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PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.

PAPERS.

1. On the Origin of Lizards.

By R. Broom, D.Sc., F.R.S., C.M.Z.S.

[Received November 24, 1924: Read February 17, 1925.]

(Text-figures 1–8.)

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In the last twenty years Palæontology has thrown much light on the origin of Mammals, and given some new facts which seem to help us a little nearer to an understanding of the origin of Birds. In neither case is the complete history known, but still we cannot now be very far from the truth. In the case of two other living groups—Lizards and Chelonians—we are still in much uncertainty. We have very little palæontological evidence bearing on the origin of the Chelonia, and what little we seem to have does not help us much. Towards a solution of the question of the origin of Lizards, on the other hand, it seems to me that we have much palæontological evidence of a most helpful nature. And as the extent and importance of this evidence is not, I think, at present fully realized, I propose in this paper to state the palæontological facts bearing on the question a little more fully than has previously been done.

The solution of the question of the origin of Lizards depends largely on whether it is decided that the superficial resemblance between *Sphenodon* and the Lizards indicates a real affinity or only a parallel development.

In *Sphenodon*, as is well known, there are two temporal openings on each side of the skull. The upper is bounded by four bones which everyone, so far as I am aware, agrees in calling the postfrontal, the postorbital, the squamosal, and the parietal. The lower temporal opening is bounded by the postorbital, the jugal, and the squamosal; but a fourth bone, the quadratojugal, forms part of the bony ring though it does not reach the border of the opening. As all present-day morphologists and palæontologists agree in accepting these names and determinations, we may take the *Sphenodon* skull as our basis of reference.

The typical Lizard has a skull which at first sight seems to resemble that of *Sphenodon* considerably, but when the bones of the temporal region are examined certain difficulties manifest themselves. There is a supratemporal opening much like that of *Sphenodon*; but what seems to be a lower temporal opening differs in that the lower bar is missing, the quadrate which in *Sphenodon* is firmly held by the squamosal, the quadratojugal, the jugal, and the pterygoid is here loose, the quadratojugal, if present, is not situated as in *Sphenodon* low down on the quadrate, and the large squamosal of *Sphenodon* seems to be here replaced by two slender splint-like bones. And the problem arises, has the lower temporal region in the Lizard arisen from a condition somewhat similar to that in *Sphenodon* by the loss of the lower bar, or is it of an entirely different nature?

Following Huxley and Parker, who looked on *Sphenodon* as only a primitive Lizard, the large majority of workers of the last forty years have believed that the typical lizard condition has arisen by the loss of the lower bar and with it the quadratojugal from a skull not unlike that of *Sphenodon*.

An entirely different view has had the able support of Owen, Gegenbaur, Baur, and Watson. Watson, the most recent exponent of this view, believes "that the Lizards have always had a single temporal fossa and that their present curious arrangement results from the gradual reduction of a formerly broad temporal arch, the process culminating in the upward retreat of the quadratojugal to allow of the freeing of the quadrate."

Huxley, Parker, and most others have held that the outer of the two small bones in the supra-posttemporal region of the typical Lizard skull is the squamosal and that the inner one is a supratemporal lost from or not developed in the *Sphenodon* skull. Gegenbaur, Baur, and Watson, however, believe that the outer bone is the true quadratojugal and that the inner bone is the squamosal.

Watson derives the main support for his view from the study of a skull of *Pleurosaurus* in the British Museum. This skull, he believes, has only a single upper temporal fossa, and a broad

outer temporal bar formed mainly by the postorbital and the jugal. Behind the upper temporal fossæ is a large bone which he believes to be the squamosal, and adjacent to its outer and hinder side are two bones which he believes to be the quadrate and quadratojugal. This British Museum skull is crushed to an extreme degree, so that it is hardly possible to be sure of the exact condition of affairs. It might be suggested in criticism of Watson's view that the eye is likely to have been subglobular, and to accommodate such an eye the back part of the skull must have been much deeper than Watson shows in his restoration of the side view. Watson believes that the temporal region in *Pleurosaurus* agrees pretty closely with Lortet's figure of the temporal region in *Sauranodon* (*Sapheosaurus*) and that this latter form also has thus only a supratemporal fossa.

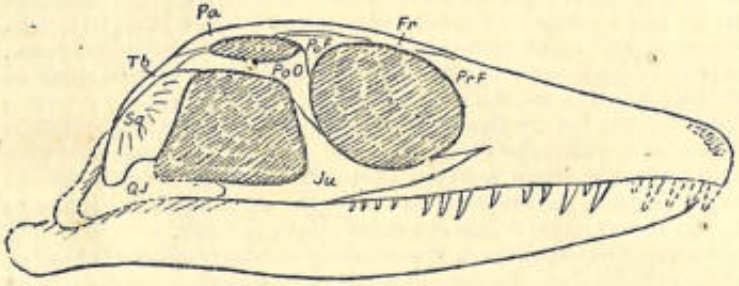
Lortet believed *Sauranodon* (*Sapheosaurus*) to have two complete temporal fossæ, and hitherto most have accepted Lortet's opinion. In view of the doubt raised, Boulenger in 1919 made a special re-examination of Lortet's types and satisfied himself that in *Sauranodon* (*Sapheosaurus*) there are two temporal fossæ, an upper and a lower, and that the lower bony arch is complete. As *Sauranodon* is thus undoubtedly possessed of two temporal fossæ, and as *Pleurosaurus* has a supratemporal fossa very similar to that in *Sauranodon*, we will require very much stronger evidence than is afforded by the extremely crushed skull in the British Museum to persuade us that it has not also a complete lower fossa. Boulenger is satisfied that there are two bones in the supra-posttemporal region, and of these he believes the inner to be the supratemporal and the outer the squamosal.

In 1902 I showed from the study of the skeletogenesis that in at least the lizards *Eremias*, *Mabuia*, and *Zonurus* in the young skull, even at a time when all the bones are already ossified, the quadrate is completely fixed by a cartilaginous bar which joins its lower part to the base of the epipterygoid almost exactly as in *Sphenodon*. There is, of course, no quadratojugal, but in all other respects the very young lizard is essentially a Rhynchocephalian. As will be shown presently, the bone in the lizard regarded by Watson and the others as the quadratojugal cannot possibly be the quadratojugal, and is manifestly the squamosal. There is thus no evidence of the quadratojugal having moved from the position low down on the quadrate which it always occupies in Rhynchocephalians, and we are thus led to believe that it simply became lost when in the Rhynchocephaloid ancestor of the lizard the lower bar became incomplete.

In 1914 I described, under the name *Youngina capensis*, an extremely interesting skull from the *Cistecephalus* zone of the Beaufort Beds of South Africa. As the horizon is low down in the *Cistecephalus* zone, we may regard it as highly probable that the age of the skull is not later than Upper Permian. The skull has two complete typically Rhynchocephalian temporal fossæ, and is thus the earliest satisfactorily known two-arched

reptile. The type-skull is a little weathered and imperfect at the front of the snout, the nasal region, and the quadratojugal region. Most of the temporal region is, however, well preserved on both sides. I figured the skull as preserved and as I identified the elements. In my opinion, it shows an upper temporal fossa bounded by the postorbital, the postfrontal, the parietal, and a bone which I regard as the tabular. The lower temporal fossa is bounded by the jugal, the postorbital, a large squamosal, and doubtless a quadratojugal, which is largely lost from the specimen. Watson had some doubts about my determinations, and I left the specimen temporarily in his hands that he might give an independent view, but, so far as I am aware, he has published no separate opinion. Since 1914 two other specimens of *Youngina* have been found. One with a bad skull but with a good deal of the skeleton is now in the Pretoria Museum; the other, a fair skull, is in my own possession. This second skull, though it gives us a

Text-figure 1.

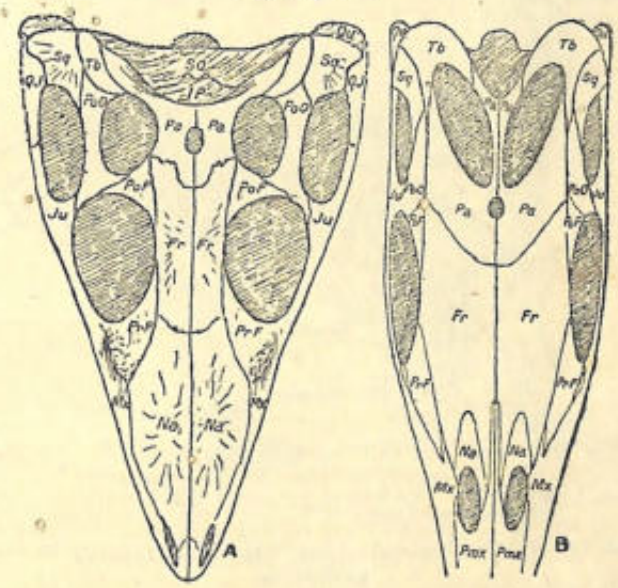


Side view of skull of *Youngina capensis* Broom. About 1½ times natural size. From the type-specimen, further restored from a second specimen.

nearly perfect snout, with practically the whole of the right side of the skull, has lost the occiput. Unfortunately, in the latter skull the bones from the posttemporal region have been mostly weathered off. We do get, however, further light on the squamosal, and we have some portions of both quadrate and quadratojugal unfortunately rather badly crushed. We have no further evidence of the structure and relations of the bone which I regard as tabular. Though much of the type-skull is well preserved, the condition of the posttemporal region is not so satisfactory as one could desire, and one cannot complain if doubts have been expressed as to the correctness of my determinations. Fortunately, an almost perfect skull of another type of two-arched reptile, *Mesosuchus*, has recently been discovered which agrees sufficiently closely with *Youngina* as to leave no reasonable doubt that the drawing I gave of the *Youngina* skull in 1914 is essentially correct. The drawings I now give are further restored in the light of the more recently discovered *Youngina* skull.

The main noteworthy points in the temporal region of *Youngina* are the presence of a large squamosal which, as in *Sphenodon*, forms the back of the lower temporal fossa, and a small upper bone lying between the latter and the parietal. If we only knew of two-arched reptiles like *Sphenodon* with a quadratojugal and a large squamosal above it, and lizards also with two posttemporal bones, we might perhaps reasonably conclude that the lizard elements are also the quadratojugal and the squamosal, and that the two elements preserved in the type-skull of *Youngina* are the quadratojugal and the squamosal.

Text-figure 2



A. Skull of *Youngina capensis* Broom. From the type-skull, further restored from a second specimen. 1½ nat. size.

B. Restoration of greater part of the skull of *Thalattosaurus alexandræ* Merriam. Further restored from Merriam's figure in the light of the later researches of v. Huene.

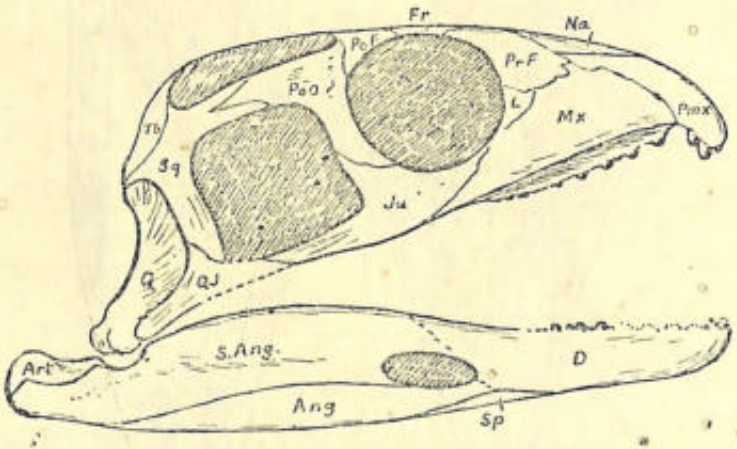
But by comparison with the skull of *Mesosuchus* there can now be no doubt that I was right in 1914 in regarding the large lower element as the squamosal.

In 1912 Watson named a very imperfect skull in Mr. Alfred Brown's collection *Mesosuchus browni*. Beyond this very badly-preserved skull, which I figured a year later, and a considerable part of the skeleton, also badly preserved, nothing has been known further of *Mesosuchus* till recently. Last year (1924), however, a nearly perfect skull was acquired by the South African

Museum from the same or a near locality as the type. It is one of the most beautifully-preserved skulls that has ever been discovered in the Karroo formation, and, indeed, one of the finest ever discovered in the history of palæontology. Haughton has recently described it in a paper read before the Royal Society of South Africa; but he has allowed me to make some independent drawings of it.

The skull bears considerable resemblance to that of *Rhynchosaurus*, and there is little doubt it is a near ally. The nostrils are united, and the premaxillæ are bent down in front to form a sort of beak. The nasals are large, as are also the frontals. The maxilla has, as I showed in 1913, a number of round teeth anchylosed to the bone. There is a distinct small lachrymal,

Text-figure 3.



Side view of skull of *Mesosuchus browni* Watson. Very slightly less than natural size.

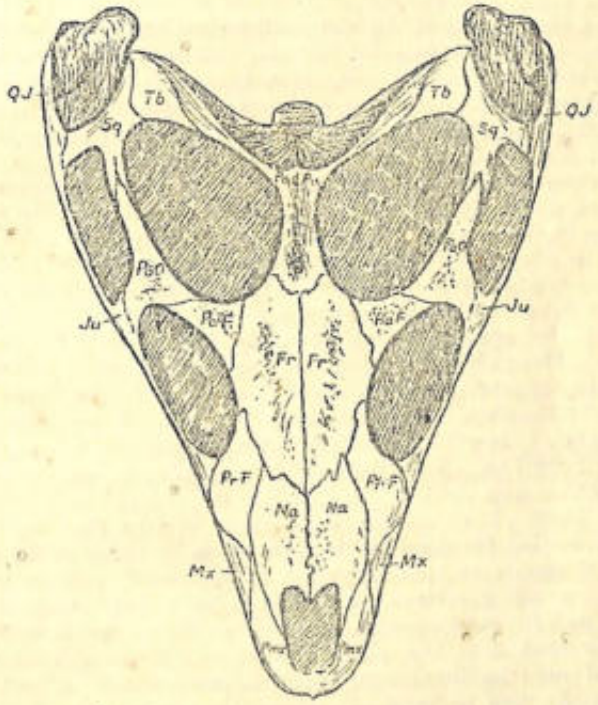
and the prefrontal is large. The postfrontal is a rather small triangular bone which forms the anterior border of the large upper temporal fossa. The postorbital is a large tri-radiating bone which forms most of the back of the orbit, and about two-thirds of the bony bar which divides the upper and lower fossæ.

The parietals are united into a single bone which in front forms the intertemporal portion of the skull. Near the anterior end is a small but not rudimentary pineal foramen. Posteriorly the united parietals send out well-developed processes which form much of the hinder border of the supratemporal fossa. The squamosal is a large bone which forms most of the posterior border of the infratemporal fossa and unites with the postorbital to form the bony bar between the fossæ. Between the upper part of the squamosal and the outer end of the parietal is a

triangular-shaped bone which I believe to be the tabular. It forms a considerable part of the posterior border of the supratemporal fossa. It also forms a considerable part of the occipital face, and its lower end passes down and articulates with the quadrate and the paroccipital. A very considerable part of the squamosal also shows on the posterior aspect of the skull.

The jugal is completely and perfectly preserved, and is seen to form, besides the lower orbital wall, the greater part of the bony

Text-figure 4.



Upper view of skull of *Mesosuchus browni* Watson. Nat. size.

bar below the infratemporal fossa. The quadrate is beautifully preserved on both sides. It is relatively large, and its upper end is apparently moderately firmly articulated with the squamosal. On the outer side of the lower part of the quadrate lies the quadratojugal. Unfortunately, owing to slight crushing the bone is not quite perfect on either side. Haughton believes that the quadratojugal did not reach the posterior end of the jugal and that thus the lower temporal fossa was open, as in lizards, though to a much less extent. I am very strongly of

opinion that this is not so. On each side the posterior part of the quadratojugal is fractured, and on the right side the posterior end of the jugal seems to me to have an articular surface for the anterior end of the quadratojugal. Further, the fossa is so nearly closed by the long posterior process of the jugal that I hold the bony bar must have been complete, otherwise there would have been here a most dangerous mechanical weakness. I have therefore restored the side view as I believe the bones must have been. The only part of any bone in the figure that is open to any doubt is the anterior part of the quadratojugal. The posterior part of the quadratojugal is well preserved and in position.

In the view I give of the occiput the relations of the quadrate to the tabular, the squamosal and the quadratojugal are shown. The basioccipital, exoccipitals, paroccipitals, and possibly supra-occipital are firmly anchylosed, and this occipital piece is somewhat displaced in the actual specimen. In the drawings I give I have replaced it in what appears to be its natural relations.

The determination of the quadratojugal and the squamosal admits of no doubt. The quadratojugal is quite similar in its relations to the quadrate to the quadratojugal in *Sphenodon*, and the bone above the quadratojugal agrees sufficiently closely with the squamosal of *Sphenodon* to leave out the slightest doubt that the determinations are correct.

Above the squamosal we have the bone which I call the tabular. Haughton, following Boulenger and others, prefers to call it the supratemporal. Though I am strongly of opinion that this is the bone which in Therapsids and Anapsids we are calling the tabular, I do not think it advisable at present to press the point. I shall be quite satisfied if I can persuade every one that it is not the squamosal.

This skull of *Mesosuchus* shows very clearly that in early Rhynchocephaloids there are three membrane-bones in the post-temporal region—a quadratojugal, a squamosal, and an upper element which I believe to be the tabular but which others prefer to call the supratemporal. In *Sphenodon* it is quite manifest that it is the quadratojugal and squamosal that are retained and the tabular or supratemporal which is lost. In Lizards the two bones that are usually retained are, I think, quite manifestly the upper two, the outer of which is the much reduced squamosal and the inner the reduced tabular or supra-temporal.

A comparison with *Youngina* shows that the three bones I identified in the type-skull are manifestly the same three that are more satisfactorily preserved in *Mesosuchus*.

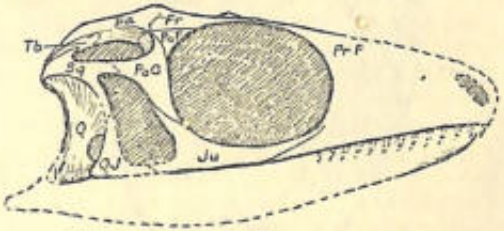
The beautifully-preserved *Mesosuchus* skull, which shows us in perfect condition the squamosal and the well-developed bone above and within it which I call the tabular, strongly supports Boulenger's view that in *Pleurosaurus* and *Sauranodon* (*Saphæosaurus*) the two bones seen on the upper side behind the upper

temporal fossa are the squamosal and the supratemporal or tabular. Another reptilian type on which the *Mesosuchus* skull seems to throw some further light is the aquatic Triassic reptile *Thalattosaurus* of Merriam.

When Merriam first described *Thalattosaurus* he believed that the nearest affinity was with the lizards, and this opinion has been followed by most. Von Huene, re-examining Merriam's specimens, discovered what he regarded as a supratemporal, and it seems to me that v. Huene is right. If, however, the preserved portions of the skull are thus rightly identified, it may be regarded as almost certain that there was a complete supratemporal fossa as I restore it. Further, while a quadratojugal is not preserved, I think it most highly probable that *Thalattosaurus* had one, and even a large one, and that the infra-temporal fossa was perfect as in *Sphenodon*.

In 1903 I described, under the name *Paliguana whitei*, a small but fairly well-preserved skull in the Albany Museum collection,

Text-figure 5.



Side view of skull of *Paliguana whitei* Broom. × 2. All sutures and bone limits in unbroken line are beyond doubt. The sutures and limits in broken line are all probably correct, but subject to a little doubt.

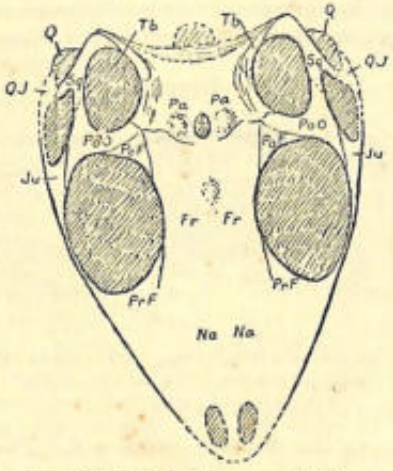
and believed it to be the oldest known lizard. The skull is only about an inch in length, a little crushed, and considerably weathered. The bones are a good deal cracked: so that altogether the specimen is much less satisfactory than could be desired. When I first saw the specimen in 1902 I believed the quadrate to be large and lizard-like both in shape and in being free from the jugal, and figured the skull as accurately as I was then capable of doing. In 1911 Watson re-examined the specimen, and, while admitting that my figures accurately represented the specimen as preserved, he expressed doubts as regards it being a lizard. As I was most anxious to restudy the type, and to see whether in the light of our 20 years' later knowledge anything further could be made of it, Mr. Hewitt, Curator of the Albany Museum, has very kindly sent it to me on loan, and I am thus able to say a good deal more about this most important animal than I was in 1902.

The re-examination now leads me to believe that the top part of what in 1902 I regarded as quadrate is really part of the

squamosal, and the outer side of the lower part is really part of the quadratojugal. It must be clearly understood, however, that the bones are in such a condition that sutures in this region are not as clear as could be desired.

In the lower part of the quadrate region is what appears to be a foramen. If this is, as it appears to me to be, the foramen between the quadrate and the quadratojugal, then clearly *Paliguana* is not a lizard. The position is so exactly similar to that of the foramen in *Mesosuchus* that I believe it to be the quadrate foramen; and in the restoration which I now give of the skull, I figure what I believe to be the greater part of the quadratojugal. Though there is no complete arch preserved joining it to the jugal, a complete arch was most probably present. What in 1902

Text-figure 6.



Upper view of skull of *Paliguana whitei* Broom. × 2.

I regarded as the articular, I now believe to be in part the lower end of the quadrate.

Though the squamosal is imperfectly preserved the outline of its upper part at least can be restored with certainty. There is clearly a lizard-like inner portion, an anterior process to meet the postorbital, and doubtless a descending feeble process to join with the quadratojugal as I restore it.

Internal to the squamosal is a slender splint-like tabular, quite lizard-like in its position, shape, and slenderness.

Behind and internal to the tabular is the posterior and outer process of the parietal. When I described the specimen first, I thought the parietals probably paired. The bone is too much cracked to enable one to be quite certain. I now rather think the parietals were united. One interesting point is that probably on each side of the pineal foramen there is a small bony boss which

probably supported a bony scale or horn. The boss of the right side is well-preserved: that of the left side lost. The back part of the parietal region is broad, and posterior to the upper flat part of the parietal is a narrow broad part sloping downwards and backwards. Whether this is part of the parietal proper or the interparietal, the evidence does not conclusively show. I incline to think it may be interparietal. About the middle of the frontal region is a small bony boss which doubtless supported a horny scale.

There is clearly a distinct postfrontal bone which I did not recognize in 1902. On no other part of the structure can I throw much further light.

If I am right in believing that there is a quadratojugal, it is very highly probable that there was also a complete quadratojugal arch, and this being so, we must remove *Paliguana* from the Lacertilia as at present defined. For the present I think it will be most convenient to place it with *Youngina* in the Eosuchia.

Text-figure 7.

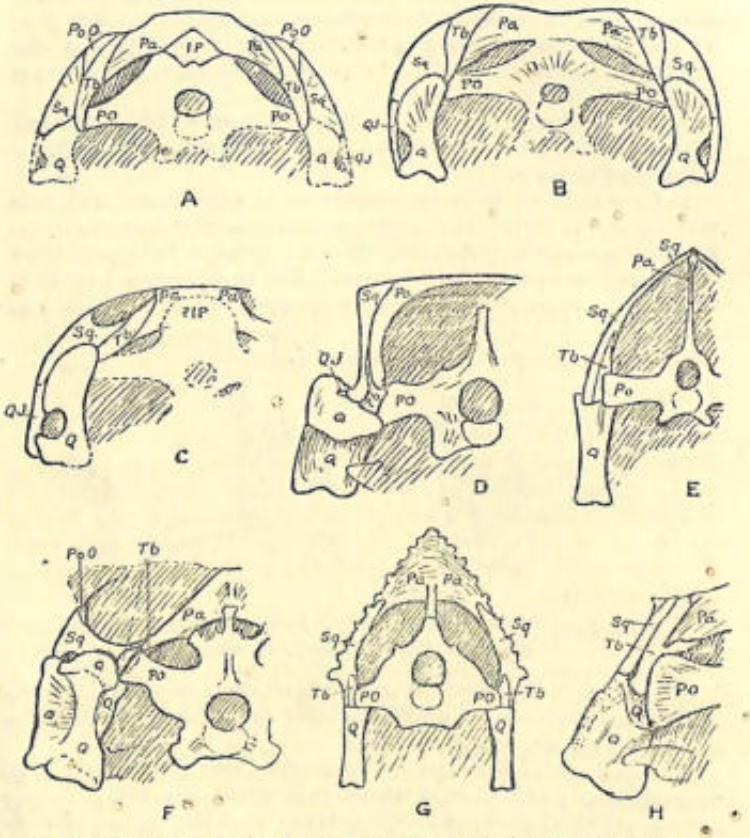
Quadrate and epipterygoid of (A) embryo *Sphenodon* (after Howes and Swinnerton) and (B) embryo *Zonurus*.

Youngina may be regarded as a primitive generalized representative, *Paliguana* as a late member far advanced along the line that gave rise to the lizards.

Though I would thus remove *Paliguana* from the Lizards, it is, nevertheless, perhaps even more interesting, as being in my opinion a Rhynchocephaloid which is nearly a lizard. As already stated, Huxley and Parker both regarded *Sphenodon* as a true but primitive lizard, and certainly *Paliguana* is much nearer to the typical lizard than is *Sphenodon*. The tabular and squamosal are almost typically Lacertilian in structure and relations—the splint-like tabular is very similar to the tabular of *Varanus*, and the squamosal is no longer the large bone seen in *Youngina* or *Mesosuchus* or even *Sphenodon*, but it is, as in lizards, much reduced and very similar in most respects to the squamosal of such lizards as *Agama*. The quadratojugal is relatively small. If, some day, a perfect skull of *Paliguana* is discovered, and it is found that the small quadratojugal does not meet the jugal, and that the lower bar is thus incomplete, a nice question will arise as to whether *Paliguana* will not again have to be restored to

the Lacertilia. I have in my possession a skull of *Tiliqua scincoides* which shows a small ossicle of undoubtedly membrane-bone lying external to the squamosal above the quadrate. I am

Text-figure 8.



The Tabular bone and its relatives in some Lizards and allied early Reptiles. Various magnifications and reductions.

A. *Youngina capensis*. A primitive Eosuchian.
B. *Mesosuchus browni*. A Rhynchosaurian.
C. *Paliguana whitei*. A late Eosuchian.
D. *Tiliqua scincoides*, showing rudimentary quadratojugal. A Scincid.
E. *Chamæleon gallensis*. A Chamæleonid.
F. *Chlamydosaurus kingi*. An Agamid.
G. *Lophosaura pumila* juv. A Chamæleonid.
H. *Varanus albigularis*. A Varanid.

inclined to regard it as a rudimentary quadratojugal, and if this be so, then quite possibly some lizards will be found normally to retain a rudimentary quadratojugal.

As already stated, some lizard embryos have the quadrate fixed to the base of the epipterygoid by a well-chondrified bar. When I looked into this question in 1902 I was only able to examine embryos of five different lizard families, and I have never been able to get embryos of representatives of any other families, and, so far as I am aware, no one else has ever studied the question. I found in the Lacertidæ as represented by *Eremias*, the Scincidæ as represented by *Mabuia*, and the Zonuridæ as represented by *Zonurus*, a quadrate fixed almost exactly as in *Sphenodon*, as will be seen by the figure I give of the quadrates in *Sphenodon* and *Zonurus*. In the Agamidæ as represented by *Agama*, and in the Chameleonidæ as represented by *Lophosaura*, there is no longer a chondrified bar connecting the quadrate and the epipterygoid, but there clearly is a membranous one. The peculiar fixing of the base of the quadrate to the base of the epipterygoid in these lizards is so strikingly similar to the condition in the embryo *Sphenodon* that it seems to me impossible to doubt that there is some close affinity. The immediate ancestor of the lizard must have had a fixed quadrate as in Rhynchocephalians. Though doubtless some embryologists have done much to discredit "Recapitulation," the evidence that there is something in it is overwhelming.

I had intended, in this paper, to discuss at some length the comparative morphology of the lacertilian squamosal and tabular, but as I find that to do the subject justice considerably more space will be required than I had anticipated, and as the matter can be more satisfactorily dealt with in a separate paper, I shall only here briefly deal with the condition in the two types *Agama* and *Chameleon*.

In *Agama* the squamosal is fairly large, larger than in most other lizards. It forms, with the postorbital and part of the jugal, the arch that bounds the outer side of the upper temporal fossa. It also forms part of the postorbital arch with the very powerful jugal. Internally it sends in above the tabular a process which articulates with the parietal. It gives a considerable articulation for the quadrate but does not come in contact with the paroccipital. The tabular is moderately developed and lies almost entirely below the squamosal and the parietal. Posteriorly and inferiorly it has a large articulation with the quadrate and the paroccipital, and it gives practically the whole of the support to the suprastapedial. The upper surface of the bone is largely hidden by the squamosal and the parietal, though a very small part is seen behind the squamosal and much of the anterior process lying external to the posterior process of the parietal. A small part appears on the occipital face. No fibres of the temporal muscle are inserted into the tabular, though the muscle passes over part of the bone.

In *Chamæleon* there has been much confusion of views as regards the structure of the posttemporal region. Both Kitchen Parker and Boulenger have misunderstood the structure.

Boulenger, in his British Museum Catalogue of Lizards (vol. iii. p. 437), says as regards *Chameleon*: "Parietal single, often much narrowed and compressed, forming a crest, and meeting posteriorly the extremities of a pair of bones, the supratemporals, which, on each side, connect it with the squamosal." This is quite wrong. The arched bones which pass up to meet the parietal crest are beyond question homologous with the bones which Boulenger has, in my opinion, quite rightly identified as squamosals in other lizards. The squamosal in *Chameleon* forms, as in *Agama*, part of the postorbital arch and part of the outer arch of the supratemporal fossa. It sends downwards a well-marked process to give articulation to the head of the quadrate, and forms almost the whole of the posterior bar of the supratemporal fossa. In *Chameleon quilensis* the squamosals of the two sides meet each other in the middle line above the parietal crest. The tabular is a little rudimentary bone which lies entirely behind the lower part of the squamosal. It gives a considerable articulation to the quadrate and a large articulation to the paroccipital and almost entirely separates the paroccipital from the squamosal. No single fibre of the temporal muscle is inserted into the tabular or comes near to the bone.

In the small Chameleons (*Chameleon pumilus*) the condition of the bones differs so considerably that I feel compelled to accept Gray's genus *Lophosaura* for these small viviparous Chameleons of the *C. pumilus* group. Here the parietals form a wide roof to much of the temporal region, and the squamosals are much smaller and extend upwards not quite half-way to the top of the crest. The parietals not only form an upper median roof to the temporal regions but send down processes which form a large part of the posttemporal arch. The tabular is a very small bone wedged in between the tip of the paroccipital and the squamosal. It passes upwards only about half a millimetre above the paroccipital, but occasionally meets the descending process of the parietal. It forms the greater part of the articulation for the head of the quadrate, and completely separates the squamosal from the paroccipital. No fibres of the temporal muscle are inserted into it, and it is almost entirely a bone of the occiput.

The identification of the squamosal in lizards may now be regarded as beyond all doubt. Such a form as *Mesosuchus* shows us clearly the early structure of the squamosal, and there is no difficulty in tracing it through the well-developed undegenerate lizards. When in some lizards, such as the Geckos, only one bone is found in the posttemporal region, there is, of course, some doubt as to whether it is the squamosal or the tabular, and it is with this question that I wish to deal in a later paper. But in such forms as *Varanus*, *Agama*, or *Tiliqua* the identification of the squamosal is a matter of certainty. It is invariably the outer bone, which usually joins with the postorbital to form the bar bounding the supratemporal fossa, gives support to at least

part of the quadrate, and joins with the parietal in all cases when the tabular is small or rudimentary.

The inner bone, which I identify as the tabular, can be traced without any difficulty from such forms as *Youngina* and *Mesosuchus*. And it is beyond doubt that the inner bone of the lizard is the homologue of the bone that lies between the parietal and squamosal in *Mesosuchus*. Whether this be, as held by Boulenger and others, the supratemporal or, as I hold, the tabular, may be argued at some length.

A supratemporal we know in a few primitive Amphibians and one or two early Reptiles. Among Reptiles it is seen in the Diadectids and in *Pantylus* but in no other reptile that I know of. It is a roofing bone of the temporal region and doubtless gave insertion to much of the temporal muscle. With the formation of the supratemporal fossa, it seems to have been immediately lost and is never again met with.

The tabular, on the other hand, is a bone of much greater importance. It is invariably present in all undegenerate Stegocephalians and primitive Reptiles. In all the "Cotylosaurs" we find it—*Pantylus*, *Diadectes*, *Captorhinus*, *Pareiasaurus*. Even in the very lizard-like *Procolophon* we find not a supratemporal but a tabular. In all the Therapsids known it is a well-developed element, whereas a supratemporal is never met with. Further, the tabular has been retained in all these early reptiles as a coupling which holds together the parietal, the squamosal, the paroccipital, and the quadrate. And in the lizard the greatly reduced element is still present supporting the quadrate and invariably attached to the paroccipital and articulating with the squamosal and the parietal. Further, in lizards, so far as I know, it never gives any attachment to fibres of the temporal muscle and is always, apparently, an occipital element. I cannot understand why the rare supratemporal which, where known, is a temporal roofing-bone, which is only known among lower forms where the temporal region is roofed and which apparently gave a large attachment to the temporal muscle should be conjured up to explain the meaning of the inner bone in lizards when we have an element the tabular almost invariably present in lower forms, and an element which seems to agree very closely in relations and functions with the lizard element. And until some strong reason can be brought forward by those who advocate the view that the inner lizard bone is the supratemporal I shall continue to hold the view first proposed by Williston, and supported by me in 1913, that the element is the tabular.

But whether the scientific world will agree with me or not in regarding the inner bone as the tabular, it will, I think, readily agree that the two bones in the lizard are homologous with the two in *Mesosuchus* and *Youngina*. And even with no knowledge of such a type as *Paliguana*, we might be strongly inclined to regard some primitive form such as *Youngina* as a Lacertilian ancestor. The knowledge of *Paliguana* confirms this

view. In *Paliguana* we have a form which, though not a lizard, is nevertheless almost a lizard. The squamosal and tabular are very lizard-like. The squamosal is reduced and almost all above the quadrate. The quadratojugal is manifestly small. In fact, the only point in *Paliguana* that prevents it from being a lizard is the presence of a quadratojugal and presumably an entire lower arch. As already mentioned, we know that the immediate ancestor of the lizard had a fixed quadrate and presumably a quadratojugal and entire lower arch.

From *Paliguana* to the lizard is only a very short step and one easily understood. Most lizards have osseous scales, and we find such osseous scales in a large number of different families—families so different that we can regard it as much more probable that the ancestral lizard had osseous scales than that osseous scales have been independently developed in a large number of different families. If a pre-lizard like *Paliguana* developed osseous scales such as we find in, say, *Zonurus* or *Tiliqua*, or *Gerrhosaurus*, and the lower temporal fossæ were covered by such scales as we find in these types mentioned, it is in the highest degree probable that the quadratojugal would become aborted and the lower arch lost, both being superfluous, and a lizard in the strict sense would be developed. The presence of osseous scales in the abdominal region would also result in the loss or great reduction in the development of abdominal ribs, and would perhaps also account for the loss of the proatlas.

It is an interesting point that the three families in which a fixed quadrate is known to occur in the embryo—Lacertidæ, Zonuridæ, and Scincidæ—are all families in which osseous scales are retained and thus probably early types: while the Agamidæ and Chameleonidæ, in which the quadrate is no longer fixed by a cartilaginous bar to the epipterygoid, have also lost the osseous scales.

Many years ago Owen expressed the opinion that the peculiar large cutting teeth of *Plagiaulax* were developed for the preying on hard-scaled lizards, and years afterwards, without knowing that Owen had expressed this opinion, I independently came to the same conclusion. If we are right in this, it adds a little further evidence in favour of the early lizards, at least as far back as Jurassic, having had bony scales. *Heleosaurus*, the imperfectly known Karroo genus from beds which are probably Upper Permian, is evidently an Eosuchian allied to *Youngina*, and we know that it had osseous scales at least along the dorsal region.

2. The External Characters of an American Badger (*Taxidea taxus*) and an American Mink (*Mustela vison*), recently exhibited in the Society's Gardens. By R. I. Pocock, F.R.S.

[Received November 4, 1924 : Read February 17, 1925.]

(Text-figures 1–5.)

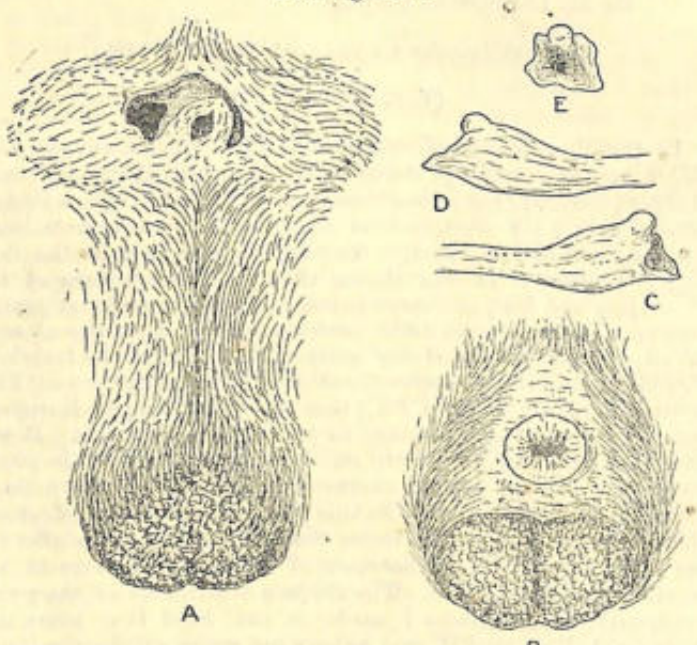
In the Proceedings of this Society for 1920, pt. iii. pp. 423-436, I gave an account of the external characters of the American Badger (*Taxidea taxus*=*americana*) and of the European Badger (*Meles meles*), my observations on the American species being based upon a female example that died in that year in the Zoological Gardens. It was shown that in the structure of the rhinarium and feet, and more particularly of the anal and genital regions, the two species differ profoundly, and that the absence of all trace of the glandular subcaudal pouch in the female of *Taxidea* diametrically contradicted the statement of Coues ('Fur-bearing Animals,' 1877, p. 267,) that the American and European animals resemble one another in possessing this pouch. It was necessary, however, to bear in mind the possibility of this pouch being a secondary sexual character, restricted to the male of *Taxidea*, admittedly remote as this possibility was. I welcomed, therefore, the chance to examine the male of this species afforded me by the death, in the summer of 1924, of the mate of the female above referred to. The absence of all trace of the pouch confirmed the inference I made on that head four years ago (text-fig. 1, B). That it may or may not occur within the limits of the genus is in the highest degree improbable, and it would be useless to speculate about the source of the error committed by Coues. Probably his examination was made upon dried skins. This supposition will also help to explain his failure to detect in the male of *Taxidea* the presence of a pair of large abdominal glands of which there is no trace in *Meles*.

These *abdominal glands* are capacious integumental pouches with a somewhat constricted orifice, each opening towards the middle line at the side of a depression in the skin of the abdomen in which the extremity of the penis, enveloped in its hairy prepuce, lies. This is the only part of the penis which is free, the rest of the organ, as in other Mustelidæ, being embedded in the abdominal skin, and extending some distance in front of the scrotum, all the posterior half of which, in the specimen examined, was covered with naked, coriaceous skin. (Text-fig. 1, A, B.)

The *penis* itself when extracted from its sheath is seen to be thickened and slightly upturned at its distal end, whence it

terminates above in a smooth rounded knob which is the tip of the embedded baculum. Beneath the tip of the baculum lies the orifice of the urethra, flanked on each side by a flap of flaccid, probably erectile tissue, the flap on the left side being considerably larger than on the right. Behind its thickened terminal

Text-figure 1.



A. External genital organs of the male of *Taxidea taxus*, showing the corrugated scrotum, the long perineum, and the tip of the penis lying in the depression and turned to the left to expose the orifice of the right glandular sac. The position and size of the glandular sacs represented by dotted lines.

B. Anal area of the same with scrotum below and anus above, showing the absence of the subcaudal glandular pouch present in *Meles*.

C. Tip of the protruded penis of *Taxidea taxus* from the right side.

D. The same from the left side.

E. Apex of the penis, showing the orifice and the tip of the baculum above it.

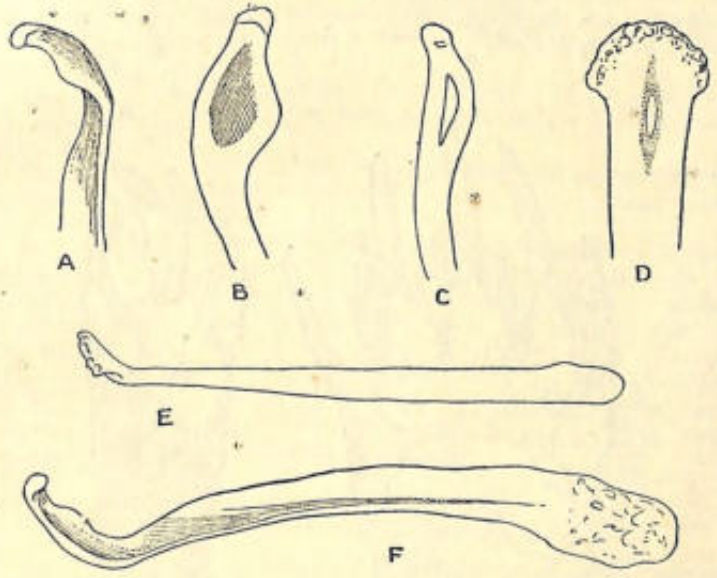
portion the penis is nearly straight and subcylindrical. (Text-fig. 1, C, D, E.)

The *baculum*, briefly and not very intelligibly described by Coues, is a relatively large * and massive bone, measuring 93 mm. in length. Its main shaft from above is nearly straight; from the side it is slightly convex above and correspondingly concave

* Actually the largest Musteline baculum I have examined.

below. Its pelvic or proximal end is roughened, clavate, and directed downwards at an angle of about 135° to the axis of the shaft, with which the thickening gradually blends. The shaft is evenly rounded above from side to side, but somewhat flattened and lightly grooved below; running along the lower portion of each side there is also a groove or gutter, scarcely traceable in the proximal half, but deeper and wider distally, where it vanishes on the upturned distal portion. This is gradually curved upwards at about an angle of 45°, and is laterally and asymmetrically widened into a cordate or subovate expansion twisted

Text-figure 2.

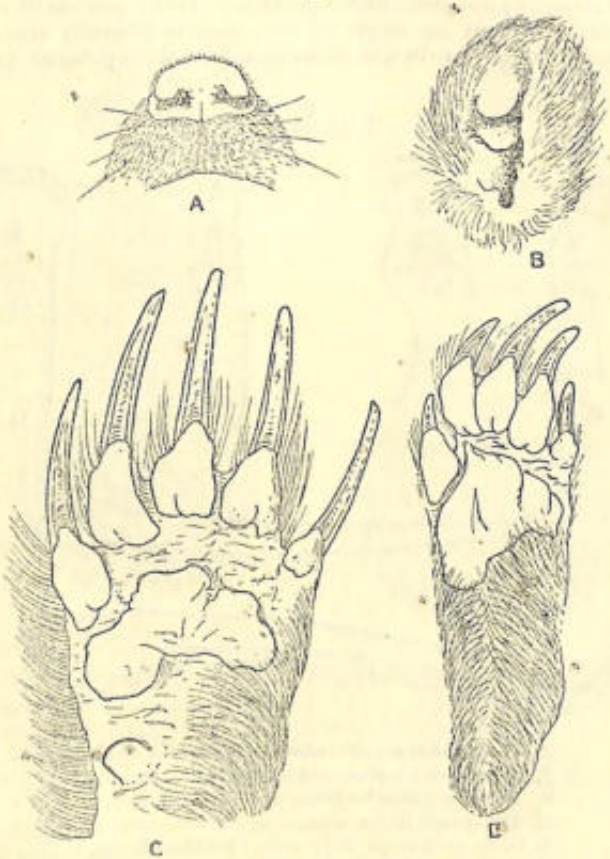


A. Tip of baculum of *Taxidea taxus* from the right side.
B. The same from above and behind.
C. The same of *Martes foina*.
D. The same of *Meles meles*.
E. Entire baculum of *Meles meles* from the left side.
F. The same of *Taxidea taxus*.

slightly to the right and ending in a single, rounded, condyle-like boss. The lower side of this expansion, facing forwards and to the right, is almost flat, but its upper side, looking correspondingly backwards and to the left, shows a marked median oval longitudinal excavation. The left edge of the expansion is evenly and lightly convex, the right edge strongly convex in its proximal portion and concave distally towards the rounded tip of the bone. (Text-fig. 2, A, B, F.)

This baculum is quite distinctive of *Taxidea* and unlike that of any genus of Mustelidæ in which the bone has been described. Oddly enough, it is more like the baculum of *Martes* than of any genus known to me, more like that of *Martes*, indeed, than is the baculum of *Charronia*. The profound differences between the

Text-figure 3.



A. Rhinarium of *Taxidea taxus* from the front.
B. Ear of the same closed.
C. Right fore foot of the same with the digits slightly spread.
D. Right hind foot of the same with the digits not spread.

bacula of *Martes* and *Charronia* show that such differences are not necessarily correlated with pronounced differences in the skull or other parts. But in the case of *Taxidea* and *Meles* such a correlation exists, the bacula of the two genera being entirely dissimilar. That of *Meles* is much shorter, thinner, straighter,

less incrassate proximally, and less upturned distally. Its upper surface is compressed and carinate, its lower much more deeply and widely grooved, especially distally, and its laterally expanded apex is symmetrical, with roughened, convex, sometimes quadrilobate edge, and a shallow median groove generally perforated by one or more orifices. (Text-fig. 1, C, D, E.)

With regard to other external structural characters, I have very little to add to my previous description. The *feet* show a few individual differences. In the fore foot, for example, the single small carpal pad lies close to the outer side of the carpus behind the large outer lobe of the plantar pad, not near the middle of the carpus, as shown in the female; and in the hind foot the plantar pad is wider, a little wider than its median length, and nearly as wide as the digital and metatarsal areas, not narrower, as in the female, in which this pad was a little longer than wide. (Text-fig. 3, C, D.)

The *rhinarium* is generally similar to that of the female, but its superior edge and angles form a more evenly convex line. (Text-fig. 3, A.)

The *ear* also is similar; but for comparison with my previously published figure, I here add one of the ear as it appears when unexpanded. (Text-fig. 3, B.)

In conclusion, it may be added that the secondary sexual characters of the male of *Taxidea*, represented by the pair of glandular pouches alongside the prepuce and the structure of the baculum, confirm the claims, based upon the examination of the female, that *Taxidea* and *Meles* have nothing in common apart from superficial adaptive resemblances, that the retention of *Taxidea* in the subfamily Melinæ is inadmissible, and that *Taxidea* should be regarded as the sole representative of the subfamily Taxidiinæ of the family Mustelidæ.

The American Mink (*Mustela vison*).

Minks, as is well known, are species of Mustelidæ differing from their near allies—the Weasels, Stoats, and Polecats—in being semiaquatic in habits. They are, indeed, expert swimmers and readily take to the water, swimming when submerged, by means of powerful strokes of the hind legs working in unison, not alternately, as in the case of typically terrestial mammals. On the land they unquestionably look very like little Otters; but in the water they have not learnt the Otter's method of swimming at full speed by the sinuous serpentine action of the body and tail combined. They are, however, not closely related to Otters, and, as I shall show, exhibit no trace whatever of convergent resemblance to them in adaptation to similarity in mode of life, except in the nature of the thick under-fur, which is developed to exclude the water from the skin.

By some authors it was thought that the Minks should rank as generically distinct from *Mustela*, and three names—*Lutreola*,

Vison, and *Hydromustela*—were proposed for them. From the typical forms of *Mustela*, indeed, they differ, as Miller has shown *, in tolerably well-marked cranial and dental characters; but as that author has also shown, and no one, on the evidence available, will question his verdict, they completely intergrade with true *Mustela*, as represented by the Stoat, *M. erminea*, through such Asiatic species as *M. sibirica* and *M. canigula* †, which presumably may be called either Stoats or Minks according to fancy. Hence, although Miller provisionally retained for them the name *Lutreola* as a subgenus, he remarked that it may well be questioned whether the name should remain in use.

From Miller's researches it may be inferred that the Minks may be regarded as modified Stoats rather than as modified Polecats, although in size they resemble the latter. They also resemble the Polecats, and, indeed, in my experience excel them, in the intensity of the Skunk-like odour they emit. The atmosphere round the pond in the Zoological Gardens where two specimens were recently kept was redolent with the scent. I have never known a Stoat in captivity objectionable in that way, although the secretion of their glands is by no means pleasant.

The following observations on the species were made from one of the two female examples recently exhibited in the Gardens, which died in May 1924:—

The *facial vibrissæ* are normally developed and slender, with no trace of the thickening and stiffness commonly found in aquatic mammals which hunt their prey in water.

The *rhinarium* is entirely naked and roughened. Viewed from above it has a straight posterior border and rounded anterolateral angles. From the front its upper edge is lightly convex in the middle, strongly convex at the sides, where it curves down to the margin of the nostrils. The nostrils are tolerably widely separated and open outwards and forwards. The infranarial portion is broad and deep, its sides converging inwards and downwards to a short median point. The upper lip is very weakly grooved mesially, but there is no definite philtrum. (Text-fig. 4, A, B.)

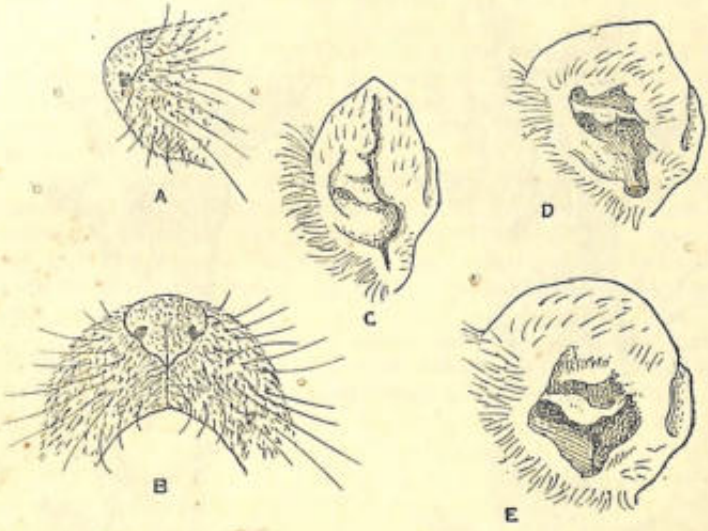
The *ears* are rather small, and relatively smaller than in the Stoat. Miller, for example, gives 21 mm. as the length of the ear in an adult female English Stoat, with the hind foot 43 mm. The ear in the adult female Mink is 19 mm., and the hind foot 53 mm. The upper border is somewhat pointed. There is a tolerably well-developed bursa and the cavity above the shelf-like, mesially thickened supratragus is provided with a flap-like lobe. The anterior edge of the upper portion of the cavity turns backwards beneath the supratragus and dies away

* Cat. Mamm. Western Europe, 1912, p. 415.

† A study of the baculum of the various species now assigned to *Mustela* may throw new and important light upon their mutual affinities.

without being continued inferiorly to the tragus, which is tolerably large and separated by a distinct intertragal notch from the antitragal thickening. When the ear closes the posterior border of the cavity is brought forwards towards the anterior border, the supratragus is obliquely depressed upon the thickening which occupies the lower portion of the cavity, and the antitragus in pressed against the tragus, within which

Text-figure 4.



A. Rhinarium of *Mustela vison* from the side.
B. The same from the front.
C. Ear of the same closed.
D. The same normally distended.
E. The same of *Mustela erminea*, much expanded.

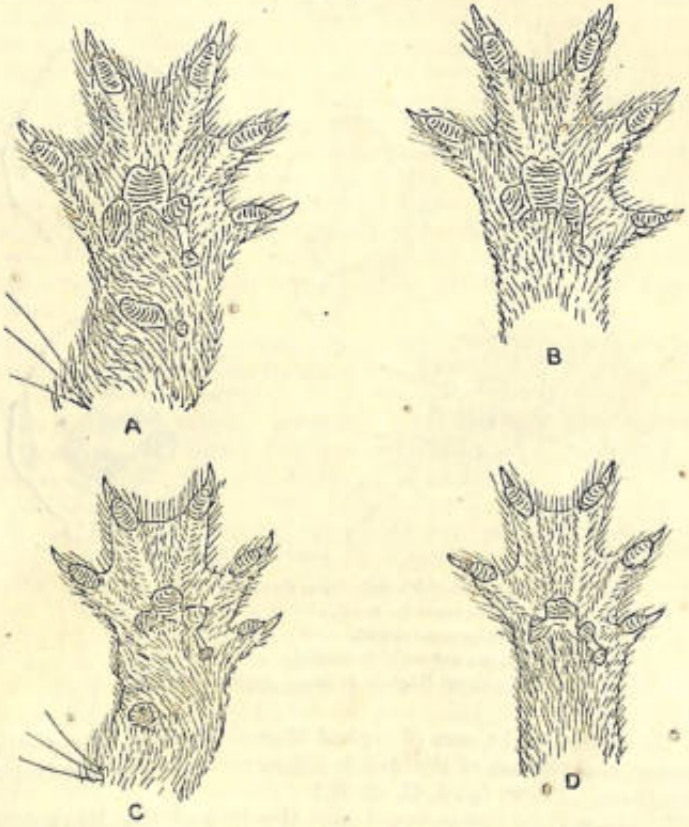
lies the orifice. The ears of typical Mustelidæ close in a similar manner, and the ear of the Mink differs in no important respect from them. (Text-fig. 4, C, D, E.)

The feet.—It has been stated that the feet of the Mink differ from those of the Polecats, Stoats, and Weasels, "by the toes being partially webbed and by the absence of hair in the intervals between the naked pads of the soles of the feet"*. The first part of this sentence suggests that the feet in Polecats, Weasels, and Stoats are unwebbed. They are, on the contrary, webbed up to the proximal end of the digital pads, and the digits of the Mink are webbed to approximately the same extent, certainly not more so.

* Flower & Lydekker, 'Mammals Living and Extinct,' p. 556.

The *fore foot* is a little wider than the hind foot as in the terrestrial Mustelidæ, not narrower as in the aquatic Otters. The underside, apart from the pads, is covered with hair, although not quite so thickly as in the Polecat, Stoat, and Weasel. As in these three species, the digital pads are oval and transversely striate, and the margins of the webs between the digits are concave when

Text-figure 5.



A. Right fore foot of *Mustela vison*.
B. Right hind foot of the same.
C. Right fore foot of *Mustela erminea*.
D. Right hind foot of the same.

the digits are spread. The plantar pad is transversely striate, as in the Stoat, but is better developed, its three main lobes being larger and more confluent. Behind the inner lobe lies a small but distinct and striate spherical pollical lobe connected with the inner lobe of the plantar pad by a strip of naked skin similar

to that of the Stoat, but broader. The carpal pad is about as large as the outer lobe of the plantar pad and striate; close to it, on the inner side, there is a minute radial carpal pad. This latter pad is generally not detectable as such in Stoats and Polecats, but a vestige of it sometimes persists as a small area of naked skin. The carpal vibrissæ are present and normal. (Text-fig. 5, A, C.)

The *hind foot* has the margins of the webs somewhat more concave than in the fore foot. The development of these webs does not suggest that they perform any special function in swimming, although these limbs are the main organs of propulsion in the water. The hair on the sole is scantier round the plantar pad than towards the digital pads; and the plantar pad, which, like the digital pads, is striate, is, as in the fore foot, larger, with more confluent lobes than in the Stoat, Weasel, or Polecat. (Text-fig. 5, B, D.)

In the larger size of the plantar pads, the Mink somewhat resembles the naked-footed Polecat from Sumatra, the feet of which I described and figured in 1921 (Proc. Zool. Soc. ii. pp. 818–819, text-fig. 33, A & B); but in this species the entire sole, including the area round the two carpal pads of the front foot, is entirely naked.

The *anus* and *external genitalia* are like those of typical Weasels and Stoats. The vulva is naked and piriform, and the perinæal area between it and the anus is covered with hair.

3. Additional Notes on the External Characters of some Platyrrhine Monkeys. By R. I. Pocock, F.R.S.

[Received November 17, 1924: Read February 17, 1925.]

(Text-figures 6–12.)

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This paper may be regarded as amplifying and supplementary to the one I published some years ago upon the external characters of the South American Monkeys (Proc. Zool. Soc. 1920, pp. 91–113). Since that date a few specimens showing special features of interest died in the Society's Gardens, and were examined by me in the Prosectorium.

The White-nosed Saki (*Chiropotes albinasa*).

Reasons for assigning this rare species to the genus *Chiropotes* are given below (p. 29). For many years it has by common consent been regarded as belonging to *Pithecia*, which it tolerably closely resembles in external characters; and since *Pithecia*, apart from *Brachyteles*, was the only genus of Platyrrhine monkeys of which I had not seen a fresh example when the paper above referred to was written, the following note upon a young female of *albinasa* may be of interest:—

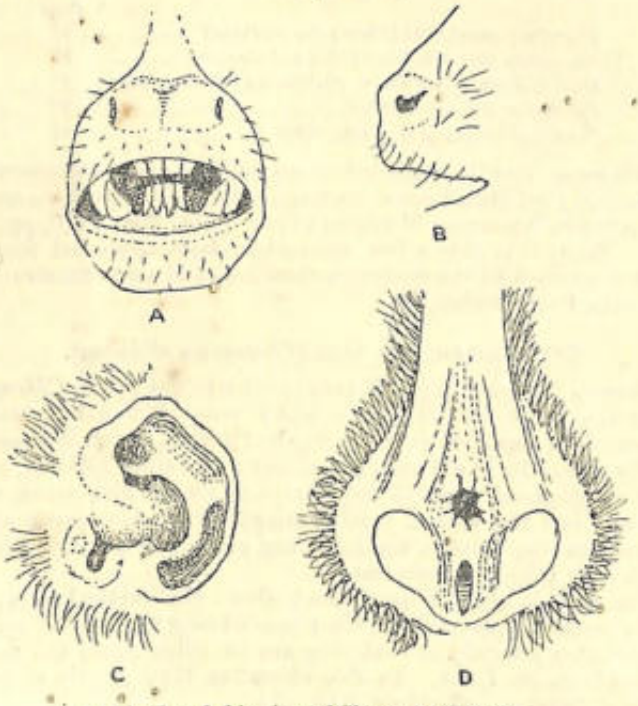
The *nose* is slightly prominent above the vertical upper lip and is markedly platyrrhine, the nostrils being very widely spread, and opening laterally so that they are invisible when the face is viewed from the front. In this character they closely resemble those of *Cacajao*. (Text-fig. 6, A, B.)

The *ear* is normally developed and, in a general way, is like that of *Cacajao* or *Cebus*. It is angular or slightly pointed above; its posterior edge is convex, and its inferior free portion forms a widely-rounded lobe projecting well below the level of the intertragal notch and some distance behind it. The edge is overfolded throughout its extent. The tragus is present as a stiff rounded ridge, and the antitragus, on the posterior side of the well-defined intertragal notch, is also well developed. The deep and wide groove in the lower half of the ear between the outer margin and the edge of the cavity extends downwards to the lower lobe, but not so far forwards towards the intertragal notch as in *Cebus*. The orifice is set high up behind the middle of the tragus and well above the intertragal notch. (Text-fig. 6, C.)

The *tongue* has a bilobed frenal lamella as in other genera of the Cebidæ.

The *fore foot* (*hand*) has the skin of the wide sole smooth and creased, the pads being poorly defined. The arrangement of the digits differs from that of *Cebus*, *Callicebus*, *Saimiris*, and *Aotus* (*Nyctipithecus*), and resembles that of *Cacajao*, *Lagothrix*, and *Alouatta* in having the 2nd digit more widely separated from the

Text-figure 6.



A. Mouth and rhinarium of *Chiropotes albinasa*.
B. Rhinarium of the same from the side.
C. Ear of the same.
D. Anal and genital area of young female of the same.

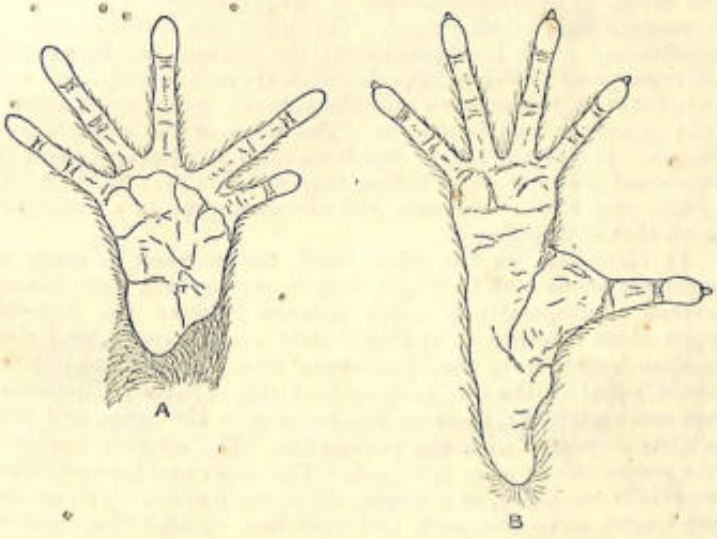
3rd than the latter is from the 4th, or the 4th from the 5th. It is closer to the short pollex, and acts in unison with it for grasping. The pollex shows no sign of a basal lobe, and can hardly be described as opposable. The length of the digits in order is 3, 4, 2, 5, 1 ; the inequality between 2, 3 and 4 is not very marked, and 1 (the pollex) is about two-thirds the length of 5. (Text-fig. 7, A.)

The *hind foot* is much longer than the fore foot as it is in *Cebus*, *Callicebus*, *Saimiris*, and *Cacajao*. The skin of the sole

is smooth and wrinkled, the pads being poorly defined. Digits 3 and 4 are subequal, and surpass by their terminal segments digits 1 and 5, which are also subequal. The 1st digit, or hallux, is rather slender and short, scarcely reaching the base of the 2nd when turned forwards. It is, however, approximately as well developed as in *Cacajao*. (Text-fig. 7, B.)

The skin of the *anal* and *genital area*, and round it, is smooth and naked. The ischia form prominent cushions. The vulva is a narrow vertical cleft a short way below the anus, and there is no distinct external pendulous clitoris, such as is seen in *Ateles*, *Lagothrix*, *Alouatta*, *Cebus*, and *Callicebus*. (Text-fig. 6, D.)

Text-figure 7.



A. Right hand of *Chiropotes albinasa*.
B. Right foot of the same.

From the above-given description it will be seen that the external characters of *Chiropotes* confirm the conclusion that the genus is more nearly allied to *Cacajao* than to any other Platyrrhine monkey in which they have been described.

The Genera *Pithecia*, *Chiropotes*, and *Cacajao*.

In recent text-books, systematic treatises, and faunistic lists there is a curious mistake connected with the genera *Cacajao*, *Chiropotes* and *Pithecia*, referred to the subfamily Pitheciinæ—*Chiropotes* is not admitted. To the genus *Cacajao*, formerly called *Brachyurus* or *Ouakaria*, are referred *rubicundus*, *calvus*, and *melanocephalus*. To *Pithecia* are referred *pithecia*, *monacha*,

albinasa, *chiropotes*, *satanas*, and, by Elliot, a few more of doubtful specific standing. The two genera as constituted are distinguished by the shortness of the tail in *Cacajao* and its length in *Pithecia*.

A glance at the skulls, however, shows that that allocation of the species is entirely indefensible, and that *Pithecia*, as above defined, contains two sharply-distinguished genera, typified respectively by *pithecia* and *chiropotes*.

In *pithecia* the crown of the cranium is lower. The *frontals* extend far back between the parietals, where they form an acute angle, their median length from this angle to the fronto-nasal suture being nearly, or quite, twice the median length of the parietals. The *nasals* are broad and noticeably bulging above the nares. The alveolar border of the *premaxillæ* is produced to a comparatively small extent. The upper and lower *incisors* are smaller and much less prominent; the canines smaller and less divergent and tusk-like, the diastema above and below on each side between the incisors and the canines being much smaller. The *zygomatic arch* is stouter. The walls of the *mesopterygoid fossa* are higher and longer, the fossa itself being deeper, with the combined posterior nares higher than wide. (Text-fig. 8, A, B.)

The skulls of *P. monacha* and *albinasa* agree in all essentials with that of *P. pithecia*.

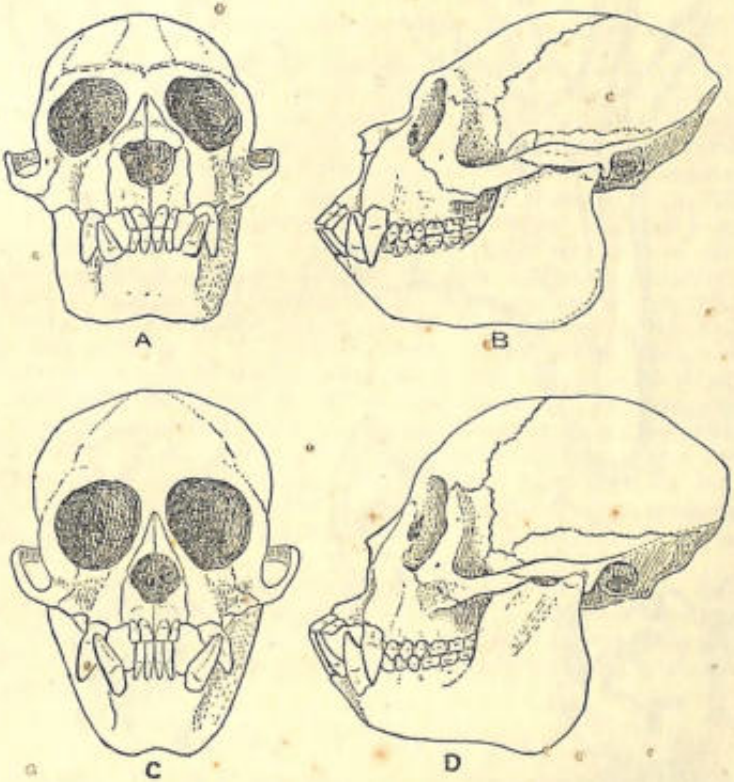
In *chiropotes*, on the other hand, the *cranium* is relatively more capacious both in height, length, and breadth; the *frontals* extend a comparatively short distance between the parietals, their sides meeting at approximately a right angle, and their median length from the fronto-nasal suture to the angle being about equal to the median length of the parietals. The *nasals* are much narrower, show no expansion over the nares, and form a narrower union with the premaxillæ. The alveolar border of the *premaxillæ* is more produced. The upper and lower *incisors*, especially the latter, are longer and more porrect. The *canines* are longer, more divergent, and tusk-like, so that the diastema above and below between them and the incisors is larger. The *zygomatic arch* is thinner. The walls of the *mesopterygoid fossa*, formed by the ectopterygoid plate of the alisphenoid, are lower and shorter, the fossa itself being shallower, with the combined posterior nares wider than high. (Text-fig. 8 C, D.)

The skulls of *satanas* and *albinasa* agree in all essentials with that of *chiropotes*.

The differences above pointed out show clearly that *chiropotes*, *satanas*, and *albinasa* cannot be regarded as closely allied to *pithecia*, *monacha*, and their allies. Two genera are clearly involved, and the names *Chiropotes* and *Pithecia* are available for them. There are also two external characters of less importance by which the two may be distinguished. In *Pithecia* there is a whorl or parting in the hairs far back on the nape of the neck or on the shoulder, those in front of the whorl turning forwards and growing over the neck and crown, covering the latter as a

cap or hood up to the level of the anterior edge of the ears; and the throat is naked in the middle line between the whiskers. In *Chiropotes*, on the contrary, there is a distinct whorl on the summit of the crown, and from this the hair radiates in all directions; the whiskers also extend across the middle line of the throat.

Text-figure 8.



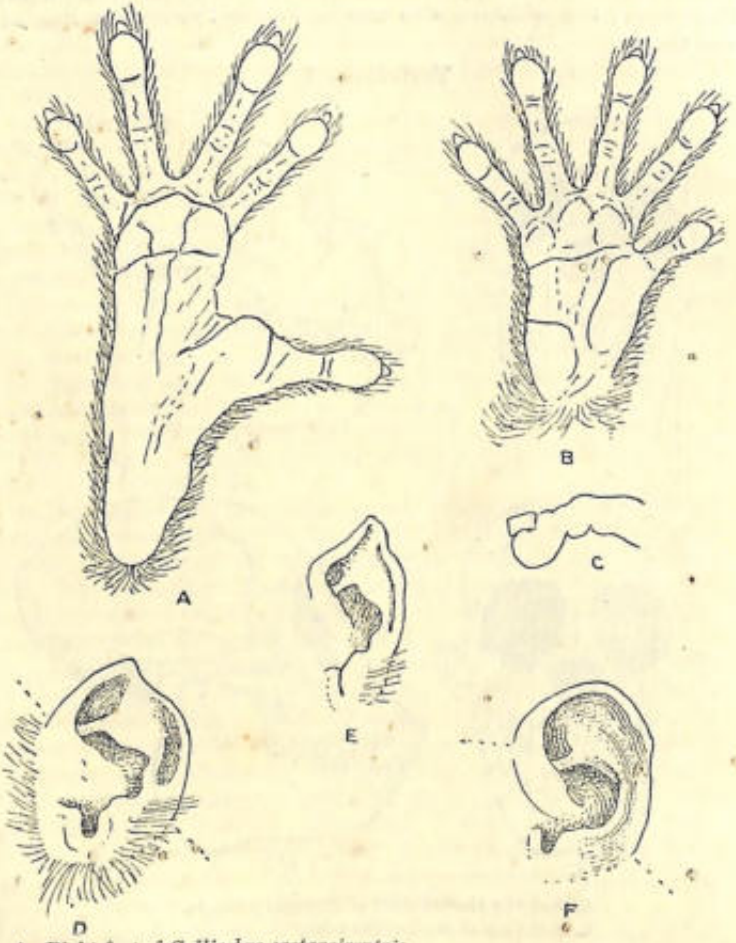
A. Anterior view of skull of *Pithecia pithecia*.
B. Side view of skull of the same.
C. Anterior view of skull of *Chiropotes chiropotes*.
D. Side view of skull of the same.

Reverting to the cranial characters, an interesting point connected with them is that in all structural points in which the skull of *Chiropotes* differs from that of *Pithecia*, it resembles the skull of *Cacajao*, as may be seen at once by comparing my figures of the skull of *Chiropotes chiropotes* with those of *Cacajao calvus* as shown in Elliot's monograph *; and it cannot be doubted that

* 'A Review of the Primates,' i. pl. xxxi. (facing p. 290), 1912.

Chiropotes is more nearly akin to *Cacajao* than it is to *Pithecia*. This was perfectly obvious to Gray *, who assigned *Pithecia* to

Text-figure 9.



A. Right foot of *Callicebus castaneiventris*.
B. Right hand of the same.
C. Tip of hallux of the same showing thick digital pad.
D. Ear of the same normally spread.
E. The same contracted.
F. Ear of *Ateles pan* from Mexico, the point of attachment to the head shown by dotted lines.

the tribe Pithecina of the family Cebidæ, and *Chiropotes* and *Cacajao* (*Ouakaria*) to the tribe Brachyurina. The reasons he

* Cat. Monkeys, Lemurs, etc., 1870, pp. 36-62.

assigned for this classification were not, however, very convincing; and this may account for the neglect of his views by subsequent authors; but the failure of the latter to detect the differences between *pithecia*+*monachus* and *chiropotes*+*satanas*, and the resemblances between the latter and *rubicundus* + *calvus* + *melanocephalus*, can only be ascribed to misplaced reliance upon written statements and neglect to examine actual specimens.

The Chestnut-bellied Teetee (*Callicebus castaneiventris*).

In 1920 I described the rhinarium, the ears, and the hands and feet of an immature example of *Callicebus*—identified doubtfully as *moloch*—and the external genitalia of an adult male and female of *C. personatus*. The ear of an adult of *C. castaneiventris* which died on June 2nd, 1920, differs in some interesting particulars from that of *C. moloch* as figured (*op. cit.* text-fig. 3, D, p. 95). In that specimen the posterior margin of the ear emerged from the side of the head at a point slightly below the line of the bottom of the intertragal notch, and the deep depression extending round the pinna within its posterior edge reached inferiorly to a point on a level with the middle of the antitragal thickening. In the example of *C. castaneiventris*, on the other hand, the posterior margin of the ear starts as a free edge at a point on a level with the top of the intertragal notch, and the marginal groove ceases inferiorly at a point approximately on a level with the middle of the cavity of the ear, some distance above the upper end of the antitragus. The posterior margin of the ear, too, is not evenly convex, but is concave at the summit, meeting the anterior margin at a well-defined angle (text-fig. 9, D, E, p. 32).

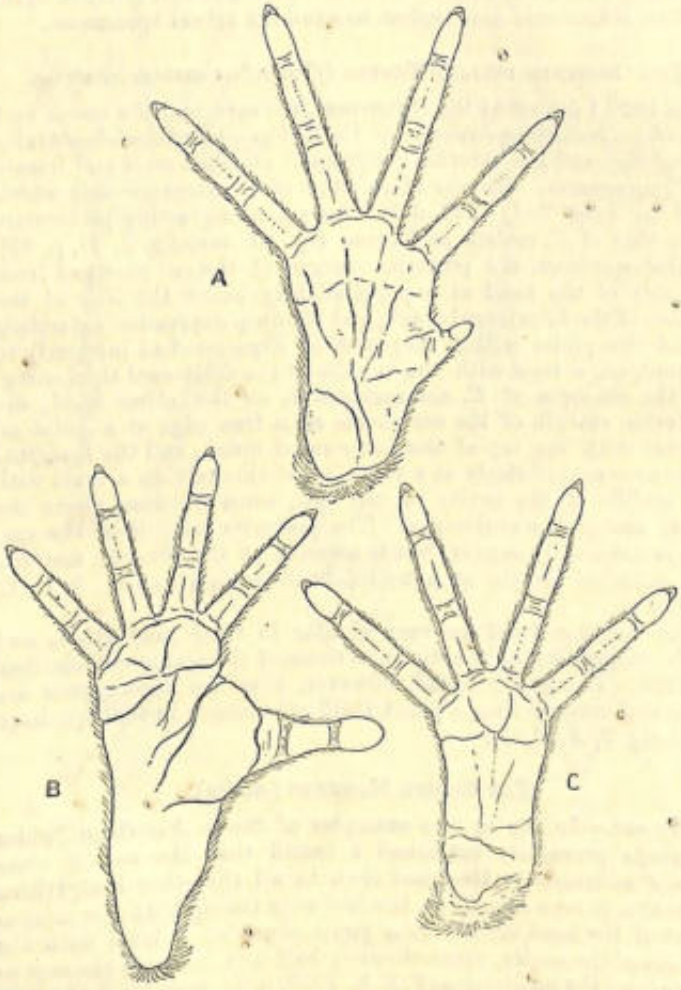
The *hands* and *feet* are very similar in their proportions and in the disposition of the digits to those of the specimen described in 1920. It may be added, however, that the digital pads are large and cushion-like, a point I did not observe in that specimen (text-fig. 9, A, B, C).

The Spider Monkeys (*Ateles*).

The ear.—In one or two examples of South American Spider Monkeys previously examined I found that the ear is more closely adherent to the head than in all the other Platyrrhine monkeys, except *Lagothrix*, the free edge fusing with the integument of the head behind at a point about on a level with the middle of the cavity, approximately half-way between the supratragus and the antitragus (P. Z. S. 1920, p. 95, text-fig. 3, G & H); and I considered this would probably prove to be a generic feature common to all the species. But in a specimen from Mexico (*Ateles pan*) I find that the free edge extends considerably below that point, below indeed the level of the lower edge of the cavity, to a point in a line with the bottom of the intertragal notch. The anterior edge of the pinna is also free

from a point on a level with the supratragus. In the South American specimens the point of attachment is above the level of that ridge. (Text-fig. 9, F.)

Text-figure 10.



A. Right hand of *Ateles paniscus*, with pollex retained.
B. Right foot of another specimen of the same species showing the well-developed base of the hallux.
C. Right hand of the same specimen with pollex suppressed.

The description I gave in 1920 of the *hands* and *feet* of *Ateles paniscus* was taken from a young and wasted specimen, and

I remarked that the foot is characterized by the reduction in the size of the hallux, which is both shorter and weaker than in other genera, the big muscular lobe at the base being scarcely visibly developed. But subsequent examination of an adult example of the same species shows that, although true in the particular case cited, the character does not apply to the full-grown animal in good condition. In this specimen the hallux is as well developed, both in length and grasping power, as in other genera, its basal portion being as thick and muscular as in any. (Text-fig. 10, F.)

In connection with the *hand*, I also said that digits 2, 3, 4, and 5 are evenly spaced as in *Cebus*, *Callicebus*, etc., showing no grasping space between digits 2 and 3 as there is in *Alouatta* and *Lagothrix*; and from this fact arose the inference that the hand of *Ateles* is not derivable from the type of hand seen in *Lagothrix*, but from the more primitive type seen in *Cebus* for example. The spacing of the digits, however, is variable. In the adult example of *A. paniscus* referred to above, the four digits in question are evenly spaced. But in another adult example of the same species, the hand of which retains the pollex as a small excrescence, the 2nd digit is noticeably more deeply divided from the 3rd than the 3rd from the 4th or the 4th from the 5th. It is therefore capable of greater divarication as in *Lagothrix*, *Alouatta*, *Pithecia*, *Chiropotes*, and *Cacajao*. But it is noticeable that the vestigial pollex is remote from the 2nd digit, remoter even than is the fully-developed pollex of *Cebus*, *Saimiris*, *Aotus*, and *Callicebus* in that it projects from the middle of the inner margin of the hand as in the monkeys of the Old World*. (Text-fig. 10, A, C.)

I have not found any noticeable variation in its position in dried skins of *Ateles* and *Brachyteles*. In these genera, as others have observed, the presence of the vestigial pollex has no systematic value. In both of them it may be present on one hand and absent from the other.

My description of the *female genitalia* of *Ateles* was very brief, and was based upon the unsatisfactory examination of living examples. Since then an adult female, apparently of *A. paniscus*†, which died in the Gardens, 26. viii. 20, came into my hands, and the following is a description of the organs in question:—

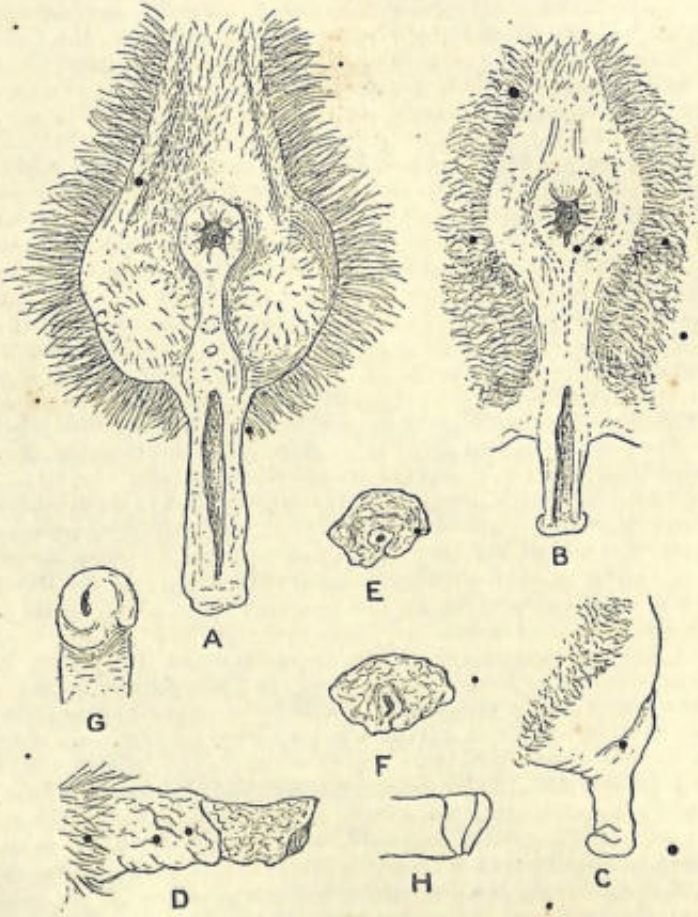
The ischial prominences are scantily hairy. From the lower rim of the area between them arises the long, thick, peniform, naked clitoris, which is supported by a cartilaginous rod extending from the pubic region to its extremity. This clitoris is about twice the length of the area above it, lying between the ischia at

* In this connection it may be recalled that the pollex or 1st digit of the hand in typical Platyrrhini closely resembles in position and its limited opposability the corresponding digit in *Tarsius*, whereas in the typical Old World Monkeys the pollex is in those particulars like the pollex of the Lemur (see P. Z. S. 1918, pp. 34–35).

† The species of *Ateles* are but little understood.

the sides and the anus above. It is relatively and actually much larger than in any other genus of Platyrrhini, and further

Text-figure 11.



A. Anal and genital area of adult female *Ateles paniscus* showing the long grooved clitoris. The position of the orifices of the urethra and vagina indicated by dotted circles.
B. Anal and genital area of adult female *Lagothrix infumata*.
C. Lateral view of the clitoris of the same.
D. Penis of adult male of *Ateles paniscus*.
E and F. Apex of the same from the front showing degree of contraction of terminal field.
G. Tip of penis of *Ateles pan*, from Mexico, from below.
H. Side view of same.

differs in having the apex undifferentiated into a disk- or button-shaped glans. Its posterior surface is deeply and widely grooved

from the base almost to the apex, but the apex itself is ungrooved. The margins of this groove or gutter fold over it and meet in the middle line *.

At its upper end the groove communicates with the passage between the ischia containing the small urethral and vaginal orifices, which are completely concealed from view by the superficial skin extending between the ischia from the anus to the proximal end of the groove of the clitoris. A precisely similar arrangement was observed in female examples of *Cebus*, *Alouatta*, and *Lagothrix*. (Text-fig. 11, A.)

My previous description of the female genitalia of *Lagothrix* was taken from an injected example of *L. infumata* with the labia of the generative orifice turgid, it was supposed, from the injected fluid. An uninjected female of the same species shows that the swollen condition was due to the injection. In this specimen the labia or margins of the groove of the clitoris are not swollen, and the groove itself opens below on the posterior surface of the transverse disk-shaped glans, the clitoris in length, thickness, and grooving closely resembling that of *Cebus*, except that the glans is not enveloped in a preputial flap of skin. (Text-fig. 11, B, C.)

The *penis* of *Ateles paniscus* is very short as compared with that of *Cebus* and most other genera, and it has no disk-shaped or button-shaped glandular termination. The skin of its apex is flaccid and retains no definite shape, the orifice lying in the lower half of the terminal area sometimes to one side of the middle line. But in the Mexican *Ateles* (*A. pan*), whose ear was described above, the apex of the penis is much more regular in shape, forming a smooth, definitely circumscribed, rounded area, marked with grooves and with the orifice to the right of the middle line. The tip of the penis in this species recalls that of *Cebus* rather than of *Ateles paniscus*. (Text-fig. 11, D–H.)

The Classification of the Platyrrhini.

It is needless to enumerate the characters by which the American Platyrrhine † monkeys may be distinguished from the Catarrhine † monkeys of Africa and Asia. But there is one character in connection with the skulls used by some authors, Max Weber, for instance, which does not hold good in all cases. This is the junction of the bones of the sides of the skull behind the orbit. In most cases, it is true, the parietal extends forwards to form a suture with the malar, as shown in the skulls of *Pithecia*

* When I examined the living specimen as reported in my previous paper, the juxtaposition of these edges obliterating the groove led to my describing the clitoris as "apparently ungrooved."

† These terms have been so long in use that they may still be adopted; but it must be remembered that they do not express a constant difference. The nostrils, for example, of the Howler (*Alouatta*) I figured and described in 1920 are both in direction and narrowness of separation more like those of a typical Catarrhine species than they are like the nostrils of *Chiropotes* or *Cacajao*, in which the 'platyrrhinism' reaches its highest expression.

and *Chiropotes* figured above (p. 31, text-fig. 8, B, D). But in some skulls of *Alouatta ursina* and of *Brachyteles arachnoides*, picked at random from series from Espiritu Santo, Brazil, in the British Museum, great variation in the disposition of these bones is exhibited. In one example of *A. ursina*, for instance, the alisphenoid forms a long junction with the frontal, shutting off the parietal and squamosal from the malar (text-fig. 12, A). In another the parietal forms a very narrow union and the squamosal a broad union with the malar, excluding the alisphenoid from the frontal (text-fig. 12, B). Again, in an example of *B. arachnoides* the alisphenoid forms a short suture with the frontal, the parietal and squamosal both failing to meet the malar (text-fig. 12, C). In another of the same species the squamosal is joined both to the frontal and the malar, shutting off the alisphenoid from the frontal and the parietal from the malar (text-fig. 12, D). These are merely a few instances of the many observed variations which seem to show that the method of closing the space between these four bones is a matter of complete indifference, at all events, in these two genera.

By almost common consent the Platyrrhines are assigned to two families—the Hapalidæ or Marmosets and the Cebidæ or Monkeys.

By the structure of the hands and feet and the loss of the third molar tooth above and below, the Hapalidæ are in my opinion, as expressed in 1917, clearly a specialized derivative group that branched off at an early stage from the monkey stock *. The reduction of the hallux to a comparatively useless vestige, and the conversion of the nails into long, sharp claws, were adaptations to a change in method of climbing and leaping, whereby the arboreal activities of the Marmosets came to resemble those of Squirrels.

One of the most interesting of the genera is *Callimico*, comparatively recently described by Thomas, which has retained the last molar and resembles the Cebidæ in dentition. Those who attach greater importance to the number of the teeth than to the structure of the feet will classify *Callimico* with the Cebidæ. In my opinion it is a primitive Marmoset; and its distinction from the rest of that family may be expressed by dividing the Hapalidæ into two subfamilies—the Hapalinæ for *Hapale*, *Mystax*, *Œdipomidas*, and *Leontocebus*, and the Callimiconinæ for *Callimico* †.

The well-defined genera of the second group of Platyrrhines, comprising the species with a large hallux and the digits of both hands and feet provided with nails, are usually assigned to a single family—the Cebidæ, which in most recent text-books is subdivided into four subfamilies. But since modern changes in

* I cannot agree with Prof. Elliot Smith that *Hapale* is the most primitive surviving Monkey ('Essays on the Evolution of Man,' p. 141, 1924).

† Proc. Zool. Soc. 1920, p. 113; for the characters of the well-marked genera of Hapalinæ see my paper in Ann. Mag. Nat. Hist. (8) xx. pp. 247-258; and for finer subdivisions Thomas's paper in Ann. Mag. Nat. Hist. (9) ix. pp. 196-199.

the generic names have necessitated changes in the subfamilies derived from them, it may help those unfamiliar with these changes if it be explained that :—

The Howlers, *Myostes* are now *Alouatta*.
The Night Apes, *Nyctipithecus* are now *Aotus*.
The Squirrel Monkeys, *Chrysothrix* are now *Saimiris*.
The Teetees, *Callithrix* are now *Callicebus*.
The Uakaris, *Brachyurus* or *Ouakaria* are now *Cacajao*.

Going back to 1870, we find that Gray divided the Cebidæ into two sections as follows :—

A. Gymnura.
Tribe Mycetina (*Mycetes*).
„ Lagotrichina (*Ateles*, *Brachyteles*, *Lagothrix*).

B. Trichiura.
Tribe Cebina (*Cebus*).
„ Callitrichina (*Chrysothrix*, *Callithrix*).
„ Nyctipithecina (*Nyctipithecus*).
„ Pithecina (*Pithecia*).
„ Brachyurina (*Chiropotes*, *Ouakaria*).

Subsequent authors dropped the main divisions Gymnura, based on the highly prehensile tail being terminally naked beneath, and Trichiura, based on the tail, whether prehensile or not, being terminally hairy beneath, and converted some of Gray's tribal names into subfamilies, rearranging the genera to a certain extent. Thus in 1891 Flower and Lydekker ('Mammals, living and extinct,' pp. 711–718) divided the Cebidæ into :—

Subfamily Mycetinæ (*Mycetes*).
„ Pitheciinæ (*Pithecia*, *Uakaria*).
„ Nyctipithecinæ (*Callithrix*, *Chrysothrix*, *Nyctipithecus*).
„ Cebinæ (*Ateles*, *Eriodes* (=*Brachyteles*), *Lagothrix*, *Cebus*).

This classification differs from Gray's in (1) the association of *Cebus* with *Ateles*, *Brachyteles* (*Eriodes*), and *Lagothrix*; (2) of *Nyctipithecus* with *Callithrix* and *Chrysothrix*; and (3) of *Ouakaria* with *Pithecia*, whereas *Chiropotes*, as has been shown above, was fused with *Pithecia*.

With the substitution of Alouattinæ for Mycetinæ, Flower's classification was followed by Forbes in 1891* and by Trouessart in 1898 and 1904†. It was also adopted by Max Weber in 1904‡, with the noteworthy exception that he transferred *Chrysothrix* to the vicinity of *Cebus* in the Cebinæ and gave subgeneric importance to *Chiropotes*. Elliot in 1912§ reverted to Flower, but placed

* Allen's Nat. Libr.: Monkeys, vol. i.
† Cat. Mamm. i. pp. 32–48, & Suppl. pp. 21–26.
‡ Die Säugethiere.
§ Mon. Primates, vols. i. and ii.

Chrysothrix, under its correct name *Saimiris*, in the Pithecinæ alongside *Pithecia* and *Uakaria*, citing the latter under its present name, *Cacajao*. He also altered the name Nyctipithecinæ to Aotinæ and, no doubt accidentally, referred *Callithrix* or, as he correctly called it, *Callicebus* to the Marmosets. Finally, Miller in 1924*, omitting the Pitheciinæ and *Callicebus* as aliens to the fauna of North America, arranged the genera of that continent in the families Alouattidæ, Aotidæ, Saimiridæ, and Cebidæ, dividing the latter into Cebinæ and Atelinæ.

Gray, Flower, Forbes, and Max Weber gave definitions of the groups they founded or adopted. Elliot, very wisely, made no such attempt. Trouessart and Miller, being concerned purely with nominal lists, left definitions alone.

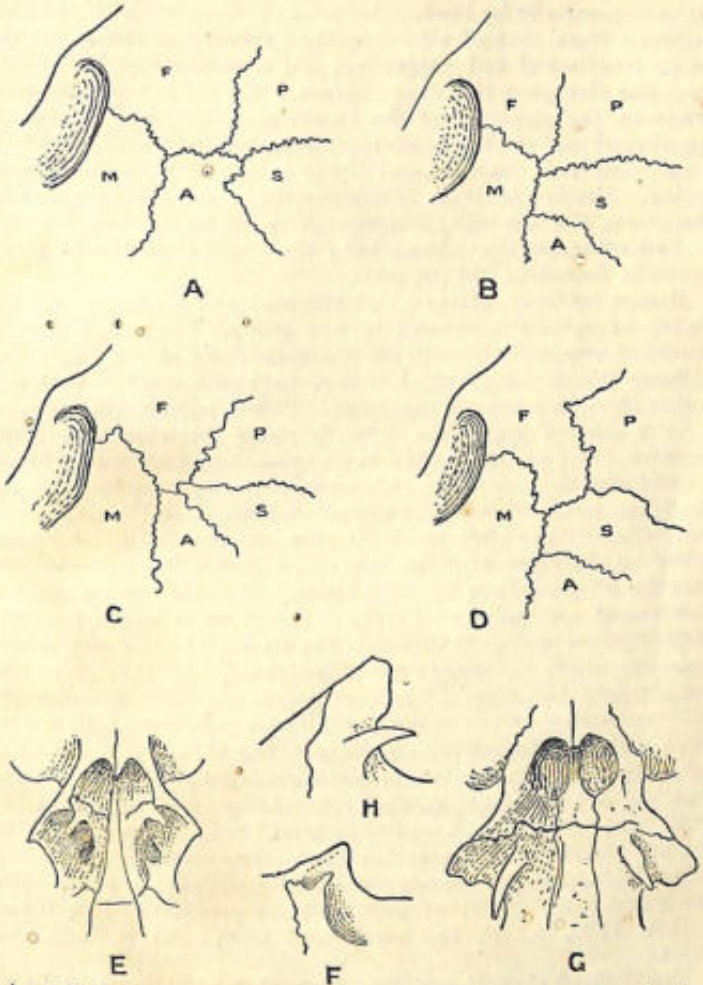
Perhaps the most interesting point connected with these classifications is the diversity of views as to the kinship of *Saimiris* (*Chrysothrix*). Associated by Gray with *Callicebus* (*Callithrix*), by Flower, Forbes, and Trouessart with *Callicebus* and *Aotus* (*Nyctipithecus*), by Max Weber with *Cebus*, by Elliot with *Pithecia* and *Cacajao*, it was finally by Miller given the status of a family to itself.

In my opinion Max Weber's allocation of it was perfectly correct. Its skull supplies no evidence of close affinity between it and *Callicebus*, or *Aotus* or *Pithecia* or *Cacajao*. On the other hand, although the back of the skull is longer and the occiput is more horizontal in *Saimiris* than in *Cebus*, the skulls of the two, making allowance for the effects of more powerful musculature in *Cebus*, agree tolerably closely in general features, in the long, low cranium, the facial angle, the shape of the jaws, the unexpanded angular region of the mandible, and the disposition and relative size of the teeth. More particularly, however, do they agree and differ from the skulls of other Platyrrhines in the structure of the mesopterygoid fossa, which shows a very pronounced space or pit between the pterygoid itself and ectopterygoid plate of the alisphenoid. In the other genera there is no such pronounced pit, the greater part of the pterygoid being fused with the ectopterygoid, so that only its terminal portion ending in the hamular process stands away from it. The two genera also agree tolerably closely in external characters, in the structure of the hands and feet, the nostrils, ears, and external genitalia of both sexes, although the glans penis is differently shaped in the two, the orifice being inferior in *Saimiris* and terminal in *Cebus*. (Text-fig. 12, E–H.)

In view, then, of the resemblances between *Cebus* and *Saimiris*, and of the isolation of the latter from the rest of the Platyrrhine genera, and of the differences between *Cebus* and *Ateles*+*Brachyteles*+*Lagothrix*, with which it has been commonly associated, I should classify the two in a group apart—the Cebinæ,—equivalent to Miller's Cebinæ and Saimiridæ.

* Bull. U.S. Nat. Mus. no. 128, pp. 167–171.

Text-figure 12.



A and B. Temporal region of skull of two examples of *Alouatta ursina* from Espiritu Santo, showing variation in the junction of the cranial bones.

C and D. The same of two examples of *Brachyteles arachnoides* from Espiritu Santo. F., frontal; P., parietal; M., malar; A^{s}, alisphenoid; S., squamosal.

E. Mesopterygoid fossa of *Saimiris* showing the pterygoid separated by a deep valley from the ectopterygoid plate.

F. Left wall of the same from the inner side.

G. Mesopterygoid fossa of *Alouatta* showing the absence of valley between the pterygoid and the ectopterygoid plate, the hamular process of the pterygoid alone projecting.

H. Left wall of the same from the inner side.

A second tolerably well-defined group—the Pitheciinæ.—

containing the genera *Pithecia*, *Chiropotes*, and *Cacajao*, is characterized essentially by the arrangement of the front teeth, which is different from that of all the other genera; the lower incisors being lengthened and projecting, and separated by a diastema from the divergent tusk-like canines. They also resemble each other in the structure of the hands and feet, the feet being lengthened and the hands having the second digit separated by a wide space from the third and acting in unison with the first or pollex. Neither of these characters, however, is distinctive of the group, the feet being scarcely longer relatively than in *Cebus* or *Callicebus* and the disposition of the digits of the hand being found in *Lagothrix* and *Alouatta*.

Except by Gray, *Aotus* (*Nyctipithecus*) and *Callicebus* (*Callithrix*) have been associated in one group. There are several points of resemblance between them in their skulls, but many differences also; and I think it is perhaps on the whole better to follow Gray and keep them apart. *Aotus*, indeed, differs from all the other Platyrrhines, including the Marmosets, in being nocturnal and provided with large eyes—hence its trivial name "owl-faced monkey"; and to accommodate its large eyes the skull has orbits enormously expanded both laterally and dorso-ventrally, so that they encroach upon the cheeks, making them lower or shallower than in any other genus. The orbits open into the temporal fossa by a big space. The nasal bones, too, are compressed and long, projecting so as to be in advance of the lower canines and vertically over the alveolar border of the premaxillæ, which is scarcely at all produced. In this sense the muzzle may be described as orthognathous. For the rest the inferior border of the mandible is approximately parallel with the alveolar border of the cheek-teeth, but its angle is produced into a large angular lamina projecting beyond the condyle. The cranium is low, short, and tolerably broad, and the bullæ are exceptionally strongly expanded in front of the meatus. Finally, the hands and feet are exceptional in having very large, coarsely-ridged pads, probably an adaptation to nocturnal prowling; and the vulva is not provided with a visible pendulous clitoris (see P.Z.S. 1920, p. 99, for hands and feet; and p. 106, for vulva).

The skull of *Callicebus* differs from that of *Aotus* mainly in having orbits of normal dimensions, a normally high cheek, and more porrect premaxillæ, so that the muzzle cannot be described as orthognathous although it is less prognathous than in most genera. The jaws are narrowed distally, and owing to the smallness of the canines, the teeth form an almost unbroken curved line, very different from that of *Saimiris*. The mandible is of immense depth, its inferior border sloping downwards and backwards from the longish symphysis and being compressed and inturned. The angle forms a lamina larger and rounder than in *Aotus* but similarly projecting. The zygomatic arch is much stouter than in that genus, and exceptional in the downward

projection of its antero-inferior maxillary angle. The bulla is inflated, but the inflation is mostly below the meatus, not in front of it as in *Aotus* and some others, *e. g.* some forms of *Ateles*. Finally, the soles of the hands and feet of *Callicebus* have pads normally smooth and poorly defined, except the terminal digitals, which are soft and cushion-like; and the vulva is provided with a short pendulous clitoris very like the penis of the male but smaller (see P. Z. S. 1920, p. 110). Neither in cranial nor external characters, therefore, are the likenesses between *Aotus* and *Callicebus* sufficiently close to justify the view that they are closely related, and I regard them as representing respectively two subfamilies—Aotinæ and Callicebinæ.

The genera *Lagothrix*, *Ateles*, and *Brachyteles* have always been associated by common consent. So far as external characters are concerned, *Lagothrix* and *Ateles* resemble one another, and differ from all the genera hitherto considered in the structure of the tail, which is covered below distally with naked, transversely wrinkled skin, and is highly specialized for prehension and very sensitive. The feet, too, are shorter, as compared with the hand, than in the others. The hand of *Lagothrix*, however, is like that of *Chiropotes* or *Cacajao*, whereas in *Ateles* the pollex is absent or vestigial, and the second digit is at most only slightly farther from the third than the third is from the fourth. *Lagothrix* and *Ateles* are also alike, or nearly so, in the attachment of the ear and in the widely-spread nostrils. The penis of *Lagothrix* is also like that of *Ateles*, but the clitoris of *Lagothrix* is more normal, being shorter and grooved to the tip, which has a button-shaped expansion. In the structure of its clitoris, *Ateles* is the most highly-specialized genus of Platyrrhines.

My knowledge of *Brachyteles* is limited to skins and skulls. So far as can be judged, the hands and the feet are like those of *Ateles*. The ears also appear to be similar. The nostrils have been described as narrowly separated as compared with those of *Ateles*. This may be the case, but the character is not convincingly shown on the skins. The external genitalia are certainly different from those of *Ateles* in at least one respect. Below the generative orifice in the female there is a distinct but not very long penis-like projection, covered with black hair apparently stuck together with secretion. This organ is very distinct from the long, naked clitoris of *Ateles* as figured above (text-fig. 11, A). The penis, too, appears to be considerably larger relatively than in *Ateles*, and to be expanded at the tip into a short but deep glans, which is irregularly oval in outline when viewed from the front, being somewhat rounded above and pointed below, and carrying a large orifice in the middle of its anterior surface. In both sexes there is a large area at the base of the tail beneath, which is naked except for a median line of hairs. The area round the anus is also naked; and in the male a narrow strip of naked skin passes from this to the scrotum, which is also naked.

The kinship of *Alouatta* is not easily determined; but so far as the external characters above discussed are concerned, the following points may be noted:—The tail is like that of *Lagothrix*, *Brachyteles*, and *Ateles*; the hand is like that of *Lagothrix* and *Pithecia* or *Cacajao*, but the foot is not long as compared with the hand, as in the last two, but short as in *Lagothrix*. The nostrils are comparatively narrowly separated as has been stated to be the case in *Brachyteles*. The ear, it is true, retains its primitive freedom from the skin of the head and is not basally confluent with it as in *Lagothrix* and some species of *Ateles*; but since this character varies within the limits of the genus *Ateles*, it has no great importance in the present connection. The male genitalia are unknown to me; but the vulva and clitoris do not differ greatly from those of *Lagothrix*.

In the sum of its external characters therefore, I can find no structural peculiarities justifying the severance of *Alouatta* from the Atelinæ. But the claim of the genus to hold a place apart in a special subfamily or family rests upon its skull and hyoid bone. It appears to me to be probable that the modifications of the skull are correlated with the well-known and extraordinary development of the hyoid bone. The mandible is exceedingly massive, with a long symphysis and receding chin, the ascending ramus being especially high and expanded, with an evenly curved posterior border. Correlated with the height of the mandible is the upward tilt of the cranial portion of the skull, so that the plane of the occiput is nearly vertical and the plane of the basi-occipital, basisphenoid and presphenoid, instead of sloping upwards from the foramen magnum behind to the posterior nares in front to form an obtuse angle with the basifacial axis, is approximately horizontal and in line with that axis. The result of this modification is that when the cheek-teeth are resting upon a flat surface the occipital condyles are raised high above it. In *Lagothrix*, *Ateles*, or *Brachyteles*, on the other hand, when the cheek-teeth are on a flat surface, the occipital condyles also rest on that surface. These and other differences, such as the lower crown and occiput, obtain both in male and female skulls; but most of them are much less pronounced in the female than in the male. If the less-modified female skull be compared with that of *Lagothrix*, *Ateles*, and *Brachyteles*, it does not seem extravagant to claim *Alouatta* as a divergent genus of that stock, differing mainly therefrom in the huge expansion of the hyoid and the cranial modifications correlated therewith*. The teeth of *Alouatta* are not very different from those of *Brachyteles*, although the molars and premolars are relatively larger and the last lower molar has a larger "heel." *Alouatta*, indeed, stands alone amongst the Platyrrhini in having the last lower molar longer than the first.

* The skull of a young *Alouatta*, with the first molar already fully in use, differs very little in general conformation from adult skulls of *Ateles* or *Brachyteles*, the upper surface of the cranium being well arched, the occipital plane inclined, and the basicranial axis also more inclined than in the adult.

The distinguishing characters of the subfamilies and genera here admitted may be tabulated as follows: —

a. Orbits very large, their combined width about equal to length of cranium; cheeks low; muzzle orthognathous, upper rim of nares in front of lower canine; hands and feet with large coarsely-striated pads ..... Aotinæ (*Aotus*).

a'. Orbits normal, their combined width much less than length of cranium; cheeks high; muzzle more or less prognathous owing to projecting premaxillæ; hands and feet with comparatively smooth and less well-developed pads.

b. Posterior (outer) wall of orbit evenly convex, with compressed edge, which is not thickened or crested; muzzle short and compressed; bullæ markedly inflated below the meatus; mandible with horizontal ramus gradually expanding, its angle developed into a large lamina projecting backwards some way beyond the condyle ..... Callicebinæ (*Callicebus*).

b'. Outer margin of orbit thickened and defined by a ridge from the posterior surface; muzzle not short *and* compressed; bullæ not markedly inflated below meatus; mandible variable, its expanded angle seldom projecting noticeably beyond condyle when the horizontal ramus is expanded.

c. Lower incisors long and compressed, separated from the divergent tusk-like canines by a distinct diastema, their combined width at most slightly exceeding their height ... Pitheciinæ.

d. Frontals low and long, nasals swollen above nares; incisors and canines more normal; tail long ..... *Pithecia*.

d'. Frontals higher and shorter; nasals not swollen above nares; incisors and canines abnormal, jaws markedly prognathous.

e. Tail longer than hind limbs ..... *Chiropotes*.

e'. Tail shorter than hind limbs ..... *Cacajao*.

c'. Lower incisors not elongated, not separated from more vertical canines by a distinct diastema, their combined width usually as much as twice their height or more.

f. Pterygoid not confluent with ectopterygoid, separated from it by a deeper and wider space; supraoccipital noticeably bi-impressed. Tail hairy distally beneath. Feet long as compared with hands; the pollex well developed and not working in unison with digit 2 ... Cebinæ.

g. Posterior region of cranium very long; supra-occipital plane horizontal; orbits communicating; no brow ridge. Tail not prehensile ..... *Saimiris*.

g'. Posterior region of cranium not abnormally long; plane of supraoccipital inclined; orbits not communicating; brow ridges present. Tail prehensile ..... *Cebus*.

f'. Pterygoid, apart from hamular process, confluent with ectopterygoid, or nearly so, at most a narrow shallow space between. Supraoccipital not noticeably bi-impressed. Distal end of tail beneath naked and wrinkled. Feet short as compared with hand; pollex, when normally developed, close to digit 2 and acting in unison with it.

h. Hyoid normal, mandible at most moderately inflated, with short rounded symphysis, its last molar not markedly longer than the others; jaws less massive and shorter; cranium higher; supraoccipital high and sloped; basicranial axis forming obtuse angle with basifacial ..... Atelinæ.

j. Pollex well developed and close to digit 2, which is widely separated from digit 3. Jaws shorter; interorbital septum more prominent above, more hollowed below ..... *Lagothrix*.

j'. Pollex absent or, when vestigial, remote from digit 2, which is scarcely farther from digit 3 than the latter is from 4. Jaws longer; interorbital septum less prominent above, less hollowed below.

k. Incisors and canines small, upper median incisors not larger than laterals, the series underlapped by lower incisors; mandible more expanded ..... *Brachyteles*.

k'. Incisors and canines larger, upper median incisors larger than laterals, the series not underlapped by lower incisors; mandible less expanded ..... *Ateles*.

k''. Hyoid hollow and inflated; mandible greatly expanded, with long sloped symphysis, and evenly convex posterior border, its last molar longer than the others; jaws longer and more massive; cranium and supraoccipital low, the plane of the latter nearly vertical; basicranial axis in same plane as basifacial. Hands as in *Lagothrix* ..... Alouattinæ (*Alouatta*).

Note (Dec. 15th, 1924).—Not until this paper was completed and accepted by the Publication Committee did I see Winge's account of the Platyrrhini ('Pattedyr-Slægter,' ii. pp. 267–77, 1924). Since this author's views always command careful attention, I venture to give a free translation of the classification of this group that he proposed*.

Family Cebidæ.

a. Brain smaller; lumbar vertebræ longer.
b. Third molar present; nails flat ..... Mycetini.
c. Lumbar vertebræ long, their spinous processes normal; tail not prehensile; hyoid normal.
d. Lower incisors normal ..... Callitriches (*Callithrix, Nyctipithecus*).
d'. Lower incisors abnormal ..... Pitheciæ (*Pithecia, Brachyurus*).
c'. Lumbars generally short, their spinous processes ridge-like; tail prehensile; hyoid abnormal ..... Mycetes (*Mycetes*).
b'. Third molar absent; nails secondarily modified as claws ..... Hapalini (*Hapale, Midas*).
a'. Brain larger; lumbar vertebræ usually shorter ..... Cebini.
c. Pterygoids confluent with ectopterygoids; tail not pointed, hairy at end; lower end of upper arm narrow ..... Cebi (*Cebus, Chrysothrix*).
c'. Pterygoids not confluent; tail pointed and naked beneath at end; lower end of upper arm wide ..... Ateles (*Lagothrix, Ateles, Eriodes*).

The author's adoption of such obsolete names as *Mycetes*, *Callithrix*, *Chrysothrix*, *Brachyurus*, and *Nyctipithecus* is a matter of no real moment. The points to be noted in his classification are:—

(1) All the South American Primates are referred to the family Cebidæ, which is equivalent to the Platyrrhini of other authors.

(2) The Marmosets (Hapalini) are regarded as a subfamily of the Cebidæ and as a modified offshoot of a small-brained stock of the group which also contains the five genera *Callicebus* (*Callithrix*) and *Aotus* (*Nyctipithecus*); *Pithecia* and *Cacajao* (*Brachyurus*); and *Alouatta* (*Mycetes*). Winge's view that Hapalini are a derivative, not a primitive, group agrees with the view I expressed in 1917. He does not, however,

* Since this paper is written in Danish, I enlisted the kind services of Mr. Martin Hinton for the translation.

take *Callimico* into account. In all probability its inclusion would not have materially altered his opinion regarding the status of the Hapalini.

(3) In keeping *Callicebus* and *Aotus* in one section and *Pithecia* and *Cacajao* in another, Winge agrees with Weber and some other authors; and his decision of these points calls for no special comment. But his grouping of these genera with *Alouatta* (*Mycetes*) in a subfamily is a novel idea. It may, however, perhaps be doubted if the characters, the smaller brain, and the longer lumbar vertebræ, upon which the association is based, have the value assigned to them. From Winge's analytical key it appears that the vertebræ themselves are variable, and judging from the convex curvature of the crown of the skull in *Chiropotes* and *Cacajao*, those genera have a considerably larger brain than *Pithecia*, as large indeed as in *Lagothrix* or *Brachyteles*. Yet the kinship between *Chiropotes* and *Pithecia* is generally admitted. Winge appears to think, and in my opinion rightly, that an exaggerated importance has been attached to the abnormality of the hyoid in *Alouatta*; but in spite of his removal of that genus from the neighbourhood of *Lagothrix* and *Ateles*, I am disposed to retain my opinion that the structural peculiarities of the Howlers may be explained on the hypothesis that they are in some ways specialized, in some ways degenerate members of that stock.

(4) He adopts Weber's view that *Saimiris* (*Chrysothrix*) is akin to *Cebus*, and it will be noticed that we independently made use of the characters presented by the mesopterygoid fossa as evidence of their association and of their dissociation from *Lagothrix* and *Ateles*, with which *Cebus* at all events had been generally classified.

4. Descriptions of New Acari, mainly parasitic on Rodents.

By Stanley Hirst, F.Z.S.

(Submitted for publication by permission of the Trustees of the British Museum.)

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(Text-figures 1–15.)

Myonyssoides, gen. nov.

Allied to *Myonyssus* Tiraboschi. *Tritosternum* with a pair of spinules at the base. *Sternal plate* trapezoidal and furnished with four pairs of hairs. *Genito-ventral plate* rather like that of *Myonyssus*, but much shorter, and only widened a little posteriorly; apparently only one pair of hairs is present on this plate. *Anal plate* very large, being shaped like that of *Myonyssus*.

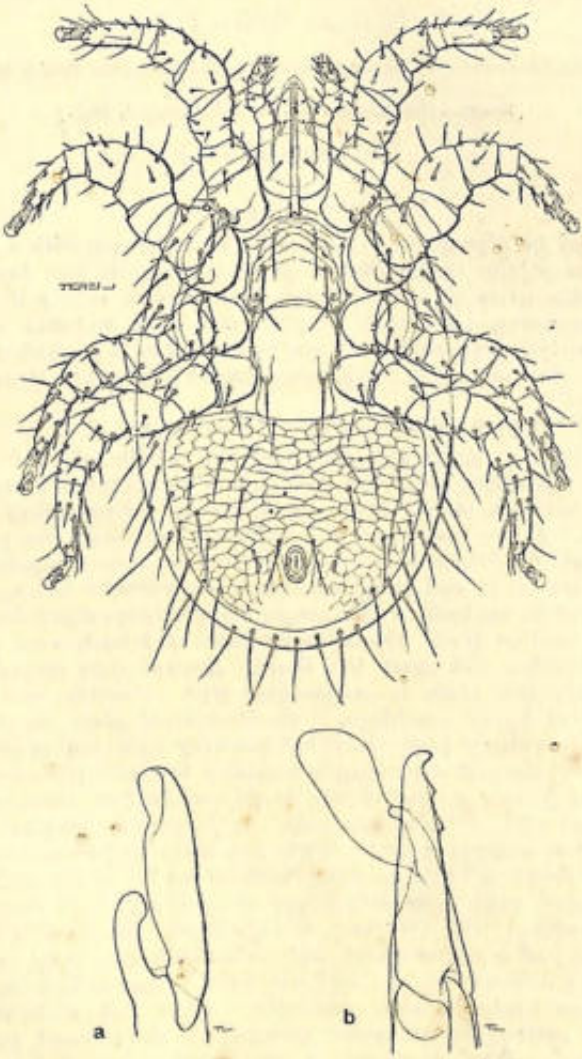
Myonyssoides capensis, sp. n. (Text-fig. 1.)

♀. *Scutum* undivided, covering the whole of the dorsal surface; it is smooth in the middle, but ornamented posteriorly with a network of fine linear markings and microscopical punctations. A few very short and inconspicuous hairs are present in the middle of the scutum; laterally there are some comparatively long hairs on it, and there are also a few anterior hairs. Base of *capitulum* ventrally with a single file of minute sharp denticles in the median line. Denticles on base of *tritosternum* placed close together and stout but short. *Sternal plate* trapezoidal; anteriorly this plate is ornamented with reticulate and some transverse linear markings. *Genito-ventral plate* short and gradually widened posteriorly, but not very wide, and practically truncated, the posterior margin touching the anterior margin of the anal plate. *Anal plate* very large, and most of its surface is furnished with reticular markings; anal aperture situated near the posterior margin; about thirty-one hairs are present on this plate. *Peritremal tube* reaching forwards as far as the middle of the second coxa. Movable finger of *chelicera* well developed and furnished with two very minute teeth; immovable finger consisting of a rather short, but well chitinized, basal portion bearing a delicate lobular distal structure. Coxa of first leg with a curious knob-like spur ventrally. Coxæ 2–4 without any ventral spurs; the posterior margin of the second coxa is somewhat salient, however; a well-developed and forwardly directed spur is present dorsally on the second coxa.

♂. Very like the female in most respects. *Sternal plate* united with the *genito-ventral plate* and the usual anterior male sexual fore is present; posterior end of this plate narrower and more rounded off than in the female sex; five pairs of hairs are

present on this ventral plate. *Anal plate* contiguous to the ventral plate, but separate and shaped as in the female. Coxa of

Text-figure 1.



Myonyssoides expensis, gen. & sp. n., ♀. Ventral view.
a. Chelicera of male. *b*. Chelicera of female.

first leg with a little knob-like spur ventrally as in the female. Second leg enlarged and differs from that of the female sex in

having a strong ventral spur on its femur; fourth and fifth joints also with small tooth-like spurs. One of the fingers of the *chelicera* is comparatively long, being somewhat spatulate and hollowed out; the other finger is very much smaller.

♀. *Length* (not including the capitulum) ·93 mm.; greatest width ·68 mm.

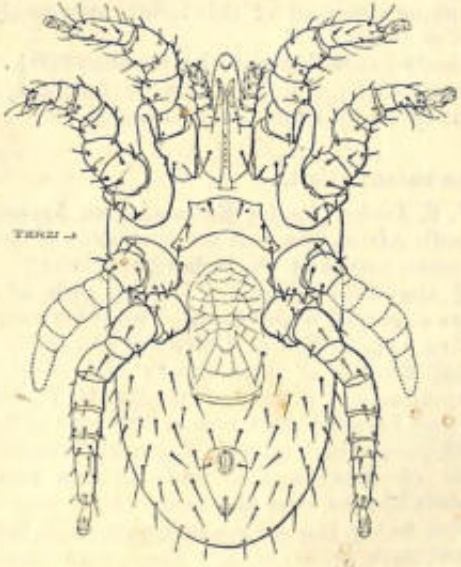
♂. *Length* (not including the capitulum) ·76–·82 mm.; greatest width ·54 mm.

Host: *Cryptomys hottentotta*, Grahamstown; a number of specimens collected by John Hewitt, of the Albany Museum.

ECHINONYSSUS, gen. nov.

Closely allied to *Liponyssus* Kolenati, but the anterior end of the dorsum scutum produced in the median line to form a large hook-like process. Posterior end of *genito-ventral plate* truncated; two pairs of hairs are present on this plate. *Anal plate* pear-shaped as in *Liponyssus*.

Text-figure 2.



Echinonyssus nasutus, gen. & sp. n., ♀. Ventral view.

ECHINONYSSUS NASUTUS, sp. n. (Text-fig. 2.)

Dorsal scutum large and not divided; it does not cover the entire dorsal surface, a short area of softer integument being left at the posterior end of the body. Hairs on *scutum* very short and inconspicuous, not numerous; they are symmetrically

arranged. Base of *capitulum* with a single median file of very minute forwardly-directed denticles ventrally as in *Liponyssus*, etc. *Sternal plate* short and wide, the posterior margin being rather strongly concave; there are three pairs of hairs on this plate. *Genital operculum* large and very delicate, and some rather scale-like markings are visible on it; it is continued posteriorly by the *genito-ventral plate*, which is rather short, its posterior end being truncated; two pairs of hairs are present on this plate, one pair being situated on the posterior margin. *Anal plate* pear-shaped and bearing the usual three hairs. Hairs on *venter* fairly numerous, fine, stiff, and rather short. *Peritremal tube* reaching as far forwards as the first coxa. Coxa of first leg furnished with a single sharp spur; the second coxa has a very large curved hook-like spur anteriorly, and posteriorly it is furnished with two sharp little subequal spurs; third coxa with two sharp little subequal spurs posteriorly; fourth coxa with a single quite short posterior spur.

Tarsus of second leg with a pair of short but stout spinules ventrally at its distal end. A spinule is also present in the same position on the tarsi of the posterior legs. *Chelicera* difficult to see in our unique specimen of this mite; apparently the fingers are devoid of denticles?

Length of body (including anterior process) 630 μ.

Host. Tupaia picta; a single damaged female specimen from this host sent to me by Professor Trouessart.

LIPONYSSUS BACOTI Hirst.

Mr. R. W. E. Tucker, Senior Entomologist, Agricultural Dept., Union of South Africa, has sent me specimens of this mite found attacking human beings at Pretoria (April 1924). Some of the examples of the mite occurring in the beds of the persons attacked were engorged with blood. Two other instances of this mite attacking man in South Africa are known to Mr. Tucker. The Imperial Bureau of Entomology has recently received a number of specimens of *L. bacoti* from Mr. H. P. Thomasset, who states that they invaded the whole of the post office at Weenen, Natal, biting people and causing much unpleasantness. There are numbers of bats in the roof of this post office, and Mr. Thomasset thinks that the mites came from them. The specimens sent to the Bureau are referable to *L. bacoti*, however, and it seems more probable that they were brought into the building by rats.

LIPONYSELLA, gen. nov.

I propose the new generic name *Liponysella*, for *Liponyssus madagascariensis*, mihi, Proc. Zool. Soc. 1921, p. 780, differing chiefly from *Liponyssus* in having the posterior end of the *genito-ventral plate* truncated instead of pointed or rounded off; and with three pairs of hairs on this plate instead of only one pair.

Dermanyssus gallinæ Redi.

Specimens attacking human beings at Cape Town (November 1923) received from Mr. R. W. E. Tucker.

Dermanyssus muris Hirst.

A single example of this mite was collected by Mr. W. A. Lamborn at Faliwas, 36 miles, S.W. of Karonga, North Nyasaland (7. xi. 1919).

Genus Lælaps Koch.

Only the species of *Lælaps* (s.s.) having four pairs of hairs on the genito-ventral plate of the female are included in the present paper. It is hoped to deal with the species of *Hæmolælaps* and *Androlælaps* occurring on rodents in another note.

Key to the African species of Lælaps (*females*) *present in the British Museum Collection.*

1. Small species (·62–·76 mm.) ..... 2.
   Large species (·9–1·80 mm.) ..... 9.

2. Coxa of first leg ventrally with two stout spinules ... 3.
   Coxa of first leg ventrally with one stout spinule and one longer seta ..... 5.

3. Base of capitulum ventrally with a pair of very short but stout spinules ..... *L. parvulus* Hirst.
   Base of capitulum ventrally with fine hairs only ..... 4.

4. Spines at distal end of second tarsus not very large. Anal plate shaped as figured, the paired hairs replaced by stout spines ..... *L. vansomereni* Hirst.
   A cluster of heavy spines distally on the second tarsus. Anal plate shaped as figured, the paired hairs on it fine ..... *L. æthiopicus*, sp. n.

5. Lateral margin of dorsal scutum conspicuously thickened ..... *L. algericus*, sp. n.
   Lateral margin of dorsal scutum not conspicuously thickened ..... 6.

6. Sternal plate shaped as shown in figure, being longer than wide ..... *L. liberiensis*, sp. n.
   Sternal plate shaped otherwise ..... 7.

7. Genito-ventral plate rather wide posteriorly; this plate and also the sternal plate are very strongly chitinized and without distinct markings. Coxal platelet is distinct ..... *L. orangiensis*, sp. n.
   Genito-ventral plate not so wide posteriorly. Ventral plates with distinct linear markings. Coxal platelet distinct, being comma-shaped ..... 8.

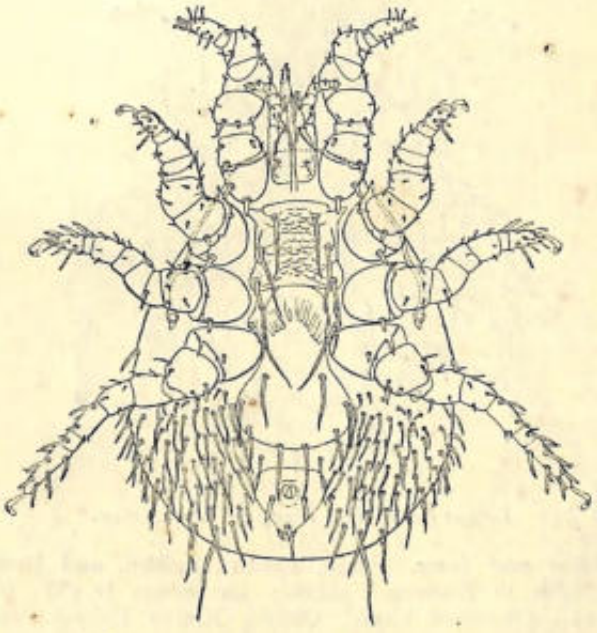
8.	Coxal platelet wide comma-shaped. Chelicera of male slender and elongated	*L. lamborni*, sp. n.
	Coxal platelet quite narrow, being elongate comma-shape. Chelicera of male much shorter	*L. nuttalli* Hirst.
9.	Coxal platelet unusually large and shaped as shown in figure	*L. ugandanus* Hirst.
	Coxal platelet much smaller and shaped otherwise	10.
10.	Genito-ventral plate very much widened behind the last coxæ	11.
	Genito-ventral plate narrower	12.
11.	Size very large and body strongly chitinized. Posterior margin of genito-ventral plate only slightly concave. Coxal platelet rather wide. Chelicera of male very long and styliform	*L. muricola* Trägårdh.
	Size smaller and body less strongly chitinized. Posterior margin of genito-ventral plate strongly concave. Coxal platelet narrower. Chelicera of male styliform but not very long	*L. echidninus* Berlese.
12.	Posteriormost hairs on margin of genito-ventral plate placed close together. Paired hairs on anal plate long	13.
	Posteriormost hairs on margin of genito-ventral plate wide apart from one another. Paired hairs on anal plate short	*L. grandis*, sp. n.
13.	Posterior hairs on venter rather sparse and fine. Plates on venter not very strongly chitinized and with fairly distinct linear markings. Genito-ventral plate with the sides strongly curved	*L. giganteus* Berlese.
	Posterior hairs on venter dense and stout. Plates on venter all very strongly chitinized, linear markings being weak or absent. Genito-ventral plate narrower, the sides being less strongly curved	*L. giganteus*, var. *bakeri* Hirst.

LÆLAPS PARVULUS Hirst. (Text-fig. 3.)

♀. Chiefly characterised by the presence of a very short but stout spinule on each half of the ventral surface of the *capitulum*, replacing the fine hair usually present in this position. Other details as follows:—Body narrowed anteriorly, being widest behind the last pair of legs. *Sternal plate* long and narrow, but not very strongly chitinized, being ornamented with distinct scale-like markings; its posterior margin concave; the usual three pairs of hairs are present on this plate in this species (not four pairs as stated in the preliminary description). *Genito-ventral plate* well expanded behind the last pair of legs and rounded off posteriorly, the posterior hairs being situated close to one another; there are no distinct markings on this plate. *Anal plate* shaped as figured, the paired hairs on it fairly stout. Little lateral (coxal) platelet short and fairly wide. *Peritremal tube* apparently reaching forwards slightly in front of the second coxa. *Venter*

densely furnished with hairs posteriorly, a few of them being quite short, but most fairly long and slender. Coxa of first leg with two stout spinules ventrally as in *L. vansomereni* and *L. æthiopicus*; trochanter of this leg with three stout spinules ventrally, but two of them are quite small; its femur ventrally with a minute stout spinule and a longer seta.

Text-figure 3.



Lælaps parvulus Hirst, ♀. Ventral view.

Measurements:— ♀. Length of body (not including capitulum) ·73–·75 mm.

Hosts. *Arvicanthis dorsalis*, South Africa (Peringueys Coll.); and *Otomys irroratus*, Grahamstown, April 1923 (J. Hewitt).

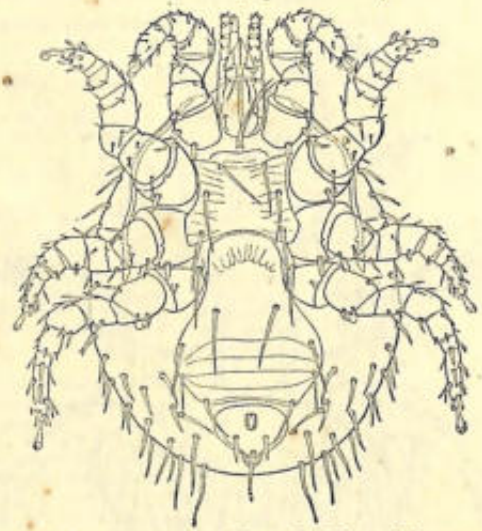
Lælaps vansomereni Hirst. (Text-fig. 4.)

♀. This little species differs from *L. nuttalli* in having two stout spinules or thorns ventrally on the coxa of the first leg, instead of a thorn and a longer bristle. *Sternal plate* shaped as figured, being strongly chitinized, linear markings being only visible at the sides. *Genito-ventral plate* fairly well expanded behind the last pair of legs, and with distinct transverse linear markings on its surface; last pair of hairs on this plate widely separated from one another as in *L. grandis*, but the strip of margin between them is slightly concave instead of being straight.

Paired hairs on *anal plate* fairly stout. Hairs on posterior part of *venter* also rather stout and fairly numerous. Little lateral (coxal) plate usually fairly wide. *Peritremal tube* reaching a little further forwards than the second coxa.

Measurements:—♀. ·71–·74 mm.

Text-figure 4.



Lælaps vansomereni Hirst, ♀. Ventral view.

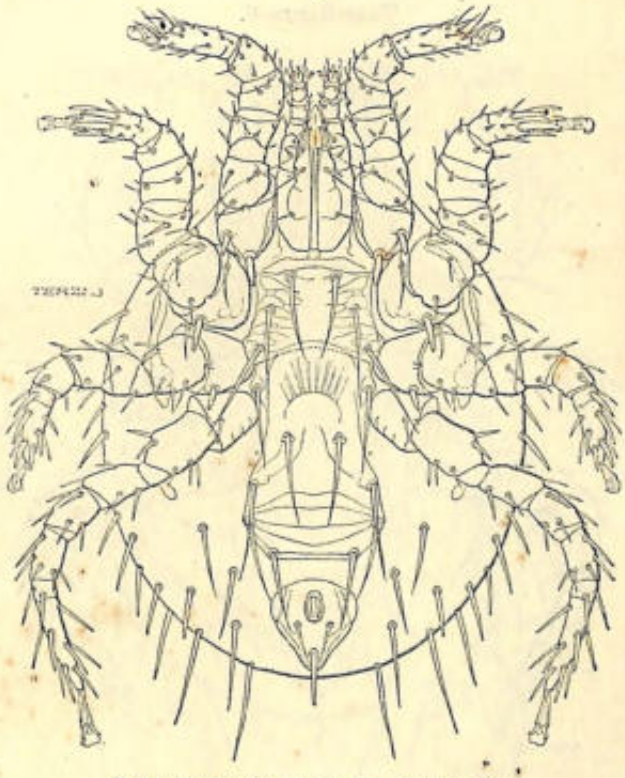
Localities and hosts. Busiu, South Bigishu, and Bumungi, Bugwe, both in Eastern Uganda; on rodent D (W. N. van Someren). Okwara's Camp, Ohayo, Kenya Colony; on rats (W. N. van Someren). Mfongosi, Zululand; specimens found by W. E. Jones on *Mus chrysophilus*; ex E. C. Chubb's Coll.

LÆLAPS ÆTHIOPICUS, sp. n. (Text-fig. 5.)

♀. Very closely allied to *L. vansomereni* Hirst, the first coxa having two strong ventral spinules as in that species; the anal plate is, however, differently shaped, being more elongate pyriform, the paired hairs on it quite fine instead of stout. Tarsus of second leg with a cluster of three quite stout and rather elongated spinules. Other details of structure are as follows:—*Sternal plate* rather like that of *L. nuttalli*, but strongly chitinized, the linear markings on it only visible at the sides, but faint maculate markings are also present as in *L. muricola*, *L. grandis*, etc. *Genito-ventral plate* moderately expanded behind the last pair of legs and furnished with transverse linear markings as in *L. nuttalli*, posteriormost pair of hairs widely separated from one another, the

strip of margin between them is straight. Lateral (coxal) platelet of moderate width ? *Peritremal tube* reaching just beyond second coxa. Hairs on venter finer than in *L. vansomereni*, those at the posterior end of the body longer than in that species.

Text-figure 5.



Lælaps æthiopicus, sp. n., ♀. Ventral view.

Measurements:— ♀. Length (not including capitulum) ·70–·76 mm.; greatest width ·54–·56 mm.

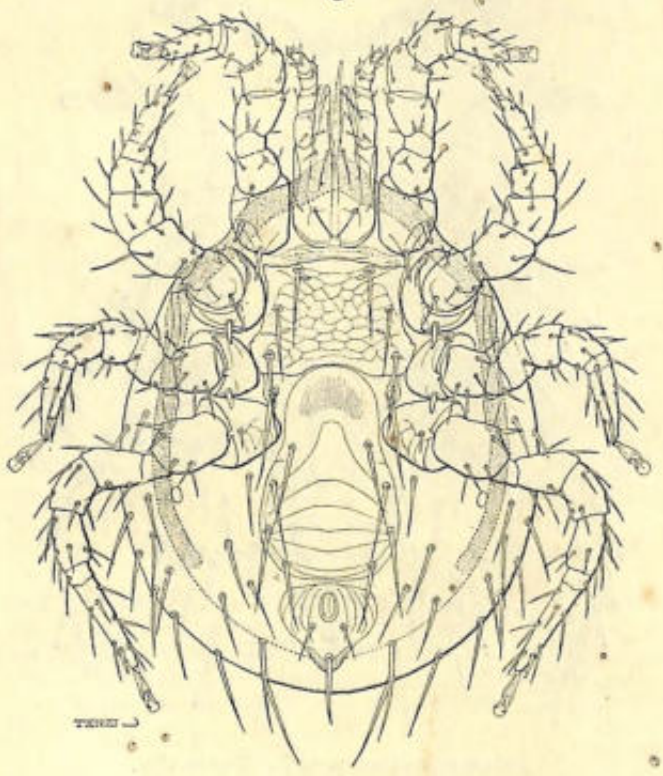
Locality and host. Ashundwa's Camp, Wanga, Kenya Colony; on rats (W. N. van Someren).

LÆLAPS ALGERICUS, sp. n. (Text-fig. 6.)

♀. A small species resembling *L. nuttalli* in many respects. Anteriorly and laterally, however, the *dorsal scutum* is furnished with a conspicuous strongly chitinized thickened edge, which is not present in *L. nuttalli*. Hairs on *dorsum* fine and of moderate length. *Sternal plate* trapezoidal in shape, its length in the median line being slightly less than the width of the anterior margin, but much less than the width of the posterior margin

its surface is faintly sculptured with reticulate markings. *Genito-ventral plate* about the same width as in *L. nuttalli*, and with transverse linear markings as in that species. *Anal plate* shaped as figured. Lateral (coxal) platelet fairly wide. Hairs on *venter* fine and of moderate length. Coxa of first leg with a rather

Text-figure 6.



Lælaps algericus, sp. n., ♀. Ventral view.

short stout spinule and a longer bristle as in *L. nuttalli*. Second and third coxæ with the usual stout posterior spinule or thorn.

Length of body (not including capitulum) ·70 mm.

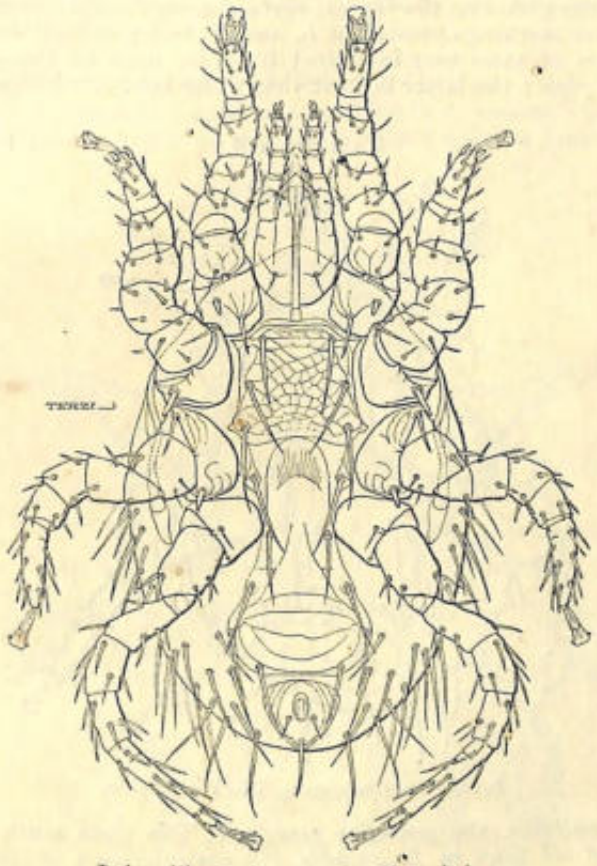
Locality and host. Tougourt, Algeria, 6. iii. 1920, several specimens from *Mus algericus* collected by Dr. Karl Jordan.

LÆLAPS LIBERIENSIS, sp. n. (Text-fig. 7.)

♀. *Sternal plate* longer than in *L. nuttalli* and differently shaped; the median length of this plate is about equal to the width of its anterior margin, but considerably less than that of the posterior margin; it is ornamented with distinct

reticulate linear markings. *Genito-ventral plate* with transverse linear markings as in *L. nuttalli*, but wider behind the posterior legs, being shaped very like that of *L. grandis*, the last pair of hairs on it being widely separated from one another. Coxal platelet wide. *Peritremal tube* shorter than

Text-figure 7.



Lælaps liberiensis, sp. n., ♀. Ventral view.

in *L. nuttalli*, reaching forwards only as far as the second coxa. Hairs on posterior part of *venter* few in number and fairly long. A spinule and a longer bristle are present on the first coxa as in *L. nuttalli*; second and third coxæ with the usual spinule, which is only moderately stout; fourth coxa only with a fine hair. Second leg much the stoutest. Some of the setæ on the ventral surface of the second and third legs are subspiniform, and there is a terminal pair of stout spinules on the second tarsus.

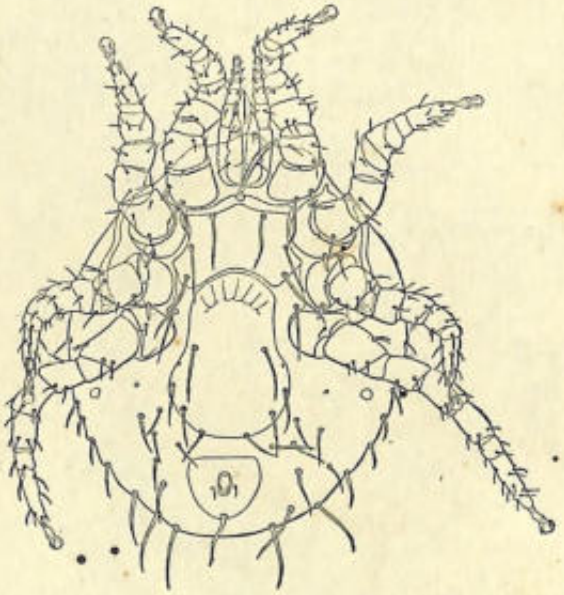
Measurements:— ♀. Length (not including capitulum) ·66 mm.; greatest width ·45 mm.

Locality and host. Gonyon Country, Liberia; a single female example (the type) from *Epimys defua*, 4. xii. 1910 (R. H. Bunting); ex N. C. Rothschild's Coll.

LÆLAPS ORANIENSIS, sp. n. (Text-fig. 8.)

♀. A small species rather like *L. nuttalli*, but differing in having the plates on the ventral surface more strongly chitinized, the linear markings present in *L. nuttalli* being absent, with the exception of some very indistinct irregular lines on the *genito-ventral plate*; the latter is somewhat wider behind the legs than

Text-figure 8.



Lælaps oraniensis, sp. n., ♀. Ventral view.

in *L. nuttalli*; the posterior margin of this plate much more rounded off than in *L. grandis*, the posteriormost of the four pairs of hairs closer together than in that species. The further details of structure may also be useful:—Hairs on *dorsal scutum* short and fine; just in front of the middle of the posterior margin there is a pair of exceptionally minute hairs, followed by a rather long pair. *Sternal plate* wider than long, its posterior margin rather strongly concave. *Peritremal tube* reaching forwards as far as the middle of the second coxa. Hairs on *venter* not very numerous, being fine and fairly long, especially the posterior ones. Coxa of first leg furnished with a thorn or spinule which is not

very stout and also with a longer seta. Second and third coxæ each with a rather stout posterior thorn; thorn on fourth coxa comparatively slender. Second coxa also with a short but distinct antero-dorsal denticle resembling that present in some species of *Liponyssus* (for instance in *L. flavus* Kolenati). Tarsus of second leg with a pair of rather stout terminal spines.

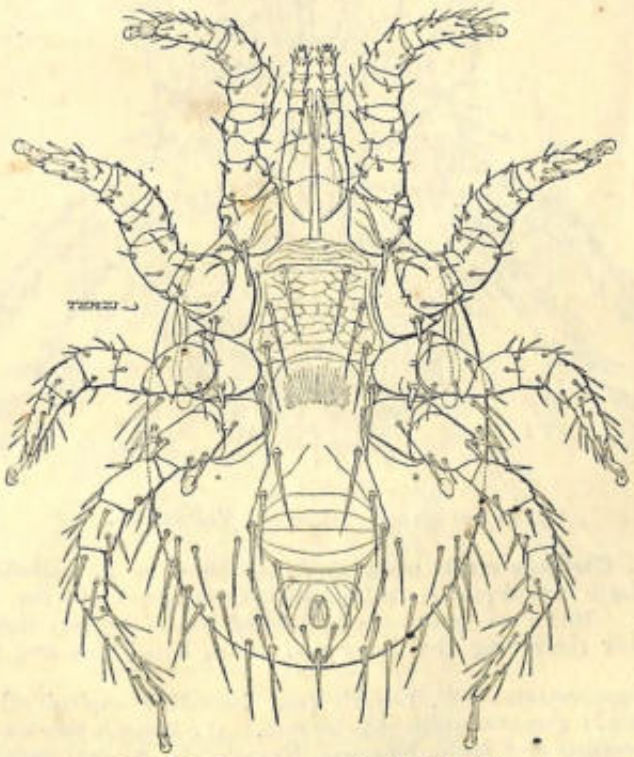
Measurements:—♀. Length (not including capitulum) ·66–·72 mm.; greatest width ·51–·57 mm.

Locality. Mt. Marabut, Oran, N. Africa; on field mice; ex N. C. Rothschild's Coll.

LÆLAPS LAMBORNI, sp. n. (Text-fig. 9.)

A small species of *Lælaps* closely allied to *L. nuttalli* Hirst, but the posterior margin of the sternal plate (of the female) less

Text-figure 9.

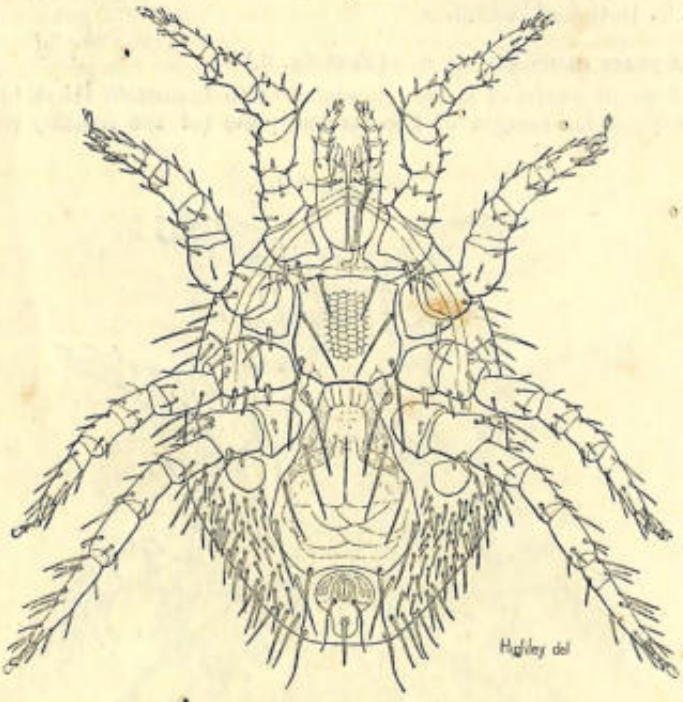


Lælaps lamborni, sp. n., ♀. Ventral view.

concave than in that species, being almost straight, and the little lateral (coxal) platelet wider and less elongated. Styliform chelicera of male very much longer than in *L. nuttalli*. Further

details of structure as follows:—♀. *Sternal* and *genito-ventral* shields ornamented with linear markings as in *L. nuttalli*. *Peritremal tube* shorter than in *L. nuttalli*, only reaching forwards as far as the middle of the second coxa. Hairs on venter few in number. First coxa armed with a spinule and also a longer seta as in *L. nuttalli*. Second and third coxæ with the usual stout posterior spine or thorn.

Text-figure 10



Laelaps ugandanus Hirst, ♀. Ventral view.

♂. *Chelicera* much more elongated than in *L. nuttalli*, the styliform digital portion being very slender, especially the distal half. Hairs on *genito-ventral shield* about twenty-three in number (including the three anal ones), being fine and fairly long.

Measurements:—♀. Length (not including capitulum) ·64–·69 mm.; greatest width ·42–·50 mm. ♂. Length ·48–·51 mm.

Localities and hosts. Karonga, Nyasaland. Several specimens including the type off the rat called "Kapuku." Other specimens off a rat called "Majancha" at the same locality (Lamborn Coll.). N. Kitosh and Wamia, Kenya Colony; on rats (van Someren).

LÆLAPS UGANDANUS Hirst. (Text-fig. 10.)

Proc. Zool. Soc. London, 1923, p. 971.

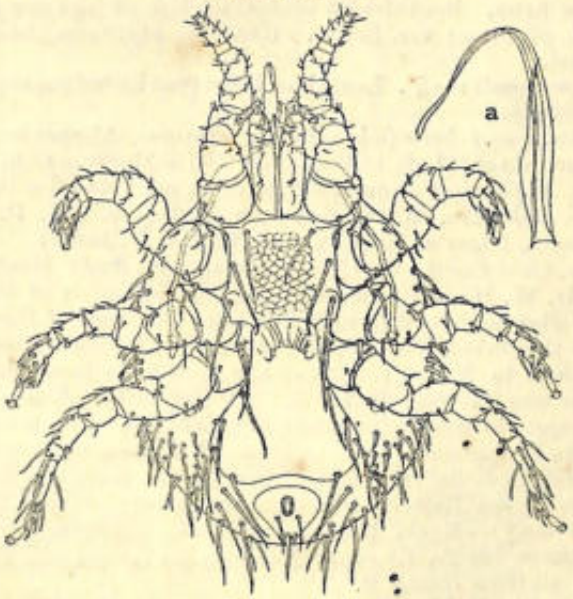
The largest species of the genus *Lælaps* occurring in Africa. Lateral (coxal) platelet unusually wide for the genus. For further details see the original description.

♀. *Length* of body (not including capitulum) 1·82 mm.

Localities. All the specimens of this mite which I have been able to examine are from the Eastern Province of Uganda. Unfortunately the exact host is still unknown, but is some species of rodent. Mr. W. N. van Someren collected specimens at Budadiri, Mujembe, and Kabaroni, these three localities being in N. Bugishu. At Paya, Budama, and at Busolwe, Bunvuli. Also at three localities in Bugwe, viz., Busia, Bumungi, and Masabi. All these localities mentioned above seem to be in the Bukedi District.

Mr. C. J. Baker collected specimens of this mite at Kanyum Teso, Uganda.

Text-figure 11.



Lælaps muricola Trägårdh ♀. Ventral view.
a. Chelicera of male, greatly enlarged.

LÆLAPS MURICOLA Trägårdh. (Text-fig. 11.)

L. muricola Trägårdh, in Sjöstedt's Schwedischen Zoologischen Expedition nach dem Kilimandjaro, dem Meru, Band iii. pp. 34–57, pl. ii. (figs. 17, 22), pl. iii. (figs. 1, 4, 12, 13 and 31), 1910.

A very large and strongly chitinized species. ♀. *Sternal plate* shaped very like that of *L. echidninus*, very strongly

chitinized, and sometimes ornamented with maculate markings which are not very distinct, however. *Genito-ventral plate* very greatly expanded behind the last pair of legs, its surface smooth; but a very faint pattern of linear markings (similar to that present in *L. giganteus*) is sometimes discernible. Little lateral coxal platelet fairly wide; it is usually oval in shape, but in specimens from Accra on *Cricetomys* this platelet is almost round in outline. *Anal plate* shaped as figured, the paired hairs on it fairly long. Hairs on *venter* fairly numerous and rather thick. The usual stout spinule is present on coxæ 1–3, but is not so stout as in *L. giganteus*. *Cheliceræ* with rather slender fingers, the denticles rather small, those on the immovable finger being quite minute.

♂. Hairs on *genito-ventral plate* all long and fine, the middle ones on the expanded portion being about as long as the ones situated between the coxæ. Hairs on uncovered posterior part of *venter* mostly shorter than those on the plate, but not nearly so short as those present in the same position in the male of *L. giganteus* var. *bakeri*; there are, however, some quite long posterior hairs. Spinules on ventral surface of legs not so stout as in *L. giganteus* var. *bakeri*. *Cheliceræ* styliform, being very elongated.

Measurements:—♀. Length of body (not including capitulum) 1·48–1·62 mm.

Localities and hosts (when given). Harrar, Abyssinia; 22. iii. 1904, sur un rat (M. de Rothschild); Paris Museum Coll. Addis Abbeba, Abyssinia; June 1904, sur un rat (Maurice de Rothschild). Lake No, White Nile; on *Rattus* sp. (W. P. Lowe). Near Lagos, Nigeria; on mouse no. 63 (W. P. Lowe).

Accra, Gold Coast; on *Cricetomys* sp. (W. Scott Macfie). In 1922, Mr. W. N. van Someren collected specimens of this mite at the following localities in the Eastern Province of Uganda, all being in the Bukedi District, viz., at Bugobu, Budadiri, Butandika, and Bulago in North Bugishu; the specimens from these four localities are all from *Rattus* B. At Batiru (on *Rattus* B) and at Lwanjusi in South Bugishu (on rodent D). At Kwapa and Mulanda, in Budama. Also at Bumugi, Bugwe, on rodent D.

Captain C. J. Baker obtained the species from the following localities in the Eastern Province of Uganda, during the year 1922, namely:—Kyeri Teso, Serere Teso, Kabiremaido Lango, and Ekwere Lango, Kagwata Lango, Lira Lango, and Kachung Lango; all from *Rattus* B.

On S.S. 'Speke,' on *Rattus rattus alexandrinus*.

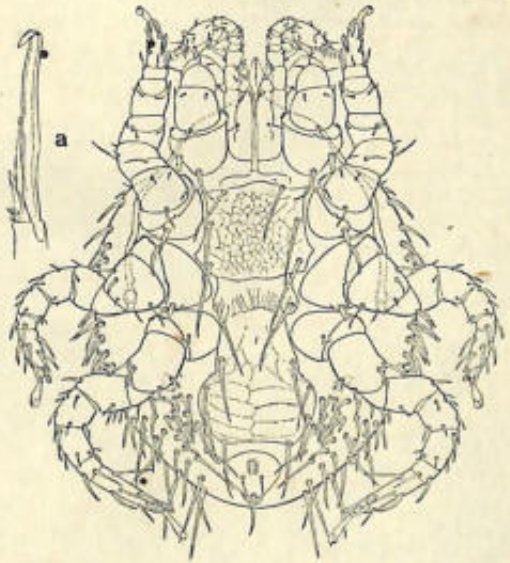
On *Rattus hildebrandti* and on *Lemniscomys ibeanus* at Nairobi (van Someren). Wamia and North Kitosh, in Kenya Colony; on rats (van Someren).

Karonga, N. Nyasa, 1919, on rat called "Kapuku" and on rat "Chitutú" (the latter=*Saccostomus campestris*); W. A. Lamborn Coll. Also specimens from *Mus equcha*, South Africa, sent to me by Professor Antonio Berlese. Grahamstown, Cape Colony, from *Mus silaceus* (John Hewitt).

LÆLAPS GRANDIS, sp. n. (Text-fig. 12.)

♀. *Sternal plate* shaped as shown in figure, resembling that of *L. echidninus* very closely; both this plate and the genito-ventral one are very strongly chitinized, the reticulate linear markings present in some species being absent or only faintly visible. *Genito-ventral plate* shaped very like that of *L. giganteus*, but the posteriormost of the four pairs of hairs are widely separated from one another, and the margin between these two hairs is straight instead of slightly concave. Paired hairs on *anal plate* very short

Text-figure 12.



Lælaps grandis, sp. n., ♀. Ventral view.
a. Chelicera of male, greatly enlarged.

instead of long as in *L. giganteus*. Lateral (coxal) platelet behind last pair of legs fairly wide. Hairs on *venter* rather numerous, being fairly fine but stiff. Coxæ of legs 1–3 furnished with the usual stout thorn or spinule, but it is more slender than in *L. giganteus*; spinule on fourth coxa quite weak. Movable finger of *chelicera* rather strongly curved at the distal end, overlapping the immovable one.

♂. Hairs on posterior part of *genito-ventral plate* slightly more numerous than in *L. muricola*. *Cheliceræ* fairly elongated, but much shorter than in male of *L. muricola*.

Measurements:— ♀. Length (not including capitulum) 1·25–1·36 mm.; greatest width ·96–1 mm.

♂. *Length* 1·05 mm.; greatest width ·73.

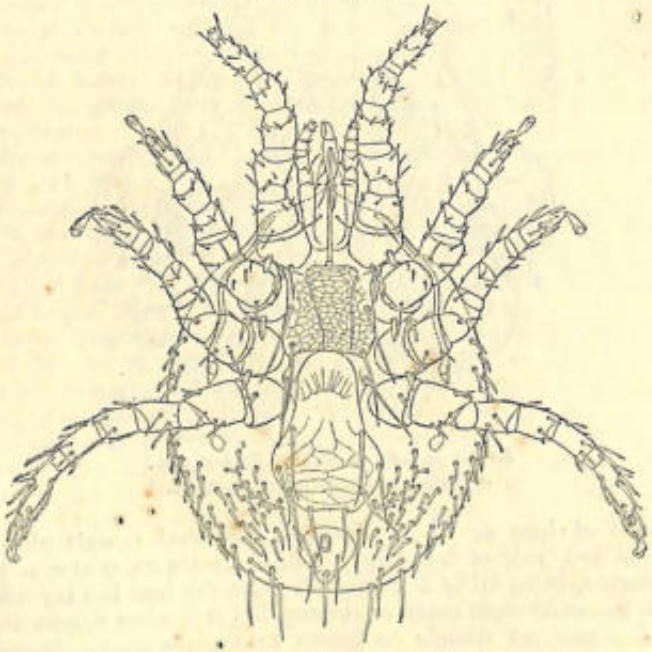
Locality and hosts. Bumungi, Bugwe, Eastern Province of Uganda. One specimen (the type) on rodent D (W. N. van Someren). Also two males and several female examples from rats, Ashundwa's Camp, Wanga, Kenya Colony, 4. vii. 1921.

LÆLAPS GIGANTEUS Berlese. (Text-fig. 13.)

L. giganteus Berlese, Redia, xiii. pp. 129–131 (1918).

A large and rather strongly chitinized species. ♀. *Sternal plate* shaped very like that of *L. echidninus* Berl., *L. muricola*, etc., and ornamented with a faint network of linear markings. *Genito-ventral plate* well expanded behind the last pair of legs, its sides being strongly curved; the two posteriormost hairs of this plate are placed close together, being separated only by a short slightly concave strip of the margin; linear markings, which are

Text-figure 13.



Lælaps giganteus Berlese, ♀. Ventral view.

mostly transverse in direction but sometimes connected by short longitudinal or oblique lines, are generally distinctly visible. *Anal plate* shaped as figured; the paired hairs on it are rather long. Lateral (coxal) platelet fairly wide comma-shape. Hairs on *venter* much finer than in the variety *bakeri*. *Chelicera* with

rather stout fingers, the denticles on them being well developed; the movable finger is rather strongly curved at the tip.

Measurements:— ♀. Length of body (not including capitulum) 1·33–1·53 mm.

Localities and hosts: Begwai, Bassa, Liberia, on *Rattus tulbergi* and *Dasymys rufulus* (R. H. Bunting); ex N. C. Rothschild's Coll. Gonyon Country, Liberia, 4. xii. 1910, on *Epimys defua* (R. H. Bunting).

Near Lagos, Nigeria, on mouse no. 61 (W. P. Lowe).

Bubungi, N. Bugishu, Eastern Province, Uganda, 27. i. 1922. On rodent D (W. N. van Someren).

Budadiri, N. Bugishu, 1. ii. 1922. On rodent D (W. N. van Someren).

Lanyo, Semia, Uganda, 28. iv. 1922. On rodent D. (W. N. van Someren).

Kangai Lango, Uganda, 22. v. 1922. Host not given (C. J. Baker).

Wamia, Kenya Colony, 23. vii. 1921. On rats (W. N. van Someren).

Nairobi, 29. iii. 1921. On rats (W. N. van Someren).

Mfongosi, Zululand. On *Arvicanthis dorsalis* (W. E. Jones). Specimens sent to the Museum by Prof. Antonio Berlese.

LÆLAPS GIGANTEUS var. BAKERI Hirst. (Text-fig. 14.)

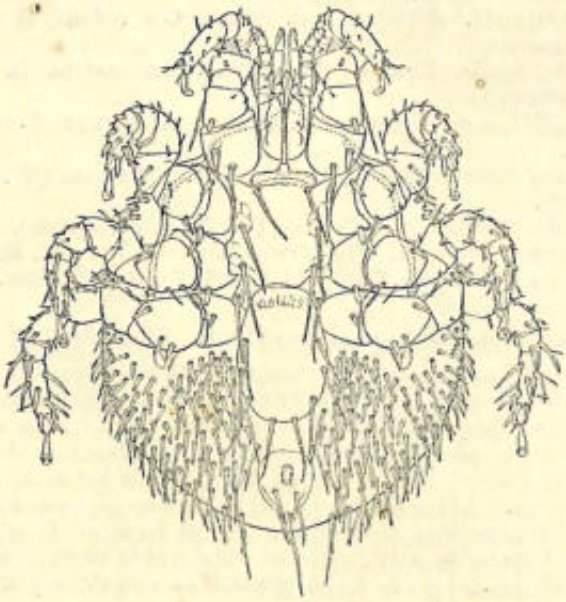
♀. Hairs on *scutum* finer than those at the sides of the body and on the venter. Posteriorly on the softer marginal strip of integument there is the usual pair of hairs longer than the rest. *Genito-ventral plate* distinctly narrower and lacking the slight concavity present in the typical *L. giganteus* between the last pair of hairs. Little lateral (coxal) platelet narrow comma-shape, being narrower than that of the typical form of *L. giganteus*. *Sides* and *venter* densely furnished with rather short setæ, which are much stouter than those present in the same position in *L. giganteus*.

♂. Some long hairs are present anteriorly and also at the sides of the *dorsum*, and there are also two or three pairs of these long hairs at the posterior end of the body; towards the middle of the dorsal surface, however, the hairs become much shorter, and the posterior half is furnished with numerous quite short fine hairs. The five pairs of hairs present on the *genito-ventral plate* between the coxæ are long, but those on the expanded part of this plate behind the coxæ are very short, especially the lateral ones; paired hairs near anal orifice also short, but the unpaired hair is long. Uncovered part of *venter* with numerous very short but stiff hairs, which are not thickened. There is also a pair of long hairs posteriorly on the venter. Style of *chelicera* fine but not very long.

Measurements:— ♀. Length (not including capitulum) 1·48–1·55 mm.

Localities and hosts. Algiers, 24. iii. 1912. On *Arvicanthis barbarus*; ex N. C. Rothschild's Coll. Hamman Rirha, Algeria, on *Arvicanthis barbarus*; ex N. C. Rothschild's Coll. Mr. W. N. van Someren collected specimens of *L. giganteus* var. *bakeri* at the following six localities in N. Bugishu, viz., Bubungi, Budadiri, Sipi, Kyepetekoi, Kabaroni, and Walasi. In three cases the host was *Lemniscomys striatus massaicus* Pag.; in the others the exact host is not known. Van Someren also obtained specimens at

Text-figure 14.



Laelaps giganteus var. *bakeri* Hirst, ♀. Ventral view.

Bubulu and Bupota in S. Bugishu, and at Tororo, Bučama, 26. iii. 1922, on *Lemniscomys striatus massaicus*. All these localities of van Someren are in the Bukedi District, Eastern Province, Uganda. Mr. C. J. Baker collected specimens of this mite at Soroti Teso, Kellelango, Kangia Lango, and Lira Lango, all in the Eastern Province of Uganda, the host when identified being *Arvicanthis abyssinicus nubilans* Wrought.

Kakawega, Kenya Colony, 20. vi. 1921. On *Rattus rattus rattus* (W. N. van Someren). Also specimens collected by the same from Nairobi and Ohayo, the name of the host not being given.

West foot of Aberdare Mountains, British East Africa, 1. iii. 1911. On mouse skin no. 238 (Dr. S. Neave).

Karonga, N. Nyasa, 6. xi. 1919. On rat called "Mengi" (W. A. Lamborn).

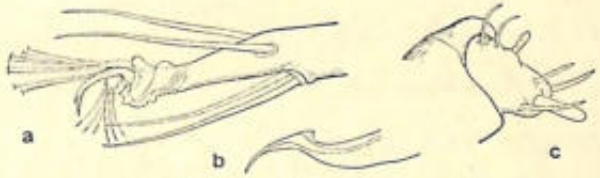
Bothaville, Orange Free State. On striped mouse (G. A. H. Bedford).

Grahamstown, Cape Colony. On *Arvicanthis pumilio* (J. Hewitt).

PARATETRANYCHUS BIHARENSIS, sp. n. (Text-fig. 15.)

♂. *Penis* strongly curved; its tip is shaped rather like that of *Tetranychus* (*Schizotetranychus*) *schizopus*, *T. crataegi*, etc., having two barbs, one very short but distinct, the other long and very slender. Claw of penultimate segment of *palp* blunt, being almost truncated distally as in *Tetranychus fijiensis* mihi. Terminal finger of tarsus of palp long and slender, being rather

Text-figure 15.



Paratetranychus biharensis, sp. n., ♂.
a. Tarsus of foot. *b*. Penis. *c*. Distal end of palp.

like that of *T. tiliarium*. Dorsal finger of tarsus of palp not very long, but slender and almost cylindrical, being only very slightly club-shaped. Claws of *legs* normal for the genus, the dorsal claw-like portion as usual well developed, and it has a very slight and inconspicuous dorsal hairlet or offshoot; ventral part of claw split distally into about six fine hairs.

♂. *Length* of male (including palpi) about ·35 mm.; length of tip of penis 12 μ, length of terminal finger of tarsus of palp 9 μ, its width about 2 μ; length of dorsal finger of tarsus of palp slightly over 5 μ, the longer of the two rod-like setæ 8½ μ.

Locality and host plant. On rose leaves, Pusa, 6. ii. 1918 (T. B. Fletcher).

5. On *Natrix olivacea* (Peters), from Pemba Island, and other Notes on Reptiles and a Murænid Fish. By Arthur Loveridge, C.M.Z.S., F.E.S.

[Received November 4, 1924: Read February 17, 1925.]

In a small collection of reptiles obtained by the writer's mammal collectors on Pemba and Zanzibar Islands in 1923, there is an interesting specimen of *Natrix olivacea* (Peters), a species as yet unknown from Pemba Island though several times recorded from Zanzibar. Pemba is twenty miles due west of Tanga on the mainland of Tanganyika Territory; Zanzibar is about the same distance from Saadani, a coastal town lying between Tanga and Dar es Salaam. Chakechake on Pemba Island is spelt Chakchak on some maps.

Natrix olivacea (Peters).

Coronella olivacea Pfeffer, Mitt. Natur. Mus. Hamb. 1889, vi. pt. 2, p. 10.

Coronella olivacea Pfeffer, Mitt. Natur. Mus. Hamb. (1892), 1893, x. pt. 1, p. 11.

Tropidonotus olivaceus Boettger, in Voeltzkow, Reise in Ostafrikas, 1913, Bd. iii. H. 4, p. 347.

A single female from Chakechake, Pemba, 6.x.23 (M.C.Z. No. 19112). Total length 288 mm.; tail 78 mm.; mid-body scale-rows 15 mm. Ventrals 127, caudals 56; labials 8, of which the fourth and fifth enter the eye. Coloration normal.

The number of scale-rows at mid-body for this species is 19, and this has held good for specimens taken all over Tropical and South Africa by many collectors during the last seventy years. Presumably it holds good for the specimen taken by Stuhlmann on Zanzibar, 20.x.1888, and that taken by Voeltzkow on Zanzibar in 1889, as neither Pfeffer nor Boettger makes any comment on the scalation of these specimens, though both collections were critically examined. Fifteen scale-rows in the present specimen may be an individual aberration or indicate an island race.

There are 17 scale-rows on its neck and backwards (counting from the parietals) to the 67th scale-row, where there are 16: these continue to the 71st row, where there are 15 onwards to the anus. For purposes of comparison I made scale-counts at neck, mid-body, and in the præ-anal region of all the available material here in the Museum of Comparative Zoology, Cambridge, Mass. These seem to point to a reduction of scale-rows in this species as you cross the continent from West to East.

M.C.Z. No. 6334.	Lagos, West Africa	21	19	17
6254.	South Africa	19	15	17
18185.	Kabare, Bukoba, Victoria Nyanza	19	19	16
18445.	Bagilo, Ulegura Mtns., T.T.	17	19	17
18446.	„ „ „ „	17	19	17
19112.	Chakechake, Pemba Island	17	15	15

LYCOPHIDIUM ACUTIROSTRE (Gunther).

Boulenger, Cat. Snakes in Brit. Mus. 1893, i. p. 338.
Boettger in Voeltzkow, Reise in Ostafrikas, 1913, Bd. iii. H. 4, p. 362.
Loveridge, P. Z. S. 1923, p. 877.

In 1923 I remarked that this species was only known from Zanzibar prior to my finding a doubtfully determinable specimen at Dar es Salaam. Recently I came across a record from Manene near Tanga of a specimen collected by Voeltzkow in 1903 and recorded by Boettger. This reference seems to have escaped Mr. Boulenger when compiling his "List of the Snakes of East Africa, . . ." which appeared in P. Z. S. 1915, pp. 611–640.

The other reptiles collected by my natives were:—

LEPTOTYPHLOPS EMINI (Boulenger).

Glauconia emini Boulenger, Cat. Snakes, 1893, i. p. 64.
Glauconia emini Boettger in Voeltzkow, Reise in Ostafrikas, 1913, Bd. iii. H. 4, p. 351.

Three specimens from the following localities on Pemba:—

Wete.....	8.ix.23.	Total length	135 mm.	Tail	16 mm.	Body diameter	3 mm.
Chakechake.	4.x.23.	„	200 mm.	„	18 mm.	„	4 mm.
„ ...	6.x.23.	„	140 mm.	„	12 mm.	„	2·5 mm.

This series gives a diameter of body into total length of 45 to 56 times as against 50 to 57 times as previously recognized. The tail length goes 8 to 11 times into the total length instead of 9 times. In other respects these specimens, which are wholly black, agree perfectly with the mainland forms. Its type locality is Karagwe, Victoria Nyanza. Boettger has already recorded specimens from Pemba, but the species does not appear to have ever been found on Zanzibar.

PHILOTHAMNUS SEMIVARIEGATUS (Smith).

A single specimen from Wete, Pemba, 8. ix. 23. Already known from both Pemba and Zanzibar.

HEMIDACTYLUS MABOUIA (Moreau de Jonnès).

Fourteen examples from Zanzibar City, 3–6. vii. 1923.
One from Chakechakè, Pemba Island, 6. x. 23.

LYGODACTYLUS PICTURATUS PICTURATUS (Peters).

Seventeen examples from Zanzibar City, 4–7. vii. 1923.

PHELSUMA LATICAUDA (Boettger).

Four males and three females from Zanzibar City, 3–6. vii. 23. All have median clefts on the rostral, which was a character of *Phelsuma dubium* (Boettger), to which species former Zanzibar

specimens have been referred, but which I have shown elsewhere is not a constant character. In the oldest male of this series the cleft is very slight. Two of the specimens have 2 scales separating the upper nasals, whilst the remaining five have 3 scales, like the type of *dubium*. Four specimens have 9 upper labials on both sides, the others range from 9 to 12. Three specimens have 9 lower labials on both sides, the others are irregular and range from 8 to 10. The upper caudal scales are smooth excepting in one old individual, where some are distinctly keeled.

MABUYA COMORENSIS (Peters).

Loveridge, P. Z. S. 1923, p. 956.

A male (M.C.Z. No. 19128) from Kokotoni, Zanzibar, 28.vi.23. A fine specimen measuring 248 mm., of which 168 mm. is tail. It is quite typical, excepting for a division of the right nuchal into two scales. Voeltzkow also collected one of these scarce skinks in the same locality on 12. viii. 1889.

Mainland records of this species are so uncommon that I was interested in finding an unidentified specimen (M. C. Z. No. 12089) in the Agassiz Museum collected by Dr. Glover Allen at Mombasa, Kenya Colony, 24. vi. 89. It agrees with the description excepting in two minor points, viz., anterior labial is *not* in contact with the first labial, and the supranasals are *not* in contact behind the rostral.

MABUYA MACULILABRIS (Gray).

A female from Mkoani, Pemba, and five examples from Chakechake taken ix–x. 23. A female from the last locality collected on 6. x. 23 holds three eggs measuring 14 × 8 mm. which distend the abdominal region to its capacity.

MABUYA STRIATA (Peters).

A male and female from Zanzibar City, 3. vii. 23.

LYGOSOMA (RIOPA) PEMBANUM Boettger.

Boettger in Voeltzkow, Reise in Ostafrikas, 1913, B. iii. H, 4.

Three specimens from Chakechake, Pemba, 5. x. 23. Boettger's species appears a good one, differing from *L. sundevalli* in the complete absence of præfrontals and the lower number of scale-rows.

LYGOSOMA (RIOPA) SUNDEVALLI (Smith).

Two examples from Zanzibar City, 11. viii. 23. The collector has made a note that the native name for this species is "Kiumambazi."

CRYPTOBLEPHARUS BOUTONII var. PERONII (Cocteau).

Ablepharus boutonii var. *peronii* Blgr. Cat. Liz. iii. p. 347 (1887).

Examples from Zanzibar have been referred to *boutonii* (Desj.), and it is to be regretted that the collectors did not get any Zanzibar material, as I strongly suspect that such specimens will belong to the above-mentioned variety, as have all the mainland examples which I have taken at Mombasa, Dar es Salaam, and Mozambique, and 5 specimens now collected on the marine rocks at Vitongezi, Pemba, 20. x. 23, which agree in having 24 mid-body scale-rows. The coloration is like that of those on the adjacent mainland and does not conform to that given in Boulenger's 'Catalogue of Lizards in the British Museum,' vol. iii. p. 347, presumably based on Australasian specimens. All East African *peronii* are of a blackish bronze hue above with rather indistinct lighter lateral bands *not* edged above and below by black bands, *nor* are there any signs of light dots on the sides and limbs.

PELUSIOS NIGRICANS (Donndorff).

Six specimens of the Black Turtle from Vitongozi reached England alive; more than a score were collected. The species has already been recorded from Pemba.

MORINGUA ABBREVIATA (Bleeker).

One from Vitongozi, Pemba, 20. x. 23, has been kindly identified for me by Dr. Garman. This interesting minute-eyed Murænid was taken by the collectors as a "Sea snake," for which they were told to be on the look out, as *Pelamydrus bicolor* is known to occur along the coast. In reply to enquiries, fishermen will always tell you that sea snakes are common, but hitherto all examples brought me have proved to be murænids, of which there are many species in these waters.

In conclusion, I should like to express my grateful thanks to Dr. Wm. Aders, F.Z.S., who has done so much to extend our knowledge of the Zanzibar fauna, and whose oversight of my collectors made the trip possible. Also to Dr. Thomas Barbour, of the Museum of Comparative Zoology, Cambridge, Mass., for permission to publish these notes.

6. On the Origin of the V-shaped Branchial Arch in the Teleostomi.

By EDWARD PHELPS ALLIS, Jr., F.Z.S., F.L.S., Menton, France.

[Received November 6, 1924: Read February 17, 1925.]

It has long been well known that in the branchial arches of fishes there are two distinctly different forms of skeletal bar, the sigma-shaped and the V-shaped, the one found typically exemplified in the Plagiostomi, and the other in the Holostei and Teleostei. In the mandibular and premandibular arches, however, not only in these two groups of fishes but in all others of the Gnathostomata, the skeletal bars are sigma-shaped, if I am correct in my recent conclusions (Allis, 1923, 1925). Assuming that I am correct in this, some explanation must be sought for the abrupt change, in the Holostei and Teleostei, from the sigma form in the mandibular arch to the V-shaped one in the first branchial. The hyal arch, which lies between these two, has undergone several special transformations which will be explained immediately below.

In the early ancestors of all fishes, the cartilaginous bar of each visceral arch, whether primarily formed by a single piece or by the several well-known elements, quite unquestionably lay in a single plane. As the mouth, with biting jaws, developed, and the skeletal bars of the mandibular and premandibular arches acquired the sigma form, a similar form was necessarily more or less strongly impressed on the skeletal bars of the more posterior arches. During this period, the postmandibular arches and the intervening clefts apparently increased considerably in volume relative to the metameric segments to which they are generally considered to have been primarily related, and the arches were progressively pushed farther and farther posteriorly, their dorsal ends consequently lying posterior to the neurocranium, opposite the anterior portion of the spinal column, as they actually do in recent Plagiostomi.

When, in these early fishes, the ventral portion of the hyomandibular cleft became closed, the articulating ends of the epi- and cerato-mandibulars acquired, in certain fishes, contact with the corresponding and adjoining ends of the epi- and cerato-hyals, and the hyostylic suspensorium of the Selachii arose, the pharyngohyal becoming reduced, or completely disappearing, as the otic capsule developed and gave articulation to the epihyal (Allis, 1915). In certain other fishes the hyal and mandibular arches were separated by so considerable an interval that the articulating ends of the epal and ceratal elements of the two arches did not acquire contact, and the pharyngohyal was prolonged antero-ventrally until it acquired contact with the dorsal edge of the epimandibular (palatoquadrate), this giving rise to the

hyostylic suspensorium of the Batoidei (Allis, 1915), which is thus totally different from that in the Selachii. In still others of these early fishes, branchial-ray bars were developed in the preauditory segments, and gave origin, in the hyal arch, to a hyomandibula that is characteristic of all of the Teleostomi and differs markedly from that of the Plagiostomi (Allis, 1918). A symplectic was also developed in these fishes, either as an independent cartilage or as the ventral portion of a hyomandibulo-symplectic bar, and this independent cartilage, or the fused bar, gave articulation to the epimandibular, two types of hyostylic suspensorium thus arising, the one exemplified in the Chondrostei and the other in the remainder of the Teleostomi, these two types of hyostylic suspensorium differing but little from each other but differing markedly from those in the Selachii and Batoidei.

In these early ancestors of the Teleostomi, the dorsal halves of the branchial arches were sigma-formed, as above explained, and because of this the distal end of each pharyngobranchial articulated with the hind edge of the articular facet on the dorsal end of the related epibranchial (Allis, 1923), the anterior edge of the articular facet projecting antero-mesially as a short process serially homologous with the orbital process of the palatoquadrate of the Plagiostomi. The hyomandibula of these fishes being of the teleostomean type, and articulating with the otic capsule dorsal to the vena jugularis (capitis medialis or lateralis), there was no skeletal element between the pharyngeal elements of the first branchial and mandibular arches, and the space thus left has actually, in recent fishes, been invaded by the dorsal ends of the internal openings of the anterior branchial clefts, deep grooves being formed in the roof of the branchial chamber and extending dorso-anteriorly toward the mid-dorsal line, as shown in one of my figures of *Amia* (Allis, 1897, fig. 60, pl. 37). As these dorso-anterior prolongations of the branchial openings developed, the primitive pharyngobranchials necessarily became reduced, and this doubtless led to a prolongation of the anterior processes on the dorsal ends of the epibranchials, these processes necessarily lying between the dorso-anterior prolongations of the branchial clefts. If these processes were then each to be segmented off from the remainder of the related epibranchial, a series of cartilages would arise which would have all the topographical relations to the other cartilages, and to the nerves and blood-vessels of the region, that the infrapharyngobranchials of van Wijhe's (1882) descriptions do, and the primitive pharyngobranchials, greatly reduced, would have the topographical relations of the supra-pharyngobranchials. The V-shaped arch would thus have been established, and this seems the only reasonable explanation of its origin, for the assumption that independent cartilages were developed in the lines prolonged of the epibranchials seems unwarranted. That the primitive pharyngobranchials were swung around from a dorso-posterior to a dorso-anterior direction seems improbable, as does also the assumption that the skeletal bars of

these arches retained their primitive positions in a single plane and these planes were then inclined posteriorly. Under this latter assumption, which is, I believe, the generally accepted one, it is difficult to explain the abrupt change in direction of the bars from the mandibular to the first branchial arches, and equally difficult to explain the pharyngeal elements in the branchial arches of *Acipenser*, as described and figured by Parker (1882).

The infra- and supra-pharyngobranchials above referred to have been described, or figured, in many of the Teleostomi, the infrapharyngeal always articulating with the anterior corner of the dorsal end of the epibranchial of its arch and the supra-pharyngobranchial articulating with its posterior corner, excepting only in *Acipenser*, as described by van Wijhe (1882), where these relations to the epibranchial are reversed, but this would seem to be due to a typographical error. On the posterior arches there is usually but one pharyngeal element to each arch, or a single large pharyngeal related to two or three arches, and in each such case van Wijhe considered the element, or elements, to be infra-pharyngobranchials, the single large one probably being formed by the fusion of elements belonging to two or more arches. In Parker's (1882) figures of *Acipenser*, however, the single pharyngeal elements shown on the third and fourth arches would certainly seem to be the primitive pharyngeals, and hence suprapharyngobranchials.

Several fishes in which these infra- and supra-pharyngo-branchials are found were referred to in my work on the homologies of the hyomandibula (Allis, 1915), and I there came to the conclusion that the suprapharyngeals were derived from the extrabranchials of the Plagiostomi, which I now consider to be incorrect. In my recent work on *Polypterus* (Allis, 1922), the infrapharyngeal elements are said to represent the primitive pharyngobranchials, which is also not in accord with my present determinations. In the adult of this latter fish, both pharyngeal elements were found on each of the first three arches, and all fused with the epibranchials.

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7. Zoological Results of the Third Tanganyika Expedition conducted by Dr. W. A. Cunnington, 1904–1905. Report on the Cestoda. By Prof. O. Fuhrmann, Ph.D., and Jean G. Baer, D.Sc.*

[Received October 23, 1924: Read February 3, 1925.]

(Text-figures 1–14.)

Introduction.

Of the five species of Cestoda collected from fishes in Lake Tanganyika, all have been found to be new to science, including two new and very interesting genera, thus lengthening the already considerable list of the fauna inhabiting this lake.

It is perhaps of interest to note that two of the species of Cestoda were found in a fish, which, according to Cunnington†, is only to be found in Lake Tanganyika, whereas the other hosts, also Siluroids, are to be found in other waters.

Systematic Description.

Monobothrioides cunningtoni, g. n., sp. n.

Host: *Auchenoglanis occidentalis* C. & V.

Locality: Mtondwe Bay.

A large number of specimens of this new genus of the subfamily *Caryophyllæinæ* Nybelin was obtained from the gut of the above Siluroid.

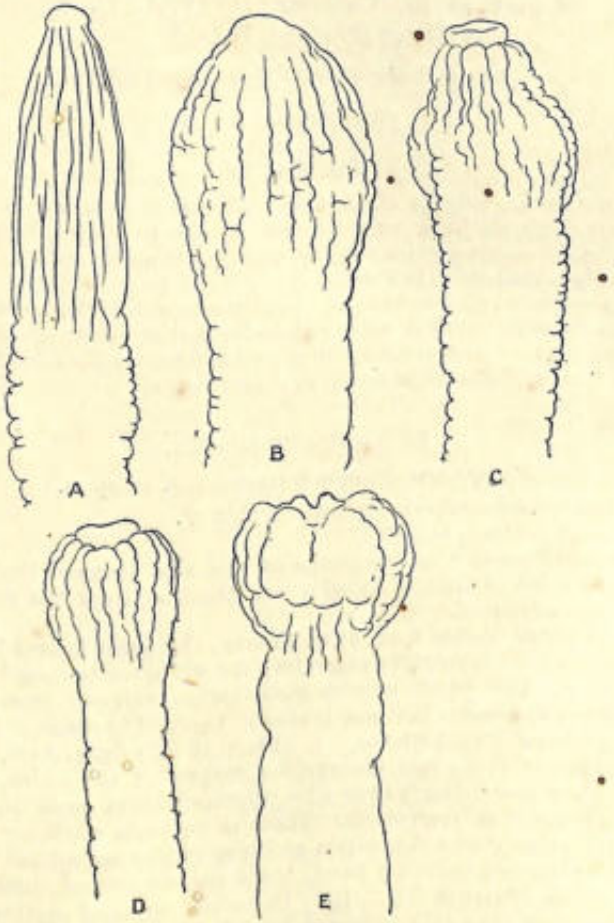
The length varies from 14 to 40 mm., the lesser figures being of contracted or immature examples; the width varies from 0·5 to 0·7 mm. The aspect of the scolex is so variable from one specimen to another that one is almost tempted to consider them as so many different species. A glance at text-fig. 1, A–E, will immediately bring out the various aspects of the scolex, and will show more clearly than a lengthy description could do, this extraordinary polymorphism. There is no trace whatever of a ventral and a dorsal depression which might be assimilated with bothria, but, on the other hand, there are to be found numerous longitudinal furrows (B, C, D). In certain stages of contraction the apex of the scolex may acquire an apical depression (C, D) which may, on the other hand, not be marked at all (A, B). The dimensions of the scolex vary from 0·93 to 1·3 mm. in length, and from 0·7 to 1·6 mm. in width.

* Communicated by Dr. W. A. Cunnington, F.Z.S.

† "The Fauna of the African Lakes: A study in Comparative Limnology, with special reference to Tanganyika," Proc. Zool. Soc. 1920, p. 507.

From the foregoing it is clear how careful one must be when using the scolex of a Bothriocephalid as a specific character, a point to which Fuhrmann * has already drawn attention.

Text-figure 1.



Monobothrioides cunningtoni, g. n., sp. n.
A–E. Different aspects of the scolex.

The transverse sections of the scolex (text-fig. 2, B, C) show clearly the numerous longitudinal furrows, which can be quite

* Die Cestoden der Deutschen Süd-Polar-Expedition, 1901–1903.—XVI. Zoologie, 8, p. 469, 1921.

deep in certain cases, and which contribute to fix the Cestode more firmly in the gut of its host. Behind the scolex there is a region devoid of genitalia and very variable in length; then comes the testicular region containing also the vitellaria, the latter surrounding the testes. This region is also very variable in length, measuring from 6·4 mm. in the smaller specimens to 23 mm. in the larger and well-expanded ones. The posterior region containing the ovary and the uterus, on the other hand, varies much less in length (from 4 to 5 mm.); *i. e.*, the genital pores are situated 4·2 to 5·2 mm. from the posterior extremity of the worm.

The muscular system is very powerfully developed, the entire medullary zone of the scolex and of the neck being occupied by muscle-fibres consisting principally of longitudinal fibres. This medullary zone is surrounded in the scolex by a cortical zone, in which are found longitudinal fibres radiating obliquely from the centre. The transverse and dorso-ventral fibres are relatively weak.

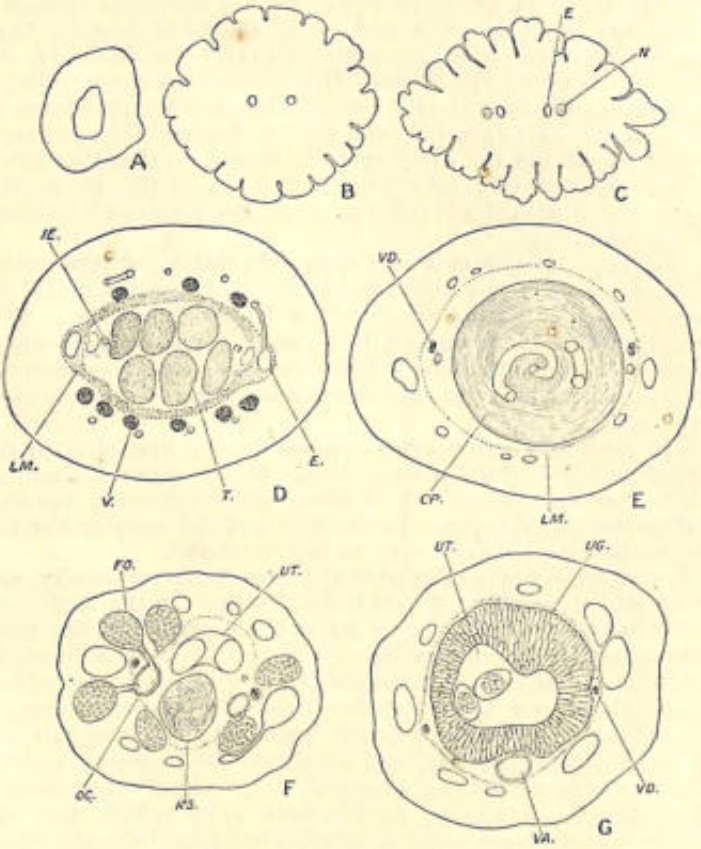
The medullary parenchyma appears for the first time in the region occupied by the male gonads. In this region the musculature forms a narrow ring of fibres without forming bundles, and surrounds the testes. In the region of the ovary and of the uterus the musculature is very weakly developed.

The excretory pore is situated at the posterior extremity, and opens into an excretory vesicle 0·2 mm. long. In the medullary parenchyma, and extending as far as the neck-region, two pairs of longitudinal excretory vessels are to be found. The vessels of one pair are narrow, surrounded by a sheath of longitudinal muscle-fibres, and united at intervals by a transverse vessel. The other pair of vessels, situated laterally to the first pair, are of much larger diameter, and open into the excretory vesicle; they are surrounded by a lateral longitudinal musculature. From the latter vessels, ramifications arise which join the peripheral vascular network situated exterior to the longitudinal musculature and to the vitellaria. In transverse sections passing through this region there are generally to be found four dorsal and four ventral vessels. In the scolex there are only two internal longitudinal vessels, forming a large ring at the apex. Exterior to the musculature of the scolex, at a fairly large distance from the surface of the latter, there is a very well-developed peripheral vascular network.

The two longitudinal nerve-cords are very thin.

The male gonads are extremely numerous, and form a double layer of testes which occupy the whole of the medullary parenchyma. The first testes are situated slightly posterior to the first follicles of the vitellaria, and disappear anterior to the cirrus pouch, where the vas deferens forms several coils. The cirrus pouch occupies the entire medullary parenchyma, and possesses fairly distinct muscular walls which touch the longitudinal musculature of the strobila. According to the state of

Text-figure 2.



Monobothrioides cunningtoni, g. n., sp. n.

Transverse sections, passing through different regions :—

A. Through the anterior portion of the scolex.

B. „ „ middle of the scolex.

C. „ „ posterior extremity of the scolex. E. Excretory vessel. N. Nerve.

D. „ „ testicular region. IE. Internal longitudinal excretory vessel. LM. Longitudinal musculature. T. Testes. V. Vitellaria.

E. „ „ cirrus pouch. C.P. Cirrus pouch. VD. Vitelline duct. The other letters as above.

F. „ „ ovary. FO. Ovarian follicles. OC. Ovarian duct. RS. Receptaculum seminis. The other letters as above.

G. „ „ uterine region. UG. Uterine glands. UT. Uterus. VA. Vagina. The other letters as above.

contraction, the length of the cirrus pouch varies from 0·68 to 0·97 mm., and its diameter from 0·19 to 0·3 mm. The male pore opens slightly anterior to the female pore.

The disposition of the female genitalia is extremely characteristic. The ovary is very distinct, and presents two anterior and two posterior wings, the latter meeting in the mid-field. The structure of the ovary is not that usually met with in Cestodes, *i. e.*, a more or less lobed gland, but is here distinctly follicular in structure. The very numerous follicles situated exterior to the longitudinal musculature open into anterior and posterior ducts provided with a thick wall similar to that of the ovarian reservoir and distinct from the envelope of the ovarian follicles, which meet in a common ovarian reservoir, oval in shape and situated between the wings of the ovary. The anterior wings are 0·9 to 1·2 mm. long, and the posterior wings 0·6 to 0·7 mm. long; the ovarian reservoir measures 0·18 : 0·16 mm. The oviduct is situated slightly laterally and passes into the mass of the shell-gland; the latter is slightly larger than the ovarian reservoir. The vagina terminates in the anterior region of this glandular mass, whereas the yolk-duct terminates near the centre of the mass (text-fig. 3).

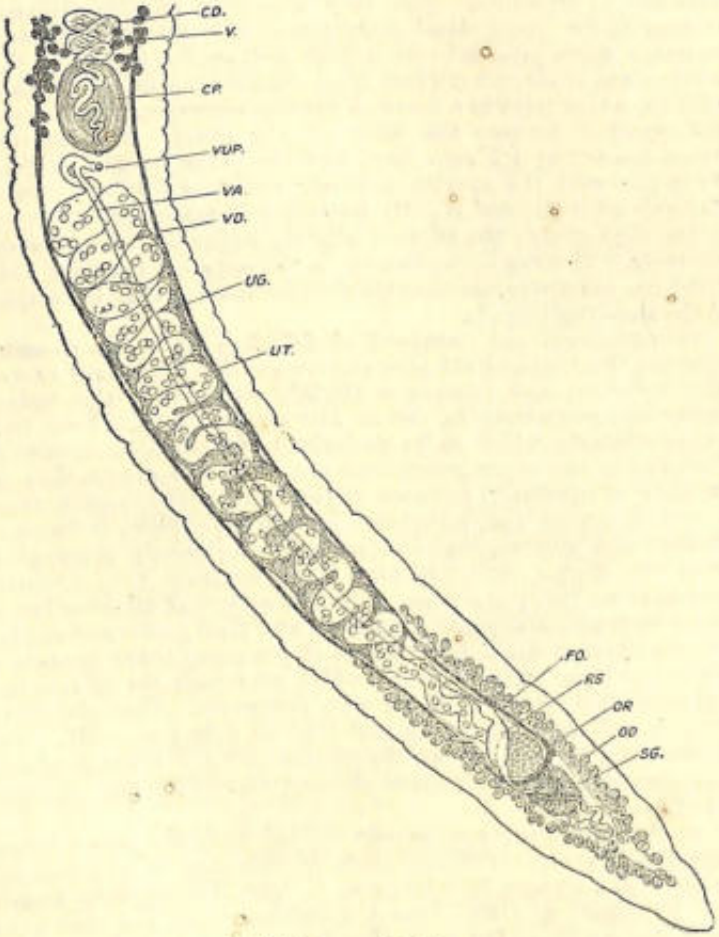
The vitellaria are composed of follicles; they are situated between the longitudinal musculature and the peripheral excretory network, and commence slightly anterior to the testes, extending posteriorly as far as the cirrus pouch, where two yolk-ducts arise which unite posterior to the ovarian reservoir. Contrary to the other genera and species of this group, *there is no trace of vitellaria posterior to the ovary*. The vagina runs a ventral course, and, just before joining the oviduct, it forms a distinct elongate *receptaculum seminis*. Anteriorly the vagina joins the uterus, both opening by a common pore situated posterior to the male pore. The uterus first of all describes a few coils behind the ovarian reservoir, and then passes anteriorly. On the level of the anterior wings of the ovary there appears a glandular layer 0·09 mm. thick which surrounds the uterus, the latter continuing to wind its way anteriorly. This glandular zone is 2·5 to 3 mm. long and 0·28 to 0·34 mm. wide. On approaching the female pore the uterine coils lose their glandular envelope and become somewhat irregular. The ova measure 54 : 36 μ.

At first sight our species seems to belong to the genus *Monobothrium* Diesing, of which there is only one species known, namely *M. wageneri* Nybelin (syn. *M. tuba* Diesing, from *Tinca*: see Nybelin*, p. 118). However, further study has shown us that the species is the type of a new genus which differs from *Monobothrium* by the following characters:—The scolex is not hexagonal, and does not present any dorsal and ventral bothria. The male and female genital pores are separate, and do not open into a common genital atrium. The vagina presents a distinct *receptaculum seminis*, absent in *Monobothrium*, and, contrary to the latter, the ovary is follicular, and there are no vitellaria

* "Anatomische-Systematische Studien über Pseudophylliden." Göteborgs Kungl. Vetenskaps- och Vitterhets-Samhälles Handlingar, Fjärde Följden, xxvi. p. 1.

posterior to the ovary. If we compare our genus with *Caryophyllæus*, we find that the scolex is totally different, and does

Text-figure 3.



Monobothrioides cunningtoni, g. n., sp. n.

A whole mount of the posterior half of the worm. CD. Vas deferens. OR. Ovarian reservoir. SG. Shell-gland. VUP. Vagino-uterine pore. The other letters as in text-fig. 2.

not present the spatulate appearance peculiar to the latter. The utero-vaginal duct is short instead of being long, and the ovary is follicular instead of being compact, also the oviduct

does not arise from the middle of the bridge uniting the wings of the ovary. The vitellaria do not reach posterior to the ovary, and are situated outside of the longitudinal musculature, whereas in *Caryophyllæus* the vitellaria reach beyond the ovary, and are situated in the medullary parenchyma.

Since our species cannot be placed in either of the above genera, we propose to create a new genus, *Monobothrioides*, which may be defined as follows :—*Caryophyllæinæ* with a scolex devoid of bothria, but bearing numerous longitudinal furrows. The apex of the scolex may be withdrawn, forming a kind of funnel. Male and female genitalia open on the surface by two separate pores. Utero-vaginal duct short. Large *receptaculum seminis* present. Ovary follicular, with a large median ovarian reservoir. Oviduct arises to the right of the mid-line. Uterus never reaching anteriorly beyond the female pore; present as a long regularly-wound tube surrounded by uterine glands. Vitellaria situated in the cortical parenchyma and never reaching beyond the ovary.

Adult in Siluroids. Type: *M. cunningtoni*, sp. n.

Our new genus is closely related to the genus *Lytocestus* Cohn. It has in common with the latter the absence of vitellaria posterior to the ovary, and the follicular structure of the latter, the follicles lying in both cases outside the longitudinal musculature. It differs, however, from this genus, as far as we can judge from the incomplete description given by Cohn *, by the shape of the scolex, the disposition of the musculature, which consists of a double layer of longitudinal fibres, the excretory system, the position of the uterus, which does not reach beyond the anterior wings of the ovary, and by the absence of a *receptaculum seminis*, and also of a special structure of the vagina.

The numerous specimens of *Lytocestus adhærens* from *Clarias fuscus*, collected in Hong Kong, were considered by the author as isolated proglottides of a Tetraphyllidean Cestode; but Pintner, and especially Nybelin (p. 135), have shown that this species must be referred to the Cyathocephalidæ. This theory is supported by the existence of two or more species belonging to this genus, and described by Woodland † under the names of *Caryophyllæus filiformis* Woodland and *Caryophyllæus chalmersius* Woodland, the former from *Mormyrus cashive* and the latter from *Auchenoglanis occidentalis*. Although these two descriptions are incomplete, there seems to be no doubt that these species should be referred to the genus *Lytocestus* Cohn.

Woodland (*loc. cit.*) has attempted to revise the Caryophyllæidæ and the Cestodaria; we are, however, unable to accept this

* "Die Anatomie eines neuen Fischcestoden." Centralbl. f. Bakt. u. Parasit. xlvi. 1908, p. 134.

† "On some remarkable new forms of Caryophyllæidæ from the Anglo-Egyptian Sudan, and a Revision of the Families of the Cestodaria." Quart. Journ. Micr. Sci. lxvii. p. 435.

"On a new Species of the Cestodarian genus *Caryophyllæus* from an Egyptian Siluroid." Proc. Zool. Soc. 1924, p. 509.

revision. Woodland once more places the Caryophyllæidæ among the Cestodaria, and unites them with the Gyrocotylidæ in a new order, the Paralinidea. This return to ancient systematic dispositions is to be regarded as a regression, because the only character of any importance allowing the Caryophyllæidæ to be placed with the Gyrocotylidæ is the fact that both these groups are monozootic. However, Loennberg*, as far back as 1897, showed that the Caryophyllæidæ are secondarily monozootic, whereas the Gyrocotylidæ are primitively monozootic. Their anatomy and even their morphology are but distantly related, whereas the anatomy of the Cyathocephalidæ is much more closely related to the Pseudophyllidea and especially to the genera *Diplocotyle*, *Bothrimonus*, *Cyathocephalus*, and *Didymobothrium*, all of which are contained in the family Cyathocephalidæ Nybelin †, 1918.

Woodland characterises his order Paralinidea as follows:—Cestodaria: (*a*) with three sexual apertures situated close together; (*b*) with the uterus and vagina running parallel to each other in the same dorso-ventral plane along the median longitudinal axis of the body; (*c*) with the testes restricted to the anterior end of the body; (*d*) with a bilobed ovary; (*e*) without calcareous bodies; (*f*) with a reticulate excretory system; (*g*) with a hexacanth larva (?).

This vague diagnosis shows the lack of sufficient basis for the order. The character (*a*) does not exist in the Gyrocotylidæ, since the male and female pores are to be found on both surfaces of the worm; the character (*g*) is only found in the Caryophyllæidæ, the Gyrocotylidæ possessing ten hooked embryos; the character (*b*) is common to the majority of the Pseudophyllidea; and the character (*d*) is found in nearly all the Cestodes. What remains to characterize the order Paralinidea?

Woodland seems to disregard Poche's ‡ recent re-classification of the Amphilinidea, but a fuller consideration of it might have convinced him that nowadays it is impossible to create genera and even orders for Platodes based on purely morphological characters.

In his family Caryophyllæidæ Woodland, the author only retains the genera *Caryophyllæus*, *Archigetes*, and *Wenyonia*; he is unaware of the genera *Caryophyllæides* Nybelin and *Lytocestus* Cohn, and removes the genera *Monobothrium* Diesing and *Glaridacris* Cooper. This latter genus seems to be identical with *Monobothrium*, which must be retained as a well-characterized genus.

Consequently the family Caryophyllæidæ Woodland = *Caryophyllæinæ* Nybelin contains, not three, but no fewer than seven

* "Beiträge zur Phylogenie der parasitischen Plathelminthen." Centralbl. f. Bakt. u. Parasit. xxi. 1897.

† The family Caryophyllæidæ Woodland is identical with the subfamily *Caryophyllæinæ* Nybelin. The family Cyathocephalidæ, in addition to the above genera, contains the *Caryophyllæinæ*.

‡ "Zur Kenntniss der Amphilinidea." Zool. Anz. liv. 1921, p. 276.

genera, counting our new genus; all of these genera are well characterized.

The diagnoses of the genera and of the species as given by Woodland are insufficient. For instance, his diagnoses of *Caryphyllæus* and of *Archigetes* only differ by the presence of a caudal appendage in *Archigetes*, when there are distinct anatomical differences, clearly shown in the diagnoses of these genera as given by Nybelin.

With regard to Woodland's diagnoses of the species, we again find the same fault; for instance, that of *C. fennicus* (type-species of the genus *Caryophyllæides* Nybelin). He has failed to draw attention to the fact that the uterine coils are also found *anterior* to the cirrus pouch, a character only found in that genus. He says in a note on p. 456 that he has found two specimens of *C. laticeps* possessing uterine coils anterior to the utero-vaginal pore, but this only means that his specimens were *C. fennicus* and not *C. laticeps*.

To Woodland's list of species of the genus *Caryophyllæus* we must add *C. caspicus* Annenkova Klopin, 1919, and *C. fimbriceps* Annenkova Klopin 1919*. As this paper is written in Russian we are unable to state whether these species are valid or not.

Proteocephalus dinotopteri, sp. n.

Host: *Dinotopterus cunningtoni* Boulenger.

Localities: Mbete and Niamkolo.

This species was in the same bottle as the next species, and at first sight we thought that we had before us a much extended specimen of *P. cunningtoni*, sp. n. A closer examination, however, revealed the fact that we had before us a distinct species also new to science.

These specimens are slightly macerated, so that we are compelled to leave out certain histological details.

The total length of this worm is 290 mm. and the greatest width 1·6 mm. The scolex, viewed from above, is almost square in shape and measures 2·1 : 1·85 mm. The suckers are 0·85 mm. in diameter; a fifth sucker or a rostellum are entirely absent. The first segments are 0·85 mm. long and 1·6 mm. wide, the mature segments 2·2 mm. long and 1·5 mm. wide, and, finally, the gravid segments, much extended, are 4·7 mm. long and 1·1 mm. wide.

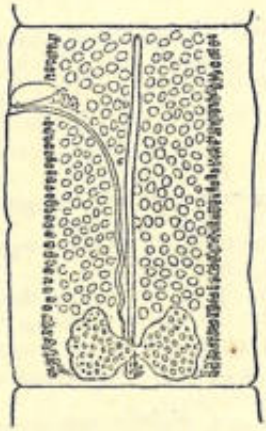
The cuticle is very thin, probably due to the macerated condition of the worm, and does not measure more than 2 μ in thickness. The subcuticular-cell layer is 8 μ wide. The longitudinal musculature is well developed: the muscle-bundles are 19 μ in diameter and contain 16 to 20 fibres. The transverse

* "Two new Species of the Genus *Caryophyllæus* parasitic in Cyprinidæ." Bull. Acad. Sci. Petrograd, 1919, p. 97.

and dorso-ventral muscles are weakly developed. Of the excretory system we have only been able to find the two longitudinal excretory vessels.

The genital pores alternate irregularly, and are situated in the anterior quarters of the segments. The cirrus pouch is 0·29 mm. long and 0·13 mm. in diameter; it possesses a thin muscular wall not exceeding 3 μ in thickness. The cirrus is 0·27 mm. long and is fairly stout. Several coils of the *ductus ejaculatorius* are contained within the cirrus pouch. The *vas deferens* forms several coils much dilated with spermatozoa. There are about 240 testes occupying the entire field between the vitellaria anterior to the ovary; they are situated in a single dorsal layer and measure 62 μ in diameter.

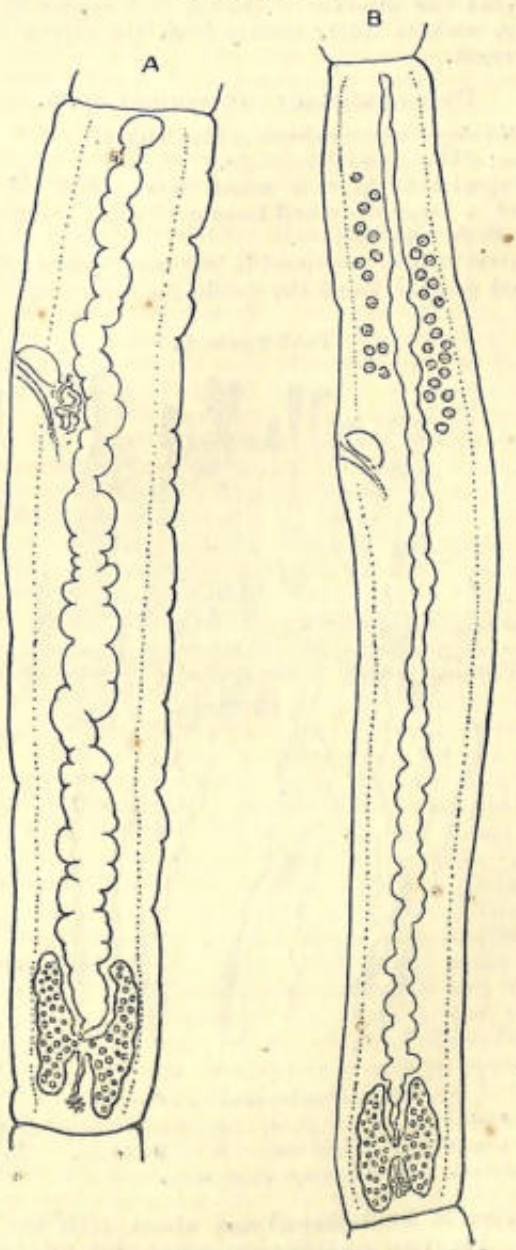
Text-figure 4.



Proteocephalus dinotopteri, sp. n.
Whole mount of a mature segment.

The vagina opens anterior or posterior to the cirrus pouch, and its proximal portion is somewhat dilated. From the genital pore the vagina runs in a curve towards the ovary. The latter is bilobed, the two lobes being fan-shaped and measuring 0·82 mm. across. The shell-gland, 0·13 mm. in diameter, is situated posterior to and between the two lobes of the ovary. The vitellaria occupy two lateral bands reaching beyond the posterior border of the ovary. The uterus first appears as a straight tube, which soon branches off laterally and forms 25 to 30 diverticulæ. These diverticulæ are extremely short, not more than one-third of the width of the segment. The uterus possesses 8–12 distinct uterine pores. The ova are 15 μ in diameter and contain an embryo 12 μ in diameter.

Text-figure 5.



Protocephalus diuotopteri, sp. n.
A & B. Two gravid and much extended segments.

As can be seen from text-fig. 5, when the segments are very much extended the internal anatomy, and especially the shape of the ovary, tends to differ totally from the aspect of a normal mature segment.

PROTEOCEPHALUS CUNNINGTONI, sp. n.

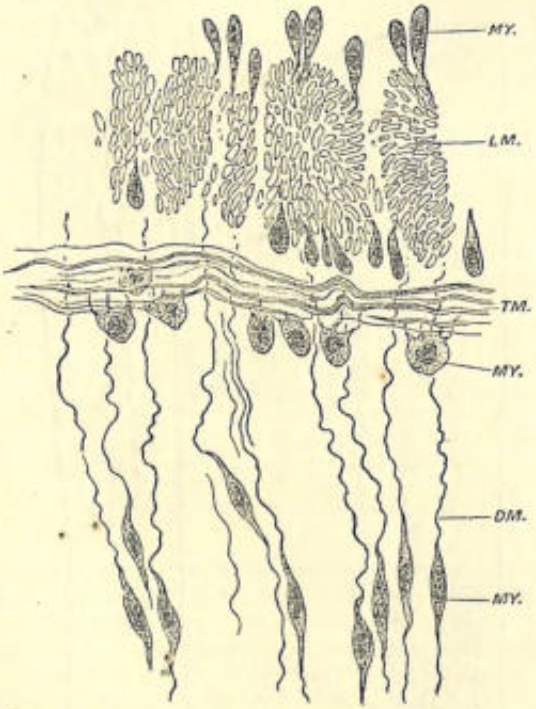
Host: *Dinotopterus cunningtoni* Boulenger.

Localities: Mbete and Niamkolo.

Several specimens of this worm were obtained from the intestines of a large male and female "Singa," caught at Mbete and at Niamkolo respectively.

The greatest length measured is 250 mm., but must in reality be somewhat greater, as all the specimens were much contracted.

Text-figure 6.



Proteocephalus cunningtoni, sp. n.

A portion of the musculature highly magnified and showing the myoblasts. LM. Longitudinal musculature. MY. Myoblasts. DM. Dorso-ventral musculature. TM. Transverse musculature.

The scolex is knob-shaped and about 1·75 to 2·1 mm. in diameter. The four suckers open anteriorly and are spherical;

they measure 0·67 mm. in diameter. There is no trace whatever of a fifth sucker or of any rostellar-like structure. Behind the scolex there is a distinct neck 7 mm. long; the first segments are 0·4 mm. long and 2·7 mm. wide, the mature segments 1·85 mm. long and 3 mm. wide, and the gravid segments 2·4 mm. long.

The cuticle is extraordinarily thick, measuring on transverse sections as much as 23 μ. Beneath the cuticle lies the usual layer of longitudinal and circular muscles. The subcuticular cells are exceedingly long and spindle-shaped; they form a layer 57 μ wide.

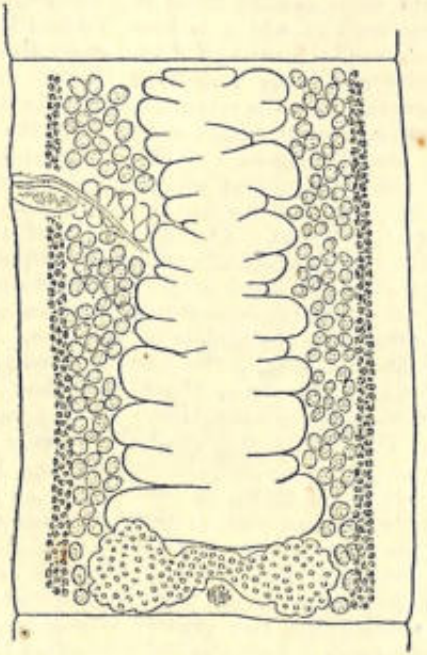
The longitudinal musculature is exceedingly well developed, and consists of stout bundles 38 to 40 μ in diameter containing about 95 fibres, each of which is from 3·8 to 4·7 μ in diameter. The transverse muscles consist of 4 to 6 stout fibres; the dorso-ventral muscles are fairly numerous though very fine. An interesting feature about the muscular system is the presence of very large and distinct myoblasts, not only on the dorso-ventral but also on the transverse and longitudinal muscles. The myoblasts of the longitudinal muscles are pyriform, and are situated at the periphery of the muscle-bundles and perpendicular to the latter (text-fig. 6). The myoblasts of the transverse musculature are almost spherical, and present a Spider-like aspect, reminding one of a nerve-cell with its characteristic prolongations. The dorso-ventral muscles possess the usual spindle-shaped myoblasts situated near the middle of the fibre. We have not observed any chalk bodies. The two longitudinal nerves are exceptionally stout and measure 56 μ in diameter.

The excretory system is much more distinct in quite young segments, and consists of the usual dorsal pair of excretory vessels, 15 μ in diameter, situated dorsally and lateral of the ventral pair, which is 22·8 μ in diameter. As the excretory vessels are displaced more than is usual towards the centre of the segment, they lie dorsal to the vitellaria, a disposition that we have not seen recorded before. Both the dorsal and the ventral vessels possess numerous secondary branches. A transverse vessel uniting the two ventral vessels is absent. The genital pore alternates irregularly, and is situated in the anterior half of the segment; the genital ducts pass ventral to the excretory vessels and to the nerve. The cirrus pouch is pear-shaped and measures 0·34 to 0·38 mm. in length and 0·15 mm. in diameter. The musculature of the pouch is not very well developed, and consists chiefly of longitudinal fibres forming a wall 4 μ thick. The cirrus is very stout and possesses a very thick cuticula; it measures 0·27 mm. in length and 0·04 mm. in diameter. The *ductus ejaculatorius* forms several coils within the cirrus pouch. The *vas deferens* is very long and much coiled, the coils being much distended with spermatozoa, thus replacing functionally a *vesicula seminalis*. In transverse sections the coils of the *vas deferens* are seen to fill the entire medullary parenchyma in the poral half of the segment. The testes occupy

one to two dorso-ventral layers, and occupy nearly the whole field contained between the vitellaria; in gravid segments the testes are pushed aside by the growing uterus, so that there are no testes dorsal of the latter (text-fig. 8). There are altogether about 200 testes, the latter being 98 μ in diameter.

The vagina appears as a thick-walled tube, opening anterior to, and ventral to, the cirrus pouch; there is no *receptaculum seminis*. The ovary is situated in the posterior half of the segment; it is

Text-figure 7.



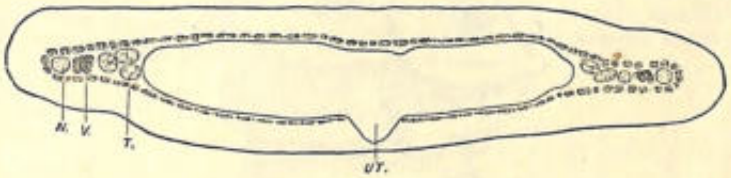
Proteocephalus cunningtoni, sp. n.
A gravid segment.

bilobed and measures 1·65 mm. across. The shell-gland is well developed, and is situated between the two lobes of the ovary and posterior to the latter. The vitellaria form two lateral bands reaching as far as the posterior border of the ovary. The uterus forms 12 to 15 lateral diverticulæ, of which the two posterior ones may sometimes overlap the anterior border of the ovary; in transverse sections the gravid uterus is seen to occupy nearly the whole of the medullary parenchyma (text-fig. 8). The ova measure 19 μ in diameter. The embryo measures 11·4 μ,

and is surrounded by a very fine membrane. There are no uterine pores present, but the gravid segments open along the middle to expel their ova.

As far as we have been able to ascertain, there has only been a single species of *Proteocephalus* reported from Lake Tanganyika, and that is *P. sulcatus* (Klaptocz), reported by Beauchamp * from

Text-figure 8.



Proteocephalus cunningtoni, sp. n.
A transverse section through a gravid segment. Letters as in text-fig. 2.

a Siluroid *Chrysichthys* sp. collected by Stappers in 1912. Thanks to the kindness of Prof. Beauchamp we have been able to examine the original slides, and find that this is a new species, for which we propose the name:

PROTEOCEPHALUS BEAUCHAMPI, sp. n.

Syn. *Proteocephalus sulcatus* (Klaptocz), Beauchamp, 1914.

As only fragments are present, it is impossible to estimate the length of this worm. The width of mature and gravid segments is 2·2 mm. The scolex is about 2 mm. in diameter, only the openings of the suckers being visible. The anatomy differs from that of *P. sulcatus* by the much smaller number of testes, about 80 instead of 200, and by the fact that the vagina lies anterior to the cirrus pouch and never posterior to the latter as in *P. sulcatus*. The cirrus pouch is pear-shaped, about 0·25 mm. long and 0·19 mm. in diameter. It contains a long unarmed cirrus which, when fully everted, measures 0·48 : 0·06 mm. The gravid uterus has 7 to 8 lateral outpocketings, distinctly separated from one another; the ova measure 15 μ in diameter.

LOENNBERGIA TANGANYIKÆ, g. n., sp. n.

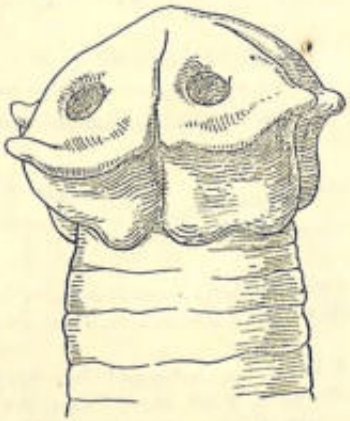
Host: *Clarias lazera* C. & V. (?).
Locality: Vua.

Several specimens of this interesting new genus were obtained from the gut of a very large female Siluroid, probably *Clarias lazera* C. & V., caught at Vua. These worms are from 90 to 150 mm. long and from 2 to 3·5 mm. wide. The scolex viewed

* "Sur quelques Parasites du Congo Belge." Rev. Zool. Africaine, iv. p. 100 (1914).

from above is almost square and measures 1·45 to 1·85 mm.: 0·85 to 1·35 mm. The four suckers are deeply embedded in the tissues and open anteriorly, the openings being flush with the

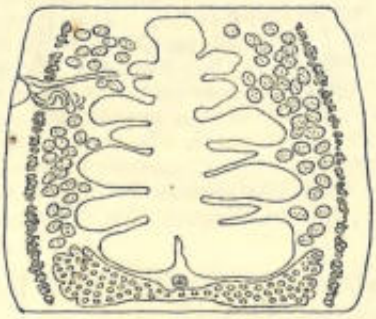
Text-figure 9.



Proteocephalus beauchampi, sp. n.
The scolex.

surface of the scolex; these suckers are nearly spherical and measure 0·5 to 0·7 mm. in diameter. We could find no trace of a vestigial fifth sucker or of any rostellar-like structure either in

Text-figure 10.

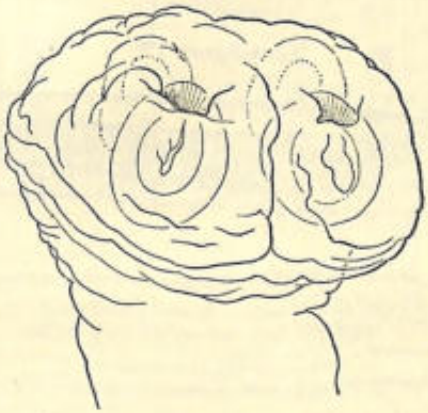


Proteocephalus beauchampi, sp. n.
A gravid segment.

whole preparations or in sections of the scolex. The latter presents an interesting feature which seems to place this genus as an intermediate form between the genera with a simple scolex,

i. e. *Proteocephalus*, and those with a scolex surrounded by a kind of frill derived from an expansion of the tissues, like *Corallobothrium* for instance. The base of the scolex presents a certain amount of loose tissue, not sufficient to form a distinct frill, but enough to give an irregular and characteristic aspect to the whole structure (text-fig. 11). Behind the scolex there is a distinct neck 4 mm. long; the first segments are 0·11 mm. long and 1 mm. wide; mature segments measure 1 mm. in length and 3·2 mm. in width. The greatest width of 3·5 mm. is reached in the gravid segments. The cuticula is 11 μ thick, and beneath the latter there lies a single layer of longitudinal muscle-fibres; the subcuticular cell-layer is 30 μ wide.

Text-figure 11.



Loennbergia tanganyikæ, g. n., sp. n.
The scolex.

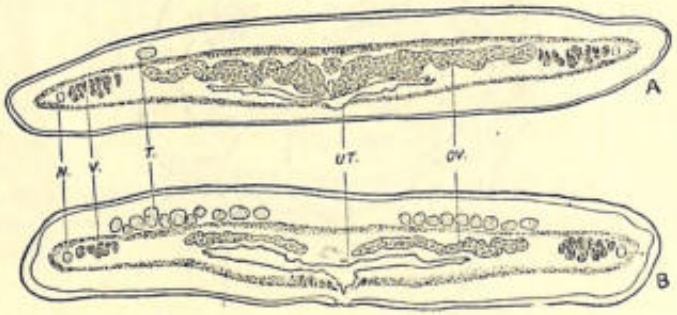
The longitudinal musculature is powerfully developed, and reminds one, by its general appearance, of that of certain species of *Diphyllobothrium*. In transverse sections (text-fig. 12, A & B) it appears as a muscular ring 0·06 mm. wide, made up of stout isolated fibres, each of which is about 1·6 μ in diameter. Under a higher power we could observe that this muscular ring consists of about 12 concentric layers of fibres, the latter presenting very large and conspicuous myoblasts situated towards the periphery of the muscular ring. The dorso-ventral musculature is represented by occasional but very distinct fibres, which appear, owing to contraction, to be twisted corkscrew-wise. The transverse musculature is very weak, consisting of only 2 to 3 fibres.

After forming a complicated network in the scolex, the excretory vessels follow a somewhat winding course throughout the entire length of the strobila. The dorsal excretory vessels lie dorsally and laterally to the ventral vessels and are situated

next to the nerve; they measure 23 μ in diameter, whereas the ventral vessels measure 38 μ in diameter. *Foramina secunda* are present throughout the entire strobili. The two longitudinal nerve-cords are 45 μ in diameter, and are situated within the longitudinal musculature.

The genital pore is situated laterally in the anterior half of the segment, and alternates irregularly; the genital ducts pass between the excretory vessels and beneath the nerve. The cirrus pouch is 0·48 to 0·55 mm. long and 0·21 to 0·23 mm. in diameter; it possesses a weak muscular wall, not more than 4 μ thick, consisting almost entirely of longitudinal muscle-fibres. The cirrus itself is 0·47 mm. long and 0·04 mm. in diameter; it is inerme, but possesses a thick cuticula. The cirrus pouch also contains several coils of the *ductus ejaculatorius*. The *vas deferens* is extremely coiled and much dilated with spermatozoa, thus

Text-figure 12.



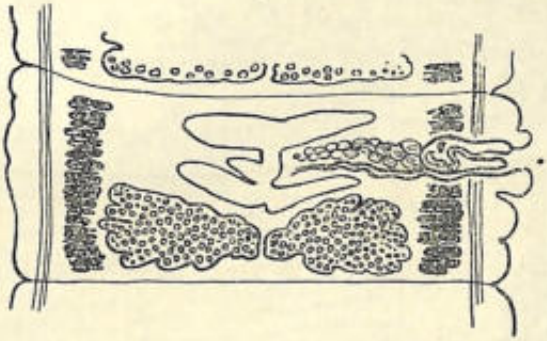
Locumbergia tanganyikæ g. n., sp. n.
A & B. Transverse sections through a gravid segment. Letters as in text-fig. 2.

replacing functionally a *vesicula seminalis* which is absent. The testes, about 200 in number, are situated entirely in the cortical parenchyma and occupy a single dorsal layer; a single testis is about 76 μ in diameter.

The vagina opens posterior to the cirrus pouch, although in certain segments it may be found anterior to the latter, and is lined with a thick cuticula surrounded by a layer of dark staining cells. From the genital pore the vagina runs a fairly horizontal course as far as the centre of the segment, then turns to join the oviduct, shortly before reaching which it forms a distinct *receptaculum seminis* situated between the two lobes of the ovary. The latter consists of two broad lobes situated in the posterior half of the segment. The vitellaria form two lateral bands situated *within* the longitudinal musculature and reaching as far as the posterior edge of the ovary. The shell-gland is well developed, and is placed dorsally between the two lobes of the

ovary. The uterus lies ventral to the ovary and presents 5 to 8 diverticulæ, which may in turn be subdivided into 2 or 3 diverticulæ situated in the same dorso-ventral plane. The width of the gravid uterus is one-third of that of the entire segment; there are from 5 to 8 uterine pores. The ova measure 20 μ in diameter, and the embryo is surrounded by a very fine membrane 11 μ in diameter. The ova in the same uterus seem to be very irregularly mature, ripe ova being found alongside ova which have only just begun to segment.

Text-figure 13.



Loennbergia tanganyikæ, g. n., sp. n.
Horizontal section through a mature segment.

La Rue* created the new family Monticelliidæ to accommodate the genus *Monticellia* La Rue, which, owing to its curiously aberrant anatomy, could not be placed in the family Proteocephalidæ. A later paper by Fuhrmann † has brought to light the existence of two new genera, *Goezeella* Fuhrmann and *Rudolphiella* Fuhrmann = *Ephedrocephalus* Diesing (Mola) ‡. Both these genera, together with our new genus *Loennbergia*, present the same aberrant anatomy as *Monticellia*—*i. e.*, part of the genitalia are situated in the cortical parenchyma. They are therefore to be included in the above family, which must be re-defined as follows:—

Family Monticelliidæ La Rue, em.

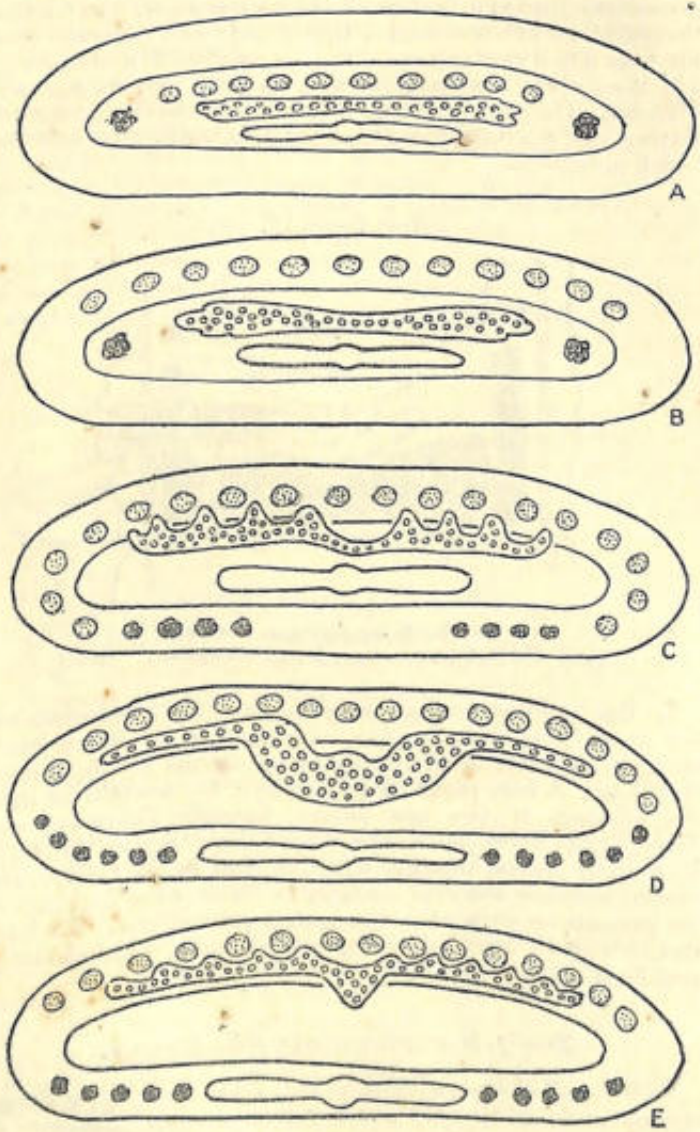
Scolex small globose, with or without folds of encircling tissue; suckers sessile, fifth sucker and rostellum absent. Anatomy of

* "A Revision of the Cestode family Proteocephalidæ." Illinois Biol. Monogr. no. 13.

† "Eigentümliche Fischcestoden." Zool. Anz. xlvi. p. 13.

‡ "Di alcuni specie poco studiate o mal note di Cestodi." Ann. Mus. Zool. Napoli, ii. p. 1.

Text-figure 14.



Diagrams of the internal anatomy of the genera of the Monticelliidæ as compared with the genus *Proteocephalus*.

A. *Proteocephalus*. B. *Loennbergia*. C. *Ephedrocephalus*.
D. *Monticellia*. E. *Goezeella*.

the typical Tetraphyllidian type. Testes occupy a dorsal or dorso-lateral field in the cortical parenchyma only, whereas the female genitalia may be partly in the cortical and partly in the medullary parenchyma.

Adult in Siluroids. Type-genus: *Monticellia* La Rue.

A glance at the diagrams* in text-fig. 14 will immediately show the differences which exist between the genera of the Monticelliidæ. These genera may be defined as follows :—

1. Loennbergia, g. n.

Scolex globose, without folds of encircling tissue. Testes in a single dorsal field, situated in the cortical parenchyma. Ovary, uterus, and vitellaria situated entirely in the medullary parenchyma.

Adult in African Siluroids. Type: *L. tanganyikæ*, sp. n.

2. Ephedrocephalus Diesing = *Rudolphiella* Fuhrmann.

Scolex globose, with folds of encircling tissue. Testes dorsal and lateral, situated in the cortical parenchyma. Uterus and part of the ovary situated in the medullary parenchyma; vitellaria situated ventrally in the cortical parenchyma.

Adult in South American Siluroids. Type: *E. microcephalus* Diesing. Further species: *E. lobosus* (Riggenbach).

3. Monticellia La Rue.

Scolex globose, without folds of encircling tissue. Testes dorsal, situated in the cortical parenchyma. Vitellaria ventral and lateral, uterus ventral; both situated in the cortical parenchyma. Ovary partly in the cortical, partly in the medullary, parenchyma.

Adult in South American Siluroids. Type: *M. coryphicephala* (Monticelli). Further species†: *M. diesingi* (Monticelli) and *M. macrocotylea* (Monticelli).

4. Goezeella Fuhrmann.

Scolex globose, with folds of encircling tissue. Testes dorsal, situated in the cortical parenchyma. Vitellaria and uterus ventral, situated in the cortical parenchyma. Ovary almost entirely in the cortical parenchyma.

* In these diagrams the limits of the medullary and of the cortical parenchymæ are indicated by a simple line. The testes are lightly dotted and the vitellaria heavily dotted. The ovary is represented with small circles and the uterus as an oblong sack.

† We do not consider *T. malopteruri* Fritsch to be a member of this genus, and leave it under the above name until its anatomy has been worked out. Woodland has lately published a paper (Parasitol. xvi. p. 441) in which he creates a new genus *Gangesia* possessing an armed scolex. It seems highly probable that *T. malopteruri* should be referred to this genus.

Adult in South American Siluroids. Type: *G. siluri* Fuhrmann.

From the diagrams it will be seen that the genus *Loennbergia* seems to form the connecting-link between the Monticelliidæ and the Proteocephalidæ.

Of the four genera and seven species of Monticelliidæ, *Loennbergia tanganyikæ*, g. n., sp. n., is the first and at present the only genus and species to be recorded from the African continent.

8. The Comparative Morphology of the Cæcal Gland (Rectal Gland) of Selachian Fishes, with some reference to the Morphology and Physiology of the similar Intestinal Appendage throughout Ichthyopsida and Sauropsida.

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(Plates I.–III.*; Text-figures 1–44.)

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* For explanation of the Plates and Text-figures, see p. 188.

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INTRODUCTION.

The characteristic appendage of the post-valvular segment of the intestine of Selachii has been given a variety of names. The one in most general use at the present time is "rectal gland," but since the terminology of this portion of the intestine is confused because the portion still called the "rectum" in most text-books probably corresponds to the whole of the large intestine in higher vertebrates, it seems inadvisible to designate this appendage the "rectal gland." Frequently it is not digitiform in shape, so that the term "digitiform appendix" is not appropriate. Consequently, while deprecating the complication caused by multiplication of nomenclature, it seems advisable to follow Owen and Morgera in using the term "cæcal gland" because of its cæcal or diverticular origin.

My interest in the subject was first aroused by Dr. H. W. Marett-Tims, who suggested to me that the knowledge of the morphology and physiology of this organ was contradictory and required further investigation. I am greatly indebted to him for advice during the earlier pursuit of this work.

Material.—The description of the comparative gross anatomy of the gland is based on the examination of a number of freshly-caught specimens examined at Plymouth through the kindness of Dr. Allen and the Staff at the Biological Station; also preserved specimens of twenty-six genera of Elasmobranchs from the Natural History Museum Collection, which Mr. Tate Regan kindly put at my disposal. To Professor Cole, I am indebted for a portion of the viscera of a large female *Chlamydoselachus*, to Dr. Esdaile for the loan of Salmon material for comparative study, and to Dr. Shann for the loan of the only male *Lamna* embryo which has been recorded. I also wish to express my sincere thanks to these zoologists and to Professor Boulenger for advice.

HISTORICAL SUMMARY.

The literature dealing with the structure and function of the cæcal gland of Elasmobranch Fishes is somewhat extensive. The early references are naturally fragmentary, while the more recent ones are conflicting and incomplete.

The earliest record of the existence of the gland is probably that in Severini's 'Zootomia Democritæ,' 1645. Professor F. J. Cole has drawn my attention to Severini's figure of the alimentary canal of "*Galeus*" (?), in which the organ is shown attached to a band of "fat," passing through which appears to be an artery reaching to the tip of the gland.

Monro figures it in relation to the other viscera of the Skate in his 'Structure and Physiology of Fishes,' 1785. In his text he refers to it as a secretory gland, but apparently on hypothetical grounds, and in his brief references the terms "appendix digitiformis," "appendix vermiformis," and "cæcum" are used. The first term was obviously used because of the shape of the gland in the Selachians most commonly seen, and this name came into general use during the XIXth Century (Pixell, 1908, attributed the first adoption of this name to Sanfelice in 1888).

The cæcal gland was briefly referred to in the works of the early anatomists, Cuvier, Blainville, Home, Retzius, Rathke, and Owen.

Blainville, in his 'Mémoire sur le Squale pèlerin,' 1811, showed the spongy nature of the gland in this Shark (*Selache maxima*). His was the first investigation of the internal structure.

In 1814, Home gave two figures showing the shape of this organ in *Spinax*. Plate xcvii. in his 'Lectures on Comparative Anatomy' shows that the gland is suspended by mesentery and has an anteriorly-directed duct. He compared the organ with the "bursa Fabricii" of birds and its duct with that of the ink-sac of the Cuttlefish.

The similarity to the bursa in birds was supported in 1819 by Retzius, who adopted the name "bursa cloacæ" for the cæcal gland.

Rathke (1824–27) gave a summary of the earlier descriptions, but added no original observations.

The name "cæcal appendage" was given by Owen in 1846. The first investigations showing the glandular nature of the structure were due to Leydig (1852). By maceration he observed clusters of closely adherent vesicles opening by short ducts and well supplied by blood-vessels. He compared them, both in structure and function, with Brunner's glands. Leydig made a further very interesting observation, which has been attributed to later writers, that in *Chimæra*, where the appendix is absent, the glandular element is contained in the thickness of the walls of the post-valvular intestine.

Hyrtl, in 1853, attributed a totally different function to the gland. He believed it to be an accessory reproductive structure.

Another possible function, that of an urinary bladder, was suggested by Milne-Edwards in 1860.

Some of the earlier references were briefly summarised by Duméril (1865) in his 'Histoire Naturelle des Poissons.' He described the "appendix digitiformis" as occurring near the

origin of the rectum, having a very narrow cavity opening by a narrow canal with a very constricted opening. He considered that the thickness of the glandular walls was so great in proportion to the size of the cavity that not more than half the expected quantity of secretion could be contained. He assumed, therefore, that the gland is very actively secretory.

Turner (1875) described the visceral anatomy of the Greenland Shark, and referred to the presence of the digitiform appendix. He noticed the ovoid shape and the "duct" passing nearly to the distal end, into which "beyond doubt" the gland discharged secretion.

Gegenbaur (1878) gave a diagram of the shape of the gland in *Squatina*.

From this date onwards the cæcal gland has been studied from various standpoints. The most important works are those of Blanchard, Sanfelice, Howes, Crawford, Morgera, and Hoskins.

The first work on the development of the gland and also the first experimental investigations of the physiological importance of the gland were due to Blanchard (1878 and 1882). He examined sections of the embryo of *Acanthias vulgaris* (23 mm. long) and of older embryos of *Mustelus vulgaris* (5·5 and 11 cm.). He arrived at the conclusion that the gland arises as an anlage on the left dorsal wall of the intestine; the parenchyma is of mesodermal origin (all writers except Hoskins have read this as "endodermal") and develops comparatively late in ontogeny, although it is almost completely formed when the embryo is still in the maternal "uterus." He disagreed with Leydig's view that the parenchyma consists of acinous glands, and found that it is composed of compound tubular glands, is surrounded by a connective-tissue envelope, and its duct-opening is guarded by a fold of the mucous membrane of the intestine. Because the gland is not always digitiform, he decided to name it the "glande superanale." His physiological tests showed the presence of ferments of a decided diastatic and emulsifying nature.

Pillet (1885) added to the slight histological knowledge of the adult gland by describing the epithelium of the tubules as "cuboid," with large central nuclei with three or four nucleoli and indistinct cell walls.

In the 'Challenger' Reports, 1887, Günther figured the "rectal" gland with other viscera of *Chlamydoselachus*, but the relative position of the gland is left vague. He stated that it is a globular organ about the size of a large pea, and discharges its secretion into the *cloaca*.

Sanfelice, in 1888, continued the embryological and histological investigations. He found that the gland is of endodermal origin, repeated outpouchings of the intestinal epithelium taking part in the formation of the parenchyma. His conclusions were based on examination of sections of embryos of *Pristiurus* and *Torpedo* (15 mm. and 20 mm. long). He observed that the

central lumen was bounded by "squamous stratified" epithelium, but the epithelium of the primary and secondary tubules differs in *Scyllium* and *Raia*.

The account given by Howes in 1891 in his paper "On the Intestinal Canal of the Ichthyopsida, with special reference to the Arterial Supply and Appendix Digitiformis," was the first to deal with the comparative gross anatomy of the cæcal gland and of a series of similar appendages, possibly of the same origin, occurring in other members of the Ichthyopsida. He described the lumen and duct of the gland in *Chlamydoselachus*, *Heptanchus*, *Cestracion*, *Læmargus*, *Scyllium*, *Zygæna*, *Rhina* (*Squatina*), *Acanthias* (*Squalus*), and *Raia*, and simple diagrams are given of five of these. The greater part of his work concerned the arterial supply of the alimentary canal and its appended glands and diverticula. By a comparison of the superior and inferior mesenteric series throughout the Ichthyopsida, he concluded that the "rectal" gland is supplied by the most posterior artery of the superior mesenteric series, and is therefore the original form of the cæcum coli and vermiform appendix. Howes decided that further investigation was required in two directions: firstly, to find if the cæcum is generally represented in at least the young of Teleostei; and, secondly, to work out the histology and development of the gland, and to study the comparative histology of the cæcum coli and vermiform appendix.

Mazza and Perugia (1894) again described glandular tissue in the wall of the intestine in *Chimæra*.

In 1899, Crawford published a short account of the histology of the "rectal" gland of the Skate. He remarked on the richness of the blood-supply and its peculiar arrangement; he found large sinuses in the central and peripheral regions connected by capillaries. The central lumen epithelium was described as transitional; the "acini" cells of the glandular part showed no peculiar feature and resembled those of kidney. He therefore suggested an excretory function accessory to that of the kidney. This conclusion was supported by tests for urea carried out by Noel Paton on extracts of the gland.

Carazzi (1905) described the arterial system of *Seluche maxima*, and suggested the possibility of a blood function for the cæcal gland.

Sullivan (1907) concluded there is no digestive activity, as extracts of the gland produced no effect on fibrin, starch, and ethyl butyrate. His description of the histology was almost identical in wording to that of Crawford.

A preliminary paper by Pixell (1908) followed, in which she stated she was unable to agree with Crawford in the resemblance of the tubule cells to those of kidney. The absence of lymphatic tissue which is so characteristic of the vermiform process was remarked on, but she considered this to be expected, as Berry (1901) had made the remarkable statement that the Skate has no lymphoid tissue and it is unnecessary in cold-blooded animals.

Pixell repeated Noel Paton's tests for urea with negative results. She agreed with Blanchard in finding a diastatic and an emulsifying ferment.

A preliminary note by Morgera appeared in 1909. He stated very briefly that he supported Howes's hypothesis that the "digitiform" gland is homologous with the vermiform appendix of Man and other mammals. He believed in the identity of the nerve- and blood-supply in the ontogeny of both. The function of the gland he considered is to secrete a substance ("hormone") which accelerates the peristaltic movements of the intestine, thus aiding in defæcation.

This preliminary note was followed in 1915 by a more complete account of this author's work. Following Sanfelice, he described minute secretory granules arranged in rows in the cells of the glandular tubules; he thought these granules were central in position when the cells were active and peripheral during inactivity. Otherwise there is nothing new in his short account of the histology. His paper, like that of Howes, contains a great deal of discussion on the blood-supply of the gland. He used this and the nerve-supply as the basis for establishing a homology with the vermiform appendix of mammals, while Howes confined his comparisons to the cæcum throughout the Ichthyopsida. Morgera stated that the arterial circulation of the gland is derived from the dorsal intestinal artery ("appendicular artery"), which he, in opposition to Howes, considered is homologous with the superior mesenteric artery of mammals. The artery passing to the distal end of the organ (posterior branch of the superior mesenteric series of Howes) he believed to be the inferior mesenteric artery of mammals, and maintained that it is only of secondary importance in the blood-supply of the gland. In the more complete account of his physiological experiments he stated that defæcation was stopped in fishes in which the gland had been extirpated or isolated by distal and proximal ligatures. When an extract of the gland was used to bathe the mucous membrane of the terminal portion of the intestine, or was injected into this region, he found that the valvular and post-valvular intestine contracted, producing regular defæcation in these fishes with ablated cæcal gland. He believed that the physiological value of the secretion of this gland and of the appendix of any Vertebrate is the same.

Hoskins, in 1915, briefly described the development of the digitiform gland in *Squalus acanthias*. In the 'Journal of Morphology,' 1917, he gave a fuller account, together with a description of the post-valvular segment of the intestine. He showed that the anlage of the gland is formed of five or six layers of stratified columnar epithelium. The peculiar method of tubule formation in the gland of this fish was described. He found blood-vessels present from the first, the arterial supply being from a branch (the "digitiform artery") of the dorsal

aorta, which Howes considered to be the posterior branch of the superior mesenteric series. Signs of degeneration were noticed in the adult gland.

E. R. and M. M. Hoskins (1918–19) gave an account of the "Reaction of Selachii to injections of various non-toxic solutions and suspensions and to excretory toxins." The experiments concern the cæcal gland among other organs. Intra-muscular injections of Weed's solution, trypan blue, carmine, and potassium chromate produced undecided effects on the gland; nevertheless, they concluded that the gland reacted as an inefficient excretory organ.

The "rectal" gland was described in an addendum to a paper on "Comparative Morphology of the Secondary Sexual Characters of Elasmobranch Fishes" by Leigh-Sharpe in 1921.

The present position of the knowledge of the cæcal gland leaves work to be done on the gross anatomy, histology, and embryology of the gland, and a great deal of the comparative morphology is untouched. Adequate and accurate diagrams are needed. The conflicting views of Howes and Morgera emphasize the danger of placing too much trust in a comparison of blood vessels for deciding the homology of structures. A much more comprehensive field of observation is required to establish the homology of the cæcal gland with the cæcal diverticula and appendages of higher Vertebrates.

Almost every possible function has been ascribed to the gland, although many of these are merely hypothetical suggestions, and the physiological significance is still in doubt.

There has been no attempt to find if there is any individual or seasonal variation of the cæcal gland.

The Gross Anatomy of the Cæcal Gland in Selachian Fishes.

A large number of freshly-caught and living specimens of *Scyliorhinus* and of *Squalus* were examined at Plymouth, and a detailed account of the macroscopic features of the gland in these two genera will be given.

Scyliorhinus (Scyllium) canicula.

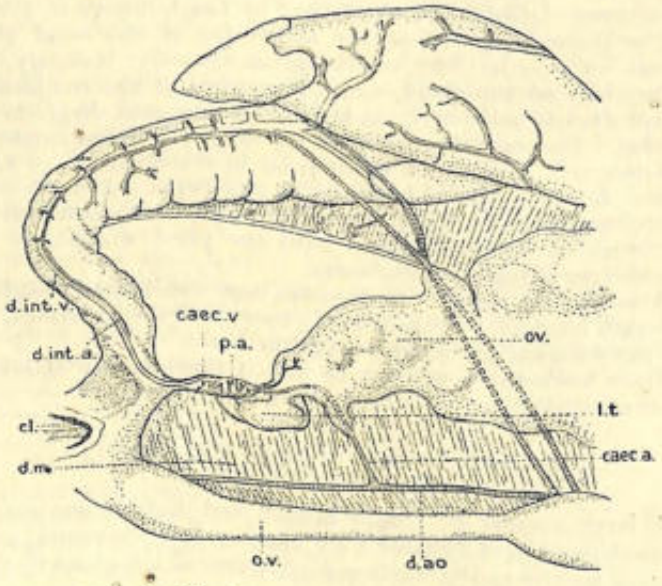
One hundred and twenty specimens, roughly equal numbers of male and female fishes, varying in size from 12 cm. to 72·5 cm. were examined.

The gland is a dorsal diverticulum of the post-valvular intestine displaced to the left and situated nearer to the termination of the spiral valve than to the anus. It is cylindrical, with a blunt distal extremity which is held in an anterior position by a continuation of the mesovarium or mesorchium extending to suspend the gland throughout its length. This mesentery, in the Rough Dogfish, always encloses a mass of lymphoid tissue, which is continuous with the posterior end of the ovary or testis. The

anterior part of the gland is frequently embedded in this lymphoid mass (see text-fig. 1). Splanchnic peritoneum invests the gland.

The colour of the organ is pink or very red, according to the amount of blood present, which varies very greatly in freshly-killed specimens. Frequently the gland looks highly vascular. It has a turgid appearance because of the great development of glandular tissue. In the proximal end of the gland this tissue is absent, and there is a sudden narrowing into a very short and exceedingly narrow duct opening to the intestinal lumen. The orifice

Text-figure 1.



Scyliorhinus (*Scyllium*) *canicula* (60 cm.). Cæcal gland and adjacent viscera. × ½.

cæc.a., cæcal artery; *cæc.v.*, cæcal vein (origin of dorsal intestinal vein); *cl.*, cloaca; *d.ao.*, dorsal aorta; *d.int.a.*, dorsal intestinal artery; *d.m.*, dorsal mesentery of gland; *d.int.v.*, dorsal intestinal vein; *l.t.*, lymphoid tissue; *ov.*, ovary; *ov.*, oviduct; *p.a.*, peripheral branch of cæcal artery.

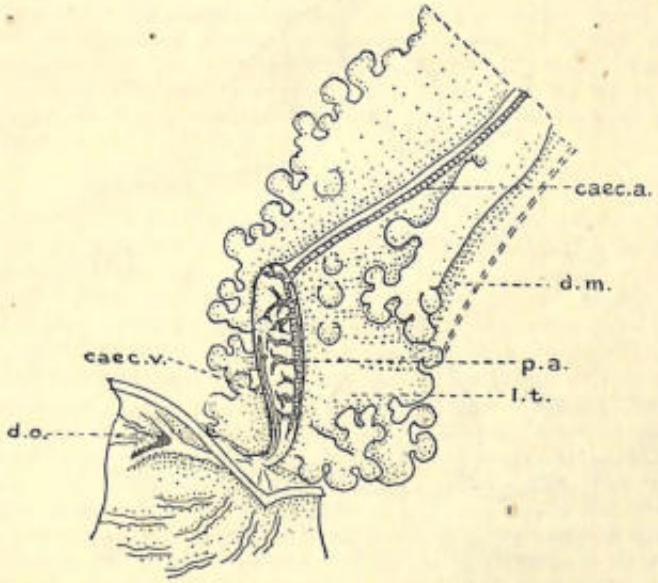
of the duct can be made out with difficulty. It is minute, and is directed toward the spiral valve by a tiny fold of mucous membrane, making a small additional portion of duct out of axis with the primary duct and gland and skirting the inner dorsal wall of the intestine (text-fig. 17). Morgera stated that a valve, similar to the one noticed by Blanchard in *Acanthias*, is sometimes present in *Scyllium*, but it appears to be constantly present, although the additional duct is frequently extremely short. It is

shown by Howes (pl. ii. fig. 11), but he considers it to be formed by an anteriorly-directed fold of the whole intestinal wall; but I find that it arises in ontogeny as a simple duplication of the mucous membrane and underlying connective tissue (see Embryology, p. 179).

The circulation of the gland is interesting, and has given rise to controversy (see Historical Summary, p. 106).

Injected specimens show that it is supplied by the cæcal artery, whose origin from the dorsal aorta is very considerably anterior to the tip of the gland. It passes posteriorly through the mesovarium or mesorchium, and is frequently partially embedded in the lymphoid tissue at the apex of the gland before reaching the organ's distal extremity, or a little below it, on the dorsal side.

Text-figure 2.

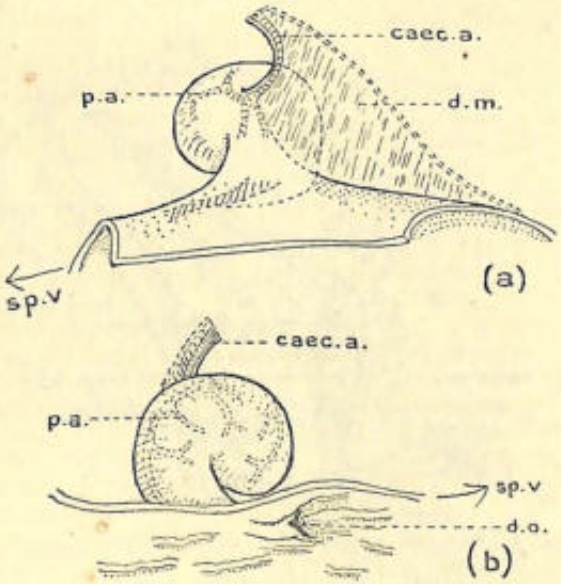


Mustelus vulgaris (40 cm.). × 1.
d.o., orifice of duct of cæcal gland. Other lettering as in text-fig. 1.

It penetrates into and supplies the peripheral envelope of the gland, a main vessel following the dorsal side of the gland in the position of its attachment with the mesentery, giving off numerous branches on both sides almost completely surrounding the gland and sometimes anastomising on the ventral surface. According to Morgera and Diamare this very noticeable artery is a posterior mesenteric artery, and is only of secondary importance to the dorsal intestinal artery (ileo-colic artery of human anatomy) in the blood supply of the gland. Morgera's text-

figure 3 gives a very limited area of supply to the former artery compared with that shown by my injection in *Scyliorhinus*. I have been unable to trace the dorsal intestinal artery passing into the cæcal gland either by injections or in sections of the gland in the embryo and adult. The anterior position of origin of the cæcal artery is used by Howes to support his view that this artery is one of the anterior mesenteric series. Minute arterial branches sometimes pass from the cæcal artery into the lymphoid tissue at the base of the gonad, and I have also observed small arterial and venous branches connecting patches of the lymphoid tissue with the gland. The terminal portion of the intestine posterior to the gland is supplied by two or sometimes three small posterior mesenteric arteries.

Text-figure 3.



Læmargus (68 cm.). × 1. (*a*) to show mesentery; (*b*) to show orifice of duct. *sp.v.*, spiral valve. Other lettering as in text-figs. 1 and 2.

Blood is conveyed away from the gland by the dorsal intestinal vein, which commences in the cæcal gland by large central and several basal peripheral collecting vessels. These unite near the gland duct into a ventral vessel, which follows the forward direction of the duct and then the dorsal wall of the spiral valvular intestine, increasing in size as it receives the encircling factors from this part of the intestine and then passing to the portal system.

When the gland is cut through longitudinally a small lumen is seen extending distally, so that little more than the lateral thickness of glandular substance is left at the apex (text-fig. 17). The lumen is generally oval in transverse sections, and contains a minute quantity of pale yellow substance of viscid nature, which is also sometimes seen at the intestinal orifice of the duct. Sanfelice thought this substance had the same appearance as the semi-fæcal matter mixed with mucus in the terminal part of the intestine, but it seems to be of smoother consistence and is paler in colour. Duméril described it as a bloody liquid, but probably most of the blood he saw in it was caused by extravasation from the venous vessels surrounding the lumen. The lumen is lined by a thin white layer of epithelium, similar to, but thinner than, the mucosa lining the duct and intestine, and immediately under this lie the central blood vessels. The parenchyma of the gland wall is pale pink. After maceration in weak hydrochloric acid (Sanfelice's method), minute racemose tubules are isolated. Peripherally there is a white band of connective tissue, becoming thicker in the duct where the glandular tissue is absent and continuing into the connective tissue of the intestine. Small blood vessels are cut through in this tissue. The whole is enveloped in visceral peritoneum continuous with that of the intestine.

Size of the Gland in Scyliorhinus canicula.

Table I. gives a comparison of the size of the gland and its relative position in the embryo and in older fishes, both in this genus and in *Squalus*.

These figures lead to a suggestion that the gland anlage in *Scyliorhinus* arises considerably nearer the spiral valve than the anus, and that from the first development of a duct orifice it becomes relatively and progressively nearer the spiral valve as the fish grows to maturity. Howes suggested that in young forms the "appendix digitiformis" is situated further forwards than in the adult. The relative length of the post-valvular intestine appears to diminish with the growth of the fish, but this portion of the intestine is difficult to measure, for in the older embryos it is folded in S-shape and in adult fishes there is some variation in its length. In embryos of about 30 mm. in length until several weeks after birth the relative length of the gland is noticeably greater than in the older fishes. I believe that Howes's suggestion that the position of the gland alters during ontogeny may have arisen from this fact and from the relatively greater length of the post-valvular intestine in the embryo. In *Heptanchus*, however, where the gland-duct is simple in the adult as in the embryo, the duct orifice, unlike that of *Scyliorhinus* and *Squalus*, becomes nearer the anus in the adult.

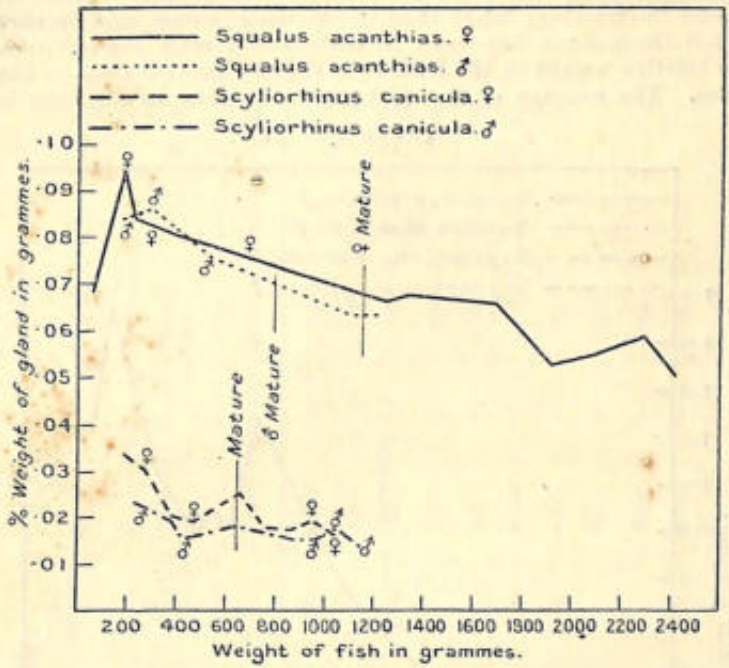
The weight of the gland percentaged for the body-weight in male and female *Scyliorhinus* is shown for fishes of increasing size in Graph 1. In order to reduce the range of individual variation,

TABLE I.

	Scyliorhinus canicula.					*Squalus acanthias.*	
	Mature.	Hatched 2 months.	Embryo.	Embryo.	Embryo.	Mature.	Embryo with large yolk-sac.
Length of fish	600	217	30	21·5	15	812	255
Length of cæcal gland (glandular portion)	14·5	5·25	·9	·34	Only anlage.	47	15
Diameter „ „ (greatest)	4·5	1·0	·2	--	--	7	2
Length of duct free from intestine	4·0	--	--	--	--	9·5	1
„ „ additional duct (adherent portion)	3·0	--	--	--	--	19	2
Total length of duct	7·0	1·5	·42	--	--	28·5	3
Distance from duct orifice to termination of spiral valve	10·0	3·0	·65	·6	·5	8·0	8·5
„ „ „ „ to anus	27·0	5·0	1·9	1·6	1·4	32·0	14·5
Percentage distance from spiral valve (for length of fish)	1·7	2·3	2·1	2·8	3·3	·98	3·3
„ „ „ anus (for length of fish)	4·5	4·7	6·3	7·4	9·3	3·9	5·6

N.B.—All measurements are in millimetres. -- = Too small to measure.

Graph 1.



the average figures for several individuals of approximately the same body-weight have been grouped as shown in the following data:—

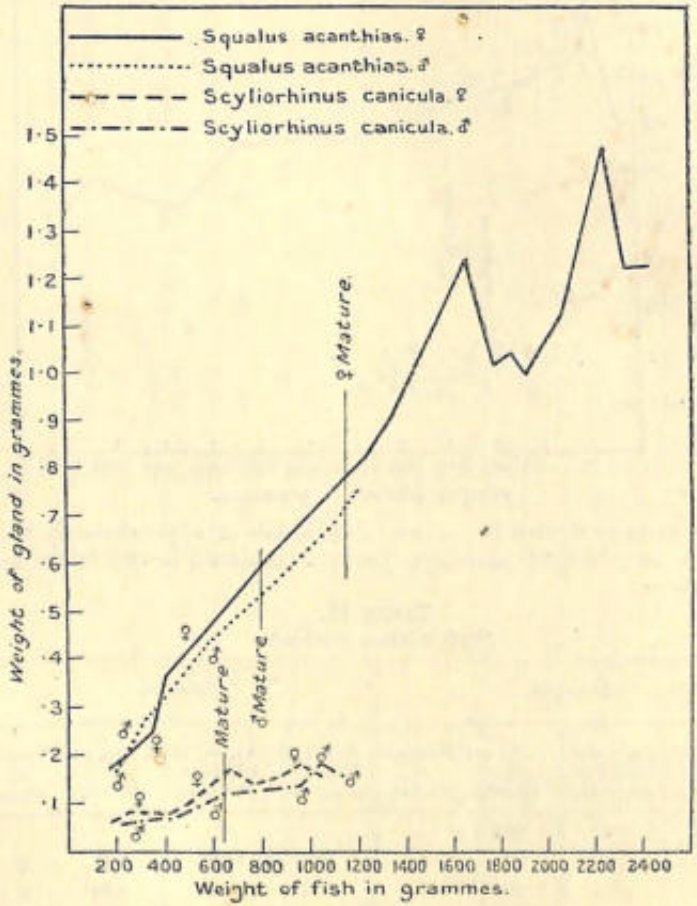
TABLE II.

Scyliorhinus canicula.

Females.				Males.			
Av. wt. of Fishes in grammes.	Av. wt. of Gland in grammes.	Av. % wt. of Gland.	Number of Fishes.	Av. wt. of Fishes in grammes.	Av. wt. of Gland in grammes.	Av. % wt. of Gland.	Number of Fishes.
176	·06	·034	1				
262	·08	·031	1	228	·0525	·023	2
378	·075	·02	2	382	·075	·019	2
475	·09	·01	1	409	·065	·015	2
561	·128	·022	3	—	—	—	—
661	·169	·025	4	632	·12	·018	1
756	·140	·018	5	759	·123	·016	8
861	·151	·017	6	859	·128	·015	8
948	·180	·019	4	962	·144	·015	6
1034	·162	·016	3	1040	·183	·017	2
				1146	·15	·013	2

Graph 1 shows that the percentage weight of the gland is greater in immature fishes than in the mature ones, and appears to fall throughout life both in male and female *Scyliorhinus*. The relative weight in the females is slightly greater than in the males. The average of the percentage weights in all females

Graph 2.



examined is ·019, and in all males it is ·015. When net weights are used instead of percentage weights, ascending curves result (Graph 2), and, as before, the curve for the females is slightly higher than for the males.

Seasonal Variation.

As the weighings were taken from fishes caught in the spring (March and April) and in the autumn (September and October), the two batches have been separated to find if there is any

indication of seasonal variation. Table III. shows the weighings on which Graph 3 is based.

Table III.

Scyliorhinus canicula.

Males.

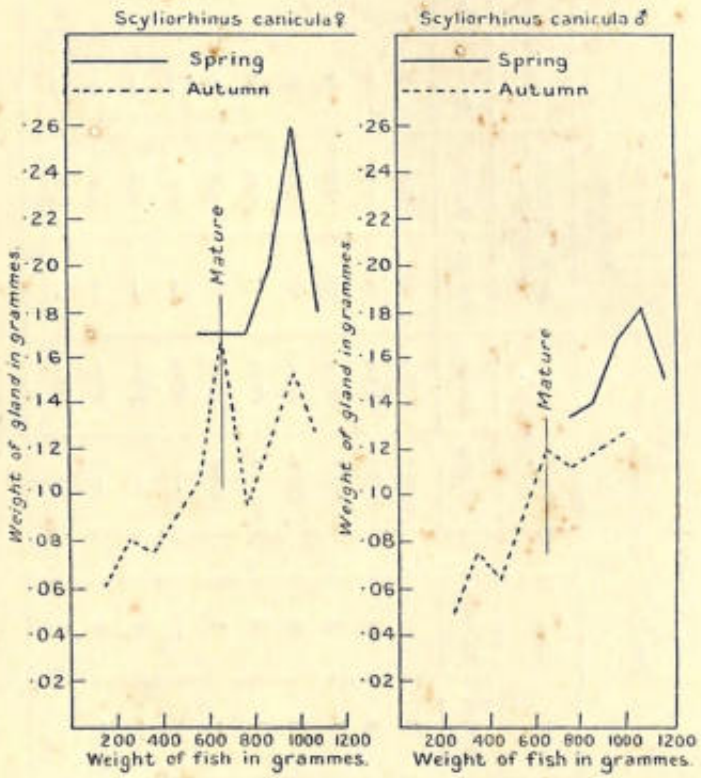
Av. wt. of Fishes in grammes.		Av. wt. of Gland in grammes.		No. of Fishes.	
Spring.	Autumn.	Spring.	Autumn.	Spring.	Autumn.
1100+	—	·15	—	2	—
1000+	—	·182	—	2	—
900+	900+	·168	·126	5	1
800+	800+	·142	·118	2	5
700+	700+	·134	·113	4	4
—	600+	—	·12	—	1
—	—	—	—	—	—
—	400+	—	·065	—	2
—	300+	—	·075	—	2
—	200+	—	·052	—	2

Females.

Av. wt. of Fishes in grammes.		Av. wt. of Gland in grammes.		No. of Fishes.	
Spring.	Autumn.	Spring.	Autumn.	Spring.	Autumn.
1000+	1000+	·18	·125	2	1
900+	900+	·26	·153	1	3
800+	800+	·20	·126	2	4
700+	700+	·17	·095	3	2
600+	600+	·17	·165	3	1
500+	500+	·17	·107	1	2
—	400+	—	·09	—	2
—	300+	—	·075	—	2
—	200+	—	·08	—	1
—	100+	—	·06	—	1

Graph 3 gives some indication that the cæcal gland is slightly heavier in spring than in autumn in both male and female *Scyliorhinus*, but undoubtedly data are required in many more

Graph 3.



fishes to establish this seasonal variation. It must be noted that no allowances have been made for the variation in weight of the reproductive organs and their products in mature and immature fishes at different times of the year. If such were made, the difference in relative weight of the gland in mature male and female fishes and in spring and autumn weights would probably be greater. (It has been shown by Ford that egg-deposition in *Scyliorhinus* occurs chiefly during spring and summer, and is at its minimum during autumn.)

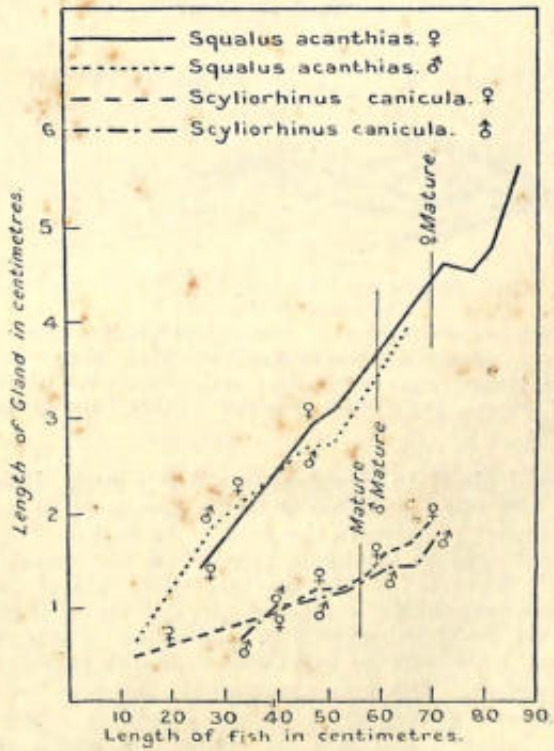
The length and other variable dimensions of the gland were measured in one hundred and twenty fishes. For Graph 4 the figures given in the following table were plotted in order to compare the length of the fish with the length of the cæcal gland :—

TABLE IV.

Scyliorhinus canicula.

Length of Fishes in mm.	Average length of Gland in mm.		Number of Fishes.	
	Females.	Males.	Females.	Males.
700+	20	17·8	1	4
650+	16·9	14·6	10	14
600+	15·8	14·8	16	16
550+	13·9	13·2	11	4
500+	12·0	11·7	4	3
450+	11·9	10·9	4	8
400+	10·3	10·3	9	8
350+	9·3	9·5	4	2
300+	—	7·0	—	1
100+	4·9	—	2	—

Graph 4.



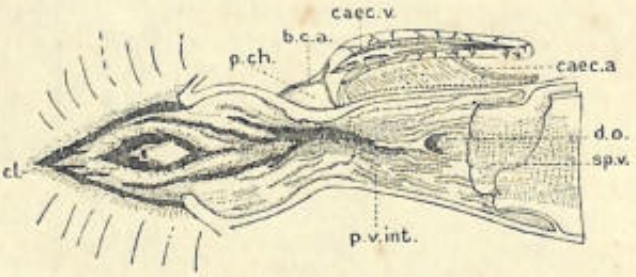
This graph shows that the organ is somewhat longer in females than in males, and the small difference is probably worthy of note when it is remembered that Graphs 1, 2 and 3 show a similar difference in the weight of the gland.

In *Scyliorhinus stellaris* (*catulus*) the gland is slightly larger, with a slightly longer portion of duct adhering to the internal dorsal wall of the intestine; the duct orifice is more noticeable. The cæcal artery frequently divides into two branches before reaching the dorsal surface of the gland, one branch passing to the apex of the gland, and the other to the middle of it.

SQUALUS ACANTHIAS.

Twenty-seven female and eleven male Spur Dogfish were examined. They ranged from 13 cm. (uterine embryos) to 87 cm. in length. Blanchard and Hoskins have given some account of the macroscopic as well as of the histological features of the gland in this fish, and Hoskins has figured the gland of the late embryo. It is necessary to compare the gross anatomy of the gland with that of *Scyliorhinus*, and to add what is new from an examination of a number of freshly-killed fishes.

Text-figure 4.



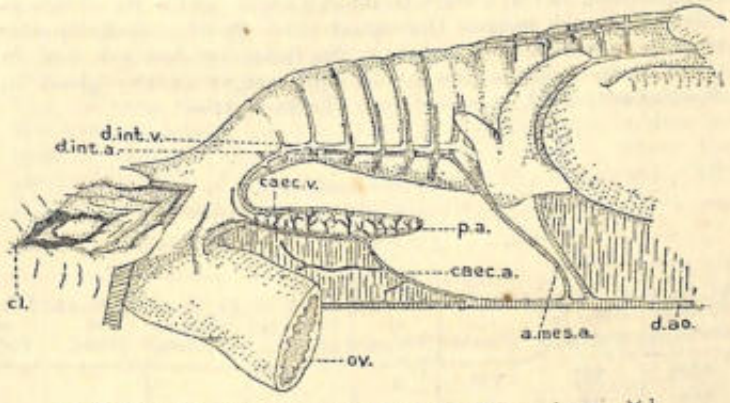
Squalus acanthias (86 cm.). Cæcal gland opened to show lumen, intestine opened to show duct orifice. × ½.

b.c.a., branch of cæcal artery to intestine; *pch.*, deep pouch of post-valvular intestine; *p.v.int.*, post-valvular intestine. Other lettering as in previous figures.

The cæcal gland in *Squalus acanthias* is large, digitiform, and arises in the same situation as in *Scyliorhinus*; it is frequently in a mid-dorsal position in the adult. In mature females carrying the ovoviparous young it is crushed between the enlarged "uterine" portions of the two oviducts. (Hoskins says that it is characteristically displaced to the right from an early stage in its development.) The suspension of the organ from the dorsal body-wall is markedly different from that in the Rough Dogfish. The dorsal mesentery suspends the gland with its artery and that portion of the intestine posterior to this viscus exclusively, and has no connection whatever with the

gonad mesentery, which terminates in a more anterior position in the cœlom than in *Scyliorhinus*. Another outstanding feature is the absence of lymphoid tissue near the gland. It is buff-coloured, with the rich supply of superficial blood-vessels showing clearly. The organ tapers anteriorly, and is always somewhat flattened laterally. The cæcal artery has relatively a much more posterior origin than in *Scyliorhinus*. It follows the free border of the mesentery, and may bifurcate before reaching the gland or pass straight to it less than one-third from its tip, where it gives rise to anterior and posterior dorsal branches, which have bilateral ramifications passing fairly completely over the periphery and sometimes uniting on the ventral surface of the gland, as Hoskins noticed. In injected specimens a basal arteriole of the gland may be seen to extend beyond the duct of the gland

Text-figure 5.



Squalus acanthias (81 cm.). Cæcal gland and adjacent viscera. × ½.
Lettering as in text-fig. 1.

to the intestinal wall (see text-figs. 4 & 5). It is important to notice that the venous system seems to be exclusively central, except near the duct, and the arterial and venous systems are more distinctly separated than in *Scyliorhinus*. A large branched sinus, seen when the gland is cut longitudinally, distends the lumen epithelium, causing definite ridges bulging into the lumen in injected specimens (text-fig. 4). Depressions are seen in the surface of the lumen which lead to the primary tubules of the glandular substance. The duct leads excentrically and anteriorly to skirt the intestinal mucosa of a dorsal pouch of the post-valvular intestine, as shown in text-fig. 4. The portion of the duct formed by the fold of mucosa takes exactly the same direction as the dorsal intestinal vein; it is very much longer than in *Scyliorhinus*, and opens very near the termination of the spiral valve by a much wider aperture, although still small. Frequently furrows with a central gutter in the mucous membrane lead from

the orifice towards the spiral valve (text-fig. 4). All these points concerning the duct lead one to suppose that there is some special reason for careful conduction of the viscid liquid of the gland towards the posterior end of the spiral valve. Blanchard first noticed the presence of valve-like folds of mucous membrane preventing the entrance of fæcal matter into the duct, but there are never two valves as he suggests. The substance contained in the gland and sometimes in the duct looks similar to that found in *Scyliorhinus*, but because of the much greater size of the gland it is of quite perceptible quantity.

Size of the Gland.

Comparative measurements of the gland and of its position in the embryo and adult *Squalus* are given in Table I., so that they can be compared with those for *Scyliorhinus*. It will be seen that these figures suggest the same conclusions as in *Scyliorhinus*, but the duct is much longer, while its orifice is relatively much nearer the spiral valve in the adult *Squalus* than in the adult *Scyliorhinus*. The following data are used in Graph 1 to compare the percentage weight of the gland in *Squalus* with that in *Scyliorhinus* (Table II.):—

TABLE V.

Squalus acanthias.

Females.				Males.			
Av. wt. of Fishes in grammes.	Av. wt. of Gland in grammes.	Av. % wt. of Gland.	Number of Fishes.	Av. wt. of Fishes in grammes.	Av. wt. of Gland in grammes.	Av. % wt. of Gland.	Number of Fishes.
*35·5	·037	·068	4				
180	·17	·094	1	195	·165	·084	1
220	·185	·084	1	288	·25	·086	3
385·5	·311	·08	3	559	·432	·075	2
831	·613	·073	3				
1252	·835	·066	1	1105	·70	·063	1
1339	·903	·067	2	1200	·76	·063	1
1720·5	1·135	·065	2				
1852	1·043	·056	3				
1913	·998	·052	2				
2076	1·133	·054	2				
2290·5	1·351	·058	3				
2418	1·23	·050	1				

* Fœtus with umbilical scar just healed.

The graph shows that the fæcal gland is relatively much heavier than in *Scyliorhinus*. The percentage weight increases

after birth and then falls throughout life, as in *Scyliorhinus*. The average weight of the gland percentaged for the body-weight in all female *Squalus* weighed is ·066, for mature females it is ·057, and for immature females ·08. In male *Squalus* only two mature fishes were obtainable, and the percentage weight is ·08 in immature and ·063 in mature males. It is interesting to compare these figures with those obtained by Kearney for *Mustelus vulgaris* in his investigations on the embryonic and post-natal relative growth of the viscera. He found that, in common with most organs, it is relatively heavier in the embryo than after birth, decreasing from ·105 per cent. body-weight in the embryo to ·032 per cent. at birth (Kellicott ·0398 per cent.) and increasing to ·046 per cent. shortly after birth, thereafter decreasing to ·022 per cent. in fishes weighing 1499 grammes. In a mature female *Mustelus vulgaris* weighing 3250 grammes the writer found the percentage weight of the gland to be ·018. *Mustelus*, therefore, seems to have a gland intermediate in weight between that of *Squalus* and *Scyliorhinus*. Graph 1 gives an indication of a low percentage weight immediately previous to birth, with a rise after birth followed by a decrease throughout life for *Squalus*. As in *Scyliorhinus*, the average weight of the organ is slightly more in females than in males. This is also shown in Graph 2, where the absolute weight of the fishes and glands are compared. The following are the data for comparison shown in Graph 4:—

TABLE VI.

Squalus acanthias.

Length of Fishes in mm.		Average length of Gland in mm.		Number of Fishes.	
Females.	Males.	Females.	Males.	Females.	Males.
863	—	56·5	—	2	—
815	—	48	—	8	—
783	—	45·5	—	3	—
719	720	43·4	45·5	4	1
631	650	39·5	40	3	1
510	550	31	31	1	2
470	450	29·3	27	3	3
408	—	25	—	2	—
*250	275	14	18·6	1	1
—	130	—	·65	—	1

* "Fœtus" with small yolk-sac.

Graph 4 shows that the cæcal gland in *Squalus* is more than twice the relative length in *Scyliorhinus*. It increases in length

up to maturity, and afterwards shows variability. The graphs appear to indicate that the organ is slightly larger in the female than in the male, but it must be remembered that the males of *Squalus* mature earlier than the females (Ford). Bearing in mind these indications in *Scyliorhinus* and *Squalus*, it is curious that in nine female and nine male specimens of *Mustelus* averaging 73 cm. long, examined by Hoskins, the gland averaged 23·5 mm. in length in the females and 22·5 mm. in the males, if this difference is merely normal variability as he suggests.

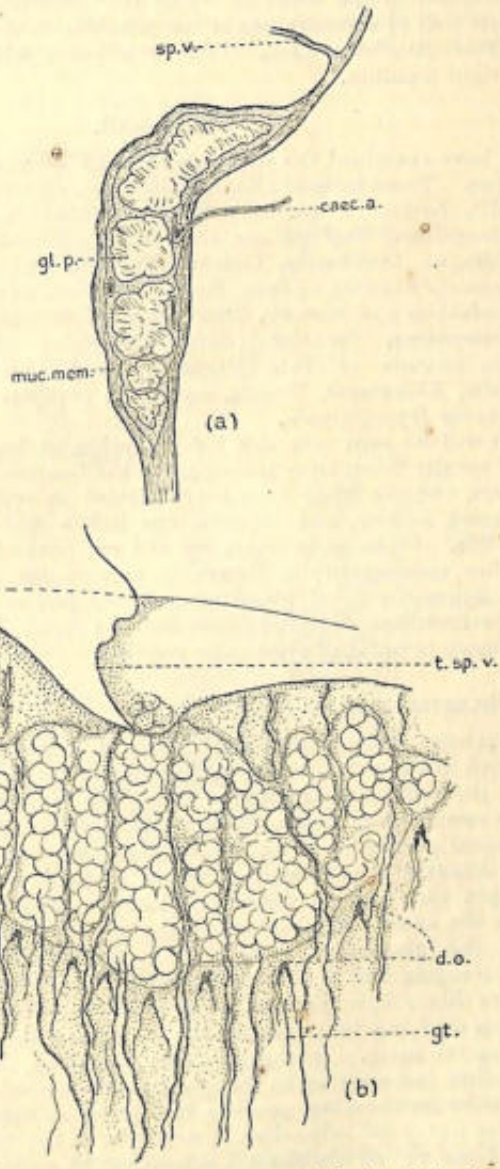
Unfortunately all the *Squalus* were examined in autumn, so there are no data for judging the possibility of seasonal variation in this genus.

The Cæcal Gland in other Selachii.

(*a*) Holocephali.

Chimæra has a patch of glandular substance in the dorsal wall of the post-valvular intestine which may be the cæcal gland in its original form. The presence of tissue in *Chimæra* similar to the glandular substance of the cæcal gland was first noticed by Leydig in 1852, and described somewhat incompletely by Mazza and Perugia in 1894. Apart from these two references, there seems to be no information concerning the disposition of the glandular tissue in the terminal portion of the intestine of this fish. There is a considerable patch of this tissue beginning at, or a little posterior to, the termination of the well-developed spiral valve and extending to within a short distance from the cloacal opening of the short post-valvular intestine. In a fish measuring 62 cm. in total length this portion of the intestine was cleared in winter-green oil after benzole (text-fig. 6 *b*); the glandular substance is 20 mm. in length, the posterior termination of it is 1·2 cm. from the anus, and it extends more than half-way round the intestine, tapering laterally. The thickness of the tissue in the wall is 4·5 mm. (text-fig. 6 *a*). This tissue was present in the three fishes examined, but it varied in extent; an irregular bulging of the mucous membrane of the intestine marked its limits. The cleared specimen shows the glandular tissue divided into nine more or less definite patches with longitudinal ridges separating them; the patches are again subdivided into lobes, giving a nodular appearance. Where this tissue terminates posteriorly there are small pocket-like openings into the intestinal cavity in the furrows between the longitudinal ridges of mucous membrane (text-fig. 6 *b*). A seeker will only push a short distance into these openings, which I find were pointed out as the efferent ducts by Mazza and Perugia. It appears, therefore, that in *Chimæra* a group of tubulo-acinar (alveolar) glands with their apices anteriorly placed and their efferent ducts posteriorly placed, occur in the intestinal wall in the same region as the cæcal gland in other Selachian Fishes. Histological details are given later in this paper.

Text-figure 6.



Chimæra (62 cm.). (*a*) Longitudinal section of post-valvular intestinal wall. × 1⅔.
(*b*) Cleared portion of post-valvular intestine seen from internal surface. × 1⅔.
gl.p., glandular portion; *gt.*, gutter: *muc.memb.*, mucous membrane; *t.sp.v.*, termination of spiral valve. Other lettering as in previous figures.

It is important to notice that an artery, which appears to correspond to the cæcal artery of the Euselachii, passes to the dorsal wall of this segment of the intestine to the central portion of this glandular mass. This is a point which has escaped previous mention.

(*b*) Euselachii.

I have examined the cæcal gland in 26 genera of Euselachian Fishes. These include *Chlamydoselachus*, *Heptanchus* (fœtus and adult), *Lamna* (fœtus and adult), *Mitsukurina*, *Ginglymostoma*, *Chiloscyllium*, *Scyliorhinus* (*Scyllium*) (*canicula* and *stellaris*), *Pristiurus*, *Carcharias*, *Galeus*, *Mustelus* (*vulgaris* and *lævis*), *Zygæna* (*Sphyrna*), *Spinax*, *Cestracion*, *Squalus* (fœtus and adult in *acanthias* and *lebruni*), *Centrophorus*, *Læmargus*, *Echinorhinus*, *Pristiophorus*, *Squatina* (*Rhina*) belonging to the Suborder Pleurotremata of Tate Regan's classification; and *Torpedo*, *Pristis*, *Rhinobatus*, *Trygon*, and *Raia* (various species) of the Suborder Hypotremata.

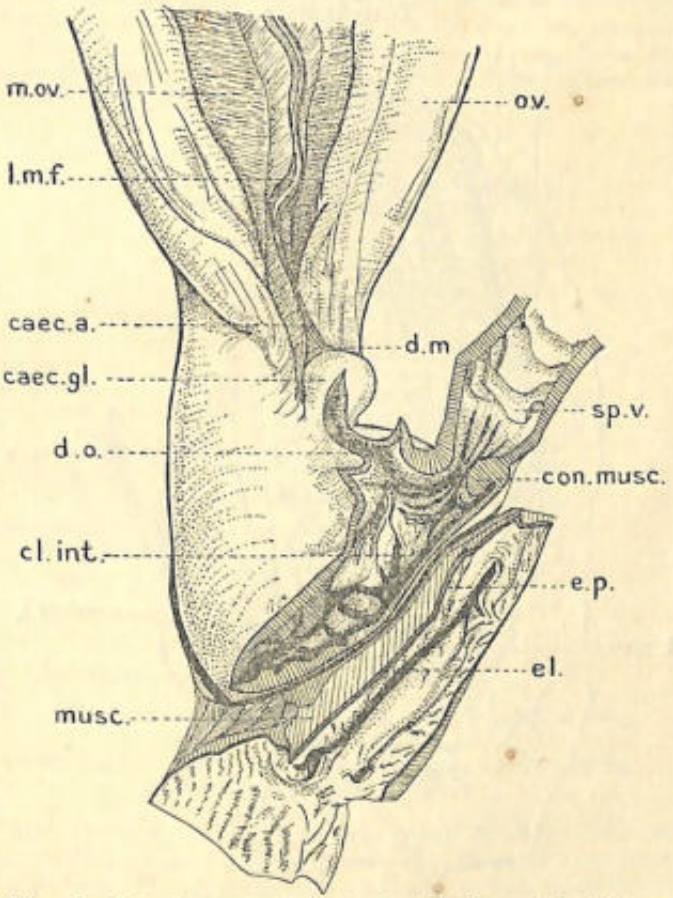
It will be seen that this list comprises at least one member, and usually more, from almost all of the families of the two sub-orders, and the fishes have been selected to represent as widely different feeding and reproductive habits and distribution as possible. In order to follow up and verify the few comparative studies commenced by Howes, it seemed desirable to describe and figure the cæcal gland in as many genera as possible, so that correlations and conclusions could be made. The descriptions are made in order of systematic position.

Chlamydoselachus anguineus.

Text-fig. 7 shows the cæcal gland of a female 165 cm. long, opened to show the lumen and communication with the intestine and the positional relation of the gland with the other viscera. It is small and globular, and is a mid-dorsal diverticulum of the terminal portion of the post-valvular intestine. This portion of the intestine is extremely short, so that the gland-duct seems to open very near to the anus, although it is actually 2·3 cm. from the anus. This portion of the intestine is dilated dorsally, and the gland-duct runs in the much-thickened intestinal wall merging into the common wall of the oviducts. The figure shows this unique position. The intestinal opening of the short simple duct is a little nearer the anus than the termination of the spiral valve. In the specimen examined the post-valvular intestine just anterior to the cæcal gland has undergone marked muscular contraction, so that the gland orifice appears to be nearer the spiral valve than it would be in the dilated condition. The distal end of the gland is suspended by a very narrow dorsal mesentery, which is not continuous with that of the gonad. There are two small lateral folds of mesentery at the sides of the gland mesentery, slightly thickened by lymphoid tissue.

The cæcal artery passes in the peritoneal fold supporting the gland almost along the free edge, and passes to the top of the gland. The cavity of the gland is fairly large, and is slightly flattened laterally. The organ is 1·4 cm. long, and its greatest

Text-figure 7.



Chlamydoselachus (165 cm.). Cæcal gland and intestine opened. × $\frac{2}{3}$.
caec.gl., cæcal gland; *cl.int.*, position of cloacal opening of intestine; *con.musc.*, contracted muscle; *ep.*, epidermis; *l.m.f.*, lateral mesenteric fold; *m.ov.*, mesentery supporting oviduct. Other lettering as in previous figures.

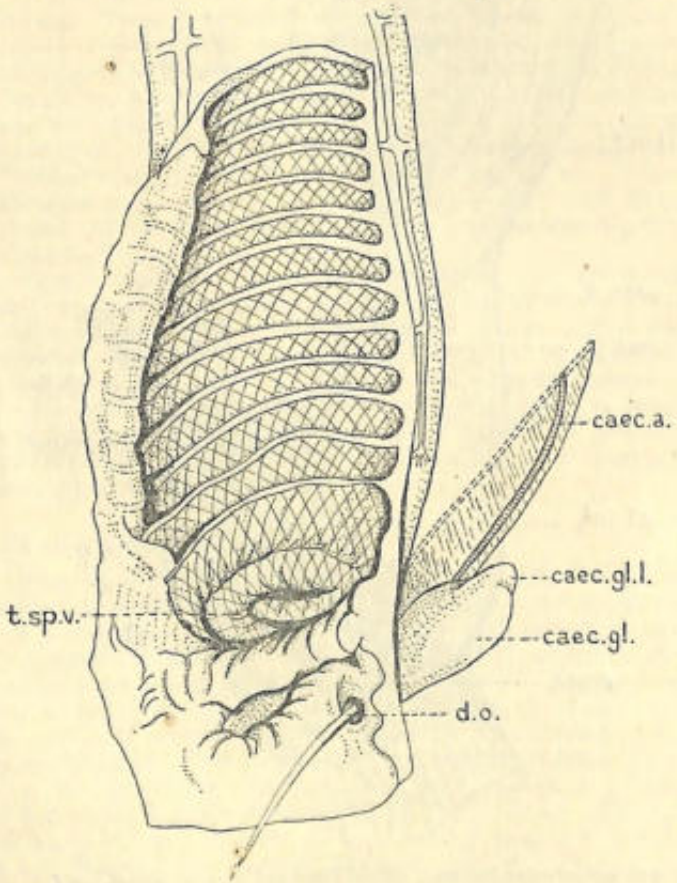
diameter is 1·3 cm.; the glandular tissue is about 3 mm. thick from periphery to central lumen; the duct is 1 cm. long.

The cæcal gland of this fish was first described by Günther in the 'Challenger' Reports. In a *Chlamydoselachus*, 4 ft. 10 ins.

long, he found it the size of a large pea, discharging its secretion by a short duct into the "cloaca." In fig. lxv. he shows the "rectal" gland, but its position in relation to the other viscera is left vague.

Howes stated that the organ is situated further back than in any other Selachians, and correlates this position with the gland

Text-figure 8.



Heptanchus (83 cm.). Intestine opened. × 1⅓.
cæc.gl.l., second lobe of cæcal gland. *d.o.*, bristle in duct opening of gland.
Other lettering as in previous figures.

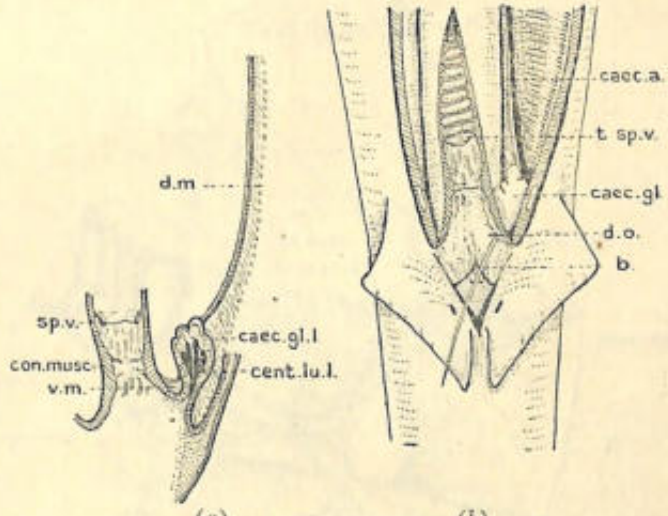
being the smallest known. I cannot agree with him, as I consider there are cæcal glands in a similar position and others with relatively much less glandular tissue. The globular shape of the gland must be taken into account.

HEPTANCHUS CINEREUS.

This genus is interesting to compare with *Chlamydoselachus*, as both belong to the primitive division Notidanoidei.

The description of the gross anatomy of the cæcal gland in *Heptanchus* is based on the examination of two young fœtuses 7·5 cm. and 13·8 cm. long, the smaller one supplied from Naples and the larger from the Natural History Museum Collection; a fœtus 25·5 cm., with the yolk-sac almost absorbed, obtained from Naples; and two older fishes—one 75 cm. from the Museum Collection, and one 83 cm. from Naples. These five fishes were all females.

Text-figure 9.

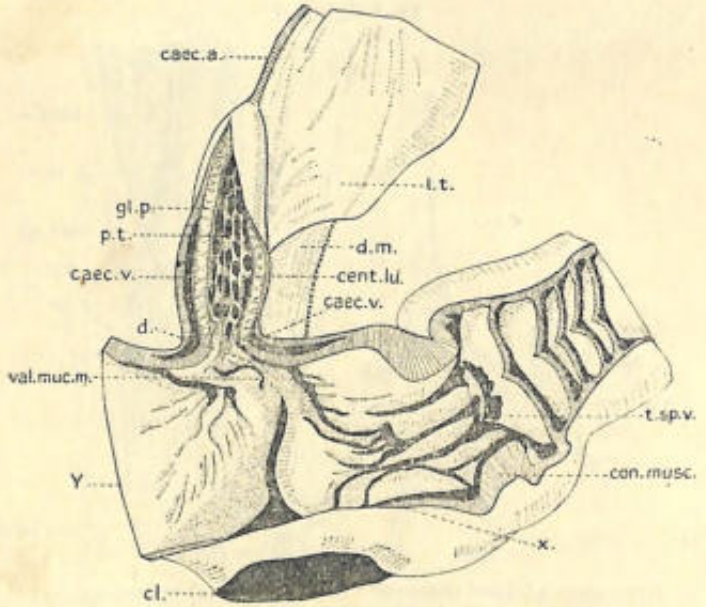


Heptanchus (advanced embryo 25·5 cm.). × 1⅓. (*a*) sagittal section; (*b*) gland and adjacent viscera.
b, bristle; *cent.lu.l.*, central lumen of gland lobe; *v.m.*, ventral mesentery.
Other lettering as in previous figures.

As text-figs. 8, 9, and 14 show, the gland is lobed, the lobes varying in distinctness and in number; two, three, or four lobes may be present. In all cases it is displaced to the animal's left side. In the smallest fœtus its intestinal orifice is about half-way between the anus and the termination of the spiral valve, but in the fishes 13·8 and 25·5 cm. long and in the larger fishes it is relatively nearer the anus. As in *Chlamydoselachus* the post-valvular intestine is very short, and in the two older fishes there is a dilation immediately above the intestinal opening of the duct, with a muscular contraction of the wall of the intestine between the pouch and the spiral valve termination. The suspending dorsal mesentery is small and simple as in

Chlamydoselachus, and the cæcal artery skirts the free border of the mesentery to enter near the anterior end of the gland. There is a small ventral peritoneal fold connecting the dorsal wall of the intestine with the proximal portion of the organ. In the fish 75 cm. long the gland and related parts were cleared in winter-green oil after injection of the lumen, and this specimen showed the dorsal intestinal vein commencing near the central lumen at the base of the gland and passing to the intestinal wall through the small mesentery mentioned (text-fig. 14). The

Text-figure 10.



Mitsukurina (189 cm.). Cæcal gland and intestine opened. Y, cut edge turned back away from X. × ½.

cent.lu., central lumen; *d.*, primary duct of gland; *p.t.*, primary tubule; *val. muc.mem.*, valve-like fold of mucous membrane. Other lettering as in previous figures.

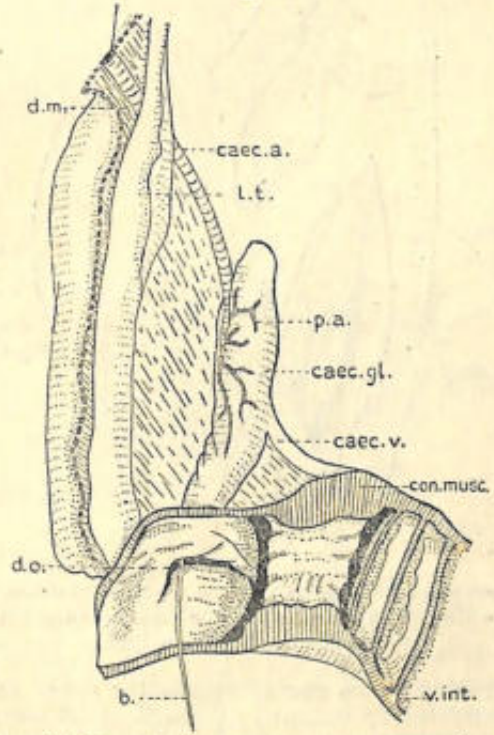
gland-duct is short and simple, of very minute diameter in the smaller fishes, while in the larger fishes a thick bristle will pass through. In the transparent gland mentioned above it is seen that the duct passes immediately into a double gland lumen, so that this viscus appears like two adhering racemose glands. Sections of the glands of smaller fishes show this division of the lumen and glandular substance to be a characteristic feature in this genus.

I am unable to agree with Howes, who figured and described the gland of this fish with a duct of "maximum attenuation." In a fœtus 15 cm. long he described the duct as "much shorter and relatively wider than in the adult, and not bound down to the intestinal wall," as he showed it in the adult gland in his diagram on pl. ii. His figure corresponds with the condition I have described in *Squalus*.

MITSUKURINA.

This specimen, which I examined at the Natural History Museum, was immature and was a male measuring 189 cm. in length. (*Mitsukurina* is most interesting because it may be

Text-figure 11.



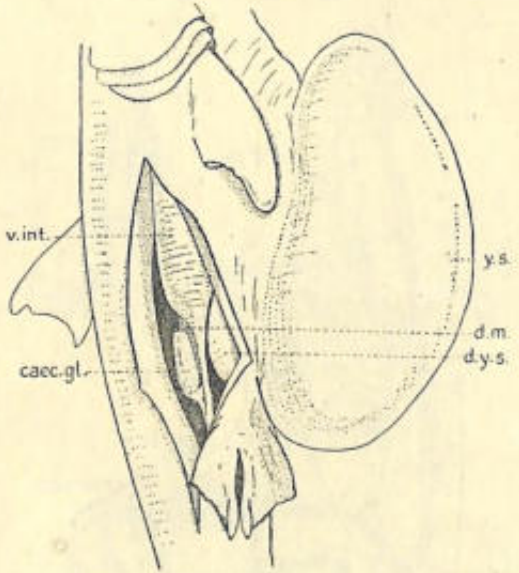
Lamna spalanzanii (70·5 cm.) Intestine opened to show opening of gland-duct. *e.int.*, valvular intestine. Other lettering as in previous figures. × ⅔.

synonymous with the Upper Cretaceous *Scapanorhynchus* generally believed to be extinct [Smith-Woodward (1899)]. Bashford Dean believes in its very close relationship to *Odontaspis*, but

retains the name *Mitsukurina* because fossil characters are still so imperfectly known. Tate Regan (1906) calls it *Scapanorhynchus owstoni*.)

The cæcal gland of this Elphin Shark is the largest, in relation to the size of the fish, of all those I have examined (taking the three variable dimensions of length and greatest and shortest diameter into account). It is digitiform, is displaced to the animal's right side, and appears to lie very near to the anus as in *Chlamydoselachus* and *Heptanchus* (text-fig. 10). The post-valvular intestine is exceedingly short, and its muscular wall is greatly contracted immediately posterior to the termination of the spiral valve. Deep furrows in the mucous membrane pass from the

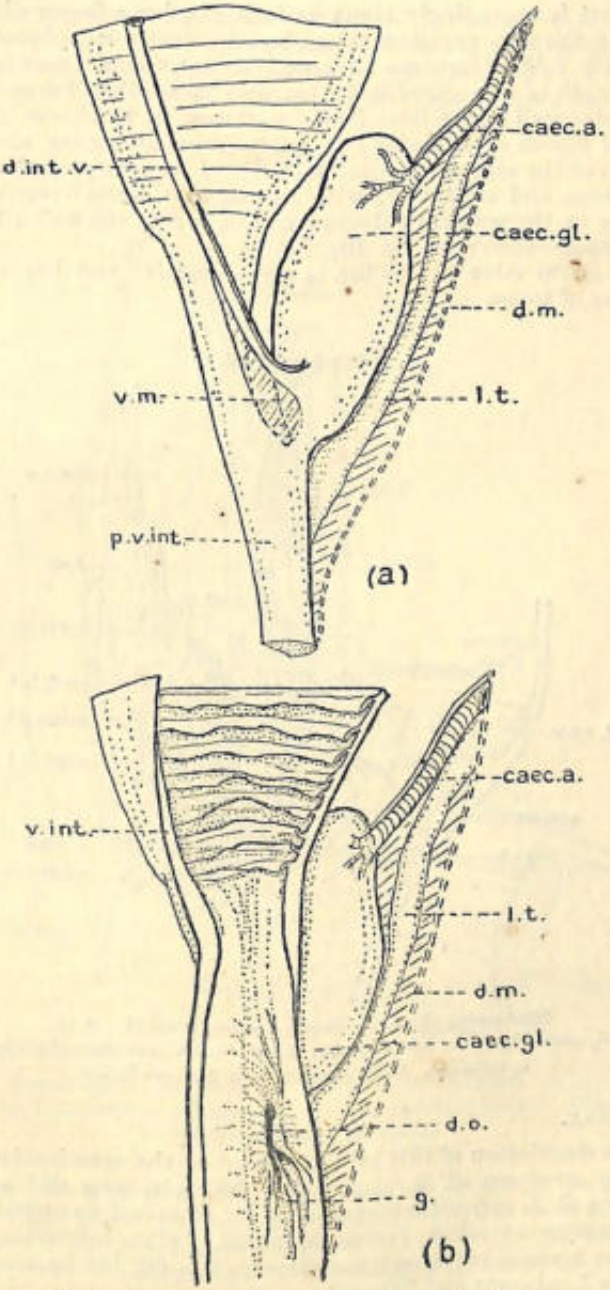
Text-figure 12.



Lamna cornubica (embryo 35 cm.) Gland in relation to viscera. × ½. *d.s.y.*, dorsal surface of yolk stomach; *y.s.*, yolk stomach. Other lettering as in previous figures. (See Shann, 1923.)

intestinal opening of the gland towards the spiral valve. The gland is suspended by mesentery throughout its entire length. This dorsal mesentery carries an enormous fold of lymphoid tissue, which is closely applied to the dorsal side of the gland except in the proximal quarter of it. The mesentery and lymphoid tissue pass directly to the gonads. The cæcal (dorsal mesenteric) artery is prominent at the free border of the mesentery, and passes to the extreme tip of the gland. A large vein extends from the middle of the length of the gland to the dorsal intestinal vein.

Text-figure 13.

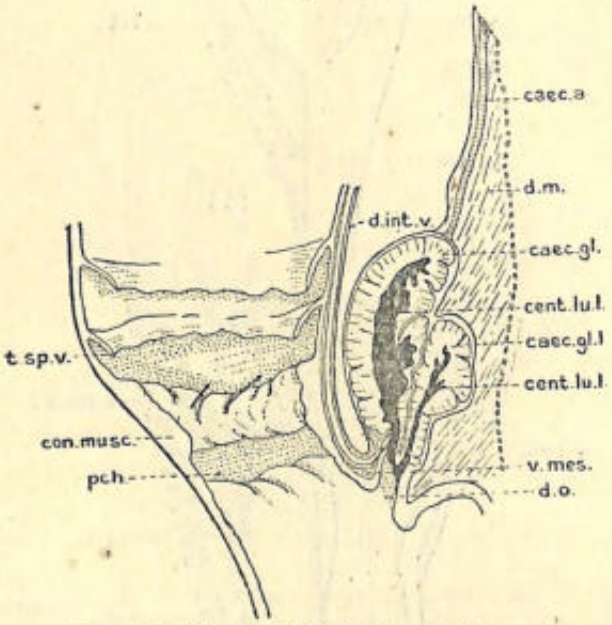


Lamna cornubica (embryo 35 cm.). (*a*) dorsal view of gland; (*b*) ventral view with intestine opened to show duct orifice. *g.*, groove. Other lettering as in previous figures. × 2½.

The duct is exceedingly short and simple, has a larger diameter than in the two previous fishes, but its orifice is reduced by a posterior fold of mucosa directing it anteriorly (text-fig. 16). The length of the gland is 6·2 cm. and its width is 1·6 cm. The glandular wall varies from 5 mm. to 8 mm. in thickness, and the central lumen of the gland is fairly large, extending almost to the tip of the organ. Villus-like folds of mucosa projecting into the lumen and connecting with one another, leave irregular pits leading to the primary tubules between, giving the wall a honeycomb appearance (text-fig. 10).

The spiral valve of this fish is very extensive and has a large number of turns.

Text-figure 14.



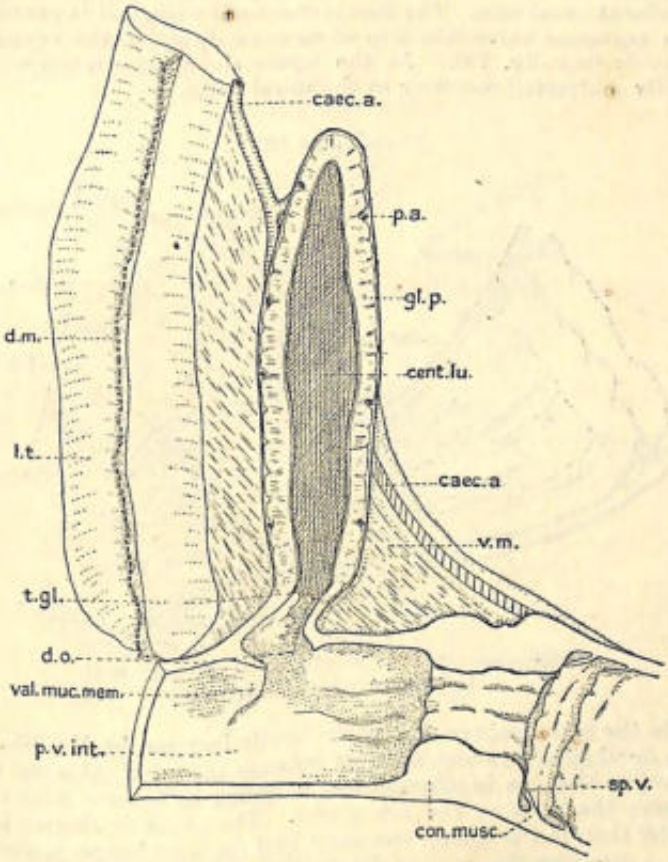
Heptanchus (75 cm.). Sagittal section of gland. × 1½.
cent.lu.l., central lumen of lobe of gland; *v.mes.*, ventral mesentery attaching gland to intestine. Other lettering as in previous figures.

LAMNA.

The description of this genus is based on the examination of a female specimen of *L. spalanzanii* 70·5 cm. long and a male embryo of *L. cornubica* 35 cm. long. I have had no opportunity to examine an adult Porbeagle Shark. (The interesting and unique mode of embryonic nutrition in this fish has been pointed out by Lohberger and Shann.)

In the female specimen the cæcal gland is similar in shape and postion to that of *Mitsukurina* (text-fig. 11). The gland is 4·9 cm. long, and its greatest and shortest diameters are 1·1 cm. and ·6 cm. respectively. The size, bearing in mind the three

Text-figure 15.

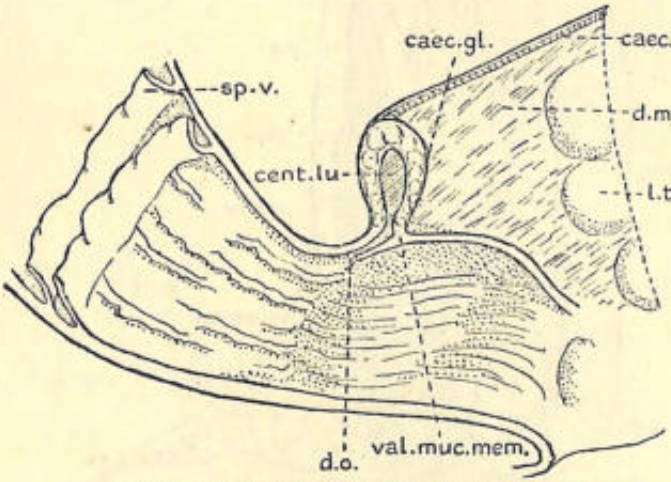


Lamna spalanzanii (70·5 cm.). Sagittal section of gland. × 1½. *t.gl.*, termination of glandular portion; *v.m.*, ventral mesentery. Other lettering as in previous figures.

variable dimensions of the gland and the length of the fish, is large, although smaller than in *Mitsukurina*. The post-valvular intestine is still short as in Notidanoids and in *Lamna*, and the gland is near the anus. The dorsal suspending mesentery of the gland is continuous with that of the gonad as in *Mitsukurina*,

and there is a large fold of lymphoid tissue lying close to the dorsal attachment of the mesentery and extending as far as the anus. The cæcal artery is large, and passes through the lymphoid fold of the gland mesentery to 1 cm. from the apex of the organ, and forms distinct branches over the surface of the gland. There is a small ventral mesentery extending half-way up the gland across to the dorsal wall of the intestine, carrying the very prominent cæcal vein. The duct is short and wide, and is guarded by a posterior valve-like flap of mucosa directing the opening forwards (text-fig. 15). As the figure shows, the intestine is greatly contracted posterior to the spiral valve.

Text-figure 16.



Chiloscyllium (38 cm.). Sagittal section of gland. × 2½.
Lettering as in previous figures.

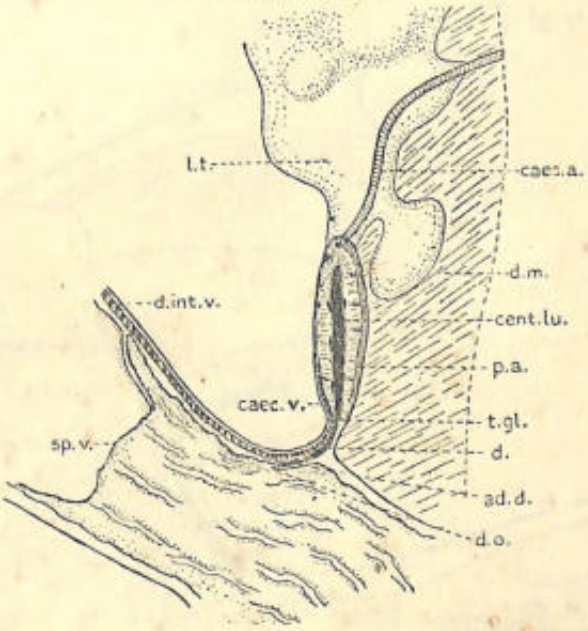
In the male embryo Porbeagle kindly lent me by Mr. Shann the cæcal gland is about half-way between the spiral valve and the anus, so that, as in *Heptanchus*, it seems to become relatively nearer the anus as the fish grows. The gland is shorter and wider than in the female specimen, and the duct has no posterior valve directing the opening forwards. On the contrary, grooves in the mucous membrane lead posteriorly from it (text-fig. 13). The central lumen of the gland is minute in the male embryo, but fairly large in the older female fish.

Chiloscyllium ocellatum.

A male 38·2 cm. long and a female 23·7 cm. long of this small shore fish of the Indian Ocean were examined. In the former the cæcal gland was 0·55 cm. long, while in the latter it measured

only 0·4 cm. With the exception of *Rhinobatus*, no Selachian fish appears to have a gland of such small size. It is globular, but resembles that of *Scyliorhinus* in having a mesentery in common with the gonad, and in the presence of a small anteriorly-directed duct valve and minute orifice (text-fig. 16). The post-valvular intestine is relatively longer than in the Notidanoidei and the more primitive families of the Galeoidei, and because it has outgrown the length of the body-cavity it is bent in S-form as in *Scyliorhinus*. The gland is situated half-way between the spiral valve and the anus.

Text-figure 17.



Scyliorhinus (*Scyllium*) (60 cm.). Sagittal section of cæcal gland. × 1⅓.
Lettering as in previous figures.

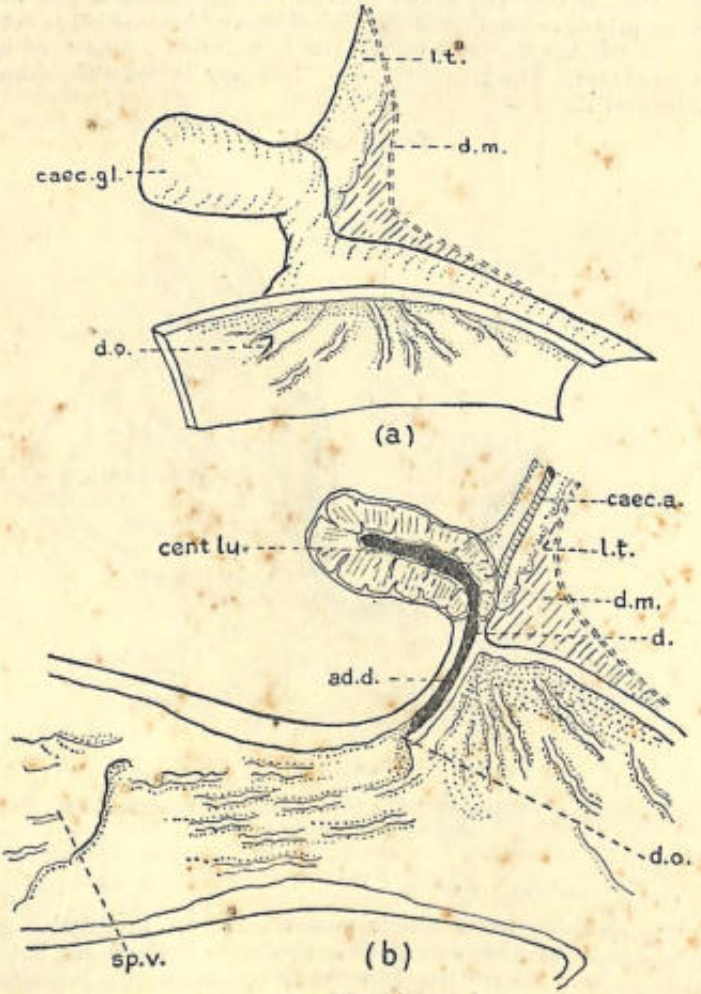
GINGLYMOSTOMA CIRRATUM.

The specimen was a female measuring 73 cm. in length. In this pelagic fish the cæcal gland is similar to *Scyliorhinus* but a little smaller; the portion of the duct adhering to the intestinal wall is longer and wider. Furrows of mucous membrane lead from the wider duct orifice towards the termination of the spiral valve. The dorsal mesentery extends to the tip of the gland, but the cæcal artery is some distance from the free edge of the mesentery, and branches into two before reaching the gland. There is no lymphoid tissue in the mesentery.

Pristiurus melanostoma. (Male 52·5 cm., and female 56 cm.)

The Black-mouthed Dogfish is closely related to *Scyliorhinus*, and has a very similar cæcal gland, with the difference that it is

Text-figure 18.



Cestracion philippi (26·5 cm.).

(*a*) to show shape of gland; (*b*) sagittal section of cæcal gland. × 2½.

ad.l., adherent portion of gland-duct; *d*, primary duct of gland; *d.o.*, intestinal orifice of gland-duct. Other lettering as in previous figures.

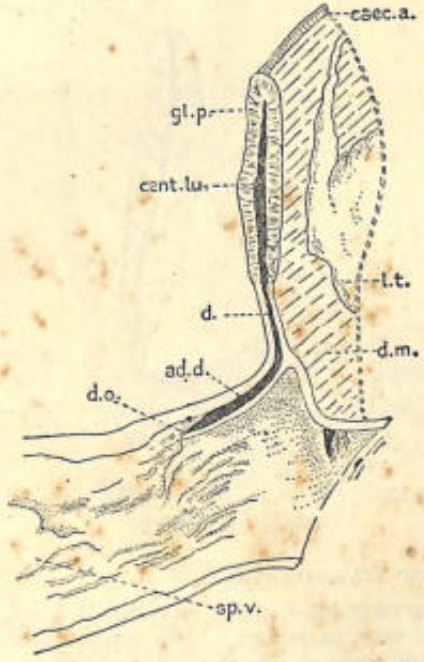
more attenuated. It was 2·1 cm. long and 0·35 cm. in diameter in a fish 52·5 cm. in length. The portion of its duct free from

the intestinal wall is longer, but the portion adhering to the intestinal wall is exceedingly short and opens about half-way between the spiral valve and the anus. The dorsal mesentery extends to the tip of the gland and carries lymphoid tissue surrounding the cæcal artery.

MUSTELUS (VULGARIS and LÆVIS).

Several specimens of *M. vulgaris* were examined in fresh condition. In two specimens the blood-vessels were injected. The gland has the same shape but is larger than in *Scyliorhinus*. The duct is also longer, the superadded portion being especially

Text-figure 19.



Mustelus lævis (40 cm.). Sagittal section of cæcal gland. × 1⅔.
Lettering as in previous figures.

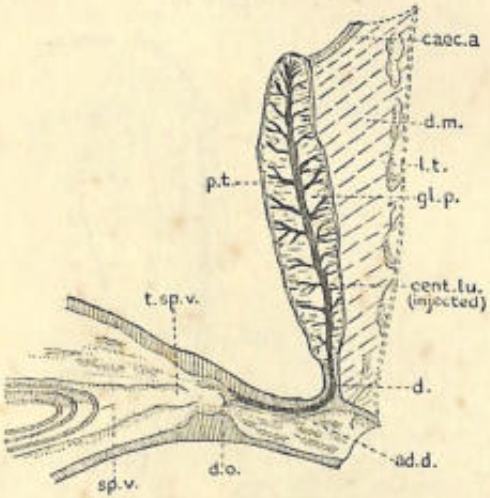
long in *M. lævis* (text-fig. 19). It has a spout-like opening between two ridges of mucous membrane similar to that described for *Squalus*, and this orifice is slightly nearer the termination of the spiral valve than the anterior end of the cloaca. The gland is suspended as in the Rough Dogfish, but curious lobed folds of lymphoid tissue hang on both sides of the organ in *M. vulgaris* and adhere closely to it throughout its length (text-fig. 2). These

folds were present in all the specimens of *M. vulgaris* I examined. The peripheral portion of the cæcal vein commences about a quarter of the way from the tip of the gland and is therefore more superficial than in *Scyliorhinus*.

Carcharias and Galeus.

The cæcal gland in these two fishes has characters very similar to those in the nearly-related Galeoid fishes just described. In both the duct opens considerably nearer the spiral valve than in *Scyliorhinus*.

Text-figure 20.



Zygæna (embryo 47·5 cm.). Sagittal section of gland. × 1½.
Lettering as in previous figures.

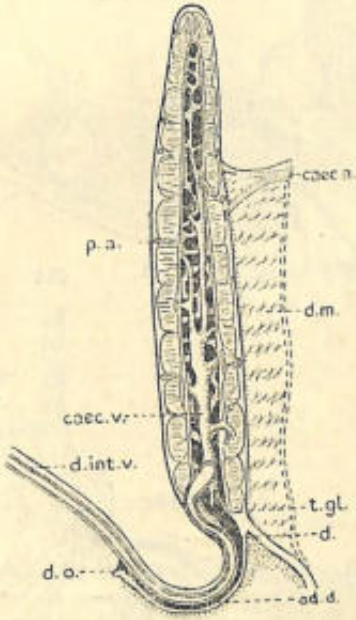
Zygæna (Sphyrna) malleus.

Two Hammer-headed Sharks, a male 47·5 cm. long and a female 46 cm., were examined. Both specimens were advanced embryos and had cæcal glands of somewhat greater relative bulk than in *Mustelus*, with stout digitiform shape. The duct is long and narrow, and the portion adhering to the intestinal wall is elongated and passes anteriorly to within 0·25 cm. of the termination of the peculiar scroll-like spiral valve (text-fig. 20). Although the gland itself appears to be a little nearer the anus than the spiral valve, the intestinal opening of the duct is extremely near the spiral valve. When a gelatine injection mass, coloured with Berlin blue, was passed into the duct, and the gland was cleared with methyl salicylate, a narrow central lumen was

seen leading into many primary and secondary tubules penetrating into the somewhat massive glandular tissue. The post-valvular intestine has an exceedingly narrow cavity, but this condition must change in the adult. The dorsal mesentery extends to the gland apex and has patches of lymphoid tissue.

It is impossible to agree with Howes in his remark that in *Zygæna* the duct retains its primitive condition, being short and wide as in the fœtal *Heptanchus* (*Notidanus*). The gland has a more highly-specialized duct than in other Galeoid fishes. (According to Tate Regan these Sharks ought probably to constitute a separate subfamily of the Carchariidæ.) In the character

Text-figure 21.



Squalus acanthias (86 cm.). Sagittal section. × 1⅔.
Lettering as in previous figures.

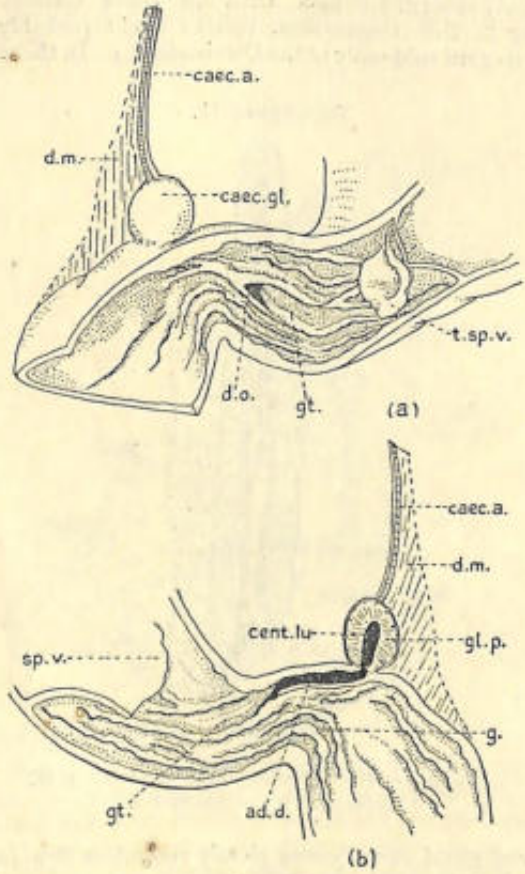
of its cæcal gland duct *Zygæna* closely resembles *Squalus*, details of which have been already given.

CESTRACION PHILIPPI.

The systematic position of the Port Jackson Shark has been changed at various times. According to Tate Regan it is included in the Suborder Squalidæ of the Division Squaloidei because of the structure of its paired fins.

The cæcal gland of *Cestracion* exhibits some peculiarities. It has a stumpy club-shape, with a swollen anterior end and a right-angled bend at its base. The whole of its duct is therefore out of the axis of the gland. There is a small portion of it free from the intestine, and the longer portion is adherent to the intestinal wall (text-fig. 18 *b*). The orifice is a little nearer the spiral valve

Text-figure 22.



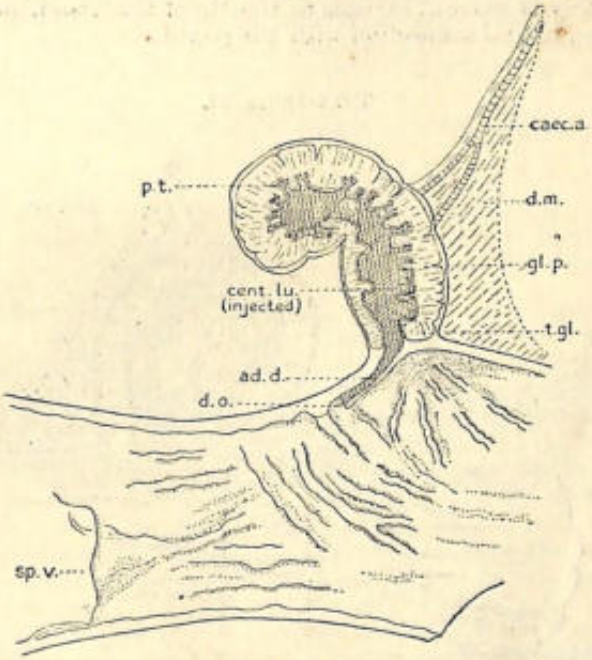
Pristiophorus (75 cm.).
(*a*) to show shape of gland and duct orifice; (*b*) sagittal section of gland. × 1½.
Lettering as in previous figures.

than the anus. The large intestine widens suddenly at the duct-opening. The suspending mesentery is unique in extending only to the proximal portion of the gland (contrast Howes's diagram, 1891, pl. ii. fig. 12). A patch of lymphoid tissue passes completely

round the cæcal artery to adhere to the base of the gland (text-fig. 18 *a*). The mesentery carrying it is continuous with that of the gonad.

Howes stated that in this Shark the spiral valve terminates "at a point lineally below the orifice of the appendix digitiformis," but in the specimen I examined, the two appear to be comparatively widely separated.

Text-figure 23.



Squatina (74·5 cm.). Sagittal section of gland. × 1¼.
Lettering as in previous figures.

SPINAX NIGER.

This Black Dogfish is closely related to *Squalus*. Of the two specimens examined, one 36·5 cm. long was collected at Plymouth, and the other, a larger fish, at Aberdeen. The cæcal gland shows a resemblance in general characters to that of the Spur Dogfish, except that the duct is considerably shorter. Home (1814) gave poor figures of this gland (pls. xcvii. & xcviii.).

CENTROPHORUS FOLIACEUS.

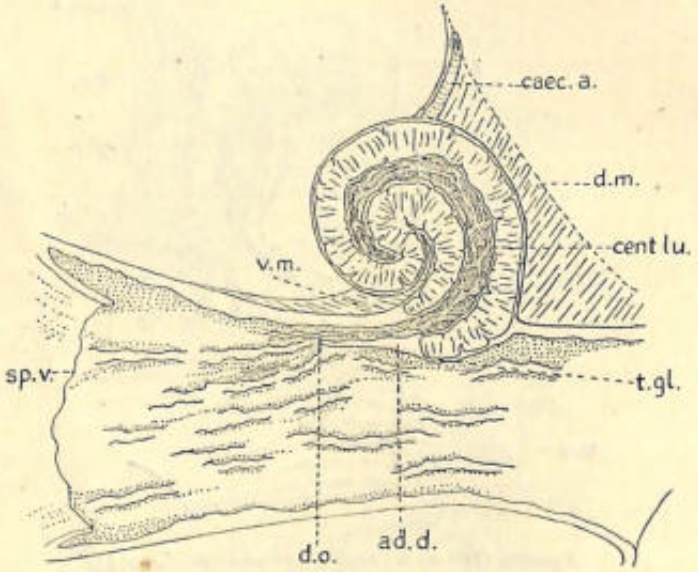
The gland is very like that described for *Squalus*, but the duct is more reduced than in *Spinax*.

PRISTIOPHORUS CIRRHATUS (male 75 cm.).

According to Regan and Jaekel this fish with its saw-like rostrum is closely related to *Squalus* in anatomical features.

The cæcal gland is small and globular as in *Chiloscyllium*. There is no duct free from the intestine, and the duct adhering to the dorsal wall of the intestine is long as in *Squalus*, but wider and with a more spout-like opening, which is further from the termination of the spiral valve. Definite deep furrows lead from the opening to the spiral valve (text-fig. 22 *a* and *b*). The dorsal mesentery is narrow, extends to the tip of the gland, and, as in *Squalus*, has no connection with the gonad.

Text-figure 24.



Læmargus (68 cm.). Sagittal section of gland. × 1¼.
Lettering as in previous figures

LÆMARGUS ROSTRATUS (female 68 cm. and female 274 cm.).

Turner, in his description in 1873 of the anatomy of the Greenland Shark, described the gland as ovoid, and pointed out a striking peculiarity of the alimentary canal in the presence of two large cæca opening into the commencement of the small intestine co-existing with a well-developed pancreas.

The cæcal gland is fairly large, and is peculiar in having a coiled shape as shown in text-figs. 3 and 24. In female specimens it is flattened laterally, owing to the pressure of the two oviducts upon it. As in *Pristiophorus*, there is no duct free from the

rectum, and the glandular substance is peculiarly embedded in intestinal wall on its posterior side and protrudes into the fold of mucous membrane which forms the short adherent duct (text-fig. 24). (It is possible that further modification in this direction would lead to the presence of glandular substance embedded in the intestinal wall as in *Chimæra*.) The duct opening is nearer to the spiral valve than to the anus. The figures show the attachment of the short dorsal mesentery to the left side of the gland, so that the gland is slightly displaced to the right. A small fold of mesentery passes from the coiled tip of the gland binding it down towards the dorsal wall of the intestine.

Howes's statement that the duct is shortest where the gland is most massive (as in *Læmargus*) does not hold when more genera have been examined.

According to Turner the spiral valve has twenty-three turns.

E[illegible]INORHINUS (124 cm. long).

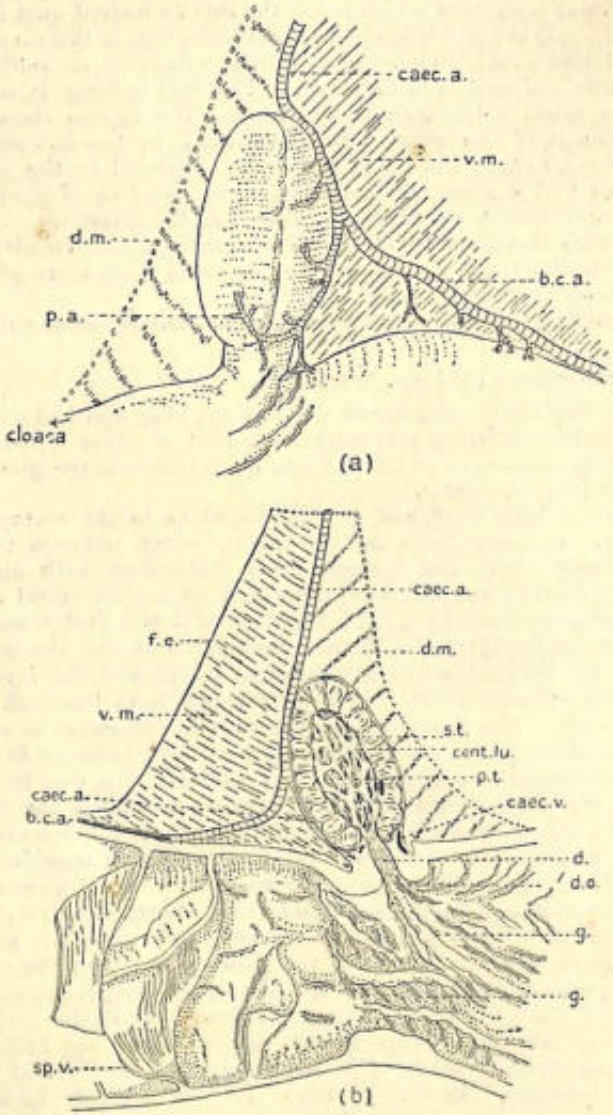
[illegible]eep-sea Ground-Shark was 124 cm. long, and had a cæcal di[illegible]m differing markedly from that of other Squaloidei i[illegible]respects in which it shows resemblance to the gland in [illegible]Hypotremata).

[illegible]s a large bulk, and is club-shaped as in the embryo of [illegible]*na*. It has a large central lumen, which narrows to an exceedingly short and comparatively wide duct with simple opening to the large intestine, somewhat nearer the spiral valve than the anus (text-fig. 25 *b*). The length of the duct is merely the same as the thickness of the intestinal wall, and the orifice is directed backwards without guarding valves, and the furrows lead in a posterior direction. The duct axis is in line with the gland axis. The terminal portion of the intestine is much dilated, although the whole of the post-valvular intestine is very short in comparison with the size of the fish. In this feature and in the short simple duct *Echinorhinus* resembles the Notidanoidei and the Batoids. The mesentery of the gland is unique in the presence of a large ventral fold extending considerably beyond the organ; it connects the gland and dorsal mesentery with the intestine (see text-fig. 25 *a* and *b*). There is no lymphoid tissue in the mesentery, which is not continuous with the gonad mesentery. The circulation of the gland is unique; the cæcal artery passes through the middle of the suspending mesentery to the tip of the gland to pass completely down its anterior surface, giving off branches ramifying over the surface; but half-way down the gland it sends off a large branch to the dorsal wall of the intestine. This very unique feature is shown in text-fig. 25 *a* and *b*.

SQUATINA.

According to Tate Regan, but contrary to the text-books, this remarkable genus is a "typical Squaloid in all essential features,"

Text-figure 25.



Echinorhinus (124 cm.).

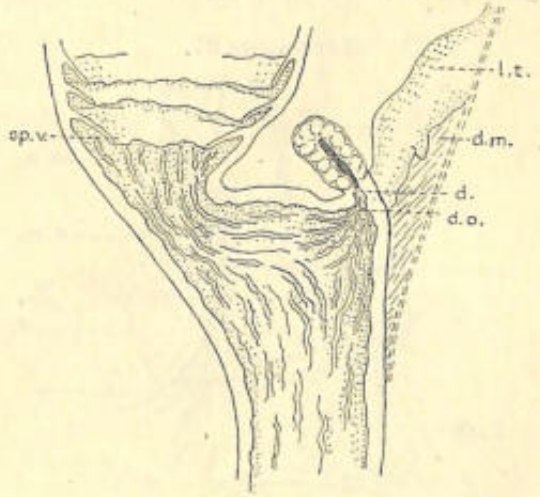
(*a*) lateral view to show shape of gland and peculiar distribution of cæcal artery, × 1⅔; (*b*) sagittal section of cæcal gland. × 1¼.

b.c.a., branch of cæcal artery to dorsal surface of intestine; *f.e.*, free edge of ventral mesentery; *s.t.*, secondary tubule. Other lettering as in previous figures.

and shows specially close relationship to the family Squalidæ, but there is also some indication of Batoid affinity. Two freshly-killed specimens and one preserved specimen were examined.

The cæcal gland is of large bulk and is club-shaped, with the swollen distal extremity bent anteriorly. The glandular tissue is massive; the central lumen is wide, and follows the curve of the gland; it leads into tubules, as shown in an injected and cleared specimen (text-fig. 23). Proximally the lumen passes to a short adherent duct, without the interpolation of a duct free from the intestine; it is out of the axis of the gland, is of

Text-figure 26.



Torpedo (21 cm.). Sagittal section of cæcal gland and intestine. × 1½. Lettering as in previous figures.

narrow calibre, and opens into a greatly widened terminal portion of the intestine a little nearer the anus than the spiral valve. The gland is suspended by a simple mesentery for from half to three-quarters of its length. The cæcal artery branches into two or several factors in the mesentery before reaching the gland.

Owen (1868, pl. 75) showed the "appendix" in *Squatina* with the intestine opened to show the communication, but the nature of the duct is not shown.

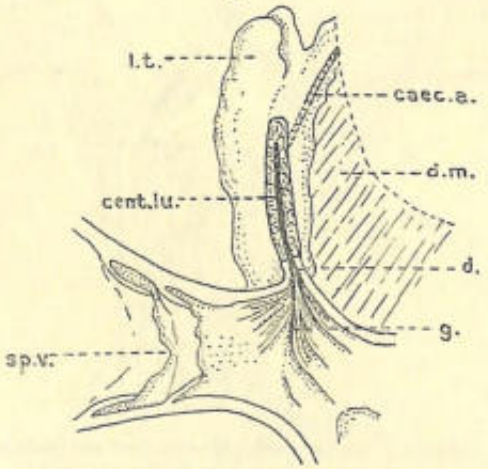
Howes gives a rough idea of the shape of the gland in this fish in his pl. ii. fig. 15, and assumes that the duct is simple, remarking that it is intermediate in constriction between Batoids and Selachoids. From the examination of several specimens it is impossible to agree with Howes.

Batoids.

TORPEDO.

The cæcal gland in *Torpedo* is small, club-shaped, and bent anteriorly at its base. The central lumen is rather small, and communicates by an exceedingly short, simple duct with a pocket-like diverticulum of the enormously dilated terminal portion of the intestine (text-fig. 26). The duct is constricted and has thick walls; passing from its opening are folds of mucosa leading both posteriorly and in the direction of the extensive spiral valve. The duct opening is nearer the spiral valve than the anterior end of the cloaca, and although the simple duct opening closely resembles that found in Notidanoids, the post-valvular intestine is longer and even more dilated in the region of the

Text-figure 27.



Rhinobatus (32·5 cm.). Sagittal section of cæcal gland. × 2½.
Lettering as in previous figures.

cæcal gland than in Squaloids. The dorsal mesentery does not suspend the gland throughout its length; it passes to the duct only, carrying the cæcal artery covered by lymphoid tissue to the extreme base of the gland. A similar condition was found only in *Cestracion*.

Howes reports that the "processus digitiformis" in Batoidei has a non-constricted duct, which is identical in *Torpedo*, *Trygon*, and *Hypnos*.

PRISTIS PECTINATUS.

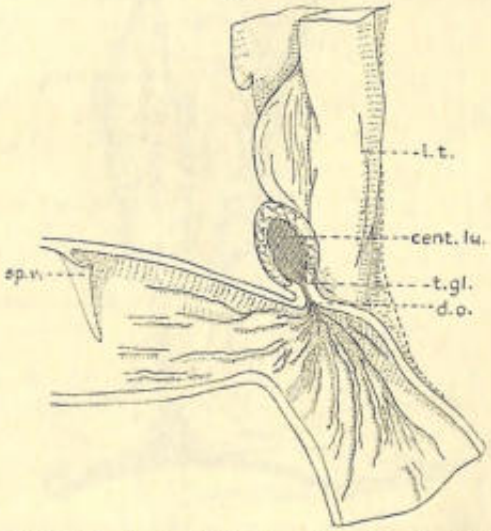
In *Pristis* the gland is rather larger than in *Torpedo* and is ovoid in shape. The central lumen is larger. The duct has the

same characters as in *Torpedo*. The opening is half-way between the spiral valve termination and the anus. The suspending mesentery attaches almost from the tip of the gland, is continuous with the mesorchium, and has thick masses of lymphoid tissue adhering round the organ and connecting anteriorly with the testes (text-fig. 28).

RHINOBATUS BLOCHII.

The gland in this fish is the smallest I have seen, and has an elongated digitiform shape. It opens to the intestinal lumen as in *Torpedo* and *Pristis*. The suspension is the same as in *Pristis*,

Text-figure 28.



Pristis (54 cm.). Sagittal section of cæcal gland. × 1¾.
Lettering as in previous figures.

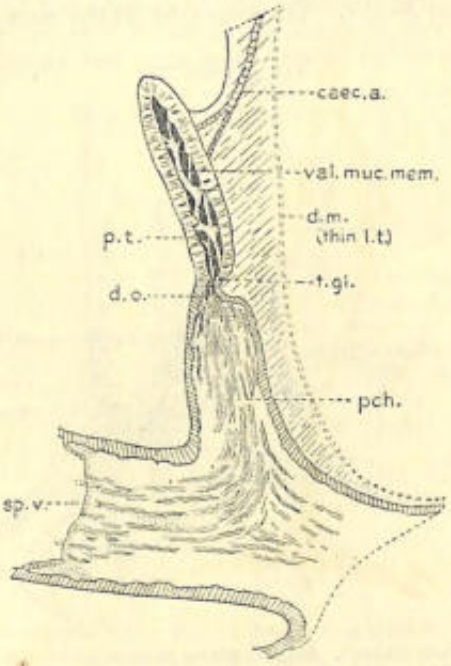
but a pouch of lymphoid tissue projected between the gland and the valvular intestine when the body-cavity was opened, so that the gland was completely surrounded by lymphoid tissue as in *Mustelus*, although more closely imbedded in it, as shown in text-fig. 27. In Batoid fishes the organ appears to be displaced to the left.

RAIA.

In *Raia* the gland has approximately the same relative bulk as in *Læmargus*, and is the seventh largest of those I have examined. It has a stout and short digitiform shape and a simple short duct. In some species (e.g. *circularis*) this duct is very wide; the

reduction in external girth in this region is caused simply by the absence of glandular tissue (text-fig. 30). In other species (e. g. *R. batis*), the duct is more constricted (text-fig. 29). In all cases it opens into a dorsal pouch of the dilated post-valvular intestine at roughly the middle of its length. In some cases (e. g. *R. batis*) this pouch may be narrowed so as to form a diverticulum or cæcal-like portion. This resembles the cæcum in other vertebrates, and the gland resembles the vermiform

Text-figure 29.



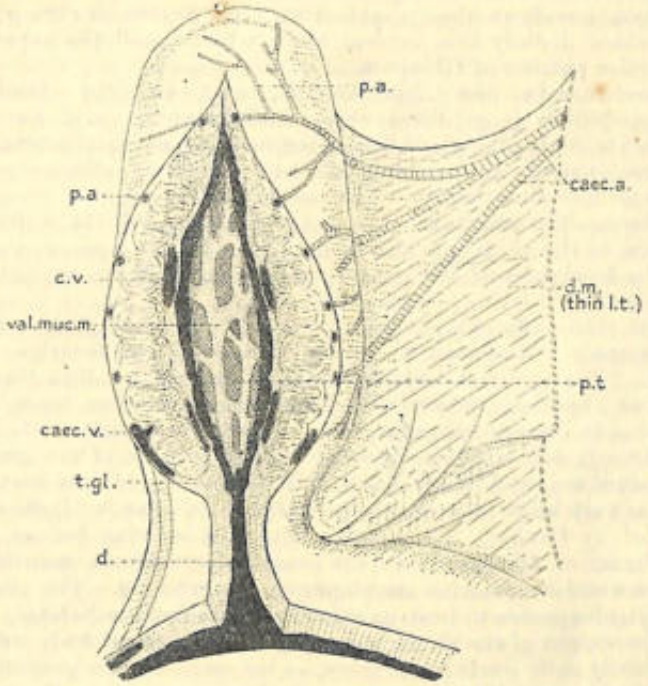
Raia batis. Sagittal section of cæcal gland. × 1½.
Lettering as in previous figures.

appendix of higher Vertebrata in its position (text-fig. 29). The suspending mesentery does not reach to the tip of the gland; lymphoid tissue varying in quantity is present in it, and there are veins connecting with the cardinal sinus; the supplying artery passing through it usually branches several times, and the branches pass to the surface of the gland at various levels. The glandular tissue is firm and thick; the central lumen is very large and is filled with a great quantity of sticky straw-coloured liquid. The mucous membrane of the lumen is raised into prominent longitudinal folds with oblique connections, leaving deep pits showing mucous folds at a deeper level and giving a latticed appearance (text-fig. 30).

In fresh glands slit open, the peripheral arterial system and central venal system can be well seen by the cut ends of the blood-vessels, which are gorged with blood (text-fig. 30).

Crawford also points out that the duct "from the gland proper

Text-figure 30.



Cæcal gland of *Raia circularis* opened to show lumen and circulation. × 1½. *c.v.*, central vein. Other lettering as in previous figures.

to the rectum" in *Raia* is short and wide, and opens into a posterior dilation of the rectum. It is difficult to understand Pixell's remark that in *Raia punctata* the duct is "long and wide and looks like the short gland."

Summary of the Macroscopic Features of the Gland throughout Selachian Fishes.

The cæcal gland appears to be present in all living Selachian fishes. Its original form is probably similar to that found in *Chimæra*, where a number of tubular glands form longitudinal ridges beneath corresponding folds of the mucosa at the commencement of the post-valvular intestine. These glands have

separate efferent ducts opening posteriorly by a number of intestinal orifices at the same level. The position of this glandular tissue and its blood-supply in *Chimæra* are the same as those of the cæcal gland in Euselachii.

In primitive Euselachian fishes (*Chlamydoselachus* and *Heptanchus*) a diverticulum of the post-valvular intestine separates the glandular tissue into a definite gland with a proximal constriction forming a short simple duct. In *Heptanchus* the gland is divided distally into several lobes, which recall the separate glandular patches of *Chimæra*.

Position.—In the Notidanoidei, and in the families Odontaspididæ (e. g. *Mitsukurina*) and Lamnidæ (e. g. *Lamna*) of the Galeoidei, the gland is situated near the anus; this position is accompanied by a straighter and relatively shorter post-valvular intestine than in other Sharks and Rays.

Shape.—The shape of the gland varies greatly in different genera, as the diagrams show; it is constant for a genus, and is similar in closely-related genera. (Howes said it was variable in closely-related forms.)

Size.—In different genera the size of the cæcal gland varies enormously; it appears to bear no relation to the length of the duct. The greatest relative bulk is found in *Mitsukurina*, *Lamna*, *Squalus*, *Squatina*, *Echinorhinus*, *Læmargus*, *Raia*, and *Zygæna* in descending order. Unfortunately records of the size of the egg and reproductive habits of a number of the genera examined are unobtainable, but it is interesting to note that the egg is very large in genera with large cæcal glands (Doflein, as quoted by Graham Kerr, states that *Mitsukurina* has an egg 220 mm. in diameter); in the ovoviparous genera mentioned above the intra-uterine development is very long. The size of the gland appears to bear no relation to the feeding-habits.

The weight of the gland percentaged for the total body-weight gradually falls during ontogeny, as has been shown graphically for *Squalus* and *Scyliorhinus*.

The relative length of the gland increases from the time the organ is definitely constricted off from the intestine in embryos of *Scyliorhinus* 30 mm. long until shortly after birth in fishes 127 mm. long.; after this the percentage length is considerably less. (Further details are given in the Embryological Section.)

In all dimensions the cæcal gland of *Squalus* is relatively much larger than that of *Scyliorhinus*. In both genera it is probably slightly larger in all measurements in mature female than in mature male fishes.

There is some indication of seasonal variation in the relative weight of the organ in *Scyliorhinus*. It is slightly heavier in both males and females during the breeding-season, but this needs verification from more numerous statistics.

Duct characters.—In Notidanoids the duct is short and simple. Progressive stages in specialization of the intestinal portion of the duct are shown in genera of the Galeoidei and Squaloidei.

Mitsukurina and *Lamna* exhibit the simplest of these stages in the presence of a valve-like fold of mucous membrane, on the posterior border of the duct orifice, with its free edge directed anteriorly. *Zygæna* and *Squalus* show the longest and most complex duct, adhering for a considerable length to the dorsal intestinal wall (text-figs. 20 & 21). *Læmargus*, *Squatina*, and *Echinorhinus* show intermediate stages in the simplification of the duct, culminating in the Batoids, where it is short and simple as in Notidanoidei.

Where the efferent duct is most specialized there is marked proximity of the orifice to the termination of the spiral valve; the direction of transmission of viscid liquid, which is undoubtedly present in the gland and duct, is controlled by the narrow calibre of the duct and by gutters in the mucosa leading towards the spiral valve.

Where the gland-duct is simple, the spiral valve appears to have a large number of turns as in *Heptanchus* and *Raia*; where it is specialized, there are fewer spiral turns as in *Squalus*, or the valve is scroll-like as in *Zygæna* or *Carcharias*.

The position of the duct orifice becomes progressively nearer the spiral valve termination during ontogenesis in those fishes which develop a specialized duct. The distances percentaged for the length of the fishes in *Squalus* and *Scyliorhinus* show this.

The simple duct in Hypotremata (Batoids) opens into a larger dilation of the post-valvular intestine than in Squaloidei and Galeoidei. In some species of *Raia* the pouch is long and narrow, and suggests the cæcum of higher vertebrates, while the gland at its apex suggests the appendix.

Mesentery.—The cæcal gland may be suspended in one of two ways: firstly, a continuation of the gonad mesentery may suspend the gland dorsally throughout its length, in which case lymphoid tissue, continuous with the posterior end of the gonad, is always near the gland, and may be packed closely round it as in *Rhinobatus*, *Mustelus*, and *Scyliorhinus*; secondly, the mesentery may be independent, in which case it supports only the gland and its artery and carries no lymphoid tissue. A ventral mesentery, connecting the ventral surface of the gland with the dorsal wall of the intestine and carrying the cæcal vein, may be present. It is small in *Heptanchus* but extensive in *Echinorhinus*.

Circulation.—The organ is highly vascular. In all cases it is supplied by the cæcal artery, which passes in the dorsal mesentery from the dorsal aorta directly to the gland. Frequently this artery supplies this viscus alone, and in all cases principally. In genera in which the gland mesentery is continuous with the gonad mesentery, minute arteries may pass to the lymphoid tissue in the neighbourhood before the artery reaches the gland, as in *Scyliorhinus*; in *Echinorhinus* an arterial branch passes ventrally to the valvular intestine (text-fig. 25). The principal branches of the arterial circulation are exclusively peripheral; capillaries penetrate near the central lumen region (see Histology,

p. 156). The major portion of the venous system is central, except at the proximal end of the gland where the ventral cæcal vein is formed by the union of venous factors. This constitutes the beginning of the dorsal intestinal vein, which is a factor of the portal system. The venous system is remarkably internal in *Squalus*, but in *Scyliorhinus* it is also superficial in the proximal half of the gland. These and other important points in the circulation are dealt with in greater detail in the Histological Section.

Suggestions Concerning the Physiology.

These facts suggest the possibility of a double physiological significance of the gland. On the one hand, the discharged viscid liquid may have some action on the intestinal lumen; the arrangements for controlling the direction of this discharge in Galeoidei and Squaloidei suggest a possible physiological relation with the spiral valve, which may be less important in the Notidanoids and Batoids (Hypotremata), which lack these arrangements. On the other hand, the marked vascularity and importance of the blood-supply of the gland suggest a problematical rôle in changes in the composition of the blood. The larger relative size of the organ in advanced embryos and in fishes shortly after birth, the slightly larger size in mature females than in mature males, together with the possible seasonal variation and the proximity of lymphoid tissue in many genera, may all conceivably be concerned with an obscure blood function.

Histology of the Cæcal Gland.

Material and Technique.

The fresh material for this investigation was obtained at Plymouth. It includes glands of *Scyliorhinus* (*Scyllium*) *canicula* from male and female fishes of various sizes and at different times of the year; of *Mustelus vulgaris*, *Squalus acanthias*, *Squatina*, and *Raia*; and a series of embryos of *Scyliorhinus canicula* from 12 mm. in length. In addition, the glands were sectioned in *Chimæra*, *Heptanchus*, *Mitsukurina*, and *Torpedo*.

Various fixing and hardening fluids were used. The best results were obtained with Bouin's formula and with corrosive acetic mixture. The paraffin sections were cut from 5 to 10 μ thick. After staining the tissue with osmic acid, sections were cut with a freezing microtome and examined in glycerine jelly for fat globules in the epithelial cells.

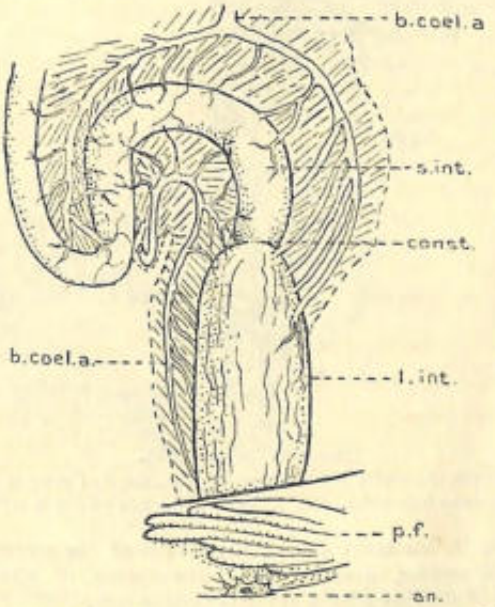
Several staining methods were adopted. For general cytological purposes Delafield's hæmatoxylin, counterstained with eosin or orange G, was used. Heidenhain's iron hæmatoxylin was employed to show nuclear structure and to test for the presence of zymogen granules. Connective-tissue distribution was shown by Mallory's stain. This stain was useful to show mucin, but the

more specific stains—thionin, toluidin blue, methylene blue, and muchæmatein—were also used. For hæmatological purposes Mann's methyl blue eosin, in which the eosin is particularly specific for white corpuscles, and Gram's alum carmine with gentian violet (Weigert's modification for phagocytosis) were found useful. Gold chloride was used to show nerve endings.

Thick hand-sections of the cæcal gland were cut after injection of the arterial and venous systems. A microscopic injection of the lymphatic system was made by subperitoneal injection from the attachment of the mesentery at the tip of the gland.

Some of the histological drawings were made with a projection apparatus, and others with a camera lucida.

Text-figure 31.



Pleuronectes. Junction of large and small intestine. × 2½.
an., anus; *b.coel.a.*, branch of cœliac artery; *const.*, constriction; *l.int.*, large intestine; *p.f.*, pelvic fin; *s.int.*, small intestine. (See p. 180.)

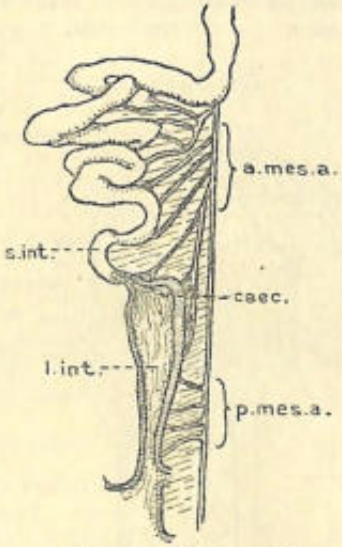
Microscopic Structure of the Adult Gland.

As already mentioned in the Historical Summary, Blanchard was the first to show that the organ consists mainly of branched tubular glands, which are lacking where the gland-duct joins the intestine, and the tubular parenchyma is bounded by a connective-tissue envelope. Apart from these points, his paper is confined to the development in *Acanthias vulgaris* and *Mustelus vulgaris*.

Ten years later, Sanfelice added that in *Raia* the connective-tissue capsule contained smooth muscle, and that the epithelium of the central lumen and collecting-ducts is of the "stratified pavement" variety with some goblet cells.

Crawford gave a somewhat more complete account of the histology of the adult gland in *Raia*. He noted large central sinuses among the collecting-ducts of the tubules. He considered that the cells of the gland "acini" resembled kidney cells.

Text-figure 32.



Cæcum of *Triton*. × 2½.

a.mes.a., arteries of anterior mesenteric series; *caec.*, cæcum; *p.mes.a.*, arteries of posterior mesenteric series. (See p. 181.) Other lettering as in text-fig. 31.

Hoskins, in his more adequate account of the embryology in *Squalus acanthias*, gives a good description of the peculiar method of branching of the tubules in this fish.

These accounts omit precise information on the vascular system of the gland, which appears to have peculiar features, which, considered in the light of modern hæmatological work, probably have important physiological significance. Particular attention has, therefore, been paid to the blood system of the gland in this investigation.

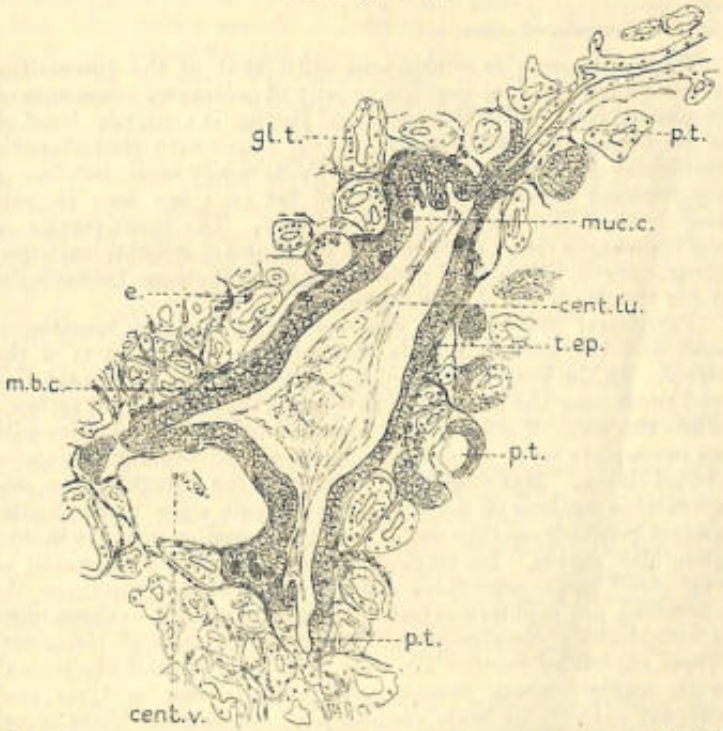
Scyliorhinus canicula.

Serial transverse sections show that the apex of the gland consists of a solid mass of glandular tubules cut transversely and surrounded by a thin connective-tissue capsule enclosed by

peritoneum. Towards the proximal end of the gland the connective tissue gradually thickens as the glandular parenchyma decreases in diameter. In the middle of its length the gland can be divided into three regions:—

A. The thin peripheral zone of connective tissue with unstriped muscle, enclosing arterial branches in sections cut at all levels, and

Text-figure 33.



Scyliorhinus (*Scyllium*) *canicula*. T. S. through central lumen of cæcal gland of mature female (middle region of gland). Drawn under projection apparatus. × 70.

cent.lu., central lumen; *cent.v.*, central vein; *e.*, erythrocyte; *gl.t.*, glandular tubule; *m.b.c.*, migrating blood cell; *muc.c.*, mucous cell; *p.t.*, primary tubule; *t.e.*, transitional epithelium.

venules and the ventral vein in sections placed in the proximal half of the organ. The whole is covered externally by peritoneum.

B. An intermediate glandular region, consisting of vast quantities of much-branched tubules separated by blood vessels and an exceedingly scanty amount of connective tissue.

C. A middle region enclosing the central lumen, which is bounded by epithelium continuous with that of the primary tubules, among which is a central venous circle of vessels separated from the lumen epithelium by a very variable amount of connective tissue, which may, or may not, surround the blood vessels.

These three regions with the variations found in different specimens will be described in detail.

A. *The Peripheral Zone.*

The peritoneum is continuous with that of the suspending dorsal mesentery, and consists usually of columnar, sometimes of squamous, cells. The subperitoneal portion is a narrow band of white fibrous connective tissue, which stains with characteristic feebleness with ordinary stains. Occasionally small patches of longitudinal muscles and others of fat cells are seen in this tissue; the latter are near the mesentery. The inner portion of the connective tissue envelope is a thin band of circular unstriped muscle fibres, which may penetrate a short distance between the outer tubules of the middle region.

Peripheral blood vessels are seen between the subperitoneal coat and the smooth muscle layer, and in various parts of the latter. In the anterior part of the gland they are mainly arterial, and those near the mesentery have walls typical of small arteries, while the walls of others are typical of pre-capillary arteries with an incomplete layer of smooth muscle fibres covering the endothelial lining. Many of these pass round the circumference, and transverse sections of microscopic injections show these circular vessels breaking up into radial branches passing into the middle glandular region. In transverse sections below the middle of the gland large superficial venules are seen to loop over the encircling pre-capillary arteries to pass externally to them, often a considerable distance round the circumference of the gland. These superficial venules are wide, have only an endothelial wall with scanty smooth muscle cells, and in some sections they connect directly by wide venules with the central blood vessels (Pl. I. fig. 1). The ventral, superficial venous vessel gradually increases in size as the sections approach the gland-duct; the venules are tributaries to it. The proportion of leucocytes to erythrocytes in these vessels appears to be great. The oval erythrocytes, as is well known, are larger than in Teleostomes. Their longer diameter averages approximately ·025 mm.; their shorter diameter is ·02 mm.

Microscopic injections show a rich, delicate plexus of lymphatic vessels accompanying the superficial blood vessels; their capillaries penetrate as fine arborizations through the glandular region.

The capsule of the gland is innervated by branches from sympathetic nerve strands in the dorsal mesentery (Monti, 1898,

and Hoskins, 1917). I find that these branches give a rich supply of nerve-endings to glandular tubules of the region within the capsule.

The lymphoid tissue carried in the supporting mesentery of the gland frequently presses as a dense mass against the connective tissue of the gland capsule. The relation of this tissue to the organ was pointed out in the first portion of this paper (text-figs. 1 & 17). In places the subperitoneal layer of the gland is absent and the smooth muscle layer may be incomplete. In four glands patches of lymphoid tissue were lying immediately under the smooth muscle and encroaching on the connective tissue and the outer glandular tubules. Pl. I. fig. 3 shows this. The adjacent lymphoid tissue of the mesentery has a fine reticulum with branching connective-tissue cells with clear nuclei, interspersed by many small arteries and veins. The stroma is difficult to see because of the dense mass of leucocytes present. These include many small lymphocytes with characteristically very little cytoplasm, a few large lymphocytes (mononuclears or transitional leucocytes) with more basic cytoplasm, and a lightly-staining large nucleus in which a nucleolus may be seen, unlike the mono-nuclears of higher vertebrates. There is also a large proportion of polymorpho-nuclear leucocytes (granulocytes) with very varied granulations in their cytoplasm. Many of these have coarse oxyphil (acidophil) granules, which show very distinctly with Orange G or with eosin. Others have finer oxyphil granules with a few basophil granules amongst them.

(Drzewina, in 1905, first recorded the presence of these last polymorphs, which she found did not fit in with the orthodox series of leucocytes for higher Vertebrates. Drzewina and Ladreyt (1921) show a series of transitional forms in the blood of Elasmobranchs from small lymphocytes to mono-nuclears and granular leucocytes. These authors and most modern hæmatologists believe these leucocytes constitute an essentially monophyletic series in contrast to the classical Pluralist scheme of Ehrlich and his followers.)

The simple small masses of leucocytes lying under the gland peripheral capsule and following its inner wall are in the neighbourhood both of the blood-vessels and lymphatics of the peripheral coat, and of the external lymphoid tissue in some cases. Small lymphocytes form the bulk of these groups of leucocytes. Occasional oxyphil polymorphs are seen and, still more occasionally, a large lymphocyte.

B. *Intermediate Glandular Region.*

The whole of this zone consists of a parenchyma formed by the epithelium of the tubulo-racemose glands with the small interspaces filled mostly with a capilliform network with large quantities of blood corpuscles. Connective-tissue cells are

extremely few except in the most external portions. In some places the blood has a remarkably close association with the glandular cells.

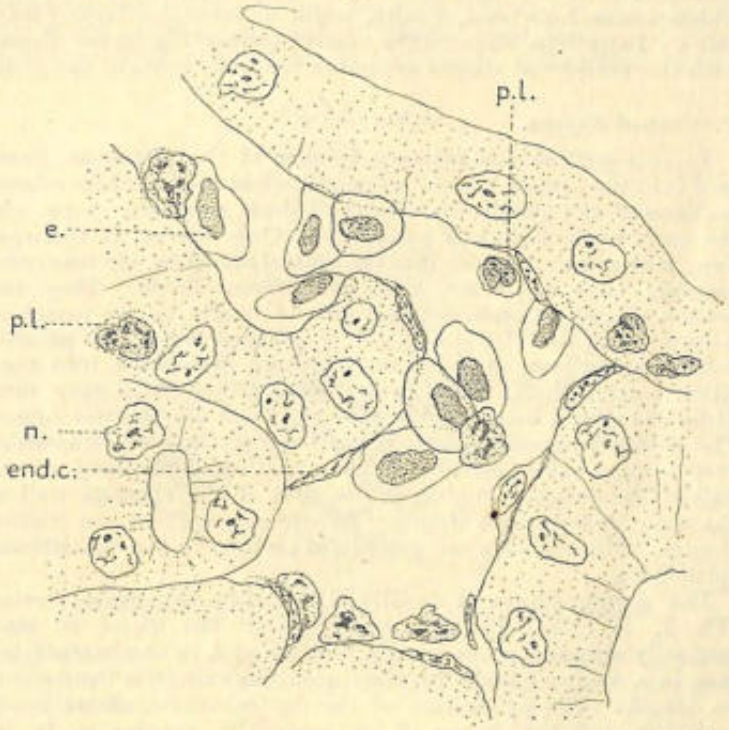
The glandular parenchyma consists of the tubules of the compound racemose glands, which are cut in various directions. In transverse sections most of them are cut transversely or obliquely. The primary tubules therefore run in a longitudinal or oblique direction. The arrangement of tubule branchings is similar to that described by Hoskins for *Squalus* embryos 95 mm. long with tubules of many more orders, and is in contrast with that found in the gland of adult *Squalus*, where the central tubules run longitudinally and the bulk of the glandular parenchyma consists of unbranched radial tubules. The addition of innumerable small branches seems to continue in the adult *Scyliorhinus*. The peripheral terminations of these tubule branches are seldom enlarged. They lie directly beneath the circular smooth muscle-ring of the peripheral coat. The epithelial cells of the tubular gland are usually columnar, with a short diameter directed towards the interior of the tubule; this diameter averages ·037 mm. The adjacent cell walls are difficult to see, but can be made out with Mallory's stain. The nuclei are usually oval in the radial direction, and are generally placed centrally. They have clear nucleoplasm, with one to several nucleoli and chromatin granulations among filaments. The nuclei resemble those of the follicular epithelium of the thyroid gland of *Scyliorhinus*. The cytoplasm has a coarse reticulum, which stains darkly with Mallory's stain, with clear unstainable granules in the meshes, which are very difficult to see after some fixing fluids and after some stains. In sections stained with methylene blue they are unstained and refractive. In glycerine-jelly preparations, after osmic acid fixation, they are denser (text-fig. 40). Where the tubules are cut longitudinally or obliquely they are arranged in parallel lines, and frequently in tubules cut transversely they are aggregated towards the centre. The cytoplasm granules were first seen by Sanfelice in the epithelial cells of the cæcal gland of *Raia*. He and Morgera have called them secretory granules, but Crawford denied their presence. Morgera stated that they are placed externally during inactivity and centrally during secretion. This is difficult to see in fresh or preserved material, and granules are rarely seen in the lumina of the tubules. Osmic acid brings out coarse, brown dots in the cytoplasm, the size and disposition of which can be seen in text-fig. 40. These are probably fat globules. There are occasionally large vacuoles in the glandular cells of the middle region, and still more occasionally goblet cells with their contents staining with specific mucin stains. The terminal tubule cells under the connective-tissue coat are sometimes polyhedral, owing to compression.

The quantity of blood corpuscles present in the capilliform network of the interspaces between the tubules varies enormously

in cæcal glands of different individuals of this genus. In some, the blood-spaces are packed tightly and distended with corpuscles as if they had been injected, while in others the corpuscles are in smaller numbers, but in all cases the tissue is highly vascular.

The radial vessels from the encircling pre-capillary arteries of the connective-tissue capsule penetrate between the glandular

Text-figure 34.



Scyliorhinus (*Scyllium*) *canicula*. T.S. of portion of glandular tubules with interstitial blood-space. (Camera lucida.) × 860.
end.c, endothelial cell; *n.*, nucleus of gland-cell; *p.l.*, polymorpho-nuclear leucocyte. Other lettering as in text-fig. 33.

tubules; their endothelial wall is soon laid bare by the disappearance of the scanty smooth muscle-cells; they break up abruptly into a capillary plexus, which occupies the connective tissue between the epithelial tubules.

Microscopic injections show this capillary plexus pervading the entire glandular region; it is less dense near the central lumen. The endothelial walls are in direct contact with the adjacent glandular epithelial cells, which in places appear to impinge

upon the lumen of the capillary vessel. Frequently little groups of blood corpuscles lie pressed against the glandular cells. Leucocytes are often present in excessive numbers, and it is important to notice that they are seen in various stages of penetration into the intercellular spaces and, apparently, into the cytoplasm of the gland-cells. These leucocytes include lymphocytes and oxyphil polymorphs. The infiltration is most noticeable in the inner tubules (text-fig. 34). The blood from the venous capillary plexus is collected into thin-walled and wide venous vessels, which anastomose and, finally, unite to form the large central veins. Injections show wide vessels connecting these directly with the peripheral venous system in the basal parts of the gland.

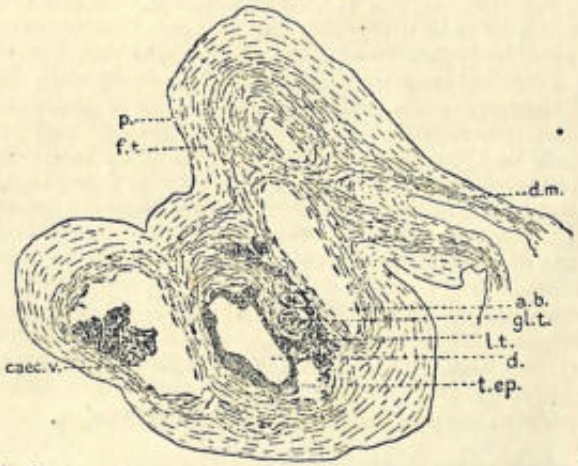
C. *Central Region.*

In this portion the primary tubules of the racemose glands lead into the central lumen. The epitheloid cells of these efferent portions of the glands are usually of deep, columnar shape, with the ovoid nucleus slightly peripheral. Only one or, at the most, two primary tubules open into the central lumen in one transverse section; they, therefore, arise at different levels. They may branch almost at once, or may extend nearly to the periphery before doing so. In the gland of mature fishes the primary tubule epithelium has frequently become elaborated into transitional epithelium, which may extend either for a very short distance or for a considerable distance from the central lumen. The change from columnar to transitional epithelium is sometimes very abrupt. The epithelium may be three cells deep on one wall of the primary tubule, while that of the opposite wall at the same level remains simple. In other cases there is a gradual change. Mucous cells are sometimes present in the transitional epithelium.

The central lumen is usually elliptical in transverse section (Pl. I. fig. 2). Towards the duct of the gland it may gradually assume a more ventral position and, in one exceptional case, in a mature female fish the lumen was excentric throughout its length. The epithelium of the central lumen shows much variation, and the degree of its complexity appears to be in direct relation to the age of the fish. In very immature fishes it consists of simple low columnar cells averaging ·031 mm. in depth, while in other immature fishes it is squamous in the distal portion but transitional towards the proximal end. In fishes nearing maturity the central lumen epithelium is simple only in its most distal portions, and shows progressive but sometimes erratic changes to transitional epithelium of four or five cells deep, where the lumen merges into the gland duct. Mucous cells are present in the superficial, very frequently in the deeper, layers of this epithelium; there is an increase in their number in the duct, but there is never a complete surface row of goblet cells such as are seen in the neighbouring intestinal epithelium. (The anteriorly-directed valve forming the small additional duct shown

in text-fig. 17 is covered by transitional epithelium resembling that of the general intestinal mucosa.) The variations in the central lumen epithelium are well shown in longitudinal sections. The surface cells of the transitional epithelium may show the characteristic flattening, or the cells at all levels may be polyhedral and much enlarged. In all cases there is invasion of leucocytes in the epithelium, but the number of migratory leucocytes varies very much. Sometimes diffuse masses of lymphoid corpuscles are found in close proximity to and encroaching on the lumen epithelium, and in these cases there are many migratory leucocytes among the epithelial cells which have a

Text-figure 35.



Scyliorhinus (*Scyllium*) *canicula*. T. S. through duct of gland. (Camera lucida.) × 36.

a.b., arterial branch; *d.*, primary duct of gland; *f.t.*, fibrous tissue; *gl.t.*, glandular tubule; *l.t.*, lymphoid tissue; *p.*, splanchnic peritoneum; *t.ep.*, transitional epithelium.

very changed appearance, similar to the invaded stratified epithelium of tonsils. The more definite of the small lymphoid patches lie near vessels of the central venous circle, and they appear to have developed at the expense of parts of the glandular tubules, the interstitial connective tissue, and the epithelium in the vicinity. (See Pl. I. fig. 2 and text-fig. 35.)

The size and disposition of the central venous vessels varies greatly according to the region of the gland in which a transverse section is cut. In the extreme distal portion there are usually no large central veins. In the middle part of the gland there are several vessels varying in size and sometimes forming an incomplete circle external to the central lumen epithelium. The vein on the ventral side of the lumen increases in size as the

sections become nearer the base of the gland. This increase is due to the inflow of the smaller central vessels of the venous circle. It becomes still larger near the commencement of the duct by the addition of factors from the peripheral coat, which are seen among the peripheral arteries in the basal half of the gland. The vessel so formed is the cæcal vein, which passes away from the gland on the ventral side of the duct in the fibro-muscular tissue, which wholly replaces the glandular tissue in the duct region (text-fig. 35). As has been mentioned in the first section of this paper, this vein becomes the dorsal intestinal vein, which is a factor of the portal system.

The central venous vessels are limited by an endothelial wall, which is sometimes strengthened by an envelope of fibrous connective tissue varying greatly in amount. When the central lumen epithelium is transitional, as in the gland of older fishes, this connective tissue is usually thick. Its varying thickness is well seen in longitudinal sections stained with Mallory's connective-tissue stain. It is continuous with the same tissue which forms a layer of separation between the central lumen epithelium and the central glandular tubules in places where the venous sinuses are absent. In immature fishes this layer of connective tissue is absent, and the venous sinuses are separated from the lumen epithelium merely by their endothelial walls, which are occasionally seen to be defective. In such cases the central sinuses have a very thin covering to separate them from the central lumen. Little groups of free blood corpuscles lying in the lumen close to its epithelium, and so placed that they have probably not been extravasated from the central sinuses, are sometimes seen.

Lymphatic channels accompany the central veins.

Contents of the Central Lumen.

It is difficult to discover the nature of the lumen contents from serial sections. Usually a finely granular substance with only a slight affinity for stains is present (Pl. I. fig. 2). In this, isolated blood corpuscles in various stages of degeneration are sometimes seen. The granules of polymorpho-nuclear leucocytes may be in the process of discharge from the cytoplasm. Occasionally the free blood corpuscles are pressed against the lumen epithelium, but when large patches of blood-cells are seen in the lumen, they have probably been displaced from the central vessels. The goblet cells of the lumen and primary tubule epithelium are, undoubtedly, seen discharging mucin into the lumen, but the proportion of mucin in the lumen content is always very small; chemical tests also show this. When a gland from a freshly-killed fish is removed, after the precaution of ligaturing the duct to prevent the intestinal contents entering, and a little of the viscid secretion is examined in eosin and sea water, numerous small refractive granules with occasional blood corpuscles are seen with high magnification.

There seems to be no constant difference in the general histological characters either of the glands of male and female fishes or of the glands at different seasons. The variations noticed seem to be largely due to the varying ages of the individuals.

Histology of the Homologous Structure in Chimæra.

The arrangement of similar glandular tissue embedded in the valvular intestinal wall without a diverticulum in *Chimæra* has been described in the macroscopic section of this paper.

As the material was spirit preserved, it was indifferently fixed in places, but sufficiently well to determine the general histological features.

The peripheral region of the swollen portion of the intestine shown in text-fig. 6 consists of splanchnic peritoneum covering a thick band of muscular tissue, the outer part of which is chiefly longitudinal muscle, and the inner wider portion is circular muscle with fibrous connective tissue. This peripheral region, the mucosa and sub-mucosa, are of about the same thickness as that of the general intestinal wall, and the increased thickness of the wall is due to the presence of definite nodular masses of glandular tissue which are the dense bulges seen in the whole specimen viewed as a transparency (text-fig. 6 *b*). In the transverse sections nearest the spiral valve these masses consist of small tubules, which are branches of racemore glands cut mostly in a transverse direction, so that they are running parallel with the intestine in this region. Strands of connective tissue, in which small blood-vessels are seen, separate the various nodules, and finer strands pass between the tubules. In this anterior region, very small isolated patches of diffuse lymphoid tissue are sometimes observed. At times the epithelium of the tubules is invaded by leucocytes. The glandular epithelial cells are considerably smaller than in *Scyliorhinus*. They are usually about ·01 mm. in radial diameter, often smaller, while in *Scyliorhinus* they average ·037 mm. The cytological features are very similar. The nuclei are clear and oval, with one to three nucleoli, and granules are seen in the cytoplasm mitochondria with an oil immersion lens.

In transverse sections further removed from the anterior end some of the tubules are cut obliquely and longitudinally, and their epithelium may pass into a row of goblet cells with deep chalices; these goblet cells line cylindrical large lumina which connect with one another (Pl. II. fig. 7, *s.d.*) They increase in size in sections placed nearer the anus, and there is a marked decrease in the quantity of glandular tissue present; ultimately it entirely disappears, and gives place to a row of several large separate ducts. These are lined by transitional epithelium, the superficial layer of which is composed of goblet cells. They open to the intestinal lumen at the same level beneath folds of mucosa. The lumina seen in the anterior sections are secondary ducts, leading on all sides to the posterior primary ducts. The rows

of goblet cells are frequently loose from the duct walls, and lie in a finely granular substance in the lumina. Primary ducts have been observed to unite, but this is exceptional.

It therefore appears that the longitudinal ridges of glandular tissue in *Chimæra*, which are homologous with the cæcal gland of the Elasmobranchs (Leydig), are simple racemose glands opening by separate duct orifices to the intestine. Their terminal branches are similar to, but smaller than the tubules of a typical cæcal gland; the primary ducts and secondary ducts differ remarkably from the primary tubules leading to the central lumen of a typical cæcal gland in the presence of a complete lining of goblet cells. The character of the epithelial cells changes abruptly to cells similar to, but smaller than, those of the cæcal-gland tubules immediately the ultimate branches of the gland are reached.

The main ducts and their intestinal orifices in *Chimæra* were described by Mazza and Perugia (1894), but their figures give little idea of the nature of the glands.

Heptanchus cinereus.

The histology of the cæcal gland of *Heptanchus* has not been previously described. It shows interesting features which are probably of significance when compared with the glands of *Chimæra*.

A complete series of transverse sections of the gland of an advanced embryo of *Heptanchus cinereus* with the yolk-sac absorbed were made. As in other fishes at this stage the cæcal gland is completely developed. It will be remembered, from the description of the macroscopic features in this Shark, that the gland is lobulated. In the sections placed most anteriorly, only one of these lobules, the larger one, is cut. A little lower, however, the sections pass through two lobules, and in the middle region through three and four lobules (Pl. II. fig. 5). At varying levels in the gland a definite lumen for each lobule can be traced. Near the proximal end the smaller lobules and lumina merge at different levels into the larger one, and the common lumen passes directly to the short, simple gland duct.

The peripheral capsule is similar to that described for *Scyliorhinus*. The white fibrous tissue and inner circular smooth muscle are thicker at the tip of the lobules, and relatively thin in the middle sections. Where more than one lobule is cut in a section, this tissue is seen to form very definite partitions between adjacent lobules. In a few places it penetrates into the peripheral glandular part of each lobule, as seen in Pl. II. fig. 5. The peripheral arterial branches show no peculiar feature. In sections nearing the duct a large ventral vein (the cæcal vein) is present in this now thicker connective tissue. As Pl. II. fig. 6 shows, this vein is full of blood; the proportion of leucocytes is large. In sections through

the simple duct the glandular tissue has disappeared, and the muscular connective tissue occupies the thickness. The cæcal vein is seen to leave the gland and to pass near the free border of a ventral mesentery, which is present in this region in addition to the dorsal mesentery. Successive sections show that this passes into the connective tissue on the dorsal side of the intestine.

The glandular tubules are very similar to those of *Scyliorhinus*, and frequently run in a longitudinal or oblique direction. The nuclei of the glandular epithelial cells are placed near the peripheral border of the tubules, as I have found them in embryos of other genera and at all ages. They are more round than in the adult gland of *Scyliorhinus*. One or more nucleoli are present. The granular nature of the cytoplasm can be well seen in sections stained with Mallory's stain. The cell walls are rather more distinct than in *Scyliorhinus*. Except where the definite partitions of connective tissue with muscle fibres penetrate between the tubules (in some cases to the centre), the connective tissue is very scarce. As in *Scyliorhinus*, the blood corpuscles may be in very close proximity to the gland cells. All varieties of leucocytes may be present, and, particularly in the proximal half of the gland, they are seen to invade the glandular epithelium. Near the duct small patches of a lymphoid nature develop at the expense of the glandular tissue and interstitial connective tissue (Pl. II. fig. 6).

The anterior portion of the central lumen of each of the lobules is bounded by simple columnar epithelium. In sections a little lower, the epithelium becomes transitional with a few mucous cells in the superficial layer. Beneath the transitional epithelium a band of connective tissue is developed, which is continuous with the partitions from the peripheral capsule. The central venous sinuses are surrounded by this tissue in the lower sections. A lobule with the central lumen epithelium of simple columnar character, and no surrounding connective tissue, may be seen in the same section as one with transitional epithelium and much central connective tissue. Free blood corpuscles are seen against the peripheral walls of the tubule cells in increasing numbers as the sections near the duct. In many sections near the duct, in the region where the glandular tubules are reduced to very few, two very distinct lymphoid follicles are seen immediately under the central lumen epithelium; Pl. II. fig. 6 shows these. They bear a close resemblance to the lymphoid nodules which Berry has described in the mucosa of the vermiform appendix of the Rabbit soon after birth, and to Peyer's patches. These lymphoid follicles in *Heptanchus* seem to have replaced the central venous factors which have united into larger vessels in the preceding sections and have formed the ventral cæcal vein in these sections.

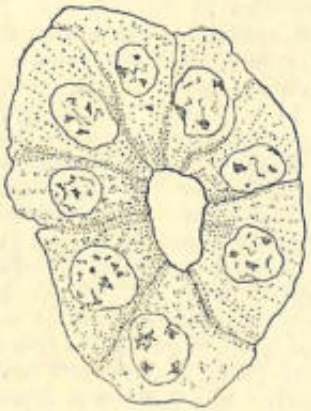
The cæcal gland lobes placed side by side in *Heptanchus* are reminiscent of the separate longitudinal glands of *Chimæra*

It is probable that in *Chimæra* the gland anlagen push into the connective tissue of the intestine in an antero-longitudinal direction, while in *Heptanchus* the whole intestinal wall forms part of the hollow bud which may divide into several pits to form the lobes of the gland. Later the organ in *Heptanchus* is separated from the gut by a proximal constriction which is the common duct of the lumina of the lobes.

Mitsukurina.

It will be remembered from the description of the anatomical features of the gland and related parts in this Japanese Shark that the organ is relatively the largest of those described, that

Text-figure 36.



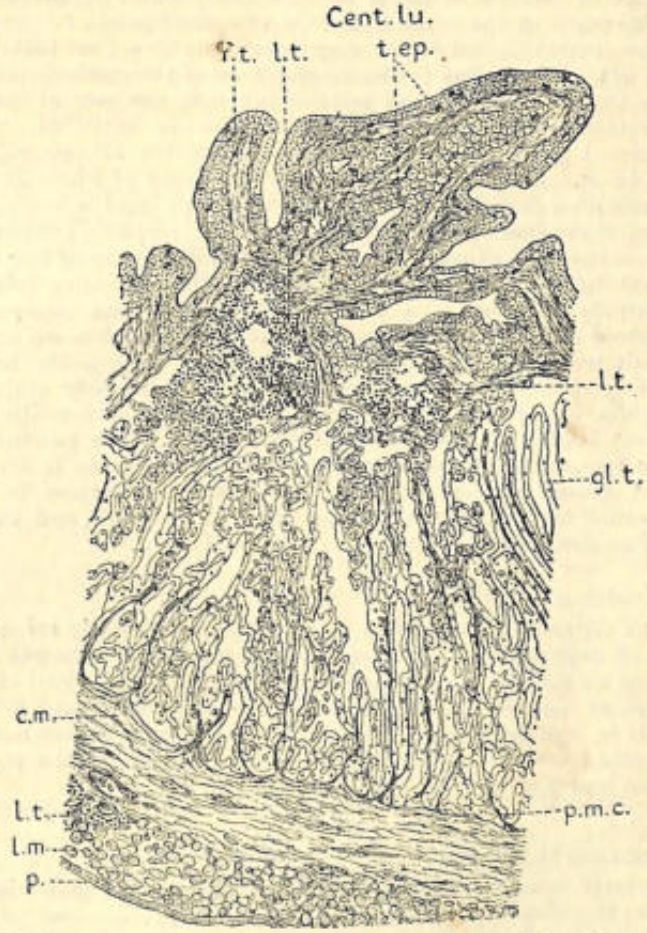
T.S. of glandular tubule of *Squatina* after Mallory's stain, showing minute granules in cytoplasm. (Camera lucida.) × 730.

its duct characters come next in simplicity to those of the Notidanoidei, and that a heavy fold of lymphoid tissue follows the gland mesentery packing closely against the gland throughout its length. The association of this lymphoid tissue with the organ is much more close than in *Scyliorhinus*, where it does not usually extend more than one-quarter or one-half of the length of the gland. It was important, therefore, to section a portion of this gland with the adherent lymphoid tissue.

The sections show that this lymphoid tissue consists of a fine reticulum which is almost hidden by the extremely dense crowding of lymphoid corpuscles. Lymphocytes, mono-nuclear leucocytes, and polymorphs are present, and among the latter coarsely granular eosinophilous cells are unusually abundant. In places, groups of these leucocytes, some of which are actively dividing, are developed in the outer peripheral capsule of the

gland, which consists mainly of longitudinal smooth muscle, and in the inner peripheral coat, which consists mostly of circular muscle.

Text-figure 37.



Mitsukurina. Portion of T.S. of cæcal gland (middle region) to show lymphoid nodules (*l.t.*). (Projection apparatus.) × 25.

p.m.c., penetrating muscle cells; *c.m.*, circular muscle; *cent.lu.*, central lumen *l.m.*, longitudinal muscle. Other lettering as in text-fig. 35.

The middle glandular portion consists of tubules cut in various directions, but in many cases longitudinally, so that primary tubules are seen to take a radial course, sometimes without

branchings, until they near the periphery. The tubule cells have a smaller diameter than those in *Scyliorhinus*, but they are larger than in *Chimæra*. An average diameter is ·02 mm. In places where diffuse lymphoid tissue occurs in the peripheral coat the glandular tubules may lie close to it, and the small amount of connective tissue between the tubules appears to be continuous with the reticulum of the lymphoid patch.

The central lumen has a very erratic outline (see text-figs. 10 & 37). This is due to the development of the epithelium into villus-like folds of mucosa penetrating into the central lumen in various directions. The epithelium is stratified, with occasional goblet cells. Migrating leucocytes are sometimes seen in it. Beneath the epithelium is a band of white fibrous tissue with a few circular muscle-fibres. This band is lacking in places where free blood corpuscles of central lymphoid follicles lie close to the epithelium. These lymphoid follicles are of fair size, as text-fig. 37 shows; they encroach on the glandular tubules externally. There is a fine reticulum as in the mesenteric lymphoid tissue, but the corpuscles lying in its meshes are not so densely packed. Erythrocytes are present; among the leucocytes, lymphocytes are most abundant, while coarsely granular oxyphils are scarce. The clear, transparent nuclei which are present belong to the cells of the reticulum. The presence of these lymphoid follicles may be of great importance in solving the function of the gland. There are no references in the literature to its presence in the gland of any fish, and this is the first description of the organ in *Mitsukurina*.

MUSTELUS VULGARIS.

The histology of the cæcal gland in this fish closely resembles that of *Scyliorhinus*. The only points worthy of note are that leucocytes appear to be abundant in the interstitial blood of the glandular portion, particularly in the peripheral and central portions, and in these regions migratory leucocytes are seen in the glandular epithelium. The epithelium both of the central lumen and the primary ducts is transitional.

SQUALUS ACANTHIAS.

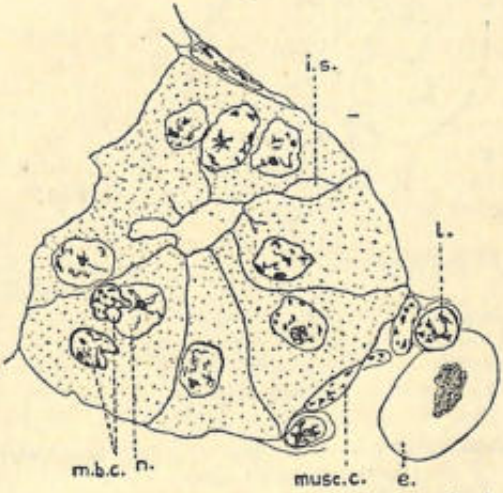
A brief description of the histology of the adult gland in the Spur Dog-fish was given by Hoskins in his account of the embryology of the gland in this genus. In connection with the glandular portion, it is only necessary to mention the fact that, unlike that of *Scyliorhinus*, it is divided into two very definite regions: an inner narrow portion, in which the tubules are cut transversely in transverse sections, and therefore have a longitudinal course; and an outer wide portion, in which the tubules are cut longitudinally, forming semi-complete unbranched radii. In this region the nuclei are frequently placed with their longer diameter parallel with the tubule. It is further

necessary to point out the new facts in the blood system. The blood-supply closely resembles that of *Scyliorhinus*, but the venous system is more exclusively central; the cæcal vein becomes ventral only at the extreme proximal end of the gland. The blood-spaces between the central glandular tubules, which are cut transversely, are larger than those between the radial tubules. In places the adjacent endothelial cells are wide apart, as in *Scyliorhinus*, and migratory corpuscles are seen in the epithelium in all parts of the gland, but more frequently in the central regions.

SQUATINA.

In the gland of *Squatina* the glandular parenchyma is divided into definite radial portions by five or more partitions of fibrous

Text-figure 38.



T. S. of glandular tubule of *Raia* to show migrating blood-cells. (Camera lucida.) × 940.
i.s., intercellular space; *l.*, lymphocyte; *musc.c.*, muscle-cell. Other lettering as in text-figs. 33 & 34.

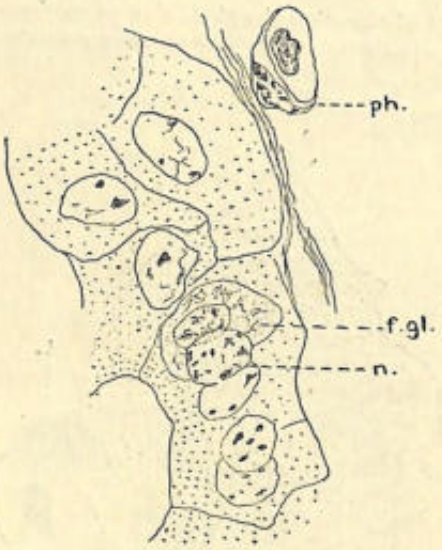
tissue strengthened by muscle cells; these partitions are continuous with the peripheral capsule, near which they are thicker; centrally they are continuous with the connective tissue underlying the central lumen epithelium.

The tubule cells are slightly larger than in *Scyliorhinus* and have more definite walls (text-fig. 36). Granules are present in the cytoplasm; they are frequently denser towards the centre of the tubule and near the approximating cell-walls. The cells are probably actively secretory. The stratified epithelium of the

central lumen is roughly four times as deep as in *Scyliorhinus*, but is otherwise similar.

The circulation is the same as in *Scyliorhinus*, in spite of the curious shape of the gland. In proximal transverse sections the large central vein can be seen penetrating through the thick mass of glandular tissue to take up a ventral peripheral position. This cæcal vein appears to have a large proportion of leucocytes. There is the same very intimate relationship of the blood-stream with the glandular epithelium as in *Scyliorhinus* (Pl. II. fig. 4).

Text-figure 39.



T. S. of tubule cells of *Raia* to show migration of finely granular lymphocyte (*f.g.l.*). (Camera lucida.) ×700.
n., nucleus of tubule cell; *ph.*, phagocyte.

Raia and Torpedo.

No new histological features are exhibited by the sections of the cæcal gland of *Raia* and *Torpedo*. Both the primary ducts and the central lumen are lined by epithelium of the stratified type, which may be as much as eight cells in depth. Sanfelice and Pixell refer to the lining of the "central main duct" as "low cylindrical epithelium, which can only be distinguished from that of the 'ducts' and tubules by the size of the lumen." From my investigations I believe the glands they examined must have been from very immature fishes which had not yet developed the more elaborate epithelium. The blood-relationships are similar to those already described in other glands (text-figs. 38 & 39).

Summary of the New Facts in the Histology.

The histology of the gland in *Heptanchus*, *Mitsukurina*, and *Squatina* is here described for the first time. Previous descriptions of the gland in *Scyliorhinus* are inadequate, and give no mention of the interesting points in the circulation. Leydig's account of the glands in *Chimæra* is fragmentary, and the account given by Mazza and Perugia adds extremely little to Leydig's original report.

The simplest type of cæcal gland is probably that found in *Chimæra*, where several branched tubular glands with separate intestinal ducts have developed in an antero-longitudinal direction into the intestinal wall. From this origin the more complicated type found in *Heptanchus* may have been derived by the gland anlage pushing in a horizontal direction, remaining partially separate, as shown by the definite lobes lying side by side, but having a common duct which is probably produced by constriction. The innumerable tubulo-racemose glands which are typical of the parenchyma of the adult cæcal gland of Elasmobranchs arise from the central lumen at different levels, and their complicated method of branching varies in different genera. In *Scyliorhinus*, for example, the branches continue to multiply in the extreme peripheral regions even after maturity, but in *Squalus* the additional branching is limited in mature fishes to the central parenchyma, while the peripheral tubules are all radially placed and increase in length with the increased girth of the gland.

The gland tubules have a peculiarly close relation to the blood-stream in all genera.

The arterial supply is exclusively of external origin, while the main factors of the venous system are central and exclusively so, except at the proximal half of the gland in some genera. The cæcal artery passing directly through the mesentery to the gland breaks up in the capsule into a rich plexus of encircling pre-capillary arteries; radial branches from these penetrate between the glandular parenchyma, and abruptly give rise to a capillary plexus which occupies almost the whole of the connective tissue between the glandular tubules. The venous capillaries are collected into large thin-walled venules which anastomose in the central glandular region; these form large central veins which join into a large cæcal vein; this becomes superficial near the gland-duct, and constitutes the beginning of the dorsal intestinal vein. The blood-plexus filling the spaces between the glandular tubules takes the shape of these spaces. The endothelial walls are in direct contact with the glandular epithelial cells; the endothelial cells are frequently very wide apart, so that blood corpuscles are pressed immediately against the epithelial cell walls. Leucocytes may migrate into the epithelium in all regions. There is a delicate superficial lymphatic plexus, and lymphatic vessels follow the central veins. The glandular tubules are well supplied

with nerve-endings from the sympathetic nerve branches of the capsule.

The absence of lymphoid tissue in the cæcal gland has been cited by several authors as a point of contrast with the vermiform appendix of higher vertebrates.

The present investigations show that a simple form of lymphoid tissue is present in the organ in varying degrees of development in different genera. Isolated groups and diffuse patches of lymphoid corpuscles are found in the peripheral and central regions in *Scyliorhinus*, *Mustelus*, *Squalus*, and *Squatina*. More definite lymphoid follicles occur near the central lumen epithelium in *Heptanchus* and *Mitsukurina*. These follicles contain free erythrocytes and numerous leucocytes in various stages of development scattered in an obscure reticulum. Although these are simple types of lymphoid tissue similar to those met with in the embryo of higher vertebrates, they are also of the same type as the lymphoid patches and nodules which Drzewina and others have found in a number of organs throughout the Ichthyopsida, and which they consider compensate for the absence of the more orthodox lymphatic glands, which it is well known are lacking in these animals. They may be concerned in the destruction of effete corpuscles or in the formation of new leucocytes.

Embryology of the Cæcal Gland.

Notes on the Previous Embryological work.

The investigations of Blanchard, Sanfelice, and Hoskins have been mentioned in the Historical Summary (pp. 104 & 106).

Blanchard (1878) noticed the gland bud in an embryo *Acanthias* 23 mm. in length developing on the left dorsal side of the intestine. He erroneously described the inner lining of this bud as connective tissue.

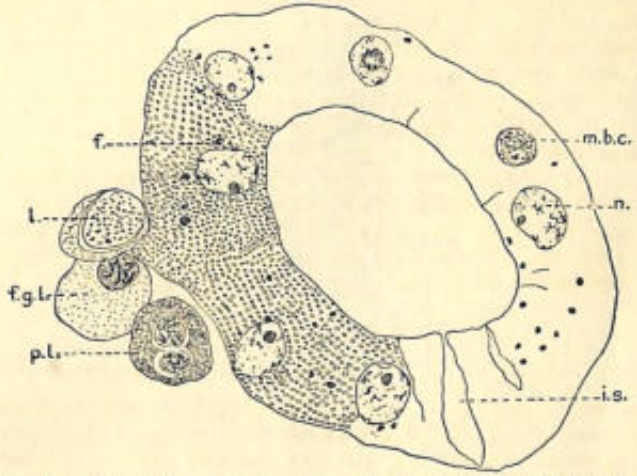
Sanfelice (1889) first reported the endodermal origin of the cells lining the lumen of the bud; he showed that successive evaginations of this layer give rise to the glandular tubules of the organ. He saw the gland anlage in embryos of *Torpedo* and *Pristiurus* 15 mm. long.

Hoskins (1917) found the anlage in *Squalus acanthias* embryos of the same length, but he disagrees with Blanchard in finding it invariably placed in a right dorso-lateral position. His paper gives an exhaustive account of the peculiar manner of formation of the tubules in this genus, and this constitutes the major portion of his work. He shows that by repeated outpouchings of the endoderm wall six orders of tubules may arise; a primary tubule may pass to the periphery without branches; it may divide dichotomously near its origin; it may extend to the periphery, with lateral branches at right angles; lastly, it may divide near the central lumen into a cluster of secondary tubules.

The development of the organ in *Scyliorhinus* (*Scyllium*) *canicula* has not been worked out. In the adult the arrangement of

the tubules is different from that in the adult *Squalus* gland. Other differences in the adult cæcal glands of the two fishes have been pointed out. It was thought desirable to follow the embryology in *Scyliorhinus* and pay attention to the vasculogenesis, which has been almost neglected; knowledge of this is necessary because of the interesting feature in the circulation of the adult gland. Embryos of *Squalus*, *Heptanchus*, and *Torpedo* were used for comparison.

Text-figure 40.



T. S. of glandular tubule of *Scyliorhinus* (*Scyllium*) treated with osmic acid. (Camera lucida.) × 600.
l., lymphocyte; *f.*, fat particle. Other lettering as in previous figures.

Development of the Cæcal Gland in Scyliorhinus canicula.

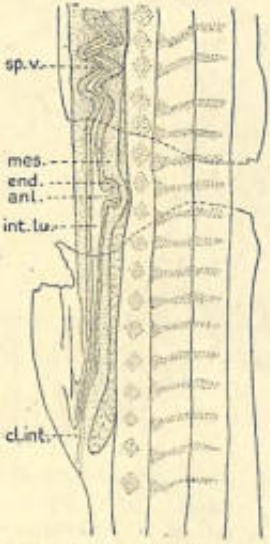
Examination of Transparent Embryos.

The general appearance of the developmental stages can be well seen in embryos, from 13 mm. upwards, which have been stained in bulk and then cleared in benzole and methyl salicylate. After an examination of the positional relations of the gland, this portion of the intestine could then be dissected out with the aid of a binocular microscope. Transverse and longitudinal serial sections of selected stages were cut.

The anlage of the gland is first seen in embryos 14 to 14·5 mm. long as a slight evagination of the endoderm, causing a small dorsal bulging of the mesoderm. In embryos 15 mm. long the evagination is more easily seen; it involves no thickening of the endoderm in this region. In two embryos 15 mm. in length two shallow pockets were seen close to one another (text-fig. 41). This is interesting when compared with the several-lobed

gland of *Heptanchus*, but may be a transitory phase caused by unequal growth of the epithelial cells, for in the immediately succeeding stages the internal wall of the pocket is a simple curve. The anlage is considerably nearer the spiral valve than the anus, as is shown in Table I. in the early portion of this paper. The table also shows that the position in *Squalus* embryos is similar, although Hoskins stated that it is about half-way between the spiral valve and the anterior end of the cloaca.

Text-figure 41.



Scyliorhinus (Scyllium) canicula embryo (15 mm. long). Cleared entire. Part of body-wall removed to show gland anlage. (Camera lucida.) × 20.
anl., anlage of cæcal gland; *cl.int.*, position of cloacal opening of intestine; *end.*, endoderm; *int.lu.*, intestinal lumen; *mes.*, mesenchyma; *sp.v.*, spiral valve.

In embryos of 16 mm. to 18 mm. long the more pronounced gland-bud is a hollow pocket extending at right angles to the gut and pointing dorso-laterally. It is usually directed to the right side of the embryo; Hoskins said it was invariably to the right in *Squalus*.

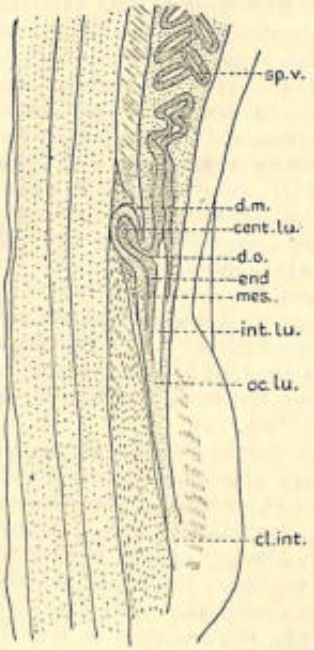
In embryos over 19 mm. long the apex of the bud extends cephalad. The dorsal mesentery of the gland can now be seen extending in an antero-dorsal direction from the blunt tip; its anterior border is quite free from the intestine, so that the valvular intestine is left without mesentery from this stage onwards.

A little later, in embryos of 21 to 22 mm., the cavity of the bud

is partially lost by a narrowing at the proximal end of the gland; the epithelial walls are closely approximated in this future duct region, so that the lumen, with wavy outline, is only left at the blunt end of the bud. At this stage the gland is about 0·34 mm. long. The lumen of the intestine between the gland-bud and the base of the spiral valve is also occluded in these embryos (text-fig. 42).

The next stages, in embryos of 23 to 26 mm. long, show marked changes. The gland increases rapidly in length, more than in

Text-figure 42.



Scyliorhinus (*Scyllium*) *canicula* embryo (21·5 mm. long). Cleared entire. (Camera lucida.) × 20.
cent.lu., central lumen of gland; *d.m.*, dorsal mesentery of gland; *d.o.*, opening of gland-duct; *oc.lu.*, occluded intestinal lumen.

width; the central lumen has an erratic outline which deepens in places into evaginations at right angles to the long axis of the tubules; in embryos of 25–26 mm. the primary tubules have already formed from these evaginations. At this time the post-valvular intestine begins to curve because the intestine has outgrown the length of the body-cavity. The point of greatest curvature is immediately posterior to the duct of the cæcal gland (Pl. III. fig. 10). With the rapid increase in the length of

the gland, the length of the duct grows rapidly, and is slightly curved proximally by the curving of the intestine. It is, therefore, decidedly directed towards the spiral valve. The intestine posterior to it has grown rapidly, but that portion between the gland duct and the spiral valve has not grown in length, so that the duct orifice is relatively nearer the spiral valve. In *Squalus* most of the duct is involved in the curving of the intestine, but in *Scyliorhinus* the extreme proximal end alone is involved (see Hoskins).

In embryos of about 30 mm. long the gland is relatively larger than in the adult. Its tip reaches as far forwards as four and a half turns of the spiral valve; this is clearly shown in Pl. III. fig. 10. The duct is also relatively longer than in the adult. Its intestinal orifice shows an outgrowing posterior lip of mucosa, which is caused by the curving of the duct with the curving of this part of the intestine. This is the anteriorly-directed short intestinal portion of the duct noticed in the adult. In *Squalus* this portion of the duct is very long at this stage, and remains relatively long in the adult (Hoskins). In the embryo and the adult of *Heptanchus* and *Torpedo* the duct remains unchanged from the earlier condition. In the embryos of *Scyliorhinus* at this stage, smaller secondary tubules have already branched from the primary tubules.

In embryos 40 mm. long the gland is still relatively long, and is much wider because of the development of tubules of several orders; the duct is relatively long; the large intestine posterior to it is still more bent, and the posterior part of the valvular intestine is also bent, but in an opposite curve, so that an S-shape is produced (Pl. III. fig. 11).

In older embryos the duct ceases to grow, and its orifice gets progressively nearer the spiral valve; the gland increases in length and width with additional gland branchings. In embryos 50 mm. long, and over, there is a very definite thickening of the dorsal mesentery, adhering closely to the tip of the gland and passing fully half-way down the dorsal side of the organ. This is identical in position with the adherent lymphoid tissue of the adult mesentery. In the embryos it is indistinguishable from the developing gonad both of the male and female embryos.

The relative length of the cæcal gland throughout life is shown in the following table:—

	Length of Fish (in mm.).	*Length of Gland* (in mm.).	*Length of Gland percentaged for length of Fish* (in mm.).
Embryos:			
Large yolk-sac	21·5	0·34	1·58
Large yolk-sac	30	0·9	3·0
Large yolk-sac	60	1·75	2·91
Yolk-sac 12 mm. in diam.	83	2·5	3·04
Yolk-sac 5 mm. in diam.	87·5	2·75	3·14
Yolk-sac absorbed	98	3·25	3·31

Other Fishes:	*Length of Fish* (in mm.).	*Length of Gland* (in mm.).	*Length of Gland percentaged for length of Fish* (in mm.).
Average of 2 fishes	124	4·9	3·93
„ „ 7 fishes	370	8·6	2·32
„ „ 27 fishes	447	10·8	2·4
„ „ 22 fishes	550	12·7	2·3
„ „ 56 fishes	641	15·5	2·4

Additional Observations from Serial Sections.

In the earliest stages, up to 20 mm. embryos, the endoderm of the cæcal-gland bud has four, and sometimes five, rows of oval nuclei placed rather more closely together than in the neighbouring intestinal endoderm. The cell walls are exceedingly indistinct. Small vascular channels are seen in the mesenchyme in the anlage; they were noticed by Hoskins in *Squalus* embryos. The mesoderm cells and their nuclei are flattened in the direction of the evagination.

The gland endoderm is still smooth in embryos 18 to 20 mm. long; the nuclei are not so crowded, but there are still four layers of cells. The vascular channels are now much larger. In an embryo 18 mm. long a wide channel was seen in the mesenchyme at the proximal end of the gland, and from examination of the preceding and succeeding sections, this appeared to link up with a wide dorsal intestinal channel in one direction, and to pass close to the gland lumen in the other. This is probably the beginning of the cæcal vein.

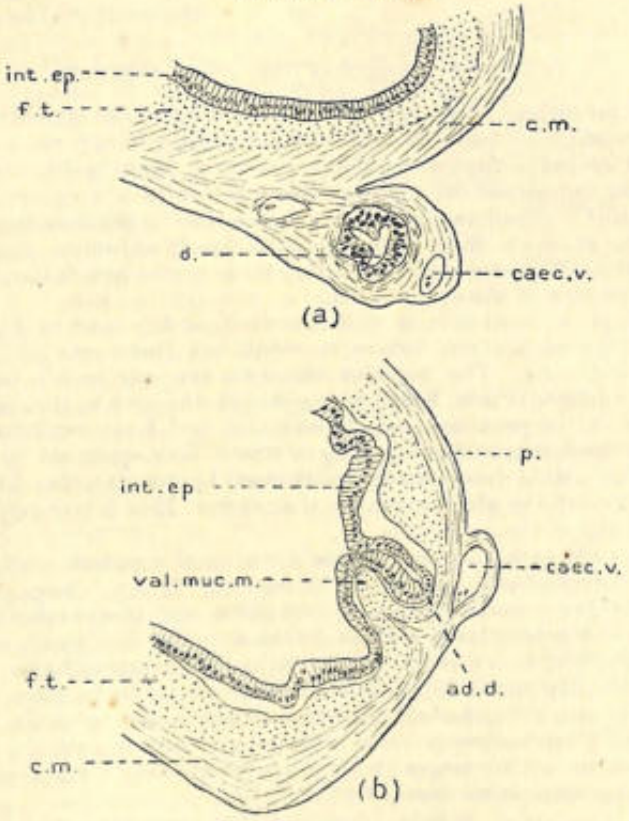
Text-fig. 44 is a camera lucida drawing of a vascular channel in a longitudinal section of an embryo 23 mm. long. The channel lies close to the lumen epithelium, and is separated from it only by a very incomplete endothelial wall. The scarce endothelial cells closely resemble the cells of the mesenchyme, and are probably not differentiated from it at an early stage, as a strictly specific endothelium. The channels are so wide that several blood corpuscles can lie side by side in it. White corpuscles in various stages of development are seen; the erythrocytes are as large as they are in the adult.

At this stage, tubule formation has commenced. Large evaginations of the lumen epithelium bulge very deeply into the mesenchyme. The epithelial nuclei in these regions are round and much less crowded than in the central portions; the epithelial cells are only one or, at the most, two cells deep in the evaginated parts.

From this stage and in older embryos the epithelial cell nuclei have a peripheral position. This characteristic position is also noticeable in the sections of the glands of *Heptanchus* and *Squalus* embryos, but has not been mentioned by previous writers.

In embryos about 35 to 40 mm. long the gland lumen is wide and very irregular, because of the part it plays in rapid tubule formation at this stage. The lumen epithelium now consists of simple columnar cells with peripheral nuclei. It is interesting to notice that it is stratified in the earliest stages, then becomes

Text-figure 43.



Scyliorhinus (*Scyllium*) *canicula* embryo (40 mm. long). (Camera lucida.) × 40.
(*a*) T.S. through duct of cæcal gland; (*b*) T.S. through portion of duct adherent to intestinal wall.

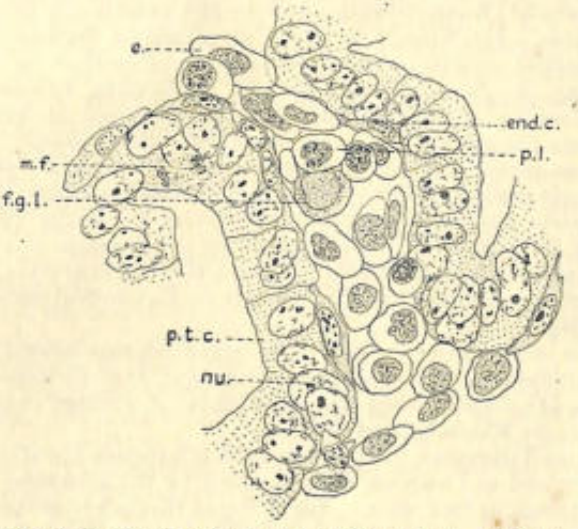
ad.d., adherent portion of duct; *int.ep.*, intestinal epithelium; *val.muc.m.*, valve-like fold of mucous membrane. Other lettering as in text-figs. 35 and 37.

of simple character, which is retained until the fishes are nearing maturity, when it becomes stratified once more. There are tubules of first, second, and third order in the 40 mm.-embryo. The anteriorly-directed and valve-like intestinal portion of the duct can be seen clearly in transverse sections. It is clear that

this involves only the epithelium and underlying mesenchyme, and not the peritoneum (text-fig. 43 *a* and *b*). It is therefore impossible to agree with Howes, who considered that the whole of the intestinal wall was invaginated to form this "super-added" duct.

There are three or four orders of tubules in the embryo of about 83 mm. This corresponds to the number found by Hoskins in *Squalus* embryos 95 mm. long. In *Scyliorhinus*, unlike *Squalus*, additional orders of branches appear to be added throughout life. In longitudinal sections of the whole posterior half of the embryo stained with Mallory's triple stain, the

Text-figure 44.



Scyliorhinus (*Scyllium*) *canicula* embryo (23 mm. long). L.S. through primary tubules and blood sinusoid. (Camera lucida.) × 650.
e., erythrocyte; *end.c.*, endothelial cell; *f.g.l.*, finely granular leucocyte; *m.f.*, mitotic figure; *nu.*, nucleus of tubule cell; *p.l.*, polymorph leucocyte; *p.t.c.*, primary tubule cell.

epithelial nuclei of the gland stain intensely with fuchsin, and contrast sharply with those of the intestinal epithelial cells and with those of the kidney tubules, which stain faintly.

In this stage the cæcal vein is very distinct; the portion of it which is in the gland has been compressed internally by the development of the numerous tubules, and lies close to the central lumen. The venous system has still a sinusoidal character. The cæcal artery in the mesentery is very distinct, and there are arterial branches in the gland capsule.

COMPARATIVE STUDY, IN OTHER ICHTHYOPSIDA AND IN SAUROPSIDA, OF THE ORGANS WHICH MAY BE HOMOLOGOUS WITH THE CÆCAL GLAND.

From the work of Howes, Kostanecki, and Morgera it seems probable that the cæcal gland of the Selachii is homologous with the cæcum of all vertebrates which possess this organ. An attempt has therefore been made to examine the junction of the large and small intestine in other Ichthyopsida and in Sauropsida, particularly in cases where the existence of this organ is in doubt.

1. Teleostomi.

Howes considered that a cæcal diverticulum is probably present in the young of all Teleostei; it is homologous to the cæcal gland of Elasmobranchs and to the cæcum coli of higher vertebrates. He figured a small diverticulum formed by the asymmetrical anterior end of the large intestine in young specimens of *Trigla gurnardus* and *Cyclopterus lumpus*; the small intestine opens into the large intestine on one side, and the opening is guarded by a circular "ileo-colic" valve.

In post-larval and young specimens of *Pleuronectes platessa*, *P. limanda*, and *P. microcephalus* I find that a distinct increase in diameter marks the commencement of the large intestine (text-fig. 31); internally it is marked by the presence of a valve, around which the large intestine forms a circular dilatation, which is sometimes asymmetrical. There is no histological peculiarity in this region.

Cuvier and Valenciennes (1830) regarded this lateral or bilateral dilatation, in such fishes as *Box salpa*, as of no importance.

Owen (1846) described the occurrence of distinct cæcal processes in the Flounder and in *Box*.

In some Teleostomi the large and small intestine are of uniform diameter, and can only be distinguished by the character of the internal wall, as in *Salmo*. According to Howes's hypothesis, the young of *Salmo* should have a cæcal process. To verify this, I examined a series of post-larval and young Salmon which were kindly put at my disposal by Dr. Esdaile. In no case was there any indication of a rudimentary cæcum; the terminal portion of the intestine was symmetrically dilated.

Among Ganoids, I have examined *Acipenser* and *Polypterus*. In both cases the spiral valve is very extensive, and may reach to within 1 cm. of the anus. Sections of the reduced post-valvular intestine show no histological peculiarity.

Among Dipnoi, I have examined the intestine of *Ceratodus* and of a small *Protopterus*, and have found no glandular mass in the terminal portion of the straight intestinal wall; the spiral valve is present throughout the length of the intestine.

W. N. Parker (1889) compared the cloacal cæcum in *Protopterus* with the "appendix digitiformis" of Selachii. This view was shown to be incorrect by Graham Kerr (1901), who described

the development of the cloacal cæcum. He followed the early anatomists, Owen and Hyrtl, in showing this organ to be a projection of the urinogenital sinus, probably homologous with the sperm-sacs of Selachii and the urinary bladder of Teleostei.

2. Batrachia.

According to some morphologists, there is no cæcal pouch in Batrachia; the short hind-gut commences at the constriction of the intestine and has an increased diameter.

Perrault has described a small cæcum in *Salamandra terrestris*, but Funk, as cited by Milne-Edwards, denied its existence in *Salamandra maculosa*. Marshall figures an asymmetrical dilatation at the origin of the terminal portion of the intestine in *Rana*. Howes affirms this (pl. i. fig. 3 of his paper); he shows that this diverticulum is supplied by a posterior branch of the superior mesenteric artery, which he believes to be the homologue of the cæcal artery in Elasmobranchs, and therefore he considers that the cæcum in *Rana* corresponds morphologically with the "digitiform appendix" of Selachii.

Wood-Jones (1900) made a very brief note on an abnormal "outgrowth of lymphoid nature" at the junction of the large and small intestine of *Rana*. In 25 per cent. of Frogs fed with fatty meals he found a small movable and highly vascular appendage supported by mesentery at the anterior end of the large intestine. This outgrowth was wholly composed of lymphoid tissue, with connective tissue and blood-vessels, and the lining of the gut did not pass into it. This lymphoid tissue was continuous with that of the intestine in this region.

I have examined the intestine of Axolotl, *Salamandra maculosa*, and *Triton*, and have found a small lateral "cul de sac" lying to the left side in all cases. It is made obvious by the externally and internally constricted opening of the small intestine into the large intestine (*Triton*, text-fig. 32).

Pl. III. fig. 8 shows the beginning of the large intestine and the anterior end of the cæcum of a young Axolotl in transverse section. In sections slightly more posteriorly placed the cæcum has a cavity continuous with that of the large intestine. Diffuse lymphoid tissue is beginning to develop extensively in the wall of the cæcum. The intestinal wall is thickened, and supplied with this tissue at the junction of the large and small intestine and for a number of sections posterior to it. The remainder of the large intestine has a thinner wall.

Little attention seems to have been paid to the nature of this cæcum in Amphibia.

3. Reptiles.

According to Gadow, in the 'Cambridge Natural History,' a short cæcum is sometimes present at the beginning of the "rectum" in Lacertilia, more particularly in the herbivorous

forms, where the intestinal canal is longest; it is absent in Chelonia and Crocodilia. Owen (1846) stated that in *Draco*, some species of *Agama* (*Ardiscosoma*), *Galiotes*, *Stellio*, and *Monitor* there is a small cæcum at the commencement of the colon which is distinct from the slender rectum. Milne-Edwards states that the ileum opens by a slit guarded by mucous membrane folds in a ridge of the cæcum, and there is a second orifice for egress of contents. Home figured a cæcum at the origin of the large intestine in the Skink and *Iguana*. In *Iguana tuberculata* and *Cyclura teres* there is a sacculated cæcal pouch of considerable size derived from the proximal segment of the colon. The opening of the first portion of the cæcum is guarded by an annular sphincter. A second circular valve separates this portion from the second portion of the cæcum, and the remainder of the complicated cæcum is divided by semicircular valves, and its opening to the terminal portion of the gut has a small valve. This cæcum in *Iguana* has been found to contain portions of the less digestible portions of vegetable food. It is absent in the carnivorous Heloderma. The lateral pouch is large in Ophidia, and, according to authors other than Gadow, a rudimentary cæcum is present in many Chelonia.

I have noticed a lateral dilatation in the Tortoise similar to that which is always present in the Lizard. Weidersheim, in 1886, stated that the cæcum of *Amphisbæna*, which is of ordinary Lacertilian type, resembles the "appendix digitiformis" of Selachii. Howes adopted this view from his belief in the homology of the arterial supply.

In the Lizard I find the cæcum is characterized by the presence of lymphoid tissue.

In Reptilia the cæcum appears to be absent only in the Crocodilia. In some Lacertilia it is well developed and complicated.

4. Aves.

Milne-Edwards and Chalmers Mitchell have described the bilateral cæca at the junction of the large and small intestine in Birds. These two diverticula usually have their entrance to the commencement of the short, large intestine guarded by a valve, and they vary enormously in development. According to Milne-Edwards, the varying development of these organs follows a physiological rule. In granivorous, insectivorous, omnivorous, and rapacious birds, such as the Hen, the Duck and the Swan, etc., the cæca are much developed, while in Piscivorous birds they are little developed. Berry, in 1901, appears to be the first to mention the predominance of lymphoid tissue in the cæca of birds. He found that when the cæca are short, as in the Pigeon, this tissue is very dense, but when they are long, as in the Fowl, it is diffuse. He and other authors therefore assign a blood function to these organs.

In his valuable and exhaustive account of the "Intestinal

Tract of Birds," 1901, Chalmers Mitchell classifies the various modifications of the cæca. He distinguishes a primitive type (*i. e.* near the reptilian type) in which the digestive function is retained, but in some cases there is also the beginning of a glandular function. Modifications of this type are in the direction of increase or decrease in size. When the cæca are enlarged the digestive function is retained, but the function is also "partly secretory or excretory." Reduced cæca are of two types. A vestigial type is especially noticeable in frugivorous birds. The other type of reduction is characterized by well-developed lymphoid tissue. Chalmers Mitchell decides that "diet is no complete explanation of the character of the cæca."

Conclusions.

Functional cæca at the junction of the large and small intestine are probably absent in the Teleostomi. In Batrachia, Reptilia, and Aves, cæcal diverticula are developed in varying degree, but in the same position. A digestive and a problematical blood function for these organs have been established in Birds. In Reptiles the function has been regarded as solely digestive, but the double function most probably exists both in the Reptilia and in Amphibia because lymphoid tissue characterizes the cæca in both groups.

There appears to be no literature on the development of these cæca.

The cæcal gland of Selachian fishes is probably homologous with the cæca in Batrachia, Reptilia, and Aves. Howes was the first to suggest this homology (with Batrachia and Reptilia) from his observations on the circulation. The presence of simple lymphoid tissue in the cæcal gland, which has been shown in the histological section of this paper (p. 172), is another point of similarity. All other writers have supposed that the gland differs markedly from the vermiform appendix and cæcum because of the absence of this tissue.

Note on the Physiology of the Cæcal Gland.

From the preceding account of the macroscopic and histological features of the gland throughout Selachian Fishes, the suggestion of a double functional rôle arises. Firstly, it undoubtedly discharges a liquid into the intestinal lumen; the physiological effect of this is doubtful, but it appears to be most important in the Galeoidei and Squaloidei, in which the duct is highly specialized to convey the liquid in the direction of the spiral valve. Secondly, the importance of the blood-supply, the highly vascular nature of the organ, the intimate relation of the glandular tubule cells with the blood-stream, and the presence of simple lymphoid tissue, point to an obscure blood function. The endodermal origin of the gland and anteriorly-directed duct in many genera seem to indicate that a urinary function is unlikely.

I have performed the tests recommended by Sullivan (1907) in his experiments on the digestive tract of Elasmobranchs, on glycerin extracts of the gland, and on the secretion only of a large *Raia* gland. The result showed a lipolytic activity, but no proteolytic or amylolytic enzymes appeared to be present. In this I agree with Morgera.

The characteristic biuret, nitro-benzaldehyde, furfural, and sodium hypobromite tests were performed to test for the presence of urea. Negative results were obtained.

The lumen content of the gland was tested for mucin, which was found to be present in very small quantities.

It is desirable to repeat all these tests a number of times in order to be confident of the results. This I hope to do, and, in addition, to proceed with some further experimental investigations which have already been commenced.

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EXPLANATION OF PLATES I.–III.

Plate I. (figs. 1–3). *Scyliorhinus* (*Scyllium*) *canicula*.

Fig. 1. Photomicrograph of transverse section through proximal half of cæcal gland. Venous sinus passes from centre to periphery. × 25 diam.

Fig. 2. Photomicrograph of portion of transverse section of cæcal gland to show the lumen region. × 75.

Fig. 3. Photomicrograph of portion of transverse section of cæcal gland to show its dorsal mesentery with adherent lymphoid tissue. × 40.

PLATE II. (figs. 4–7). *Squatina, Heptanchus, Chimæra.*

Fig. 4. Photomicrograph of portion of transverse section of cæcal gland of *Squatina* to show migration of leucocytes into the glandular tubules. × 500.

Fig. 5. Photomicrograph of transverse section through proximal half of cæcal gland of *Heptanchus cinereus* (advanced embryo, 25·5 cm.) to show gland lobes. × 30.

Fig. 6. Photomicrograph of transverse section of cæcal gland of *Heptanchus cinereus* cut immediately anterior to duct region, to show patches of lymphoid tissue. × 50.

Fig. 7. Photomicrograph of transverse section of homologous gland in intestinal wall of *Chimæra*, near openings of primary ducts to intestinal lumen. × 40.

PLATE III. (figs. 8–11). Axolotl cæcum, *Scyliorhinus* (*Scyllium*) embryos.

Fig. 8. Photomicrograph of transverse section through anterior end of large intestine and cæcum of Axolotl. × 50.

Fig. 9. Photomicrograph of portion of embryo of *Scyliorhinus* (*Scyllium*) *canicula*, 21·5 mm. long, to show origin of cæcal gland a little below termination of spiral valve. × 25.

Fig. 10. Photomicrograph of cæcal gland and spiral valvular intestine of embryo of *Scyliorhinus* (*Scyllium*) *canicula*, 30 mm. long. × 25.

Fig. 11. Photomicrograph of cæcal gland and intestine of embryo of *Scyliorhinus* (*Scyllium*) *canicula*, 41 mm. long. Gland duct opens towards spiral valvular intestine, which is on the right. × 25.

Explanation of Lettering of Text-figures and Plates.

a.b., arterial branch; *abd.p.*, abdominal pore; *ad.d.*, adherent portion of duct of cæcal gland; *a.mes.a.*, artery of anterior mesenteric series; *an.*, anus; *anl.*, anlage of cæcal gland; *b.*, bristle; *b.c.a.*, branch of cæcal artery to dorsal surface of intestine; *b.coel.a.*, branch of cœliac artery; *c.m.*, circular muscle; *c.v.*, central vein; *cæc.*, cæcum; *cæc.a.*, cæcal artery; *cæc.gl.*, cæcal gland; *cæc.gl.l.*, cæcal gland second lobe; *cæc.v.*, cæcal vein or origin of dorsal intestinal vein; *cent.lu.*, central lumen of gland; *cent.v.*, central vein (origin of dorsal intestinal vein); *cent.lu.l.*, central lumen of lobe of gland; *cl.*, cloaca; *cl.int.*, cloacal opening of intestine (position of); *con.musc.*, contracted muscle in intestinal wall; *const.*, constriction; *d.*, primary duct of cæcal gland; *d.ao.*, dorsal aorta; *d.int.a.*, dorsal intestinal artery; *d.int.v.*, dorsal intestinal vein; *d.l.c.*, diffuse lymphoid corpuscles; *d.m.*, dorsal mesentery of cæcal gland; *d.o.*, orifice of duct of cæcal gland; *d.y.s.*, dorsal surface of yolk stomach; *e.*, erythrocyte; *end.*, endoderm; *end.c.*, endothelial cell; *ep.*, epidermis; *f.*, fat; *f.e.*, free edge of ventral mesentery; *f.y.l.*, finely granular lymphocyte; *f.t.*, fibrous tissue; *g.*, groove; *g.t.*, glandular tubule (in Microphotograph 3); *gl.p.*, glandular portion; *gl.t.*, glandular tubule; *gt.*, gutter; *i.s.*, intercellular space; *int.b.c.*, interstitial blood corpuscles; *int.ep.*, intestinal epithelium; *int.l.*, intestinal lumen; *int.m.*, intestinal mesentery; *l.*, lymphocyte; *l.int.*, large intestine; *l.m.*, longitudinal muscle; *l.m.f.*, lateral mesenteric fold; *l.t.*, lymphoid tissue; *m.b.c.*, migrating blood corpuscle; *m.f.*, mitotic figure; *m.oe.*, mesentery supporting oviduct; *mes.*, mesenchyme; *muc.c.*, mucous cell; *muc.memb.*, mucous membrane; *musc.*, muscle; *musc.c.*, muscle cell; *n.*, nucleus of tubule cell; *nu.*, nucleolus; *oc.lu.*, occluded intestinal lumen; *ov.*, oviduct; *p.*, peritoneum; *p.a.*, peripheral branch of cæcal artery; *p.c.*, peripheral coat of gland; *p.d.*, primary duct; *p.f.*, pelvic fin; *pch.*, deep pouching of gut lumen; *ph.*, phagocyte; *p.l.*, polymorph leucocyte; *p.m.c.*, penetrating muscle cells; *p.t.*, primary tubules; *p.t.c.*, primary tubule cell; *p.v.int.*, post valvular intestine; *s.d.*, secondary duct; *s.int.*, small intestine; *s.musc.*, smooth muscle; *s.t.*, secondary tubules; *sp.v.*, spiral valve; *t.ep.*, transitional epithelium; *t.gl.*, termination of glandular portion; *t.o.*, temporary closing of duct lumen; *t.sp.v.*, termination of spiral valve; *v.*, vein; *v.int.*, valvular intestine; *v.m.*, ventral mesentery of gland; *val.muc.m.*, valve-like fold of mucous membrane; *v.s.*, venous sinus; *y.s.*, yolk stomach.

9. Some Observations on the Female Urogenital Organs of the Didelphyidæ.

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(Plates I.–VII.*; Text-figures 1–6.)

Introduction.

The material on the examination of which the present paper is based was obtained partly from specimens collected by one of us (J. P. H.) during the Percy Sladen Expedition to Brazil in 1913, and partly from specimens in the collection of the Natural History Museum through the kind offices of Mr. Oldfield Thomas. To him, as well as to Mr. M. A. C. Hinton, we desire to express our thanks for the help they have afforded us. We are also indebted to Prof. J. Graham Kerr for a specimen of *M. pusilla*, and to Mons. A. Touchon, late of Theresopolis, Brazil, for specimens of *M. americana* and *M. theresa*.

The organs of some eleven species belonging to six out of the seven existing genera have been examined in serial sections, and it is thus possible to provide, for the first time, a comparative account of the relations of the female genital ducts in the South American Marsupials, our knowledge of which, in comparison with that of the Australian forms, has remained singularly incomplete.

We have made no attempt in this paper to provide exhaustive descriptions of the organs examined, but have confined ourselves, in the main, to the elucidation of the variations in the structure of that distinctive part of the marsupial female genital system, the vaginal apparatus, comprising the lateral vaginal canals and the median vaginæ (vaginal culs-de-sac).

On developmental grounds, the term median vaginæ should be applied to the cæcal outgrowths which arise from the Müllerian ducts just where they bend outwards, *i.e.*, to those portions of the median culs-de-sac situated in the adult behind the apparent origins of the lateral vaginal canals, but we continue to use the term in a topographical sense as indicative of the median chambers in their entirety, into which the ora uteri open.

We are much indebted to Mr. F. J. Pittock for the care he has taken in the preparation of the microphotographs and to Mr. A. K. Maxwell for working up the figures on Plates I., II. & VII.

Historical.

The earliest description of the anatomy of the female organs of a Didelphyid known to us is that by "that learned and accurate

* For explanation of the Plates see p. 217.

anatomist," Dr. Edw. Tyson, in his account of the anatomy of an Opossum (*? Didelphys virginiana*) published in vol. xx. of the Philosophical Transactions for the year 1698, and apart from the naming of the parts, an excellent description it is, considering he had only a single specimen at his disposal for the investigation of its entire anatomy. He recognized and described the two ovaries, Fallopian tubes, and uteri. The latter he termed the "cornua uteri," since he regarded what are really the median vaginal culs-de-sac as the true uteri. "These 2 cornua," he says (1), "empty themselves into the 2 uteri, just in the middle where they are conjoined together." He observed the median vertical partition which completely separates the vaginal culs-de-sac ("uteri"), "though outwardly they both seemed as one continuous body," and he described how the latter are continued out in a lateral direction, near the neck of the bladder, to form expansions in the form of turns or loops (really the expanded anterior portions of the lateral vaginal canals or vaginal loops) which "are continued thence into the two vaginæ which lie just under [really above] the urethra." He showed, further, that the two vaginæ and the urethra open into a common passage (urogenital sinus) and that this finally leads to the exterior by an aperture common to it and to the rectum.

In 1763, Daubenton (in Buffon, 'Histoire Naturelle,' T. x.) described and figured the female genital organs of "le Sarigue ou l'Opossum" [=*Metachirus opossum*], one of his specimens having five mammæ and four pouch-young, measuring "deux pouces" from the vertex of the head to the root of the tail, the other having seven mammæ (the typical number for the species). According to Daubenton's account, the median vaginæ were very incompletely separated by a kind of septum ("raphé") in the form of a crescent, situated between the openings of the uteri. Behind this, apart from the presence of a few transverse fibres in the canal near the neck of the bladder, there were no other vestiges of the median partition, so that the two median vaginæ formed a single canal extending down the length of the urethra. This canal, Daubenton states, opened into the urogenital sinus by a definite aperture of its own, which lay above that of the urethra.

In our example of this species the two median vaginæ are separated by a well-marked septum which, however, is perforated in front and is absent at their posterior extremities, so that there is formed a short median canal which terminates blindly some distance in front of the sinus. Behind it, there are traces of a pseudo-vaginal passage but no indication of a median opening into the sinus, and in view of the size of the pouch-young in Daubenton's specimen, we think it highly improbable that the median aperture he describes was a genuine opening from the median canal into the sinus.

Daubenton also gives a short account (*loc. cit.* p. 335) of the genital organs of another Didelphyd under the name of "la

Marmose," which Mr. Hinton has been good enough to determine for us as *Marmosa murina*. The female had ten attached pouch-young, four lines in length, four vacant nipples, and no pouch, though two slight lateral folds bounded the mammary area. The two median vaginæ are devoid of a longitudinal partition and form a common canal proportionately wider than in the Sarigue and extending the length of the urethra. This canal is here again described as terminating in an aperture, leading into the sinus. The lateral vaginal canals are said to form an oval.

This description differs widely from our own of *M. murina* and, apart from the median aperture, is more suggestive of *M. cinerea*.

Owen (**18**), in 1834, in his paper "On the Generation of the Marsupial Animals," gave a brief description and a good figure of the female organs of *D. dorsigera* [=*M. murina*] and also referred to the condition of the median vaginal culs-de-sac in *D. virginiana*, stating that, like those of *Dasyurus*, they "descend to the urethro-sexual passage and are connected to but do not communicate with it." In *D. aurita*, we show, however, that the median vaginæ terminate about half-an-inch or so above the anterior end of the sinus.

In 1880, Brass (**2**) also described and figured (his figs. 4 & 5) the female organs of two young individuals of *D. dorsigera* [*M. murina*], as well as those of a "Didelphiden-Embryo," and made a brief reference to those of *M. opossum*. Fig. 4 of Brass was reproduced by Weidersheim in his text-book and thence copied into others, with the result that the condition of the median vaginæ therein depicted has come to be regarded as that typical for the Didelphyidæ as a whole.

In more recent times, W. H. Osgood (**17**) has given an account of the female organs of that rare and interesting form, *Cœnolestes obscurus*, whilst C. Hartman (**8, 9, 10**) has contributed to our knowledge of those of *D. virginiana*. Detailed reference to the observations of Osgood and Hartman will be found in the sequel.

Descriptive.

Didelphys aurita. (Pl. I. fig. 1; Pl. III. figs. 11–14; text-fig. 1.)

Of this species, locally known as the "Gamba," we have available a fair amount of material, collected in Brazil in 1913. A figure of the organs of a full-grown female is reproduced on Pl. I. fig. 1. The organs from which our sectional figures Pl. III. figs. 11–14 are taken, are those of a female (A. 21.7.13) with seven young in the pouch, measuring 8 mm. H.L. and 32 mm. D.C.L.

We have compared the organs of this species with those of *D. virginiana* and find, as was to be expected, that they are very similar.

The uteri are ovoidal in form and are distinctly marked off

from the Fallopian tubes. They are continued back as the uterine necks and open into the median vaginæ by large papillæ, which project freely into the vaginæ and have richly folded surfaces.

The lateral vaginal canals, on leaving the median vaginæ, run at first forwards and outwards and then bend sharply back again to form very prominent, freely projecting U-shaped loops, the two limbs of which are in close approximation and are often irregularly bent. The anterior or ascending limb of the loop is much thicker than the descending, and, indeed, is frequently very greatly enlarged (fig. 1). In one of our specimens we observed a second smaller loop behind the main loop. The descending limbs join the urogenital cord about on a level with the neck of the bladder and pass back in that dorso-laterally to the urethra (Pl. III. figs. 12 and 13) to open with the latter into the urogenital sinus.

The lateral canals as far back as the hinder limit of the remains of the pseudo-vaginal passage (text-fig. 1, *pv.p.*) have their lining produced into prominent longitudinal folds which are especially well developed in the region of the loops. The lining epithelium in this region is a relatively thin stratified layer with a distinct stratum corneum, desquamating in thin layers. In the grooves between the folds is a variable amount of amorphous debris, evidently derived from the latter.

Behind the above-mentioned level the lumina of the canals (Pl. III. fig. 13, *l.vag.c.* left) become considerably reduced, though they remain patent, right back to their openings into the sinus. At the same time the lining becomes much less folded and the epithelium alters in character. It is distinctly thicker, is devoid of a cornified layer, and small nucleated squames are being given off from its surface. Below it is indented by ingrowths of the underlying connective tissue. It is noteworthy that the urogenital sinus is lined by an epithelium of an identical character.

In a pouch-young of H.L. 18 mm. we find a corresponding condition of the epithelium of the lateral canals. Their anterior portions are lined by a quite thin epithelium, their posterior portions by a much thicker layer, similar to that of the sinus, whilst the lumina are here reduced and completely occluded in the terminal thirds of the canals. Hartman (9) points out that in *D. virginiana* the lateral vaginæ do not open into the urogenital sinus until puberty. They are at first solid posteriorly and only become patent during the first proœstrum.

These details in regard to the character of the lining in the anterior and posterior segments of the lateral canals are of interest in view of the possibility of a difference in the origin of the two regions, and also in view of the recent observations of Hartman (9) on the changes undergone by the vaginal epithelium in the course of the œstrous cycle in *D. virginiana*.

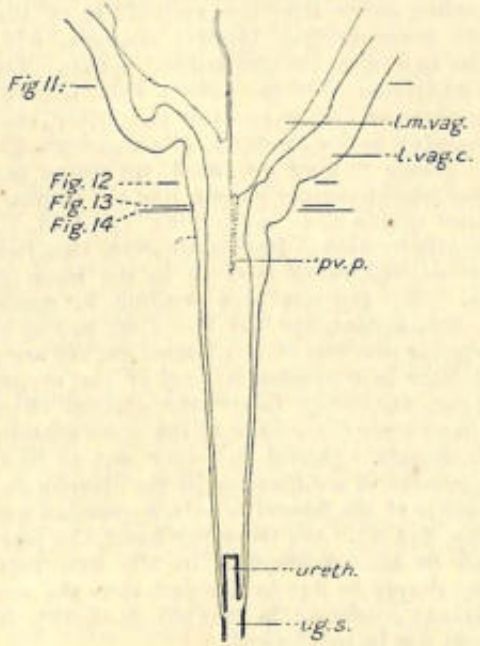
According to Hartman, the epithelium of the vaginal canals thickens during proœstrum and develops a well-marked stratum corneum which commences to slough off thin cornified lamellæ. Desquamation continues during œstrus and ovulation, and as the result some twelve to fifteen or more days after the latter event, the lumina of the canals are found to be filled by a thick cheesy mass, formed from the exfoliated lamella as the result, Hartman states, of bacterial action. The desquamation process is described as continuing after parturition, Hartman's fig. 71, pl. xii. from an animal with young three weeks old, being very similar to our sections of the anterior vaginal epithelium of specimen A. Hartman further shows that the epithelium of the urogenital sinus exhibits corresponding cyclical changes, but the cornification begins later than in the vaginal canals. Desquamation reaches its maximum during œstrus and ovulation and is completed in three or four days after the latter, the epithelium gradually returning to the condition of a non-cornified squamous epithelium. Lastly it may be noted, he states that "during anœstrum, the lateral vaginal canals, like the vagina [urogenital sinus], are lined with a clear epithelium" (p. 393).

It is apparently implied in Hartman's paper that the epithelium of the lateral vaginal canal behaves in the same way over its entire extent. We are not in a position to speak with any authority on this matter, but the fact that in our specimen A, the more posterior portions of the lateral vaginæ are lined by an epithelium similar in character to that of the urogenital sinus, tends to suggest that they follow the cyclical changes of the urogenital sinus rather than those of the more anterior segments of the lateral canals. Should this turn out to be the case, it would be suggestive of a difference in the developmental origin of the two regions of the lateral canals, a question which is dealt with later (pp. 214–5). On the other hand, the possibility that the difference in the epithelium in the two regions, above described, may simply be due to the fact that the return to the ancestral (resting) condition is effected gradually from behind forwards should not be overlooked.

The median vaginæ in specimen A consist of two relatively large sacs which together reach a width of 1·3 cm. They form what appears in the dorsal view of the organs as a single, transversely oblong, median swelling, from which the lateral canals pass off antero-laterally, and which extends back between the hinder portions of the vaginal loops, dorsally to the neck of the bladder, to enter the urogenital cord. Sections show that the two sacs are completely separated by a thin vertical partition and that the left sac is somewhat larger than the right (Pl. III. fig. 11, *vag. s.*). From their walls, as well as from the septum, there arise numerous pinnately-branched folds which largely fill up their lumina (fig. 11). The folds are supported by thin cores of connective tissue and are clothed by a columnar epithelium with light staining cell-bodies provided with terminal bars and

possessing basally situated nuclei. Possibly the cells of this epithelium secrete the viscid fluid which Hartman (**10**) describes as filling the vaginal canals at the time of œstrus. Traced posteriorly, in the sections, the vaginal sacs are seen to undergo a gradual diminution in size, their tapering posterior extremities being situated between the upper ends of the straight posterior segments of the lateral canals, dorsally to the neck of the bladder. The smaller right sac terminates blindly just behind the level

Text-figure 1.



Graphic reconstruction of the posterior portions of the median and lateral vaginæ in *D. aurita* (A). *pv.p.*, remains of pseudo-vaginal passage extending back from the longer left median vaginal (*l.m.vag.*). 3·6

of the openings of the ureters into the latter, whilst the larger left sac continues on for a distance of not quite 2 mm. before it also ends blindly about 14·5 mm. in front of the anterior end of the urogenital sinus. In the terminal part of its extent, it comes to lie axially in the urogenital cord (Pl. III. fig. 12, *m.vag.*), its wall consisting simply of folded epithelium, outside which is the connective tissue occupying the triangular area enclosed by the two lateral vaginæ dorsally and the urethra ventrally.

Round the terminal extremity of the sac, the connective tissue

is on the one side dense and very cellular but on the other side, as well as directly behind the sac, it is loose, lightly staining, and composed of small anastomosing fibroblasts, and thus presents all the characters of young or embryonic connective tissue, recently formed to fill up a cleft or space. In the third section behind that containing the last trace of the epithelium of the vaginal sac, there appears a definite space, ovalish in section, in the direct backward continuation of the latter, which is more or less completely occupied by this young connective tissue, and, adjacent to it, is another similar area but less definitely bounded by the surrounding tissue and more completely filled up. The appearance presented is shown in Pl. III. figs. 13 & 14 (*pc.p.*). In the higher power view seen in fig. 14 (·19 mm. behind the last trace of the vaginal epithelium), the main space above referred to is clearly visible, and ventro-laterally to it, two smaller areas of similar character. Behind this level, these spaces can be followed continuously in the serial sections until they gradually become reduced and disappear as definite structural differentiations some 3 mm. behind the extremity of the vaginal cul-de-sac (*cf.* text-fig. 1, *pc.p.*).

There can be no doubt these longitudinal tracts, more or less completely filled by embryonic connective tissue, are the last remains of the split or cleft in the connective tissue of the urogenital cord, originally described by one of us (H.) in *Perameles* (**11**) under the name of the pseudo-vaginal passage, which, stretching from the hinder end of the vaginal cul-de-sac back to the anterior end of the urogenital sinus, a distance in this species of about 14·5 mm., provided a direct median passage for the birth of the young during parturition.

We have not been able to detect any break in the epithelium of either the vaginal cul-de-sac or the urogenital sinus, and conclude that in both cases the wounds have become completely healed. It may be recalled that in *Dasyurus* (Hill, **14**) obliteration of the pseudo-vaginal passage and of the breaks in the epithelium of the median vagina and sinus produced during parturition, proceeds with remarkable rapidity. On the second day following parturition, the epithelial ruptures are completely healed, and on the third day the pseudo-vaginal passage itself is no longer patent.

We conclude accordingly that in *D. aurita*, the young reach the exterior by way of one or other of the median vaginal culs-de-sac and of a pseudo-vaginal passage which is formed in the connective tissue of the urogenital cord, lying in the direct backward prolongation of the vaginal cul-de-sac and that the passage becomes obliterated after parturition to be reformed anew at each succeeding act.

The occurrence of a pseudo-vaginal passage in this species was first recorded by one of us (H.) in these Proceedings for 1917, and subsequently Hartman (**8**) has stated that it is present also in *D. virginiana*.

METACHIRUS OPOSSUM. (Pl. I. fig. 3; Pl. IV. figs. 15–17.)

We have examined the organs of a female (22.8.13.) with seven young in the pouch (H.L. 13 mm., D.C.L. 4·5 cm.).

The organs of this species are readily distinguishable from those of *D. aurita* by the characters of the vaginal loops. They are relatively much smaller than those of that species and project freely forwards and downwards in front of the uterine necks, whilst their ascending and descending limbs are more equal in size.

The uterine necks run back to become imbedded in the dorsal walls of the median vaginæ and finally open into the latter by numerous small slit-like apertures situated on prominent papillæ. These are attached practically throughout their length, their tips only being free, and their surfaces are folded like the lining of the vaginæ.

The lateral canals are lined throughout by a stratified epithelium, non-cornified, thicker in their anterior portions where the lining is thrown into thickish longitudinal folds (Pl. IV. fig. 15, *l.vag.c.*), thinner in their posterior segments where the folds are reduced or absent, and the lumina of the canals for some distance in front of their openings into the sinus are completely, or all but completely, obliterated. Where traces of the lumina are preserved, they are largely occupied by masses of shed nucleated cells.

The condition of the median vaginæ is of added interest in view of Daubenton's account already referred to (p. 190). They have the form of large transversely wide sacs, the lining of which is produced into irregular folds, much less prominent than in *D. aurita* (Pl. IV. fig. 15, *m.vag.*), and clothed for the most part by a low columnar epithelium, the nuclei occupying the basal two-thirds of the cells. The median septum between the sacs is thick (fig. 15, *vag.s.*), but incomplete. About 0·75 mm. behind the origins of the lateral canals, it is perforated by an aperture about 0·16 mm. in diameter. Behind this, the septum continues complete for a distance of about 1·5 mm., and then it again becomes perforated and reduced to dorsal and ventral folds. These gradually disappear behind until there is left a single median vagina. This further back becomes subdivided by oblique folds into several small channels (fig. 16, *c.m.vag.*), which finally end blindly. The length of the median vagina is about 0·96 mm., and it terminates about 4·6 mm. in front of the urogenital sinus.

In view of the condition of the median vaginal septum, we might very well expect to find evidence of the former existence of a pseudo-vaginal passage and such evidence, we think, is present. Fig. 17 illustrates a section through the urogenital cord 0·2 mm. behind the termination of the median vagina. In the connective tissue situated between the lateral vaginæ and dorsally to the urethra, there will be seen a light-staining tract (*pv.p.*) which is similar to the tracts in a corresponding position in *D. aurita*, though the young connective tissue is perhaps a

little more compact than in that species and is not so distinctly marked off from the surrounding tissue. This tract is traceable right up to the hinder extremity of the median vagina, and in front of that it is more or less definitely in continuity with the two areas of light-staining connective tissue, seen in fig. 16, between the sub-divisions of the median vagina and the urethra. The presence of these two areas suggests that the young during parturition had ruptured the epithelium of the median vagina at two points, shortly above its tip.

The dorsal lip of the cloaca is produced to form a blunt triangular projection, above the transverse or crescentic opening. The cloaca itself is shallow and the clitoris simple.

METACHIRUS NUDICAUDATUS. (Pl. I. fig. 2; Pl. IV. fig. 18.)

We have examined six sets of organs of this species, two of them in serial sections, viz., A, an adult female (2.28.7.13) with a recognizable pouch-area, but we have no evidence as to whether or not this female had bred, and B, an adolescent female.

The uteri (fig. 2) are more elongated than in the two preceding species. They are distinctly marked off from the Fallopian tubes, but pass over without definite limit into the uterine necks, which are very thick. The necks pass back distinct from each other and connected only by the continuation of the median peritoneal fold between the uteri. Externally they seem to pass into direct continuity with the ascending limbs of the lateral vaginal loops (fig. 2), the organs presenting in this respect a somewhat primitive appearance. Internally they terminate in large freely projecting papillæ which bear the slit-like uterine ora and largely fill up the anterior portions of the median vaginal lumina.

The lateral vaginal loops are large and prominent, recalling those of *D. aurita*. Their ascending and descending limbs are both markedly thickened (especially so at œstrus), and their surfaces, instead of being smooth, are crossed by a number of irregular grooves which give them a very characteristic rugose appearance (fig. 2). The lining of the anterior segments of the lateral canals is produced into close-set parallel folds (fig. 18, *l.vag.c.*), covered by a relatively thin stratified epithelium, non-cornified. In the hinder segments, the epithelium is thicker and its under surface is produced into irregular processes. Here also the lining is more coarsely folded. In specimen A, in this hinder region, the lumen is on one side almost obliterated and on the other, much reduced, but both lumina communicate with the sinus. In the younger specimen B, however, the lateral canals are solid for a distance of 4·6 mm. in front of their connection with the sinus.

The median vaginæ in specimen A are seen in transverse section in Pl. IV. fig. 18, *m.vag.* They appear as dorso-ventrally flattened, but transversely wide sacs, situated between the lateral vaginal canals and separated by a thick but low median septum which extends as a complete structure throughout

their length. Posteriorly they gradually become reduced in size and more laterally compressed and eventually end blindly about 12 mm. in front of the sinus, one of them being wider and slightly longer than the other.

The lining of the vaginal sacs is only very slightly folded, in marked contrast with those of *D. aurita* and *M. opossum*, whilst the epithelium is similar to that of the vaginal loops, a somewhat exceptional condition. In the sacs there is present a granular material containing desquamated cells in small numbers, and traces of the same material are present in the vaginal loops.

The connective tissue immediately behind the terminations of the median vaginæ is very vascular, and there are present in it a number of spaces and clefts which disappear further back, but, apart from these, no definite remains of a pseudo-vaginal passage are recognizable.

In the younger specimen, the median vaginæ have the same disposition as in the older, but one of them is very distinctly longer than the other and is almost circular in cross-section.

CALUROMYS PHILANDER. (Pl. I. fig. 4; Pl. V. figs. 19 & 20.)

Our material consists of the organs of a female with four pouch-young (H.L. 8·5 mm., G.L. 18·5 mm., D.C.L. 3·5 cm.).

In their general form the organs of this species recall those of *M. opossum*, but are readily distinguishable from those of the latter, and, indeed, of all Didelphyds, through the presence of a median cylindrical structure situated between the uterine necks and the origins of the lateral vaginal canals and measuring about 5 mm. in length by 6·5 mm. in breadth. This structure really represents the drawn out anterior portion of the median vaginæ into which the uterine necks open and is distinctive of the species.

The uteri are broadly oval in outline (8 × 5 mm. in diameter) and are sharply marked off from the Fallopian tubes, which are singularly short and thick. The uterine necks are also very short (about 2·5 mm.). They pass back enclosed in a common connective tissue sheath, and entering the median vaginal prolongation form well-marked papillæ which terminate considerably in front of the openings of the lateral canals. The free surfaces of the papillæ (Pl. V. fig. 20, *pt.p.*) are provided with numerous richly branched folds, and these, along with the similar folds arising from the walls of the median vaginæ, practically completely occupy the lumina of the vaginal prolongation at this level, and so produce the remarkable appearance seen in fig. 20.

The lateral vaginal canals take origin from the median vaginæ about 5 mm. behind the anterior margin of the median prolongation. They form well marked closed loops which project freely outwards and forwards, the left loop being more prominent than the right in our specimen. The anterior segments of the canals, including the loops, are lined by a non-cornified stratified epithelium with a smooth surface produced below into papillæ,

frequently of some length and branched. The lining is irregularly grooved, but folds like those found in the preceding species are absent (fig. 19, *l.vag.c.*). The posterior segments of the canals are similar to the anterior in histological structure and are patent throughout. They open into each other 0·6 mm. above their common opening into the sinus.

The median vaginæ (and their anterior prolongation) form together a slightly flattened cylindrical structure, with an apparent length in the entire organs of 11 mm., and a greatest breadth at the level of penetration of the ureters of 7·5 mm. The two sacs are separated over the greater part of their extent by a relatively thin septum (Pl. V. fig. 19, *vag.s.*). From the surfaces of this, as well as from the vaginal walls, there arise numerous slender dendritically branched folds which project inwards, leaving only the central parts of the lumina free (fig. 19). The folds are covered by an epithelium composed of cylindrical cells with pale-staining cell-bodies and basally situated nuclei. In the lumina of the vaginæ there is present a granular material containing numerous remains of detached epithelial cells.

Some 5 or 6 mm. behind its anterior margin, the vaginal septum becomes perforated at the middle of its height, and behind this the ventral half of the septum gradually becomes reduced and disappears, the two sacs being in communication with each other over a distance of about 1·5 mm. Behind this gap the septum again becomes complete and continues so back to the blind terminations of the two sacs. The latter are separated from the sinus by a distance of about 6·6 mm. The connective tissue in the direct continuation of the vaginæ appears dense and very vascular, but in the sections immediately behind the latter we can detect in the centre of the denser tissue a small irregular patch of lighter staining tissue which probably marks the site of the pseudo-vaginal passage.

The cloaca is shallow, the clitoris simple, and the dorsal cloacal lip spout-like.

In the structure of its genital organs, and especially of its median vaginæ, *Caluromys* exhibits a considerable degree of specialisation and occupies a somewhat isolated position in the family.

MARMOSA CINEREA. (Pl. II. fig. 6; Pl. VI. figs. 24–27; text-fig. 2.)

The organs of this species have not hitherto been described. They present features of some interest. We have examined the organs of two adults: A, 30.7.13, pouch absent, mammæ ?4–1–4; and B, 1.8.13, pouch absent, mammæ 5–1–5.

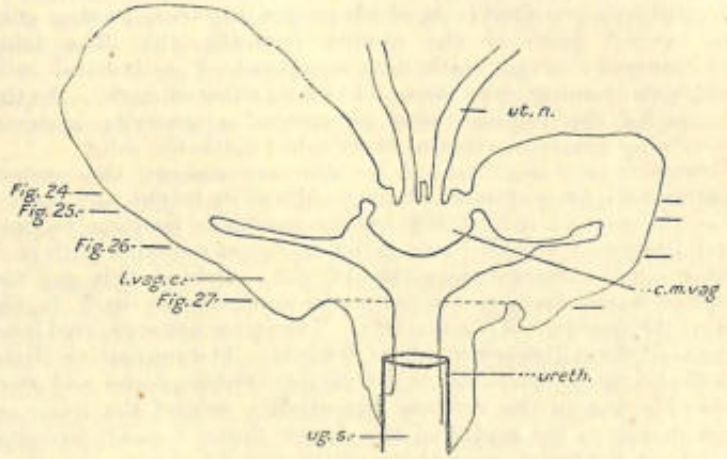
The uteri (fig. 6) are elongated (about 7 mm.–8·5 mm. in length) and spindle-shaped in form. They are fairly distinctly marked off from the thin convoluted Fallopian tubes but pass over gradually into the uterine necks, though the junction of the two is readily perceptible in A, the uteri being lightish brown, the necks white.

The uterine necks pass back in contact with each other and open by well-marked papillæ which project freely in A into the median vaginæ (fig. 24, *ut.p.*), but in B are attached to the lateral walls of the latter, practically along their length.

The general configuration of the lateral and median vaginæ is shown in text-fig. 2.

The median vaginæ are represented here by a single relatively short chamber, oblong in cross-section (figs. 24, 25, *c.m.vag.*), measuring only a little over 1 mm. in length by about 1·8 mm. in breadth. The median partition, no doubt originally present, has

Text-figure 2.



M. cinerea. Graphic reconstruction of the lateral vaginal canals (*l.vag.c.*) and the common median vagina (*c.m.vag.*). The parts of the lateral canals below the dotted lines have occluded lumina. × 9.

all but completely disappeared, all that remains of it being in the form of a low vertical fold, with a crescentic posterior edge situated in A between the bases of the uterine papillæ but rather more extensive in B, where it extends back to behind the level of the openings of the uterine necks. The lining of the median vagina is quite thin and smooth, being entirely devoid of folds of any sort.

In A there is no definite trace of a pseudo-vaginal passage in the connective tissue behind the blind termination of the median vagina. In B there is given off from the hinder extremity of the vagina, a curious tubular diverticulum, lined by a quite thin epithelial layer, which runs back in the connective tissue for a distance of 0·18 mm. Possibly this is related to the birth of the young, since the connective tissue immediately behind it tends to be loose and light-staining in character, but, apart from this,

we cannot positively identify the remains of a pseudo-vaginal passage. Nevertheless, we think there can be little doubt the young in this species are born through a direct median passage constituted by the single median vagina in front and a pseudo-vaginal cleft behind.

In both specimens the median vagina is separated by a distance of about 2·7 mm. from the urogenital sinus.

The lateral vaginæ are also characteristically developed (fig. 6 & text-fig. 2, *l.vag.c.*). The vaginal loops are well marked but are short and compact, with their two limbs in close contact. The anterior limb communicates with the median vagina by a slit-like aperture (fig. 24) and runs forwards laterally to the corresponding uterine neck as a thick bulbous expansion (that of the right side being in both specimens larger than the left), with relatively thin walls and a spacious lumen. The anterior limb constricts rather suddenly where it passes at the bend into the much thinner posterior limb. This runs medially and then bends back to form the straight hinder segment of the canal, situated in the urogenital cord. These hinder segments in this species are remarkably short (indeed the canals as a whole are short), having a maximum length in A of about 2 mm.

The urogenital sinus is correspondingly elongated, measuring in A close on 12 mm.

The vaginal loops possess well-marked lumina and their lining is thrown into longitudinal folds, best developed on the outer sides of the canals. The straight hinder segments, however, down to a level immediately in front of their junction with the sinus, have their lumina completely obliterated by the fusion of their epithelial lining to form a solid irregularly star-shaped core (fig. 27).

The cloaca is extensive and the clitoris simple and imbedded.

Marmosa murina. (Pl. II. fig. 7; Pl. V. figs. 21 & 22; text-figs. 3 & 4.)

The organs of this widely-distributed species, as already noted, have been described by Daubenton, Owen, and Brass. We have examined three sets of organs, all derived from specimens in the collection in the British Museum (Natural History), viz.:—

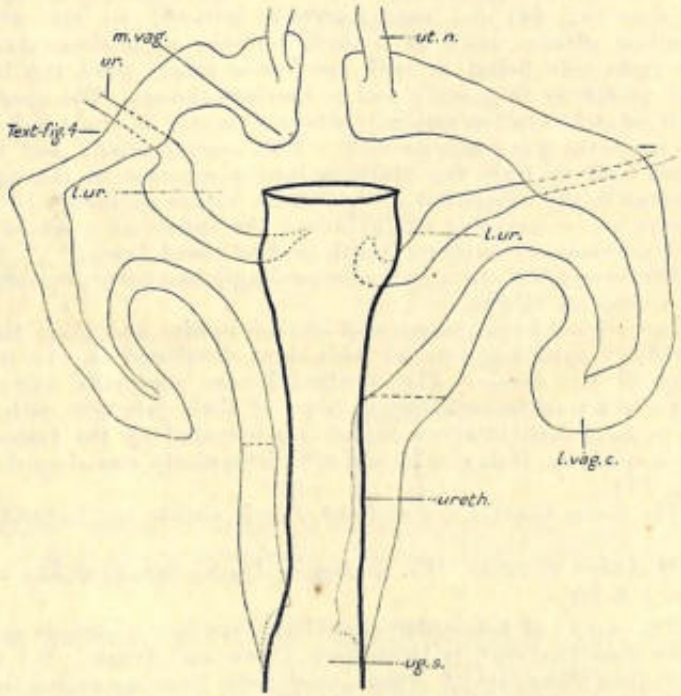
A. Adult female (5.1.8.12), Cayenne, mammæ 4–1–4, mammary glands large.
B. Adult, L. de Jeude Collection, mammæ 5–1–5.
C. Immature, 81.9.7.3 & 28, North Peru.

The bodies of the uteri in our specimens, as in those described by Owen and Brass, are elongated (about 6–8 mm. in length by 2·5 mm. in thickness), and spindle-shaped. They graduate off above into the long and convoluted Fallopian tubes and below into the relatively long uterine necks. The latter, widely separated above, converge below and open into the median vaginæ, opposite the openings of the lateral canals. The papillæ

are attached to the dorsal walls of the vaginæ, their tips alone being free.

The lateral vaginal canals are more highly specialized than in *M. cinerea*. In both adults their anterior segments are characteristically coiled to form two double or S-shaped loops, one on each side, in which the coils may be disposed in one plane, as in B (text-fig. 3), or in two superimposed planes, as in A. Owen's description (**18**, p. 352) is as follows: "each tube after embracin

Text-figure 3.



M. murina (B). Graphic reconstruction of the genital ducts, ureters (*ur.*), neck of bladder and urethra (*ureth.*); *l.ur.*, level of entrance of ureters into urogenital cord; *m.vag.*, median vaginal cul-de-sac. The parts of the lateral vaginæ below the dotted lines are solid. × 15.

the os tincæ, is immediately continued upwards and outwards, then bends downwards and inwards, and after a second turn upwards, descends by the side of the opposite tube to terminate parallel with the extremity of the urethra in the common passage."

The descending limbs of the canals are, as in *M. cinerea*, very short, their openings into the sinus in A being about 2 mm., and

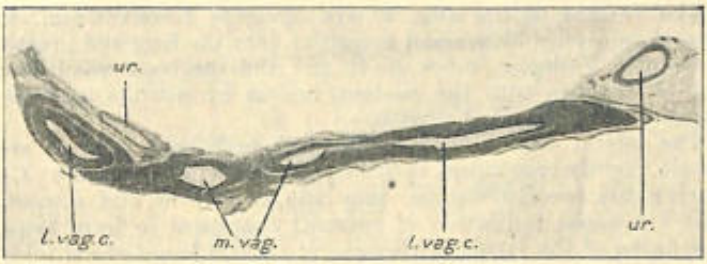
in B about 4 mm. behind the terminations of the median vaginal culs-de-sac.

The first loop of the lateral canal in A is of smaller diameter than the second and is lined by a stratified epithelium, only a few cells in thickness and thinner than that of the second loop. The straight posterior segment is also of smaller diameter than the second, and has its lumen occluded right back to its opening into the sinus.

In the immature specimen C there is but a single vaginal loop on each side, much as depicted by Brass in his fig. 4, and the solid portions of the lateral canals are longer in proportion to the whole than in the adult specimens.

The median vaginæ in our specimens, as in those described and figured by Owen and Brass, are in an exceedingly simple and primitive (indeed practically persistently fœtal) condition. They

Text-figure 4.



M. murina (B). Trans. sect. passing through the median vaginal culs-de-sac (*m.vag.*) at the level indicated in text-fig. 3. × 23·3.

have the form of extremely short culs-de-sac, ovoidal in section, which project back into the connective tissue of the genital cord: they are separated and surrounded by the same, but can hardly be said to possess a differentiated septum (Pl. V. fig. 21, *m.vag.*; text-figs. 3 & 4). In A, where the culs-de-sac are best developed, they extend back behind the posterior margins of the openings of the lateral vaginal canals for a distance of about 0·6 mm., and, as above mentioned, they terminate in A, 2 mm., and in B, 4 mm., in front of the sinus. Behind them, the connective tissue of the urogenital cord situated medianly between the lateral vaginæ and dorsally to the bladder-neck is quite compact (Pl. V. fig. 22, *c.t.*), and presents no indication even in A (a multipara) of the former presence of a pseudo-vaginal passage. Nevertheless, we think it probable that the young follow the median track during parturition, since it is difficult to imagine them safely negotiating such a convoluted path to the exterior as is provided by the lateral vaginal canals.

MARMOSA PUSILLA.

The organs of a quite immature female of this species generally resemble those of the immature specimen (C) of the preceding species. The median vaginæ are here again in the form of quite minute culs-de-sac, and the lateral canals form simple loops and are occluded posteriorly for about two-fifths of their entire length.

MONODELPHIS (PERAMYS) AMERICANA. (Pl. II. fig. 8; Pl. VII. figs. 28–31; text-fig. 5.)

We have examined the organs of an adult female which, judging from the condition of the mammæ, had but recently completed suckling the young. There is no pouch and the mammæ, according to O. Thomas, are in this species 5–5–5. In our specimen there appear to be two lateral rows of three (with possibly a minute additional one at the anterior end of the left row), and three, arranged in triangular fashion, between them. Seven of the nipples are well developed.

The uterine bodies (fig. 8) are elongate (about 6 mm. in length) and pass by gradual transition into the long and greatly convoluted Fallopian tubes above and the uterine necks below. The latter open into the median vaginæ by slit-like apertures situated on well-marked papillæ.

The lateral vaginal canals (fig. 8 & text-fig. 5, *l.vag.c.*) are simple slightly bent tubes, their loops being little prominent. On leaving the median vaginæ, they run backwards and inwards with but slight indication of outward curvature to form loops. The lining of the latter is thrown into coarse longitudinal folds, covered by a quite thin stratified epithelium, only two or three cells in thickness. Towards the hinder end of the median vagina (text-fig. 5), the canals diminish in diameter, their lumina become reduced (fig. 30), and their lining epithelium alters in character and takes on the structure of a typical, though thin, stratified epithelium. Over the posterior part of their extent (forming about one-quarter of their total length), the canals are devoid of lumina almost up to their opening into the sinus.

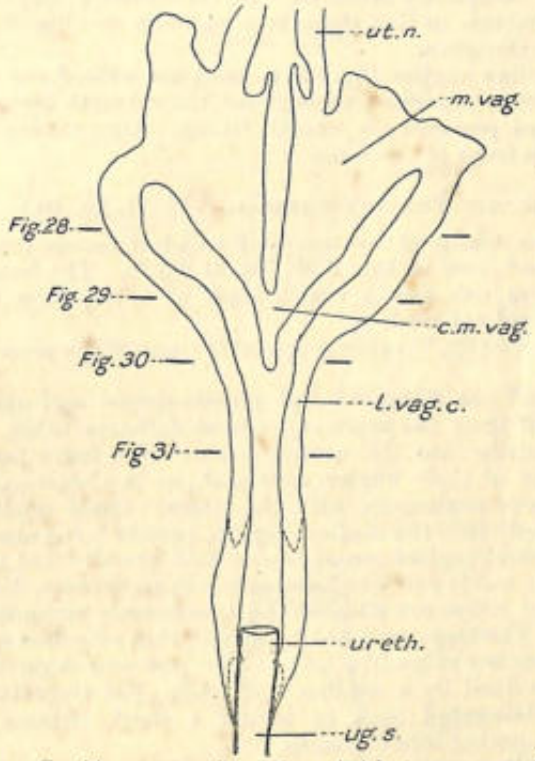
The median vaginæ are much in advance of those of *Marmosa murina* and appear as relatively large sacs, transversely wide in front, where their lining is thrown into a few coarse folds (fig. 28, *m.vag.*). Over about three-quarters of their length, they are separated from each other by a thick median septum, but this becomes incomplete posteriorly (fig. 29, *p.vag.s.*) and finally disappears, and the two sacs are then continued back as a short median vagina of flattened tubular form (fig. 30, *c.m.vag.*) and about 1 mm. in length. This ends blindly about 3·3 mm. in front of the sinus. The total length of the median vaginal apparatus is a little over 3 mm.

The connective tissue immediately behind the median vagina is loose and open for a stretch of about 0·4 mm., though not

apparently composed of young tissue, and then gives place to the dense tract visible in fig. 31 (*c.t.*) between the lateral vagina and the bladder-neck.

We think the disappearance of the septum at the hinder end of the median vaginæ points to the birth of the young through the direct median passage. The urogenital sinus has a length of about 6·5 mm., the cloaca is extensive, and the clitoris simple and imbedded.

Text-figure 5.



M. americana. Graphic reconstruction of the genital ducts. *m.vag.*, median vagina; *c.m.vag.*, common median vagina. The parts of the lateral vaginæ (*l.vag.c.*) below the dotted lines are solid. × about 11.

MONODELPHIS (PERAMYS) DOMESTICA. (Pl. II. fig. 9; Pl. VII. fig. 32.)

We have available a single set of organs of this species, taken from B.M. specimen 3.10.1.123. This species, according to O. Thomas, is larger than the preceding, but the organs at our disposal are smaller than those of our example of the latter;

moreover, the uteri are quite slender. Accordingly we judge the organs to be those of a virgin.

In their main features (fig. 9), the organs of this species resemble those of *M. americana*. The uteri are elongated and slender (about 1 mm. in thickness). The uterine necks run down on either side of the vaginal septum and open by slit-like ora, provided with definite lips, but there are no free papillæ.

The lateral vaginal canals form distinct but simple loops, which project more prominently outwards and forwards than those of *M. americana*. The posterior segments have their lumina reduced but never completely occluded. At their hinder ends they open into the urethra, so that there is a common opening of all three tubes into the sinus.

The median vaginæ (fig. 32, *m.vag.*) are wide dorso-ventrally flattened sacs, separated throughout their length by a median septum and possessing a smooth lining. They terminate about 2·9 mm. in front of the sinus.

MONODELPHIS (PERAMYS) THERESA. (Pl. II. fig. 10.)

We have examined the organs of an adult female (the type of the species *, now in the B.M. No. 21.8.6.2). The fact that the mammæ are not clearly visible leads us to conclude that this specimen had not bred.

The organs (fig. 10) closely resemble those of the preceding two species.

The uteri are elongated and spindle-shaped and are sharply marked off from the much convoluted Fallopian tubes, but pass over gradually into the uterine necks. The latter become approximated at their hinder ends and, as in *Caluromys*, appear to be directly continuous with the lateral vaginal canals. They open directly into the median vaginæ, papillæ being absent.

The lateral vaginal canals run at first laterally and then bend backwards and inwards to form simple loops between the anterior portions of which are situated the transversely expanded median vaginæ. The loops are lined by a quite thin stratified epithelium and possess low ridge-like folds. The posterior segments of the canals are lined by a similar epithelium, but their lumina are largely obliterated back to within a short distance of their common opening into the sinus.

The median vaginæ have essentially the same relations as in the preceding species. They are dorso-ventrally flattened but transversely wide sacs, about 0·9 mm. in length, and are separated by a complete septum. They terminate blindly about 2 mm. in front of the sinus. They are lined by a quite smooth two-layered epithelium.

The cloaca is well marked, and the clitoris simple and situated relatively far forwards on the ventral wall, close behind the crescentic opening of the urogenital sinus.

* O. Thomas, "A new short-tailed Opossum from Brazil," Ann. & Mag. Nat. Hist. ser. 9, vol viii., 1921.

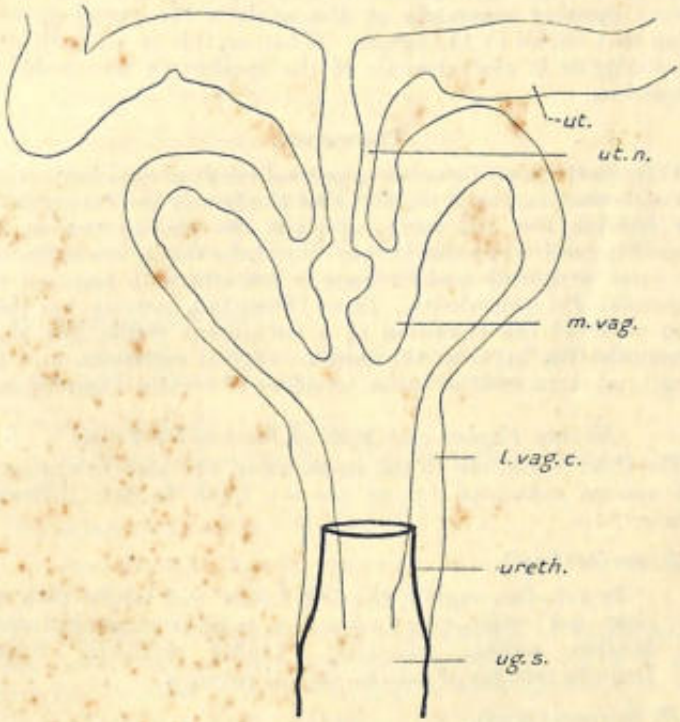
Characteristic of the genus *Monodelphis* are the spindle-shaped uteri, the simple vaginal loops, and the transversely wide median vaginæ with simple non-folded lining.

CHIRONECTES MINIMUS. (Pl. I. fig. 5; text-fig. 6.)

We have examined a single set of organs derived from B.M. specimen No. 94.8.6.15, a young female.

The Fallopian tubes are relatively short and thick and merge quite gradually into the uteri, which are also short (about 4·5 mm.

Text-figure 6.



Chironectes minimus. Graphic reconstruction of the genital ducts. *ut.*, uterus; *m.vag.*, median vaginal culs-de-sac. × 20.

in length). The uterine necks converge to meet in the middle line and their terminal portions run down attached on either side of the vaginal septum and open by slit-like apertures, bounded by prominent lips which extend well down into the median vaginæ.

The lateral vaginal canals (text-fig. 6) run outwards and forwards and then bend postero-medially to form simple loops; their posterior segments are quite short (about 1·4 mm. in length).

The median vaginæ are well-marked culs-de-sac, dorso-ventrally flattened but not so wide transversely as in *Monodelphis*. They are separated by a thickish septum and terminate some distance behind the openings of the ureters into the neck of the bladder and about 1·7 mm. in front of the sinus.

A striking feature in the entire view of the organs (fig. 5) is the clitoris, which appears freely exposed as a blunt dorso-ventrally compressed structure, 1·25 mm. in length by about 1 mm. in breadth. This exposure is apparently the result of the fact that there is in this specimen no cloaca, the urogenital sinus and rectum opening separately at the surface, the rectal opening being that visible in the figure. Whether this is an individual peculiarity or is characteristic of the species we are unable to determine.

Discussion.

Perhaps the most interesting general result of our observations is the demonstration of the fact that the female genital organs of the Didelphyidæ, and more especially the median vaginæ, far from being uniformly simple throughout the family are subject to the same structural modifications as are met with amongst the Australian Polyprotodonts. In no Didelphyd, however, has there been observed the condition of a permanent epithelially lined communication between the median vaginal apparatus and the urogenital sinus such as is characteristic of certain Diprotodonts.

Median Vaginæ and Mode of Birth of the Young.

The chief variations in the structure of the median vaginæ in the species examined by us are set forth in the following summary:—

D. aurita (bred).

Two median vaginæ, the left longer and larger than the right and terminating 14·5 mm. in front of urogenital sinus. Median septum complete. Lining markedly folded. Definite remains of pseudo-vaginal passage.

M. opossum (bred).

Two median vaginæ. Septum perforated in front and absent behind where there is a short median vagina, terminating 4·6 mm. in front of sinus. Lining folded. Traces of pseudo-vaginal passage.

M. nudicaudatus (probably not bred).

Two median vaginæ, terminating about 12 mm. in front of sinus. Septum complete. Lining only very slightly folded.

Caluromys philander (bred).

Two median vaginæ, with anterior prolongation: terminate about 6·5 mm. in front of sinus. Septum thin and perforated in two places. Lining markedly folded. Traces of pseudo-vaginal passage.

Marmosa cinerea (B, probably bred).

Single median vagina, but remnant of septum in front; terminates about 2·7 mm. in front of sinus, which is long (nearly 12 mm.). Lining smooth.

M. murina (A, bred).

Two median vaginæ, short and separated by thick septum. Lining smooth. No trace of pseudo-vaginal passage.

M. pusilla (not bred).

Two quite short median vaginæ.

Monodelphis (*Peramys*) *americana* (bred).

Median vaginæ transversely wide and paired in front and separated by a thick septum, unpaired behind where there is a median vagina (about 1 mm. in length). Latter terminates about 3·3 mm. in front of sinus, which has a length of about 6·5 mm. No evidence of a pseudo-vaginal passage.

M. domestica (not bred).

Two median vaginæ, septum complete; terminate about 2·9 mm. in front of sinus. Lining smooth.

M. theresa (probably not bred).

As in preceding species. Vaginæ terminate about 2 mm. in front of sinus.

Chironectes minimus (not bred).

Two median vaginæ, separated by a thickish septum; terminate 1·7 mm. in front of sinus.

It is somewhat remarkable that the extremes of modification in the median vaginæ are encountered within the limits of one genus, viz. *Marmosa*. *M. murina* exhibits what appears to be the most primitive condition of these structures in the Didelphyd series, inasmuch as they have the form of simple small culs-de-sac which extend back quite separately from each other and for only a very short distance in the connective tissue of the genital cord. Apart from their size, they have retained what is practically the persistently embryonic or fœtal condition, and in this respect strikingly recall those of the adolescent *Perameles* and *Myrmecobius* (Hill, **12**, **13**). *M. cinerea*, on the other hand, through the all but complete loss of the median septum, has come to possess a single median vagina, but as to whether the

septum breaks down before or, as is perhaps more probable, during the first act of parturition, we have no evidence. The condition in this species finds its parallel in that of *Petaurus breviceps* (Hill, **13**) amongst the Australian forms.

In the genus *Monodelphis* (*Peramys*), the median vaginæ in our virgin specimens of *M. domestica* and *M. theresa* are rather more highly differentiated than in *M. murina*, while in *M. americana* the septum has disappeared between their terminal ends so that there is present a short median vagina, the existence of which points, like the single median vagina of *M. cinerea*, to the birth of the young through the direct median route. The condition in this species is similar to that in multiparous females of *Perameles* and *Acrobates pygmæus* (Hill, **12** & **13**).

It is amongst the larger species that the median vaginæ reach their maximum development both as regards size and the differentiation of their lining to form folds, markedly developed and richly branched in *D. aurita* and *Caluromys philander*. In our multiparous example of the latter, the septum is perforated, and this is also the case in *M. opossum* (likewise a multipara), but here in addition, the septum has disappeared at the hinder extremities of the vaginæ, so that there is present a short terminal unpaired canal like that of *M. americana*. In our multiparous example of *D. aurita*, on the other hand, the septum is complete, whilst at the same time there are present unmistakable remains of a pseudo-vaginal passage, so that we may conclude that the incomplete or perforated condition of the vaginal septum is not a necessary concomitant of the median mode of birth.

The chief interest of these variations in the structure of the median vaginal apparatus centres in their bearing on the question of the mode of birth of the young Marsupial, whether by the lateral vaginal canals or through a more direct median passage involving the median vaginæ.

This question has long attracted attention. Home (**15**) in 1795 was the first to describe the existence in a "Kanguroo" of a direct opening between the median vagina and the urogenital sinus. This observation has been confirmed by numerous subsequent investigators for many species of the Macropodidæ (*cf.* especially Lister and Fletcher (**16**), and Fletcher (**6**, **7**)), and for *Tarsipes* among the Phalangeridæ (Hill, **13**). The opening is normally absent in the virgin animal and only appears during and subsequently to the first act of parturition, and through it the young pass directly from the median vagina into the urogenital sinus and so are born by way of a direct median passage.

In other Marsupials in which the median vaginæ terminate at some distance from the urogenital sinus, and in which no permanent communication between the two has been shown to exist subsequently to the first parturition, it was held that the young must necessarily be born through the lateral vaginal canals.

Fresh light was, however, shed on this question by the

investigations of one of us (H.) on the mode of birth of the young in *Perameles* (11, 12), which showed that in this genus, in spite of the fact that the median vaginæ are extremely short and terminate a long way in front of the urogenital sinus, the young are nevertheless born through a direct median passage, constituted in front by the median vaginæ and behind by an elongated cleft-like rupture in the connective tissue of the genital cord, in the direct backward continuation of the median vaginæ. To this cleft the name pseudo-vaginal passage was applied. Like the direct opening in Diprotodonts, it appears to be formed actually by the young during their passage backward, and from it they reach the sinus through a temporary break in its epithelial lining. Subsequently a precisely similar mode of birth was shown to hold good for *Dasyurus* (14) and for *Trichosurus* (13) amongst the Diprotodonts.*

Turning now to the observations bearing on the mode of birth of the young in the Didelphyidæ, set forth in the present paper, we find we have examined specimens of six species (*Metachirus nudicaudatus*, *Marmosa murina*, *M. pusilla*, *Monodelphis domestica*, *M. theresa*, *Chironectes minimus*) which present no evidence of having bred, and in all of these the median vaginal septum is intact. In addition, we have examined examples of five species which present definite evidence of having bred (viz., *D. aurita*, *M. opossum*, *C. philander*, *Marmosa murina* (A), and *Monodelphis americana*), and two examples of *Marmosa cinerea* which we think had probably bred. Our observations on these specimens may be summarized as follows:—

(*a*) In *D. aurita*, the vaginal septum remains complete (in the specimen studied), the median vaginæ are of unequal length, and definite remains of a pseudo-vaginal passage are present. The young reach the urogenital sinus not by way of the lateral vaginæ, but through a direct median passage constituted in front by the longer of the two median vaginæ and behind by a cleft-like rupture or pseudo-vaginal passage (about 14·5 mm. in length) in the connective tissue of the genital cord leading back from the median vaginæ. Hartman (8) has observed a similar mode of birth in *D. virginiana*.

(*b*) In *M. opossum* and *C. philander*, the vaginal septum is incomplete, more so in the former, where there is present a short common vagina. In both, there are traces of a pseudo-vaginal passage. The median mode of birth is indicated.

(*c*) In *Monodelphis americana*, the two vaginæ terminate in a short common canal, whilst in *Marmosa cinerea* there is a single median vagina, with only an anterior remnant of the septum. Though in neither is there definite evidence of a pseudo-vaginal passage, the condition of the vaginal septum, as well as the presence of the tubular diverticulum at the extremity of the median vagina in *M. cinerea* (B), point, we think, to the median mode of birth.

* Unpublished observations show that the like holds true also for the Native Bear, *Phascolarctos*. (J. P. H.)

(*d*) In *M. murina* (A), the vaginal culs-de-sac remain intact, and no trace of a pseudo-vaginal passage is recognizable, so that it looks, at first sight, as if birth through the lateral vaginal canals held good in this species. On the other hand, the intact condition of the culs-de-sac may very well be explained by the thickness of the connective tissue between them, whilst the absence of any remnant of the pseudo-vaginal passage may simply be due to the fact that a sufficient interval had elapsed in which it could become completely healed up, the specimen having but recently finished suckling the young. Lastly, we would lay emphasis on the fact that in this species the lateral vaginal canals attain the highest degree of coiling we have observed in the Didelphyidæ and consequently do not afford a very favourable channel for the outward passage of the young. We accordingly hold that the median mode of birth, even in this species, is not definitely excluded.

Indeed, taking into account all the facts, we are inclined to think that this median mode of birth will ultimately be found to hold good for the whole of the Marsupialia, and in that event it would come to constitute a class character.

Our observations show that the median vaginæ terminate at very varying distances from the urogenital sinus in the different species examined, as is perhaps to be expected, seeing that the distance depends on at least two variables, viz., the length of the median vaginæ and the length of the sinus. The distance is greatest in *D. aurita*, viz., 14·5 mm., the vaginæ being long and the sinus short. In the smaller species, the distance varies from about 1·7 mm. in *Chironectes minimus*, 2 mm. in *M. murina* (A), 2·7 mm. in *M. cinerea* (*B*), to 3·7 mm. in *M. americana*. In the latter, the sinus has a length of 6·5 mm. and in *M. cinerea* of nearly 12 mm.

Short median vaginæ are no doubt in a more primitive condition than long, but it is more difficult to evaluate the length-relations of the sinus, though Hill (12) has regarded the extremely short sinus in *Perameles* as a primitive character.

Lateral Vaginal Canals.

The lateral vaginal canals, like the median vaginæ, exhibit a considerable degree of generic and specific variation. They are simplest and least differentiated in *Monodelphis* (*Peramys*) *americana*, where they pass almost directly backwards to form quite short simple loops which project but slightly outwards. In the other two species the loops are slightly more prominent.

In the two species of *Marmosa*, *M. cinerea* and *M. murina*, the canals are strikingly different. In the former they are remarkably short, their loops are simple but markedly enlarged and very prominent. In both our specimens the ascending limb of the left vaginal loop is greatly distended and much larger than the right. In *M. murina* the canals are narrower and of greater

length than in *M. cinerea* owing to the fact that the loops are convoluted and freely projecting.

Chironectes possesses simple vase-handle-like loops. In *D. aurita* the lateral canals are highly differentiated. The loops are large and project freely, their ascending limbs being markedly enlarged, especially during the breeding-season, and much thicker than the descending. The lining of the loops is thrown into prominent longitudinal folds, clothed by a stratified epithelium with a well-marked stratum corneum. The posterior segments of the canals retain their lumina and are lined by a thicker non-cornified epithelium, similar to that lining the urogenital sinus.

The lateral canals in *M. opossum* and *M. nudicaudatus* generally resemble those of *D. aurita*, but are readily distinguishable from each other and from the latter by peculiarities in form. In *M. opossum* the loops are simple, they project freely forwards, and their limbs are of about the same thickness. In *M. nudicaudatus* the loops are massive, are characteristically rugose, and project markedly outwards.

In *C. philander* the vaginal loops recall those of *M. opossum*, but differ internally in having a practically smooth lining, whilst the posterior segments of the canals have a common opening into the sinus.

In connection with the function of the lateral canals in transmitting the spermatozoa to the uteri and Fallopian tubes, some interesting observations have been recorded by Hartman (10) in a recent paper. He shows that in the Virginian Opossum the canals during œstrus are highly motile and become greatly distended by a viscous secretion. During copulation the semen is mixed with this fluid by the active peristaltic contractions of their walls, and at the same time some of the fluid contents are carried up by these contractions to the ora uteri, possibly almost instantaneously, he thinks, since the contents soon undergo coagulation to form solid "vaginal plugs" which enclose the remaining spermatozoa as well as desquamated cornified cells and bacteria, "the normal flora of the canals at this stage." Hartman's account of these so-called "plugs" is based on the examination of a single female and leaves us in some doubt as to the constancy of their occurrence, especially as he states that he failed to find any remains of them in the lateral vaginæ of several hundred opossums specially examined. He suggests that the plugs may be promptly expelled or that they may be disintegrated by bacterial action.

On the other hand, the fact that there are present in *Perameles* (and also in certain other Marsupials, *Peragale*, *Chæropus*, *Potorous*) vaginal cæca which have been seen to be filled by "a clear viscid semi-fluid material" containing numerous spermatozoa, together with masses of hard caseous-looking substance, and which must accordingly be regarded as receptacula seminis*

* The markedly enlarged vaginal loops seen in certain forms (e.g., *D. aurita*, *M. cinerea*) doubtless also subserve a similar function.

(Hill **12**), rather militates against Hartman's account of the formation of these vaginal "plugs" holding good generally for the Marsupials.

In the descriptive part of this paper we have had occasion to direct attention to the fact that in many species the terminal portions of the lateral vaginal canals are constricted and have their lumina either wholly or partially obliterated, owing to the more or less complete soldering together or fusion of their lining epithelium, and also to the fact that in some cases, e.g. *D. aurita*, where the lumina are patent throughout, the epithelium of the terminal portions differs from that of the anterior segments and is identical with that of the urogenital sinus, whereas in others, as in *Caluromys philander*, the epithelium appears uniform throughout.

Home (**15**), in 1795, and Owen (**18**), in 1834, described the constricted terminal regions of the lateral canals in *Macropus*. Owen states (p. 354): "at the distance of three-quarters of an inch from their terminations there is a sudden contraction, with a small valvular projection in each," and goes on to say these projections "do not exist in the Opossums and Petaurists, in which there is simply a contraction of the vaginal canals at the corresponding part."

In 1880 Brass (**2**) again described this constricted region in *M. major*, and, in 1881, Lister and Fletcher (**16**) examined a large number of Macropodidæ, and in all of them, with the exception of *Bettongia* (*Hypsiprymnus*) *gaimardi*, they found that the terminal parts of the lateral vaginal canals were constricted and had their muscular layer thickened, whilst in many cases a definite valvular fold was present. In *B. gaimardi* they describe the canals as being uniform throughout their extent.

The precise significance of this differentiation when present, whether functional or developmental, is somewhat difficult to determine. A possible developmental explanation of the condition is perhaps to be found in the fact, first observed by Lister and Fletcher (**16**), that in the pouch-young of *M. rufus*, the Wolffian and Müllerian ducts do not enter the urogenital sinus separately, but instead, the Müllerian duct joins the Wolffian duct shortly above its opening into the sinus, with the result that there is formed on each side a short common duct. Van den Broek (**4**) subsequently described the same condition in *M. ruficollis* and *M. thetidis*, and Buchanan and Fraser, in a paper on the development of the genital system in *Trichosurus vulpecula* (**5**), have shown that it also holds good for this species, and that in the adult there is a constriction situated about one-third of the length of the lateral vagina from its posterior end which appears to mark the former point of union of the two ducts. It is accordingly suggested that in *Trichosurus* and the Macropodidæ the terminal segment of the lateral vaginal canal is derived from the Wolffian duct alone.

As regards the Didelphyidæ, the developmental evidence is not sufficient to clear up the question. In the paper just referred to, some observations are recorded on the genital ducts of pouch-young of *D. aurita*. In pouch-young, H.L. 8 to 10·5 mm., "the Müllerian duct joins the wall of the urogenital sinus just medially to the Wolffian duct and the connection is apparently solid." In a later stage, H.L. 18 mm., the two lateral vaginæ become solid, posterior to the passage of the ureters through the genital cord and shortly behind this level, in the region of the hinder third of the lateral vagina, the epithelium alters in its staining character, and the canal continues back solid almost up to its opening into the sinus. It is clear that the terminal segment in *Didelphys* does not arise from the Wolffian duct, but it may be formed by an outgrowth from the dorso-lateral part of the urogenital sinus as suggested by Buchanan and Fraser (**5**). Further observations are, however, necessary to settle this point.

The Female Genital Organs of *Cænolestes*.

In his important monograph on the anatomy of that interesting form, *Cænolestes obscurus* Osgood (**17**) gives an account with two figures (his figs. 1 & 2, pl. viii.) of the female organs, the specimen dissected being a virgin, but reference is also made to the organs of a pregnant female.

The following is a brief résumé of his observations:—The Fallopian tubes are rather short and stout and pass over without definite limits into the uteri. The ora tincæ of the uterine necks are completely coalesced and have thick rugose walls. In the virgin they are of extraordinary size, extending the full length of the vaginal culs-de-sac, though in an older female they are relatively much smaller. The vaginal culs-de-sac are completely separated by a septum and extend nearly to the base of the bladder. "In a pregnant and probably multiparous female, a possible connection was observed between the median vagina and the urogenital sinus. An irregular opening was found, but some destruction of tissue had occurred before the specimen was examined, so the point needs verification." The lateral vaginal canals are characterized by having their loops coiled so as to form a double loop on each side which projects freely backwards. The urogenital sinus in the virgin is long (9 mm.). The cloaca is short (3 mm.), and the clitoris is highly developed and bifid.

Osgood concludes that the female organs of *Cænolestes* are "distinctly of a diprotodont rather than a polyprotodont type. This is evidenced at once by the deep median vaginæ and the long lateral vaginal canals." In coming to this conclusion he is also influenced by the possibility of the occurrence of a direct connection between the median vaginæ and the urogenital sinus, though he is careful to emphasize that the opening observed between the two may be due to adventitious circumstances.

We think the observations we record in this paper rather discount Osgood's conclusion. Should the occurrence of the median mode of birth be established for *Cænolestes*, we show herein that there is no need to go outside the limits of the Didelphyidæ for a parallel, and even were the presence of a permanent opening to be demonstrated, we should not be inclined to regard it as necessarily a mark of affinity with the Diprotodonts but rather as an interesting parallel development, since the presence or absence of a permanent opening simply depends on the degree of approximation between the median vaginæ and the sinus.

As concerns the degree of backward extension of the median vaginæ to which Osgood attaches importance as a mark of affinity, it is not quite clear from his account at what level they do terminate in *Cænolestes*. On p. 67 he states that they "extend nearly to the base of the bladder," and on p. 69, "almost to contact with the urogenital sinus." If the latter statement is correct, then the same may be said of *Chironectes minimus*, where a distance of only 1·7 mm. separates the median vaginæ from the sinus.

Lastly, in regard to the length of the lateral vaginal canals, that is due in great measure to their convoluted character, a feature, so far as our knowledge extends, unknown amongst the Diprotodonts, but which finds a ready parallel in *Marmosa murina* amongst the Didelphyidæ and *Myrmecobius fasciatus* amongst the Australian Polyprotodonts. So far as the structure of the female organs goes, we see no valid reason for regarding *Cænolestes* as other than a member, and indeed a somewhat specialized member, of the Didelphyd series.

Finally, as concerns the bearings of our study of the female genital organs on the question of the mutual relationships of the genera of the Didelphyidæ, our observations show that the pouchless genera, *Marmosa* and *Monodelphis* (*Peramys*), exhibit the most primitive relations in respect of their genital ducts. This is in agreement with the conclusions of Bensley (1) and Bresslau (3), reached after detailed studies on the dentition and foot-structure, and the mammary apparatus respectively.

Bensley's scheme, illustrative of his views of the relationships of the genera, indicates three diverging lines of evolution radiating from *Marmosa* as the parent form, one short basal line terminating in *Peramys*, a second passing through *Metachirus* and terminating in two divergent branches, representing *Chironectes* and *Didelphys*, and a third line terminating in *Caluromys*.

With that scheme our results are in general agreement, except that they indicate no very close relationship between *Chironectes* and the *Metachirus* group. *Caluromys*, according to Bensley, represents an advanced form of one of the larger Marmosas, and in the structure of its genital organs, it clearly occupies an isolated position in the family.

List of Papers referred to in Text.

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(2) Brass, A.—"Beiträge zur Kenntniss des weiblichen Urogenitalsystems der Marsupialen." Inaug.-Diss., Leipzig, 1880.

(3) Bresslau, E.—"Die Entwicklung des Mammarapparates der Monotremen, Marsupialier u. einiger Placentalier.—III." Semon, Forschungsreisen, Bd. iv., 1912.

(4) Broek, A. J. P. van den.—Beiträge zur Kenntnis der Entwicklung des Urogenital apparates bei Beuteltieren." Petrus Camper, Dl. iv., 1907.

(5) Buchanan, G., & Fraser, E. A.—"The Development of the Urogenital System in the Marsupialia, with special reference to *Trichosurus vulpecula*." Part I. Journ. Anat. vol. liii., 1918.

(6) Fletcher, J. J.—"On the Existence after Parturition of a direct communication between the median vaginal cul-de-sacs, so-called, and the urogenital canal, in certain species of Kangaroos." Proc. Linn. Soc. N.S.W. vol. vi., 1881.

(7) Fletcher, J. J.—"On some Points in the Anatomy of the Urogenital Organs in Females of certain species of Kangaroos." Part I. Proc. Linn. Soc. N.S.W. vol. vii., 1882. Part II., *ibid.* vol. viii., 1883.

(8) Hartman, C. G.—"Breeding-habits, Development and Birth of the Opossum." Smithsonian Report for 1921. Washington, 1923.

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(10) Hartman, C. G.—"Observations on the Motility of the Opossum Genital Tract and the Vaginal Plug." Anat. Rec. vol. xxvii., 1924.

(11) Hill, J. P.—"The Placentation of *Perameles*." Quart. Journ. Micros. Sci. vol. xl., 1897.

(12) Hill, J. P.—"Contributions to the Morphology and Development of the Female Urogenital Organs in the Marsupialia.—I. (*Perameles*)." Proc. Linn. Soc. N.S.W., 1899.

(13) Hill, J. P.—"Contributions etc.—II.-V." Proc. Linn. Soc. N.S.W., 1900.

(14) Hill, J. P.—"On the Fœtal Membranes, Placentation, and Parturition of the Native Cat (*Dasyurus viverrinus*)." Anat. Anz. Bd. xviii., 1900.

(15) Home, E.—"Some Observations on the Mode of Generation of the Kanguroo, with a particular description of the organs themselves." Phil. Trans., 1795.

(16) Lister, J. J., & Fletcher, J. J.—"On the Condition of the Median Portion of the Vaginal Apparatus in the Macropodidæ." P. Z. S., 1881.

(17) Osgood, W. H.—"A Monographic Study of the American Marsupial, Cænolestes." Field Mus. of Nat. Hist., Publication 207, Zool. Ser. vol. xiv. no. 1. Chicago, 1921.

(18) Owen, R.—"On the Generation of the Marsupial Animals, with a Description of the impregnated uterus of the Kangaroo." Phil. Trans., 1834.

EXPLANATION OF THE PLATES.

List of reference-letters.

bl., bladder; *c.m.vag.*, common median vagina; *c.t.*, connective tissue between lateral vaginal canals (fig. 31); *l.vag.c.*, lateral vaginal canal; *m.vag.*, median vaginal cul-de-sac; *p.vag.s.*, incomplete vaginal septum (fig. 29); *pr.p.*, remains of pseudo-vaginal passage; *ug.s.*, urogenital sinus; *ur.*, ureter; *ureth.*, urethra; *ut.n.*, uterine neck; *ut.p.*, papilla of uterine neck; *vag.s.*, median vaginal septum.

The figures of female genital organs in Plates I. & II. are all ventral views.

Plate I.

Fig. 1. *Didelphys aurita*. × about 1½.
Fig. 2. *Metachirus nudicaudatus*. × just over 1½.
Fig. 3. *Metachirus opossum*. × 2.
Fig. 4. *Caluromys philander*. × just under 2.
Fig. 5. *Chironectes minimus*. × about 4.

Plate II.

Fig. 6. *Marmosa cinerea*. × 2.
Fig. 7. *Marmosa murina* (A). × about 3.
Fig. 8. *Monodelphis (Peramys) americana*. × about 3.
Fig. 9. *Monodelphis domestica*. × about 3.
Fig. 10. *Monodelphis theresa*. × 5.

Plate III.

The sectional planes of figs. 11–14 are indicated in text-fig. 1.

Fig. 11. *Didelphys aurita*. Trans. sect. passing through the median vaginæ (*m.vag.*) and the lateral vaginal canals (*l.vag.c.*) in front of the openings of the ureters (*ur.*) into the bladder (*bl.*). × 10.
Fig. 12. *D. aurita*. Trans. sect. passing through the terminal portion of the left median vagina (*m.vag.*). × 10.
Fig. 13. *D. aurita*. Trans. sect. through the urogenital cord, shortly behind the termination of the left median vagina, showing the remains of the pseudo-vaginal passage (*pv.p.*) and also the differences in the character of the epithelial lining, and in the lumina of the lateral vaginal canal (*l.vag.c.*). × 10.
Fig. 14. *D. aurita*. Higher power view of central part of trans. sect. through the urogenital cord just behind fig. 13 and 0·19 mm. behind the termination of the left median vagina, to show the remains of the pseudo-vaginal passage (*pv.p.*). × 100.

Plate IV.

Fig. 15. *Metachirus opossum*. Trans. sect. passing through the median vaginæ (*m.vag.*) immediately in front of the openings of the ureters (*ur.*) into the bladder (*bl.*). × 15.
Fig. 16. *M. opossum*. Trans. sect. passing through the terminal part of the common median vagina (*c.m.vag.*). × 15.
Fig. 17. *M. opossum*. Trans. sect. shortly behind the termination of the median vagina, showing the remains of the pseudo-vaginal passage (*pv.p.*). × 25.
Fig. 18. *M. nudicaudatus*. Trans. sect. passing through about the mid-region of the median vaginæ (*m.vag.*). × 10.

Plate V.

Fig. 19. *Caluromys philander*. Trans. sect. through the median vaginæ, immediately in front of the openings into the lateral vaginal canals (*l.vag.c.*), showing the vaginal septum (*vag.s.*) and the branched folds arising from it and from the walls of the vaginæ. × 10.
Fig. 20. *C. philander*. Trans. sect. in front of the preceding, through the anterior prolongation of the median vaginæ, showing on the left the papilla of the uterine neck (*ut.p.*) cut through, and on the right, the tip of the same. Note the much-branched folds arising from the papillæ and from the walls of the vaginæ and practically filling up their lumina. × 10.
Fig. 21. *Marmosa murina* (A). Trans. sect. in front of the point of union of the neck of the bladder with the urogenital cord. Owing to the obliquity of the sectional plane, only one of the median vaginal culs-de-sac (*m.vag.*) is visible in the section. The lateral vaginal canals (*l.vag.c.*) are cut across twice on each side. × 25.
Fig. 22. *M. murina* (A). Trans. sect. some distance posterior to the preceding, showing the urethra (*ureth.*), and the lateral vaginal canals (*l.vag.c.*) cut thrice on each side. The posterior segments of the canals situated dorsally to the urethra have their lumina occluded. × 25.

Plate VI *.

The sectional planes of figs. 24–27 are indicated in text-fig. 2.

Fig. 24. *Marmosa cinerea*. Trans. sect. passing through the anterior portion of the common median vagina (*c.m.vag.*), showing the papillæ of the uterine necks (*ut.p.*) and the openings of the lateral vaginal canals (*l.vag.c.*) into the median vagina. × 10.

* [There is no Figure 23 on the Plates, as the figure intended for that number was transferred to the text-figures.—Ed. P. Z. S.]

Fig. 25. *M. cinerea*. Trans. sect. passing through the mid-region of common median vagina (*c.m.vag.*). × 10.

Fig. 26. *M. cinerea*. Trans. sect. passing through the hinder end of the common median vagina (*c.m.vag.*), at the level of the openings of the ureters (*ur.*) into the neck of the bladder (*bl.*). × 10.

Fig. 27. *M. cinerea*. Trans. sect. through the urogenital cord at the junction of the descending limbs of the vaginal loops with the solid posterior segments of the lateral vaginal canals (*l.vag.c.*). × 10.

Plate VII.

The sectional planes of figs. 28–31 are indicated in text-fig. 5.

Fig. 28. *Monodelphis* (*Peramys*) *americana*. Trans. sect. through the mid-region of the median vaginæ (*m.vag.*), showing the median vaginal septum (*vag.s.*), complete at this level. × 30.

Fig. 29. *M. americana*. Trans. sect. at the level where the vaginal septum becomes incomplete (*p.vag.s.*). × 30.

Fig. 30. *M. americana*. Trans. sect. through the terminal region of the common median vagina (*c.m.vag.*). × 30.

Fig. 31. *M. americana*. Trans. sect. through the urogenital cord at the level of the openings of the ureters (*ur.*) into the bladder (*bl.*); *c.t.* connective tissue between the lateral vaginal canals in which the pseudo-vaginal passage, when present, is situated. × 30.

Fig. 32. *M. domestica*. Trans. sect. passing through the median vaginæ (*m.vag.*) showing their flattened, transversely expanded form. × 30.

10. On Mammals collected in 1923 by Captain G. C. Shortridge during the Percy Sladen and Kaffrarian Museum Expedition to South-West Africa. By Oldfield Thomas, F.R.S., F.Z.S., and Martin A. C. Hinton, F.Z.S. With Field-Notes by the Collector.

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Thanks to the generosity of the Percy Sladen Trustees and to the Trustees of the King William's Town Museum, South Africa, we were in a position last year to give an account * of a valuable collection of Mammals which had been obtained in 1922 by Captain Guy Shortridge on the Lower Orange River, a region that had been previously but little explored.

That collection having been of so much scientific value, the same two bodies of Trustees were good enough in 1923 to bear the expenses of a further expedition into the territory of South-West Africa, a country still less known zoologically, and we now submit an account of the resulting collection, together with Capt. Shortridge's notes on the habits and life-histories of the various species he met with.

The area investigated forms the southern half of the territory of British South-West Africa (formerly known as Damaraland and Great Namaqualand, and more recently as German South-West Africa). Very little is known about the mammalogy of this region.

Of previous specimens obtained in this district, the only ones worthy of mention are the few collected about 1830 by Capt. (later Sir James) Alexander in Damaraland; and those obtained in 1859–1867 by the well-known Swedish collector C. J. Andersson, some of which formed the basis of a small paper by Thomas in 1882 †, while others were worked out and described by De Winton. One of Andersson's localities, Otjimbinque, was only about twenty miles from Karibib, where Capt. Shortridge was able to make a considerable collection.

Alexander's specimens were described by Mr. Ogilby in the Proceedings of this Society ‡, but as they included examples of *Amblysomus* and *Cryptomys*, genera that are not found in the area visited by Capt. Shortridge, the collection was presumably made farther north, where these animals are known to occur.

Mention should here be made of an important paper on S.W. African Mammals, published recently by Zukowsky §.

* P. Z. S. 1923, p. 483. † P. Z. S. 1882, p. 265. ‡ P. Z. S. 1838, p. 5

§ Zukowsky. "Beitrag zur Kenntnis der Säugetiere der nördlichen Teile Deutsch-Südwestafrikas unter besonderer Berücksichtigung des Grosswildes," Arch. f. Naturgesch., Berlin, &c. 1924, Abt. A, Heft 1, pp. 29–168.

This deals, however, chiefly with the game animals of the region; and since we have decided to wait for the arrival of Captain Shortridge's final collection before attempting to work out the ungulate material in detail, it has little bearing upon our present task.

Apart from a few old specimens, Capt. Shortridge's collection was made at four very well-selected localities, namely, Berseba, in the south-eastern part; Great Brukaros Mountain, an isolated peak over 5000 feet in height, near Berseba; Karibib, a place on the high inland region north-west of Walvis Bay; and Rooibank, a village down on the coast near the latter. Inland and costal regions, high and low altitudes, are therefore all represented.

Descriptions of these collecting stations are found in Capt. Shortridge's notes below, which we publish nearly in full, as they give so good an idea of the local characteristics of the places where the animals live.

The collection is an exceedingly fine one, and speaks volumes for Capt. Shortridge's energy and hard work. It consists of no less than 693 specimens, belonging to 67 species and subspecies, of which we have found occasion to describe 8 as new. We have also been able to distinguish some of the long described, but hitherto imperfectly known forms, based upon specimens collected by Andrew Smith, Alexander, and Andersson; and the good skins and skulls now obtained have enabled us to understand at last the proper characteristics and positions of these animals. In addition, a number of interesting embryos were obtained which have been placed in the hands of suitable investigators.

Altogether this new contribution of the Percy Sladen and King William's Town Trustees is one of very great value as helping forward our more exact knowledge of the mammalogy of Africa, and we have every reason to be grateful to them for it. Half the specimens come to our own National Museum, and half go to the Kaffrarian Museum, King William's Town.

The following are Capt. Shortridge's notes on the country and its mammalia:—

"In the following notes statistics have been partly taken from the 'Official Year Book of the Union of South Africa,' 1910–1921.

The area of South-West Africa is 322,450 square miles, or about three-fourths of that of the Union of South Africa.

Population (1921), European 19,432; Native 208,300 (approx.).

The rainfall varies from about 1" along the coastal belt to 6" in the South, 12" in the centre, and about 22" in the North. The climate is hot and dry, but very healthy, except in the northern districts, where malaria is prevalent during the autumn.

Except for the Kunene and Okavango Rivers on the northern, and the Orange on the southern boundary, there are no perennial

streams, although the country is intersected by innumerable dry river-beds, the most important of which is the Fish River, which, although only flowing after rain, always contains water-pools. Subterranean water is on the whole plentiful, and in river-beds frequently within a few feet of the surface.

South-West Africa consists of a series of plateaux, varying in altitude from 2000–7000 feet, diversified by hills, but generally flat, with an average height of 5000 feet. These uplands slope towards the east, where they merge into the Kalahari Desert and also slope gradually towards the north and south.

The coastline is bordered by a belt of sand, which varies in width from 20 to nearly 100 miles, known as the Namib Desert, an arid, rainless, and almost uninhabited region that extends northwards into Angola.

To the east of this belt, stretching from the Orange River to between Gibeon and Rehoboth in the north, the country known as Great Namaqualand changes from mountainous formation to a succession of flat or slightly undulating plains resembling the Upper Karroo, but with perhaps a higher percentage of grass country. At Rehoboth the railway is crossed by a narrow tongue of typical red Kalahari sand.

On reaching Damaraland, a complete change is noticed, and the Karroo gives place to mountain ranges and park-like grass country studded with large thorn-trees, which increase in number as far as Omaruru. From this point northwards the mountains gradually disappear, and the bush becomes very dense with an undergrowth of grass, and these features are maintained up to the northern border.

The eastern border, on the other hand, that merges into the Kalahari Desert, has very different characteristics. The country in the vicinity of the Orange River is a mixture of grass and karroo, whilst farther north, for a distance of about 300 miles, it consists of an endless succession of red sand-dunes thickly covered with grass and interspersed with trees, which increase in number until latitude 23° S. Here a further change takes place, and the dunes are followed by grassy, well-wooded plains, which merge into dense bush, right up to the Okavango River.

Through the kindness of Mr. G. R. Hofmeyr, C.M.G., the Administrator for South-West Africa, free game and shooting permits were obtained, and every facility was given by local officials in all districts visited. Camps were made at Berseba village and the Great Brukaros Mountain, Karibib, and Rooibank, while small collections were obtained from around Keetmanshoop and Windhuk.

The Hottentot names given may be liable to correction, as in some cases they were obtained by showing illustrations, which the natives were not always quick to recognize. The conventional signs in front of the names signify various kinds of 'clicks.'

Berseba.—Altitude 3067 feet, about the same latitude as Johannesburg. An important Hottentot village 54 miles

N.N.W. of Keetmanshoop, centrally situated in Great Namaqualand. Except for the Great Brukaros Mountain, 12 miles to the north, the surrounding country is flat and sandy or occasionally stony. Water—in some places barely below the surface—is plentiful, while the Fish River approaches within 8 miles of the village. Vegetation is sparse, resembling that of the Upper Karroo. *Rhigozum trichotomum*, the predominant bush farther south along the Orange River, is still plentiful, and, in addition to scrub, a rather thin coating of grass springs up after rain. Fleshy-leaved annual Mesembryanthemums are numerous, especially in the dry watercourses; otherwise succulent plants do not predominate.

The Great Brukaros Mountain.—Altitude 5902 feet. An isolated peak about 12 miles to the north of Berseba village. The only outstanding landmark visible from the railway between the Karas Mountains and those of Damaraland, which commence immediately to the south of Windhuk. What vegetation there is is sparse and stunted. The higher parts of the mountain consist mostly of bare precipitous rock outcrops, the slopes being covered with loose flat shingle. The mountain is horseshoe-shaped, and a watercourse runs south from a more or less permanent pool in its centre, which is practically shut off from the sun by high cliffs. The loose boulders, crevices, and slightly thicker vegetation in the bed of this watercourse had attracted a large percentage of what mammals occurred on the mountain.

Keetmanshoop.—Altitude 3286 feet. Population, White 1155; Coloured 5910. The second largest town in South-West Africa. Rainfall 6 inches. Situated about half-way between the Karas Mountains and Great Brukaros. Country very sandy and even more arid than around Berseba. Partly surrounded by stony kopjes and barren precipitous ranges of low hills.

Windhuk.—Altitude 5000 feet. Population, White 4460; Coloured 4400. 1384 miles from Cape Town and 1338 from Johannesburg. The administrative capital of South-West Africa. The town, which is situated in typical Damaraland thorn-veldt country, is surrounded on all sides by high kopjes and mountain ranges.

Karibib.—Altitude 3842 feet. Population, White 403; Coloured 5628. About half-way by rail between Windhuk and Swakopmund. Situated inside the Damaraland thorn-veldt area, but close to the eastern edge of the Namib. The country here consists of flat patches and strips of grass land studded with thorn-trees, which, however, are not so thick as they become towards Omaruru and Okahandja. Most herbaceous vegetation dries off and practically disappears during the hot weather. The flats, which are intersected by dry watercourses of no great size, are separated by chains of precipitous mountains of rocky outcrop, very sparsely covered with stunted vegetation that culminate in the Erongo Range, some 30 miles north of the town, which rises to upwards of 7000 feet.

Rooibank.—Altitude 240 feet, situated 20 miles up the Kuisib River from Walvis Bay.

Walvis Bay.—Population, White 144; Coloured 636. One of the finest natural harbours on the West Coast, and the port of entry for South-West Africa. Walvis Bay itself is surrounded by sandhills that are not typical of the Namib proper, and which stop at the Swakop River about 20 miles farther north. There is no vegetation of any description, but on crossing the sandhills, which appear permanently to have shut off the mouth of the Kuisib River from the sea, its bed, which at first is much choked up with sand and not well defined, widens out to over a mile. At the rare intervals, when up country rains have been sufficient partly to fill the river, the water percolates before reaching the sea. Subterranean water, however, occurs in the river within 10–15 feet of the surface. At first the vegetation, which is confined to the bed of the Kuisib, is scanty, and consists entirely of wild tobacco, *Mesembryanthemum marlothii*, *Tamarix articulata*, and "Narra" (*Acanthosicyos horrida*), a species of spiny leafless melon peculiar to river-beds in this part of the Namib. Twenty miles up the river at Rooibank there is a distinct increase in the vegetation, which now includes tufts of coarse grass and some large wild fig thorn-trees.

Rooibank is a very small Hottentot settlement, the river-bed vegetation here maintaining a limited number of goats and a dozen or so head of cattle. The natives themselves, who are of an extremely degenerate type, in addition to goats' milk, subsist almost entirely on the seeds of the 'Narra,' which are collected when the fruit is ripe and stored for food. At this point the south bank of the river is shut in by sandhills similar to those around Walvis Bay, while on the north bank the country has become typical Namib desert, which consists of a heavier kind of sandy grit that—except for occasional minute stone lichens—is equally devoid of vegetation. The river-bed, therefore, stunted and scattered as the vegetation is that grows in it, becomes the obvious and only hunting-ground for a local mammal fauna."

1. Papio porcarius Bodd.

♂. 923. Karibib. 3842'.

"Plentiful around Karibib, and without doubt occurring throughout the mountainous regions of Damaraland. Not resident on Great Brukaros, although the Berseba Hottentots state that they occasionally occur along the low precipitous banks of the Fish River. These may wander up from the Karas Mountains or the hill country in the neighbourhood of the Orange River.

Cercopithecus lalandei apparently does not occur in South-West Africa except among the trees that fringe the Orange River, where—I was locally informed—they extend almost to the mouth."—G. C. S.

2–6. Rhinolophus and Hipposideros.

Mr. Shortridge's collection includes a fine series of Bats belonging to the genera *Rhinolophus* and *Hipposideros*. The working-out of these involves certain questions of considerable difficulty, and we think it better to defer our description of the material until next year when, it is hoped, we shall receive a further collection from S.W. Africa.

7. Nycteris damarensis Pet.

♂. 868, 871, 1005. ♀. 869, 870. Karibib. 3842'.
♂. 1024, 1035. Windhuk. 5600'.

"Apparently plentiful in caves around Karibib and Windhuk. A late flyer."—G. C. S.

8. Cistugo seabræ Thos.

♂. 591. ♀. 510. Berseba. 3067'.

A valuable accession, as no members of this genus had been received since it was described from a single specimen in 1912. The glands in the wing, not easily perceptible on the dried skins, become readily apparent if the wings are soaked in water.

A larger bat from the Paarl district of the Cape, stated to belong to the same genus, has been described by Mr. Austen Roberts*.

"Not observed in any numbers, but probably appearing in greater quantities during the hot season.

Bats were scarce around Rooibank during my visit, but I was informed that they would become numerous later on in the year."—G. C. S.

9. Nyctinomus bocagei Seabra.

739.

"A few specimens were observed on most nights flying from the mountain, where they probably had a roosting place."—G. C. S.

10. Nyctinomus (*b*).

738.

Shot in company with *N. bocagei*.

11. Macroscelides melanotis Og.

♂. 411, 429, 430, 504, 506, 520, 544, 556, 558, 569, 588, 590, 622, 624, 650. ♀. 431, 445, 505, 507, 508, 517, 518, 519, 557, 573, 589, 597, 611, 621, 623, 631, 649. Berseba.
♂. 654. ♀. 703, 704, 733. Great Brukaros Mt.

"Extremely plentiful in Berseba District. *Elephantulus* also occurred there in equal numbers, and at a short distance they

* *Cistugo lesueuri*, Ann. Transv. Mus. vi. p. 112, 1919.

are indistinguishable. It is curious that *Macroscelides*, with its enlarged auditory bullæ, should be distinguished by the local Hottentots from the normal *Elephantulus* by a name that means 'Deaf' Mouse. Frequenting flat sandy country, studded with low scrub, under which they excavate their not very deep burrows, which are frequently almost perpendicular. The tail-gland is similar to that of *Elephantulus*, but smaller. The ears of this species are dead black, and not semi-transparent against the light as with *Elephantulus*. It will be seen from the fœtuses sent that the young of Elephant Shrews are born in pairs, in a highly advanced state, well covered with fur, and apparently with their eyes open, and extremely large in comparison with those of adults."—G. C. S.

12. Elephantulus rupestris Sm.

♂. 478, 479, 522, 579, 596, 599, 600, 603, 614, 616, 617, 639, 640, 641, 642. ♀. 412, 477, 523, 524, 546, 568, 594, 595, 598, 601, 602, 604, 615, 618, 619, 625, 632. 636, 637, 638. Berseba.

♂. 677, 690, 691, 757. ♀. 705. Great Brukaros Mt.

There is remarkable uniformity in the coloration of the typical form of this species, specimens from the Western Transvaal, Orange River, and Namaqualand all agreeing very closely with each other.

"Although, unlike *Macroscelides*, *Elephantulus* frequents rocky hills and stony country, both species were equally plentiful in the flats around Berseba, and a 'digging party' would frequently obtain equal numbers of each from the same locality. When angry they make a scolding noise rather like that of a small bird, and when several are kept together, occasionally make a curious kind of rattling sound; they also kick at each other with their hind feet, which become quite thickly tangled with tufts of fur. Ears pale brown, and semi-transparent against the light.

The snouts of Elephant Shrews are very sensitive, but are only movable from the base.

'Huni paus' (Berseba Hottentots)."—G. C. S.

13. Elephantulus intufi Sm.

♂. 955, 970, 971 (immature), 1001, 1010, 1012. ♀. 956, 1011. Karibib. 3842'.

Specimens 971 and 1010 are much greyer and less buffy than usual, especially posteriorly, so much so as to suggest the coloration of *E. rupestris*; but there is no doubt that they are really referable to this species.

The skull of *E. intufi* is smaller than that of *E. rupestris*, with a less elongated muzzle, and the combined length of the five posterior upper teeth (p^3—m^2) is normally below 10·5 mm., while in *rupestris* it ranges from 11 to 11·7.

"Fairly plentiful around Karibib, chiefly in rocky situations."—G. C. S.

14. Felis leo L.

"Lions, except as rare stragglers, are probably extinct in Great Namaqualand, but they are still well known in Northern Damaraland along the Kalahari border.

'Chimi' (Berseba Hottentots)."—G. C. S.

15. Felis pardus L.

761 (no skull).

"Apparently generally distributed throughout S.W. Africa."—G. C. S.

16. Felis nigripes Burch.

"Rare and possibly occurring only on the eastern border, where conditions are similar to those of the Kalahari. I saw no skins in local karosses, but there is a live specimen at the Windhuk Zoological Gardens, which I believe came from the neighbourhood of Gobabis. It was kept in a run with several specimens of *F. ocreata caffra*."—G. C. S.

17. Felis ocreata caffra Desm.

♂. 613. ♀. 587. Berseba. 3067'.

"Plentiful. Karosses made from the skins of these cats are easy to obtain. The Kaffir Cat is very evenly distributed throughout South Africa, and appears to be equally numerous in open and forest country. Without doubt a considerable amount of interbreeding occurs between this species and the domestic cat, and as almost invariably the females are the domestic cat, these hybrids are frequently to be found around farms and native villages, which may account for the fact that in South Africa domestic cats so readily develop into poultry thieves."—G. C. S.

18. Caracal caracal Güld.

1076 (no skull). 1078 (skull only). Damaraland.

"Karosses made from 'Red Cat' skins chiefly obtained from the Kalahari border are occasionally procurable in S.W. Africa.

For its size the Caracal is in the habit of preying on large animals and does a lot of damage to stock."—G. C. S.

19. Acinonyx jubatus Erxl.

760 (no skull). Keetmanshoop.

1019 (no skull), 1020 (no skull). Damaraland.

"Judging by the number of trade skins for sale in local stores, cheetahs would appear to be more numerous than leopards in this part of Africa. These skins are said mostly to come from Gobabis and elsewhere on the Kalahari border.

Usually referred to as the 'leopard' by colonists when distinguishing it from *Felis pardus*, which in South Africa is almost invariably called a 'tiger.'"—G. C. S.

20. Genetta felina Thunb.

471 (no skull). Berseba. 3067'.
762 (no skull). Keetmanshoop. 3350'.
842. Rooibank. 240'.
919, 1018 (no skull). Karibib. 3842'.

"Apparently generally distributed throughout Great Namaqualand and Damaraland; extending west into the Namib, but, as in the case of most of the local small carnivores, seeming to become more numerous towards the Kalahari. Genet skin karosses were not very plentiful in South-West-Africa."—G. C. S.

21. Atilax paludinosus G. Cuv.

390. Louisvale. 2600'.

"Although from the evidence of this specimen the Water Mongoose exists along the Orange River, it is probably uncommon in the south-west, and chiefly to be found in those parts of South Africa where there is rank vegetation and a heavier rainfall. Strictly nocturnal, and even where judging from tracks it is plentiful, it is seldom seen by day. As with the Otters, on account of there being no permanent rivers it is without doubt absent from S.W. Africa between the Orange River and the rivers on the northern boundary."—G. C. S.

22. Herpestes gracilis Rüpp.

♂. 713. ♀. 694, 695. Great Brukaros. 3500–5202'.
♂. 574. Berseba. 3067'.

"Quite plentiful in rocky open country judging from tracks and other indications, but as they were never put up or seen by day they may be more exclusively nocturnal than is usually the case with smaller mongooses. The grey mongoose observed last year in the rocky country near Louisville might have been this species. With the exception of *Cynictis* and *Suricata*, no mongoose skins were observed in local karosses. All of these specimens were caught in traps baited with mealies."—G. C. S.

23. Cynictis penicillata G. Cuv.

♀. 475, 476, 630. Berseba. 3067'.

"Apparently widely distributed and in many localities fairly plentiful, although on the whole possibly less so than in the Karroo.

Suricata was evidently much more local. It was not observed or spoken of at Berseba, but was said to occur around Karibib, and described as plentiful near Rehoboth. I saw several skins in a kaross that had been made in that district. It may also become more numerous in the direction of the Kalahari. *Cynictis* is incorrectly mentioned in Sclater's 'Mammals of S. Africa' as not extending so far west as *Suricata*."—G. C. S.

24. HYÆNA BRUNNEA Thunb.

1017 (no skull). Karibib. 3842'.

"Possibly more plentiful in the southern parts of S.W. Africa than *C. crocuta*. At the same time they can be by no means numerous, as the destruction done by them to stock appears to be small in comparison to that done by the wild dog.

Generally known as the "Strand Wolf" on account of its well-known habit when near the coast of feeding on dead fish and other marine refuse; also said at times to swim out to rocks at low tide for the purpose of feeding on shellfish. *Crocuta crocuta* evidently becomes more plentiful in the less disturbed country beyond Damaraland. It is recorded by Sclater as being specially common in Ovampoland."—G. C. S.

25. PROTELES CRISTATUS Sparrm.

765, 766 (no skull). Keetmanshoop. 3350'.
1021, 1022 (no skull). Karibib. 3842'.

"The Aard Wolf is well known in South Africa and, judging by the number of skins in karosses, reasonably plentiful.

It is slowly becoming recognized that they are entirely harmless to stock, and as wild ostriches have been proclaimed vermin in S.W. Africa, the fact that they have been accused of destroying eggs, would, if true, be more in their favour than otherwise. On account of their insectivorous habits their local protection is being considered. Although described by Sclater as a slow animal, one that was put up by Kaffir dogs near Berseba in fairly open country managed to get away with apparent ease."—G. C. S.

26. CANIS MESOMELAS Schr.

♂. 491. Berseba. 3067'.
♀. 831, 846. Rooibank. 240'.

"Plentiful, large numbers of Jackal karosses are made locally; trade name, 'Golden Jackal.'"—G. C. S.

27. VULPES CHAMA A. Sm.

♀. 645. Berseba. 3067'.

"Considerably less plentiful than *Otocyon megalotis*, the skins not being obtained in large numbers by local dealers, although they are much sought after. Silver Fox karosses, although not wearing well, are of comparatively high value, being rare.

The burrow in which the above specimen was trapped was extremely small for the size of the animal, and appeared to be part of a warren occupied by *Cynictis*."—G. C. S.

28. Otocyon megalotis Desm.

♂. 458, 627. ♀. 628. Berseba. 3067'.

"Delalande's Fox is believed to feed almost entirely on small rodents, reptiles, and insects; on this account, and because of the numbers that are destroyed by the kaross-making tribes, it has recently been placed on the protected game list by the Administration of S.W. Africa. This fox must not only be plentiful, but easy to capture, as enormous numbers of their skins are annually made into karosses, which chiefly come in from Gobabis and elsewhere on the Kalahari border.

There are three specimens in the Windhuk Zoo. Their long-legged and loose-haired appearance gives them a resemblance to a small jackal rather than a fox. During life the hair along the line of back forms a parting and falls over loosely on either side as in *Proteles*."—G. C. S.

29. Lycaon pictus Temm.

"The Cape Hunting Dog can hardly be considered a resident in any one locality, but practically all districts in S.W. Africa are periodically visited, and there is no doubt that the damage they do on these occasions among stock and wild game is very considerable. They are said to show no fear of Kaffir dogs, which are unwilling to face them."—G. C. S.

30. Ictonyx striatus Perry.

♂. 521. Berseba. 3067'.

"Widely distributed and well known everywhere in S.W. Africa, even in the Namib, as it is said to occur along the dry bank of the Kuisib River.

Around settlements it is a persistent poultry thief.

Except along the Orange River in the south and the permanently running Kunene and Okavango Rivers in the north, Otters are not likely to occur in S.W. Africa, as, according to Berseba Hottentots, they are not even found in the disconnected pools of the Fish River."—G. C. S.

31. Mellivora ratel Sparrm.

1067 (no skull). Karibib. 3842'.

"Probably occurring throughout S.W. Africa wherever there are rocky hills, but although widely distributed the ratel, like a true badger, is strictly nocturnal, seldom seen, and still more seldom captured. Notwithstanding their small size it is considered dangerous to disturb them in their hiding places, especially when they have young, as it is said to be quite usual for the old ones to rush out and attack anything that approaches too near. It is also said to require a good dog to tackle one singly.

Although widely distributed it cannot be described as 'plentiful everywhere in South Africa' as recorded by Sclater."—G. C. S.

32. Arctocephalus pusillus Schreb.

849 (850, 51, 52, 53, 54, & 55, skulls only). Cape Cross.

"Cape Cross, about 100 miles to the north of Walvis Bay, would seem to be the most northerly point and the only place on the mainland where the Cape Seals breed and to be their most extensive breeding grounds—others being a limited number of small islands and rocks off the coast between the Cape and Walvis Bay.

Those between the Orange River and Luderitz are: Long, Possession, Roast Beef Islands, and Black Rock. Others between Luderitz and Walvis Bay being known as Hollam's Vogel Island, Staple Rock, Staple Riff Island, Dom Futsen Island, and No. 84 Rock, all of these being close to Itshabo Guano Island. The eastern limit of its range appears to be Bird Island in Algoa Bay.

Large males are said to weigh up to 800 lbs."—G. C. S.

33. Geosciurus capensis namaquensis Licht.

♂. 469. Berseba. 3067'.

♂. 989. Karibib. 3842'.

Both specimens in worn fur, so that no very close comparison is possible.

"Not plentiful around Berseba. A single warren was found about six miles from the village.

Judging from their warrens, ground squirrels were quite plentiful around Karibib. They are apparently not evenly distributed in S.W. Africa. Diurnal, although during the hot weather seldom seen towards the middle of the day. 'Gienab' (Berseba Hottentots)."—G. C. S.

34. Gliriscus (g. n.) rupicola, sp. n.

♂. 921. ♀. 857, 894. Karibib. 3842'.

In determining these specimens we have made an examination of all the African Dormice commonly referred to the genus *Graphiurus*. It has long been obvious to us that the Cape Dormouse (*Graphiurus ocularis*) was not properly congeneric with the other African species, and we may take this opportunity of reclassifying the group.

This would seem to be divisible into three, namely, the Cape Dormouse, the ordinary African arboreal dormice, and the rock-inhabiting forms of which Capt. Shortridge has now discovered a second species.

The three genera we propose to recognize may be briefly arranged as follows:—

A. P^4 minute, simple. Surface of teeth with scarcely perceptible ridges.
   1. *Graphiurus* F. Cuv. Genotype: *G. ocularis* (*Myoxus ocularis* A. Sm.).

B. P^4 little smaller than molars; its outer edge, when unworn, notched as in the molars. Surface of teeth with distinct ridges.
   a. Skull of normal height; brain-case strongly convex upwards.
      2. *Claviglis* Jent. Genotype: *C. crassicaudatus* Jent.
   b. Skull flattened, muzzle low; brain-case scarcely convex upwards.
      3. *Gliriscus*, g. n. Genotype: *G. platyops* (*Graphiurus platyops* Thos.).

We believe that all the members of *Claviglis* are arboreal, while those of *Gliriscus* are rock-haunting, their flattened skulls enabling them to creep into low crevices in the rocks they live among.

The present species, the second known of the genus, may be described as follows:—

A large rock-inhabiting Dormouse with flattened skull and large bullæ. Size large, one of the largest of African Gliridæ. Fur close and velvety, hairs of back about 9 mm. in length. General colour above silvery grey with a faint drabby infusion. Below the hairs are broadly tipped with dull whitish, which may or may not have a slight vinous tinge*. Hands and feet white, the latter normally without any brown on the metatarsals. Tail broad and bushy, more than an inch in breadth, the hairs broadly slaty basally, with white tips, the middle area of the tail above also profusely white mixed.

Skull large and very much flattened, nearly as much so as in that of *G. platyops*, which it closely resembles with the exception that the bullæ are very much larger, so that in this part of the skull its height is much greater. But anteriorly it is low or flat, quite unlike the skull of the species of *Graphiurus*.

Dimensions of the type:—

Head and body 116 mm.; tail 99; hind foot 21·5; ear 16·5.

Skull: greatest length 32·5 mm.; condylo-incisive length 29; zygomatic breadth 17·8; nasals 13; interorbital breadth 5; greatest breadth above bullæ 15·7; height of crown from alveolus of m^1 6·1; height of brain-case from lower surface of bullæ 11; length of bullæ 11·4; upper cheek-teeth 3·6.

Hab. Inland highland region of S.W. Africa. Type series from Karibib.

Type. Adult male. B.M. No. 25.1.2.71. Original number 921. Collected 1 November, 1923.

This fine Dormouse is conspicuously different from any hitherto described, as, with the exception of *G. platyops*, all other known forms have their skull of the usual rounded and unflattened shape and are generally far smaller. *G. platyops* is considerably lighter in colour and has much smaller bullæ.

But from the Great Brukaros Mountain Capt. Shortridge obtained a series of a dormouse essentially the same as *G. rupicola*, but sufficiently different to deserve a distinct subspecific name.

35. GLIRISCUS RUPICOLA MONTOSUS, subsp. n.

♀. 685, 725, 744, 758, 759. Great Brukaros Mt. 3600'–5000'.

Similar to true *rupicola* in all important respects, but general colour darker and more slaty, less drabby; under surface darker,

* In describing four Transvaal Dormice, Mr. A. Roberts (Ann. Transv. Mus. iv. pp. 79–89, 1913) has used the presence or absence of a vinous tinge as though it were a character of importance, but in most or all cases it is merely an accidental staining of the hairs by fruits or other food. How far the described forms are valid it is impossible to determine from the descriptions.

the light tipping to the hairs both shorter and more brownish white; hind feet with the proximal half or two-thirds of the metatarsus occupied by a patch of dark brown, which may extend to the base of the digits. Tail less bushy, barely half an inch in breadth, the white ends to the hairs less in extent, especially along the middle area both above and below.

Skull as in true *rupicola*. Cheek-teeth slightly larger, but this may be a question of wear.

Dimensions of the type:—

Head and body 118 mm.; tail 108; hind foot 21·5; ear 17.

Skull: greatest length 32·5 mm.; condylo-incisive length 29·2; bullæ 11·3; upper tooth series 3·9.

Hab. Great Brukaros Mountain.

Type. Adult female. B.M. No. 25.1.2.74. Original number 744. Collected 26 September, 1923.

In parallel variation with several other cases the Brukaros form is subspecifically distinguishable from that of Karibib by its darker coloration.

As is indicated in Capt. Shortridge's notes, this *Gliriscus* is not arboreal, as are most dormice, but is an inhabitant of rocks, into whose crevices its peculiarly flattened skulls enable it to creep. We have little doubt that *G. platyops* is also a rock-liver, even though the collector of the type marked his one specimen as being "arboreal"; or, of course, it may be both. In the case of *G. rupicola* there would seem to be no trees for it to inhabit.

36. Desmodillus auricularis Sm.

♀. 571. Berseba. 3067'.

Very like the Orange River specimens obtained in 1922 by Capt. Shortridge.

"Only a single specimen was obtained at Berseba, but on account of the quantities of *Rhabdomys*, *Praomys*, etc., that got into the traps, it is impossible to determine in a limited time whether other rodents were actually scarce or merely less numerous."—G. C. S.

37. Desmodillus auricularis pudicus Dollm.

♂. 806, 832. ♀. 834, 835, 844. Rooibank, near Walvis Bay. 240'.

Apparently identical with *pudicus* of the Kalahari, in spite of the difference in altitude.

"*Desmodillus* is largely insectivorous, and the wings of large quantities of locusts were found inside the burrows of those obtained at this camp. Occasionally the burrows were discovered in the open desert at some little distance from the scrub in the river-bed.

It might be noticed that these rodents, which resemble *Macroscelides* in having enlarged auditory bullæ, make burrows that are more or less perpendicular, and quite indistinguishable from those of the Elephant Shrew."—G. C. S.

38. Gerbillus vallinus Thos.

♂. 543, 578, 633, 644, 652. ♀. 609, 610, 646, 653. Berseba. 3067'.

♂. 719. ♀. 696, 710, 729, 745. Gt. Brukaros Mt. 3500'–5202'.

This distinct species has been hitherto only known from the type, collected by Capt. H. A. P. Littledale at Tuin, Kenhart, Great Bushman's Land. That type had lost the terminal half of its tail, and we are now able to record that the tail is particularly long (138–154 mm.) and has an unusually well-developed blackish pencil along the upper side of its distal half. Proximally the upper side of the tail is lined blackish and the lower dull whitish. The large bullæ and partially hairless soles are quite the same as in the type.

"Fairly plentiful around Berseba, and at the foot of the Great Brukaros Mountain. Nocturnal; their burrows are not conspicuous, being usually hidden under the bushes that line the beds of dry water-courses, etc."—G. C. S.

39. Gerbillus swalius, sp. n.

♂. 920, 927, 961, 962, 966, 968, 988, 1002. ♀. 994. Karibib. 3842'.

Size and colour as in *G. calidus* of Molopo, the general tone of the same sandy fawn, though the dorsal hairs are more distinctly tipped with blackish. Hands and feet white, the forearms wholly in the white area. Soles completely hairy except for a small spot, about 1–2 mm. in diameter, under the calcaneum, the region under the ankle-joint fully covered. Underside of terminal pad and digits also fully clothed. In *calidus* there is a bare patch under the astragalus, and the under side of the digits is also more or less naked. Tail decidedly longer than in *calidus*, the terminal half distinctly crested and pencilled with blackish-brown hairs attaining 7 or more mm. in length, while in *calidus* there is practically no pencilling.

Skull rather longer and with larger and more highly inflated bullæ than in *calidus*; posterior palatal foramina longer.

Dimensions of the type:—

Head and body 95 mm.; tail 121; hind foot 27; ear 15.

Skull: greatest length 30 mm.; condylo-incisive length 96; nasals 12·6; breadth of brain-case 13·8; palatal foramina, anterior 5, posterior 2·4; diagonal horizontal diameter of bullæ 8·8; upper molar series 4·3.

Hab. High country inland of the Walvis Bay region. Type from Karibib, alt. 3842'. The Otjimbinque specimens collected by Andersson in 1865 and previously referred first to *G. paeba* and later to *G. calidus*, also belong, as is natural, to this species.

Type. Adult male. B.M. No. 25.1.2.88. Original number 920. Collected 1 November, 1923.

"Fairly plentiful in flat country around Karibib."—G. C. S.

Now that a number of well-collected specimens of the western Gerbil are available, we are able to distinguish it from *G. calidus* of the Kalahari by its much longer and more tufted tail, and its more inflated bullæ. Specimens from the coast, at a low altitude, are also assignable to it, but are distinguishable subspecifically, as follows:—

40. Gerbillus swalius oralis, subsp. n.

♂. 770, 789, 810, 811, 829, 833, 837, 838, 843, 847. ♀. 769, 777, 799, 814, 825, 830, 836, 839, 840. Rooibank, near Walvis Bay. 240'.

Size and essential characters as in the high ground *swalius*, but the colour is a richer and brighter buffy, the hairs of the back quite without the blackish tips which give so distinct a shading to *swalius*. Hind feet with the soles more naked than in *swalius*, the bare patch under the heel extending under the ankle-joint to the proximal quarter of the metatarsus, and in some cases further. On the other hand the character is not absolutely constant, some specimens more agreeing with *swalius*.

Dimensions of the type:—

Head and body 87 mm.; tail 116; hind foot 27·5; ear 13·5.

Skull: greatest length 28 mm.; condylo-incisive length 24·4; bullæ 8·7; upper molar series 4.

Hab. Low coast region near Walvis Bay. Typical series from Rooibank. 240'.

Type. Adult male. B.M. No. 25.1.2.95. Original number 810. Collected 17 October, 1923.

Although no doubt closely allied to *swalius* this coast Gerbil seems to represent a distinguishable lowland race characterized by its brighter colour and more naked soles.

"Plentiful among the vegetation in the bed of the Kuisib River. Well known locally on account of their habit of hopping round camp-fires at night. Seeming to prefer the neighbourhood of Narra bushes (*Acanthosicyos horrida*) which form tangled growths on the small sand dunes."—G. C. S.

41. Parotomys (Liotomys) littledalei Thos.

♂. 401, 402, 407, 413, 444, 495, 563, 565, 567, 568. ♀. 403, 404, 405, 408, 409, 410, 414, 433, 494, 564, 592, 608. Berseba.

"Diurnal, gregarious, plentiful around Berseba village, as usual not readily trapped, so that when their presence is discovered, it is more profitable to dig them out. In this locality their burrows were found among the roots of small bushes on low sand-hills close to patches of annual mesembryanthemums which they probably fed on, there being no typical salt country similar to that where the Louisvale specimens were obtained. There were also none of the usual structures of sticks above their burrows."—G. C. S.

42. Praomys namaquensis Smith.

23 ♂, 26 ♀. Berseba. 2067'.
*23 ♂, 25 ♀. Great Brukaros Mt.
18 ♂, 9 ♀. Karibib.

"There are no hills or rocky outcrops around Berseba village, but these small rock rats were extremely plentiful in any patches where there was any loose shingle, and also among the ruins of some old stone buildings in the village; otherwise they did not appear to be attracted by habitations.

This species absolutely swarmed on the Great Brukaros Mountain, both among bare rocks and in the low thickets that grew among loose boulders in the beds of the dry water-courses. Nocturnal, but coming out at dusk—extremely active.

Plentiful among rocky hills around Karibib, probably occurring in the hill-country throughout Damaraland.

'Durub' (Berseba Hottentots)—mice and rats generally."—G. C. S.

43. Praomys collinus, sp. n.

♂. 858, 859, 860, 911, 912, 925, 958, 959, 960, 976, 983, 984, 991, 1003, 1014. ♀. 892, 893, 949, 957, 977, 978, 990, 992. Karibib. 3842'.

A small Gerbil-coloured mouse with short feet.

Size quite small, although larger than in the next species. Fur fine, soft and silky; hairs of back about 8 mm. in length. General colour uniform buffy, sometimes very bright buffy, but generally a sandy buffy; younger specimens more drabby. Under surface greyish white, the hairs broadly slaty basally, with white tips. Forehead and crown lighter than back and generally perceptibly greyer. Ears long, dull brown. Hands and feet white. Tail rather longer than head and body, uniformly whitish above and below, or with very faint darker clouding. Mammæ 1-2=6.

Skull delicate, smooth, without ridges, the supraorbital edges barely squared, quite without defined beads in marked contrast to the condition in *P. namaquensis*. Anteorbital plate little projected, not undercut as it is in that species.

Palatal foramina of medium length, their hinder ends about level with the front of m^1. Mesopterygoid fossa fairly open. Bullæ of medium size.

Incisors well turned in backwards, their index about 56°. Molars small and delicate, rather variable in size.

Dimensions of the type, measured in the flesh:—

Head and body 89 mm.; tail 100; hind foot 16·5 (range 15–17); ear 16 (range 15–17).

Skull: greatest length 25·6 mm.; condylo-incisive length 23·2; zygomatic breadth 12·5; nasals 9·5; interorbital breadth 4; breadth of brain-case 11·7; palatal foramina 4·7; bullæ, diagonal diameter 3·6; upper molar series (worn) 3·7.

Hab. South-West Africa—type series from Karibib.

Type. Adult female. B.M. No. 25.1.2.166. Original number 990. Collected 8 November, 1923.

"Plentiful among rocky hills round Karibib."—G. C. S.

This mouse appears to be unlike any described South African species, and to belong rather to the group containing *P. aeta* and other more tropical forms. Its buffy Gerbil colour is evidently related to the sandy nature of the country it inhabits.

While the Karibib series, with the exception of a few immature examples, all agree with the above description, which would no doubt also apply to the corresponding mice of other South-West African localities, the specimens obtained by Capt. Shortridge on Great Brukaros Mountain show sufficient average difference to deserve a special subspecific name, and we therefore put them under a separate heading.

44. Praomys collinus bruchus, subsp. n.

♂. 727, 728, 743, 752, 753, 754, 756. ♀. 671, 696, 710, 723, 729, 742, 745. Gt. Brukaros Mt. 3500'–5200'.

Essential characters as in *P. collinus*, but colour darker and less buffy or gerbilline. Upper surface dull lined brown, the head if anything darker than the back, while in *collinus* it is a lighter and more greyish buffy. Ears a darker brown. Tail distinctly brown throughout, the hairs blackish, in marked contrast to the whitish tail of *collinus*.

Dimensions of the type:—

Head and body 86 mm.; tail 97; hind foot 17·5; ear 15.

Skull: greatest length 25 mm.; condylo-incisive length 23; upper molar series 3·8.

Hab. Gt. Brukaros Mt. Altitude 3500'–5200'.

Type. Adult female. B.M. No. 25.1.2.172. Original number 723. Collected 24 September, 1923.

This is evidently a dark mountain race of what will no doubt prove to be a widely spread buffy-coloured inhabitant of the rocky and sandy areas of S.W. Africa.

"A rock mouse, frequenting the same localities as the Dormouse, and similarly living in rock crevices."—G. C. S.

45. Praomys monticularis, sp. n.

♂. 718. ♀. 726. Gt. Brukaros Mt., near Berseba. 3500'–5200'.

A very small species with short ears and tail.

Size markedly less than in *P. collinus*. Colour and general appearance quite as in *P. c. bruchus*, with which it lives side by side. Fur thin and straight, hairs of back about 7 mm. in length. General colour above brownish buffy, clearer buffy on sides and rump; head more blackish. Under surface soiled grey, the hairs slaty basally. Ears unusually short, dark brown.

Hands and feet white. Tail shorter than head and body, well-haired throughout, but not pencilled, the scales showing through; dark brown above and below, as in *bruchus*.

Skull smaller and more delicately built than in *collinus*, the supraorbital edges inclined to be more sharply angular, though equally without beading. Palatal foramina penetrating slightly between molars. Choanæ very narrow and closed up, the mesopterygoid fossa narrowed to a mere linear slit, markedly different from the well open fossæ of *collinus*; ectopterygoids broadened and more angular laterally. Bullæ small.

Dimensions of the type:—

Head and body 77 mm.; tail 72; hind foot 15·5; ear 12·5.

Skull: greatest length 23·5 mm.; condylo-incisive length 21; zygomatic breadth 11·7; nasals 8·8; interorbital breadth 3·9; breadth of brain-case 10·6; palatal foramina 5; bullæ, diagonal diameter 3; upper molar series 3·5.

Hab. Gt. Brukaros Mt., near Berseba. Altitude 3500'–5200'.

Type. Adult male. B.M. No. 25.1.2.167. Original number 718. Collected 24 September, 1923.

This very distinct little kopje mouse, which Capt. Shortridge recognized as different from the common *collinus*, in whose company it was found, may be readily recognized by its short ears and tail, and the very marked narrowing of the mesopterygoid fossa.

"Trapped in a low rocky kopje."—G. C. S.

46. LEGGADA BELLA INDUTA Thos.

♀. 891. Karibib. 3842'.

Agreeing closely in colour and skull characters with the mid-winter type from Molopo, but with shorter fur, a difference no doubt due to season.

"Trapped in the bed of a dry water-course in flat country near the marble quarries of Karibib."—G. C. S.

47. RHABDOMYS PUMILIO BECHUANÆ Thos.

21 ♂, 30 ♀. Rooibank, near Walvis Bay. 240'.

Decidedly larger, and with less dark and strongly contrasted dorsal lines than the specimens from the higher country inland, Karibib and Berseba, which we place under the next heading.

Although this coast region can certainly not be called "Betjouanas," as the original type, purchased from a French dealer in 1857, was labelled, the identity of these specimens with that type is so exact that they clearly must be assigned to *bechuanæ*, a race which would appear to have a more or less discontinuous distribution, the smaller *griquæ* coming between. Dollman's *deserti* from the Kalahari is also similarly larger, and but little lighter than the lightest of the present series.

"Occurring in large numbers in the bed of the Kuisib River, never observed climbing among bushes; the entrances of their burrows were very conspicuous and as large as those of *Parotomys*." —G. C. S.

48. RHABDOMYS PUMILIO GRIQUÆ Wrought.

32 ♂, 12 ♀. Berseba.
♂. 974. ♀. 896, 985. Karibib.

Smaller and more strongly lineated than the coast animal. Quite agreeing with the series obtained from Louisvale on the Orange River, which we termed *R. p. bechuanæ* in our previous paper. The fine additional series now obtained indicates that this smaller and more strongly marked form occupies the Orange River area, from the Modder to the western edge of the high country, through Griqualand, the Upington region and Berseba, to Karibib, and that its proper name is *griquæ*.

"Extremely plentiful around Berseba; their burrows, which are usually under bushes, are thickly lined with fine grass and other soft materials—quite frequently they may be found in deserted birds' nests well off the ground. In this locality they are semi-arboreal, spending much of their time climbing among low thorn-trees. The skin of *Rhabdomys* is rather thick and dead black except on the under sides of the legs and throat, which are mottled with pinkish white.

Plentiful around Karibib and Windhuk."—G. C. S.

49. THALLOMYS DAMARENSIS de Wint.

Mus damarensis de Wint. Ann. Mag. N. H. (6) xix. p. 349, 1897.

♂. 466, 467, 511, 512, 516 (young). ♀. 468, 513, 514, 515 (young), 553, 554. Berseba. 3067'.

With the knowledge gained from the fine series of *Thallomys* which we owe to the Percy Sladen Trustees, we are now able to identify the immature and somewhat imperfect type of de Winton's *Mus damarensis* as a *Thallomys*, in which genus it is distinguishable by its completely white belly, little developed ocular markings, and light-coloured tail. The following are the measurements of an old male specimen:—

Head and body 134 mm.; tail 153; hind foot 27; ear 21.

Skull: greatest length 36·6 mm.; condylo-incisive length 34·5; zygomatic breadth 18; nasals 13·5; palatal foramina 8·2; bullæ 7·9; upper molar series 5·2.

"Apparently quite plentiful along the thin belts of trees that fringe the semi-dry bed of the Fish River, their large untidy nests were frequently observed among these trees from the train, where the line runs parallel to the river."—G. C. S.

50. Saccostomus anderssoni de Wint.

♂. 536, 561, 629, 643. ♀. 562, 585. Berseba. 3067'.
♂. 676. Gt. Brukaros Mt. 4000'.

Like Andersson's specimens, of which the exact locality is not recorded, the Berseba series is characterised by a drabby coloration quite different from that of the greyer *pagei*. The white ear-spot is reduced to a minimum, as it is in Kuruman *hildæ*, while in typical *pagei* from the Kalahari it is comparatively large and prominent.

51. Saccostomus pagei T. & H.

♂. 905, 1000. Karibib. 3842'.

"The cheek pouches of *Saccostomus* can be enormously distended, those of one specimen from Berseba contained 50 wild berries rather larger than pepper-corns and over 20 grains of wheat from the traps.

Apparently chiefly, if not entirely, nocturnal."—G. C. S.

52. Pedetes sp.

"The Spring-Haas is apparently rare in Berseba district, although said to be plentiful around Karibib. Great Namaqualand may be the dividing area between two species as is also possibly the case with *Suricata*. 'Goob' (Berseba Hottentots)."—G. C. S.

53. Petromys typicus tropicalis, subsp. n.

♂. 898, 900, 901, 904, 913, 916, 922, 951, 982, 996, 997. ♀. 899, 903, 909, 914, 915, 939, 944, 972, 995, 998, 999, 1013, 1015. Karibib. 3842'.
♂. 692, 751. ♀. 675. Great Brukaros Mt. 3500'–5000'.

While we did not think, when working out the Orange River collection last year, that there was sufficient evidence to show that the greater pallor of the rock-rats, as compared with those of Namaqualand, was independent of season, the present series, from still farther north, indicates that there is an undoubted difference between the northern and southern races of these interesting animals. We are still without specimens strictly comparable as to season, but the few specimens of both series which are in process of change show that in each race there is practically no essential difference in colour between the summer and winter pelages, when fresh. A direct comparison between the northern and southern series is therefore permissible.

By the help of Mr. Grant's specimens of 1903 we see that the typical Namaqualand animal is of a reddish-brown colour, the rump more strongly rufous than the fore-back, and that it has a prominently black tail.

In contrast with this the new form may be described as follows:—

General colour drabby grey, the head and fore-back clearer grey, the hinder back broadly washed with buffy or drab, very different from the deep rufous of the same parts in *typicus*. In rare cases even the buffy is absent, and the whole upper surface is grizzled grey. Hands and feet buffy. Tail, for about three-fourths its length, buffy, varying in intensity, and mixed to a certain extent with blackish, but never the deep black of *typicus*; the terminal fraction dark brown.

Skull apparently quite as in *typicus*.

Dimensions of the type:—

Head and body 175 mm.; tail 161; hind foot 32·5; ear 12·5.

Skull: greatest length 40; condylo-incisive length 36; upper molar series 9·5.

Hab. Damaraland and Great Namaqualand. Type from Karibib, just north of the tropic of Capricorn. 3842'.

Type. Young adult female, B.M. No. 25.1.2.225. Original number 944. Collected 3 November, 1923.

All the specimens of this northern race of *Petromys* are very uniform in colour, except that No. 904 is greyer and has more black on its tail than is usual. The series from the Orange River, obtained in 1922, is on the whole more similar to *tropicalis* than to *typicus*, though the specimens are mostly too much bleached for accurate comparison; those from the Brukaros Mountain tend to be a little intermediate, although also nearer *tropicalis* than *typicus*.

"Extremely plentiful among rocky hills around Karibib and said to be equally so at Windkuk. They probably occur throughout the hilly country of Damaraland, but whether still farther north remains to be seen. Farther south the eastern range of *Petromys* without doubt stops at the Great Brukaros and Karas Mountains, beyond which the flat sandy country of the Kalahari commences. Chiefly diurnal, although not exclusively so. Probably on account of its having no under-fur, the hair of this animal during life when standing out appears to be slightly spiny, and, as noticed under '*Gliriscus*,' its body, in addition to its head, is remarkably flattened, the ribs being short, and practically flat with the backbone. From specimens examined, the young are born singly or in pairs.

'Gama,' 'Harug Yeb.'

The illustration in Sclater's 'Mammals of South Africa' is quite unrecognizable."—G. C. S.

54. HYSTRIX AFRICÆ-AUSTRALIS Pet.

1067 (skull only). Damaraland.

"Probably to be found throughout S.W. Africa wherever there are rocky hills. 'Noab' (Berseba Hottentots)."—G. C. S.

55. Pronolagus crassicaudatus rupestris A. Sm.

♂. 741. ♀. 693, 716, 717. Great Brukaros Mts.
♀. 897. Karibib. 3842'.

"Fairly plentiful on the slopes of the Great Brukaros Mountain, although generally shy, making quickly for cover, and seldom wandering far from their hiding places among rocks and loose boulders; it is sometimes possible at dusk to walk almost over them. Even when crouching they seem invariably to keep their ears in an upright position.

Apparently plentiful among rocky hills around Karibib. Without doubt occurring throughout the hill country of Damaraland.

'Tsoarus' (Berseba Hottentots)."—G. C. S.

56. Lepus saxatilis, subsp.

♀. 532, 542, 570. Berseba. 3067'.

"Fairly plentiful in open plain country around Berseba. What appeared to be the same species was observed on several occasions near Karibib. The 'Kohlhaas' (*L. saxatilis*) is also said to occur.

'Karus' or 'Kaerab' (Berseba Hottentots)."—G. C. S.

57. Lepus saxatilis, subsp.

♂. 845. Rooibank. 240'.

"Occurring among scrub in the bed of the Karibib River. Not considered plentiful, although a fair number of tracks were seen."—G. C. S.

We are not in a position at the moment to deal satisfactorily with these hares, and think it, therefore, better to wait for the final collection from Mr. Shortridge next year before attempting to work them out.

58. Cephalophus (Sylvicapra) grimmi Linn.

948. Karibib.
1071 (skull only), 1072, 73, 74, 75 (horns only). Damaraland.

"This Duiker appears to be local in Great Namaqualand. In Berseba district the Hottentots say that it occurs in the thin belts of high scrub that occur at intervals along the banks of the Fish River.

Said to increase in numbers in the direction of the Kalahari, also apparently becoming widely spread in the thorn-veldt country of Damaraland.

'Doas' (Berseba Hottentots)."—G. C. S.

59. Oreotragus oreotragus Zimm.

724, 731, 732, 747. Great Brukaros.
953. Karibib.
1066 (skull only). Damaraland.
767 (horns only). Keetmanshoop.

"A dozen or so Klipspringers exist on the Great Brukaros.

On account of the comparatively few suitable localities in Namaqualand, away from the Orange River and Karas Ranges, their distribution must be patchy, and consist of isolated troops more or less out of touch with each other, but they become quite plentiful farther north among the hills of Damaraland, usually going about in parties of two or three. Although extremely active rock-jumpers, when once marked down the difficulties of approaching them are not to be compared with those of Asiatic mountain game.

'Khaisis' (Berseba Hottentots)."—G. C. S.

60. Madoqua damarensis Günth.

856, 1064 (horns only). Damaraland.

"The Damaraland Dik-dik evidently does not extend south of the mountainous parts of Damaraland. Known locally as the 'Bluebuck.'

Said to inhabit the scrub and strips of low thorn thickets in dry watercourses in the neighbourhood of hills rather than actually on hills. Possibly local and inconspicuous rather than actually scarce. Occurring at least as far north as Groetfontein in the northern terminus of the S. W. A. Railway. This Dik-dik is 'Royal Game' in South-West Africa."—G. C. S.

"A mountain buck of a larger size than a Klipspringer is said to occur in the Erengo Mountains, north of Karibib, which, from description, may possibly be the 'Vaal Rhebuck.'

The Vaal Rhebuck is recorded by Sclater from 'Great Namaqualand,' but I could get no local record of it."—G. C. S.

61. Raphiceros campestris Thunb.

575, 620, 626, 635. Berseba.
702, 709. Great Brukaros.
1065 (horns only). Damaraland.

"Apparently plentiful in flat country throughout Great Namaqualand, and probably also Damaraland, especially among the slightly denser vegetation that lines the beds and banks of dry rivers, even occasionally wandering down the bed of the Kuisib to within a few miles of Walvis Bay. One of the swiftest of the smaller buck, full-grown individuals being seldom run down by dogs. Leaving cover in the very early mornings and evenings; to a certain degree nocturnal. They feed very largely on the leaves of small trees and bushes. The immature specimens, together with the young springbuck, were caught by Kaffir dogs, which are responsible for the destruction of large numbers of half-grown game. These dogs are kept primarily for hunting game and nominally for keeping down jackals, which in reality are chiefly trapped. They are of the lurcher type and have little or no herding instincts or training. Certain of the tribes in S.W. Africa have got into the habit of living so largely on what

these dogs catch that, in their own interests, in order that they may not exterminate their own food supply, a timely effort is being made to put a check on unlimited numbers being kept.

'Aris' (Berseba Hottentots)."—G. C. S.

62. Redunca sp.

768 (horns only). Keetmanshoop.

"These horns, which were not recognized locally, were brought into Keetmanshoop by natives, together with those of several Klipspringers. They may have come from the Karas Ranges, or possibly from the hills along the Orange River."—G. C. S.

63. Strepsiceros strepsiceros Pall.

"Among other large game in Great Namaqualand and Damaraland, the Kudu appears to be the most generally distributed, being found in moderate numbers, usually in broken country and around the lower slopes of mountains wherever there is sufficient vegetation. They can conceal themselves in what, for their size, appears to be a remarkably small amount of cover.

'Chaib' (Berseba Hottentots)."—G. C. S.

"Gemsbuck occur in open country both in the Namib and Kalahari areas.

'Gaid' (Berseba Hottentots).

Cape Hartebeeste and Blue Hartebeeste become more numerous towards the eastern border, and to the north of Damaraland.

'Khamab' and 'Gaob' (Berseba Hottentots)."—G. C. S.

"Bush-pig and Wart Hog are both reported from Damaraland, and locally shot skulls of each were seen. Farther north the game list is supplemented by Waterbuck, Reedbuck, Kuku, Sassabey, Roan, Sable, Eland, Bushbuck, Buffalo, Giraffe, Hippo, Mountain and Burchell's Zebra, Black Rhino, Elephant, and, along the Okavango, possibly Sitatunga and Lechwe.

Two forms of Impala are spoken of, the northern, which is probably the Angolan species, and a southern, believed now to consist of a small isolated herd near Omaruru."—G. C. S.

64. Antidorcas euchore Zimm.

438, 451, 453, 455, 456. Berseba.

1081 & 1082 (horns only).

"Springbuck are still comparatively plentiful in the more sparsely inhabited open tracts of S.W. Africa, but they survive nowhere in their former numbers. The 'treks' of hundreds of thousands still remembered by older inhabitants have now dwindled to herds of from a dozen to a hundred at most, that during rare periods of migration may collect to a few thousand.

South-West Africa is now, without doubt, the chief stronghold for South African 'open country' big game, and under the present system of game protection in that country there is every reason to hope that it will remain so.

Many residents consider that the S.W. African Springbuck and Gemsbuck have each two distinguishable colour forms, one from the coastal Namib and the other from the Kalahari. These two deserts are sufficiently distinct to make a slight colour-variation possible.

'Sub' (Berseba Hottentots)."—G. C. S.

65. PROCAVIA sp.

473, 474, 529, 30, 31, 32, 33, 34, 577. Berseba.
902, 924. Karibib.

"Plentiful on hills and kopjes wherever there is a sufficient quantity of loose outcrop."—G. C. S.

66. MANIS TEMMINCKI Smuts.

763, 764. Keetmanshoop.
1079, 1080. Damaraland.

"Apparently comparatively plentiful in the direction of the Kalahari.

'Koom' (Berseba Hottentots)."—G. C. S.

67. ORYCTEROPUS sp.

"Aard Varks also appear to become more plentiful along the eastern border—said to be numerous in the neighbourhood of Gobabis.

A few burrows were observed near Karibib.

'Kubus' (Berseba Hottentots)."—G. C. S.

11. Contributions to our Knowledge of the Duration of Life in Vertebrate Animals.—I. Fishes. By Major S. S. Flower, O.B.E., F.L.S., F.Z.S.

[Received December 3, 1924: Read February 17, 1925.]

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1. Preface.

Buffon (1769, p. 457) mentioned two methods of obtaining information concerning the duration of life of fishes:—

1st, examination of the scales.
2nd, keeping fish in captivity.

Of the first, since Buffon's time, valuable papers have been published and work is being done not only on the external scales, but also on internal parts of fishes (*e. g.*, the otoliths).

Of the second, our knowledge is still very limited. Few records have been published, and mediæval stories, now impossible to verify, reappear in book after book.

The object of this paper is to collect records of the actual length of life in aquariums among fishes of various families—which, at any rate, must give some definite idea of their "potential longevity" (Mitchell, 1911, p. 427 *et seq.*).

2. Acknowledgments.

I wish to express my thanks to Mr. E. G. Boulenger, F.Z.S., Mr. J. R. Norman, F.Z.S., Mr. C. Tate Regan, F.R.S., F.Z.S., Lord Rothschild, F.R.S., F.Z.S., and to Capt. J. A. M. Vipan, for their kindness in answering questions and giving me advice on the subject of this paper. Above all, I have to acknowledge my deep obligation to Mr. G. A. Boulenger, F.R.S., F.Z.S., who from 1895 onward has always helped me in ichthyological matters, and especially in the identification of the Fishes of the Nile.

I am also indebted to Dr. P. Chalmers Mitchell, C.B.E., F.R.S., F.Z.S., for kind permission to examine records in the possession of this Society, and to Mr. E. Ockenden for assistance in looking up data of individual fish that I formerly knew when they were alive in the Society's collection.

3. Records of Longevity.

Dr. R. C. Osburn (1912) gave an interesting list of periods of life of fishes in the New York Aquarium. This list was

augmented and supplemented in a 'Complete List of Exhibits at the New York Aquarium,' by Miss Ida M. Mellen (1919). Out of about 360 species of fishes mentioned by Miss Mellen, 52, representing 26 families, are recorded as having lived for five or more years. Of these 52 species, 9, representing 6 families, lived for ten or more years.

Captain J. A. M. Vipan, F.Z.S., in his private aquarium at Stibbington Hall, Wansford, Northamptonshire, has made valuable records of the longevity of fresh-water fishes. Unfortunately, he has never published these, but from time to time he has very kindly allowed me to examine his collection and publish notes that he has given me.

Visits of mine to public aquariums at Alexandria, Amsterdam, Berlin, Blackpool, Brighton, Cologne, Frankfort-on-Main, Hamburg, Liverpool, London (Crystal Palace), Madras, Marseilles, Naples, Plymouth, and Trieste, though of great interest in other ways, have failed in finding any regular series of longevity records.

The Zoological Society of London, however, has useful records of the fishes that lived in its possession in the old "Fish House" and in tanks in the Reptile and Tortoise Houses, and now that the Aquarium is established, under the capable direction of Mr. E. G. Boulenger, we look forward to seeing far fuller and more comprehensive records in future years.

It is to be hoped that the publication of this paper may produce evidence, on the subject of the duration of life in fishes, from other sources than those that have been available to the author.

4. Gezira Aquarium.

Having kept various fishes in captivity whenever circumstances permitted, the decision of the Egyptian Government, in 1901, to start a public aquarium under my direction gave me the long-wished-for opportunity of trying on a large scale to see for how long fish might live.

The only information available before 1902 on the subject of Nile Fishes in captivity was that it was *not possible* to keep such forms as *Mormyrus* or *Tetrodon* alive in tanks for more than a few days. I had had previous experience of an Asiatic species of *Tetrodon* in captivity, but knew nothing of *Mormyrus*.

The system adopted was to obtain specimens of each species of fish it was intended to exhibit in the Aquarium and keep them in observation-tanks in the house I was living in in the Giza Zoological Gardens, and there experiment with different systems of water and various kinds of food till it was found what suited each species. This required much attention both by day and night. Mrs. Stanley Flower gave great assistance, and succeeded not only in keeping the fish alive but in making many individuals so tame that they would feed from her hand.

From 1903 to 1923 the general health of the fish at Gezira was good, but cold nights in winter sometimes proved disastrous. We had no means of heating the Aquarium.

The mortality among the fishes in the tanks at Gezira was

greatest at the same time of year as it was among the fishes living under natural conditions in the canals and ponds of Egypt—that is to say, in January, February, and the first part of March,—and appeared to be a result of low temperatures. If during cold weather the water in the tanks could have been kept a few degrees warmer, it is probable that, at any rate, most of the species of Egyptian fresh-water fishes would have attained to greater ages, as they probably do in large and deep bodies of water less affected by changes of the temperature of the air—as, for instance, in the Nile and in Lake Qarûn in the Fayûm.

The following table gives the numbers of species and individual fishes that were in my charge, and, where sufficient data were available, some average lengths of life of twenty selected individuals of different families.

These figures are compiled from my personal notes. Statements of longevity made by the native keepers employed in the Aquarium might show better results, but were too inaccurate to be worth recording.

Number of registered Specimens of Fishes that lived in the Gezira Aquarium during a Period of 22¼ *Years* (*January* 1902 *to March* 1924 *inclusive*).

	Number of Species.	Number of Individuals.			Average length of life of the twenty individuals that lived longest, with the number, out of these twenty, that left alive.			
		Died.	Left alive.	Total.	Years.	Months.	Days.	Alive.
CROSSOPTERYGII.								
Polypteridæ	1	1	—	1	—	—	—	—
TELEOSTEI.								
Mormyridæ	6	213	—	213	6	2	29	—
Characinidæ	7	160	6	166	5	3	0	6
Cyprinidæ	9	190	58	248	13	0	27	5
Siluridæ	9	309	71	380	12	5	10	—
Anguillidæ	1	22	—	22	—	—	—	—
Cyprinodontidæ..	1	98	14	112	—	—	—	—
Mugilidæ	1	14	—	14	—	—	—	—
Serranidæ	1	20	4	24	3	6	8	4
Osphromenidæ ...	1	4	—	4	—	—	—	—
Cichlidæ	4	25	125	150	3	10	21	17
Tetrodontidæ	1	41	2	43	2	3	4	2
Total	41	1096	280	1376	14	10	3	5
Total fishes.....	42	1097	280	1377	14	10	3	5

5. Notes by Families.

The species referred to in this paper will, for convenience, be mentioned in the following order:—

I. Class Pisces (*sens. lat.*).
1. Lepidosirenidæ.
2. Ceratodontidæ.
3. Polypteridæ.
4. Acipenseridæ.
5. Amiidæ.
6. Lepidosteidæ.
7. Mormyridæ.
8. Notopteridæ.
9. Clupeidæ.
10. Salmonidæ.
11. Characinidæ.
12. Gymnotidæ.
13. Cyprinidæ.
14. Siluridæ.
15. Loricariidæ.
16. Anguillidæ.
17. Esocidæ.
18. Cyprinodontidæ.
19. Syngnathidæ.
20. Anabantidæ.
21. Centrarchidæ.
22. Percidæ.
23. Serranidæ.
24. Lutianidæ.
25. Sciænidæ.
26. Sparidæ.
27. Labridæ.
28. Osphromenidæ.
29. Cichlidæ.
30. Scombridæ.
31. Gobiidæ.
32. Pleuronectidæ.
33. Tetrodontidæ.
34. Scyllidæ.
35. Raiidæ.
II. Class Marsipobranchii, or Cyclostomata.
36. Petromyzontidæ.
III. Class Cephalochordata, or Leptocardii.
37. Branchiostomatidæ.

1. Lepidosirenidæ.

1. Lepidosiren paradoxa. South American Lung-fish.

In London Z. G.:—

			Years	months	days.
Recd. 4.9.1908.	Died	16.1.1911.	2	4	12
Recd. 8.8.1916.	Alive	12.11.1924.	8	3	4 and still alive.

2. Protopterus annectens. African Lung-fish.

Capt. Vipan tells me that, as far as his experience goes, *Protopterus* usually lives, at most, ten to eleven years, but he had one individual for eighteen years*, and another that he received 29th May, 1912, is still alive 14th Nov., 1924 (*i. e.*, over 12 years 5 months), "but it is beginning to show signs of old age."

In the London Z. G. records seven individuals appear as having lived there for over five years:—

Received.	Died.	Years	months	days.
20.8.1889.	21. 9.1894.	5	1	1
,,	16.11.1894.	5	2	26
4. 6.1912.	22.12.1917.	5	6	18
27.6.1865.	17. 3.1871.	5	8	20
20.8.1889.	10.11.1896.	7	2	20
30.9.1887.	25. 2.1896.	8	5	22
20.8.1889.	29. 6.1899.	9	10	9

* Recd. 19 May, 1885. Died 13 May, 1903. 17 years 11 months 23 days.

2. Ceratodontidæ.

1. Ceratodus forsteri. Australian Lung-fish.

Two individuals, shipped in Australia 15th April, 1898, arrived in the London Z. G. 13th June, 1898. One died 2nd Sept., 1915, the other 30th Dec., 1917. So their life in captivity since leaving Australia was, respectively,

17 years 4 months 17 days
and 19 „ 8 „ 15 „

3. Polypteridæ.

1. Polypterus senegalus. Senegal Polypterus.

On 2nd June, 1912, I obtained a specimen in Khartoum which arrived in the Giza Z.G. 22nd July, 1912, and lived there in a small table-tank in the "Tropical House" till it died 24th Feb., 1918. Length of life in captivity, 5 years 8 months 22 days.

The two longest records in the London Z. G. appear to be:—

25 Nov., 1902—4 Jan., 1908, 5 years 1 month 9 days.
22 Nov., 1899—7 May, 1905, 5 years 5 months 15 days.

On 18th August, 1921, Capt. Vipan showed me an individual in his aquarium that he had had alive since 17th Jan., 1901, *i. e.*, 20 years 7 months 1 day, and still alive.

2. Polypterus lapradii. Gambian Polypterus.

Capt. Vipan has had six individuals alive for over 20 years, including one for 24 years, and still alive (14th Nov., 1924).

4. Acipenseridæ.

1. Acipenser sturio. The Sturgeon.

New York Aquarium (Mellen, 1919, p. 27), 6 years.

London Z. G., 26 July, 1863–21 June, 1870, 6 years 10 months 25 days.

2. Acipenser brevirostrum. Short-nosed Sturgeon.

New York Aquarium (Mellen, 1919, p. 27), 7 years.

3. Acipenser ruthenus. The Sterlet.

In July 1907, in the Aquarium of the Amsterdam Z. G., I saw four Sterlets that were said to have been there for 20 years.

The Brighton Aquarium had two Sterlets alive for about 35 years, and another, Mr. F. E. Brown told me in 1912, lived there for about 38 years (1873–1911). These three were the survivors of nine imported from Russia in 1873.

Sterlets presented to Capt. Vipan by the Czar of Russia, 8th Oct., 1888, are still alive after 36 years in England. One of these, presented to the Society by Capt. Vipan, is in our Aquarium

5. Amiidæ.

1. Amia calva. The American Mudfish, or Bowfin.

London Z. G., 15 Nov., 1901–4 July, 1916, 14 years 7 months 19 days.

New York Aquarium (Mellen, 1921, p. 73), 20 years.

6. Lepidosteidæ.

1. Lepidosteus osseus. Long-nosed Gar-Pike.

New York Aquarium (Townsend, 1920, p. 118), 20 years.

One of these American fish lived for many years in the old Berlin Aquarium, where I noted it in 1905 and 1907. When that institution was closed, this fish is said to have been sent to Frankfort-on-Main; it was pointed out to me there in October 1913—it was then called *Lepidosteus tristœchus*.

2. Lepidosteus platystomus. Short-nosed Gar-Pike.

New York Aquarium (Mellen, 1919, p. 22), 20 years, and still alive.

7. Mormyridæ.

Attempts to keep these very curious fish alive in captivity were, I had been told, entirely without success. With the able assistance of my wife, I managed to get several species to live and feed in small table-tanks in the Director's House at Giza. With the experience thus gained we were afterwards able to keep these fish on exhibition in the large wall-tanks of the Gezira Aquarium.

The maximum ascertained length of life of some individuals was:—

	Years	months	days.	
1. Hyperopisus bebe.	10	1	8	
2. Gnathonemus cyprinoides.	7	1	9	
3. Mormyrus kannume.	6	4	18	Seven individuals lived at least as long as this.
4. „ caschive.				

5. Marcusenius isidori. 5 years 2 months 6 days.

Capt. Vipan wrote to me from Stibbington Hall, 1st April, 1909, that the *Marcusenius* he received, from us, 11th Dec., 1902, was still alive, but "begins to show signs of age"; so this individual was living after being in Capt. Vipan's Aquarium for 6 years 3 months 21 days.

8. Notopteridæ.

1. Xenomystus nigri.

Capt. Vipan received specimens of this Tropical African fish 13th June, 1913; eight years later I had the pleasure of seeing

two of them in his aquarium, the longer lower fin appeared to be in constant motion, in waves in two directions at once. Capt. Vipan's maximum record for this species up to 14th Nov., 1924, is 11 years 5 months 1 day, and still alive.

9. Clupeidæ.

1. Clupea harengus. The Herring.

In October 1909, in Tank No. 32 of the Brighton Aquarium, I saw a shoal of Herrings. Mr. F. B. Brown told me that Herrings will live three to four years in captivity there.

10. Salmonidæ.

The important fishes of this family are known to be normally short-lived animals. Mr. C. Tate Regan (1917, p. 13) writes:—"It seems that Salmon seldom live longer than ten years." Mr. J. A. Milne (1913, pp. 591, 593, 595, and 607) gives interesting notes on species occurring on the Pacific coast of North America based on the examination of their scales. Dr. R. C. Osburn (1912, p. 126) gives actual records of several species of Salmonidæ that have lived in the New York Aquarium.

It appears to be a fact in certain groups of fishes that want of opportunities to breed may, under certain circumstances, prolong the life of individuals to ages far in excess of the normal longevity of the species. Thus various old stories of single Trout having been kept in wells in England and Scotland for 28, 31, or even 53 years may, or may not, be true, but cannot now be proved.

1. Coregonus clupeiformis. Whitefish.

Miss Ida M. Mellen kindly sent me a note in 1922 that this species had lived for nine years in the New York Aquarium.

The following records from the London Z. G. are of special interest, showing how well, under the circumstances, some of the Salmonidæ did in the old "Fish House."

2. Salmo salar. The Salmon.

	Years	months	days.
5 April, 1906–21 Jan., 1909.	2	9	16
24 Feb., 1906–21 July, 1909.	3	4	27

3. Salmo fario. Brown Trout.

17 Aug., 1910– 8 June, 1915.	4	9	21
31 Oct., 1907–30 Aug., 1914.	6	10	0

4. Salmo lacustris. Lake-Trout.

1863–11 May, 1870. At least	6	4	11
5 May, 1870– 5 Sept., 1880.	10	4	1

5. Salmo irideus. Rainbow Trout.

1 Nov., 1909–22 Oct., 1913.	3	11	22

6. Thymallus vulgaris. The Grayling.

5 Nov., 1906–17 Sept., 1909.	2	10	12

11. Characinidæ.

1. Three individuals of the genus *Alestes* (*A. dentex* or *A. baremose*) lived over eight years in the Gezira Aquarium, the maximum being 8 years 4 months 17 days.

2. Hydrocyon forskalii. Nile Tiger-Fish.

Locally known as "Kelb el Bahr." A series of these in the Gezira Aquarium (21 individuals), from 1902 to 1923, proved that this species grows rapidly. The maximum length of life was 7 years 11 months 17 days; this individual, placed in the aquarium when it was about the size of a minnow, became a big fish long before he died. Another individual, in just under five years, grew to a total length over all of 536 millimetres (21 inches).

3. Hydrocyon brevis.

Only a single specimen of this rare species was exhibited at Gezira; caught when quite small, it grew to a total length over all of 381 millimetres (15 inches) in 4 years 2 months 25 days.

4. Distichodus niloticus. The Nile "Lafash."

Of 15 individuals received, only two survived over 14 months in the Gezira Aquarium; but of these two, one lived 7 years 4 months 12 days and the other 7 years 6 months 9 days.

12. Gymnotidæ.

1. Gymnotus electricus. Electric Eel.

The following records of four individuals in the London Z. G. are valuable:—

Received.	Died.	Years	months	days.
9.10.1900.	15. 4.1908.	7	6	6
22.11.1897.	9.12.1907.	10	0	17
22. 7.1884.	13. 2.1896.	11	6	21
22. 7.1884.	2. 3.1897.	12	7	10

These last two were kept in the old "Insect House" near the North Gate and lived very well in spite of being very frequently caught and handled to give "shocks" to visitors.

13. Cyprinidæ.

1. Cyprinus carpio. The Carp.

"The Carp is popularly considered to rival the Pike in longevity, and has been said to attain an age of 150 years; but

it must be confessed that this and similar statements rest on very unreliable evidence, although there is reason for supposing that Carp live to a good old age" (Regan, 1911, p. 174).

"In a state of freedom," according to Heckel and Kner, "the Carp only attains the age of about 12 or 15 years" (Smitt, 1895, p. 730).

The Carp at Pontchartrain (Buffon, 1769, p. 457) had the opportunity of growing to a great age; but in the cases of supposed very old fishes in the 19th century at Versailles, Fontainebleu, Chantilly, etc., "Blanchard disposes of these fables by observing that in 1789, 1830, and 1848 the fish ponds fell under the control of the sovereign people, who loved the Carp too well to permit great size or age to be an obstacle to its ministering to their pleasure" (Seeley, 1886, p. 98).

In the New York Aquarium Carp have been six years and still living (Mellen, 1919, p. 23).

2. CYPRINUS CARPIO var. "Prussian Carp."

London Z. G.:—

6 Dec., 1904–24 May, 1911, 6 years 5 months 18 days.

3. CYPRINUS CARPIO var. (*Cyprinus rexcyprinorum*). "Mirror-Carp."

Twenty-four years and still alive in the aquarium of Capt. Vipan (Flower, 1907, p. 45).

4. CYPRINUS CARASSIUS AURATUS. The Goldfish.

Capt. Vipan told me (18 August, 1921) that from his experience the ordinary life of a Goldfish is six to seven years. This statement is confirmed by other observers, and, as would be expected, under favourable circumstances some individuals will live a few years longer.

Miss Ida M. Mellen (1921, pp. 59–61) writes:—

"Goldfishes begin to breed when in their second year, and continue six or seven years, being at their best from three to five years old." The maximum length of life of a Goldfish in the New York Aquarium is ten years (Mellen, 1919, p. 23).

In the London Z. G. a Goldfish lived from 26 Oct., 1910–18 March, 1919—8 years 4 months 22 days.

The maximum periods that I have personally noted for individual Goldfishes in the Gezira Aquarium are:—

Years	months	days.
5	4	5
5	7	20
5	11	0
6	0	24
7	3	23

but these specimens had lived for a time (not noted) in the Giza Z. G. before being transferred to Gezira.

Mr. E. R. May, of the Egyptian State Railways, kept Goldfishes for many years at Zagazig in Lower Egypt. In answer to my enquiries, he was so kind as to write to me (12 Jan., 1922):—"I have at present 21 Goldfish, all about ten to twelve years old, in a masonry enclosure, they vary from six to eight inches long, but are dying, one by one, I think owing to age."

The only statement that I know of in variance to the above is that the Rev. Gregory C. Bateman (1890, p. 112) records that Mr. T. H. Jones, of Woolwich, placed a Silverfish in an aquarium on 20 May, 1853, and that it lived there until 11 April, 1883, a period of 29 years 10 months and 21 days.

5. Leuciscus orfus. Golden Orfe.

Twelve individuals are recorded as having been in the London Z. G., 14 Dec., 1905–23 March, 1920—14 years 3 months 9 days,—when they were sent away alive.

Capt. Vipan's record for a Golden Orfe is from 9 June, 1883–29 March, 1913—29 years 9 months 20 days.

6. Leuciscus leuciscus. The Dace.

About eight years in captivity (Bateman, 1890, p. 124).

7. Scardinius erythrophthalmus. The Rudd.

In London Z. G.:—

19 Nov., 1913–7 Feb., 1921, 7 years 2 months 18 days.

In New York Aquarium, 10 years and still alive (Mellen, 1919, p. 23).

8. Phoxynus phoxynus. The Minnow.

Thirteen years in captivity (Bateman, 1890, p. 126).

9. Abramis chrysoleucas. "Common Roach, or Golden Shiner."

Seven years and still living, New York Aquarium (Mellen, 1919, p. 23).

10. Abramis chrysoleucas roseus. "Pearl Roach."

Ten years and still living, New York Aquarium (Osburn, 1912, p. 126).

11. Misgurnus fossilis. European Thunder-fish.

A specimen received by Capt. Vipan, 9 October, 1885, was still alive in June 1907, after 21 years and 8 months in his aquarium.

12. Misgurnus anguillicaudatus. Eel-tailed Loach.

Three individuals from China lived in the London Z. G.:—

28 Sept., 1908–17 Dec., 1918, 10 years 2 months 19 days.

13. Barbus bynni. Nile Barbel.

This species lives well in the Gezira Aquarium. Twenty individuals averaged 13 years 0 months 27 days: out of these twenty, five were still alive when I left Egypt, four had been at least 16 years 3 months 4 days in captivity, and one 16 years and one day.

The rate of growth in this species is remarkable for its irregularity. Mr. M. J. Nicoll, in 1919, 1920, and 1921, kindly helped me in measuring and weighing many specimens.

Individuals living together in the same tank, after twelve years, varied in weight from ·25 to 1·5 kilos (·55 to 3·3 lbs.).

A Nile Barbel in the next tank in fourteen years grew from the size of a minnow to a total length over all of 590 millimetres (23½ inches) and a weight of 2·5 kilos (5·5 lbs.).

In an out-of-doors pond in the Giza Z. G. a fish attained a total length over all of 670 millimetres (26⅜ inches) and a weight of 4·5 kilos (9·92 lbs.).

On 12 Sept., 1903, the small artificial lake in the Esbekia Garden, Cairo, being drained, I found a "Bynni" that measured in total length over all 660 millimetres (26 inches) and weighed 5·6 kilos. (12·35 lbs.). As this lake was periodically run dry, it is probable that this big fish was not more than ten years old. Whenever a pond or canal is drained in Egypt the local natives thoroughly examine the mud that is left, even to the extent of dragging wire-netting through it, to ascertain that no fishes that can possibly be edible are left in it.

14. Siluridæ.

Although several groups of Family importance are indicated, the "Catfishes" may for convenience be still "lumped" as one family—the Siluridæ.

1. Silurus glanis. European Sheatfish.

H.G. The Duke of Bedford told me (3 Dec., 1924) that two individuals of this species now alive at Woburn have been there for fifty years. They have not bred at Woburn, and the presence of the big fish is established by periodically letting the water down in the ponds *.

Lord Rothschild tells me that Sheatfish have lived for at least seventeen years in the Tring Reservoirs: one that he had turned out in 1907 was killed by an Otter in 1924.

* These two are the survivors of three that were turned out in 1874 by the Duke's uncle, Lord Odo Russell, G.C.B. The third Sheatfish died on land when it was apparently trying to pass from one piece of water to another.

In 1875, or 1876, through Mr. Frank Buckland, Lord Odo Russell, G.C.B., presented to the Museum of the Royal College of Surgeons in London particularly large specimens of two species of fish, both from Berlin, a Sheatfish (*Silurus glanis*) 5 feet 6 inches (1·67 metres) in length and 53 lbs. (24 kilos.) in weight, and a Carp (*Cyprinus carpio*) 27 lbs. (12·25 kilos.) in weight.—W. H. Flower, Annual Report, Museum, Royal College of Surgeons of England, July 3, 1876, pp. 2 & 9.

2. Hexanematichthys felis. North American Sea-Catfish.

New York Aquarium, seven years and still living (Mellen, 1919, p. 27).

3. Callichthys punctatus. South American Catfish.

One lived in the Jardin des Plantes, Paris, from 7 April, 1910–3 March, 1919—8 years 10 months 26 days (Pellegrin, 1920, p. 457).

4. Pimelodus sp. An American Catfish.

One individual I saw in the Reptile House, Jardin des Plantes, Paris, in July 1921, had been there, Dr. J. Pellegrin told me, since before July 1914, so over seven years and still alive.

5. Amiurus catus. North American Catfish.

The following records are from the London Z. G.:—

	Years	months	days.
24 July, 1914– 9 Dec., 1920,	6	4	15
? April, 1877–27 Sept., 1884,	7	5	?
10 May, 1911–16 June, 1919,	8	1	6

6. Saccobranchus fossilis. Asiatic Catfish.

Two individuals I saw in the Reptile House, Jardin des Plantes, Paris, in July 1921, had been there, Dr. J. Pellegrin told me, since July 1914, so over seven years and still alive.

The London Z. G. can show interesting records for this species:—

	Years	months	days.	
12 June, 1901–12 Oct., 1908,	7	4	0	
3 Nov., 1908–17 Nov., 1920,	12	0	14	
3 Nov., 1908–12 Nov., 1924 (alive),	16	0	9	and still alive.
2 May, 1903–23 Nov., 1920,	17	6	21	

Capt. Vipan received a specimen from Siam, 8 October, 1899, which I saw in June 1907, so about 7 years 8 months, and still alive in his aquarium.

7. African Catfishes.

The Nile species have done well in the Aquarium at Gezira. The fact that the 20 individuals that lived longest there all died during the period under review might indicate that their potential longevity is not as great as in some other Families of Fishes, but I consider the deaths due to low temperatures in the tanks, and not results of old age.

Several species, as is well known, are very tenacious of life under adverse conditions, and, compared to the Mormyridæ and Characinidæ, the Catfishes are easily cared for in captivity.

The maximum ascertained length of life at Gezira for individuals of various species is:—

	Years	months	days.	
Chrysichthys auratus	5	10	19	possibly over 17 years.
Malopterurus electricus.....	7	0	13	
" "	7	1	13	
Synodontis schall	9	0	0	
Schilbe mystus	9	8	26	
Clarias lazera	15	5	26	
" "	15	7	25	
" "	15	11	8	
" "	16	1	27	
" "	16	2	5	
Bagrus bayad	13	2	0	
" "	17	0	12	

A *Synodontis schall* received by Capt. Vipan, from us, 11 Dec., 1902, is now in his aquarium, 12 Nov., 1924, *i. e.*, 21 years 11 months 1 day, and still alive.

15. Loricariidæ.

1. Loricaria parva.

A specimen from Paraguay received by Capt. Vipan, 19 May, 1909, was still alive 14 Nov., 1924, actually 15 years 5 months 25 days.

2. Plecostomus commersonii.

One from Brazil received by Capt. Vipan 8 Oct., 1899, lived at least 7 years and 8 months in his aquarium.

16. Anguillidæ.

1. Anguilla vulgaris. The Eel.

The "specific longevity" of the Eel from when it arrives from the sea to when it finally returns to the sea may be put at five to nine years (Regan, 1911, pp. 162, 163, 164).

The "potential longevity" is unknown, but probably exceeds fifty years (Boulenger, 1904, p. 602; Flower, 1921, p. 2).

An Egyptian-caught Eel, estimated to be about 635 millimetres (25 inches) in length in 1910, died in 1916, when it had lived for over 13 years 11 months in the Gezira Aquarium.

2. Anguilla chrisypa. North American Eel.

Six years in the New York Aquarium (Mellen, 1919, p. 23).

3. Conger vulgaris (*Leptocephalus conger*). Conger-Eel.

One year in the New York Aquarium (Mellen, 1919, p. 27). Nearly six years in the Brighton Aquarium (Bullen, 1913, p. 635).

In May 1907, in the Blackpool Aquarium in a tank measuring about 28 feet long by 14 feet wide, I saw more than 27 Conger-Eels, each, apparently, from five to six feet long, fat and healthy. Mr. James Walmsley, the Superintendent, told me that the Congers were about nine years old, and that some that he had had alive in this tank weighed 112 lbs.

17. Esocidæ.

1. Esox lucius. The Pike.

"Nothing definite can be said as to the age to which a Pike may live, although it is probable that fish of 60 or 70 lbs. weight are at least as many years old. But, although Pike are reputed to live to a very great age, there are not, as far as I am aware, any satisfactory proofs that they actually do so" (Regan, 1911, p. 150).

Old stories of old Pike are found in many books (*cf.* Hamilton, 1843, p. 92; Buckland, 1873, pp. 90–93; Seeley, 1886, p. 363).

A Pike has lived for ten years in captivity in the London Z. G., and another for 14 years in a well in Derbyshire (Bateman, 1890, pp. 153, 154).

The longest record for a Pike, since 1870, that I can find in the London Z. G. is that of one presented by Mr. F. Roberts, 29 April, 1881, that lived till 11 March, 1888—6 years 10 months 12 days.

2. Esox masquinongy. Muskallunge Pike.

Ten years in New York Aquarium (Mellen, 1919, p. 24).

18. Cyprinodontidæ.

Owing to the rapidity with which some of these little fish breed in captivity, it is difficult to keep track of individuals. A specimen of *Haplochilus schoelleri* has lived, for certain, in my charge in Egypt for 1 year 5 months 20 days, another for 1 year 10 months 2 days, and others for longer periods, possibly up to 4 years 8 months 7 days.

19. Syngnathidæ.

1. Hippocampus antiquorum. Short-nosed Sea-Horse.

The average life of the ten individuals that survived longest in the London Z. G., 1883–1886, was nine months.

The maximum for an individual in London since 1870 is 1 year 3 months 28 days (28 April, 1885–26 Aug., 1886).

2. Hippocampus ramulosus. Branched Sea-Horse.

This species in the London Z. G. has not done nearly as well as *H. antiquorum*. The longest records for it are:—

5 May, 1884–12 Oct., 1884—5 months 7 days.
11 March, 1873– 5 Oct., 1873—6 „ 24 „

3. Hippocampus hudsonius. Hudson Sea-Horse.

Has lived two and a half years in the New York Aquarium (Mellen, 1919, p. 28), and over 4 years 7 months, January 1916–September 1920, in the Venice Aquarium, California (Townsend, 1920, p. 118).

20. Anabantidæ.

1. Anabas scandens. Climbing Perch.

In London Z. G., 7 Feb., 1911–26 Nov., 1918—7 years 9 months 19 days.

In New York Aquarium 8 years and still alive (Mellen, 1919, p. 26).

2. Anabas kingsleyeæ. Miss Kingsley's Climbing Perch.

Capt. Vipan received specimens from the Gambia 28th Sept., 1900, which bred in his aquarium; individuals lived at least 8 years and 8 months.

21. Centrarchidæ.

1. Eupomotis pallidus. North American Sun-fish.

Over eight years and still alive in Capt. Vipan's Aquarium.

2. Pomoxys sparoides. North American Calico-Bass.

Seven years in New York Aquarium (Mellen, 1919, p. 24).

Over seven and a half years and still alive in Capt. Vipan's Aquarium.

3. Apomotis cyanellus. North American Green Sun-fish.

Over seven and a half years and still alive in Capt. Vipan's Aquarium.

4. Micropterus dolomieu. Small-mouthed Black Bass.

5. Micropterus salmoides. Large-mouthed Black Bass.

Both 11 years and still alive in New York Aquarium (Mellen, 1919, p. 24).

6. Ambloplites rupestris. North American Rock-Bass.

Seven years and still living, New York Aquarium (Mellen, 1919, p. 24).

22. Percidæ.

1. Perca fluviatilis. The Perch.

London Z. G., 13 Sept., 1876–26 May, 1882, 5 years 8 months 13 days.

Perch probably live much longer than this. I include this note to help to call attention to how few detailed records appear to exist for even the commonest of English fresh-water fishes.

2. Perca flavescens. North American Yellow Perch.

Eight years and still living, New York Aquarium (Mellen, 1919, p. 24).

3. Percina aspro. North American Black-sided Darter.

Over seven-and-a-half years and still alive in Capt. Vipan's Aquarium.

4. Lucioperca saudra. Pike-Perch.

London Z. G., 1 Sept., 1909–14 Aug., 1916, 6 years 11 months 13 days.

23. Serranidæ.

"Striped Bass or Rock-fish," *Roccus lineatus*, have lived for 19 years in the New York Aquarium (Mellen, 1919, p. 29): these were supposed to be three years old when received, so attained to an age of 21 years (Townsend, 1911, p. 101; Osburn, 1912, p. 130).

Miss Mellen (1919, pp. 21 and 32) records eight other species of this Family as having lived from five to seven years in the New York Aquarium.

Mr. James Hornell (1922, p. 628), in an account of the Madras Aquarium, writes:—"Sea-Perches of the genus *Serranus*. Three of these have lived in the aquarium between 10 and 11 years, having been brought in quite small, soon after the building was opened. Their growth has been considerable and now they must weigh from 20 to 25 lbs. each."

The Great Nile Perch, *Lates niloticus*, has proved to be a rather difficult species to keep alive in captivity: the maximum lengths of life for individuals at Gezira being

7 years 4 months 14 days
and 7 „ 11 „ 29 „

These were both hatched in 1903, and when they died in 1911 measured, in total length, 508 and 450 millimetres (20 and 17¾ inches), and weighed 2·0 and 1·4 kilos (4·4 and 3 lbs.) respectively. This does not show that *Lates niloticus* is a slow-growing fish, but that the conditions in the Aquarium were unsuitable—probably the tanks are not large enough, as in the out-of-door ponds in the Giza Z. G. individuals found dead have weighed up to 16·5 and 21·5 kilos (36·3 and 47·5 lbs.), both probably well under 10 years old, and on 12th Sept., 1903, the small artificial lake in the Esbekia Garden, Cairo, yielded a *Lates* 1219 millimetres (48 inches) in total length and 25 kilos (55 lbs.) in weight, presumably not more than 10 years old.

In the Nile and Fayûm lake this species of Perch attains much greater dimensions. Mr. G. Paget has told me of one weighing 67 kilos (147·7 lbs.) from the Fayûm, and Mr. A. L. Butler of one from the White Nile of 111 kilos (245 lbs.).

24. Lutianidæ.

*1. Neomænis griseus. Grey Snapper.
Seven years in New York Aquarium (Mellen, 1919, p. 32).

2. Neomænis synagris. Spot or Lane Snapper.
Seven years in New York Aquarium (Mellen, 1919, p. 33).

25. Sciænidæ.

1. Pogonias chromis. Sea-drum.
Six and a half years in New York Aquarium (Mellen, 1919, p. 29).

2. Sclænops ocellatus. Channel Bass or Red Drum.
Seven years in New York Aquarium (Mellen, 1919, p. 29).

26. Sparidæ.

1. Cantharus vulgaris. Sea-Bream.
Said to have lived five years in the Naples Aquarium ('Guide pour l'Aquarium,' Naples, 1908, p. 101).

2. Archosargus probatocephalus. "Sheepshead."
Six years in New York Aquarium (Mellen, 1919, p. 33).

27. Labridæ.

1. Tautoga onitis. Tautog, or Blackfish.
Eight years in New York Aquarium (Mellen, 1919, p. 29).

28. Osphromenidæ.

1. Macropodus opercularis. Paradise Fish.
Some authorities consider that this genus should be included in the family Anabantidæ.
Has lived eight years in captivity (Mellen, 1921 (2), p. 91).

29. Cichlidæ.

In July 1921, Dr. J. Pellegrin showed me, in Paris, four individual American Cichlidæ that had been living for over seven years in the Jardin des Plantes: these were two specimens of *Acara tetramerus* and one each of *Cichlasoma nigrofasciatum* and *Geophagus brasiliensis*.

The Egyptian species of *Tilapia*, known locally as "Bolti," thrive and breed freely in captivity; in the table given above (p. 249) the average length of life of twenty individuals is given as only 3 years 10 months 21 days—this arises from the difficulty in the past of knowing individual specimens apart from each other

(and even the three species *T. zillii*, *T. nilotica*, and *T. galilæa* at times). The fact that seventeen out of the twenty selected individuals were still alive proves that the average given must be far short of the normal duration of life of these fishes.

30. Scombridæ.

1. Scomber vernalis. The Mackerel.

In October 1909, there were Mackerel on exhibition in Tank No. 37 of the Brighton Aquarium. Mr. F. B. Brown told me that Mackerel had lived in captivity from 3 to 4 years there.

31. Gobiidæ.

1. Latrunculus pellucidus. Transparent Goby.

This very small Goby is said to live for one year only, and be the first known instance of an "annual vertebrate" (Günther, 1880, p. 486).

2. Gobius minutus. One-spotted Goby.

"Maturity in this species is reached at the end of one year. Few individuals survive a second winter. This conclusion corroborates a previous statement on the subject by Holt and Byrne, Irish Fisheries Report, 1901, part ii. p. 53" (Shann, 1910. Confirmed in a letter to me of 9 Nov., 1924).

3. Periophthalmus koelreuteri. Mangrove Goby.

Individuals have lived in the London Z. G. for the following periods:—

	Years	months	days.
26 August, 1898–14 Nov., 1899	1	2	18
" 14 April, 1900	1	7	18
12 June, 1900– 8 Jan., 1902	1	6	26

4. Eleotris maculata.

5. Eleotris gyrinus.

Individuals of both species, from Cuba, were received by Capt. Vipan, 7 Nov., 1901. Both were still alive in June 1907, *i. e.*, 5 years 7 months later.

32. Pleuronectidæ.

1. Pleuronectes platessa. The Plaice.

	Years	months	days.
One received in the London Z. G., 13 Aug., 1870, is recorded to have died 30 July, 1873	2	11	17

Of four species of this family exhibited in the New York Aquarium, three lived for six months only, and one, the "Winter Flounder" *Pseudopleuronectes americanus*, for one year (Mellen, 1919, p. 31).

33. Tetrodontidæ.

1. Tetrodon fahaka.

The Nile Globe-Fish, when caught quite small, thrives and rapidly increases in size in captivity, but is not easy to keep alive for more than a few years. At Gezira one individual lived 6 years all but three days, and another 5 years 5 months 25 days.

34. Scyllidæ.

Dogfishes appear not to thrive in aquariums for more than about a couple of years at most, but Mr. Edward Boulenger tells me that some sent from Plymouth to the Aquarium in the Amsterdam Z. G. lived there for a much longer period.

35. Raiidæ.

Neither Rays, Skates, nor their allies appear to often exceed an Aquarium life of over two years; however, Lord Rothschild told me (10 Nov., 1924) that the Thorn-backed Ray, *Raia clavata*, did well in the Blackpool Aquarium, and, when he was there in 1915, some were pointed out to him by the official in charge as having been over twenty years in captivity.

36. Petromyzontidæ.

1. Petromyzon marinus. Sea-Lamprey.

In July 1907 in the Amsterdam Aquarium I saw a large specimen, a very remarkable exhibit; I was told it had been living there for two months, but was not expected to survive much longer.

In the New York Aquarium this species has lived for nine months (Mellen, 1919, p. 26).

2. Lampetra fluviatilis. River-Lamprey, or Lampern.

"Formerly the Thames alone supplied from one million to twelve hundred thousand Lamperns annually. They are very tenacious of life, and the Dutch fishermen managed to keep them alive for many weeks" (Yarrell, 1836, p. 455).

These Lamperns were used as bait. "The system of conveying them was in boats fitted with wells" (Buckland, 1873, p. 258).

From the above statement it would appear that these animals might easily be kept in captivity, but the longest record in the London Z. G. is from 11 Nov., 1882–29 April, 1883, a period of 5 months 18 days.

Capt. Vipan writes to me (1 Dec., 1924), "Lampreys never lived long with me, not much over a year."

3. "Petromyzon branchialis. Fringe-lipped Lampern." London Z. G., 12 Feb., 1881–11 April, 1881, 2 months.

4. Lampetra wilderi. North American Brook-Lamprey. New York Aquarium, 6 months (Mellen, 1919, p. 22).

37. Branchiostomatidæ.

1. Branchiostoma lanceolatum. The Lancelet, or Amphioxus. Of several individuals from Naples received in the London Z. G., 14 November, 1874:—

		Months	days.
One died	3 Jan., 1875, having lived in London	1	20
„ „	15 Jan., 1875, „ „	2	1
„ „	25 June, 1875, „ „	7	13

6. Conclusions.

Certain small fishes of the Family Gobiidæ appear to have a normal life of under two years. We have no definite evidence of other fishes not being able to live for at least five years. Both sea and fresh-water fishes of various families live to 10 years or more. Under favourable circumstances some fresh-water fishes may live for half a century.

List of Species of Fishes known, from Data given above, to reach at least the following Ages in Years:—

	Years.	
1.	50.	*Silurus glanis*, and still alive. European Sheatfish.
2.	33.	*Acipenser ruthenus*. European Sterlet.
3.	30.	*Leuciscus orfus*. European Golden Orfe.
4.	24.	*Polypterus lapradii*. Gambian Polypterus.
5.	„	*Cyprinus rex-cyprinorum*, alive. European Mirror-Carp.
6.	22.	*Synodontis schall*, alive. Nile Schall Catfish.
7.	„	*Misgurnus fossilis*, alive. European Thunder-fish.
8.	21.	*Rocus lineatus*. N. American Sea-Rockfish.
9.	20.	*Ceratodus forsteri*. Australian Lung-fish.
10.	„	*Polypterus senegalus*, alive. Senegal Polypterus.
11.	„	*Amia calva*. N. American Bowfin.
12.	„	*Lepidosteus osseus*. N. American Gar-Pike.
13.	„	„ *platystomus*, alive. N. American Gar-Pike.
14.	18.	*Protopterus annectens*. African Lung-fish.
15.	17.	*Bagrus bayad*. Nile Bayad Catfish.
16.	„	*Saccobranchus fossilis*. Asiatic Catfish.
17.	16.	*Barbus bynni*, alive. Nile Barbel.
18.	„	*Clarias lazera*. Nile Qarmût Catfish.
19.	15.	*Loricaria parva*, alive. S. American Catfish.
20.	14.	*Anguilla vulgaris*. European Eel.
21.	13.	*Gymnotus electricus*. S. American Electric Eel.
22.	11.	*Xenomystus nigri*. African Wavy-finned Fish.
23.	„	*Micropterus dolomieu*, alive. N. American Black Bass.
24.	„	„ *salmoides*, alive. „ „
25.	10.	*Hyperopysus bebe*. Nile Mormyrid Fish.
26.	„	*Cyprinus carassius auratus*. The Goldfish.
27.	„	*Scardinius erythrophthalmus*, alive. European Rudd.
28.	„	*Misgurnus anguillicaudatus*. Chinese Eel-tailed Loach.
29.	„	*Schilbe mystus*. Nile Schilbe Catfish.

	Years.	
30.	10.	*Esox lucius.* European Pike.
31.	„	„ *masquinongy.* N. American Pike.
32.	„	*Serranus* sp. Sea-Perch.
33.	„	*Salmo lacustris.* European Lake-Trout.
34.	9.	*Coregonus clupeiformis.* N. American Whitefish.
35.	„	*Callichthys punctatus.* S. American Catfish.
36.	„	*Anabas kingsleyæ.* African Climbing Perch.
37.	8.	*Lepidosiren paradoxa*, alive. S. American Lung-fish.
38.	„	*Alestes* sp. Nile "Rai."
39.	„	*Hydrocyon forskalii.* Nile Tiger-Fish.
40.	„	*Distichodus niloticus.* Nile "Lafash."
41.	„	*Amiurus catus.* N. American Catfish.
42.	„	*Plecostomus commersoni.* S. American Catfish.
43.	„	*Anabas scandens*, alive. Asiatic Climbing Perch.
44.	„	*Eupomotis pallidus*, alive. N. American Sun-fish.
45.	„	*Lates niloticus.* Nile Perch.
46.	„	*Macropodus opercularis.* Asiatic Paradise Fish.
47.	„	*Perca flavescens*, alive. N. American Yellow-Perch.
48.	„	*Tautoga onitis.* American Sea-Blackfish.
49.	7.	*Acipenser sturio.* The Sturgeon.
50.	„	„ *brevirostrum.* Short-nosed Sturgeon.
51.	„	*Gnathonemus cyprinoides.* Nile Mormyrid Fish.
52.	„	*Mormyrus* sp. „ „ „
53.	„	*Marcusenius isidori.* „ „ „
54.	„	*Salmo fario.* European Brown Trout.
55.	„	*Abramis chrysoleucas*, alive. N. American Roach.
56.	„	*Malopterurus electricus.* African Electric Catfish.
57.	„	*Pimelodus* sp. American Catfish.
58.	„	*Pomoxys sparoides*, alive. N. American Calico-Bass.
59.	„	*Apomotis cyanellus*, alive. N. American Green Sunfish.
60.	„	*Lucioperca sandra.* Pike-Perch.
61.	„	*Percina aspro*, alive. N. American Black-sided Darter.
62.	„	*Tilapia* sp., alive. Nile Cichlid Fish.
63.	„	*Acara tetramerus*, alive. American Cichlid Fish.
64.	„	*Cichlasoma nigrofasciata*, alive. American Cichlid Fish.
65.	„	*Geophagus brasiliensis*, alive. „ „ „
66.	„	*Ambloplites rupestris*, alive. N. American Rock-Bass.
67.	„	*Hexanematichthys felis*, alive. N. American Sea-Catfish.
68.	„	*Morone americana*, alive. N. American White Perch.
69.	„	*Scicenops ocellatus.* American Sea Red Drum.
70.	„	*Epinephelus morio.* „ „ Red Grouper.
71.	„	„ *striatus.* „ „ Nassau Grouper.
72.	„	*Promicrops guttatus*, alive. American Sea Spotted Jewfish.
73.	„	*Neomænis griseus.* „ „ Grey Snapper.
74.	„	„ *synagris.* „ „ Lane Snapper.
75.	6.	*Chrysichthys auratus.* Nile Abu Rial Catfish.
76.	„	*Anguilla chrisypa.* N. American Eel.
77.	„	*Pogonias chromis.* American Sea-Drum.
78.	„	*Archosargus probatocephalus.* American Sea-Sheepshead.
79.	„	*Electris maculata*, alive. Cuban Goby.
80.	„	„ *gyrinus*, alive. „ „
81.	„	*Tetrodon fahaka.* Nile Globe-Fish.

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12. Contributions to our Knowledge of the Duration of Life in Vertebrate Animals.—II. Batrachians.

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1. Preface.

The question of the duration of life in the Class Batrachia is more complicated than in the other classes of Vertebrate animals, owing to the changes that may or may not be passed through. While certain species commence their independent existence as miniature representatives of their parents, the majority pass their life in the three stages of egg, larva (Tadpole), and perfect or adult form.

The egg stage, according to the species, may last from thirty hours to twelve weeks, or may be eliminated.

The larval stage may be divided into two distinct periods, when a quiescent, clinging stage precedes the development of the active, free-swimming Tadpole.

Tadpoles may require from two or three weeks or two or three years of life before they become Frogs or Toads.

In some species the larval stage is eliminated, in others the animals may become sexually mature and reproduce their kind while still in the larval stage.

The object of this paper is to put on record what little we know so far on the subject of the longevity of Batrachians in their adult form, and give some indication of the periods of time that may be occupied in the earlier stages.

2. Acknowledgments.

To Mr. G. A. Boulenger, F.R.S., F.Z.S., I am indebted for most valuable advice and instruction, from 1886 onwards, in practical methods of keeping and caring for live Batrachians.

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I wish also to express my thanks to Dr. P. Chalmers Mitchell,

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12. Contributions to our Knowledge of the Duration of Life in Vertebrate Animals.—II. Batrachians.

By Major S. S. Flower, O.B.E., F.L.S., F.Z.S.

[Received January 30, 1925: Read February 17, 1925.]

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1. Preface.

The question of the duration of life in the Class Batrachia is more complicated than in the other classes of Vertebrate animals, owing to the changes that may or may not be passed through. While certain species commence their independent existence as miniature representatives of their parents, the majority pass their life in the three stages of egg, larva (Tadpole), and perfect or adult form.

The egg stage, according to the species, may last from thirty hours to twelve weeks, or may be eliminated.

The larval stage may be divided into two distinct periods, when a quiescent, clinging stage precedes the development of the active, free-swimming Tadpole.

Tadpoles may require from two or three weeks or two or three years of life before they become Frogs or Toads.

In some species the larval stage is eliminated, in others the animals may become sexually mature and reproduce their kind while still in the larval stage.

The object of this paper is to put on record what little we know so far on the subject of the longevity of Batrachians in their adult form, and give some indication of the periods of time that may be occupied in the earlier stages.

2. Acknowledgments.

To Mr. G. A. Boulenger, F.R.S., F.Z.S., I am indebted for most valuable advice and instruction, from 1886 onwards, in practical methods of keeping and caring for live Batrachians.

Dr. T. Barbour, C.M.Z.S., Prof. J. P. Hill, F.R.S., F.Z.S., Mr. P. C. Horn, and Mr. H. N. Milligan, F.Z.S., have all been so good as to supply interesting notes for this paper.

I wish also to express my thanks to Dr. P. Chalmers Mitchell,

Summary of Batrachians, by Orders and Families, in the Giza Zoological Gardens for October 1898 *to March* 1924 (*inclusive*).

	Number of Forms *.	Number of Individuals.			Average length of life of the twenty individuals that lived longest, with the number, out of the twenty, that left alive.			
		Died.	Left alive.	Total.	Years.	Months.	Days.	Of these 20, left alive:—
Order ECAUDATA.								
1. Ranidæ	4	35	15	50	2	10	25	5
2. Engystomatidæ	1	1	5	6	—	—	—	—
3. Cystignathidæ	1	1	—	1	—	—	—	—
4. Bufonidæ	10	120	48	168	5	8	6	10
5. Hylidæ	3	36	11	47	1	11	24	4
6. Pelobatidæ	1	12	4	16	—	—	—	—
7. Discoglossidæ	1	3	—	3	—	—	—	—
Total Ecaudata	21	208	83	291	6	0	0	13
Order CAUDATA.								
8. Salamandridæ	7	24	9	33	1	8	10	2
Total Batrachians	28	232	92	324	6	0	5	12

* Species and well-distinguished subspecies.

C.B.E., F.R.S., F.Z.S., and to Mr. E. G. Boulenger, F.Z.S., for their kindness in affording me facilities to include information as to the life of Batrachians in this Society's collection, and to Dr. Jacques Pellegrin, of the Muséum National d'Histoire Naturelle, Paris, for similar kindness regarding the famous menagerie in the Jardin des Plantes.

3. Records of Longevity.

Nothing appears to have been published on the subject of the duration of life of Batrachians in general. Incidental notes appear in several books that I have had access to (A. Duméril, 1854–5, G. A. Boulenger, 1897–8 and 1910, Gadow, 1901, Dickerson, 1907, E. G. Boulenger, 1914), and there are probably others that I am ignorant of and would be glad to be told of.

Short lists of maximum lives in captivity have been published for the Giza Zoological Gardens (Flower, 1909 and 1910), and for the New York Aquarium (Mellen, 1919).

Mr. G. A. Boulenger has dealt with the stories of Toads and Newts found fitted in walls or stones, or even in blocks of coal (1910, p. 45), and an incident reported by the late Miss Mary Cynthia Dickerson will be quoted regarding *Bufo cognatus*.

4. Giza Zoological Gardens.

Batrachians in captivity to be kept with success require special knowledge and individual attention on the part of the person in charge of them; the collection of live Frogs, Toads, and Newts in the Giza Zoological Gardens was therefore, as far as possible, kept limited to such small numbers as could be properly cared for.

The table (p. 270) shows how many were in my charge. No general conclusions can be drawn from such a small number as 324 individuals, but these figures are of interest for comparison with records from other sources.

It may be mentioned that attempts at keeping Batrachians in outdoor cages, however well sheltered from sun and wind and however well supplied with water and hiding-places, were not satisfactory. The individuals that lived longest were kept in small cages inside houses.

5. Notes by Families.

These notes are arranged by families as follows:—

Ecaudata.
1. Ranidæ.
2. Engystomatidæ.
3. Cystignathidæ.
4. Bufonidæ.
5. Hylidæ.
6. Pelobatidæ.
7. Discoglossidæ.
8. Pipidæ.

Caudata.	9. Salamandridæ.
	10. Amphiumidæ.
	11. Proteidæ.
	12. Sirenidæ.
Apoda.	13. Cœciliidæ.

Family Ranidæ.

1. Rana tigrina. Asiatic Tigrine Frog.

The two best records for the London Z. G. are:—

Received.	Died.	Years	months	days.
16.4.1902.	13.11.1906.	4	6	27
13.5.1901.	6. 1.1908.	6	7	23

Another specimen received 16.7.1920 was still alive on 13.2.1925.

2. Rana occipitalis. African Tigrine Frog.

A specimen from Malakal on the White Nile, brought to the Giza Zoological Gardens, lived there for 3 years 5 months 23 days.

3. Rana adspersa. South African Frog.

Two records for the London Z. G. are:—

Received.	Died.	Years	months	days.
20.3.1909.	19.8.1912.	3	5	0
3.1.1921.	30.7.1924.	3	6	27

4. Rana catesbiana. North American Bull-Frog.

Tadpole. "The tadpoles do not develop into frogs during the first season, as do those of the Leopard and Pickerel frogs. It is not until the second season, and sometimes the third, that a Bullfrog tadpole makes its final transformation" (Dickerson, 1907, p. 234).

Perfect Form. The following seven selected records of individuals in the London Z. G. show that, through a long series of years, this species lives well in the Regent's Park.

Received.	Died.	Years	months	days.
2. 5.1881.	29. 1.1886.	4	8	27
26. 6.1903.	30. 7.1908.	5	1	4
20. 5.1881.	19. 7.1886.	5	2	0
26. 6.1903.	27.11.1909.	6	5	1
15. 8.1894.	26. 6.1902.	7	9	11
10. 4.1885.	8. 2.1893.	7	9	28
31.10.1893.	20. 7.1909.	15	8	20

5. Rana clamata. North American Noisy Frog.

Tadpole. "The tadpoles may live two years before the final metamorphosis. It is not until the second summer, and possibly

until the third, that the change to the frog form occurs" (Dickerson, 1907, p. 204).

Perfect Form. Six London Z. G. records should be mentioned.

Received.	Died.	Years	months	days.
29.9.1892.	17. 4.1897.	4	6	18
,,	4. 8.1897.	4	10	5
10.6.1901.	17. 2.1907.	5	8	7
,,	27.10.1908.	7	4	17
,,	15. 2.1909.	7	8	5
,,	11. 8.1911.	10	2	1

6. RANA HALECINA. North American Pickerel Frog.

One lived in the London Z. G., 25.5.1900 to 7.3.1907—6 years 9 months 12 days.

7. RANA DRAYTONII. Californian Frog.

The late Miss M. C. Dickerson, in her 'Frog Book,' 1907, in "Colour Plate XV." (facing page 214), gives two beautiful coloured photographs of a "Female, four or five years old," and in "Plate LXXXI." (facing page 216) there are two photographs of a "Male frog of *Rana draytonii* Bd. and Gird., eight or more years old."

These pictures, thus described, lead one to hope for definite information on the longevity of Frogs; but from the letterpress, pages 215, 216, and especially page 242, it appears that the ages given are only estimated ones.

8. RANA ESCULENTA. Palæarctic Water-Frog.

Tadpole. From the hatching of the egg to the transformation into a frog, a tadpole usually takes about three months, but hibernation is not infrequent (G. A. Boulenger, 1897–8, p. 284).

Perfect form. In the London Z. G. so many frogs of this species have been received that it has been difficult to keep records of individuals. Mr. E. G. Boulenger agrees with me that they not infrequently live four years, and sometimes five, in the collection; some may well have lived longer, but we have no definite data on which to prove it.

The two longest London records with actual dates appear to be:—

Received.	Died.	Years	months	days.
12.4.1893.	24.2.1898.	4	10	12
2.5.1900.	11.7.1905.	5	2	9

In 1918, Major Maurice Portal, D.S.O., F.Z.S., caught some frogs of this species, of the variety *ridibunda*, in Palestine, which he presented to the Giza Zoological Gardens; when I left Egypt, two of these had been 5 years 3 months 25 days and one 5 years 11 months 3 days in the Giza Z. G., and all three alive and well.

9. Rana temporaria. Palæarctic Grass-Frog.

Although this species has been so thoroughly studied from so many points of view, apparently nothing is known of its usual or potential length of life when once it has attained its perfect form. It appears to be a difficult animal to keep in captivity.

One year and three months is the longest time I have, personally, had an individual alive for.

In the London Z. G. the longest record appears to be from 23.10.1913 to 1.8.1916—2 years 9 months 8 days.

Dr. Gadow, F.R.S., F.Z.S., has been more successful, having kept individuals *over* four years (Gadow, 1901, p. 67).

10. Rana mascareniensis. African Mascarene Frog.

These little frogs did well in captivity in Egypt. The average duration of life of twenty selected individuals was 1 year 9 months 19 days, five out of the twenty remaining alive at the period my notes ceased.

The maximum record for an individual was 4 years 4 months and 2 days.

Family Engystomatidæ.

11. Phrynomantis bifasciata. African Black-and-red Rubber Frog.

A Sudanese individual, of the variety *microps*, lived in the Giza Z. G. in 1910 for 5 months 12 days.

Family Cystignathidæ.

12. Ceratophrys ornata. South American Ornamented Toad.

This animal has often done very well in captivity; in London and on the continent of Europe there are several records of its living for over eight years. The maximum records for the London Z. G. are :—

Received.	Died.	Years	months	days.
4.5.1914.	24. 7.1923.	9	2	20
14.2.1886.	15.12.1896.	10	10	1

13. Calyptocephalus gayi. Gay's Frog from Chili.

Of two specimens received in the London Z. G., 4.5.1915, one lived there for 3 years 2 months 5 days and one for 7 years 2 months 21 days.

14. Leptodactylus pentadactylus. South American Slender-fingered Frog.

An individual lived in the London Z. G. from 22.8.1882 to 27.12.1890—8 years 4 months 5 days.

15. Leptodactylus mystacinus. South American Frog.

One lived in the London Z. G. from 31.1.1916 to 17.2.1923—7 years and 17 days.

16. Leptodactylus ocellatus. South American Ocellated Frog.

From 1881 onwards individuals have from time to time lived well in the London Z. G. The maximum record appears to be 31.1.1916 to 24.6.1921—5 years 4 months 24 days.

Family Bufonidæ.

17. Bufo calamita. European Natterjack Toad.

Tadpole. The usual life of the tadpole from the hatching of the egg to the transformation to the toad is five to eight weeks, but hibernation is possible (G. A. Boulenger, 1897–8, p. 242).

Perfect Form. The longest time I have kept a specimen myself is only 1 year 10 months and 18 days. Within recent years two have lived for over four years in the London Z. G., and there is a record of one received in Regent's Park, 13.3.1873, which died 18.8.1879, a period of 6 years 5 months and 5 days.

Mr. H. N. Milligan, F.Z.S., Zoologist of the Horniman Museum, London, kindly informed me, in a letter of 7th January, 1925:—"A male natterjack, apparently full grown when obtained, lived here for thirteen years. He died some six months ago."

18. Bufo viridis. Palæarctic Green Toad.

Tadpole. About two months (G. A. Boulenger, 1897–8, p. 234).

Perfect Form. The longest London Z. G. records are:—

Received.	Died.	Years	months	days.
11. 9.1871.	11. 6.1876.	4	9	0
,,	27. 6.1876.	4	9	16
,,	21. 4.1877.	5	7	10
20.11.1883.	17.10.1892.	8	10	27

The following are Giza Z. G. records:—

	Years	months	days.
From Palestine (Major M. Portal).....	6	9	12, and still alive.
From Palestine (Major M. Portal).....	6	4	3, and still alive.
From Maryût, N.W. Egypt	6	2	11
,, ,, ,,	6	1	27
,, Abukir, Alexandria...	6	0	7, and still alive.
Average of 20 individuals...	5	3	7 { of which 8 left alive

19. BUFO VIRIDIS ARABICUS. Arabian Green Toad.

	Years	months	days.	
Specimen from the Wadi Natrûn, Lower Egypt, in the Giza Z. G. This is a pigmy race of *Bufo viridis*.	2	0	0	
	2	1	0	
	2	11	21	
	3	1	10	
	3	8	12	
Average of 20 individuals...	1	2	24	of which 4 left alive.

20. BUFO MAURITANICUS. Moorish Toad.

Although this species attains a large size, it would appear not to do so well in captivity as its allies. The maximum record for the London Z. G. is from 7.1.1873 to 19.1.1877, *i. e.* 4 years and 12 days, and for the Giza Z. G. (an individual from Biskra, Algeria) only 2 years 5 months 13 days.

21. BUFO REGULARIS. African Square-marked Toad.

Of Egyptian specimens in the Giza Z. G. the maximum record is 6 years 10 months 8 days. Three individuals were still alive after 6 years 8 months 0 days. The average of twenty individuals was 3 years 11 months 18 days, four out of these twenty being still alive.

Although the maximum is about the same as for *Bufo viridis*, it will be noted that the average is very much shorter than for that species.

22. BUFO VITTATUS. Degen's Toad, African.

Two males of this pigmy species caught, when fully adult, at Faraskur, near Damietta, in Lower Egypt; both lived in the Giza Z. G. for 2 years 5 months 29 days.

23. BUFO PENTONI. Penton's Toad, African.

Two specimens caught in the Shata Gardens, Suakin, 24th May, 1912, arrived in the Giza Z. G., 22nd July, 1912. One died 7th January, 1914, the other 17th January, 1914, having lived in captivity 1 year 7 months 23 days.

Penton's Toad attains a fair size and should live for very much longer than this, but it would be difficult to reproduce in captivity the apparently extreme *adverse* conditions of heat and sand under which its natural life is passed.

24. BUFO DODSONI. Dodson's Toad, African.

Out of nine specimens of this little species collected by Mr. A. L. Butler, F.Z.S., in the Khor Abbat, about 25 miles from Port Sudan, the maximum length of life in the Giza Z. G. was 3 years 8 months.

25. Bufo vulgaris. Palæarctic Brown Toad.

Tadpole. Eight to twelve weeks (G. A. Boulenger, 1897–8 p. 224).

Perfect Form. The longest London Z. G. record is from 12.7.1887 to 3.10.1892, *i. e.* 5 years 2 months 21 days. This is longer than I have ever succeeded in keeping one for, but my sister, Mrs. S. T. P. Prideaux, kept a toad alive in England from August 1899 to November 1907, *i. e.* 8 years and about 3 months.

Mr. Boulenger had a female toad from Jersey alive for twelve years, 1885 to 1897 (G. A. Boulenger, 1897–8, p. 222).

Mr. Percy W. Horn, Curator, Stepney Borough Museum, London, wrote to me, 10th January, 1925:—"Tom, the Borough Toad, was a huge Italian, much esteemed by the local visitors. We had him on exhibition in the Nature Study Museum for five or perhaps six years, when unfortunately he was stolen by one of his admirers. This was fifteen years ago." In the same letter Mr. Horn gave me notes on an Essex toad, twelve years and still alive, and of another toad that lived for eighteen years in a town garden and left alive.

The toad of J. Arscott, Esq., of Tehott, Devonshire, is stated to have lived for thirty-six years. Mr. Arscott's letters on the subject deserve careful reading (Pennant, 1776, vol. iii. pp. 332, 334).

26. Bufo melanostictus. Indian Black-spotted Toad.

These two records are from the London Z. G.:—

Received.	Died.	Years	months	days.
15.8.1884.	27.11.1888.	4	3	12
,,	21.12.1888.	4	4	6

27. Bufo americanus. North American Toad.

Eggs hatch in two or three days (Dickerson, 1907, p. 5).

Tadpoles spent about six days, after hatching, in the quiescent stage, then four to six weeks as real "pollywogs," and ten to fourteen days later became "just toads" (Dickerson, 1907, p. 69).

Perfect Form. "Toads do not resort to the ponds for the breeding-season until they are three or four years old" (Dickerson, 1907, p. 72).

American Toads may live for ten or fifteen years (Dickerson, 1907, p. 79.)

28. Bufo cognatus. North American Western Plains Toad.

"At least five years must be required for full growth to be attained" (Dickerson, 1907, p. 101).

"A curious incident occurred when *Bufo cognatus* was being kept in captivity for study—an incident probably illustrative of the way in which stories have arisen regarding toads found in stones and buried in impossible places. A large fat specimen of

Bufo cognatus escaped one morning from its moss-garden in a building in Rhode Island. That day repairs had been begun on a cement floor in the basement of the building. In the afternoon of the day, while workmen were continuing to remove the cement floor—which had been put down seven years before,—they came upon a fat toad just fitting a burrow under the floor. Excitement followed, with many stories of toads found in similar situations where they had been for more than seven years. If the toad had not turned out to be the lost *Bufo cognatus* from Colorado, and had been a native of Rhode Island, there would have existed no proof that it had not been there seven years instead of a few hours" (Dickerson, 1907, pp. 101, 102).

29. Bufo arenarum. South American Toad.

London Z. G. records:—

Received.	Died.	Years	months	days.
31.1.1916.	8.5.1922.	6	3	8
,,	15.1.1923.	6	11	15
,,	18.7.1923.	7	5	18

30. Bufo marinus. American Giant Toad.

London Z. G. records:—

Received.	Died.	Years	months	days.
25.3.1881.	2. 3.1888.	6	11	7
29.9.1900.	6. 9.1908.	7	11	7
12.5.1914.	5.10.1922.	8	4	23
3.1.1880.	13. 2.1819.	9	1	10

Family Hylidæ.

31. Hyla arborea. Palæarctic Tree-Frog.

Tadpole. Usually about three months; hibernation possible (G. A. Boulenger, 1897–8, p. 258).

Perfect Form. The longest records for the London Z. G. appear to be:—

Received.	Died.	Years	months	days.
27.7.1873.	28.1.1877.	3	6	1
,,	11.5.1877.	3	9	14
7.1.1878.	4.2.1883.	5	0	27
12.7.1878.	25.8.1892.	14	1	13

In the Giza Z. G., specimens of *Hyla arborea savignii*, from Palestine, have lived:—

Years	months	days.
4	0	27
4	2	29
4	10	7
4	11	0

Prof. F. Werner, of Vienna, told me, 8 May, 1914, that from his experience frogs of this species at about eight years of age show decided signs of senility; in captivity individuals may live to be nine or ten years old.

"A man of the name of Papst, in Gotha, is said to have kept one for twenty-two years" (C. A. Boulenger, 1897–8, p. 258).

32. Hyla cœrulea. White's Tree-Frog, Australia.

This large species does well in captivity in Europe. In the London Z. G. from 1879 to the present time there have been a series of records of individuals living six, seven, or eight years in Regent's Park, and in two instances for over ten years. Mr. E. G. Boulenger tells me, 20 January, 1925, that, though we can be certain of well over ten years, it is probable that the maximum duration of life of a White's Tree-Frog in London is over twelve years.

A. Duméril (1854–5, p. 301) mentions an individual, received from M. Jules Verreaux, being still alive after six years in Paris. This may have been the famous specimen, received in the Jardin des Plantes in 1847, which was accidentally killed after it had lived there for 16 years 6 months 27 days. (I believe that Vaillant published this record, but have so far not found the quotation.)

33. Hyla aurea. Australian Golden Tree-Frog.

In the London Z. G. from 1879 to 1909 there have been a few records of this species having lived well, the maximum being from 21.10.1896 to 30.1.1904, *i. e.* 7 years 3 months 9 days.

34. Hyla pulchella. South American Tree-Frog.

London Z. G.:—

29.1.1917 to 7.5.1919. 2 years 4 months 8 days.

35. Hyla regilla. South American Tree-Frog.

London Z. G.:—

17.5.1906 to 5.8.1908. 2 years 2 months 18 days.

Family Pelobatidæ.

36. Pelobates fuscus. European Spadefoot Toad.

From 1873, to the present time eight individuals appear to have lived over two years in the London Z. G. The best records are:—

Received.	Died.	Years	months	days.
28.4.1909.	14.10.1913.	4	5	16
,,	18. 3.1914.	4	10	20

37. PELOBATES SYRIACUS. Syrian Spadefoot Toad.

The maximum length of life of an individual in the Giza Z. G., collected in Palestine by Major Maurice Portal, D.S.O., F.Z.S., was only 7 months and 6 days. It was received when in the tadpole stage. As in the two European species of *Pelobates*, the tadpoles of *P. syriacus* are very large.

38. SCAPHIOPUS HOLBROOKII. North American Hermit Spadefoot.

Eggs hatch in seven to fifteen days, according to the temperature.

Tadpoles transform in a very few weeks (Dickerson, 1907, p. 56).

Maximum life in New York Aquarium for this species is six months (Mellen, 1919, p. 35).

39. MEGALOPHRYS FEÆ. East Indian Forest Frog.

London Z. G.:—

1.9.1908 to 19.7.1911. 2 years 10 months 18 days.

40. MEGALOPHRYS ROBUSTA. East Indian Forest Frog.

London Z. G.:—

11.9.1908 to 13.7.1911. 2 years 10 months 2 days.

Family DISCOGLOSSIDÆ.

41. DISCOGLOSSUS PICTUS. European Painted Frog.

Eggs. "Thirty hours may suffice" (G. A. Boulenger, 1897–8, p. 84).

Tadpoles. One to two months, but may remain nine or ten months (G. A. Boulenger, 1897–8, p. 136).

Perfect Form. London Z. G. records:—

Received.	Died.	Years	months	days.
14.2.1897.	23.5.1901.	4	3	9
7.4.1904.	3.4.1911.	6	11	26

42. BOMBINATOR IGNEUS. European Fire-bellied Toad.

The average life of twenty individuals in the London Z. G. between 1865 and the present time is 4 years 7 months 24 days. The two longest records are:—

Received.	Died.	Years	months	days.
1.7.1882.	4.5.1892.	9	10	3
24.8.1865.	6.7.1877.	11	8	12

Mr. E. G. Boulenger (1914, p. 239) says that this species will live for twenty years in captivity.*

* Miss J. B. Procter tells me she has a *Bombinator igneus* fifteen years and still alive, 17 Febr., 1925.

43. Bombinator pachypus. European Yellow-bellied Toad.

This species has several times had individuals living for nearly, or over, five years in the London Z. G. The longest records are:—

Received.	Died.	Years	months	days.
1.7.1882.	7.2.1888.	5	7	6
,,	12.7.1888.	6	0	11
,,	18.6.1889.	6	11	17

An individual from Botzen, Austrian Tyrol, 4000 feet elevation, brought to Egypt by Mr. A. L. Butler, F.Z.S., in 1908, lived in the Giza Z. G. 5 years 10 months 25 days.

44. Alytes obstetricans. European Midwife Toad.

Eggs "take at least, under the best conditions, nearly three weeks" (G. A. Boulenger, 1897–8, p. 84).

Tadpoles. Three to five months, but may remain nearly two years (G. A. Boulenger, 1897–8, p. 171).

Perfect Form. In the London Z. G. from 1882 onwards these little toads have often lived well for three, four, or nearly five years; the maximum, as far as the records go, appears to be 5 years and 28 days, but I have been unable to verify the actual dates in this case.

Family Pipidæ.

45. Pipa americana. Surinam Toad.

Ten Surinam Toads were presented to this Society by Mr. F. E. Blaauw, F.M.Z.S., 14th November, 1894. The length of life in Regent's Park of five of these was:—

Died.	Years	months	days.
9.10.1897.	2	10	25
31. 8.1898.	3	9	17
17.10.1898.	3	11	3
2. 4.1899.	4	4	18
10. 4.1899.	4	4	26

The maximum length of life reached for the New York Aquarium is six months (Mellen, 1919, p. 35).

46. Xenopus laevis. African Smooth-clawed Frog.

Eggs hatch within thirty hours (Beddard, 1894, p. 102).

Tadpoles change into little frogs in about 2 months 21 days (Beddard, 1894, p. 104).

Perfect Form. London Z. G. records:—

Received.	Died.	Years	months	days.
6. 1.1890.	30. 4.1899.	9	3	24
12.10.1892.	18. 3.1902.	9	5	6
20. 8.1892.	18. 3.1902.	9	6	28 (2 individuals).
2. 6.1909.	15.10.1919.	10	4	13

Mr. G. A. Boulenger kept specimens alive for over eleven years in London, and Mr. E. G. Boulenger tells me (Jan. 1925) that the maximum length of life of individuals in the London Z. G. probably exceeds the records given above.

Family SALAMANDRIDÆ.

Subfamily SALAMANDRINÆ.

47. SALAMANDRA MACULOSA. European Spotted Salamander.

The young are born in the larval state. The larvæ take several months, at least three, before leaving the water (G. A. Boulenger, 1910, p. 116).

Although very many of these Salamanders have been in the London Z. G., cases of their living there for over three years are rare, and I have only found four records of their living over four years:—

Received.	Died.	Years	months	days.
27.10.1887.	22.10.1892.	4	11	25
17. 9.1904.	23. 6.1910.	5	9	6
29. 5.1914.	5. 8.1920.	6	2	6
,,	24.10.1920.	6	4	25

A very large female from Mount Lebanon, Syria, collected by Brigadier-General F. Fitz H. Lance, M.C., lived in the Giza Z. G. for 3 years 9 months 23 days.

48. SALAMANDRA ATRA. European Salamander.

The egg and larval stage are eliminated, the young being born alive in the perfect form (*auctorum*).

The London Z. G. records two instances of individuals living over two years in captivity, and one, 29.5.1900 to 3.8.1903, of a life of 3 years 1 month 4 days.

49. MOLGE MACROSOMA. Chakir Bey's Newt.

G. A. Boulenger, Ann. & Mag. N. H. ser. 8, vol. ii. July 1908, p. 32.

A female, the type of the species, of unknown but probably European locality, lived in the Giza Z. G. for 3 years 9 months 26 days.

50. MOLGE CRISTATA. European Crested Newt.

Of Newts of the genus *Molge* in general:—

Eggs hatch in from ten days to three weeks' time, according to the species and the temperature of the water (E. G. Boulenger, 1914, p. 250).

Larvæ. Transformation as a rule takes place three or four months after hatching, so is normally finished during the summer of the year in which the eggs are laid, but hibernation may occur (G. A. Boulenger, 1910, p. 127; E. G. Boulenger, 1914, p. 250).

Of this species, *M. cristata* in particular, the following four records of the London Z. G. may be noted:—

	Received.	Died.	Years	months	days.
	29. 7.1908.	5.9.1912.	4	1	6
	,,	18.9.1912.	4	1	15
Var. KARELINII	25.11.1913.	18.8.1916.	2	8	23
			(2 individuals).		
	bred 2. 8.1912.	18.8.1916.	4	0	16

A female, caught near Tring, Herts, lived in my care for 5 years 10 months 25 days.

51. MOLGE MARMORATA. European Marbled Newt.

The longest records for the London Z. G. appear to be:—

Received.	Died.	Years	months	days.
14.11.1887.	8.12.1891.	4	0	24
30. 3.1900.	29. 5.1905.	5	1	29

52. MOLGE ALPESTRIS. European Alpine Newt.

"Like the majority of European newts, this species does not flourish in confinement" (E. G. Boulenger, 1914, p. 253). The longest time I have kept an individual alive for was 1 year and 7 months.

53. MOLGE VULGARIS. European Smooth Newt.

The three London Z. G. records are:—

Received.	Died.	Years	months	days.
12. 4.1877.	6. 5.1879.	2	0	24
,,	6. 6.1879.	2	1	26
27. 4.1878.	8.10.1880.	2	5	11

I have myself kept a specimen alive for 2 years 9 days.

Mr. P. W. Horn, in a letter of 10th January, 1925, writes that he had been told of a Smooth Newt being kept alive in London for three and a half years.

54. MOLGE PYRRHOGASTRA. Japanese Newt.

In the London Z. G. there are *many* records of from three to four years, and the following ten records of over four years.

Received.	Died.	Years	months	days.	
12. 6.1901.	20.8.1905.	4	2	8	
23. 3.1909.	25.8.1913.	4	6	2	
12. 6.1901.	31.1.1906.	4	7	19	
27.10.1905.	5.9.1913.	7	10	8	
,,	8.9.1913.	7	10	11	(3 individuals).
,,	10.9.1913.	7	10	13	(3 individuals).
Av. of these 10 individuals =		6	10	2	

55. Molge torosa. Californian Newt.

Two individuals lived in the London Z. G. from 19.2.1907 to 20.7.1911—4 years 5 months 1 day.

56. Molge viridescens. North American Greenish Newt.

One lived in the London Z. G. from 1.7.1882 to 8.6.1885—2 years 11 months 7 days.

57. Molge waltlii. Spanish Pleurodele Newt.

This large species of Newt is well known to thrive under suitable conditions of captivity for four, five, six, or even more years.

The four longest records for the London Z. G. are :—

Received.	Died.	Years	months	days.	
20. 1.1906.	26.2.1913.	7	1	6	
6. 3.1905.	31.8.1912.	7	5	25	
11. 7.1901.	5.6.1911.	9	10	24	
14.11.1887.	30.5.1906.	18	6	16	(this was a female).

In the Jardin des Plantes, Paris, an individual received in 1864 lived for 19 years 6 months 16 days, as has been recorded by Vaillant.

58. Tylototriton verrucosus. Yunnan Newt.

Of two individuals received in the London Z. G. on 20th Sept., 1907, one lived there for 4 years 6 months 24 days, and one for 4 years 11 months 12 days.

Subfamily Amblystomatinæ.

59. Amblystoma tigrinum. American Axolotl.

"The eggs are hatched in from ten to twenty days, according to the temperature of the water. The larvæ..... are sexually mature when about a year old" (E. G. Boulenger, 1914, p. 261).

In the London Z. G. from 1866 onwards there are many records of Axolotls living for four, five, and six years, but the only record of one living for over seven years is :—

Received.	Died.	Years	months	days.
12.7.1871.	2.12.1880.	9	4	20

White Axolotls are reported to have lived for over ten years (1901–1911) in the Crystal Palace Aquarium.

The late Mr. J. Barrow, for many years manager of Robert Green & Co.'s "Bedford Aquarium" at Covent Garden Market, London, told me that a White Axolotl that died there about June 1909 had lived over twenty-five years in Covent Garden.

Subfamily Plethodontinæ.

60. Typhlomolge rathbuni. Texan Blind Salamander.

Lived one year in the New York Aquarium (Mellen, 1919, p. 36).

Family AMPHIUMIDÆ.

61. MEGALOBATRACHUS MAXIMUS. Asiatic Giant Salamander.

This species, which has been bred in the Amsterdam Aquarium, lives well in captivity, as these notes show :—

	Years	months	days.	
(1) New York Aquarium (Mellen, 1919, p. 36).....	10	0	0	still alive 1919.
(2) London Z. G., 14 Aug. 1868 to 1 Dec. 1879.....	11	3	17	
(3) Berlin Aquarium, in 1907 ..... Over	12	0	0	still alive 1907.
(4) Hamburg Aquarium (Gadow, 1901, p. 99)	14	0	0	
(5) Paris, Jardin des Plantes, 31 March, 1885 to 21 Feb. 1903. Monsieur Henri Bruyère kindly gave me this record.....	17	10	11	
(6) London Z. G., 23 April, 1884 to 20 Sept. 1903 ...	19	4	27	
(7) Schönbrunn Menagerie, Vienna, in 1910. About	20	0	0	still alive 1910.
(8) Blackpool Aquarium ; *said* to have been received about 1899, and to be still alive in 1924. About	24	0	0	still alive 1924.
(9) Paris, Jardin des Plantes: presented by Dr. Geerts in 1882 ; said to be still living in 1907	25	0	0	still alive 1907.
(10) Paris, Jardin d. P. ; presented by Dr. and Madame Phisalix in 1896; still alive there 9 Jan. 1925 .	28	0	0	still alive 1925.
(11) Paris, Jardin d. P. ; presented by Dr. Pompe van Meerdervoort, Nov. 1859 ("déjà âgée")... Over (A. Duméril, 1861, p. 458; Vaillant, 1897, p. 92.)	33	0	0	still alive 1897.
(12) Tring. Belonging to Lord Rothschild, F.R.S., F.Z.S. ..... About	35	0	0	still alive 1925.
(13) Leyden, Holland. Imported from Japan 1829 (or 1831) ; died 3rd June, 1881 ..... About	52	0	0	

62. CRYPTOBRANCHUS ALLEGHANIENSIS. North American Hellbender.

London Z. G. records :—

Received.	Died.	Years	months	days.
9.3.1869.	7.7.1872.	3	3	28
,,	19.8.1873.	4	5	10
18.9.1901.	12.5.1905.	4	7	24
9.3.1869.	9.8.1874.	5	5	0
23.9.1901.	14.1.1909.	7	3	21
New York Aquarium maximum (Mellen, 1919, p. 36).....		6	0	0

63. AMPHIUMA MEANS. North American Amphiuma.

London Z. G. records :—

Received.	Died.	Years	months	days.
8. 5.1902.	7.10.1904.	2	5	0
2. 8.1898.	21.11.1901.	3	3	19
24. 4.1879.	3. 9.1883.	4	4	9
29. 9.1902.	18. 8.1910.	7	10	19
17. 7.1902.	8.10.1911.	9	2	21
6.12.1870.	30. 9.1897.	26	9	24
New York Aquarium maximum (Mellen, 1919, p. 36)		5	0	0

Family PROTEIDÆ.

64. NECTURUS MACULATUS. North American Mud Puppy.

London Z. G. records :—

Received.	Died.	Years	months	days.
10.7.1881.	29.3.1883.	1	8	19
22.5.1886.	24.6.1889.	3	1	2
,,	9.2.1890.	3	8	17
New York Aquarium maximum (Mellen, 1919, p. 36).....		5	0	0
Vienna "Vivarium": two individuals ....."Nearly" (S. S. Flower, 'Zoologist,' 1911, p. 426).		5	0	0

65. PROTEUS ANGUINUS. European Proteus.

In September 1841, Dr. Louis Mandl presented a Proteus to the Menagerie of the Jardin des Plantes, Paris; it fed on earthworms, and died in September 1852, having lived eleven years in captivity (A. Duméril, 1854–5, p. 312).

London Z. G. records :—

Received.	Died.	Years	months	days.
17. 5.1871.	27.5.1875.	4	0	10
25. 2.1871.	27.5.1875.	4	3	2
11.10.1887.	8.3.1892.	4	4	27
24. 6.1910.	5.6.1915.	4	11	11
New York Aquarium maximum (Mellen, 1919, p. 36)		1	6	0

"In spite of the fact that in captivity Proteus often refuses to feed, it will thrive nevertheless without taking any form of nourishment at all for as long as five years" (E. G. Boulenger, 1914, p. 269).

Family SIRENIDÆ.

66. SIREN LACERTINA. North American Siren.

"When Mr. Neill's *Siren lacertina* was presented to him by Dr. Munro in 1825, it was *enveloped in a ball of mud or clay*, and received from the marshes of South Carolina. It was transferred from the greenhouse in April 1827 to the stove, where it lives in a box of water containing also moss. Here we have frequently seen this curious animal. . . . . It croaks like a frog, and is fed on worms" (Murray, 1830, p. 86).

Dr. Thomas Barbour, C.M.Z.S., writes to me from Cambridge, Mass., 31st Dec., 1924 :—"Sirens: I have here in my laboratory a specimen over two feet long and as large as one's wrist nearly. This old chap (I think the record in size) has lived well for several years. He eats worms, bits of beef, clams and small fish, provided they are dead. He gropes about very blindly and

prefers the dark. He has absolutely no voice whatever. No more have any of the others had which I have kept. . . . . I have been familiar with them all my life. . . . . I know nothing of their breeding habits. I have seen some young specimens, but have never kept any number of them for long."

Dr. Garden, who discovered the Siren in 1765 and sent a specimen to Linnæus, stated (I have not the quotation or reference, unfortunately): "it utters a sound like the voice of a young duck." Mr. E. G. Boulenger tells me that from his experience, like that of Dr. Barbour, the Siren has no voice.

"In 1841 a lively specimen was living in the Zoological Gardens. It was kept in a vessel of pond-water, with a deep bottom of mud, in which it buried itself; it fed upon earth-worms, devouring a dozen and a half every other day. It was about twenty inches long, and very eel-like in all its movements" ('Pictorial Museum of Animated Nature,' London, n.d., vol. ii. p. 135).

The late Mr. P. L. Sclater, F.R.S., when Secretary to this Society, was evidently unaware of the 1841 Siren, as in the 'Proceedings,' 1876, p. 333, he records:—

"Three Sirens (*Siren lacertina*, Linn.), from South Carolina, presented by Mr. G. E. Maingault, Curator of the Museum of Natural History, Charleston, March 29th (1876). Mr. Maingault has on a previous occasion transmitted to us an example of this rare and singular Batrachian; but these are the first that have reached us alive."

These three Sirens lived at Regent's Park for, respectively, 2 years 6 months 1 day, 2 years 8 months 5 days, and 3 years 11 months 19 days.

The longest record of a Siren in the London Z. G. is from 23.5.1901 to 27.12.1910, *i.e.* 9 years 7 months 4 days.

In the New York Aquarium the maximum is two years (Mellen, 1919, p. 36).

The first Siren received in the Jardin des Plantes was from South Carolina, presented by Dr. Smith; it eats newts and small fish, and grew considerably during its time, nearly seven years, in Paris, reaching almost half a metre in length (A. Duméril, 1854–5, p. 312).

On 6th May, 1889, Mr. H. Brown presented a *Siren lacertina* to the Jardin des Plantes menagerie, which I saw from time to time when visiting Paris. It died 27th November, 1913, having lived there for 24 years 6 months 21 days.

Family Cœciliidæ.

67. Siphonops annulatus. South American Cœcilian.

Most attempts at keeping the Limbless Batrachians, of Old or New World forms, alive in captivity appear to fail. The animals die in a few weeks, or even days.

The brilliant exception is that of Prof. J. P. Hill, F.R.S., F.Z.S., who, about the 20th October, 1913, collected at Theresopolis, Serra dos Orgaos, Brazil, and brought to London in November 1913 about three dozen living specimens of *Siphonops*.

Prof. Hill found them easy to keep in boxes containing damp mould, at a temperature of 60 degrees Fahrenheit. He had them at University College, London, where they laid eggs, from which a series of photographs of embryos were obtained.

On 4th April, 1916, Prof. Hill presented two live *Siphonops* to this Society (P. Z. S. 1916, pp. 447, 448). One of these escaped in the Reptile House, where it was refound, 7th January, 1921, in the earth round the roots of a palm; it eventually died 30th April, 1923, giving a known life of 9 years 6 months 10 days.

6. Conclusions.

(1) As with some fishes, it is possible that want of opportunity to breed may prolong life to beyond its normal length in some Batrachians.

(2) The larger the species, the longer the life. This appears to be true both in the Class in general, and in Families and Genera in particular.

(3) In only five families is there sufficient data to form an idea of the normal length of life that an individual, having reached its perfect form, may be expected to attain before fatal senility sets in—if it is fortunate enough to escape death from climatic changes or its numberless natural foes during the intervening period.

These ages, for the larger species only, I estimate to be:—

Discoglossidæ	6 years.
Ranidæ	$7\frac{3}{4}$,,
Cystignathidæ	$7\frac{3}{4}$,,
Hylidæ	$8\frac{1}{6}$,,
Bufonidæ	$11\frac{1}{2}$,,

(4) The actual ages in years to which species of Batrachians have attained, from the data given in this paper, are:—

Years.

52. *Megalobatrachus maximus.* Asiatic Giant Salamander.
27. *Amphiuma means.* North American Amphiuma.
25. *Siren lacertina.* North American Siren.
20. *Molge waltlii.* Spanish Pleurodele Newt.
17. *Hyla cærulea.* White's Australian Tree-Frog.
16. *Rana catesbiana.* North American Bull-Frog.
14. *Hyla arborea.* Palæarctic Tree-Frog.
13. *Bufo calamita.* European Natterjack Toad.
12 (perhaps **36**). *Bufo vulgaris.* Palæarctic Brown Toad.
.. (perhaps **20**). *Bombinator igneus.* European Fire-bellied Toad.
11. *Ceratophrys ornata.* South American Ornamented Toad.
,, *Xenopus lævis.* African Smooth-clawed Frog.
,, *Proteus anguinus.* European Proteus.

Years.
10. *Rana clamata*. North American Noisy Frog.
„ (perhaps 25). *Amblystoma tigrinum*. American Axolotl.
„ *Siphonops annulatus*. South American Cœcilian.
9. *Bufo viridis*. Palæarctic Green Toad.
„ „ *marinus*. American Giant Toad.
8. *Leptodactylus pentadactylus*. South American Frog.
„ *Molge pyrrhogastra*. Japanese Newt.
7. *Rana halecina*. North American Pickerel Frog.
„ „ *tigrina*. Asiatic Tigrine Frog.
„ *Leptodactylus mystacinus*. South American Frog.
„ *Calyptocephalus gayi*. Gay's Chilian Frog.
„ *Bufo regularis*. African Square-marked Toad.
„ „ *arenarum*. South American Toad.
„ *Hyla aurea*. Australian Golden Tree-Frog.
„ *Discoglossus pictus*. European Painted Frog.
„ *Bombinator pachypus*. European Yellow-bellied Toad.
„ *Cryptobranchus alleghaniensis*. North American Hellbender.
6. *Rana esculenta*. Palæarctic Water-Frog.
„ *Salamandra maculosa*. European Spotted Salamander.
„ *Molge cristata*. European Crested Newt.

7. List of Books and Papers.

1776. Pennant, T.—'British Zoology,' vol. iii.
1830. Murray, J.—'Researches in Natural History,' 2nd edition.
1854–5. Duméril, A.—"Notice Historique sur la Ménagerie des Reptiles." Archives du Muséum d'Histoire Naturelle, Paris, Tome vii. pp. 193–320.
1861. Duméril, A.—'Archives', Tome x. pp. 439, 458, etc.
1894. Beddard, F. E.—"Notes on the Tadpole of *Xenopus lævis*." P. Z. S. 1894, pp. 101–107.
1897. Vaillant, L.—'Guide à la Ménagerie des Reptiles.' Muséum d'Histoire Naturelle, Paris.
1897–8. Boulenger, G. A.—'Tailless Batrachians of Europe.' (Ray Society.)
1910. Boulenger, G. A.—'Les Batraciens.' (Paris: O. Doin et Fils.)
1901. Gadow, H.—'Cambridge Natural History,' vol. viii.
1907. Dickerson, M. C.—'The Frog Book.' (New York.)
1909. Flower, S. S.—Govt. of Egypt, Public Works Dept., Z. G. Special Report, no. 4, pp. 42–43.
1910. Flower, S. S.—Govt. of Egypt, Public Works Dept., Z. G. Special Report, no. 5, pp. 336–345.
1914. Boulenger, E. G.—'Reptiles and Batrachians.'
1919. Mellen, I. M.—New York Zool. Soc., Report of the Director of the Aquarium: "Complete List of Exhibits in the New York Aquarium," pp. 35–36.

13. On a Specimen of the rare Squid *Stenoteuthis caroli*, stranded on the Yorkshire coast.

By G. C. Robson, M.A., F.Z.S.

(Offered for publication by permission of the Trustees of the British Museum.)

[Received January 23, 1925: Read February 3, 1925.]

(Plate I.*; Text-figures 1–5.)

In January of the present year the Zoological Department of the British Museum acquired, through the promptness and courtesy of Messrs. F. Needler of Hull and E. Noble, H.M. Coastguard, Withernsea, a well-preserved specimen of the large and rare Decapodous Cephalopod *Stenoteuthis caroli* Furtado.

The animal was washed ashore at Withernsea in South Yorkshire, about ten miles north of Spurn Head, on the afternoon of Saturday, January 3rd. Three days later the coastguard at Tunstall (four miles north of Withernsea) reported a second large Squid ("apparently dead, similar to, but slightly smaller than," the Withernsea specimen). An attempt was made to secure the second specimen, but it was washed offshore and carried out to sea. From December 24th to January 3rd, the winds off this part of the English coast ranged from W.S.W. to S.S.W., except on the 31st of December, when they blew from the N.W. for a day. The wind reached gale force at frequent intervals. Mr. J. R. Lumby, of the Fisheries Laboratory, Lowestoft, informs me that even in south-westerly weather the tidal current has a *southerly* drift along the East coast of Scotland and England down to the Wash. One therefore would assume that this animal, if it was following the tidal stream, came from the North Atlantic.

Records of the stranding of large Atlantic Squids on British coasts are relatively uncommon. They have been discussed by Ritchie (1922); and I am informed by Dr. Ritchie that a further series of observations are to be published by him. All these records refer to forms of *Architeuthis* and *Stenoteuthis pteropus* (? and *bartrami*). The Withernsea specimen constitutes the first recorded case of the occurrence of *S. caroli* in British waters. The verified distribution is limited to the coast of Portugal (two complete and one damaged example in the Lisbon Museum (Furtado, 1887)), and the Faeroe Islands (one example in the Rijksmuseum, Stockholm (Lönnberg, 1892)), though Steenstrup (1887) gives references to early descriptions of a large Squid, which was stranded near Scheveningen in Holland in 1661 and

* For explanation of the Plate see p. 301.

is almost certainly referable to *S. caroli*.* It is a notable fact that, while the cosmopolitan *S. bartrami* is relatively well known off the western and Mediterranean coasts of Europe and has been obtained in surface waters far from land, *S. caroli* is known only from stranded examples.

The Withernsea example is described herein in some detail, as the previous descriptions, though careful, are not exhaustive and the variation and specific limits of this rare and otherwise interesting animal are practically unknown. The growth-stages of the large Decapoda, in which interesting and remarkable changes of form occur, are very imperfectly understood at present, and it is highly desirable that all the data available as to adult specimens should be published. Structures hitherto undescribed are also dealt with in this account.

S. caroli was first described by Furtado in 1887. It has been considered to be probably a variety of the widely-distributed *S. bartrami* (*cf.* Pfeffer, 1912, p. 488), though Grimpe (1922, p. 48, no. 90) allows it a qualified specific status. In view of the limited amount of material it is obviously waste of time to attempt to decide whether it is a separate species or not, and I have accordingly maintained the original status. It may be mentioned that the structure of the sexes of *S. bartrami* has been investigated by Naef (1923, p. 460), so that there is no likelihood that *S. caroli* may be a female of that form. The present specimen and the two complete Portuguese specimens are all females, while Lönnberg does not give the sex of his example, though it appears likewise to be a female. Both males and females of *S. pteropus* are known. *S. incerta* Pfr. seems to be quite distinct.

STENOTEUTHIS CAROLI Furtado.

An adult female stranded at Withernsea, S. Yorkshire, January 3rd, 1925.

Dimensions:—

Mantle;	dorsal length.....	760	mm.
	ventral ,, ...	710	,,
	width (relaxed)...	285	,,
Fins;	total width.....	635	,,
	anterior border	340	,,
	posterior ,, ...	365	,,
	base	343	,,
Arms:	1st pair, R.	407	,,
	L.	410	,,
	2nd ,, R.	475	,,
	L.	470	,,
	3rd ,, R.	532	,,
	L.	525	,,
	4th ,, R.	470	,,
	L.	460	,,

* It is uncertain whether Grimpe (Zoo. Anz. lii. 1921, p. 302) in his survey of the North Sea Cephalopoda had some further fragments of representatives of this species, or whether he refers to the Dutch specimen.

Tentacles; length, R.	1152 mm.	? ± 15.
L.	?	(damaged).
Head; width	200 „	? + 20.
Total length	about 2136 „	(7ft. 1½ in.).

This example is the largest of the four complete examples known, Furtado's largest specimen measuring 1700 mm. over all and Lönnberg's 1400 mm.

The *mantle* resembles that of Furtado's specimen in general, but is distinctly wider (37 per cent. of total mantle-length instead of 29 per cent.). The nuchal edge, as will be seen from the figure, is somewhat different in character from the type and markedly different from that seen in Lönnberg's figure.

The *fins* differ from those figured by Furtado and Lönnberg very markedly, in that (1) the maximum width lies below the median point of the line of insertion, and (2) the anterior border is convex, the posterior lightly concave. In Furtado's largest specimen the depth of the fins is 45 per cent. of the total length of the mantle, with which our specimen agrees. It should be noticed that both Furtado and Lönnberg agree in describing fins the greatest width of which is anterior to the median point of insertion. This feature occurs in *S. bartrami*, while the Withernsea example resembles *S. pteropus* in this respect. Furtado's figure shows the edges both convex as in *bartrami*, while Lönnberg's is like the Yorkshire specimen.

The free part of the fin is like that of *S. pteropus* in all three cases, being smaller than in *bartrami*.

The *funnel groove* is not so deep as in Furtado's figure, though it is of the same general shape. Lönnberg's figure shows the anterior edge triangular! The number of internal folds is seven, as in the previous descriptions, a number found in *bartrami*, while *pteropus* seems to range from seven to nine. There are three external folds on each side, of which the last is very faint. Those of Furtado's specimens ranged from three to five. *S. bartrami* has four, *pteropus* more than four. There are no accessory folds, and *caroli* and *bartrami* appear to differ from *pteropus* in lacking such folds.

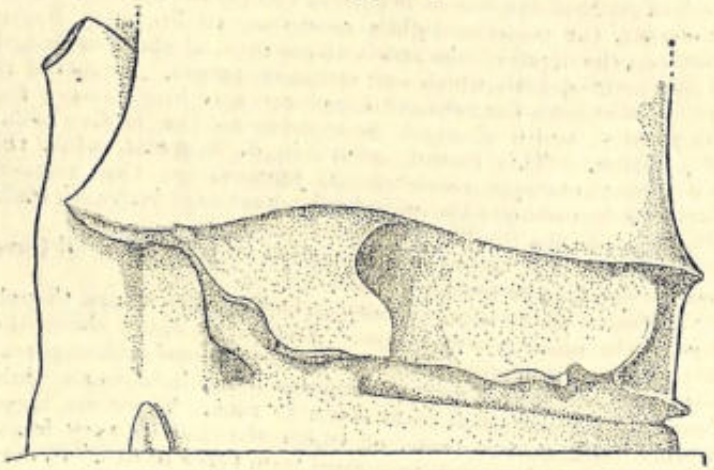
The *head*, as in previously described examples, is somewhat narrower than the mantle, though this condition is exaggerated in the photograph (Pl. I.). In *bartrami* the head is about the same width as the mantle, while in *pteropus* it is wider.

The *locking apparatus* is indistinguishable from that figured by Furtado; and *caroli* seems to resemble *bartrami* very closely in this respect, though the outer transverse ridge does not end abruptly, but curves away downwards. It is open to doubt whether there is any difference between *bartrami* and *pteropus* in this respect, except perhaps in the apical region of the mantle-plate (*cf.* Pfeffer, pl. xxxv. fig. 9, and pl. xxxviii. fig. 6).

The *funnel organ* is not very well preserved in the Withernsea specimen, nor is it figured by Furtado or Lönnberg.

The *neck-folds* are similarly not figured by these authors. Furtado's slight description is applicable to the Withernsea specimen, except that the "neck"-lappets are not triangular but rounded in the English example. The latter shows some rather important deviations from *S. bartrami* in this respect. The anterior (transverse) head ridge is alike in both cases; but the posterior ridge is much lower and weaker in *caroli*. The lappets agree in both cases in form and direction; but the relationships of the first lappet (ventral) to the ridges and funnel are singularly different (*cf.* text-fig. 1 and Pfeffer, *l. c.* pl. xxxvi. fig. 2). In the English example of *caroli* the tip of the locking apparatus lies a good deal below the first lappet. In Pfeffer's figure of *S. bartrami* (*loc. cit.*) these points coincide, while in Naef's figure (1923,

Text-figure 1.



Stenoteuthis caroli. Neck-folds.

fig. 240) the condition found in *caroli* is observed. It should be borne in mind that the proportions of various parts of these animals are subject to change with age. Until satisfactory data are obtained as to the correlation of such proportions with age, differences such as the above should not be regarded as of taxonomic value.

In *caroli* there is found below the posterior head ridge a very deep groove running half-way round the "neck." This is apparently absent in *S. bartrami*.

The *arms* have the formula 3. 2. 4. 1, while the variant 3. 4. 2. 1 is found in one of Furtado's examples. According to Pfeffer the above formula is usual in young *S. bartrami*, but 4. 3. 2. 1 or 4. 2. 3. 1 is found in old specimens. The latter formula is apparently more characteristic of mature *pteropus*. The dorsal

arms are roughly triangular in section. There is a low keel*, scarcely perceptible except in the median part of the arm. The dorsal webs* are very narrow, measuring about 5 mm.; the ventral web is wider (13 mm.), and the arm is about 18 mm. wide. The second arm has a strong, evenly developed keel. The dorsal and ventral webs measure 6 and 25 mm. respectively, the arm being 25 mm. wide. The third arm has the characteristic keel of the genus, low and weak at the base of the arm, then rising to a large triangular structure which gradually diminishes in size towards the tip of the arm. The dorsal and ventral webs measure 11 and 285 mm. at their widest. The great size of the ventral web, which is the outstanding feature of this form, is foreshadowed in *S. bartrami*, in which it is fairly prominent, but not nearly so large as in *caroli*. The web of the Yorkshire specimen resembles that figured by Furtado very closely, in that it is more or less like a lateen-sail. The outer edge in Furtado's figure is more concave. In Lönnberg's specimen the web has its apex about half-way along the arm instead of coinciding with the extremity of the latter. Pfeffer's remark that the acutely triangular form of the web may be the result of artificial distortion is not borne out by an examination of the web of the English specimen. The shape seen in Pl. I., in which the web is pinned-out, does not differ essentially from the normal (unpinned) condition.

The significance of this remarkable web is uncertain. As we have said, *S. caroli* is the female neither of *S. bartrami* nor of *S. pteropus* (*v.* Furtado, *l.c.* p. 11, for the latter case). We do not know, however, whether it may not be a sex-limited character. There is no parallel among the Decapoda for the development of the exaggerated web on one side only of a single arm pair. In a general way, one is reminded of the great extension of the web in *Histioteuthis* to form a sort of umbrella-cavity comparable to that of the Cirroteuthidæ. But in the present case the enlargement affects only a single pair of arms. The web in this case is so delicate that it is ill-suited as a locomotor apparatus. On the other hand, as Lönnberg (*l.c.* p. 31) noted, the web is traversed by the fibres of a complex musculature which give the impression that the web can be erected or stiffened, so that it seems to have some rôle in which one of these processes is involved.

The fourth arm, which is subquadrate in section, the dorsal side being longer than the ventral, has a well-developed keel along the dorsal edge. The dorsal and ventral webs average 9 and 8 mm. in width.

The carination and webbing of the arms are not described very fully by Furtado or Lönnberg. The former says the first arm-pair is bicarinate, which is certainly not the case in the Yorkshire specimen and apparently not the case in *S. bartrami*.

* It seems more desirable to retain the English words "keel" and "web" than to attempt a compromise with "schwimmsaume" and "schutzsaume" respectively.

In the relative size of the webs Furtado's description would suit our specimen, except that on the fourth pair he says the ventral web is narrower than the dorsal, while in our specimen they are approximately equal.

The main difference from *bartrami* (*i. e.* the web of the third arm) having been discussed, it remains to say that the proportions of the dorsal and ventral webs on the first and second arms of that form as described by Pfeffer do not at all agree with those of *caroli*. The curious shape in transverse section of the fourth arm in *caroli* also seems to constitute a difference between the two forms.

The *arm-suckers*. Furtado does not give the actual number found in the Portuguese specimens. Pfeffer gives 45–50 on the three upper arms of *S. bartrami*, 65 on the ventral. In our specimen we find 48 on the first, about 53 on the second, 52 on the third, and 64 on the fourth. The series is actually paired, but the pairs alternate so widely as to have the appearance of being uniserial. This feature is very marked on the third arm. The tips of all the arms are devoid of suckers for some 5–10 mm.

The largest suckers on each arm are as follows:—

1st arm:	nos. 8–14,	size 13·5 mm.	
2nd „	„ 12–14,	„ 20	„
3rd „	„ 12–13,	„ 13·5	„
4th „	„ 15–19,	„ 15	„

These data are in agreement with the previous descriptions of *caroli*, *bartrami*, and the larger specimens of *pteropus*.

The sucker-teeth of the sessile arms must be considered both with regard to the form and number of teeth on the individual suckers, the point of differentiation of the characteristic seven large distal teeth, and the point at which the proximal teeth are lost.

The second and third of these features are to be summarised as follows:—

1st arms: 1. The large group differentiated on 10–11th suckers.
2. Proximal teeth lost on 18th sucker.

2nd arms: 1. As on 1st arms.
2. Proximal teeth lost on 13th.

3rd arms: 1. As on 1st arms.
2. Proximal teeth lost on 15th.

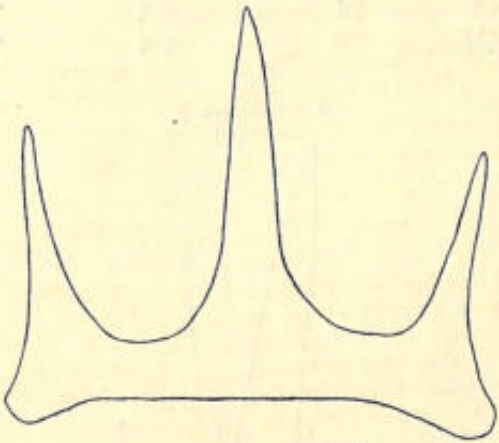
4th arms: 1. Large group differentiated on 16th.
2. Proximal teeth lost on 14th.

The total number of teeth on the first five or seven suckers is 20–23. The form of these agrees pretty closely with the previous description. I cannot wholly accept Furtado's suggestion that the intercalation of small "Nebenzähne" is regular enough to be formularized. In the Withernsea specimen the intercalation

is regular on the distal moiety of the sucker ring; but proximally it is uncertain and irregular. To judge by the present example, *caroli* differs from *bartrami* in (1) the loss of the proximal teeth at a point lower down the arm, while (2) in the former the distance between the large teeth is less than the width of the bases of the cusps, not equal to it (*cf.* Naef, 1923, pl. xii. fig. 8). Pfeffer says *S. pteropus* does not differ essentially from *S. bartrami* in the sucker-dentition; but Goodrich (1892, p. 315) figures only 13 teeth on the sessile arms.

The *tentacle* is 1·5 times the length of the mantle. It is very much distorted, but would seem to have been laterally compressed (not "depressed" (Furtado)). One of the webs is continued up

Text-figure 2.



Stenoteuthis caroli. Radula. Median tooth. × 33.

the stem for over half its distance. The *manus* agrees with that of Furtado's example and of *S. bartrami* in being about two-fifths the total length of the tentacles. The carpus consists of three knobs and sixteen suckers (if one reckons from the distal knob of the adhesive apparatus). The knobs, as usual, alternate with three smooth suckers. In Lönnberg's example there were four knobs and four suckers. There are seven suckers on the proximal side of the first knob, spread widely as in Steenstrup's (1887, p. 146) figure. In *S. bartrami* the proximal suckers are concentrated, not spread out, which is evidently a constant difference. The manus has 18–20 big rhachidian suckers with smaller dorsal and ventral rows. The distal portion (which is damaged in both cases) bears some 30 small median suckers which become disposed in one line so as to suggest that there are only three longitudinal series. The suckers of one of the outer rows are as large as those of the inner row.

The median suckers of the manus have a maximum of 22 mm. and agree in dentition with the previously described forms of *caroli*. The distal median and lateral suckers are armed in the same way as the proximal suckers of the sessile arms. In these features all the forms under review are in essential agreement. Pfeffer discovers a curious difference between *S. bartrami* and *pteropus* in the relative sizes of the largest suckers of the sessile arms and those of the tentacles expressed as a percentage of the total mantle-length.

These results are conveniently tabulated with the same measurements for *caroli* (Withernsea).

	Percentage of total mantle-length: (1) of suckers of 2nd arm.	(2) of tentacle-suckers.	Difference.
S. bartrami (8)	1·9	2·5	·6
S. pteropus (6).....	2·1	2·2	·1
S. caroli (1).....	2·6	2·8	·2

Text-figure 3.

Stenoteuthis caroli. Radula. Admedian tooth. × 33.

Expressed briefly this indicates that there is more difference between the size of the suckers of the sessile and tentacular arms in *S. bartrami* than there is in the other two species.

The *radula* of *S. caroli* is figured by Furtado (*l. c.* pl. ii. fig. 8), that of *bartrami* by Naef (*l. c.* pl. xiv. fig. 7) and Posselt (1891, pl. viii.), and that of *pteropus* by the latter (*l. c.*). It is very difficult to reconcile the figures given by Naef and

Posselt for *S. bartrami*, while the radula of the Withernsea *caroli* is very unlike that of the Portuguese examples. Whether the figures provided by the earlier authors are definitely inaccurate we cannot say, but it should be borne in mind that the radula of the Decapoda is not an easy one to figure. This is especially true of the outer lateral teeth in this case, in which the plane of curvature (if present) is at right angles to the main plane of the base. However that may be, we are obviously not in a position to decide which, if any, of the figures under discussion are inaccurate, and therefore any use of the radula as a final clue to identity is withheld. The following brief summary gives the chief points of such a comparison :—

Rhachidian teeth. The mesocone is five-sixths the length of the base; in Furtado's figure it is one-half the base. Posselt's

Text-figure 4.

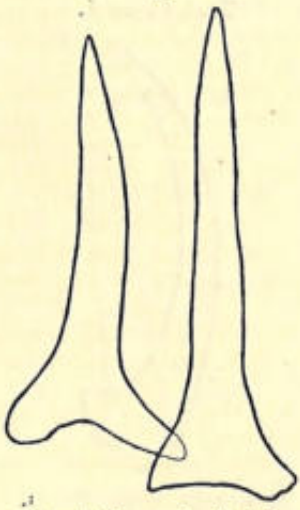
Stenoteuthis caroli. Radula.
Lateral tooth, side view. × 33.

figure of *pteropus* and Naef's of *bartrami* agree with our specimen except that in the former the base is not quite so wide and in the latter the main cusp is stouter. Posselt's *bartrami* does not agree with Naef's in this respect. The ectocones are tall and slender; those shown by Furtado are thick. Again, our specimen agrees with Posselt's *pteropus* rather than with his *bartrami*. The admedian tooth has marked internal and external "heels." The internal of these is not shown in Furtado's figure, both "heels" are found in *pteropus* (Posselt), while Posselt's and Naef's *bartrami* both show the inner "heel," but not the outer. The ectocone is very short and slender and is more like that of Naef's *bartrami*. The outer laterals are far more slender than in any of the figures given, and the bases are narrower. These teeth are nearer

Posselt's *bartrami*, but the bases differ. Posselt is the only author who illustrates differences in the base of the two laterals. Only very degenerate marginals are found in the Withernsea example; and a great part of the radula is totally devoid of them.

On the whole, the radula would be regarded as specifically distinct from all the forms previously figured. Too much importance is not to be attached to this, as we do not know if the figures are accurate; but I feel that Furtado's illustration shows differences not wholly due to differences of orientation. It should be pointed out that, if we synthesize the characters illustrated by the previous authors, we still find that the Withernsea example is unlike all the forms already described in at least three important features.

Text-figure 5.



Stenoteuthis caroli. Radula.
Lateral teeth. × 33.

Colour. The following notes were made on the animal four days after it was stranded and before it was placed in alcohol:—The dorsal surface of the mantle and head is of a deep blackish purple becoming lighter on the sides. The dorsum of the fins is lighter in tone, a purplish red predominating. The ventral surface is rather discoloured, but is obviously lighter than the dorsal surface. The under side of the fins and head is of a rich chestnut or "Indian" red. The tentacles have reddish purple stems, the manus being much darker. The first arms are more or less of a uniform medium purple. The ventral sides of the second arms are light purple to red, the dorsal sides darker; and the same is true of the third arms. Usually the keels, when present, assume a dark purple tone, while the adjacent tissues are lighter. As in neither case were observations made on the living animal, too

much importance should not be attached to the colour; but it may be remarked that Furtado's example was "violacée sur le corps et les bras," which does not suggest the deep rich purple of the Withernsea example; while the orange hue on the fins and the "rose vif" of the arms noted by Furtado were not observable in the British specimen.

Summary.

While admitting that more specimens of this interesting form are requisite for a final judgment on its taxonomic status, it would seem to be distinct from the nearest related form, *S. bartrami*, in a good many points. The web of the third arm, the various features of the neck region, the character of the carpus, and the radula present substantial differences, the first of which is, of course, far more clearly marked in all the others; while the dorsal and ventral webs of the sessile arms, the relative size of the latter, and various minor features of the arms and suckers exhibit secondary differences of some importance. Taxonomically, at least, it should be retained as a distinct species.

I have to acknowledge the courtesy with which Mr. Needler facilitated the acquisition of this specimen by the British Museum and the readiness with which he and Mr. Noble gave me all the information which they could obtain as to the stranding of the animal.

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EXPLANATION OF THE PLATE.

Plate I.

Stenoteuthis caroli. Dorsal view. ×$\frac{1}{3}$.

Stenoteuthis caroli. Ventral view. ×$\frac{1}{3}$.

The measurements given in the text are those taken before preservation, while the photographs show the animal after immersion in alcohol.

14. Notes on East African Scorpions and Solifugæ, collected 1916–1923. By Arthur Loveridge, F.E.S., C.M.Z.S.

[Received December 10, 1924: Read March 3, 1925.]

The 180 scorpions and 20 odd related arachnids mentioned in these notes were taken 1916–23, and the identifications were made by Mr. Stanley Hirst, F.Z.S., to whom my grateful thanks are due. He has also kindly seen these notes through the press and corrected proofs.

No special effort was made to secure these creatures, but native collectors brought them in from time to time, and if, when turning over stones in search of snakes the writer came across an unfamiliar scorpion, he always attempted to capture it. With the exception of sandy, more or less arid districts, such as Dodoma and around Mt. Longido, scorpions cannot be considered as numerous in Tanganyika Territory as one would expect.

From East to West and South to North the localities mentioned are :—

Portuguese East Africa.

Lumbo, site of military camp about 3 miles from Mozambique Is.

Tanganyika Territory.

Dar es Salaam District.—Outskirts of Dar es Salaam town.
Morogoro District.—Morogoro, Turiani, Ilonga, Msimba, Kimamba, Kilosa, Mbala.
Dodoma District.—Ikikuyu, Mpanira-kwa-Sagoi, Itende, Dodoma, Kongwa.
Tabora District.—Izikisia, Simbo.
Kondoa-Irangi District.—Mkalama.
Mwanza District.—Sagayo.
Usambara District.—Amani.
Arusha District.—Site of military camp on western slopes of Mt. Longido.

Kenya Colony.

Mbunyi, near Taveta and the border of Tanganyika Territory.

It will be seen that, with the exception of a dozen specimens, the bulk of the material was obtained in what was formerly German East Africa. The scorpion material has been referred

to 14 species representing 2 families. After retaining two or three examples of each species where possible for my own collection, the remainder has been divided between the British Museum of Natural History and the Museum of Comparative Zoology, Cambridge, Mass., U.S.A.

Scorpionidæ.

Pandinus cavimanus Pocock.

4 Kongwa, 21. iv. 1917.
8 Dodoma, 28. xii. 1918.
41 Ikikuyu, 12. xi. 1923.

These large, greenish-black scorpions, measuring six inches from claws to tip of tail, are exceedingly abundant in suitable localities, which for them would appear to consist of a sandy soil sufficiently stable for burrowing, more or less rock-strewn, and with scattered bushes, chiefly thorn, with here and there a euphorbia.

Such conditions were to be found at Ikikuyu, south of Igulwe on the Central Railway. Here, after clearing the site, my tent was pitched beneath an acacia thorn of considerable size. That night I was kept awake for some time by the scraping of scorpions' claws on the canvas walls, to which they were possibly attracted by the light from an acetylene lamp turned low, or possibly for the sake of prey which, in the shape of a cloud of termites, had necessitated the closing of the tent some three hours before. The native porters had already gleefully reaped a rich harvest of these into bowls of water, to be subsequently used as a seasoning for their evening meal of ground maize.

When my servant, bringing an early morning cup of tea at dawn, slipped his hand between the tent flaps to unfasten them, he touched a scorpion which was some five feet from the ground. A second was found beneath the mat beside my camp bed.

On setting forth the following morning their burrows were to be seen on every side, usually at the base of small thorn-bushes. Outside each entrance were strewn the debris of their insect prey, grasshoppers' limbs, chitinous parts of millipedes, etc. At times these formed quite a midden. Though in the early morning several were seen outside their burrows, none were observed during the heat of the day.

By offering a farthing apiece for them to a native who came asking for work, I secured more than I wanted, for he returned about an hour later with no fewer than thirty, struggling to climb upon each other to escape from the confinement of a tin. A score of these were kept alive and fed on grasshoppers and the larvæ of a giant cricket (*Brachytrypes membranaceus* Dru.) which were numerous at some spots. The scorpions were shut in a large box with a good deal of grass. They never fed while watched, but

by opening the box suddenly they were frequently surprised dismembering grasshoppers or sucking their juices. Water was sprinkled on them every night and was appreciated, as they often hurried to take up drops. About ten died during the first four months' captivity and five more when coming through the Red Sea, but the remainder were safely landed at Regent's Park nearly five months after being caught.

Both at Ikikuyu and Kongwa a great many dead scorpions were seen lying in the thorn-scrub. I asked the natives if the reason for this was known, and the reply was that everyone killed a scorpion on sight. This is not the chief cause, however, as many showed no sign of injury, and numerous others were found far from native paths or habitations. Several were recovered from the stomach of a Silver-backed Jackal at Mlowa's in Mkalama District, as recorded elsewhere.

Iomachus politus Pocock.

1 Mbunyi, K. C., v. 1916.
1 Tanganyika Territory, 1. xi. 16.
3 Kilosa, 31. i. 21.
1 Ilonga, 24. iii. 23.
2 Kimamba, 6. iv. 23.

This species inhabits grass-grown bush country and was taken beneath stones and boxes in my tent. This was the case with the two Kimamba specimens, which together with a centipede and a mygale spider shared my tent one night.

Buthidæ.

Buthus emini Pocock?

1 Sagayo, 4. xi. 22.

Buthus minax Koch.

5 ? Kilosa, 1923.

Buthus trilineatus Peters.

40 Longido West, 1. ii. 16.
1 Kongwa, 21. iv. 17.
3 Mkalama, 21. x. 21.
3 Simbo, 14. xi. 21.
1 Ikikuyu, 13. ii. 23.
1 Itende, 14. ii. 23.
1 Mbala, 26. ii. 23.

Probably this yellow scorpion is the most widely spread in the Territory. It inhabits rock-strewn, arid, thorn-bush country. Those who were at the military camp on the western slopes of Mt. Longido (then German East Africa) in February 1916, will

remember what a common occurrence it was to find one of these scorpions beneath blankets or kit-bag in the morning. I found one had excavated a little pit for itself beneath my ground-sheet (4. ii. 16), whilst an unfortunate fellow-trooper was severely stung by one which had secreted itself in his riding-breeches (11. ii. 16). In collecting boulders to build ('sangas') for the outposts it was almost the exception to find a boulder without its scorpion ensconced in a semi-burrow beneath it. It was noticeable, however, that those chiefly favoured were lying in spots exposed to the sun. Discarded sloughs were frequently found beside the burrow or chamber.

Many were found with their white, or pallid, young upon their backs, thus at Longido West on 18. ii. 16: "Eighteen on the back of a single female had rather the appearance of American Blight, for they were white excepting for a tinge of pink at the base of the chelæ and near the ocelli. This female was unusually large, another only half her size had but six young ones clinging to her; these had, however, already assumed the olive-khaki colour of the adult scorpion." At the same place another female was taken on 23. ii. 16 with 16 young, and a note records another with young found on the 25th of the same month. All these records were eclipsed by a female taken at Mbala on 26. ii. 23 with 25 young ones and many of their cast skins on her back. Two other females taken the same day held round white eggs.

At Mkomasi a scorpion which I believe was this species (the specimen was subsequently lost in transit back from the Front) was found beneath an old and battered biscuit tin with a black field cricket in its jaws; beside it was another cricket already dead and dismembered (2. vi. 16).

PARABUTHUS TRUCULENTUS Hirst.

2 Lumbo, 1. x. 18.

Though I spent six months at Lumbo in the autumn of 1918, and much clearing of land for camps was going on, I only obtained three scorpions there and came to the conclusion that they were rare.

UROPLECTES sp.

1 juv., Lumbo, ix. 18.

UROPLECTES FISCHERI var. NIGRIMANUS Pocock.

2 Mbuyi, 15. v. 16, 17. v. 16.
2 Morogoro, 22. v. 17.
3 Kilosa, 24. i. 21, 29. i. 21, 12. iv. 23.

The first individual of this bright orange scorpion, which has the tips of its legs and chelæ distinctively tipped with black, was brought me by Trooper McGregor; two days later I found a second specimen in the deserted nest of a Titmouse (*Parus* sp.) in a hollow tree-trunk.

The fourth found me, that is to say, that, having just pitched my tent on 22. v. 17, I was clearing away some stones and on lifting one about 3 P.M. was stung. The first pain was like the prick of a very sharp thorn followed immediately by acute pain in the finger (3rd of right hand) that was stung. I tied string round the base of the finger and immersed it in a strong solution of permanganate of potash for twenty minutes, then removed the ligature. At 5 P.M. toxicæmia spread to the back of my hand, which felt sore as if badly sunburned. The swelling was slight and confined to the finger, which felt like a sleeping limb; on touching anything with it a shock like that of a galvanic battery passed through it. Towards 9 P.M. it grew slightly worse, feeling at times as if it was being cut with a knife. It caused a good deal of pain, dreams, and restlessness during the night. The symptoms subsided gradually, disappearing entirely on the third day following the sting. This was the only time I received a scorpion sting during eight years in East Africa, so the creatures cannot be considered much of a menace there.

The female taken at Kilósa on 24. i. 21 was carrying three young on her back.

While in occupation of this tent on the same site, I awoke one morning to find a scorpion on the pillow within a few inches of my face, it having climbed on to my camp bed and somehow circumvented the mosquito curtain.

UROPLECTES FISCHERI VAR. NIGROCARINATUS Kraepelin.

4 Kilosa, 5. i. 21, 31. i. 21.
1 Sagayo, 4. xi. 22.
1 Mpanira-kwa-Sagoi, 12. ii. 23.
2 Itende, 14. ii. 23.

LYCHAS ASPER Pocock.

1 Morogoro, 1. ii. 18.

LYCHAS BURDOI E. Sim.

1 Longido West, 1. ii. 16.
10 Morogoro, 1. xi. 16, 4. i. 17, 22. v. 7, 1. x. 17, 1. xi. 17, 1. ii. 18.
11 Kilosa, 14. v. 21.

Both this species and *U. fischeri* were not uncommon in my house at Kilosa, though probably not more than one per month would be killed on the average. They were generally discovered in cracks of the window sills or furniture, or when moving furniture or boxes.

BABYCURUS GIGAS Kraepelin.

1 Amani, 14. iv. 14.

Found preserved, with data, but not actually collected by me.

Babycurus jacksoni Pocock.

5 Turiani, viii. 1918 and 1922.
9 Morogoro, 1. xi. 17, 1. ii. 18.
1 Msimba, 27. iii. 23.

Odonturus dentatus Karsch.

1 Morogoro, 1. xi. 17.

Isometrus maculatus De Geer.

1 Tanganyika Territory, 1. xi. 16.
4 Dar es Salaam, 4. xii. 22.

The Dar es Salaam specimens were taken in a pile of rotting fronds of the coconut palm, together with a very perfect sloughed skin. Such heaps of palm fronds are common enough on the outskirts of Dar es Salaam, and the scorpion is probably plentiful.

Tarantulidæ.

Phrynichus bacilliger Gerst.

2 Mbunyi, 15. v. 16.
2 Morogoro, 1. x. 17, 1. ii. 18.
2 Kilosa, 6. i. 23, 12. iii. 23.
3 Mbala, 24 & 26. ii. 23.
1 Ilonga, 24. iii. 23.
1 Kimamba, 6. iv. 23.

Whip scorpions, though widely distributed, are nowhere very common in the Territory. Mbunyi specimens were taken under tree-bark; Morogoro ones in holes in a bank; Kilosa specimens under boxes in house; a very perfect slough was taken beside the scorpion taken 12. iii. 23; Mbala specimens beneath stones on a hillside (a very fine pair were together under one stone). Another example was taken deep down in the passages of a termite-hill that was being demolished. Practically every whip scorpion seen was kept.

Solpugidæ.

Solpuga darlingi Pocock.

3 Longido West, 31. i. 16, 9. ii. 16.
2 Mbunyi, 15. v. 16.
3 Lumbo, 1. x. 18.

The first specimen was taken at Longido West in a snug little excavation it had made beneath my ground-sheet. When I picked it up with my forceps it champed its formidable jaw upon them in quite an alarming fashion. A second was found in the same location a week later, and its chamber was found to measure 2 inches. A comrade produced another the same morning. The

Sergt.-Major was bitten on the finger by an unknown insect a night or two before, and it was generally supposed to be a "tarantula." The finger was very swollen, but I could make nothing of his meagre description of the creature which bit him.

One of the Mbunyi specimens was found running swiftly along in a cart-wheel rut, carrying a large grasshopper minus a hind-leg. When I picked up the solpugid it dropped its prey, but on my putting the latter into the cyanide bottle with its captor, the latter seized it fiercely by the neck and continued to suck its juices until itself overcome by the cyanide fumes, when it slowly released its hold and fell over dead.

SOLPUGA ? NYASÆ Karsch.

1 Izikisia, 14.xi.21.
1 Kilosa, 12.iv.22.
1 Mbala, 26.ii.23.

At Izikisia near Tabora my tent was pitched beneath two large and heavily foliaged trees. When my acetylene lamp was lit and placed on a table in the entrance of the tent, I noticed half-a-dozen solpugids among the roots of one of these trees in the direct beam of light. I pointed them out to some local natives, who pounced upon them with their bare hands, first covering them with one hand and then picking them up. I expressed surprise, as I always considered the creatures vicious, if not poisonous, but the natives stated they were harmless.

The Kilosa specimen I erroneously referred to elsewhere * as *Solpuga darlingi*, when I gave an account of its fight with a gecko (*Hemidactylus mabouia*) which had attacked it.

A solpugid's remains, doubtfully referable to this species, were found in the stomach of a lizard (*Latastia longicaudata*) at Dodoma on 8.xii.1918.

GALEODES ARABS C. L. Koch.

1 Port Said, Egypt, 15.vi.23.

This single specimen was taken beneath a stone on waste land just outside the town; collected on the voyage home.

* Loveridge, Proc. Zool. Soc. 1923, p. 938.

15. Variation in the Colours of Palæarctic Birds in relation to the conditions under which they live. By E. Banks, B.A.*

[Received January 2, 1925: Read March 3, 1925.]

Part I. Pigmentation and Environmental Conditions.

Many years ago, J. A. Allen in America examined a large number of skins of breeding birds, particularly from the Eastern United States, but also from elsewhere; he found that among those birds with a fairly large latitudinal breeding range, the Southern representatives were (amongst other things) darker in colour than the Northern, but no confirmation of this interesting conclusion has yet been attempted with the more complete collections existing at present.

Now that the breeding-plumages of subspecies have been worked out in Europe, this conclusion of J. A. Allen is not supported in its original simple form by a study of European birds, a not very surprising fact when a continuous land-mass like the U.S.A. is compared with the irregular shape and contour of the W. Palæarctic region. It looks as if regular variation were found in a continuous land-mass, and irregular variation in a land-mass with irregular outlines and physical conditions. This paper is concerned with the correlation of locality and physical conditions with colour. It will be seen that undoubtedly some positive correlation exists.

An effort has therefore been made to compare the variations of the pigment in the feathers of eighteen groups of Passerine subspecies with the average meteorological conditions prevailing during the summer months at their respective breeding-places in the W. Palæarctic region. The standards taken in comparing the skins are only very approximate and only average meteorological conditions have been used, so that any correlation found is only of a very general nature; but as each group of subspecies varies from having much to little pigment, it is possible to say that one country has a larger percentage of dark subspecies than another country. Since this is only a very general truth the causes will probably also be of a very general nature.

Materials.

Colour variation was studied in some 160 subspecies of W. Palæarctic Passeriform species, (1) by examining thirty-

* Communicated by Prof. E. S. Goodrich, F.R.S., F.Z.S.

four skins in the British Museum of Natural History; these specimens were taken during the breeding-season (May, June, and July), and presumably, therefore, from their breeding-areas, so as to avoid the possibility of neighbouring subspecies being collected in the wrong locality. As has been noted by others, the number of breeding females taken was very small and practically only males were examined, the number of specimens from each district varying from about three to nine. (2) Subspecies not adequately represented in the Museum for the purpose were looked up in E. Hartert's book 'Die Vögel der Paläarktischen Fauna,' and as much as possible made out from the descriptions, whilst five of the eighteen species were taken wholly from this book.

Average meteorologieal conditions for a period of five consecutive years were then calculated for various districts in the Palæarctic region E. of the Ural Mountains, 'Le Réseau Mondial,' published by the Meteorological Office of the Air Ministry, being the chief source.

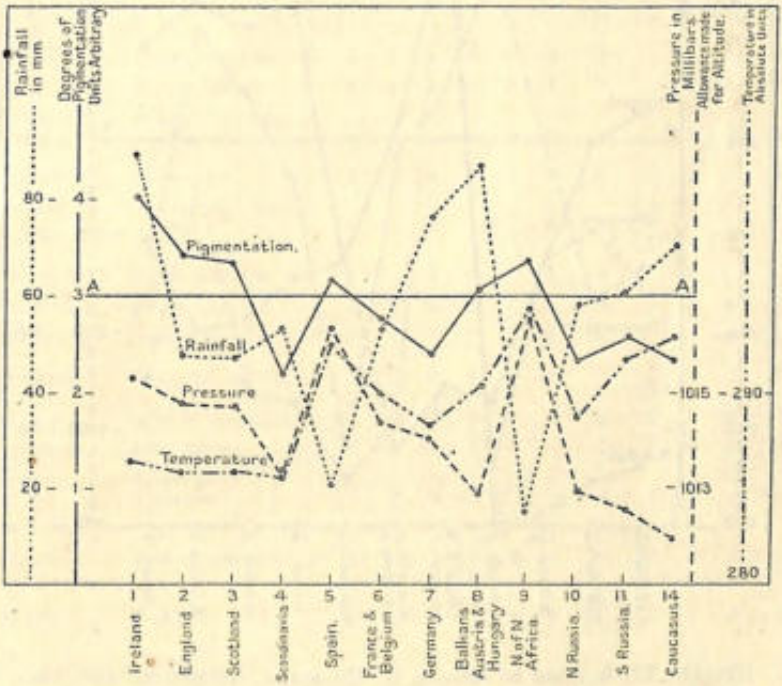
Method.

Whether from skin or description, it was necessary to examine the depth and distribution of pigment in each subspecies and to note which other forms were its nearest allies, and it was then possible to say that, judged by these standards, one subspecies had more pigment (*i. e.*, was darker) than another. Sometimes a form would vary uniformly all over its body (*e. g.*, the St. Kilda Wren), but more often pigment was just concentrated in, say, the head or wing-bar, the two subspecies being otherwise alike, in which case the race with the more pigment could still be distinguished. Thus since by careful, but not too minute examination, it was possible to say on occasions that one subspecies was darker (*i. e.*, had more pigment) than another, it was possible to arrange the subspecies in each group in descending order of pigmentation; and, for purposes of comparison, to divide each group into five shades of colour, calling the darkest 5, next darkest 4, and so on, merging very closely related subspecies together and counting them as one when necessary. These marks (5, 4, 3, and so on) only refer to each group within itself, for one cannot compare the pigment of the darkest Blue and Marsh Tits, for example, since no connection can be traced between the two patterns. Taking twelve areas into which the W. Palæarctic region may be conveniently divided, to each may be given the number of marks according to the position of its representative subspecies in the scale of pigmentation for the species, and so on for all the eighteen groups. (See Tables I. and II.) Allowing for two subspecies of different pigmentary values occurring in the same area and for areas having similar

subspecies and pigmentary values, the monopoly, say, of a large percentage of the five marks by any one area will indicate that most birds are rather dark in that region; the relations between the area can then best be shown by dividing the sum of the pigment values of an area by its number of such values (and therefore of subspecies) and plotting the numbers thus obtained for each country on a graph.

Turning to meteorological conditions, each country had about three stations at varying altitudes, and records of pressure (corrected for altitude), temperature, and rainfall could be used

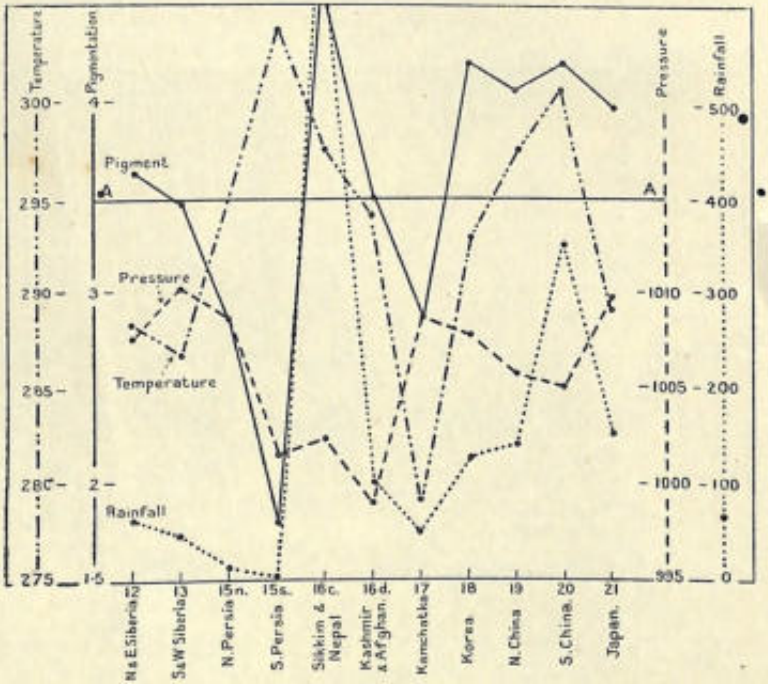
Graph 1.



for 1910–14 inclusive. Five years might seem rather a short period, but the average of annual readings for a similar period for England shows very little difference from the average of sixty-five annual readings, in spite of well-known periodicities. Average meteorological conditions were only taken during May, June, and July, the period when pigment is presumably laid down in the developing feathers which will appear at the next moult, so that as many as have only a complete autumnal moult

will have their breeding-feathers for the subsequent year laid down at the end of the previous summer. In the breeding-period the birds are sedentary, so that the climatic conditions will have more effect on them than during their winter movements; besides, climatic conditions may only affect pigment above a certain minimum not attained in winter. Knowledge of movements of subspecies in winter is not very great, but some,

Graph 2.



like the Irish, seem to remain in the same district all the time (for, with the exception of the Red Grouse in the Hebrides, one never hears of them elsewhere), though doubtless their new feathers are only susceptible to climatic conditions just before the old drop out. Having plotted average depth of pigment for each country, it is now possible to plot beside this the average temperature, pressure, and rainfall readings for each country during May, June, and July for a representative period of five years. (See graph.)

Tables showing comparative Depths of Pigmentation of various Birds in different Areas.

N.B.—Roman numerals indicate the different areas as follows:—

I. = Ireland.
II. = Scotland.
III. = England.
IV. = Scandinavia.
V. = Spain.
VI. = France and Belgium.
VII. = N. Germany.
VIII. = Balkans and Austria.
IX. = N. of N. Africa.
X. = N. Russia.
XI. = S. Russia.
XIV. = Caucasus.

TABLE I.—Birds with a comparatively large range of variation. Graph made up from these.

Area		I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XIV.
Blue Tit	*Parus cæruleus*	5	4	4	3	5	3	3	3	...	1	2	1
Marsh-Tit	*Parus palustris*	5	4	4	3	...	3	1	2	...	1	1	1
Willow-Tit	*Parus atricapillus*	...	4	4	2	3	3	2	4	...	1	{5 2}	4
Coal-Tit	*Parus ater*	5	4	3	2	...	2	1	4	4	2	2	1
Longtail Tit	*Ægithalos caudatus*	5	5	4	1	1	{2 4}	{2 3}	3	{4 1 5}			
Crested Tit	*Parus cristatus*	...	5	...	1	4	...	1	3	...	2		
Great Tit	*Parus major*	4	4	3	2	2	2	1	2	5	2	2	2
Tree-Creeper	*Certhia familiaris*	5	3	4	1	3	2	2	2	...	2	2	2
Chaffinch	*Fringilla cœlebs*	4	1	3	3	5	3	3	3	{1 2}	3	3	3
Skylark	*Alauda arvensis*	4	5	4	3	3	3	3	2	2	3	2	1
Nuthatch	*Sitta europæa*	...	2	2	2	1	3	3	4	5	2	2	4
Wren	*Troglodytes troglodytes*	2	{4 1}	3	3	2	{3 2}	3	3	2	{3 5}	3	2
Dipper	*Cinclus cinclus*	5	4	4	2	{5 4 3}	3	3	4	1	2	3	5
Magpie	*Pica pica*	2	2	2	2	{4 3}	2	2	{3 5}	5	1	2	2
Jay	*Garrulus glandarius*	4	3	3	1	2	2	1	2	{1 2}	{1 4}	1	2
Starling	*Sturnus vulgaris*	2	{2 3}	2	1	1	1	1	{1 2}	1	...	5	{4 2}
Sparrow	*Passer domesticus*	5	5	5	4	{2 4 5}	{5 4 3}	4	4	{4 3}	5	{3 1}	2 3
Great Grey Shrike	*Lanius excubitor*	...	...	...	3	{3 4}	3	3	2	{4 5}	3	{2 5}	1

TABLE II.—Birds with a comparatively small range of variation. These are not actually included in the graph, but serve to corroborate its outstanding features.

Area		I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XIV.
Goldcrest	*Regulus regulus*	2	2	2	1	1	1	1	1	...	...	...	1
Chiff-chaff	*Phylloscopus collybita*	2	2	2	1	2	2	2	1				
Blackbird	*Turdus merula*	2	2	2	2	2	1	1	1	...	...	...	1
Wheatear	*Œnanthe œnanthe*	2	2	1	2	{2 3}	2	2	2	{1 2}	2	2	{1 2}
Robin	*Erithacus rubecula*	3	3	3	1	1	1	1	1	3	1	1	{1 2}
Hedge-Sparrow	*Prunella modularis*	2	2	2	1	1	1	1	1	1	1	1	
Bullfinch	*Pyrrhula pyrrhula*		3	3	2	3	3	3	3	...	4	1	
Black Redstart	*Phœnicurus ochrurus*	...	...	...	...	...	3	3	3	...	3	1	{1 2}
Ring-Ouzel	*Turdus torquatus*	3	3	3	3	1	...	...	1	...	...	...	2
Greenfinch	*Chloris chloris*	...	1	1	1	2	2	1	1	2			
Goldfinch	*Carduelis carduelis*	...	4	4	3	5	3	3	3	5	2	2	1
Linnet	*Carduelis cannabina*	...	2	2	2	3	2	2	3	...	2	...	1
Yellowhammer	*Emberiza citrinella*	...	2	2	2	2	2	2	...	...	2	1	1
Missel-Thrush	*Turdus viscivorus*	...	3	3	3	3	3	3	2				
Song-Thrush	*Turdus philomelus*		2	2	1	1	1	1					
Reed-Bunting	*Emberiza schoeniclus*	...	2	2	2	2	2	2	1		3		

Further evidence not included in but supporting the graph is taken from sixteen birds in Table II., which have too few subspecies to be included in the graph. Whilst it is evident from the graph that Ireland, Spain, and N. Africa are dark, Scandinavia, N. Russia, and the Caucasus are light countries; this is further borne out by taking the subspecies (of these sixteen birds) in each country and comparing them with those in each of the three countries of opposite degree of pigmentation. Thus the results of Table II. may be summarized as follows:—

Ireland is darker than the three light regions in 21 cases, lighter in 2, and similar in 12;

Spain is darker than the three light regions in 16 cases, lighter in 4, and similar in 17;

N. of N. Africa is darker than the three light regions in 10 cases, lighter in 3, and similar in 8;

Scandinavia is lighter than the three dark regions in 11 cases, darker in 3, and similar in 23;

Caucasus is lighter than the three dark regions in 23 cases, darker in 3, and similar in 8;

N. Russia is lighter than the three dark regions in 8 cases, darker in 4, and similar in 9.

In a general way, therefore, the main outstanding features of the graph receive further support from other birds. In addition, it should be noted that the W. coast of Norway and the W. coast of Portugal are both said to have a heavy rainfall and a high degree of pigmentation, but they are excluded from consideration, as details and exact data are not available.

Results.

From the graph, what stands out in a general way is the tendency for pigment to vary directly, if not quite proportionally, as temperature and pressure, though there is apparently no direct connection between rainfall and pigmentation, for whilst in many cases there is an inverse relation between the two, Ireland and the Balkans stand out as countries with a rather low summer temperature but high rainfall and high pigmentation, a fact which cannot be ignored by saying that there is only one station in Ireland, for all the readings are from this same station, and either temperature or rainfall, but not both, must be considered exceptional if there is to be any correlation at all.

Starting with temperature and pressure, in the British Isles the meteorological readings evidently bear some relation to the colour variations, but are not proportional to them as in the rest of the graph. The explanation probably lies in the comparatively small number of stations, one each in England, Scotland, and Ireland, but the readings are retained as being subject to the same experimental conditions as those from other countries. Passing on to Scandinavia, Spain, France, and Germany, colour, temperature, and pressure vary together in a way which is convincing, if not quite proportional, considering that all the readings are only averages. Pressure, but not temperature, then becomes opposed to pigmentation in the Balkans, possibly through the aberration of some other factor controlling pigment (see rainfall); going on from the Atlas Mountains and N. Russia to S. Russia and the Caucasus, a certain amount of discrepancy occurs, pressure in S. Russia and temperature in the Caucasus failing to follow the general rule, the only source of error being that it is not known to what extent such a specialized region as the Caucasus mountains effects the immediately surrounding plain from which a number of readings have been taken.

Coming to rainfall, readings from the British Isles, as already mentioned, are not very conclusive, and a high rainfall and much pigment appear to go together in Ireland; Scandinavia and Spain then show high and low rainfalls correlated negatively with degrees of pigmentation. France shows a higher rainfall with comparatively less colour and Germany a still higher rainfall with still less pigment. Balkans and S. Russia are very suggestive, for here high rainfall goes with much pigment, and in both cases with comparatively low summer pressure, illustrating the difficulty of isolating the effect of any one of the factors responsible for pigment and showing how closely together

these factors work. N. Africa and N. Russia further bear out how high rainfall need not go with increased pigmentation.

The data being only a series of averages, minutely accurate and proportional results cannot be expected, but, in a general way, the colour of the feathers assumed in the autumn in different subspecies varies directly as the temperature and pressure, rather irregularly as the rainfall conditions of the preceding summer months, May, June, and July. How closely these factors are interconnected can be seen in the Balkans and S. Russia, where relatively high pigmentation goes with high rainfall and low pressure, indicating the possibility that pressure only exerts its usual influence within the limits of a certain minimum of rainfall (or, of course, *vice versa*). An extreme case (included in the data for the graph) may serve to show how approximate the results are, for examination shows that in N. Africa, Spain, and Ireland, all with relatively deeply coloured subspecies, the Wren is relatively very lightly coloured. This condition is carried on into some of the Scottish Islands and suggests the possibility either that they are a feature of a comparatively recent geographical migration and have not yet attuned themselves (a conclusion which, however appealing, has little outside evidence to support it); or, on the other hand, that they have a different susceptibility to climatic conditions, for, in addition to these light variations, they appear to be darker than the other birds of Scandinavia, Germany, N. and S. Russia, judged by the mean depth of pigmentation of a number of birds from those regions.

From this paper there appears to be a definite correlation between geographical regions and general intensity of pigmentation; and it is probable that this correlation depends on a combination of meteorological factors of which summer temperature and pressure are the most marked, rainfall being more complex.

Part 2. Pigmentation and Temperature of Breeding-areas.

The connection between the depth of pigmentation of European birds and the summer temperature of their breeding-areas was so suggestive that it was thought worth while to test this conclusion by a study of Asiatic birds on similar lines.

The material was examined at the same time as that for European birds, but the skins of only eleven species were looked at, and the descriptions of nine others were made out from E. Hartert's book, 'Die Vögel der Paläarktischen Fauna.' Meteorological conditions for an area east of the Ural Mountains, including Persia, the Himalayas, and S. China, were taken from the same source as before, viz., 'Le Réseau Mondial.'

The method followed was similar to that used for European birds; the Eastern Region was divided into eleven areas, but owing to the extreme variants of many species being wide apart, it was found convenient to divide each species into six grades of

Table showing comparative Depths of Pigmentation of various birds in different areas of Asia.

N.B.—The Roman numerals indicate the different areas as follows :—

XII. = N. & E. Siberia. XVIc. = Sikkim & Nepal. XIX. = N. China.
XIII. = S. & W. Siberia. XVId. = Kashmir & Afghan. XX. = S. China.
XVn. = N. Persia. XVII. = Kamchatka. XXI. = Japan.
XVs. = S. Persia. XVIII. = Korea.

Area		XII.	XIII.	XVn.	XVs.	XVIc.	XVId.	XVII.	XVIII.	XIX.	XX.	XXI.
Blue Tit	*Parus cæruleus*	3	3	1,2	1							
Marsh-Tit	*Parus palustris*	4,3	2	1	1	...	...	...	3	3,1	3	2
Coal-Tit	*Parus ater*	3	4	3	...	2	5	...	...	2,1	...	6
Willow-Tit	*Parus atricapillus*	2	3	...	...	...	...	1	...	...	...	2,3
Longtail Tit	*Ægithalos caudatus*	1	1	3	2	...	...	...	...	6,4	6	1,5
Nuthatch	*Sitta europæa*	3	3,4	2	...	...	...	1	5,6	6	4	6
										5	5	5
Wren	*Troglodytes troglodytes*	4	4	3,1	2	6	4	1	5	4,3	4	4
											3	3
Tree-Creeper	*Certhia familiaris*	4	4	...	...	1,5	2,4	4	4	3,4	3	2
Dipper	*Cinclus cinclus*	3	2	4	1	6,4	6,5	3	3	4	...	3
Skylark	*Alauda arvensis*	3	2	2	2	1	2,1	3	4	...	...	5,2
Great Tit	*Parus major*	5	5	4,2	...	...	3,1	...	3	3	5	6
Magpie	*Pica pica*	1	1	1,3	...	4	1	1	2	4	2	2
Jay	*Garrulus glandarius*	3	3	4	1	3	3	...	3	3	...	3,2
Starling	*Sturnus vulgaris*	1	1	1,2	1	4	2,3					
White Wagtail	*Motacilla alba*	1,3,5	2	5	3	...	2,5,6	4	...	5		
Black Redstart	*Phœnicurus ochrurus*	...	1	1,2	...	3	1	...	...	3		
Great Grey Shrike	*Lanius excubitor*	4	3,4,4	1	...	...	3	4	2			
House-Sparrow	*Passer domesticus*	2	2	1	...	3	1					
Reed-Bunting	*Emberiza schæniclus*	1,3	1	...	...	...	...	1				
Goldfinch	*Carduelis carduelis*	1	1,2	1,2,3	...	...	...	1,2,4	...	...	...	2

N.B.—Some species, *e.g.*, Tits, except Great and Longtail, do not range over the whole of this East Region, and can only be divided into three, four, or five grades of colour; these grades must then be brought up to the common standard of six to make the final addition and division correct, in determining the average for each area.

colour, rather than five, as in European birds. The meteorological data were fairly plentiful, most areas having about three stations, the Siberian areas fifteen or sixteen. Certain parts, however, *e.g.*, Mongolia, Tibet, had to be omitted because there were no observation posts.

The pigmentary data have been tabulated as before, and represented graphically together with the meteorological readings. The two graphs are, of course, only comparable as a whole, and not in detail, for the pigmentary values of the areas of the two different regions have been judged according to a different standard for each region, and not a common standard for both regions.

The most noticeable points about the graph as compared with that for European birds are as follow :—

Firstly, the extreme and general variation of pigmentation (allowing for the difference in the two scales) is not appreciably greater in Asiatic than in European birds, the former ranging between a little darker and a little lighter than the range of variation of the latter, perhaps one quarter of a grade each way when the different scales are allowed for. The actual differences in depth of colour in the two regions cannot, of course, be compared, only the extreme ranges of variation. Nevertheless, it is probable that the variation in Asia is somewhat greater than in Europe, for the grades of colour are probably farther apart for the former region than the latter.

Secondly, the range of variation of meteorological conditions in Asia is much greater than in Europe; *e.g.*, temperature ranges over more than 20° Absolute, as opposed to rather less than 15° in European conditions; and further, a good deal of this variation exceeds the highest temperature reached in Europe, so that, on the whole, the warm parts of Asia are considerably warmer than those in Europe; atmospheric pressure ranges over some ten millibars as opposed to only about four in Europe, and in no case do the highest readings approach even the lowest of the European ones, so that, speaking generally, one would expect Asia to be on a higher average level. Most striking, however, is the range of rainfall variation in Asia, so great that it is not surprising that variations of 20 mm. or so in a rainfall not exceeding 80 mm., *e.g.*, in Europe, occurred irregularly as the pigmentation, for such variations seem almost negligible beside the rainfall of most parts of Asia, where, for instance, excepting Siberia and Persia, the rainfall only once falls below 100 mm. and varies up to 300 and even 700 mm.

In spite of this increased variation in meteorological conditions, the main conclusion, that there is a connection between pigmentation and temperature, is still supported to some extent, if allowance be made for the desert conditions of Persia and the mountainous parts of Sikkim and Nepal.

Starting with temperature, the different pigmentary values of the two Siberian areas are accompanied by corresponding changes. The desert conditions of Persia appear to upset the balance of

those other factors, in the presence of which, under more normal conditions, temperature has a controlling influence on pigment; north of the Koh-Rud Mountains the birds are lighter with increasing temperature but an almost negligible rainfall, whilst south of the mountains the temperature becomes excessive with no moisture, and the birds reach their palest (the influence of other factors, in whatever direction, can be seen if South Persia is compared, for example, with South China, where the birds are well pigmented in an area which is nearly as warm, but in addition has a good rainfall). Just as in Persia the extreme lack of moisture (among other things) upsets the influence of the highest of temperatures to bring about the palest of the birds, so in Sikkim and Nepal the extreme abundance of moisture upsets the influence of by no means the highest of temperature bringing about the darkest of the birds; though, no doubt, altitude and the question of zones should be taken into consideration in this area. In Kashmir and Afghanistan (where no doubt zones of life occur as in the Himalayas, though perhaps to a less extent) and in Kamchatka there is a falling off in the depth of colour, just as there is in temperature; the rise in pigmentary scale in Korea is somewhat too great in proportion to the rise in temperature, and constitutes, perhaps, an exception to the rule; in North and South China and Japan, however, the changes in colour and temperature roughly correspond.

The readings for atmospheric pressure appear to bear no relation to those for pigmentation in this case, and the range of variation is so much greater in Asia than in Europe that it raises some doubt as to whether the difference of a few (four or less) millibars is enough to have any controlling influence in the latter region when somewhat larger differences in the former region appear to have no connection with pigmentation.

When the low rainfalls of Siberia and Persia and the high rainfall of Sikkim and Nepal are left out, the standard rainfall in Asia (more than 100 mm. and with quite considerable variations) is somewhat higher than that of Europe, and as the connection with pigmentation is only just apparent in the former region, it is not surprising that the small rainfall (never more than 80 mm. with variations of 20 mm. or so) in the latter region goes irregularly with pigmentation. It looks, in fact, as if there must be a certain minimum of rainfall present before additional variations influence pigmentation; there does, however, appear to be some connection between rainfall and pigment, from the two extremes in South Persia and Himalayas through the other countries to Japan, with a slight divergence in Korea again.

The original idea of J. A. Allen, that North American birds are found to be darker and darker as their breeding-ranges go farther south, hardly applies to the Palæarctic region, for the continents are here a good deal more broken up as discontinuous land-masses than North America, and this irregularity brings

about variation which is not uniformly in one direction, as in North America. The very fact of the more irregular conditions of the Palæarctic region accompanying the irregular trend of variation suggests that the physical conditions have some controlling influence. J. A. Allen, of course, realized that the tendency to be warmer in the more southern regions had something to do with this variation, and in the above paper, speaking very generally, it appears that there is some direct connection between depth of colour and summer temperature, which supports his conclusions in so far as the southern regions are warmer. It should, however, be realized that this connection breaks under abnormal conditions, such as the deserts of Persia, the mountains of Himalaya, and possibly the west coast of Portugal and Norway facing the Atlantic.

Experimental evidence of the direct effect of temperature on pigmentation in birds is lacking, but there is some evidence of the influence of moisture. From the graphs, however, the influence of rainfall in the Palæarctic region is not very clear, but it certainly does not reach anything like the importance of temperature.

16. On the Display of the Argus Pheasant (*Argusianus argus*). By D. Seth-Smith, F.Z.S.

[Received March 2, 1925; Read March 3rd, 1925.]

(Plate I.)

The nuptial display of male birds to their mates is one of the most extraordinary phenomena in Nature. It is indulged in to a greater or lesser extent by almost all species, but in certain groups Nature seems to have gone out of her way to decorate the males for the purpose of providing them with the means to present a startling spectacle to their mates. Decorative plumes are developed on various parts of the body such as the neck, chest, flanks, tail, or wings, and the method of display varies enormously, but in every case it is designed so as to bring the most showy plumes into special prominence.

This over-development of the plumage is not infrequently of distinct disadvantage to the bird other than in providing the means of producing a striking nuptial display. It is a great hindrance to flight in many cases, rendering the bird very liable to capture by predaceous animals. The Greater Bird-of-Paradise with its huge flank plumes, the Giant Whydah-bird with its enormous tail and wings, and the Argus Pheasant with its huge secondary wing-feathers are all very poor fliers, especially against the wind, and far less able to avoid capture than are their respective females with plumage designed purely for utility. Thus we see that the over-development of the plume is solely for the one purpose of the nuptial display, which evidently has some profound effect upon the female, although such effect is not very obvious to human observers.

In the Pheasants, special development of the plumes for the purpose of nuptial display is most noticeable in the Peacock and the Argus Pheasant, the former with enormously produced upper tail-coverts, and the latter with greatly enlarged and decorated secondary wing-feathers. In the Argus both primaries and secondaries are of extreme beauty, with delicate pattern and colouring. The secondaries, which are twice the length of the primaries and of considerable breadth, are decorated throughout their length with a series of large spots or ocelli, shaded as with the skilled brush of an artist so as to represent balls within their sockets, the remainder of these feathers being very delicately spotted and striped. The primary feathers which also come into prominence during the display are equally beautiful, the shaft being blue and the webs spotted with dark brown shaded with rufous on a cream-coloured ground, while on the inner web is inlaid a band of rufous minutely spotted with white.

When in its normal attitude, the Argus Pheasant does not present any very striking features excepting its long tail, the specialized portions of its plumage being hidden. The general effect is that of a large brown bird, which the majority of visitors to a zoological garden will pass by with a casual glance, their attention being at once arrested by a neighbouring Golden or Amherst Pheasant, but a close inspection reveals the fact that the brown effect is produced by a series of minute stripes and spots. The bird is extremely well camouflaged, its striking features being only seen to perfection during the nuptial display.

Living as this bird does in the dense forests of the Malay Peninsula, it has rarely been seen in its wild state, and Mr. William Beebe is probably the only white man who has seen its display under natural conditions; but its habit of clearing a space in the jungle as a "display ground," which it frequents during the whole of the breeding-season, has been described on more than one occasion.

The display has, however, been observed on several occasions in captivity. In the 'seventies the Argus Pheasant was kept successfully in these Gardens, and several young were hatched. The display was observed by the late A. D. Bartlett and T. W. Wood, the latter being not only a good observer but a very skilful artist. He was able to make a drawing of this, which, although an extremely difficult subject, is on the whole fairly accurate, although the position of the head in relation to the wings is not quite correct. So far as I know, this phenomenon has not been photographed until now.

Apparently the Argus Pheasant does not breed until its fourth or fifth year. The two pairs which the Society possesses came as immature birds in 1922, and have only now come into full maturity, and on two occasions during February 1925 I was able to carefully observe the display of one of the cock-birds to its mate. Once before, in 1912, I had seen the display, which did not differ on that occasion from that recently observed.

When about to display, the cock-bird assumes a snake-like attitude with extended neck, and commences to walk round the hen in a wide circle; then, bending his neck and continuing his circular walk, he commences to stamp loudly with his feet, and thus continues to circle round his mate. Then, suddenly rushing past her, he lowers his wing on the side nearest to her, and performs a lateral form of display; then, suddenly facing her, he erects his wings into a huge screen, holding them well forward, with his head concealed behind the right wing. The long upper tail-coverts are erected vertically and the tail itself swayed forwards and backwards, while a rustling sound is made by the feathers and apparently a hissing with the mouth. The head is hidden behind the wing, in every instance I have observed this being the right wing.

Bartlett asserted that the bird was in the habit of pushing its head between the secondary feathers of the wing in order to see

the hen. I have not seen this happen; Wood did not observe it, and thought that the bird looked between the wings.

A study of the photograph, which shows the right-side view of the bird, will reveal the fact that in the position in which the wings and head are held it would be impossible for the head to reach far enough to be thrust between the secondary feathers.

The display is continued for some twenty minutes, the bird now and then lowering his wings and rushing round in a circle; facing round again and repeating the display. I was able to watch, often from a distance of no more than a yard, and on several occasions, when directly in front of the bird, the hen-bird only being between us, could see the cock's left eye peering through the opening *between the wings*.

During this display the hen-bird certainly did appear to take an inquisitive interest in the proceedings. She would walk directly up to the centre of the gaily-decorated screen and peer into its depths, as if wondering what it all meant.

EXHIBITIONS AND NOTICES.

February 3rd, 1925.

Sir ARTHUR SMITH WOODWARD, F.R.S., F.Z.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the months of November and December, 1924:—

NOVEMBER.

The registered additions to the Society's Menagerie during the month of November were 115 in number. Of these 83 were acquired by presentation, 6 were deposited, 20 were purchased, and 6 were born in the Menagerie.

The following may be specially mentioned:—

1 Rufous-backed Cercopitheque (*Cercopithecus albigularis rufilatus*), from Kilimanjaro, presented by F. Ratcliffe Holmes, Esq., F.Z.S., on November 11th.

A collection of Birds and Reptiles, presented by the New York Zoological Society on November 8th, including a Yellow Palm-Warbler (*Dendræca palmarum hypochrysea*), a Phebe Warbler (*Sayornis phebe*), a North-American Oven-bird (*Siurus auricapillus*), a Grey-hooded Ground-Dove (*Gallicolumba rubescens*), 2 Kemp's Loggerhead Turtles (*Caretta kempi*), all new to the Collection.

A collection of Birds from Bushire, Persian Gulf, presented by C. E. Capito, Esq., on November 22nd, including an Isabelline Shrike (*Otomela isabellina*), new to the Collection.

A collection of Snakes, presented by the Calcutta Zoological Gardens on November 6th, including a Forsten's Cat-Snake (*Dipsadomorphus forsteni*), new to the Collection.

DECEMBER.

The registered additions to the Society's Menagerie during the month of December were 161 in number. Of these 55 were acquired by presentation, 36 were deposited, 13 were purchased, 5 were received in exchange, and 52 were born in the Menagerie.

The following may be specially mentioned:—

1 Indian Rhinoceros (*Rhinoceros unicornis*), from Nepal, presented by The Maharaja of Nepal, G.C.B., G.C.S.I., G.C.V.O., G.C.M.G., on December 13th.

16 Bennett's Wallabies (*Macropus bennetti*), presented by Lady Loder on December 19th.

8 South African Ostriches (*Struthio australis*), from Cape Colony, deposited on December 3rd.

The SECRETARY exhibited, and made remarks upon, a piece of leaden pipe which had formed a part of the water-supply piping to a waiting-room at Waterloo Station, and had been gnawed through by rats.

Dr. H. H. SCOTT, M.D., M.R.C.S., D.P.H., Pathologist to the Society, exhibited, and made remarks upon, some Hæmosporidia found in the blood of animals which had died in the Gardens during January.

February 17th, 1925.

Prof. E. W. MACBRIDE, F.R.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of January, 1925:—

The registered additions to the Society's Menagerie during the month of January were 62 in number. Of these 18 were acquired by presentation, 13 were deposited, 29 were purchased, and 2 were born in the Menagerie.

The following may be specially mentioned:—

1 Clouded Leopard (*Felis nebulosa*), from the Malay States, purchased on January 8th.

1 Abyssinian Roller (*Coracias abyssinicus*), deposited on January 28th.

1 Tuatera Lizard (*Sphenodon punctatus*), from New Zealand, presented by Sir Donald McGaven, C.M.G., D.S.O., on January 15th.

THE GREY-HOODED GROUND-DOVE (*Gallicolumba rubescens*).

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon (1) the nest of a Mouse (*Mus musculus*), and (2) a living specimen of the rare Grey-hooded Ground-Dove (*Gallicolumba rubescens*) from the Marquesas Islands in the Pacific.

The species was first discovered in 1813 when a Russian expedition under Captain von Krusenstern visited the South Sea Islands. The only record of the species brought home by the Russian captain consisted of a somewhat crude illustration, and from this Vieillot described the bird in 1818, naming it *Columba rubescens*. The species was lost sight of entirely for more than a hundred years, until 1922 in fact, when it was re-discovered by Mr. Rollo H. Beck of the American Whitney South Sea expedition, collecting for the American Museum of Natural History. It appeared to have become extinct in the island of Nukuhiva, where von Krusenstern is said to have obtained it; but a series of specimens was collected on the neighbouring islands of Hatutu

and Fatuhuku, and some living examples were brought back for Mr. E. W. Gifford, of Oakland, California. These bred in Mr. Gifford's aviaries, and some of the young birds were sent to the Bronx Park, from which one has been most generously presented by the New York Zoological Society to the Zoological Society of London.

The species is fully described by Dr. Robert C. Murphy in the American Museum 'Novitates' (No. 115, May 29th, 1924).

The Secretary exhibited, and made remarks upon, a photograph of a young Lion Cub taken in the Sudan by Mr. J. W. Gibson.

March 3rd, 1925.

Sir Arthur Smith Woodward, F.R.S., F.Z.S., Vice-President, in the Chair.

Mr. D. Seth-Smith, F.Z.S., exhibited, and made remarks upon, a series of photographs which he had recently taken in the Society's Gardens showing the courtship display of the Argus Pheasant (*Argusianus argus*).

Mr. C. Davies Sherborn, F.Z.S., exhibited and made remarks upon, a rare book on Birds, "Jarocki's 'Spis Ptakow Gab. Zool.' Warszawsk. Univ. 1821."

17. A Monograph of *Orycteropus afer*.—I. Anatomy except the Nervous System, Skin, and Skeleton.

By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society and Demonstrator of Anatomy at University College.

[Received February 2, 1925: Read March 3, 1925.]

(Plate I.*; Text-figures 1–30.)

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INTRODUCTION.

Zoological literature contains a number of descriptions of parts of *Orycteropus capensis* and *O. afer*, but there is nothing which at all approximates to a full account of one animal. And if one puts together all the partial descriptions, one finds that many regions have been quite neglected. Moreover, one finds that several parts of the other animals formerly grouped with *Orycteropus* in the Order Edentata have not been described. These defects are greatly to be regretted, for it is essential for us to have a full account of what is one of the most puzzling of Mammals. The present monograph should, therefore, fill a serious gap in our knowledge of the Edentata. It is based on the examination of a male animal which was purchased for me by the Society after its death. And I have compared it with specimens of *Tamandua* and *Dasypus* which died in the Society's Gardens. It was also compared with a young *Manis tricuspis* which Sir Arthur Keith kindly put at my disposal. Unfortunately no specimen of *Myrmecophaga* was available, but there is little which one could add to the excellent memoirs by Owen, Forbes and Pouchet. The external characters of this animal have already been described last year in the 'Proceedings' of the Society by Mr. Pocock.

The accounts of the myology of *Bradypus* constitute a supplement to my former paper on the visceral anatomy.

* For explanation of the Plate see page 437.

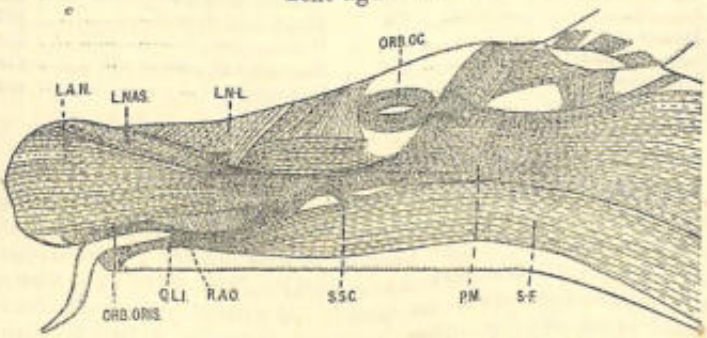
Although the existence of an Order Edentata is not now recognized, I have used the term for the sake of brevity. It is less cumbrous to say that a certain condition in *Orycteropus* differs from the same feature in other Edentata than to say that it differs from the conditions in the Pholidota and all Xenarthra.

I have inserted and acknowledged some hitherto unpublished notes by Garrod.

The Muscular System.

Panniculus Carnosus (text-fig. 1):—This very powerful muscle is divided into the following parts:—The *platysma myoides* (P.M.), which is thinnest in the face, blends with the orbicularis oculi most superiorly. The intermediate fibres are attached to the zygoma and malar bone. And the lowest fibres pass to the snout; they blend with the buccinator, receive slips from the

Text-figure 1.



The panniculus carnosus and its connections in the face. Letters in text.

compressor naris and sterno-facialis and expand on the side of the nostril, thus forming a levator labii superioris alæque nasi (L.A.N.) and dilator naris. Passing back along the neck it gives a slip to the skin behind the auricle, and, increasing in strength and coarseness, it divides into sternal and brachial parts. The mesial part fuses with the sterno-facialis, and the lateral or brachial part constitutes the *dermo-humeralis*, which is attached to the fascia over the upper half of the radius. Over the outer aspect of the elbow on each side the dermo-humeralis covers a glandular sac containing a pasty material; and each sac measures $1\frac{1}{2} \times \frac{3}{4} \times \frac{1}{2}$ inch. The *sterno-facialis* (S-F.) arises from the whole of the front of the sternum, and from the pectoral and abdominal fasciæ. It passes along the lower part of the neck and face, and is connected to the platysma and skin of the cheek (S.S.C.). It runs forwards over the

buccinator, forms a *depressor labii inferioris* (Q.L.I.) and fuses with its neighbour in the lower lips. Humphry (43) figures the platysma as dividing into two parts—one for the upper and one for the lower lip. Galton (33) points out that the sterno-facialis is a true sternalis brutorum, for it coexists with an upward prolongation of the rectus abdominis and a downward prolongation of the sterno-mastoid. Halbertsma regards it as a muscle sui generis, and Turner (93) considers it to be a differentiated part of the panniculus. The *abdomino-humeralis* extends from the axilla, where it is attached to the pectoral crest, to the knee, where it is fixed to the outer aspect of the lower end of the femur. It covers a large area of the abdominal wall.

The conditions in other Edentata are shown in the following table :—

	Platysma.	*Sterno-facialis.*	*Derma-humeralis.*	*Abdomino-humeralis.*
Bradypus	Moderate.	Absent.	Absent.	Moderate.
Myrmecophaga	...	,,	...	...
Tamandua	Present.	,,	Present.	Present.
Manis	Poor.	,,	,,	Thick.
Dasypodidæ	Panniculus much specialized in connection with the carapace.			

Windle and Parsons (101) point out that the panniculus is not highly developed in the Ungulata, but the platysma and sterno-facialis are better developed in the Suidæ than in other Families. The latter muscle is more often absent than present in the Order.

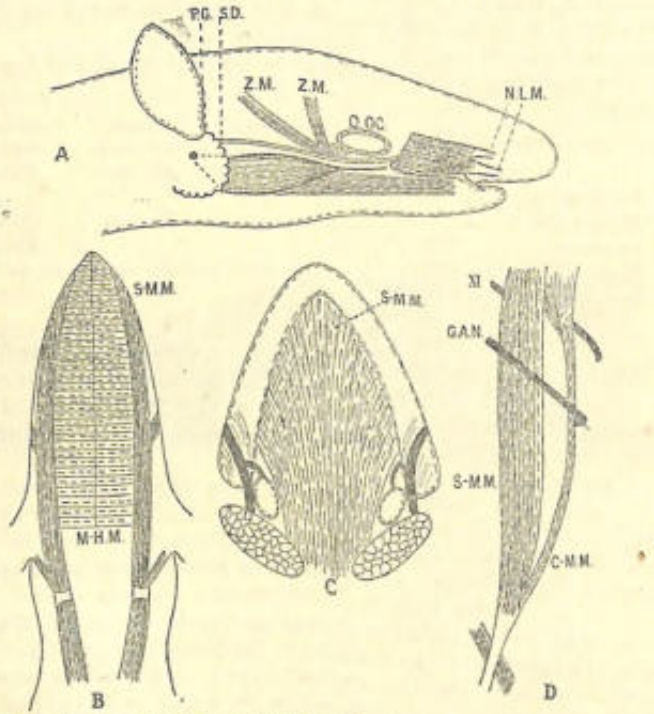
Windle and Parsons (103) also state that "the panniculus reaches a development superior to anything which we have met in our researches into mammalian musculature." I have, however, seen an extraordinary development of the cervical and pectoral regions of the panniculus in *Perameles obesula* (108). And Murie (65) has described an enormous panniculus in the Manatee, with speculations as to the reason for the great growth of some parts. As regards the cephalic parts in the Manatee, his conclusion, which is as follows, is in some ways applicable to *Orycteropus* :—"Connected with the action of this subdermal muscle it may be remarked that, as in the Cetacea, it can have little or no power over the skin itself, not being fastened thereon, a thick layer of fat intervening. On the other hand, the attachments of the muscle point to its subserving the bodily force of various parts. For instance, the fixed points to the malar bones must give the advanced segment of the muscle a very long leverage for movements of the head; at the same time the insertion on the facial bones and lips must lend power to the labial muscles, and in some ways act as a dilator oris, and impart additional strength to the thick muscles of the great

muzzle." It is to be noted that in *Orycteropus* there is no great layer of fat between the skin and the panniculus, but the connections to the skin are very few.

Muscles of the Face.

The *orbicularis oculi* (text-figs. 1 and 3, Orb.Oc.) is thin but extensive, for it covers a considerable area of the bones

Text-figure 2.



Muscles of head and neck in *Tamandua* (A, B, D) and *Dasypus* (C). G.A.N.: great auricular nerve; C.M.M: cleido-mastoid muscle; M-H.M: mylo-hyoid muscle; N-L.M: naso-labial muscles; O.OC: orbicularis oculi; P.G: parotid gland; S.D: Stensen's duct; S-M.M: sterno-maxillaris muscle; XI: accessory nerve; Z.M: zygomatic muscles.

surrounding the orbit. And the orbital fibres are coarser than the palpebral fibres, with which they are continuous. No ciliary bundles were found in any of the four eyelids. Fibres pass into it from the frontalis, platysma and anterior auricular muscles. The muscle does not differ essentially from that in other Mammals.

The *orbicularis oris* (text-figs. 1 and 3, ORB.ORIS) is a very small muscle, and is therefore difficult to display in its entirety from the surface. It produces a low, broad ridge on the mucous membrane of the lips. It receives fibres from the nasal and labial muscles and from the forward prolongation of the sterno-facialis. The buccinator does not play any great part in its formation as it does in most Mammals. When the muscle is dissected out carefully no fibres are seen to leave it to form incisivi, canini, premolares or mentales muscles. In other Edentata this muscle is of poor development. It is well-developed in the Ungulata, especially in those forms with a proboscis.

Nasal Muscles:—The thick, truncated snout is acted upon by the following muscles:—

1. Levator nasi.
2. Levator labii superioris alæque nasi.
3. Levator naso-labialis.
4. Compressor nasi.

The *levator nasi* (text-figs. 1 and 3, L.NAS.) is a long, strap-like muscle arising from the maxilla and front of the malar bone. It passes forwards and upwards to the front of the snout and then turns downwards. It is attached to the deep surface of the skin, and the posterior and lateral fibres blend with those of the levator labii superioris alæque nasi. No fibrous bands connect it to its neighbour. No fibres gain an attachment to the nasal cartilage. Beneath it the great infra-orbital nerve plexus is seen (text-fig. 3, I-O.N.).

In *Myrmecophaga* the muscle soon ends in a long, slender tendon, instead of remaining a thick fleshy mass. In *Tamandua* (text-fig. 2 A) the muscle is as in *Myrmecophaga*. The muscle is absent in *Manis* and in *Chlamydophorus* (22). In *Dasypus* this muscle is very strong. Its thick belly ends in a very powerful tendon.

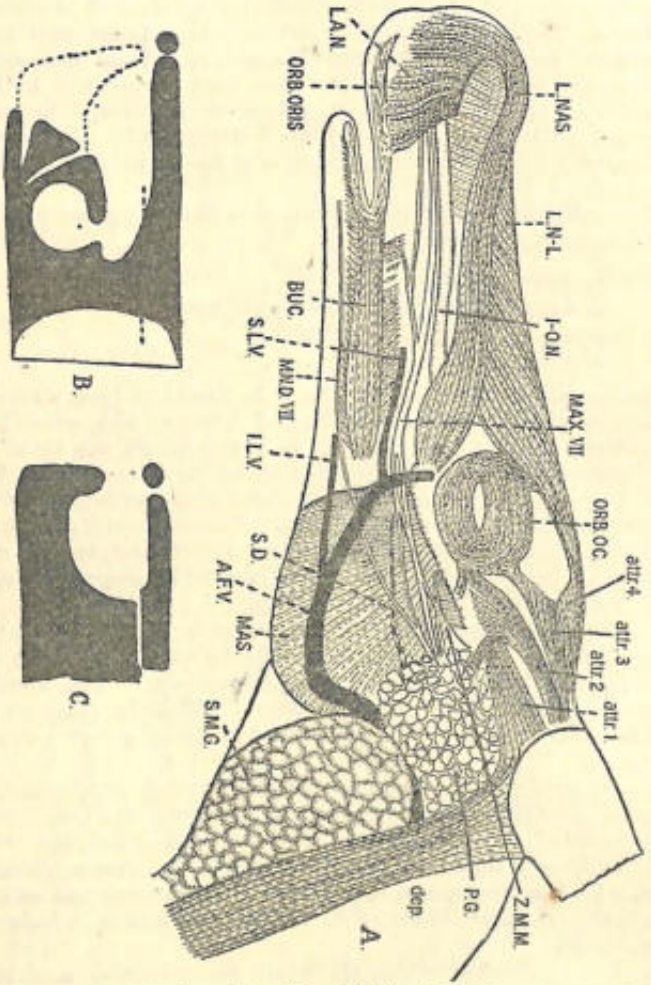
The *levator labii superioris alæque nasi* (text-figs. 1 and 3, L.A.N.) is formed by the sterno-facialis and a slip from the last muscle. It is inserted into the upper and outer surface of the snout and the lateral aspect of the nasal cartilage. Some fibres are fused with the levator nasi in the snout. It elevates and retracts the snout and dilates the nostril. This muscle mass includes the zygomaticus.

In the Myrmecophagidæ there are lateral nasal and labial muscles in long, slender tendons (text-fig. 2 A). In *Manis* the levator labii superioris is the only facial muscle apart from the orbicularis. In *Dasypus* there is a strong, fleshy levator labii superioris, and in *Chlamydophorus* (22) it is the strongest of the facial muscles. In *Tatusia peba* there is no special levator labii superioris.

The *levator* or *retractor anguli oris* (text-fig. 1, R.A.O.) is formed by the sterno-facialis and a slip from the platysma. It

is inserted into the skin of the angle of the mouth. It is fleshy throughout, whereas the corresponding muscle in *Myrmecophaga*

Text-figure 3.



The facial muscles (A) and nasal cartilage (B, C), and deep structures of the head. A.F.V: anterior facial vein; I.L.V: inferior labial vein; I-O.N: infra-orbital nerve; MAX.VII and M.H.D.VII: maxillary and mandibular divisions of facial nerve; P.G. and S.M.G: parotid and submaxillary glands; S.D: Stensen's duct; S.L.V: superior labial vein. Other letters in text.

and *Tamandua* ends in a long, slender tendon like the other nasal and labial muscles.

The *levator naso-labialis* (text-figs. 1–4, L.N-L.) is a thin sheet of fibres descending from the frontalis to the snout and upper lip. Anteriorly there is a very strong bundle forming a *compressor naris* (text-fig. 4, C.N.).

The *depressor labii inferioris* (text-fig. 1, Q.L.I.) consists of small slips running from the mandible to the lower lip under the sterno-facialis.

The *buccinator* (text-fig. 2, Buc.) rises from the maxilla and mandible and passes to the lips. No decussation of fibres occurs. It is a very thin muscle.

The risorius, triangularis and auriculo-labialis are not differentiated as separate muscles, nor is the zygomaticus entirely free from the panniculus.

Auricular Muscles (text-figs. 1–4):—Numerous muscles act on the large auricles, and these can be divided into extrinsic and intrinsic groups. The extrinsic muscles are in four sets—attrahens, attolens, retrahens and depressor. They all converge on the tubula conchæ, which is completely surrounded by fibres except on two small areas on the mesial surface (text-fig. 4, B-D).

The attrahentes consist of four slips inserted into the lower half of the outer surface of the concha. The first slip (*attr.* 1) arises from the posterior border of the mandible below the condyle; the second slip (*attr.* 2) comes from the hind end of the zygoma and receives fibres from the platysma and orbicularis oculi; the third part (*attr.* 3) from the orbicularis oculi unites with the fourth part (*attr.* 4) from the frontalis to form a large bundle. The first part is continuous with the depressor auriculæ, and the fourth part blends with the attolens muscle. These slips correspond to the muscles of the Ungulata as follows:—

attr. 1 = attrahens inferior.
attr. 2 = parotido-auricularis.
attr. 3 = attrahens anterior.
attr. 4 = attrahens superior.

The attolens (*atto.*) is a broad, thin sheet running from the mid-line of the vertex of the head to the upper surface of the concha. It is fused with the attrahens and retrahens.

The retrahens (*retr.*) runs from the mid-nuchal line to the back of the concha. It is continuous with the attolens and depressor.

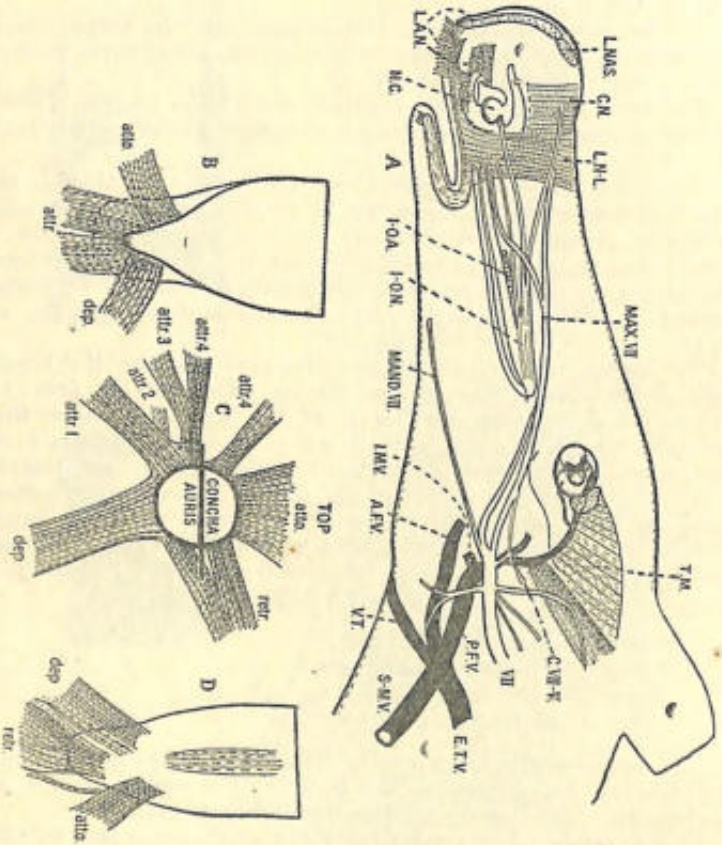
The depressor (*dep.*) arises from the manubrium sterni over the sterno-mastoid. It passes upwards to the lower and back part of the concha, where it fuses with the attrahens and retrahens.

No author has hitherto mentioned intrinsic muscles. In this animal I detected a thin bundle of longitudinal fibres on the mesial surface of the auricle (text-fig. 4). On one side it was continuous with fibres of the retractor auris.

Owen (32) described and figured the auricular muscles in

Myrmecophaga. There is a broad sheet which can act as attrahens, attolens and retrahens according to the fibres which contract; there is an additional retrahens, and there is a

Text-figure 4.



Deep structures of the face (A) and the auricular muscles (B, C, D). The ear is viewed from the side (B) and behind (D) and on cross section (C). C.VII-V: communication from facial to trigeminal nerve; E.T.V: external jugular vein; I.M.V: internal maxillary vein; N.C: nasal cartilage; P.F.V: posterior facial vein; S-M.V: submaxillary vein; T.M: temporal muscle; V.T: vena transversa; VII: facial nerve. Other letters in text and in text-fig. 3.

depressor. The depressor, unlike that of *Orycteropus*, perforates the parotid gland. The depressor also arises from the jaw

instead of from the sternum. It is thus evident that the facial muscles reach a much higher degree of development in *Orycteropus* than they do in other Edentata. They are also better developed than in many Ungulata.

No greater contrast could exist than between the small number of facial muscles in *Manis* and the large number in *Orycteropus*.

There is a greater resemblance between the facial muscles of *Orycteropus* and the Ungulata than there is between the muscles of the former and those of other Edentates.

Ueckermann (94) has given a brief account of the facial muscles of the Xenarthra.

When the muscles on the outer surface of the mandible are removed, it is seen how there are several foramina for the transmission of sensory twigs from the inferior dental nerve instead of a single foramen. But there is one large infra-orbital foramen for the transmission of the large vessels and nerves for the face and for the soft parts of the thick snout.

Muscles of Mastication.

The *masseter* (text-fig. 3, Mas.) is a thin, flat, fan-shaped muscle arising from the lower border of the anterior part of the zygoma. It is inserted into the lower border, angle and posterior border of the mandibular ramus. And it blends to a variable extent round the ramus with the internal pterygoid muscle. The vertical fibres of the zygomatico-mandibularis appear above its concave upper border. In its middle part it is bilaminar. The muscle is unilaminar in *Manis*, but it is bilaminar in *Bradypus*, *Dasypus*, and *Tamandua*. Neither Owen (70) nor Pouchet (82) mention whether it is unilaminar or bilaminar in *Myrmecophaga*.

The *zygomatico-mandibularis* (text-fig. 2, Z-M.) is composed of vertical fibres running from the lower border and deep surface of the zygoma to the outer surface of the ramus of the mandible above a line running downwards and forwards from the condyle. It is connected to the temporalis as Edgeworth points out (24). This muscle is not mentioned by writers on *Myrmecophaga*, but it is absent in *Tamandua* and *Manis*.

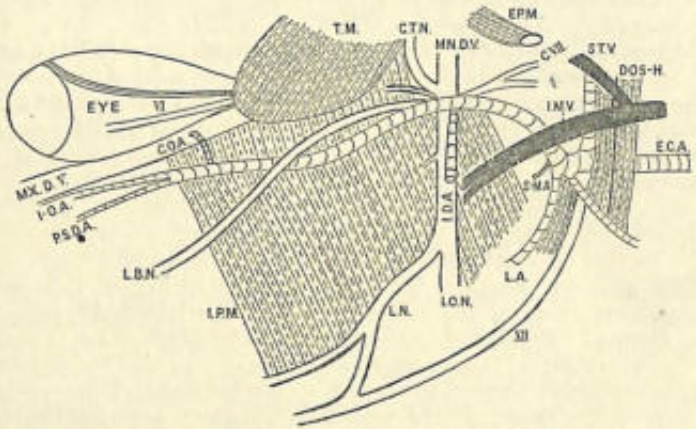
The *temporal muscle* (text-fig. 4, T.M.) extends from the frontal bone anteriorly to the occipital bone posteriorly, but it does not extend up on to the vertex in the mid line. The fibres are inserted into both sides of the coronoid process, and it is covered with strong fascia. It bounds the orbit behind, and a large vein from the nose and orbit courses down its anterior border.

This muscle varies in size in *Myrmecophaga*, Pouchet (82) describing a large muscle and Owen (70) a small one. In *Tamandua* and in *Manis* it is small. In *Chlamydophorus*,

according to Macalister (52), it is small, and in *Dasypus* it is small.

The *external pterygoid muscle* (text-fig. 5, E.P.M.) runs from the alisphenoid in front of the alisphenoid foramen to the neck of the mandible below the capsule of the temporo-mandibular joint. The *internal pterygoid muscle* (text-fig. 5, I.P.M.) arises from the outer surface of the palate bone from the frontal in

Text-figure 5.



The pterygoid region. C.O.A: communicating to ophthalmic artery; C.T.N: chorda tympani nerve; C.VII: communicating to facial nerve; E.C.A: external carotid artery; E.P.M; and I.P.M: external and internal pterygoid muscles; I.M.V: internal maxillary vein; I-O.A: infra-orbital artery; I.D.N: inferior dental nerve; L.A and L.N: lingual artery and nerve; L.B.N: buccal nerve; MN.D.V and MX.D.V: mandibular and maxillary nerves; P.S.D.A: superior dental artery; S-M.A: submaxillary artery; S.T.V: superficial temporal vessel; T.M: temporal muscle; XII: hypoglossal nerve.

front to the pterygoid bone behind. It is divided into an anterior part running backwards, a middle part running downwards and backwards, and a posterior part running vertically. There is a long insertion on the inner aspect of the mandible corresponding to that of the masseter on the outer surface. Edgeworth (24) figures a shorter insertion. The relations of the muscle are shown in text-fig. 5.

Pouchet (82) and Owen (70) do not show a triple internal pterygoid in *Myrmecophaga*, and Macalister (52) states that the inner muscle is the smaller one in *Chlamydophorus*.

The *pterygo-tympanicus* (text-fig. 6, P-T.M) arises by strong fascia from the lower edge of the tympanic ring. The fusiform muscular belly runs downwards and forwards and ends in a thin,

flat tendon, which plays over the edge of the palate bone and expands into the tensor veli palatini. These two muscles thus form a digastric muscle similar to that in Edgeworth's specimen of *O. capensis* (24).

The *tensor veli palatini* (text-fig. 6 A, T.V.P.) is very small. It is inserted into the under surface of the strong aponeurotic sheet from which the central part of the palatine muscles arise. In *O. capensis*, according to Edgeworth (24), it passes into the palatine muscles.

When the pterygo-tympanicus is pulled on, the palatal aponeurosis is raised and tightened.

Palatine Muscles (text-fig. 6 A):—The muscular mass in the soft palate is divisible into a central and two lateral portions. The former is thinner than the latter, and springs from the posterior margin of the strong palatal aponeurosis. The latter arises from the pterygoid bones. With the exception of a few oblique and transverse fibres in the central part all fibres run antero-posteriorly. The lateral parts are inserted partly into the hyoid cornua and partly into the posterior margin of the soft palate. The central part runs to the margin of the palate. A small slip descends on each side and ends in the muscular mass (L.P.). It acts as a levator of the muscular part of the palate.

The lateral bundle of palatine fibres is continuous with fibres attached to the deep surface of the mandible, and the latter is continuous with the cerato-pharyngeus muscle.

The nasal tube is continued well backwards, and the pharyngeal muscles act upon its posterior part as well as on the pharynx. A large tract is devoid of muscles anteriorly. So when the posterior aspect of the pharynx is compared with that in higher mammals, it is seen that *Orycteropus* differs from them in the absence of fibres running up to the basis cranii.

The *stylo-pharyngeus* (text-fig. 6 B, St-P.) is the highest muscle. It runs from the stylohyal and skull above it to the pharynx and nasal tube. It is overlapped by the *epipharyngeus* (Epiph.), which runs from the ceratohyal and joint between it and the epihyal to the pharyngeal wall. This, in turn, is overlapped by the *hyo-pharyngeus* (H-P.), which springs from the thyrohyal and basihyal. In contact with this muscle is the *thyro-pharyngeus* (T.H-P.), which springs from the long descending cornu of the thyroid cartilage. No fibres spring from the cricoid or from the tracheal rings.

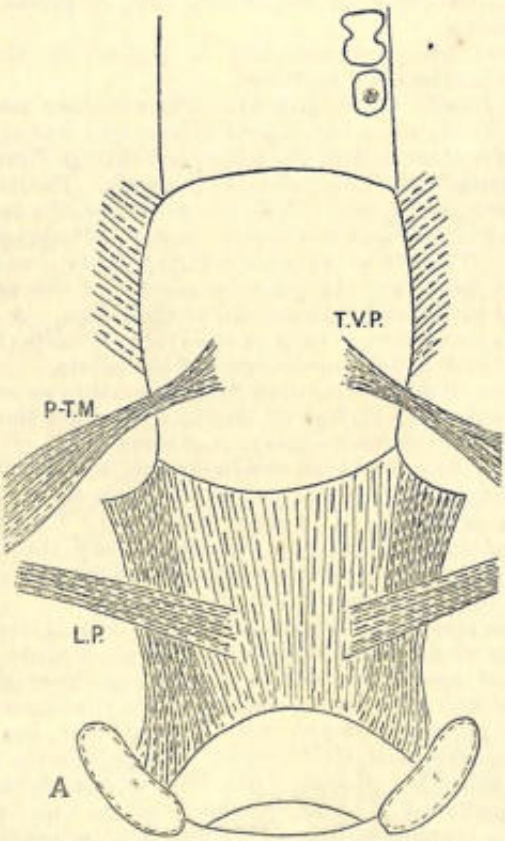
When the muscles are removed one by one till the stylo-pharyngeus is fully exposed (text-fig. 6 C) it is seen how it spreads very widely in the pharyngeal wall, and there is continuity between it and the longitudinal muscle fibres of the œsophagus. And it is side by side with a muscle which fills in the hyoid arch.

Owen (70) describes four constrictors in *Myrmecophaga*, and mentions the crico-pharyngeus as a fifth constrictor. This

animal has a retractor pharyngis connecting the scaleni and constrictors, but I could not detect this slip in *Orycteropus*.

Prevertebral Muscles (text-fig. 7 A):—The *longus colli* has no well-defined vertical part. The lower oblique part (L.O.L.C.) has

Text-figure 6 A.

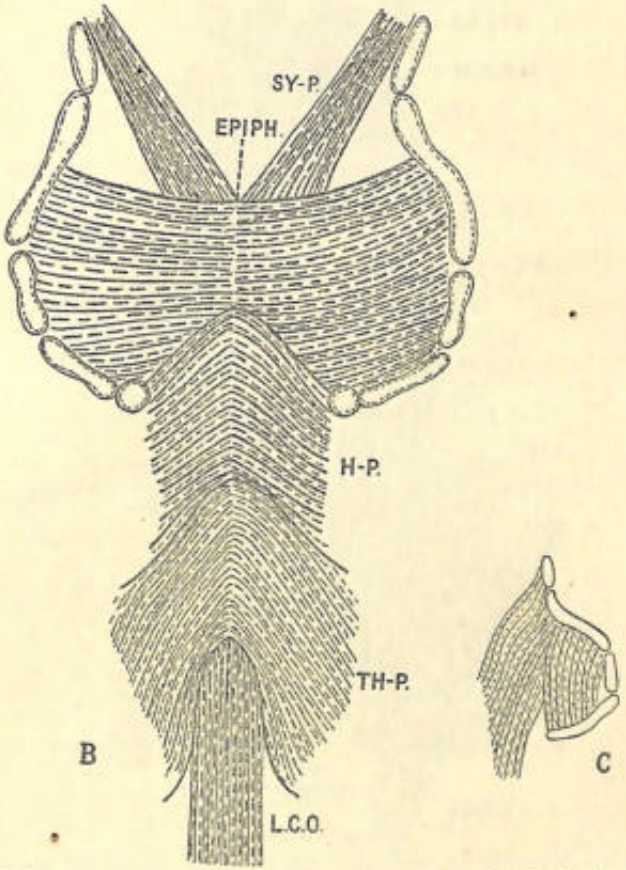


Muscles of the soft palate. L.P: levator palati; P-T.M: pterygo-tympanic muscle; T.V.P: tensor veli palatini.

a coarse lateral division running from the front of the bodies of the fourth, fifth and sixth dorsal vertebræ to the seventh cervical transverse process, and a thin mesial division on the front of the centre of the sixth cervical to the fourth dorsal vertebra. This small part may be the only representative of the vertical part of

the muscle. The longus colli is in contact laterally with a fan-shaped muscle running from the sides of the seventh, eighth and ninth dorsal vertebræ to the first six ribs. The upper oblique part (U.O.L.C.) runs from the transverse processes of the second

Text-figure 6 B.

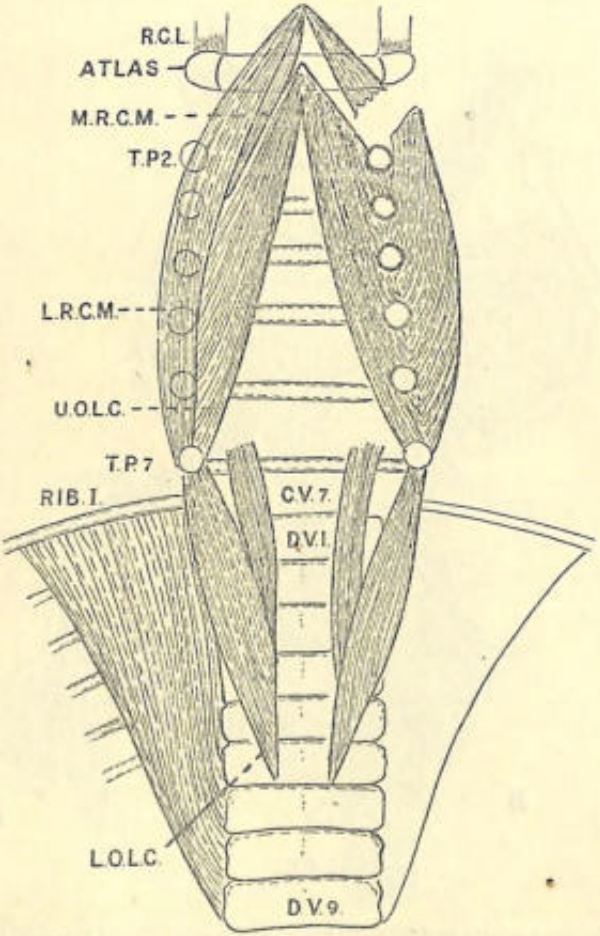


The palatine muscles in superficial (B) and deep dissection (C). L.C.O: longitudinal muscles of œsophagus. Other letters in text.

to seventh cervical vertebræ to the anterior arch of the atlas. The *rectus capitis anticus major* has mesial and lateral parts. The lateral part (L.R.C.M.) is coarse. It runs from the second to seventh cervical transverse processes to the basi-occiput. The mesial part (M.R.C.M.) runs from the second cervical transverse

process to the basi-occiput. The *rectus capitis anticus minor* is quite absent. The *rectus capitis lateralis* (R.C.L.) is strong and

Text-figure 7 A.



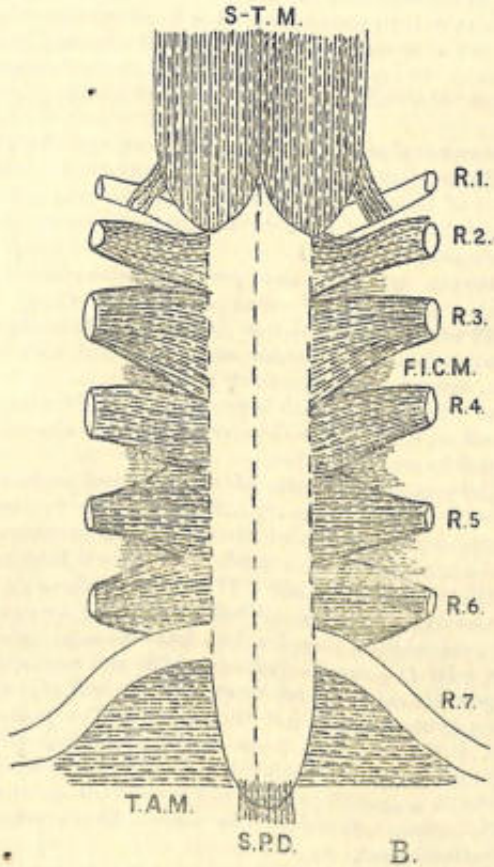
A.

The prevertebral muscles. T.P 2 and 7: cervical transverse processes; C.V and D.V: cervical and dorsal vertebræ. Other letters in text.

has the usual attachments. Macalister (54) described a rectus capitis anticus minor in seven Edentata including *Orycteropus*. In *Tamandua*, *Dasypus*, and *Manis* the vertical part of the longus

colli is absent. In *Bradypus* the vertical part of longus colli exists, and the entire vertebral centra are concealed by muscles, whereas part is exposed in other Edentates.

Text-figure 7 B.



The sternum and muscles attached. F.I.C.M: fibres of intercostal muscles; S.P.D: sternal part of diaphragm; S-T.M: sterno-thyroid muscles; T.A.M: transversalis abdominis; R 1–R 7: first seven ribs.

The vertical part of the longus colli is absent in Ungulates, but the two oblique parts are present. The rectus capitis anticus minor is frequently present, but it is exceedingly poor in *Hyrax*; indeed, Mivart and Murie (62) missed it in that animal.

In some Marsupials (87) these muscles are not well differentiated from a muscle mass.

In text-fig. 7 A there is shown a strong, flat triangular sheet of muscle lying to the side of the lower oblique part of the longus colli. It is in line with, and must be regarded as the uppermost (most anterior) of the series of long, flat muscles which cover the deep aspect of the ribs on the dorsal part of the thorax. Each of these muscles arises from one rib, crosses the rib in front of it obliquely from within outwards and is inserted into the next rib again. Thus the muscle from the tenth rib crosses the ninth and is inserted into the eighth. Only a short interval separates these muscles from the triangularis sterni, which is on the same plane.

The triangular sheet of muscle is represented by three little strands in *Tamandua*. In *Manis* and *Bradypus* I could not find any remnant of that sheet of muscle, and the two lateral masses of prevertebral muscles were relatively farther apart than in *Orycteropus* and *Tamandua*.

I am unable to give any personal observations on the prevertebral region of *Myrmecophaga*, and Owen (70) and Pouchet (82) neither describe nor figure it in their memoirs.

The peculiar lateral muscular sheet, which is well marked in *Orycteropus*, must be an expiratory muscle.

The *sterno-maxillaris*, which is present in the Myrmecophagidæ and Dasypodidæ, is absent in *Orycteropus*. It is almost absent in the Bradypodidæ and Manidæ.

The *digastric muscle* consists of anterior and posterior bellies. The anterior bellies (text-fig. 8, A.B.D.) of the two muscles are fused to form a thin sheet of fibres passing between the two halves of the mandible. No raphé exists, but Edgeworth (24) points out that this is variable. The anterior fibres do not reach as far as the symphysis mandibulæ, and the posterior fibres overlap the suprahyoid muscles, but have no attachment to the hyoid bone. In *Orycteropus capensis* (24) the posterior margin of the sheet is concave backwards. Anteriorly the intermandibularis protrudes beyond the sheet. The posterior belly (text-fig. 9, P.B.D.) arises from the paroccipital process and ceratohyal, and is inserted by a tendon into the inner surface of the angle of the mandible. It is not connected to the anterior belly at all. Some fibres of the sterno-hyoid pass into the anterior digastric sheet.

The hypoglossal nerve and lingual artery descend along the anterior border of the posterior belly, and the submaxillary duct and vein cross it. The relations are shown in text-fig. 5.

The digastric muscle has been omitted from the memoirs of Owen, Pouchet, and Forbes on *Myrmecophaga*. In *Dasypus* the anterior bellies are a broad, flat sheet.

Hence the muscle in *Orycteropus* and *Dasypus* belongs to Parson's first type, a form which is found in many Rodents (Sciuromorpha), most Cynomorph Monkeys, and in many Anthropoid Apes. Chaîne points out that the muscle has two

bellies in *Bradypus*, and there is no muscle at all in *Tatusia* as in the Monotremata and some of the Odontocete Cetacea.

The *intermandibularis* (text-figs. 8 and 9, I-M.M.) arises posteriorly from the body of the hyoid bone. The fibres run forwards and end in a strong tendon, which bifurcates, the halves running to the lower borders of the halves of the mandible. In *Orycteropus capensis* Edgeworth (24) described and figured the muscle as having two tendons. This muscle may correspond to the mylo-hyoid.

The *genio-hyoidei* (text-figs. 8 and 9, G-H.M.) arise from the inner aspects of the halves of the mandible. Passing backwards they come in contact with each other. Each is inserted into the basi-hyal and cerato-hyal. It is fused to a slight extent with its neighbour and with the genio-glossus.

The *genio-glossi* (text-fig. 8, G-G.M.) arise from the inner aspects of the anterior parts of the halves of the mandible. The muscles come together and the fibres pass to the tongue and basi-hyal.

The *hyo-glossus* (text-figs. 8 and 9, H-G.M.) arises from the side of the hyoid bone and fuses with the stylo-glossus to form a strong muscle, which passes forwards and upwards into the anterior two-thirds of the tongue.

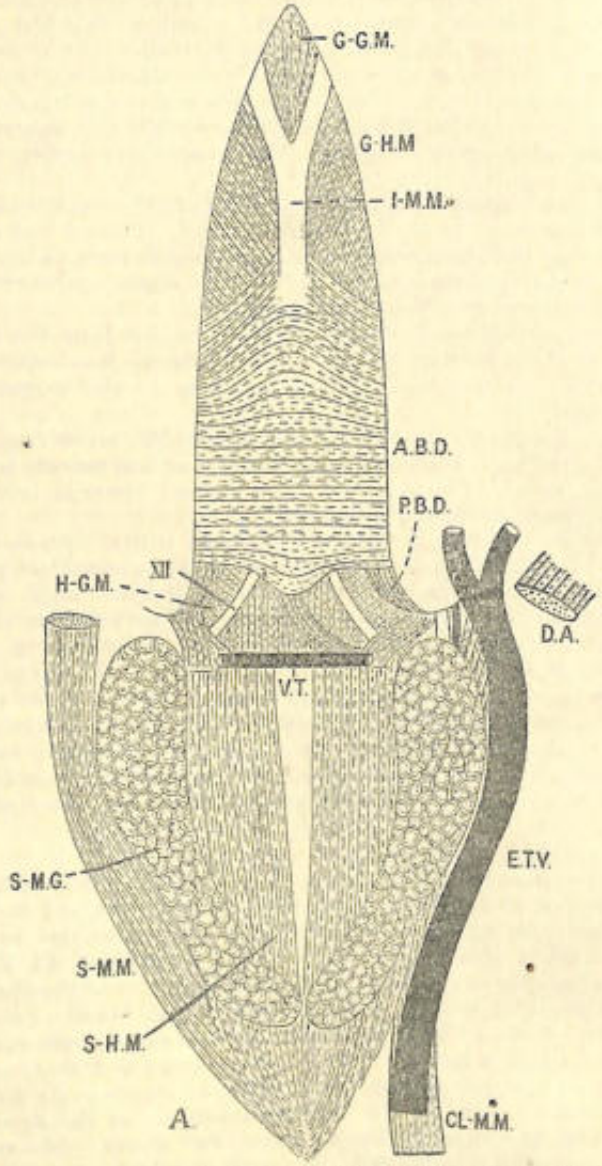
The genio-glossus is continuous laterally with a thin sheet of muscle fibres, which envelops the duct of the submaxillary gland over its entire course between the angle of the jaw and its orifice in the mouth. The fibres act probably as a constrictor of the duct. The duct and sheet are crossed by the lingual nerve.

The *stylo-hyoid muscle* (text-fig. 5, Dos-H.) arises from th upper end of the cerato-hyale, and fibres are fused with the stylo-glossus and posterior belly of the digastric. The latter covers the origin of stylo-glossus and stylo-hyoid. The muscle sweeps downwards to be attached to the hyoid bone. Fibres pass to the opposite muscle, to the hyo-glossus and to the anterior digastric sheet.

No *chondro-glossus* was seen.

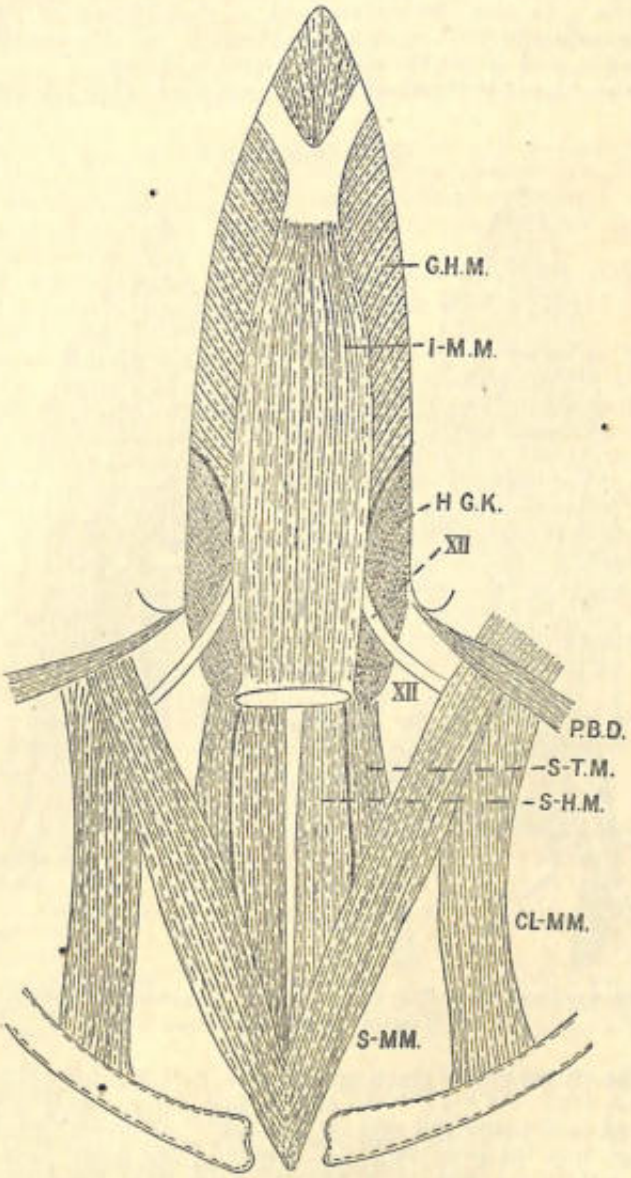
The *sterno-mastoid* (text-fig. 8, S-M.M.) arises from the anterior border and deep surface of the manubrium sterni, and there is slight fusion with its neighbourhood. It is concealed by the submaxillary gland. The *cleido-mastoid* (text-fig. 8, Cl-M.M.) arises from the middle third of the anterior border of the clavicle. It is concealed by the external jugular vein. In the anterior quarter of the neck they unite to form a *sterno-cleido-mastoid* muscle, which is inserted into the paroccipital and paramastoid regions. A strong aponeurosis connects the muscle to the auricle. A separated piece of the sterno-mastoid forms the *depressor auriculæ* (D.A.), which has been described above. The spinal accessory nerve goes between the sterno- and cleido-mastoids and, after giving a twig to the former, it pierces the latter. Various observers have described slightly different origins for the cleido-mastoid muscle. The *sterno-occipitalis* is absent.

Text-figure 8



Anatomy of the neck. D.A: depressor auriculæ; E.T.V: external jugular vein; S-M.G: submaxillary gland; V.T: vena transversa; XII: hypoglossal nerve. Other letters in text.

Text-figure 9.

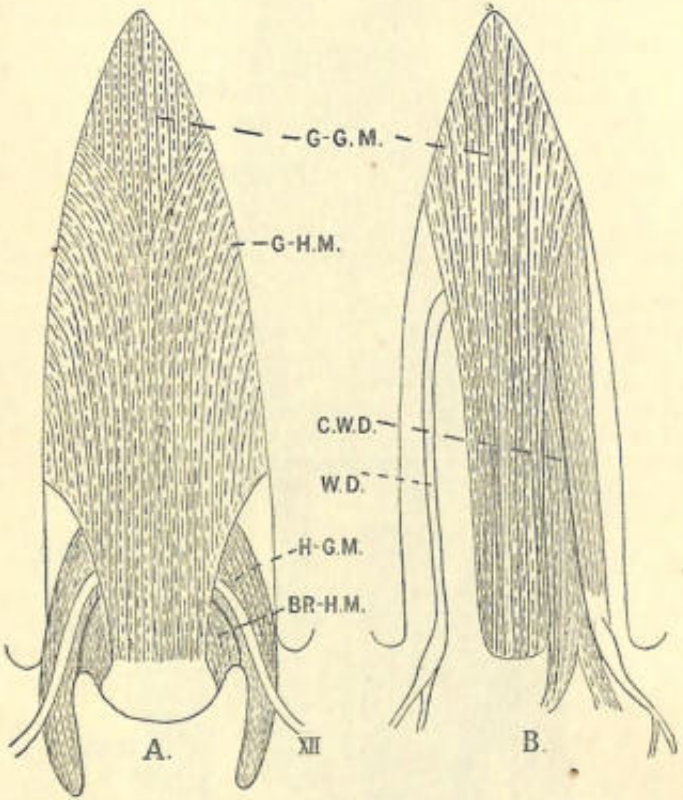


Anatomy of the neck deep to that in text-fig. 8. H.G.K: hypoglossus muscle; XII: hypoglossal nerve. Other letters in text.

In the Bradypodidæ (**53, 59, 103**) there are no separate sterno- and cleido-mastoids in *Bradypus*, but the two are separate in *Cholœpus*. In the Dasypodidæ and in *Cyclothurus* among the Myrmecophagidæ both muscles are present. In *Myrmecophaga*, *Tamandua*, and *Manis* the cleido-mastoid is absent.

The *omo-hyoid* is absent in *Orycteropus* as in other Edentata.

Text-figure 10.



Deep muscles of submaxillary region. C.W.D: compressor of Wharton's duct; W.D: Wharton's duct. Other letters in text.

The *sterno-hyoidei* (text-figs. 8 and 9, S-H.M.) have a common origin from the back of the manubrium sterni, and they remain united in the posterior fifth of the neck. Later on they diverge to be inserted into the lower border of the hyoid bone. The *sterno-thyroidei* (text-fig. 9, S-T.M.) arise from the back of the manubrium sterni and first three costal cartilages. The fibres of

origin are continuous with the triangularis. On the right side the muscle obtained a strong tendinous union to the superior cornu of the thyroid cartilage, and passed on to be attached to the hyoid bone subjacent to the sterno-hyoid; so it combines sterno-thyroid and thyro-hyoid. On the left side it is attached to the side of the thyroid ala and is continued up to the hyoid bone.

Beneath the sterno-thyroidei are two small muscles which from their attachments should be called *hyo-epiglottidean*. This occurs in the Tragulidæ and Bovidæ according to Parsons.

The sterno-hyoidei, hyoglossi and stylo-hyoidei are more or less continuous.

The *branchio-hyoid* (text-fig. 10 A, Ba-H.M.) binds together hyoid cornua on each side. Parsons and Windle (**101**) found it in some Ungulata.

Scalene Muscles:—Only two scalene muscles are present—the scalenus longus and scalenus brevis. No scalenus ventralis is present, in which all Edentata agree with each other and with some higher Mammals. The *scalenus longus* arises from the transverse processes of the second, third and fourth cervical vertebræ. It passes backwards as a compact bundle as far as the clavicle. Then it thins out and expands to be inserted into the outer surfaces of the third, fourth and fifth ribs, and to the fascia covering the external intercostal muscles. Intercostal nerves enter its deep surface. The *scalenus brevis* arises from the transverse processes of the fourth, fifth and sixth cervical vertebræ, and is inserted as a compact bundle into the anterior border and outer surface of the first rib. Immediately behind the scaleni is the levator anguli scapulæ.

The attachments of the scaleni in the above animal and in other Edentata is shown in the following table, the letters C.V. meaning cervical vertebræ and R indicating ribs.

	Scalenus longus.	Scalenus brevis.
Bradypus (**59, 103**)	C.V. 6-9 to R. 1.	C.V. 6-9 to R. 1.
Tamandua (**83**)	C.V. 3-6 to R. 1.	C.V. 4-7 to R. 1.
Cyclothurus (**21, 42**)	C.V. 4-7 to R. 1.	
Dasypus (**103**)	R. 3-5.	R. 2-4.
Tatusia (**52**)	R. 1-3.	R. 1 and 2.
Chlamydophorus (**52**)	C.V. 2-6 to R. 2.	C.V. 2-6 to R. 1.
Manis (**103**)	C.V. 2-4 to R. 2-4.	C.V. 4 and 5 to R. 1.
Orycteropus	C.V. 2-4 to R. 3-5.	C.V. 4-6 to R. 1.

It is thus evident that the conditions in *Orycteropus* resemble those in *Manis* most closely.

Parsons and Windle (**101**) point out that there is a scalenus anticus or ventralis in the Ungulata, and that the scalenus longus and brevis are so closely connected at their origin that

they are easily confused; the brevis goes to the first rib, and the longus is inserted as follows:—

Hippopotamus.	Ribs 1–3.	Sheep ...	Ribs 1.
Pig	„ 1–3 or 3 and 4.	Goat ...	„ 1–4.
Peccary	„ 1–3 or 1–4.	Antelope.	„ 1–3.
Camel.....	„ 1.	Tapir ...	„ 1–3.
Chevrotain ...	„ 1–3.	Horse ...	„ 1.
Deer	„ 1.	Ass	„ 1 or 1–3.
Brocket	„ 1.	Hyrax...	„ 1–3, 3 and 4, or 3–6.
Giraffe	„ 1 and 2.	Elephant.	„ 2–4.
Ox	1–3.		

Thus the insertion in the Pig, Elephant, and Hyrax most closely resembles that in *Manis* and *Orycteropus* in avoiding the first or first and second ribs.

Intercostal Muscles:—The external and internal intercostal muscles extend from the sternum ventrally to the vertebral column dorsally. The fibres have the usual direction and attachments, but nowhere are they replaced by intercostal membranes.

Triangularis Sterni (text-fig. 7 B) arises by tendinous and muscle fibres from the side of the posterior aspect of the body of the sternum and the inner aspects of the second to seventh costal cartilages. The fibres radiate to be attached to the second to sixth costal cartilages. The fibres to the second and third costal cartilages are coarser than those to the remainder, and appear to form two separate muscles. The fibres to the second cartilage are blended at their origins with those of the origin of the sterno-thyroid muscle. And there is almost a union of the fibres of the most posterior part of the muscle and the most anterior fibres of the transversalis abdominis. There is no continuity between the triangularis and the diaphragm. No muscle fibres are found on the back of the centre of the body of the sternum from the second costal cartilage backwards, so the two triangulares are entirely separate. The whole width of the manubrium and anterior part of the body of the sternum are covered by muscle. Fibres pass into the internal intercostal muscles.

Muscles of the Back.

The *trapezius* arises from the occiput, the entire length of the ligamentum nuchæ and the first nine dorsal spines. Some fibres arise from the lumbo-dorsal fascia, as Galton (33) pointed out. There is no insertion into the clavicle. The anterior half of the muscle is inserted into the upper border of the anterior half of the scapular spine and the fascia over the supraspinatus. There is no fusion with the scapular deltoid. The rest of the muscle is inserted into a facet on the middle of the scapular spine. The most anterior fibres of origin are covered by the retractor auris,

and the posterior ones cover the latissimus dorsi. In *Tamandua* the lower cervical and upper dorsal fibres form a marked strip.

The chief variations occurring in the Edentata are the presence or absence of an occipital origin, and the presence or absence of a combination of the trapezius and deltoid to form a cephalo-humeral muscle. These are shown as follows :—

	Occipital Origin.	*Cephalo-humeralis.*
Bradypus	0	+
Myrmecophaga	0	+
Tamandua	0	+
Cyclothurus	0 or +	0 (clavicle present).
Dasypus	+	+
Tatusia	+	
Chlamydophorus	from shield over occipital bone.	0
Manis	+	+
Orycteropus	+	0 (clavicle present).

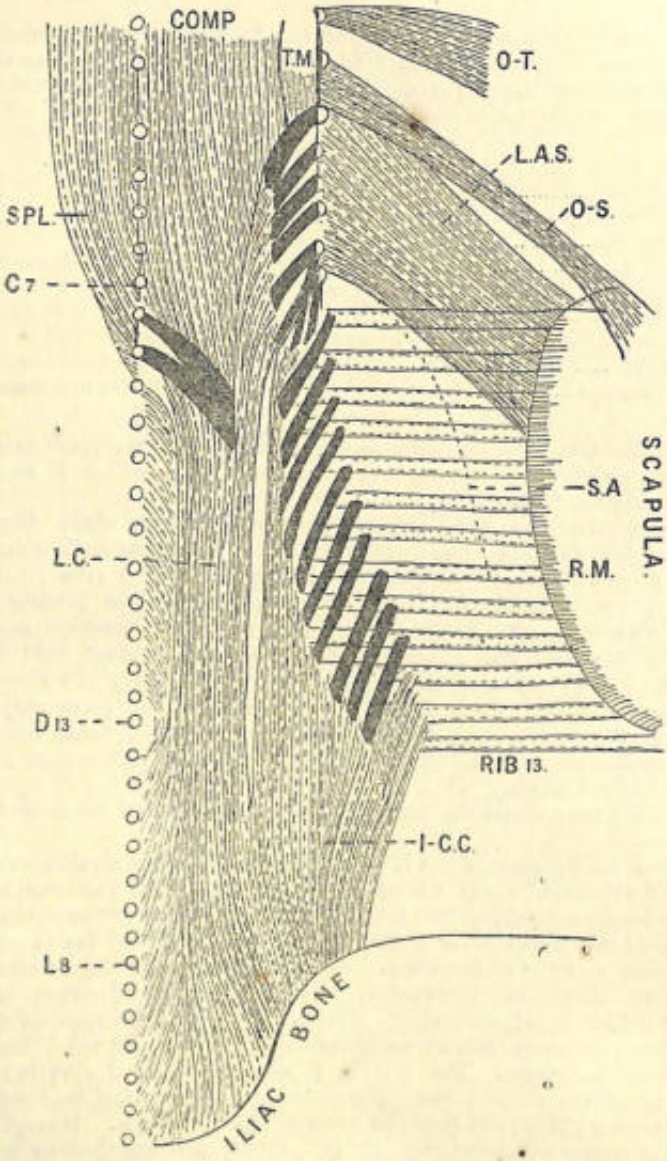
In the Ungulata the cephalo-humeralis has an occipital origin in all except the Camelidæ and Giraffidæ, in which it arises farther back in the neck.

The *latissimus dorsi* arises from the posterior eight dorsal spines and from the lumbo-dorsal fascia. No fibres spring from the pelvis. Slips of origin are also derived from ribs 10–12, and these inter-digitate with the external oblique muscle of the abdomen. No fibres take origin from the posterior angle of the scapula. The fibres converge, and are inserted into the floor of the bicipital groove of the humerus. They are closely connected to the overlying panniculus and to the teres major. Before the muscle gives way to the tendon, a strong, broad dorso-epitrochlearis is given off. Humphry (43) does not record any costal origin at all.

In *Myrmecophaga* the fusion of the latissimus and teres major is great.

Rhomboidei (text-fig. 11, R.M.):—In this animal there is a single rhomboid sheet whose origin extends from the occipital crest backwards along the nuchal ligament, spines of the seventh cervical and upper three dorsal spinous processes and fascia over the deep muscles of the back. The cervical part of the muscle is thicker than the remainder, but there is no division into R. capitis, R. major and R. minor. Galton (33) regards the thicker part of the muscle as being the R. minor and the thinner part as R. major. The muscle is inserted into the vertebral border of the scapula throughout the greater part of its length. Macalister (52) states that the occipital part is weak. Humphry (43) gives no details of any value. Fibres are continuous with those of the combined levator anguli scapulæ and serratus anterior.

Text-figure 11.



Muscles of the back. The vertebral spines and ribs have corresponding numbers. O-T: omo-trachelian. Other letters in text.

The arrangements in other Edentata and in the Ungulata are shown in the following table :—

	Occipital Origin.	Rhomboidei fused.	Rhomboidei separate.
Bradypus	0	+	0
Cholœpus	+	0	+
Myrmecophaga	0	+	0
Tamandua	0	+	0
Cyclothurus	0	+	0
Dasypus	+	0	+
Tatusia	+	0	+
Chlamydophorus	+	0	+
Manis	+		
Hippopotamidæ	+	+	0 (21
Suidæ	+	+	0 (51)
Hyracoidea	+	+	0 (62)
Other Ungulata	0	+	0 (101)

The *levator anguli scapulæ* (text-fig. 11, L.A.S.) and *serratus anterior* (text-fig. 11, S.A.) form a single, strong muscular sheet, whose origin extends from the second cervical transverse process down along the third, fourth and fifth transverse processes and the first eight ribs. The sheet is inserted into the superior angle and vertebral border of the scapula on its deep surface. Fibres are continuous round the vertebral border with the rhomboid sheet. Other authors have found a tendency to fusion between these muscles. My specimen represents the primitive arrangement. In other Edentata the degree of fusion also varies; and Parsons and Windle (**103**) have collected data regarding the variations in the origin of the two muscles. It appears from their account that the conditions are most constant in *Orycteropus*.

The *occipito-scapularis* (text-fig. 11, O-S.) runs from the transverse process of the second and third cervical vertebræ to the fascia over the supraspinatus.

Serrati Postici:—Both superior and posterior muscles are present. The former arises by an aponeurosis from the spinous processes of the dorsal vertebræ two to six; it is inserted into the outer surfaces of ribs 5–8. The latter runs from the lumbar aponeurosis to the lower four ribs. The superior muscle is present in all Edentata except *Chlamydophorus* according to Macalister (**52**).

Splenius Capitis and *Colli*:—The splenius capitis (text-fig. 11, Spl.) is a powerful muscle running from the entire length of the ligamentum nuchæ, seventh cervical and first two dorsal spines to the entire length of the occipital crest from the mid line to the paramastoid region, where it fuses with other cervical muscles. No splenius cervicis is present.

Parsons and Windle (**103**) review the literature on these muscles, and state that "the splenius colli is usually absent throughout the Order with the exception of *Bradypus*, in which

animal the splenius capitis is feeble or wanting." But I observed a splenius colli in *Tamandua*.

Sacrospinalis (text-fig. 11):—This muscular mass is clearly divisible into three columns—an outer or ilio-costalis, a middle or longissimus, and an internal or spinalis. The three columns have a common origin from the inner part of the iliac crest, the posterior sacro-iliac ligament, the back of the sacrum, and the spines of the sacral and posterior two lumbar vertebræ. In the posterior lumbar region the *ilio-costalis* (I-C.C.) is given off. This column narrows from behind forwards. It gives muscular slips to the last three ribs, and tendons to the first ten ribs and the transverse processes of the sixth and seventh cervical vertebræ. The last two slips fuse with the levator anguli scapulæ. As the column crosses the ribs it is bound down to them by muscle fibres, aponeurosis or both. The *longissimus* (L.C.) is, as usual, the broadest column, and there is a tendency for it to be divided longitudinally into two, but only the superficial part shows that trace. Anteriorly it separates into mesial and lateral parts, which diverge and expose the complexus, but there is no fusion with that muscle. The lateral part is inserted by broad bands into the transverse processes of all cervical vertebræ except the atlas. The tendons fuse with the origin of the levator anguli scapulæ. The mesial part is inserted by strong tendons into the spines of the first two dorsal vertebræ. The *spinalis* arises from the spines of all eight lumbar vertebræ, and is inserted into the spines of the third to twelfth dorsal vertebræ. These columns cannot be divided into parts corresponding to the neck and the divisions of the back.

The *complexus* (text-fig. 11, Comp.):—This muscle is exceedingly strong, and Macalister (52) showed how it is also powerful in *Tatusia*, *Chlamydophorus* and *Dasypus*. It arises in *Orycteropus* from the articular processes of the vertebræ from the second cervical to the fourth dorsal, and a long strip arises by two tendons from a dense aponeurosis on the deep surface of the longissimus. The vertebral origins are closely blended with the deep fibres of the longissimus. The entire muscle is inserted into the back of the skull, and there is no separated biventer cervicis. The long strip mentioned above may represent the biventer.

The *trachelo-mastoid* (text-fig. 11, T.M.) arises from the third, fourth and fifth cervical articular processes and from the most anterior tendon of the longissimus. It is inserted into the paramastoid region.

When the complexus is removed a strong bundle of fibres is seen to run from the inner part of the longissimus to the spine of the axis.

Sub-occipital Muscles:—A very massive muscular mass runs from the spine of the axis to the skull. The *rectus capitis posticus major* is a thick muscle running from the long spine of the axis to the occiput. It is closely applied to the massive *inferior*

oblique, which runs from the spine of the axis to the transverse process and lower border of the posterior arch of the atlas. The *superior oblique* runs from the transverse process of the atlas to the skull over the *rectus capitis posticus major*. It is thin. A small *rectus capitis posticus minor* lies deeply. It runs from the spine of the axis over the posterior arch of the atlas to the occiput with an attachment to the atlas. And a small superficial muscle runs from the posterior arch of the atlas to the occiput.

The suboccipital triangle does not exist as a space, but the muscles are disposed in a triangle. The posterior primary division of the suboccipital nerve emerges from under the inferior oblique. The muscles course over the posterior arch of the atlas and the strong occipito-atlantal membrane.

Semispinalis :—This muscle stretches from the lower dorsal region to the axis. It is composed of fibres which pass forwards and inwards. The origin is from the articular processes of the lower four cerivcal vertebræ and the transverse processes of all the dorsal vertebræ, and the insertion is into the spinous processes of all the vertebræ from the axis to the twelfth dorsal vertebra. The lowest dorsal fibres are short and run from one vertebra to that in front of it. In the mid-dorsal region the fibres are longest, for two vertebræ lie between the origin and insertion. It is only the greater closeness of the fibres which distinguishes the cervical part from the dorsal part.

Multifidus Spinæ :—The only traces of this muscle consisted of strong fibres in the lower half of the dorsal region, the lumbar and sacral regions. The short fibres crossed between three vertebræ at most, and the dorsal fibres are longest.

The *interspinales* are extensive owing to the length of the spinous processes, particularly in the cervical and upper dorsal regions; the *intertransversales* are short; and the *levatores costarum* are aponeurotic or musculo-aponeurotic. The *rotatores dorsi* I could not detect.

In *Tamandua* the sacro-spinalis is thin, and its insertion is entirely muscular, no tendons being present such as occur in *Orycteropus*. The muscle mass is continuous with the dorsal caudal muscles. The ilio-costalis is thin. The greater mass of the muscle forms the longissimus and spinalis columns. As it is traced upwards it divides into two. The lateral border gives off no processes till it reaches the neck, where it is connected by muscle slips to the cervical transverse processes. The mesial or spinalis element is connected by muscle-slips to the upper dorsal and lower cervical spinous processes. The complexus, which is strong, passes between the two divisions of the medial mass of the sacrospinalis. There is no definite sub occipital triangle. The whole sacro-spinalis is thin, and as my specimen had been hardened in spirit in the storeroom for a long time, I was unable to separate off deeper layers such as the semispinalis, multifidus, rotatores, etc., if these are actually all present.

In *Manis* the sacro-spinalis is thick in the lumbar region, and its three constituent columns are well marked in the upper dorsal region. The ilio-costalis has one tendon of insertion passing to the last cervical transverse process. The longissimus has five tendons of insertion into the preceding five cervical vertebræ, and it is prolonged as the result of direct continuity between it and the complexus to the occipital bone. In the absence of tendons of the ilio-costalis to ribs the muscle resembles that in *Tamandua*, and in the presence of cervical tendons of insertion it resembles that in *Orycteropus*. The sub-occipital muscles are pressed together into a conical mass with the apex on the axial spine as in *Oxycteropus*, so there is no triangular space. The semispinalis and multifidus are well marked.

Of *Bradypus* only a thorax and neck were at my disposal, but the main features of the muscle could be made out. It is larger than one would expect from the habits of the animal. The ilio-costalis develops tendons in the hind part of the back, and the most posterior tendon is inserted into the eighth rib. Slips from the longissimus run into the tendons where they form a thick bundle in the anterior dorsal region. In the area of thorax left to me (*i. e.* as far back as the twelfth rib) the spinalis and longissimus fuse to form a strong bundle. Slips pass mesially to be attached to all the dorsal and the lower five cervical spines. And the longissimus is fixed by muscle slips to the seventh to ninth cervical transverse processes. The remaining cervical spinous and transverse processes receive fibres which arise from the cervical articular processes. These slips form V's, the apex, which lies posteriorly, being formed by the articular processes. There is a well-marked sub-occipital triangle, in the possession of which this animal differs from all the Edentata described above.

In *Dasypus* the ilio-costalis and longissimus are muscular throughout.

Thus it can be seen that *Orycteropus* and *Bradypus* agree most closely in the great number of ilio-costalis tendons. *Manis* has very few. And the Dasypodidæ and Myrmecophagidæ have none.

Muscles of the Anterior Abdominal Wall.

The *external oblique* arises from the posterior borders and outer surfaces of all ribs, the complete line of origin running obliquely backwards and outwards across the thorax, and the fibres pass backwards or backwards and inwards. Some fibres are attached to the iliac crest and anterior superior spine of the ilium, and a few fibres end on the surface of the rectus muscle. Most end in an aponeurosis which is attached along the pelvic brim right mesially to the pubis, and it is intimately connected to the deep fascia of the hind limb. The pubic attachment is powerful. No Poupart's ligament exists. The muscle is split by the

cremaster sac, and the aponeurosis is tucked in behind the sac. Galton (33) mentions the extension of the muscle to the first rib. This high extension of the external oblique is a common feature in the Edentata, as the following list shows:—

Bradypus	ribs 6–14 (103).
Tamandua	from 4th rib backwards (103).
Dasypus	ribs 3–7 (103); to rib 1 (33).
Manis	extends to rib 1 (103).

Among the Ungulata the muscle extends farthest forwards in the Elephant, and then in order come the Horse, Hippopotamus and Tapir. In this assemblage of Orders the iliac insertion is small, and Poupart's ligament is not a well-defined structure.

The *internal oblique* arises from the iliac crest in its outer part, the anterior superior spine and the aponeurosis of the external oblique muscle. The lateral fibres pass forwards and inwards to the hinder border of the last rib. The lateral fibres are attached directly to the rib, but the mesial ones are attached through the medium of an aponeurosis. The most mesially originating fibres pass horizontally across the cremaster sac where it comes through the abdominal wall and ends over the rectus muscles. Anteriorly the muscle fuses with both rectus and transversalis. There is only a slight aponeurosis, and the muscle does not split. It gives off cremaster fibres which pass round the cremaster sac obliquely.

The costal attachments in other Edentata have been recorded as follows:—

Bradypus	to last rib (103)
Tamandua	to last five ribs (103).
Manis	to last six ribs (103).

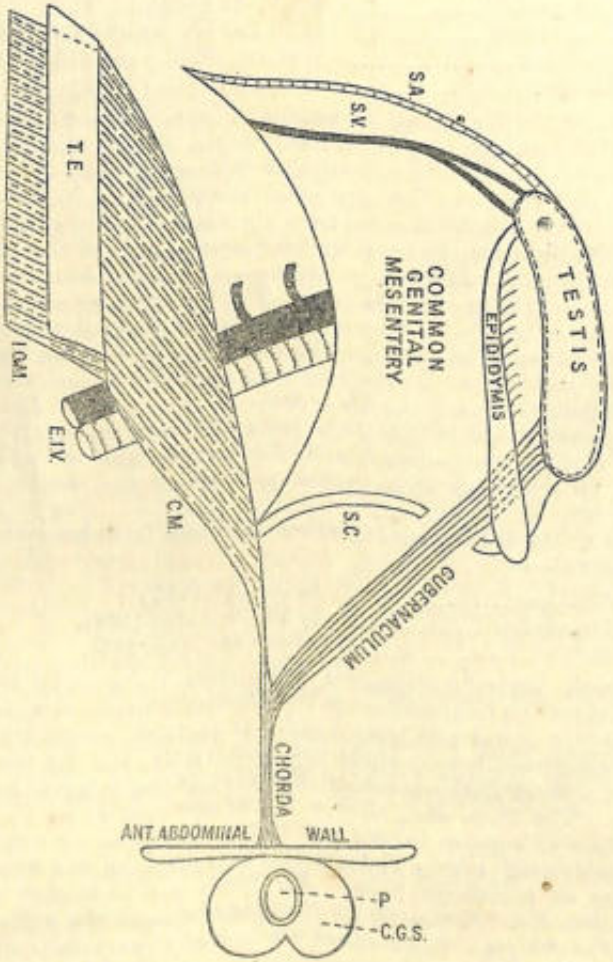
The *transversalis abdominis* arises from the anterior superior iliac spine, the deep surface of the internal oblique, and the deep surfaces of costal cartilages 7–13. It is thick anteriorly, with compact fibres, but it thins out posteriorly, and no fibres are found a short distance behind the level of the anterior superior spine. The fibres end, after a transverse course, in an aponeurosis which passes behind the rectus and joins its neighbour. Six intercostal nerves and arteries run between the fibres and appear as prominent lines. No fibres are connected to the cremaster sac. Fibres fill in the space between the xiphoid and costal cartilages. Some fibres are actually continuous with the diaphragm.

Parsons and Windle (102) record conditions in the Ungulata which are much as those described above.

The *rectus abdominis* consists of superficial and deep parts. The former springs by a strong aponeurosis from the inner $1\frac{1}{2}$ inches of the pelvic brim; it is fused with its neighbour, and it joins the deep part in the middle of the abdomen. The deep part is massive and entirely muscular. It arises from the

symphysis pubis and inner two inches of the pelvic brim. The entire muscle is inserted into the whole length of the

Text-figure 12.



Inguinal canal and contents. C.G.S: sac with genital scent glands; C.M: cremaster muscle arising from internal oblique (I-O.M.) deep to transversalis aponeurosis (T.E.); E.I.V: external iliac vessels; P: penis; S.C: spermatic cord; S.A and S.V: spermatic artery and vein.

sternum and the inner ends of the cartilages as far forwards as the first. No inscriptiones are present.

In the Edentata the muscle reaches the first rib except in *Bradypus*, in which it stops at the third or fourth rib. In the Ungulata it also goes to the first rib. And in both the number of inscriptiones varies.

The *pyramidalis* is absent as in the other Edentata and the Ungulata.

The *cremaster sac* (text-fig. 12) is a protrusion of peritoneum covered by the fascia and by a cremaster muscle derived from the internal oblique. The transversalis muscle does not cover or cross it, and the external oblique parts to give it a passage. It ends blindly, but a ligament, which Weber (99) calls the chorda gubernaculi, runs from the fundus to the deep surface of the skin surrounding the genital area. On opening the sac the testis is seen to be contained in the sac along with its mesentery (text-fig. 12), and several gubernacular bands are seen running from the globus major, under the epididymis, and along the edge of the genital mesentery to the wall of the sac and deep surface of the commencement of the chorda gubernaculi. Weber figures a narrower and more cylindrical sac than that which is present in my specimen.

Macalister (52) states that there is a wide inguinal canal for the testis in all the Edentata examined by him.

I did not have the opportunity of dissecting a female of any species of Edentata except *Manis tricuspis*, and I found that there is no large inguinal canal.

Muscles of the Perineum and Pelvis.

The cutaneous musculature sends backwards a large flat band of delicate fibres which covers the inguinal gland. Another bundle of fibres runs transversely to blend with the above on its lateral aspect.

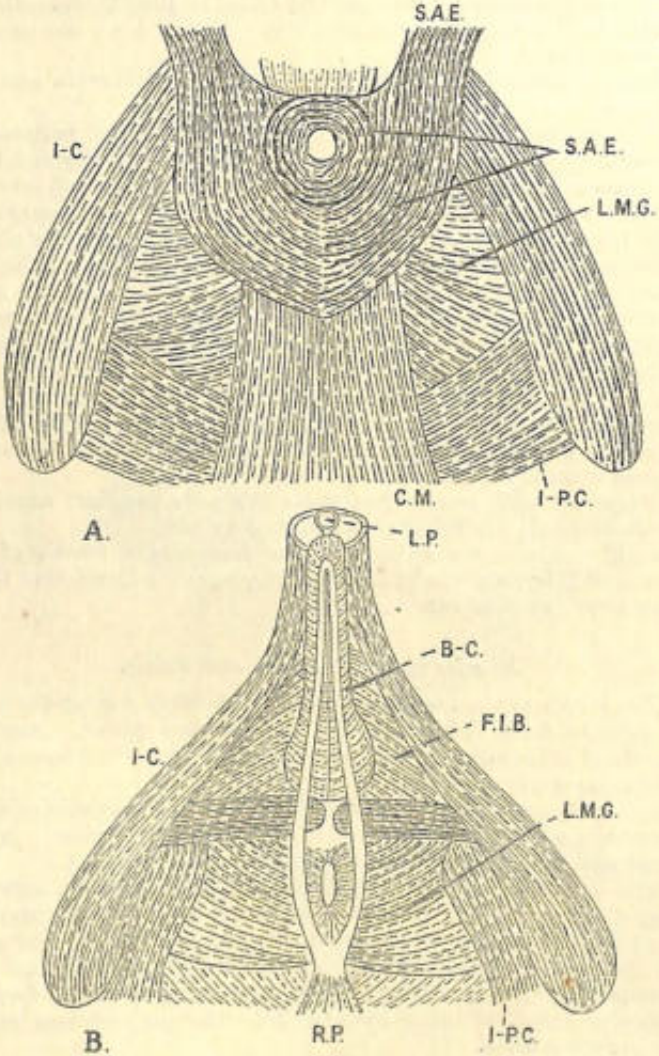
The *sphincter ani externus* is a cone of muscle fibre arising from the coccygeal fascia above to the perineal fascia below. A few fibres surround the anal orifice (text-fig. 13 A, S.A.E.).

The *retractores penis* (text fig. 13 B, R.P.) have a common origin, which blends with that of the sphincter ani externus. They form two narrow, muscular slips which pass on the sides of the anus between the sphincter ani superficially and the rectum deeply. Anteriorly they come together to form a muscular sheet, which is inserted into the prepuce and bulbo-cavernosus muscle.

The *levatores penis* (text-figs. 13 B and 14 B, L.P.) arise by muscle bellies from the deep surface and lower border of the pubic arch. After a short distance they come together, and have a strong, common tendon, which is inserted into the dorsum of the penis near the glans.

The *ischio-cavernosus* (text-fig. 13, I-C.) is a very powerful muscle arising from the tuber ischii and lower half of the pelvic arch, and it extends along the side and dorsum of the penis as

Text-figure 13.

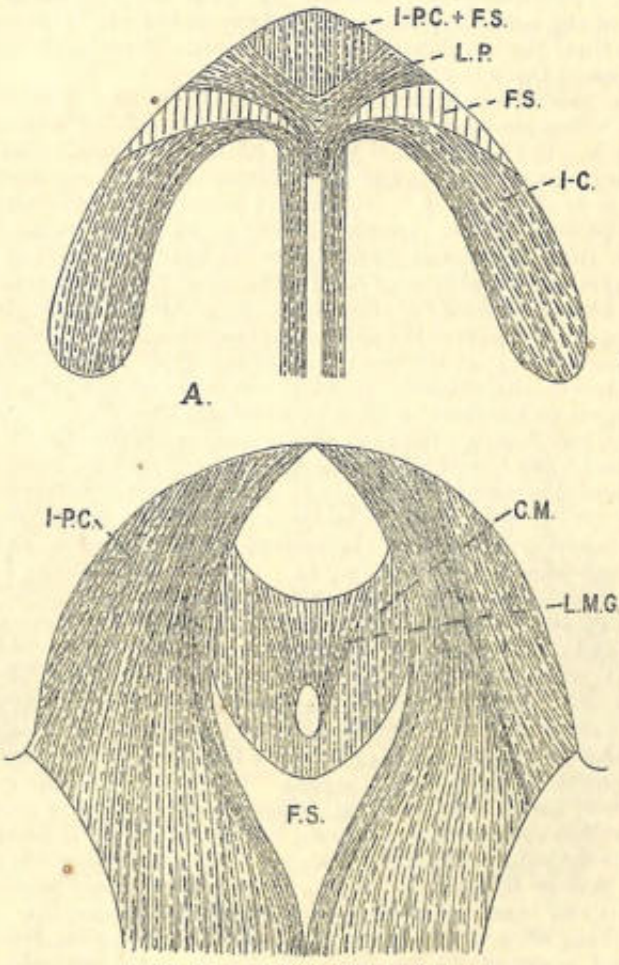


Perineal and pelvic muscles. F.I.B: connection between ischio-cavernosus and bulbo-cavernosus; L.M.G: longitudinal muscles of gut descending from above as a cone. Other letters in text.

far as the glans. The two muscles are in contact, but there is a groove on each aspect of the penis. The dorsal groove lodges the combined tendon of the levatores penis, which passes into

the ischio-cavernosi anteriorly, and the ventral groove contains the bulbo-cavernosus. Muscle fibres pass between the bulbo-cavernosus and two ischio-cavernosi. Each ischio-cavernosus

Text-figure 14.



Penile (A) and pelvic (B) muscles. F.S: fascial stratum; C.M: caudal muscles. Other letters in text.

sends a transverse bundle of fibres to the central point of the perineum between the bulbo-cavernosus and rectum. These slips are not in contact. The two ischio-cavernosi are connected

under the levatores penis to the lower border of the pubic arch by a sheet of fascia.

The *bulbo-cavernosus* (text-fig. 13, B-C.) arises posteriorly from the central point of the perineum, and its fibres run round the corpus spongiosum. On the ventral aspect there is a median raphé. Posteriorly and laterally its fibres are continuous with those of the ischio-cavernosi. Anteriorly and ventrally it receives fibres from the combined retractores penis. Beneath the bulbo-cavernosus there is a strong fibrous shelf.

The *levator ani* is absent as a distinct muscle. The coarse fibres which are seen beneath the sphincter ani and retractores penis are the longitudinal muscles of the gut wall. The gut passes through between, and is supported by two strong muscular shelves formed by the combined ilio-coccygeus, ischio-coccygeus and pubo-coccygeus muscles (text-fig. 14 B, I-P-C.). This sheet arises from the deep aspect of the pelvic brim from the symphysis pubis mesially to the sacro-iliac joint laterally. The fibres are inserted into the ilium down to the ischial tuberosity. The mesial fibres of the neighbouring muscles form the most ventral of the caudal muscles. They are connected by an aponeurosis, which is bound to the mid-ventral line of the coccygeal vertebræ by an aponeurotic septum.

The pelvic cavity has thus two lateral compartments. Each is closed behind by the fusion of the two shelves with the rest of the caudal muscles. Laterally it is closed by the pelvic bones. And it is open both mesially and towards the abdomen. Between the two shelves the rectum and urino-genital passages pass to their exits in the mid line.

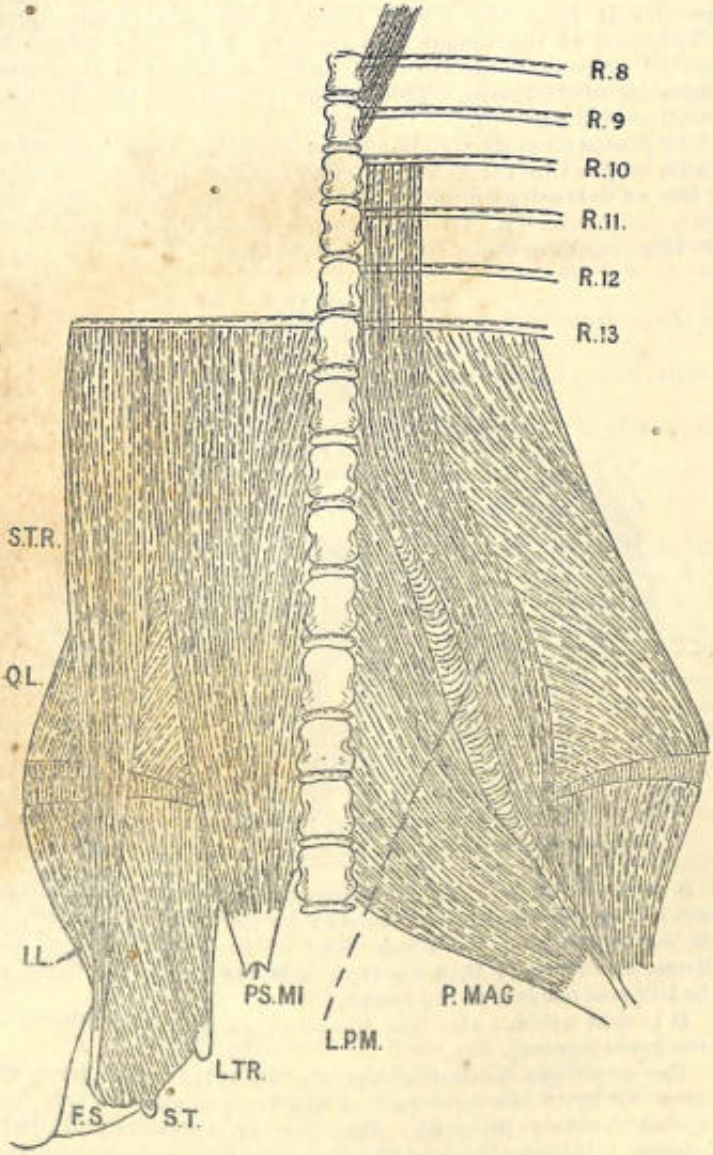
From a study of this animal one can easily understand how these sheets become attached to the rectum to form a levator ani in the adoption of the erect attitude.

The *psoas parvus* (text-fig. 15, Ps.MI.) is a muscle of very great strength. It arises by a long fascial origin from the surface of the psoas magnus and from the bony part of the last rib lateral to the psoas magnus. The fascia covers the quadratus lumborum. It gets thick muscle fibre from the sides of the bodies of the lumbar vertebræ. The insertion into the pectineal tubercle is by a strong cylindrical tendon. A slip of the muscle is detached to join the psoas magnus. The attachments show how this muscle is a flexor of the trunk. The deep surface is extensively fused by crossing slips with the psoas magnus.

A long narrow muscle (text-fig. 15, L.P.M.) arises from the ventral aspect of the transverse processes of the posterior four (10-13) dorsal vertebræ, from the ventral aspect of the inner ends of the lower four ribs, and from all the lumbar transverse processes. It joins the two parts of the iliacus where they join.

The *psoas magnus* (text-fig. 15, P.Mag.) arises from the sides of the bodies and ventral aspects of the transverse processes of all the lumbar vertebræ. It is fused with the preceding muscle and with the psoas parvus. So there is with the preceding

Text-figure 15.

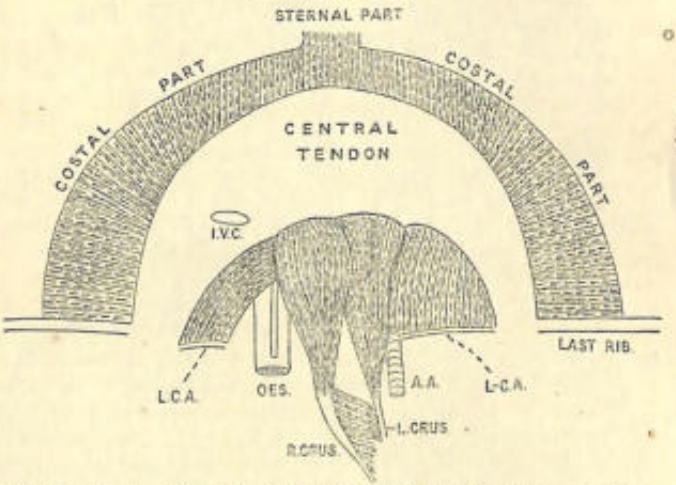


Muscles of the dorsal abdominal mass. Ribs are numbered. Letters in text.

a long and powerful muscle mass stretching from the tenth dorsal to the fifth lumbar vertebra. Only a very short distance separates it from the muscle sheet at the side of the lower oblique part of the longus colli (text-fig. 7 A). The muscle is inserted by tendon into the front and inner aspect of the lesser trochanter of the femur. This tendon is fused with the muscular insertion of the iliacus.

The *iliacus* (text-fig. 15, IL.) arises from the front and outer border of the ilium from the anterior superior spine downwards. It has an extensive muscular insertion into the femur from the lesser trochanter (L.TR.) down to the sharp tubercle (S.T.) on the ridge running down from the trochanter.

Text-figure 16.



The diaphragm. A.A: abdominal aorta; I.V.C: inferior vena cava; OES: œsophagus and left vagus nerve; L-C.A., L.C.A: lumbo-costal arches.

A muscular strip (L.TR.) running from the upper and lateral part of the psoas parvus is attached by the cord-like tendon to the spine marking the lower limit of the attachment of the iliacus, and fascia (F.S.) runs from this tendon as far down as the internal condyle of the femur.

It is thus evident that the ilio-psoas group of muscles is of very great power.

The *quadratus lumborum* (text-fig. 15, Q.L.) arises from the lower border of the inner half of the last rib and the first four lumbar transverse processes. The fibres run postero-laterally to be inserted into lateral inch of the iliac crest, the anterior superior spine and the tubercle close to it. It is fused with the iliacus.

Diaphragm:—The diaphragm is composed of several parts surrounding a horseshoe-shaped central tendon. On each side

there is a lateral part arising from the deep surface of the last rib, and there is a single slip from the back of the sternum. The two parts fuse to form a muscular semilune (text-fig. 16). On each side there is an intermediate part fused with the lateral border of each crus. The two crura form two central strips which blend with one another and with the intermediate parts. The right crus arises from the left side of the body of the seventh lumbar vertebra, and it receives slips from the other lumbar vertebræ. The left crus arises from the second, third and fourth lumbar vertebræ, and fuses with the right crus. The central tendon is moderately large.

The aorta passes through between the left crus and left middle parts. If this is the usual arrangement in *Orycteropus* it is a very uncommon condition.

The œsophagus passes through between the right crus and right middle parts.

The inferior vena cava passes through the tendon, and receives the phrenic veins as it does so.

There is no connection between the lateral parts of the diaphragm and the central parts.

Muscles of the Fore Limb.

Pectoralis Major (text-fig. 17 A):—The muscle is divisible into three parts. The first, or thickest part (P.Ma. 1), arises from the manubrium sterni, where it fuses with the sterno-mastoid and depressor auriculæ. No fibres come from the clavicle, but the muscle covers the sterno-clavicular joint. It is inserted into the outer part of the pectoral crest of the humerus and the fascia over the great tuberosity. The second part (P.Ma. 2) arises from the front of the gladiolus and xiphoid cartilage; and it is inserted into the outer and inner aspects of the pectoral crest by tendon of the aponeurosis. Aponeurosis connects it to the tendon of the biceps and clavicular deltoid. Humphry (**43**) observed a direct continuity of muscle fibres. The third part, or pectoral quartus (P.Ma. 3), fuses with the external oblique muscle of the abdomen, and rises from the outer surfaces of some hind ribs, interdigitating with the latissimus dorsi. It is inserted by aponeurosis into the aponeurosis of the gladiolar fibres, the inner aspect of the pectoral crest and the fascia over the great humeral tuberosity. Galton (**33**) points out that there is a closed aponeurotic sac concave upwards.

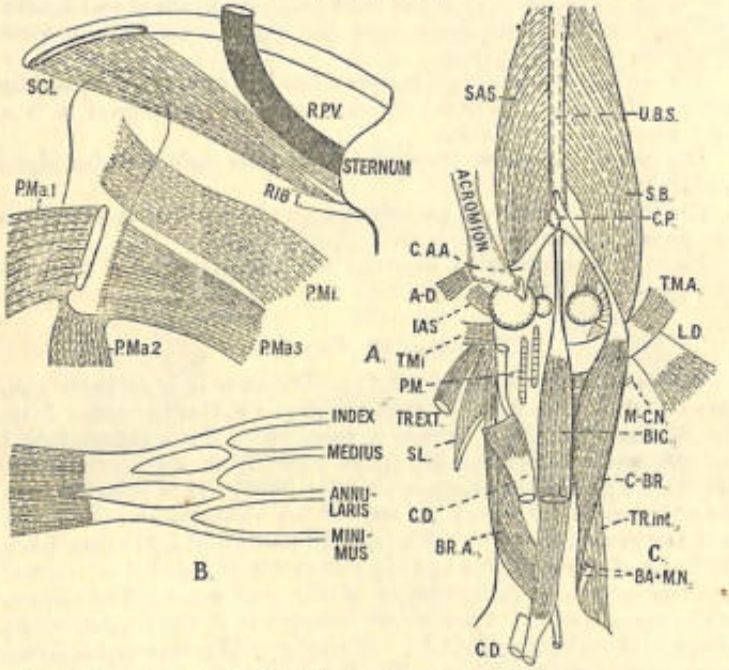
In the absence of the clavicular fibres the muscle is similar to that in the Manidæ, Myrmecophagidæ and *Cyclothurus*, and it differs from that in *Dasypus*, *Tatusia*, *Chlamydophorus* and *Bradypus*, which has such fibres.

There is no special affinity between the pectoralis major of *Orycteropus* and that in the Ungulata.

The *pectoralis minor* (text-fig. 17 A, P.Mi.) arises from the 5th, 6th and 7th costal cartilages, and is inserted into the aponeurosis

connecting the second and third parts of the pectoralis major to the fascia over the shoulder joint. Galton (33) gives the origin as the 4th, 5th and 6th costal cartilages and its insertion much as that in my specimen. Humphry (43) gives the origin as from two costal cartilages near the hinder part of the sternum, and the insertion as the outer bicipital ridge.

Text-figure 17.



Muscles of the pectoral region (A), fingers (B), and arm (C). In C the scapula and humerus are in line and viewed from above. A-D: acromio-deltoid; B.A+M.N: brachial artery and median nerve; C-A.A: coraco-acromial arch; C.D: clavicular deltoid; C.P: coracoid process; L.D: latissimus dorsi; M-C.N: musculo-cutaneous nerve; P.M: pectoralis major; R.P.V: right precaval vein; U.B.S: upper border of scapula. Other letters in text.

This muscle is absent in *Chlamydophorus*, *Tatusia*, *Cyclothurus*, *Tamandua* and *Myrmecophaga*. Meckel and Maclister (53) saw no muscle in *Bradypus*, but Cuvier and Humphry did. In Ungulates the muscle is present.

The *subclavius* (text-fig. 17 A, SCL.) is a very powerful muscle, but the costo-coracoid membrane and ligament are absent. It arises by two heads. One head springs from the side of the manubrium sterni, and the other arises from the junction of the first costal cartilage and the manubrium. After a short course

the lower head receives the upper one, and a strong muscle is formed. This passes over the shoulder joint and under the outer part of the clavicle; and it is inserted into the back of the outer half of the clavicle, the acromion and the fascia over the supraspinatus. Other authors give a greater scapular and smaller clavicular insertion: indeed Windle and Parsons (**103**) say that the muscle approaches the sterno-scapularis of several Rodents. In the insertion there is a sesamoid bone as described by Galton (**33**) but denied by Macalister (**53**). Humphry (**43**) gives the origin as the first two costal cartilages.

Galton (**33**) traced a connection between the fibres of the subclavius and those of the upward prolongation of the rectus abdominis to the first rib, and Rolleston (**84**) homologized the subclavius with the levator humeri of Birds. In this animal there is no connection on either side.

Hyrtl (**45**) described the subclavius as consisting of three parts, but the only possible trace of such a division in this animal is the presence of two heads of origin.

The subclavius is absent in the Myrmecophagidæ and Manidæ. In the Dasypodidæ there is some similarity to the conditions described above, for it is inserted into the acromion and the fascia over the supraspinatus. In the Bradypodidæ the bony insertion is greater than in *Orycteropus* and the Dasypodidæ, for it is into the clavicle, acromion and coracoid.

As regards the Ungulata, Parsons and Windle (**101**) say: "As the clavicle is always wanting the subclavius, if it is present at all, is always continued from the junction of the first or more ribs with the sternum to the fascia over the supra-spinatus."

Deltoid:—This muscle is composed of three parts—clavicular, acromial and scapular. The clavicular part is separated from the pectoralis major by a well-marked delto-pectoral triangle. The clavicular part is triangular in shape. It arises from the front of the lateral half of the clavicle, and overlaps the acromial deltoid and lateral part of the pectoralis major. It is also connected to the fascial insertion of the pectoralis major. It ends in a tendon which joins that of the biceps. When an attempt is made to separate the tendons of the biceps and clavicular deltoid, it will be found that they are inseparable only at the insertion into the radius; fascia only binds the two together down to the insertion. The acromial part arises from the under surface of the acromion process, and is inserted into the deltoid ridge. The scapular part is a narrow muscle arising from the scapular spine and being inserted into the deltoid ridge along with the acromial part. Galton (**33**) and Cuvier (**21**) observed three parts as above, but Humphry (**43**) saw only the clavicular and acromial parts.

Parsons and Windle (**103**) point out that the Edentata, as a rule, have the usual three parts of the deltoid, and the clavicular part unites with the trapezius to form the cephalo-humeral when there is no clavicle. There are variations in the insertions as

well, there being differences in the extent of humeral and radial attachments as follows:—

	Cephalo-humeralis.	*Attachment to humerus.*	*Attachment to radius.*
Bradypus	+	All three parts.	None (103).
Choloepus	+	(1) All three parts.	None (103, 55).
		(2) Spinous part.	Clavicular and acromial parts.
Tamandua	+	All three parts.	None (21, 103).
Myrmecophaga...	+	All three parts.	None (54, 82, 103).
Cyclothurus		All three parts.	None (21, 42, 60).
Manis.....	+	All three parts.	(42, 54, 103).

In the Ungulata the acromial part is suppressed except in *Elephas*, *Hippopotamus*, *Tragulus*, *Tapirus* and *Hyrax*. The clavicular and spinal parts are present.

Scapular Muscles:—The *supraspinatus* (text-fig. 17 C, Sas.) is larger than the infraspinatus, and arises from the entire supraspinous fossa. It passes under a strong coraco-acromial ligament and has a wide insertion into the inner aspect and upper border of the great tuberosity of the humerus.

The *infraspinatus* (text-fig. 17 C, Ias.) arises from the whole of the infraspinous fossa, and is inserted by tendon into the outer border of the great tuberosity of the humerus. It excludes the teres minor from the tuberosity.

Parsons and Windle (103) point out that the supraspinatus is larger than the infraspinatus in the Edentata, and the same condition holds in the Ungulata (101). The supraspinatus is cleft in the Ungulata and embraces the long head of the biceps, but there is no cleavage in *Orycteropus*, the two muscles only lying side by side.

The *subscapularis* arises from the whole of the subscapular fossa of the scapula. It passes under the tendinous and aponeurotic origin of the coraco-brachialis, and is inserted into the lesser tuberosity of the humerus (text-fig. 17 C, Sb.). The muscle is not cut up by aponeurotic septa.

The characters of the subscapularis, with the exception of the septal planes cutting it into bundles, are generally similar in Edentates and Ungulates. In some forms a special scapulo-humeralis is delaminated.

The *teres minor* (text-fig. 17 C, T.Mi.) has a musculo-aponeurotic origin from the lateral half of the axillary border of the scapula, but the muscular origin is only from the lateral inch. It is inserted into the humeral shaft just below the great tuberosity.

Parsons and Windle, in their paper on the Edentata (103), state that "in some cases it is fused with the infraspinatus or subscapularis, but from our experience of the Order we can quite easily understand how two observers, in the instances in which the muscle is not well marked, might readily differ in their description of the same animal, so we shall content ourselves by

saying that it is usually a distinct entity throughout the Edentata." In the Ungulata the muscle arises from the middle third of the axillary border of the scapula.

The *teres major* (text-fig. 17 C, T.Ma.) is a powerful muscle. It arises from the inner third of the axillary border of the scapula, where it is fused with the latissimus dorsi and most posterior part of the scapular origin of the triceps. I did not observe any fusion with the subscapularis, but Galton (33) did. The muscle ends in a ribbon-like tendon, which overlaps the ribbon-like tendon of the latissimus dorsi, and is inserted into the bicipital groove of the humerus.

Parsons and Windle (103) point out that the teres major is a powerful muscle in all Edentata except the Myrmecophagidæ, and Pouchet (82) describes the closely-blended teres major and latissimus dorsi as one muscle in *Myrmecophaga*.

The *biceps flexor cubiti* (text-fig. 17 C, Bic.) has only one head. This arises from the margin of the glenoid cavity of the scapula, the root and the under surface of the coracoid process. It passes over the shoulder capsule and between the two prominent humeral tuberosities. Up to this point it is a strong tendon. Soon it develops a long, fusiform muscular belly, which is inserted along with the clavicular deltoid into the inferior surface of the radial shaft. In Galton's specimen the following points of difference have been mentioned :—

1. The origin is restricted to the glenoid margin.
2. The muscle is fused with the clavicular deltoid.
3. The insertion is by a strong tendon instead of muscle.

There is no community of origin with the coraco-brachialis. There is no muscular insertion into the ulna, but strong fascia connects muscle and ulna. No lacertus fibrosus exists, and no fibres join the brachialis anticus.

It is possible, from the extensive origin, that both parts of the biceps are really combined.

The arrangements in other Edentata and some Ungulata are as follows :—

	Short head.	*Long head.*	*Humeral head.*	*Radial insertion.*	*Ulnar insertion.*	
Bradypus	+	+	+	+	+	(42, 53, 56, 103).
Choloepus	—	+	—	+	+	(55, 103).
Myrmecophaga.	+	+	—	+	+	(103).
Tamandua ...	+	+	?	+	+	(21, 83, 103).
Cyclothurus ...	—	+	—	+	+	(42, 54).
Dasypus	+	+	—	—	...	(35, 103).
Tatusia	—	+	—	—	+	(59).
Chlamydophorus	—	+	—	—	+	(52).
Manis	—	+	—	—	+	(103, 42).

	Coracoid origin.	*Glenoid origin.*	*Radial insertion.*	*Ulnar insertion.*
Tragulus	—	+	+	— (101).
"	+	—	+	+ (48).
Elephas	—	+	—	+ (21).
Hyrax	—	+	—	+ (62).
Antilope	—	+	—	+ (101).
Deer	—	+	+	— (101).
Brocket	—	+	—	+ (101).

In *Equus* and *Tapirus* the tendon is outside the shoulder capsule, but it is inside in the Artiodactyla.

The *coraco-brachialis* (text-fig. 17 C, C-Br.) arises from the inner aspect of the root of the coracoid process by a strong tendon, and this tendon is connected to the lesser tuberosity of the humerus by a strong fascia under which the subscapularis passes to its insertion. The muscle is inserted into the distal fifth of the shaft of the humerus and the internal supracondylar ridge. Delicate fascia connects the muscle to the humerus shaft higher up. The musculo-cutaneous nerve passes under the muscle on its way to the biceps. This muscle is really the coraco-brachialis longus. No brevis nor medius are present at all. At its insertion it splits to allow the median nerve and brachial artery to pass to the condylar foramen.

Galton (**33**) observed a trace of the coraco-brachialis brevis on one side in his animal.

The parts of the muscle as they have been recorded by other observers in the other Edentata and in the Ungulata are as follows:—

	Pars brevis.	*Pars medius.*	*Pars longus.*	
Bradypus	—	+	—	(103).
Cholœpus	+	—	+	(103).
Myrmecophaga.....	—	—	+	(given from biceps) (82).
Tamandua	—	—	+	(given from biceps) (21, 83).
Cyclothurus	—	—	—	(21, 54).
Dasypus	+	—	+	(103).
"	+	—	+	(33).
Tatusia	+	—	+	(52).
"	—	—	+	(59).
Chlamydophorus ...	—	—	—	(109).
"	+	—	—	(52).
Manis	—	—	—	(103).
"	—	—	+	(54).
Hippopotamus	—	—	+	
"	—	—	—	(21)?
Suidæ	—	+	—	(101).
Tragulus	—	+	—	(101).
"	+	+	+	(48).
Cervidæ	—	+	—	(101).
"	—	+	+	

	Pars brevis.	*Pars medius.*	*Pars longus.*	
Bovidæ	—	+	—	(101).
"	—	+	+	
Tapirus	—	+	+	(101).
Equidæ	+	+	—	(51).
Rhinoceros	—	+	—	(40).
"	—	—	+	
Hyrax	—	+	—	(62).
Elephas	—	+	+	

The *brachialis anticus* (text-fig. 17 C, Br.A.) is found only on the outer side of the deltoid. In this animal it has a very extensive origin, for it derives fibres from the whole outer border of the humerus from the lower limit of the great tuberosity above to the external condyle below. Fibres spring from the deltoid ridge, and some fibres connect it below to the biceps. It ends in a cylindrical tendon, which is inserted into the ulna below the coronoid process. It is covered by the supinator longus.

In the Edentata the variations occur in the number of the heads, in the degree of fusion with the biceps and in the insertion. These are shown as follows:—

	Outer head.	*Inner head.*	*Radial insertion.*	*Ulnar insertion.*	*Bicipital connection.*
Bradypus.....	+	—	+	+	+ or —
"	+	+			
Myrmecophaga	+	(In biceps.)	...	...	Extensive.
Tamandua	+	"	...	...	"
Dasypus	+	—			
Manis	+	—			
"	+	+			

In the Ungulata the outer head only is present. The insertion is usually ulnar, but sometimes there is an ulnar insertion.

The *triceps* is a very powerful muscle with four heads of origin.

The *internal head* (text-fig. 17 C, Tr. int.) arises from the posterior surface of the whole humeral shaft and internal supracondylar ridge, and is inserted into the back of the olecranon. It is crossed in its upper part by the tendons of the teres major and latissimus dorsi, and it fuses at its insertion with the dorso-epitrochlearis and flexor profundus digitorum. The *outer head* (text-fig. 17 C, Tr.Ext.) arises from the back of the anatomical neck of the humerus, and is fused at its origin with the inner head. It is under the teres minor and superficial to the supinator longus and brachialis anticus. It is inserted into the outer aspect of the olecranon, but much of it is fused with the anterior scapular head. The *anterior scapular head*, which is very large, runs from the anterior and middle thirds of the axillary border of the scapula to the whole of the back of the olecranon. It fused with the outer head and with the posterior scapular head. The *posterior scapular head* runs from the

posterior third of the axillary border of the scapula to the back of the olecranon. It is fused with the latissimus dorsi, dorso-epitrochlearis and anterior scapular head of the triceps.

Parsons and Windle (**103**) have reviewed the numerous observations of other anatomists on the triceps, and conclude as follows: "all the Edentata except the Bradypodidæ are remarkable for the great development and complexity of the extensor cubiti and for the presence of additional scapular origins." In the Ungulata the usual three parts are present, but they are liable to more or less subdivision. Still, the division of the scapular head into two planes is not quite the same thing as the presence of additional heads.

The *dorso-epitrochlearis* springs from the latissimus dorsi just before the latter becomes tendinous, and it fuses at the insertion with the posterior scapular portion of the triceps. It receives slips from the teres major and from the inferior angle of the scapula. In some other Edentates it has extra slips of origin, and it is frequently very powerful.

Parsons and Windle (**101**) make the following generalization regarding this muscle in the Ungulata: "the Ungulates have as a group an ill-defined latissimus dorsi, and that as an effect or coincidence the dorso-epitrochlearis is feeble and tends to shift its upper attachment (*i. e.* to the axillary border of the scapula or infraspinatus), but in the Tapirs, where the latissimus is very well developed, the dorso-epitrochlearis is also large and has the usual mammalian attachments."

The *epitrochleo-anconeus* shows nothing peculiar.

The *supinator longus* (text-fig. 17 C, S.L.) has a long origin from the posterior aspect of the shaft of the humerus from the neck above, and from the upper part of the external supracondylar ridge. As it progresses along the forearm the fibres from this broad attachment converge. It has a tendinous insertion into a tubercle on the lower end of the radius, and a fascial expansion over the flexor and extensor tendons as they pass over the wrist. There is no trace of lamination into two parts as is the case in the Bradypodidæ and Myrmecophagidæ. The muscle is absent in the Dasypodidæ, and it is variable in the Manidæ. When present in *Manis* it is connected to the deltoid. In a former paper I showed that some of these conditions are present in Marsupials (**87**). Thus in *Phascolarctos* the muscle is double, and there is a slip from the deltoid, and in *Phascolomys* the muscle is single, but is connected to the deltoid. In *Phascolarctos* it is inserted into the scapho-lunar bone. The muscle is absent in all Ungulata except *Hippopotamus*, *Rhinoceros* and *Elephas*.

The *extensor carpi radialis* is not divisible at its origin into long and short parts. It arises from the external supracondylar ridge below the lowest fibres of the supinator longus. At the lower end of the radius it gives off two tendons. The smaller tendon goes to the dorsum of the base of the metacarpal bone of

the index, and the larger one goes to the corresponding part of the middle metacarpal. Galton (33) gives their insertions as the radial aspects of these bones. Humphry (43) only mentions the slip to the medius. So it is evident that the extensor longior of human anatomy is small or absent; and Galton states that the "longior element is of secondary development." The important point in the muscles of other Edentata, and of Ungulata and Marsupialia are shown in the following table :—

	Origin.	*Extensor longior tendon.*	*Extensor brevior tendon.*
Phascolomys	Single.	+	+ (87).
Phascolarctos	Double.	+	+ (87).
Phalanger	"	+	+ (very large) (87).
Bradypus	Single.	+	+ (42, 53).
"	"	0	+ (103).
Cholœpus	Double.	+	+ (103).
Myrmecophaga	Single.	0	+ (very strong).
Tamandua	"	0	+ " "
Dasypus	"	+	+
Manis	"	0	+ (42, 103).
Suidæ	"	0	+ (21).
Tragulus	"	0	+ (48).
Dorcatherium	"	+	+ (101).
Camelidæ, Cervidæ, Giraffidæ, Bovidæ, Equidæ, Rhinocerotidæ	Single.	0	+ (101).
Procaviidæ	Double.	+	+ (62).
Elephantidæ	Single.	+	+ (97).

The conditions are such that *Orycteropus* agrees with some Marsupialia, Edentata and Ungulata in the characters of this muscle.

The *extensor communis digitorum* is a powerful muscle. It arises from the lower part of the external supracondylar ridge, and from the tubercle on the external condyle, whence the supinator brevis arises. It splits into two parts in the distal part of the forearm, and one of these gives rise to three tendons which are interconnected (text-fig. 17B), and all four divide. The lateral belly gives rise to two tendons, one of which supplies the index and communicates with half of the second to send a tendon to the medius. Half of the second tendon of the lateral belly unites with half of the solitary tendon of the inner belly to form the tendon to the annularis. And the inner half of the tendon of the inner part of the muscle furnishes the tendon to the minimus. In the other Edentata and in the Ungulata the chief differences are found in the number of digits to which the tendons are attached.

Extensors of the Pollex :—The extensor primi internodii and extensor secundi internodii pollicis are, as is to be expected, absent. The *extensor ossis metacarpi pollicis* has a long origin

from the lower two-thirds of the ridge on the inner aspect of the ulna and from the neck of the radius and interosseous membrane; and it is inserted into the dorsum of the trapezium. It is not divided into parts. In other Edentata it is inserted into the trapezium or the first metacarpal bone.

The *extensor indicis* runs from the inner border of the ulna to the proximal phalanges of the index and medius, passing deeply to the tendons of the extensor communis to the same digits. The *extensor annularis* arises from the external condyle, and its tendon sends slips to the proximal phalanges of the medius and annularis digit deep to the extensor communis. Galton (33) saw this arrangement, but Humphry (43) did not observe a connection to the medius in his specimen. Strong fascia connects the tendon to the minimus.

Parsons and Windle (103) do not mention the extensor annularis as a separate muscle, but they review the numerous observations on the extensor profundus digitorum, which includes the extensor indicis. They also seem to have included the extensor annularis.

The *extensor minimi digiti* arises from the outer aspect of the external humeral condyle. Its fusiform belly ends in the lower part of the forearm in a very powerful cord-like tendon. The tendon has a strong fibrous expansion, which is inserted into the whole width of the base of the proximal phalanx of the minimus, the sesamoid bone on the ulnar side of that digit and the ulnar side of the distal phalanx of the minimus. Galton (33) describes arrangements as above, but Humphry (43) and Cuvier (21) observed a slip to the annularis.

The *extensor carpi ulnaris* arises from the external condyle of the humerus. Its strong tendon divides into two slips, which run to the bases of the metacarpal bones of the annularis and minimus. Hence, with the extensor radialis each metacarpal bone gives an attachment to an extensor tendon. These are shown in the following table. An attachment marked M is to a metacarpal, all the rest being into digits.

	Index.	*Medius.*	*Annularis.*	*Minimus.*
Extensor radialis	M	M	—	—
„ ulnaris	—	—	M	M
„ communis	+	+	+	+
„ indicis	+	+	—	—
„ annularis	—	—	+	+
„ minimi digiti ...	—	—	+	+

The *palmaris longus* is fused with the flexor sublimis. As regards other Edentata, the muscle is present in the Bradypodidæ and *Tamandua*. In *Manis* it is either present or fused with the flexor sublimis.

The *flexor carpi radialis* arises from the internal humeral condyle below the pronator radii teres. Its strong tendon is

inserted into the palmar aspect of the base of the first metacarpal bone, the sesamoid bone over the base of the first metacarpal, the styloid process of the radius and the strong fascia over the carpal joints. Parsons and Windle (103) review the literature, which shows that the insertion of the muscle varies very much in the Edentata, and some specimens of *Manis* agree with some examples of *Orycteropus*.

The *flexor carpi ulnaris* is an extensive muscle arising from the distal two-thirds of the shaft of the ulna, and fibres spring from the flexores sublimis and profundus. It is inserted into the whole length of the style-like pisiform bone, the hook of the unciform bone, the base of the fifth metacarpal bone and the sheath of the innermost tendon of the flexor profundus digitorum. There is no trace of the small deep part of the muscle which Galton (33) described.

The *flexor sublimis digitorum* arises from the internal humeral condyle by an exceedingly powerful tendon which passes through the mass of the flexor profundus. At the level of the carpo-metacarpal joint the flattened muscle gives off four bands—one to each joint. Galton (33) points out that each tendon divides into two parts opposite the metacarpo-phalangeal joint. One of these is attached along the sides of the phalanges and forms a sheath for the flexor profundus; the other corresponds to the flexor perforatus. I am able to confirm this observation. *Bradypus* has no trace of this muscle, as is the case in some examples of *Manis*; in the latter the conditions are most variable.

The *flexor profundus digitorum* has humeral, ulnar and radial parts. The humeral part arises from the lower and back part of the internal condyle of the humerus and from the tendon of origin of the flexor sublimis. The ulnar factor arises from the distal two-thirds of the palmar and interosseous aspects of the shaft of the ulna, the coronoid process of the ulna, and by a strong bundle with the humeral factor and the tendon of origin of the flexor sublimis. The radial factor arises from the ventro-medial aspect of the radial shaft deep to the insertion of the pronator radii teres. All the factors come together to form an expansion which gives off four lumbrical muscles from its deep aspect, and a strong tendon to the terminal phalanx of each of the four digits. Parsons and Windle (103) point out how the factors composing the muscle vary in the Edentata.

The *pronator radii teres*, as in other Edentata, runs from the internal condyle of the humerus to the distal half of the radius.

The *pronator quadratus* occupies the entire interosseous space. It has a powerful tendon which passes downwards and outwards to join the expansion of the tendon of the flexor carpi radialis. Galton (33) described an equally large muscle, but Humphry (43) described a small one. In the other Edentata the muscle is small in the Bradypodidæ, large in the Myrmecophagidæ and absent in the Dasypodidæ and Manidæ.

Lumbricales:—Four lumbrical muscles are given off from the deep aspect of the expansion of the flexor profundus digitorum. Each muscle is attached to the radial side of the proximal phalanx of a digit. All except the lumbrical muscle to the minimus have tendons, but that one is muscular throughout. The number of muscles in other Edentata vary considerably (**103**).

The *palmaris brevis* is absent.

The *pollical intrinsic muscles* are absent.

The *intrinsic muscles of the manus* are as follows:—

1. *Abductor minimi digiti* from the front of the unciform bone to a sesamoid bone at the base of the fifth proximal phalanx. Galton (**33**) observed a continuity between it and the superficial interossei, but I did not do so.

2. *Adductor minimi digiti* or first superficial interosseous muscle from the palmar ligament in front of the unciform bone to the radial side of the proximal phalanx of the minimus.

3. *Adductor indicis* or second superficial interosseous muscle from the palmar ligament close to the base of the third and fourth metacarpals and to the ulnar side of the proximal phalanx of the index.

4. *Deep interossei*:—These arise from metacarpal ligaments, and one goes to each side of the index, medius and annularis, the minimus not receiving any, so there are six muscles. Galton (**33**) gives a very full account of these interossei, and I am quite in agreement with his statements. Parsons and Windle (**103**) describe each digit as receiving two flexors breves, but they have erroneously reviewed the writings of the authors whom they quote in calling the interossei flexores breves.

5. *Abductor indicis* which is really the interosseous of the index and not a separate muscle.

There is some confusion in reading the accounts of the arm muscles, for it is not certain what is meant by the first digit. There are only four digits, the thumb being absent. So the first digit of the writers is really the second digit of the hand. To avoid confusion in the foregoing account of the arm muscles I have used the names which are usually applied to digits instead of numbers.

The two superficial interossei are really contrahentes muscles, and they are the only contrahentes. Their muscle bellies are arranged like the limbs of an X.

There is no *flexor brevis digitorum* such as exists in the Myrmecophagidæ. *Bradypus*, *Myrmecophaga* and *Tamandua* have pollical muscles. *Manis* has a quite different arrangement from *Orycteropus*, for it has adductors of the index and minimus, and four dorsal but no palmar interossei.

Muscles of the Hind Limb.

The *gluteus maximus* is a broad, thin muscle arising from the iliac crest and sacral aponeurosis, and it is inserted by tendon

into the third trochanter of the femur. The posterior part is overlapped by the biceps femoris, and it overlaps the tensor fasciæ anteriorly. Galton (33) describes conditions similar to the above, but Humphry (43) describes a muscle which combines the tensor fasciæ, gluteus maximus and biceps and running to the heel; he does not describe the biceps at all in his paper. Cuvier (21) figures the muscle being inserted into the middle of the femur.

The *gluteus medius* arises from the outer surface of the ilium and edge of the sacrum, and it is inserted into the outer and inferior part of the great trochanter, covering the insertions of gluteus minimus and pyriformis. A slip of the muscle is attached to the outer and inferior part of the femoral shaft as far almost as the third trochanter. It is fused with the gluteus minimus over a large area, and with the pyriformis at its origin. And it appears that imperfect separation of these three muscles is an Edentate character. The *gluteus minimus* is inserted into the upper part of the great trochanter.

The *pyriformis* is a very powerful fan-shaped muscle lying between the gluteus medius and minimus. It arises from the outer surface of the ilium close to its junction with the sacrum, and slightly from the inner surface of the bone. Its strong tendon is inserted into the outer surface of the great trochanter below the insertion of gluteus minimus. Between it and the subjacent gluteus minimus lies the superior gluteal nerve.

The *obturator externus* arises from the bony margin of the obturator foramen and from the outer surface of the fascia filling the opening. Its strong tendon is implanted into the digital fossa of the femur.

The *quadratus femoris* is absent, as pointed out by Galton (33) and Humphry (43).

The *obturator internus* arises in the usual Mammalian manner, contrary to the condition in other Edentata, and, after a very short extrapelvic course, it fuses with the strong tendons of the gemelli. The *gemelli* are strongly developed, and each has two heads of origin. But there is a conjugation of the tendons to form one, which fuses with the obturator internus. And the combined insertion is into the digital fossa above that of the obturator externus.

Galton (33) points out that there is frequently, but not always, a compensatory enlargement of the gemelli when the quadratus femoris is absent in the Mammalia.

The *rectus femoris* is a strong muscle arising from the superior and posterior aspects of the acetabulum; and it is inserted into the upper border of the patella, being fused on either side with one of the vasti muscles.

The *vastus externus* in my specimen differs considerably from that in Galton's account. It arises from the front and lateral surfaces of the femur as far up as the edge of the great trochanter,

and it passes on to the top of the trochanter under cover of the gluteus medius. It is inserted into the lateral part of the patella, and slightly into the lateral condyle of the femur.

The *vastus internus* has a linear origin from the inner border and anterior surface of the shaft of the femur, so the origin curves obliquely round the bone. It fuses with the vastus lateralis in front, and the two muscles cannot be separated. It is inserted into the inner part of the patella and into the internal femoral condyle. The aponeurosis of the sartorius fuses with it superficially.

The ligamentum patellæ is not peculiar, but there is a lateral ligament to the external femoral condyle.

The *crureus and subcrureus* are absent, in which respect I agree with Galton (33).

Parsons and Windle (103) make the following generalizations regarding the quadriceps in the Edentata:—

1. The rectus femoris has a single origin in which the acetabular and iliac heads are fused. In Man they are separate in association with the erect attitude.

2. The vastus lateralis is always larger than the medialis.

3. It is always difficult to separate the medialis from the vastus profundus (crureus).

As regards the Ungulata we note:—

1. There is always evidence that the rectus femoris has two heads of origin.

2. The vastus externus is larger than the vastus internus except in the Tapir.

3. The crureus is more distinct than in many other Orders of Mammals, and arises from the inner side, front and outer side of the femoral shaft.

The *sartorius* arises from the ilio-pectineal tubercle. It crosses the thigh from the inner to the outer side, whereas the reverse is the case in other Mammals. The difference is due to the fact that the origin has shifted from the anterior superior iliac spine. Its lowest fibres are in contact with the highest fibres of the gracilis. It is inserted into the aponeurosis of the gracilis and the fascia over the rectus femoris, but it has no bony insertion.

The internal saphena vein lies under cover of the sartorius, and the vein and saphenous nerve pierce the aponeurosis of the gracilis.

Galton (33) describes conditions similar to the above, but Humphry (43) states that the muscle arises from the last rib external to the psoas.

In *Bradypus* and *Choloepus* the sartorius arises from the iliac crest and it is inserted into the inner side of the head of the tibia; but Macalister (53) gives a larger origin from the iliac spine and Poupart's ligament, and an additional insertion into the inner condyle of the femur.

In *Chlamydophorus* and *Dasypus* it arises from the psoas tendon, whilst it springs from Poupart's ligament in *Tatusia*.

In *Tamandua* according to Parsons and Windle (103) and in *Cyclothurus* it springs from the psoas tendon, but in *Myrmecophaga* it has human attachments.

In *Manis* it is iliac in origin, and patellar in insertion.

From these records it is evident that the sartorius in all Edentates except the Bradypodidæ and *Myrmecophaga* is displaced inwards as in many Ruminants and Rodents, the displacement being greatest in *Orycteropus*.

The sartorius and gracilis cover a large area of the inner side of the thigh.

The *gracilis* has a long origin from the pectineal line just mesial to the tubercle, and from the whole length of the symphysis pubis. It is thick at its origin, but it thins out and has a long fascial insertion into the whole length of the tibia from the knee to the ankle. There is no trace of a division into two parts as in many other Edentata.

In *Bradypus* one part, running from the inner end of Poupart's ligament to the inner surface of the tibia, is separated from the symphysial part running to the fascia on the outer side of the leg along with the insertion of the biceps. In *Choloepus* (103) it is also double. Of the Myrmecophagidæ, *Tamandua* has a single muscle (103) but *Myrmecophaga* (103) has a double one. In the Manidæ and Dasypodidæ the muscle is single or double, and is extensive.

Pectineus:—This muscle consists of two parts. The superficial part arises from the ilio-pectineal tubercle below the sartorius, and is inserted into the linea aspera of the femur below the level of the ilio-psoas. The deep part runs from the ilio-pectineal line below the gracilis to the posterior intertrochanteric line of the femur. Galton (33) and Cuvier (21) record a double muscle, but Humphry (43) saw a single one only. In *Bradypus* and *Tamandua* it is double, but it is single in *Myrmecophaga*, *Cyclothurus*, the Dasypodidæ and the Manidæ.

The *adductor longus* is a narrow, thin muscle running from the ilio-pectineal line and pubic spine below the pectineus and gracilis to the linea aspera of the femur close to the pectineus.

In some Edentata the presemimembranosus muscle is included in the adductor mass, and one of these is *Orycteropus*.

The *adductor brevis* and presemimembranosus are united to form a very strong mass arising from the symphysis pubis and greater part of the descending ramus, but no fibres reach the tuberosity of the ischium. The insertion on the back of the femur extends from the third trochanter to the origin of the gastrocnemius.

The *adductor magnus* is represented by the part known as the adductor minimus. This arises from the ascending ramus of the ischium and from the space between the tuber ischii and obturator foramen. It has a cylindrical tendon which is inserted into the sharp tubercle on the ridge running down from the lesser trochanter.

There are great variations in the adductors of the Edentata, and the following list analyses the recorded observations of other authors:—

Bradypus : Four adductors and a pectineus (Meckel, 59).
" : Adductor longus and another mass (Parsons and Windle, 103).
Myrmecophaga: One mass with three heads of origin (Meckel, 59).
" : Mass split into two planes.
Tamandua : Mass split into two planes (Parsons and Windle, 103).
Cyclothurus : Mass split into three layers (Galton, 34; Humphry, 42; Meckel, 60).
Dasypodidæ : Mass indivisible.
Manidæ : Mass split into three layers (longus, brevis, magnus).

In the Ungulata the following facts are noteworthy:—

1. The pectineus is sometimes difficult to differentiate from the adductor longus when
2. The adductor longus is not clearly delaminated from the rest of the adductor mass.
3. There is no distinct adductor brevis (Parsons and Windle, 102).

The *semimembranosus* is a very powerful muscle overlapping the posterior border of the adductor brevis. It arises from the tuber ischii, the lower part of the ischiadic ramus and the fascia over the caudal muscles. It is inserted along with the sartorius and gracilis and also into the shaft of the femur above the internal condyle. This muscle is very similar in all Edentates. The *presemimembranosus* is included in the semimembranosus. In the Manidæ and Dasypodidæ it is closely united to the semimembranosus. In the Bradypodidæ and Myrmecophagidæ it is a very distinct muscle (Parsons and Windle, 103). In the Ungulata these muscles are fused for a considerable distance, beginning at the origin. In the Artiodactyla the mass has only an ischial head, but the Perissodactyla have both ischial and caudal heads of origin. The insertion is by a rounded tendon.

The *semitendinosus* is a powerful muscle, which has only the ischial head of origin, in which it agrees with the muscle in the Bradypodidæ alone, as can be seen from the following:—

	Ischial head.	Caudal head.
Orycteropus	+	0
Bradypus	+	0
Cholœpus (103)	+	0
Myrmecophaga (103)	+	+
Tamandua	0	+
Cyclothurus (103)	Variable.	+
Dasypus	+	0
Tatusia (103)	+	+
Manis	Variable.	+

The insertion in *Orycteropus* is into the upper third of the inner surface of the shaft of the tibia.

Parsons and Windle (102) summarize the conditions in the Ungulata as follows:—"A caudal head is rarely found in the Artiodactyla, Chatin's Water Chevrotain and the Pig being the only exceptions we know. In the other suborders the Horse, Tapir and Hyrax have two heads."

The *biceps* is closely blended with the gluteus maximus, and it is difficult to distinguish between them in places. It arises from the fascia over the dorsal muscles. The upper part of the muscle is inserted by means of a tendon into a tubercle on the head of the fibula close to its union with the tibia, and this part of the muscle is continuous with the fascia into which the tensor fasciæ femoris is inserted. It is also fused with the semimembranosus. The rest of the muscle is inserted into the calcaneum. Galton (33) gives the insertion as the fascia of the leg close to that bone, but Cuvier (21) gives the insertion into the bone. There is no femoral origin to the biceps. The origin of the muscle in other Edentata and in Ungulata is as follows:—

	Long head.	Short head.
Bradypodidæ	+	+
Myrmecophaga	+	+
Tamandua	+	—
Cyclothurus	+	+
Dasypodidæ	+	—
Manidæ	+	+
Orycteropus	+	—
Ungulata	+	—

The *tibialis anticus* is a powerful and thick muscle arising from the upper ends of the tibia and fibula, from the patellar ligament and from the tendon of the biceps. It has two tendons which pass under a ligamentous band in the lower part of the leg, and are inserted into the base of the first metatarsal bone and entocuneiform respectively. Humphry (43) and Galton (33) describe similar conditions. It is easy to distinguish it from the other muscles of the region.

In the other Edentata the muscle varies in the extent of origin and in the number and attachments of the tendons. These differences are shown as follows:—

Bradypus	*origin*:	tibia and fibula;	*insertion*:		first metatarsal.
Choloepus	,,	,,	,,	,,	flexor tendons of leg.
,,	,,	,,	,,	,,	3 slips to flexor tendons.
Myrmecophaga	,,	upper 3/4 of tibia;	,,		as in *Orycteropus*.
Tamandua	,,	tibia and fibula;	,,		sesamoid on foot.
Cyclothurus	,,	,,	,,	,,	entocuneiform.
Dasypus	,,	,,	,,	,,	entocuneiform.
Manis	,,	,,	,,	,,	as in *Orycteropus*.

It is thus evident that *Orycteropus* resembles *Manis* most

closely in the characters of this muscle. The attachments to the first metatarsal and entocuneiform occur in Mammals belonging to other Orders.

The *extensor longus digitorum* arises from the outer surface of the external femoral condyle and from the interval between the tibia and fibula. It divides into four tendons which pass under the ligamentous band described above. They run to the outer four toes. The main part of the first tendon, which bifurcates, goes to the outer aspect of the index; and the small inner slip passes to join the tendon of the extensor hallucis, and then returns to join the inner part. The two parts then form an expansion over the first and second phalanges, and sends a slip to the ungual phalanx. The second tendon remains single, but the third and fourth divide and go to adjacent sides of the third and fourth toes. Thus each toe except the hallux, which receives one only, gets two tendons from the extensor longus.

This muscle varies in origin and insertion as follows:—

	Origin.	*Insertion.*
Bradypus.....	Femoral.	Metatarsals 1 and 3.
Tamandua	,,	Toes 2–5.
Dasypus	Fibular.	Toes 2–5.
Manis	Tibia and Fibula.	Toes 2–5 or 3–5.

The *extensor longus hallucis* is a delicate muscle arising by a flat belly from the front of the middle of the fibula. The slender tendon passes under the ligamentous band and passes to the terminal phalanx of the hallux. It is connected to the innermost tendon of the extensor longus.

The *extensor brevis digitorum* arises from the outer and anterior aspects of the os calcis, and from the calcanean tubercle, which articulates laterally with the astragalus. It ends in three tendons to the three middle toes. It is also connected to the tendon of the long extensor, which sends a slip to the extensor hallucis.

The extensor tendons of the toes are as follows:—

	I.	II.	III.	IV.	V.
Extensor hallucis	+	—	—	—	—
Extensor longus digitorum	+	+	+	+	+
Extensor brevis digitorum	—	+	+	+	—

Peroneal Muscles:—The peroneal muscular mass arises from the head and outer aspect of the fibula, the external lateral ligament of the knee joint and the external semilunar cartilage, and the tendons form four peronei:—

(*a*) *Peroneus brevis* to the outer side of the base of the proximal phalanx of the fifth digit.

(*b*) *Peroneus tertius* to the tubercle on the outer side of the base of the fifth metatarsal.

(*c*) *Peroneus quarti digiti* and *peroneus quinti digiti* combined. It is inserted into the bases of the proximal phalanges of the fourth and fifth toes (text-fig. 18).

(*d*) *Peroneus longus*, which crosses the sole and is attached to the base of the metatarsal of the hallux. Galton (**33**) described a slip running to the fifth metatarsal from the tendon.

Gastrocnemius:—The outer head arises from the outer side of the femur above the condyle by means of a strong tendon. The origin contains a large sesamoid bone, which plays on the femur just below the tendon. The cavity of its joint is continuous with the cavity of the knee joint. This sesamoid or fabella is present in other Edentates and in *Phascolarctos*, and many other Mammals. The inner head arises from the inner border of the femur above the condyle. Both heads join in the middle of the calf, and the strong tendo Achillis goes to the back of the os calcis. A muscular slip connects the gastrocnemius and soleus.

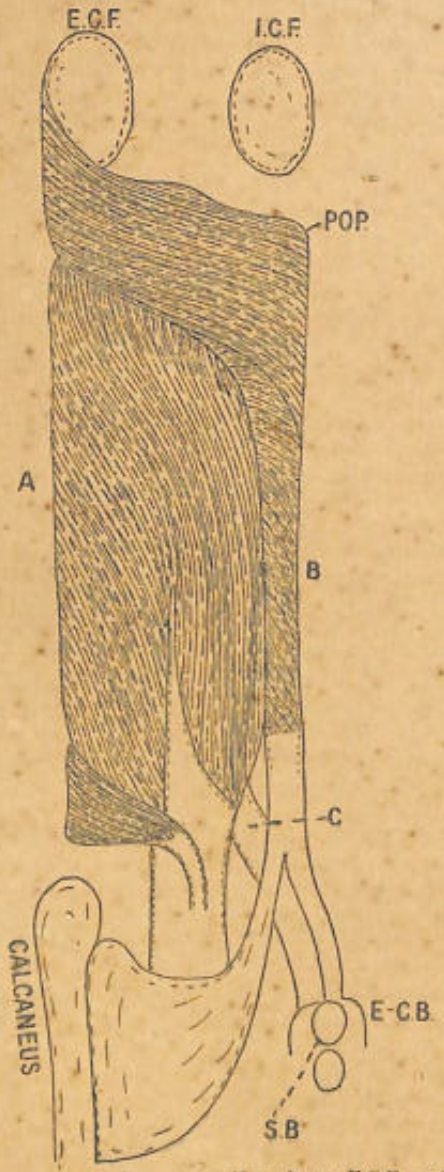
Soleus:—This broad muscle springs from a tubercle on the back of the head of the fibula, and it is inserted into the supero-mesial aspect of the os calcis. A sheet of fascia connects it to the back of the tibia on the line which a tibial head would be attached if present. Sometimes this muscle is described as a deep or third head of the gastrocnemius. The Edentate characteristic is the separate attachment of the tendo Achillis and of the soleus. It is a variable muscle in the Ungulata (**102**).

The *plantaris* is absent in this animal, but other observers have recorded it in *Orycteropus*. When present it shows the generalized arrangement of passing behind the medial malleolus and forming a flexor brevis digitorum of the four outer toes.

The *popliteus* (text-fig.18, POP.) is a powerful muscle with a muscular and tendinous origin from the back of the femur above the external condyle. It winds round below the condyle, and is very closely related to the back of the capsule of the knee joint. And it is inserted into the whole length of the back of the tibia from the head above to the malleolus below. No sesamoid bone occurs in the origin such as is present in the Bradypodidæ, Myrmecophagidæ and Manidæ. The Dasypodidæ have no sesamoid in the origin, which may be by two tendons. In all Edentata the muscle is large. In the Ungulata this muscle is not large, and Windle and Parsons (**103**) point out that a sesamoid bone is not usually present in the origin, though they observed one in the Tapir.

The conditions of the flexor longus digitorum, flexor longus hallucis and tibialis posticus in this animal differ in several respects from those recorded by Galton (**33**), Humphry (**43**) and others; and there is fusion between parts of them. Most superficially there is a large muscle (text-fig. 18 A) covering in parts of the peronei and popliteus. It arises from the posterior part

Text-figure 18.



Posterior tibial muscles. E.C.B: entocuneiform bone; E.C.F. and I.C.F: external and internal femoral condyles; S.B: sesamoid bone. Other letters in text.

of the fibula, the lateral part of the interosseous membrane and the interosseous surface of the tibia. The muscle fibres from the bones are planted into the sides of a tendon, which begins in the middle of the leg as a thin cord, but widens out to become a large tendon of very great power. A fan-shaped muscle, fusing above with the fibular component and rising from the back of the distal fourth of the fibula, is implanted into the ventral aspect of this large tendon. The tendon passes under a strong ligamentous bridge and splits into five tendons—one for each digit, including the hallux. The second muscle (text-fig. 18 B) arises from the head of the fibula, and is fused with the first muscle and with the popliteus. Its long tendon divides into two parts. Of these one goes to the sesamoid over the ento-cuneiform bone, and the other expands into a strong aponeurosis which covers the other muscles of the foot and is attached to the os calcis. The third muscle (text-fig. 18 C) arises from the interosseous membrane, and is fused with the other flexors and with the popliteus. Its powerful tendon is grooved, and is attached to the entocuneiform bone. It is probable that the first muscle combines the flexor longus digitorum and flexor longus hallucis, and the other two muscles are tibiales posticus. Galton (33) believes that it is difficult to distinguish the tibialis posticus from the flexor hallucis. No slip connects the first and second muscles as some have seen.

It appears that a double tibialis posticus is characteristic of the Edentata, except the Bradypodidæ in Windle and Parson's account, but the same condition occurs in some Marsupials and in the Seal. And the two long flexors are more or less fused. In the Manidæ they are more separate than in the other Families; and in them there is no tendon to the hallux, whereas tendons go to all digits in the other Families.

Lumbricales:—The number of lumbrical muscles is as follows:—

Bradypus and *Choloepus*—none.
Tamandua—none.
Myrmecophaga—four.
Dasypus—four.
Manis—three.
Orycteropus—four.

The *abductor hallucis* is reduced to fibrous tissue. It is absent in *Bradypus*, and it is present in the Myrmecophagidæ, Dasypodidæ and Manidæ.

The *abductor minimi digiti* is a flat muscle running from the outer surface of the calcaneus to the tubercle on the outer side of the base of the fifth metacarpal bone. It is closely related to the peronei, extensor brevis digitorum and flexor brevis minimi digiti. It is also present in all other Edentata except the Bradypodidæ.

The *flexor brevis minimi digiti* arises from the calcaneus and plantar ligament, and is inserted by a slender, but powerful, tendon into the base of the proximal phalanx of the fifth digit.

The *opponens minimi digiti* is a fan-shaped muscle arising from the plantar ligaments over the bases of the third and fourth metatarsal bones. It joins the extensor tendon on the dorsum of the proximal phalanx of the fifth digit.

The *adductor hallucis* is a fan-shaped muscle arising from the plantar ligaments over the base of the second metatarsal bone and from the plantar surface of the entocuneiform bone. It is inserted into the lateral side of the base of the proximal phalanx of the hallux. Galton (33) describes the two origins as separate; and he likens the entocuneiform head to the interosseous primus volaris, and the metatarsal origin to the outer head of the flexor brevis.

The *accessorius* is absent.

Interossei:—There are six interossei—one to each side of each of the three middle digits. They arise from the sides of strong ligaments running from the metatarsal to the sesamoid bones at the sides of the base of the proximal phalanx of each digit. They are inserted into the sides of the expansions of the extensor tendons at the metatarso-phalangeal joints.

There is no *flexor brevis digitorum*.

Ocular Muscles:—There are the usual four *rectus muscles*, of which the internal one is small. The external rectus has the usual two heads. The two *oblique muscles* are not noteworthy. The *levator palpebræ superioris* has a wide origin from the periosteum at the back of the orbit, and divides into two parts. The *retractor bulbi* divides into four parts, which are inserted behind the recti. The inner and inferior slips are small, the external slip is wide and thin and the superior slip is thick and strong. Pouchet (82) has described and figured the muscles in *Myrmecophaga*. He notes, among other facts, the following:—

1. The internal, inferior and external rectus muscles have a common tendon of origin, and they envelop the retractor bulbi.
2. The superior rectus is connected to the superior oblique by a small slip.
3. The four recti are almost equal in volume, and they are long for the diameter of the globe.
4. The oblique muscles are almost cylindrical.
5. The retractor bulbi divides into four slips arranged in external and mesial pairs.

The retractor bulbi is rarely absent in Mammalia below the Simiidæ.

In the Ungulata, according to Windle and Parsons (102), the retractor bulbi is divided into two in the Chevrotain, but it is

divided into four in the Horse and Ass; and the Horse and Ass differ from other Ungulata in the presence of a middle oblique muscle.

The *laryngeal muscles* are described on p. 429.

The Joints.

The *temporo-mandibular joint* is flat. It has a lax, but strong capsule, which is most powerful behind. Only a posterior ligament exists. No meniscus is present. The external pterygoid muscle is not attached to the capsule.

The *spinal ligaments* are strong. The supraspinous ligament is strongly blended with the origin of some muscles. The interspinous ligament consists of a strong, though thin, sheet on each side of an interspinous muscle. These ligaments are continued down to the sacral region. The intertransverse ligaments are strong, and consist of two thin sheets, between which the intertransverse muscles lie. The metapophyses of the dorso-lumbar vertebræ have no ligaments, but they give attachments to the tendons of the multifidus spinæ.

Costo-vertebral Articulations:—The posterior costo-transverse ligament is short and strong. It runs from the dorsal surface of the tubercle of the rib to the transverse process and centrum of the vertebra below. The anterior costo-vertebral ligament is short. It is simply a specialization of the posterior part of the ventral half of the articular capsule. The posterior ligament comes right round to the side of the centrum immediately below that to which the rib articulates.

The *anterior common ligament* is a thin, membranous structure stretching the whole length of the vertebral column, and surrounding both sides and front of the centra. It is not markedly thickened in any particular position.

The *ligamentum nuchæ* is thin and membranous, and extends from the atlas back to the enormous spine of the first dorsal vertebra.

A well-marked band runs from the spine of the axis to the posterior arch of the atlas.

Pelvic Joints:—The transverse process of the eighth lumbar vertebra is connected by a short, very strong *anterior lumbo-iliac ligament* to the anterior inferior iliac spine. The ligament is fan-shaped, and its most posterior fibres are blended with the strong capsule of the sacro-iliac joint. The *obturator membrane* is a very thin sheet lying between the obturator internus and externus.

A dense sheet fills in the interval between the sacrum and ilium behind, and this is continuous with the *sacro-tuberous ligament*. The latter is a band of very great strength. It arises from the posterior inferior iliac spine and the side of the entire length of the sacrum in its free part to the ischial tuberos

The *sacro-spinous ligament* is absent. The sacro-tuberous ligament is continuous anteriorly with the lowest fibres of the *posterior sacro-iliac ligament*, which runs from the mesial aspect of the posterior iliac spine to the dorsum of the sacrum on and between two hindmost metapophyses.

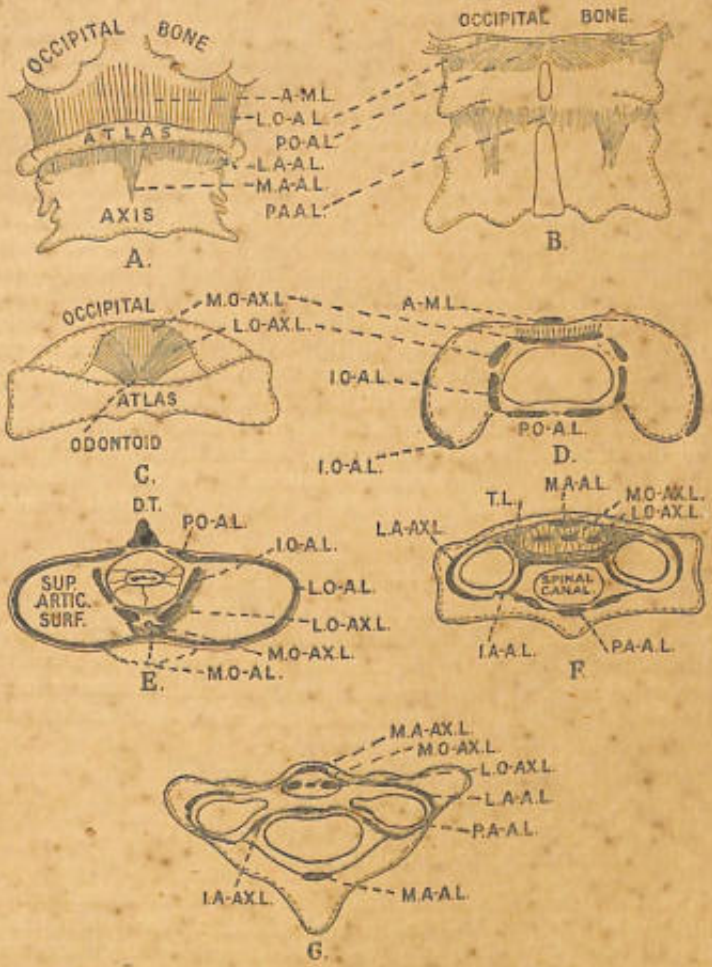
Atlanto-axoid Joint (text-fig. 19 A & B):—This joint has a single joint cavity. The capsule is quite complete. And all the ligaments are localized thickenings of the capsule. The *median atlanto-axoid ligament* (M.A-A.L.) consists of a median part, which is attached above to the under surface of the median part of the anterior arch of the atlas. Below it is fixed to a median ridge on the upper half of the anterior surface of the axial centrum. The lateral parts are thin membranous sheets extending laterally as far as the lateral auricular surfaces of the axis; the fibres run antero-posteriorly. The *lateral atlanto-axoid ligaments* (L.A-A.L.) are strong fibrous bands extending from the under surface of the atlas, round its articular surface, to the lateral border of the upper articular surface of the axis. They act as check ligaments in the rotatory movements of the atlas on the axis. The median part of the ligament blends insensibly with the median atlanto-axoid ligament. The *posterior atlanto-axoid ligament* (P.A-A.L) consists of three parts. A median thickening connects the tubercle on the posterior arch of the atlas with the upper part of the spine of the axis. The two postero-intermediate parts are thin sheets of fibres blending medially with the median ligament and laterally with a strong band of fibres—the postero-lateral atlanto-axoid ligament. The latter is strong and fan-shaped, and blends laterally with the lateral atlanto-axoid ligament. The two postero-lateral parts act also as check ligaments in rotation. The *ligamentum flavum* is absent as a separate ligament.

Atlanto-occipital Joint (text-fig. 19 A & B):—There is a complete capsule as in the last joint. The *anterior median ligament* (A-M.L) is a slight thickening of the anterior part of the capsule. It runs from the ridge between the two occipital condyles to the upper part of the anterior arch of the atlas. The lateral parts of the anterior ligament are thin membranous bands running laterally from the top of the condyles to the upper edge of the anterior arch of the atlas. They are tense in extension. The *lateral occipito-atlantoid ligament* (L.O-A.L) is a short, strong band running from the paroccipital process to the lateral articular process of the atlas. There is no rotation possible in this joint. The *posterior occipito-atlantoid ligaments* (P.O-A.L.) consist of median and lateral parts. The former is the posterior occipito-atlantal ligament, whose fibres run from the postero-superior part of the articular surface of the atlas to the median ridge on the occipital bone above the foramen magnum. Some fibres cross the mid line and decussate with those of the neighbouring ligament. Thus a strong fibrous roof is formed to protect the spinal cord just after it leaves the cranial cavity. The latter

blends with the lateral occipito-atlantoid ligament, and its fibres run antero-posteriorly.

Occipital-axial Ligaments:—Two very strong ligaments connect the postero-medial edge of the occipital condyle to the upper

Text-figure 19.



Joints of the skull, atlas and axis. Letters in text.

surface of the odontoid (text-fig. 19 C & D). The median ligament M.O-AX.L. connects the median part of the crest between the two condyles of the apex of the odontoid (text-fig. 19 C); thus it forms a weak superior crus of the cruciate ligament.

These occipito-axial ligaments do not check rotation, but prevent hyper-extension of the skull on the vertebral column. By this means the spinal cord is saved from being nipped between the sharp upper edge of the foramen magnum and the upper surface of the odontoid. The odontoid process does not enter the cranial cavity.

The *internal occipito-atlantoid ligament* (text-figs. 19 D, I.O-A.L.) is strong. It bounds the internal surface of the occipito-atlantoid joint. Above it is fixed to the inner and posterior aspect of the condyle, and below it is attached to the internal and posterior part of the superior articular surface of the atlas. It is continuous anteriorly with the lateral occipito-axoid ligament, and posteriorly with the posterior occipito-atlantoid ligament. There are two distinct joint cavities in the occipito-atlantoid articulation.

The *internal atlanto-axial ligament* (text-figs. 19 F, I.O-Ax.L.) is a semicircular band with three main thickenings—a median, blended above with the posterior surface of the transverse ligament, and attached below to the base of the odontoid process; it is tense in all positions. The two lateral thickenings form the internal part of the atlanto-axial joints. These are fan-shaped, and appear to be tense alternately in rotation.

The *transverse ligament* (text-fig. 19 F, T.L.) is strong. It is attached to the anterior arch of the atlas, and has neither bone nor cartilage. It forms a definite groove on the posterior surface of the odontoid. There is one joint cavity in the atlanto-axial joint; it is reniform, and the transverse ligament is included within the cavity.

Joints of the Fore Limb.

Sterno-clavicular Joint (text-fig. 20 A & B):—This joint is peculiar in that the inner end of the clavicle is bound by strong ligaments to the inner surface of the anterior part of the manubrium sterni, and considerable traction is necessary to get it on to the anterior border of the bone. It has no articulation with the first rib. The ligaments are:—

1. Lateral sterno-clavicular (L.S-C.L.).
2. Mesial sterno-clavicular (M.S-C.L.).
3. Posterior sterno-clavicular (P.S-C.L.).
4. Inter-clavicular (I-C.L.).

When viewed from the front the two lateral and mesial ligaments are seen to form a pocket (PKT.) for the clavicle. The ligaments are all continuous. The capsule is very dense, and no meniscus is present.

The *coraco-acromial arch* (text-fig. 17 C, C-A.A.) is a narrow but powerful band running from the side of the coracoid process to the side of the acromion and the sesamoid bone into which the subclavius is inserted. The supraspinatus muscle passes under

it. It is also attached to the deep surface of the acromial end of the clavicle and the *coraco-clavicular ligament* is absent. The sides of the arch are connected to fasciæ overlying the scapular muscles under the deltoid.

Shoulder Joint:—The upper part of the capsule is strong and is attached to the root of the coracoid process, and strong mesial and lateral coraco-clavicular ligaments pass from the process into the capsule, which is weak elsewhere. The tendon of the biceps passes over and not through the joint, and there are no bursæ passing under the muscles. The joint is strengthened by the surrounding scapular muscles, the tendons of the coraco-brachialis and biceps and the coraco-acromial arch.

Elbow Joint (text-fig. 20 C–F.):—When all the surrounding muscles are dissected away it is seen how the capsule is lax. Its attachments are peculiar, for the forearm is held midway between pronation and supination. The line of humeral attachment runs along the upper border of the olecranon fossa, under the mesial condyle, along the humerus where it forms the posterior border of the entepicondylar foramen up to the junction of the shaft and the bar of bone bounding the foramen. It then runs distally and laterally across the front of the humeral shaft, passes under the lateral border of the external condyle and reaches the olecranon fossa. A line drawn vertically downwards from the junction of the shaft of the humerus and the bar of bone bounding the entepicondylar foramen marks the innermost limit of the part of the front of the capsule attached to the radius. None of the posterior part of the capsule is attached to the radius at all. All the strengthening ligaments are on the mesial aspect of the joint, and are connected to the humerus and ulna. Strong oblong fibres are on the lateral part of the front of the capsule (L.O.F.), but they have no bony attachments. The radial attachment of the capsule is small compared with the ulna attachment, which runs from the coronoid process in front to the middle of the long olecranon process behind.

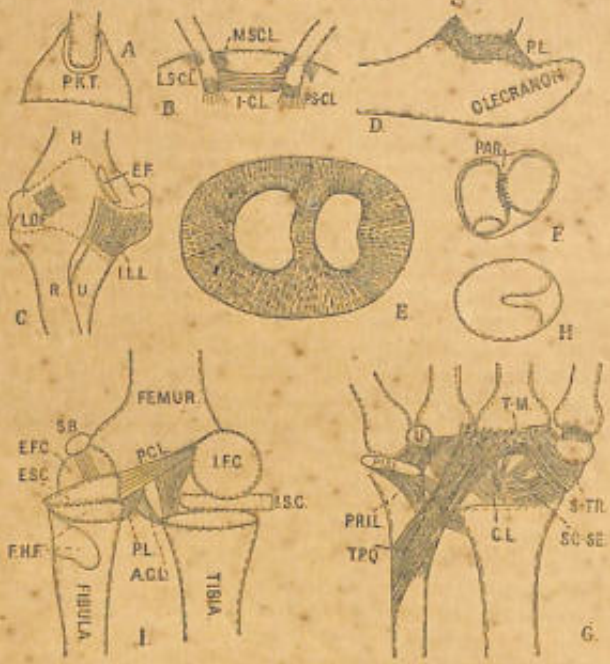
A broad anterior bundle (I.L.L.) of very thick, strong fibres runs from the shaft of the humerus along the margin of the entepicondylar foramen to the coronoid process, and a posterior ligament (P.L.) runs from the back of the lateral condyle to the olecranon.

A nutrient artery arches over the back of the joint capsule and gives several branches to it.

On opening into the joint the lateral part of the capsule is seen to be of very great strength, and a strong partition (PAR.) given off from it passes into the interval between the radius and ulna. This septum partially divides the joint cavity into two compartments—a small lateral radial cavity and a large mesial ulnar cavity. A septum from the anterior compartment does the same, and between the septa is the communication between the elbow and superior radio-ulnar joints (text-fig. 20 F).

Superior Radio-ulnar Joint:—The radius has an expanded head. On the ulnar aspect it is like the common form. Laterally it is merely a lip. The capsule of the elbow joint is attached along the anterior, lateral and posterior parts of the neck. Mesially the two septa from the elbow capsule described above come together and make a floor for the joint cavity, and, with the assistance of the strong upper fibres of the interosseous membrane,

Text-figure 20.



Joints of the limbs. E.F: entepicondylar foramen; E.F.C. and I.F.C: external and internal femoral condyles; E.S.C. and I.S.C: external and internal semilunar cartilages; F.H.F: facets on head of fibula; H: humerus; U: ulna or unciform; R: radius; PISI: pisiform.

hold the bones together. No orbicular ligament as such is present. The joint cavity is deepest on the ulnar side.

The *interosseous membrane* is strong at its upper end, where strong fibres run forwards and downwards from the radius to the ulna.

To dissect out the inferior radio-ulnar and carpal joints one must first remove the strong aponeurosis formed by the tendons of the flexor carpi radialis, flexor carpi ulnaris and pronator quadratus.

The *tendon of the pronator quadratus* is really an exceedingly powerful ligament receiving the muscle fibres of the muscle (text-fig. 20 G, T.P.Q.). By its proximal end it is fixed to the front and interosseous surface of the lower end of the shaft of the ulna. By its distal end it is attached to the front of the distal row of carpal bones in the centre, and to the palmar aspect of the bases of the metacarpal bones of the index, medius and annularis. It is superficially connected to the tendons of the flexores carpi radialis and ulnaris. Deeply it is connected by ligaments to the radius, trapezium, pisiform and unciform bones.

When the tendon of the pronator quadratus is removed, the strong *anterior inferior radio-ulnar ligament* is seen running obliquely between the ends of the radius and ulna; and it is connected by a ligament with the pisiform bone (text-fig. 20 G, P.R.I.L.). The *posterior radio-ulnar ligament* is short and connects the lower ends of the bones on their dorsal aspect. Both radius and ulna articulate with the carpus.

Radio-carpal Joint:—There is a continuous ligament connecting the front, back and sides of the forearm bones to the front, back and sides of the carpal bones. On the palmar aspect and radial border the capsule is strong, but it is thin and lax on the dorsum between the carpal bones. On the dorsum the capsule can easily be traced to the bases of the metacarpal bones. An interosseous ligament passes from the inferior radio-ulnar joint to the semilunar-cuneiform joint.

A short, very powerful ligament runs between the lower ends of the radius and ulna. It is connected to the anterior and posterior radio-ulnar ligaments to form part of the combined capsule of the inferior radio-ulnar and the radio-carpal joint. It is bisected by the ligament which passes between the semilunar and cuneiform bones, and connecting the anterior and posterior ligaments (text-fig. 20 G).

The *pisiform bone* has the following connections:—1. A ligament running to the unciform bone; 2. A ligament running to the anterior inferior radio-ulnar ligament; 3. A connection to the dorsal aspect of the radio-carpal capsule; 4. A ligamentous connection to the tendon of the pronator quadratus.

The *carpal bones* (text-fig. 20 G) are all connected to the capsule on both aspects either by long bands or by direct adhesion. The following interosseous ligaments are present:—

1. Scapho-semilunar (Sc-Se.).
2. Semilunar to os magnum and unciform and trapezoid (C.L.).
3. Semilunar to scaphoid and trapezoid (contained with last ligament).
4. Trapezoid to os magnum (T.M.).
5. Cuneiform to unciform (contained in C.L.).
6. Scaphoid to os magnum and trapezoid (S-Te.).

There is one common synovial cavity for all the intercarpal joints. The shapes of the articular surfaces are such that there

is much interlocking between the bones of the two rows, and between the distal row of carpal bones and the four metacarpals. The result is a very strong carpus with little movement between the bones.

Joints of the Hind Limb.

The *hip joint* consists of a large femoral head working in a shallow acetabular socket. The capsule is thin and moderately lax. It has fibres circularly arranged on the dorsal aspect of the joint, but no extrinsic bands are present on that side. A short anterior ligament runs from the anterior inferior iliac spine to the capsule of the joint, but there is no true ilio-femoral ligament. The cotyloid ligament is powerful and forms a complete ring. No transverse ligament is present. The ligamentum teres is very large, and its iliac attachment fills in most of the concavity of the crescentic articular cartilage, whose posterior limb is slightly wider than its anterior limb (text-fig. 20 H). No Haversian gland is present.

Knee joint (text-fig. 20 I):—*The fibular collateral ligament* is a very strong band two and a half inches long. It runs from the side of the anterior aspect of the lower end of the femur at a point level with the middle of the lateral condyle to the neck of the fibula. It lies in a groove on the head of the fibula. It arches over the popliteus muscle and gives an origin to it. And it is connected by a fine thread to the external semilunar cartilage. The *tibial collateral ligament* is attached above to a ridge on the middle of the internal condyle of the femur. It is fixed below to the tibia just above the place where the large, expanded upper end reaches the narrower shaft. It arches over the popliteus, and it has a small connection to the internal semilunar cartilage. The *popliteus muscle*, which passes under the two collateral ligaments, forms a support for the lower half of the joint. A strong *posterior ligament* (P.L.) runs obliquely from the inner aspect of the external femoral condyle to the inner surface of the head of the fibula. The *posterior cruciate ligament* (P.C.L.) runs from the internal condyle to the lateral condyle and external semilunar cartilage. The *anterior cruciate ligament* (A.C.L.) runs from a tubercle on the postero-lateral side of the head of the tibia to the medial side of the lateral femoral condyle, the depression between the condyles and the lateral side of the internal condyle. It is nearly parallel to two bands connecting the posterior cruciate ligament to the back margin of the upper articular surfaces of the tibia and fibula.

A strong band connects the external semilunar cartilage to the large sesamoid bone (S.B.) on the top of the external condyle. And this is the bone whence the outer head of the gastrocnemius arises.

The *external semilunar cartilage* is very thick in its middle part. It is connected along its margin with the edge of the

articular surface. Its posterior cornu is continued as the posterior cruciate ligament to the internal condyle. Its anterior cornu is connected by a band, which is united by fascia to the anterior cruciate ligament, to the lateral condyle.

The *internal semilunar cartilage* is larger and thinner than the external cartilage. It is connected by its margin to the edge of the articular surface of the tibia. Its cornua are attached respectively to the tibia in front and behind the spine. It projects well on the mesial side.

The *interosseous membrane*, which is not very thick, fills in the distal two-thirds of the interosseous space.

Inferior Tibio-fibular Joint:—The lower ends of the tibia and fibula are bound together by powerful anterior and posterior ligaments. The anterior ligament consists of strong fibres running downwards and outwards from the tibia to the fibula. The posterior ligament is composed of strong fibres whose direction is horizontal.

Ankle Joint:—The astragalus articulates with both tibia and fibula, but the ligaments, which are of very great strength, connect each of the tibia and fibula to the astragalus (talus) and os calcis (calcaneus). These ligaments are:—

1. A mesial ligament running from the extreme tip of the distal end of the mesial surface of the tibia to the astragalus.
2. A mesial ligament beginning above with the last ligament and running to the calcaneus. It gives a strong slip to the navicular bone.
3. A lateral ligament running from the front of the distal end of the fibula to the lateral surface of the calcaneus. It is long and powerful.
4. A lateral ligament running from the fibula at the attachment of the preceding ligament to the talus. It is short, and is concealed by the previous one.

A strip of the capsule running between the tibia and entocuneiform bone is thickened.

The talus is connected on its mesial aspect to the calcaneus and navicular by very powerful ligaments. It is also connected by strong bands to the cuboid and ectocuneiform.

The calcaneus is connected to the tibia and fibula by relatively long ligaments, which are of great strength. It is also united by short, powerful bands to the talus, navicular and cuboid bones. It also gives an attactment to the great plantar ligaments which run distally and give origins to the interosseous muscles.

When the large plantar ligaments are removed the tendon of the peroneus longus is seen crossing the sole to be inserted into the base of the hallucial metatarsal on its lateral (fibular) aspect. It is, consequently, an adductor of the hallux.

The navicular bone is connected by strong dorsal and volar ligaments, of which the latter is the more powerful, and is strongly

fixed to the middle cuneiform bone. A strong interosseous ligament passes from the navicular to the interval between the external and middle cuneiforms.

The strong capsule holds together the navicular, cuboid, cuneiforms and bases of the metatarsals. And the cuboid is connected to the exceedingly strong bundle of ligaments crossing the bases of the metatarsals.

No particular ligaments, apart from the capsule, hold the cuneiform bones together.

A single cavity of synovial membrane runs between the tarsal bones and tarso-metatarsal joints except that of the hallux.

A powerful palmar transverse metatarsal ligament connects the bases of the lateral four metatarsal bones. There is one thick root attached to the fifth metatarsal, and separate slips to the second, third and fourth. No dorsal ligament is present.

The internal cuneiform bone has a most peculiar surface for articulation with the hallux. It is large and concave from above downwards, and narrow and convex from side to side.

The Alimentary Canal.

The thick lips are adherent to the gums, and the upper one is not cleft. There is merely a trace of the upper labial frenum. And the vestibulum is almost non-existent round the small orifice of the mouth. The cheeks are thin, and the buccinator muscle is thinly spread out over them. The vestibule is slight behind, and Wharton's duct has no terminal papilla. Cheek-pouches are absent. On the inner surface of the mandible the mucous membrane forms a comb-like fold (text-fig. 21 A).

In *Tamandua* the thick lips are also adherent to the gums. On the inner aspect of the mandible there is on each side a large fold of mucous membrane which runs upwards and backwards to the soft palate. The tongue can be retracted below them so that it is enclosed in a sheath (text-fig. 21 B), and another fold projects inwards from the cheek. Similar folds have been observed in *Myrmecophaga* by Pocock (76). The large mandibular fold corresponds to the very small, functionless fold in *Orycteropus*. Small folds, which bound a trough in the centre of the floor of the mouth, are also present in *Manis* (text-fig. 21 C). In *Dasypus* these structures are not present at all.

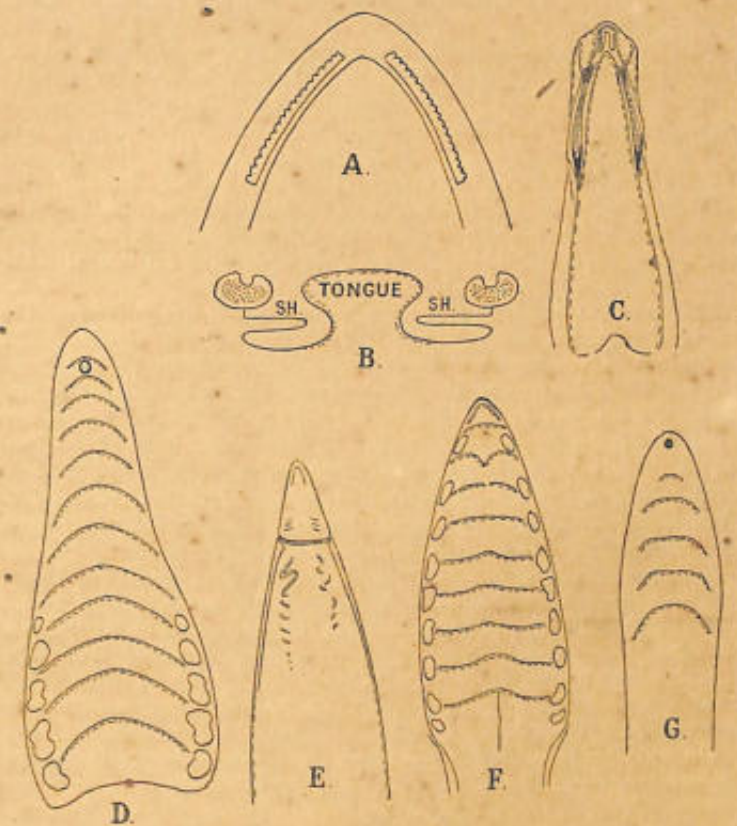
In a previous paper (89) I showed how comb-like ridges are present on the under surface of the tongue in Ruminants, and the points fit into the grooves between the teeth.

Palate (text-fig. 21 D):—The hard palate is long and narrow, and increases slightly in width when traced backwards. It has a long, low, incisive papilla, and it is crossed by twelve ridges, of which the most anterior three are close together. These ridges are thin and low. The junction of the hard and soft palates is well seen. The soft palate has no uvula. Beneath the mucosa

there is a stratum of closely-packed glands. The anterior part of the soft palate is aponeurotic, but the posterior part is muscular.

Forbes (29) describes and figures seven, irregular, notched ridges in *Myrmecophaga*, but does not mention the uvula. In *Tamandua* (text-fig. 21 E) there is a cluster of small ridges anteriorly, but

Text-figure 21.



The mouth in the Edentata. A: mandible and comb in *Orycteropus*; B: tongue and shelves in *Tamandua*; C: floor of the mouth in *Manis*; D–G: palates in *Orycteropus*, *Tamandua*, *Dasypus* and *Manis* respectively.

there is neither an incisive papilla nor a uvula. In *Manis* (text-fig. 21 G) there is no papilla nor uvula, and the palate is traversed by five, strong, widely-spaced ridges. In *Dasypus* (text-fig. 21 F) the palate is ridged and there is a nodule like a rudimentary uvula. The number of ridges varies in different

individuals. And in *Bradypus*, as I showed in a former paper (85), the palate has well-marked tubercles and lines, but neither an incisive papilla nor a uvula.

The entire mouth is short in the Bradypodidæ, but it is long in the Anteaters, the Armadillos being intermediate. In most Anteaters, if not in all, the epiglottis passes up into the posterior nares, so that the air-passage is guarded while the animal is mixing ants with saliva prior to deglutition. Similar arrangements are found in the mammary fœtus in the Marsupialia and in the Cetacea.

I have already described the *tongue* (88), and I pointed out that *Orycteropus* agrees with *Manis* and differs from the American Edentata in the possession of three circumvallate papillæ arranged in a triangle; and *Manis* differs from *Orycteropus* in the possession of a lytta. I also showed that the tongues exhibit many adaptive features, so they are no test of affinity.

Pharynx and *Œsophagus*:—The pharynx is capacious, and the communication with the nose is bounded by strongly-developed folds of mucous membrane. The Eustachian tube opens into the nasal tube as in *Tamandua*, and no torus exists.

The cervical part of the œsophagus lies entirely behind the trachea, and its mucosa has a few longitudinal folds. The thoracic part is connected to the side of the aorta by a pleural fold as in the Marsupialia. In the lower thoracic and abdominal parts the mucosa is thrown into longitudinal rugæ, which are continued for a short distance into the stomach. The abdominal part is about an inch long. The muscular coat is thick, and consists of an external longitudinal and an inner circular layer. No valve guards the entrance to the stomach as is found in some Pangolins. The œsophagus is narrow as in *Tamandua*.

Stomach (text-fig. 22 A):—The stomach is simple and capacious, and appears externally to consist of a sac with a very hard, globular pyloric region. There is no fundus, but the sac projects backwards and to the left. The duodenum emerges from the anterior part of the thick pyloric globe, and the lesser curvature is of moderate length. The peritoneal connections are not in any way peculiar.

On cutting into the stomach the mucous membrane is seen to be comparatively smooth, but Owen (71) described it as very rugose. To the right side, around the pyloric globe, it has the usual honycomb-like pits. There are no triturating teeth or spines anywhere. The muscular coat, which is of moderate thickness in the gastric sac, becomes greatly hypertrophied to form a kind of gizzard in the pyloric globe. The gizzard consists of a globular part and of a concavo-convex part, which become continuous, and the pyloric canal runs between them. No septa divide up the gastric sac into compartments. In *Tamandua* the stomach is elongated with a thick pylorus, and its mucosa is rugose. In *Manis* the muscular coat is thickened, but not as

Text-figure 22.

Alimentary canal. A: stomach; B: cæcum; C: a part of the ileum and mesentery; D: a mesenteric gland; D: duodenum; P.M. and P.C: pyloric musculature and canal.

much as in *Orycteropus*, the mucosa has triturating teeth in the pyloric region and there is a special gastric gland. In *Dasypus vellerosus* the pylorus is not very muscular. In *Tatusia peba* the

stomach is in two compartments with a wide communication, and the pylorus is very muscular.

In *Myrmecophaga* there is a gizzard like that in the pyloric region in *Orycteropus*, but there is no specialized gland similar to that in *Manis*. And in *Tamandua* there is also a thick pyloric region, but no specialized glandular area. The stomach in *Manis* has been specially studied by Oppel (**67**), and that of *Tamandua* by Neuville (**66**). In all these genera the stomach is simple, but it is complex in the Bradypodidæ. I have already shown (**85**) how the pyloric region forms a grinding apparatus in *Bradypus*.

Intestinal Tract:—The duodenal loop is differentiated from the rest of the small intestine, but there is no marked flexure between them. There is, however, a sharp differentiation between the thin-walled duodenum and the enormous globular pylorus. On cutting into the duodenum no valvulæ conniventes are present, and the biliary-pancreatic orifice is not placed on a papilla. The remainder of the small intestine is placed round the margin of an oval mesentery, and it has many minor loops. It is drained by the middle mesenteric vein (Chalmers Mitchell, **106**). It is of great length. The mucous membrane is studded with innumerable villous projections; in some places these are scanty, but there are no extensive areas without them. No Peyer's patches are present. No folds of the mucosa are present.

The terminal part of the ileum runs upwards to enter the cæcum, and a cluster of eight large lymphatic glands surrounds the termination. The ileo-cæcal opening is surrounded by a collar valve, and a ridge runs from the proximal end of the ascending colon to the proximity of the valve. Chalmers Mitchell suggests that this may indicate a former division of the cæcum into two cæcal pouches.

The form of the cæcum with its peritoneal connections is shown in text-fig. 22 B.

The large intestine is sacculated in its proximal part only. It has a pendent loop as in many Ungulates and *Lemur*. The loop and remainder of the colon as far as the beginning of the rectum are thrown into coils, but the rectum is straight. The muscular coat is not disposed in longitudinal bands, and no appendices epiploicæ are present.

The mucosa of the large intestine is comparatively smooth. After the pendent loop is past it develops longitudinal rugæ. In the rectum there are large transversely-directed folds but no longitudinal ones. No valves of Ball are present.

Bradypus has a very small cæcum. *Myrmecophaga* has a cæcum 1½ inches long. Several species of *Dasypus* have two cæca. *Tatusia* and *Tolypeutes* have no cæca. *Xenurus* has indications of cæca at the ileo-cæcal valve (Garrod).

Chalmers Mitchell (**106**) draws the following conclusions:—

1. The gut-pattern of *Orycteropus*, except for the specialization of the hind-gut, has not moved far from the primitive condition,

the two chief changes being the lengthening of Meckel's tract* and of the hind-gut.

2. The patterns of the intestinal tracts of the Tubulidentata, Pholidota, and Xenarthra afford no evidence in favour of the existence of a super-order, "Edentata." Such resemblances as they present are best explained as a common inheritance from the primitive type, and so afford no evidence of affinity. In the Xenarthra the most characteristic features are the presence of paired cæca, which seem to be more conspicuous in the young than in the adult, and the tendency of a great elongation of Meckel's tract and the proximal part of the hind-gut. The hind-gut varies considerably both in the different groups and even individually. The distal limb of the pendent loop always approaches the duodenum closely, and distad of this the hind-gut may pass nearly straight back to the rectum and may form a shallow or a well-marked and complex loop. In both Marsupials and Edentates the hind-gut appears to be still in a variable or almost experimental stage.

Any resemblances in the mouth, salivary apparatus and stomach are due to adaptation to diet and mode of feeding. As regards the lingual muscles, *Orycteropus* resembles other mammals than the Xenarthra and Pholidota. In the projection of the epiglottis up into the larynx, thereby removing the air-passage from the pharynx, the Anteaters resemble the mammary fœtuses in Marsupials and the Cetacea.

Hence one can see that the characters of the entire alimentary canal from mouth to anus show no affinities between *Orycteropus* on the one hand and the Manidæ and Xenarthra on the other.

No typhlosole is present such as that described in *Tamandua* and *Myrmecophaga* by Beddard (**5**).

The Salivary Glands.

The *parotid gland* (text-fig. 3, P.G.) is quadrangular in shape and very thin. It extends upwards to the zygoma and auricle. Anteriorly it extends on to the masseter and zygomatico-mandibularis muscles. Posteriorly it is covered by the depressor auriculæ. Inferiorly it is in contact with the submaxillary gland and anterior facial vein. Superficially it is covered by the platysma and by thin fascia. It is composed of small brown lobules held together by delicate connective tissue. No socia parotidis exists. The duct emerges from the lower part of the anterior border of the gland and has the usual course. It is slender. The facial nerve gives off numerous branches in the gland. The total mass of the gland is small. Rapp (**83**) and Oppel (**69**) describe small glands.

The *submaxillary gland* (text-fig. 8, S-M.G.) is a bow-shaped structure extending backwards and inwards across the neck from

* Meckel's tract is composed of the jejunum and ileum.

the angle of the mandible to a short distance anterior to the manubrium sterni. Posteriorly the two glands are in contact. Each has expanded extremities, and the anterior end is more massive than the posterior one. The anterior facial vein deeply grooves the anterior extremity. The gland consists of lobules of different sizes.

Two ducts leave the anterior pole, one of which is large and the other is small. Within the gland the ducts receive small ductules almost perpendicularly. The two glands unite to form one. At no place is there a salivary reservoir as there is in the Dasypodidæ and Myrmecophagidæ, but there is a slight increase in the calibre of the tube as it crosses the posterior belly of the digastric muscle. Shortly after it has crossed the muscle and gained the inner side of the mandible it becomes surrounded by muscle fibres which are fused mesially with the genio-glossus. These fibres may act as a propelling agent driving the saliva to the mouth just within the labial orifice. The submaxillary apparatus is described in many papers.

The *sublingual gland* is a thin, elongated piece of glandular tissue on the inner side of the muscle surrounding Wharton's duct.

Such resemblances as exist between the salivary organs of the Orycteropodidæ, Dasypodidæ and Myrmecophagidæ are associated with diet and are not signs of any blood-relationship. And the differences between them and the glands in the Bradypodidæ are due to the same cause.

The Peritoneum.

The *great omentum* has very little fat, and can be stretched out till its lower border reaches the symphysis pubis. The free margin is attached to the lowest limit of the hilum of the spleen, and it ends at the right side on the first part of the duodenum. The posterior layers pass to the colon and, after encircling it, form the mesocolon, in which is contained the left part of the pancreas. The pancreas is found in it between the colon and spleen.

The duodenum is connected by a fold of peritoneum to the colon, where the pendent loop turns down into the descending colon. And this connecting fold is also attached to the posterior abdominal wall.

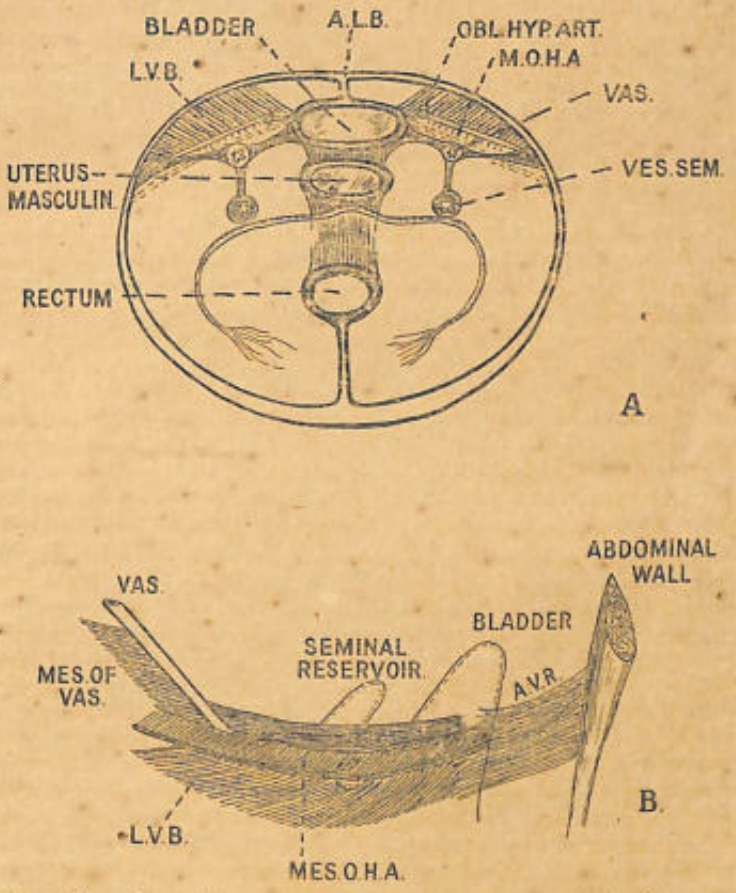
The *mesentery proper* extends throughout the entire small intestine. Within it are contained numerous lymph vessels and glands, which were all well marked owing to the time of digestion during which the animal died. The mesenteric vessels form few arcades.

The upper limit of the pendent loop of the colon is attached to the posterior abdominal wall on the right side of the inferior vena cava.

The entire large intestine has a mesentery. The meso-rectum stops at the level of the lower border of the symphysis pubis.

A triangular fold of peritoneum fills in the space between the cæcum and the lower end of the ileum (text-fig. 22 B). No artery runs along the free margin of this fold. A small fold runs from the cæcum and the right side of this sheet and encircles a small pocket.

Text-figure 23.



The pelvic peritoneum *. A.V.B. and L.V.B: anterior and lateral vesical ligaments; M. or MES.O.H.A: mesentery of the obliterated hypogastric artery.

Part of the mesentery of the small intestine with its contained lymph vessels and glands is shown in text-fig. 22.

The mesentery of the descending colon and rectum and the two *genital mesenteries* form three sheets which actually meet. Each genital mesentery crosses the posterior abdominal wall and

* Uterus masculinus and seminal reservoir are the same structur *

external iliac vessels obliquely, and the root enters the cremasteric sac. From before backwards the free margin contains the spermatic vessels running to and from the globus minor of the testis, the testis and the gubernaculum. The epididymis has its own little peritoneal fold jutting up from the side of the main mesentery. The vas deferens is at first between the layers of the main mesentery. But as it passes into the pelvis it carries away its own fold from the common mesentery. That mesentery passes into the pelvis, where it becomes continuous with the peritoneal investment of the bladder, seminal receptacle and seminal vesicles. The pelvic peritoneum is described further on p. 433.

The Pancreas.

This organ is dark in colour, finely lobulated and small. Otherwise it has no peculiar features. In other Edentates it is pale. In *Tamandua* it is long, flat and triangular. In one *Dasypus villosus* the massive pancreas stretched from the spleen to the cæca.

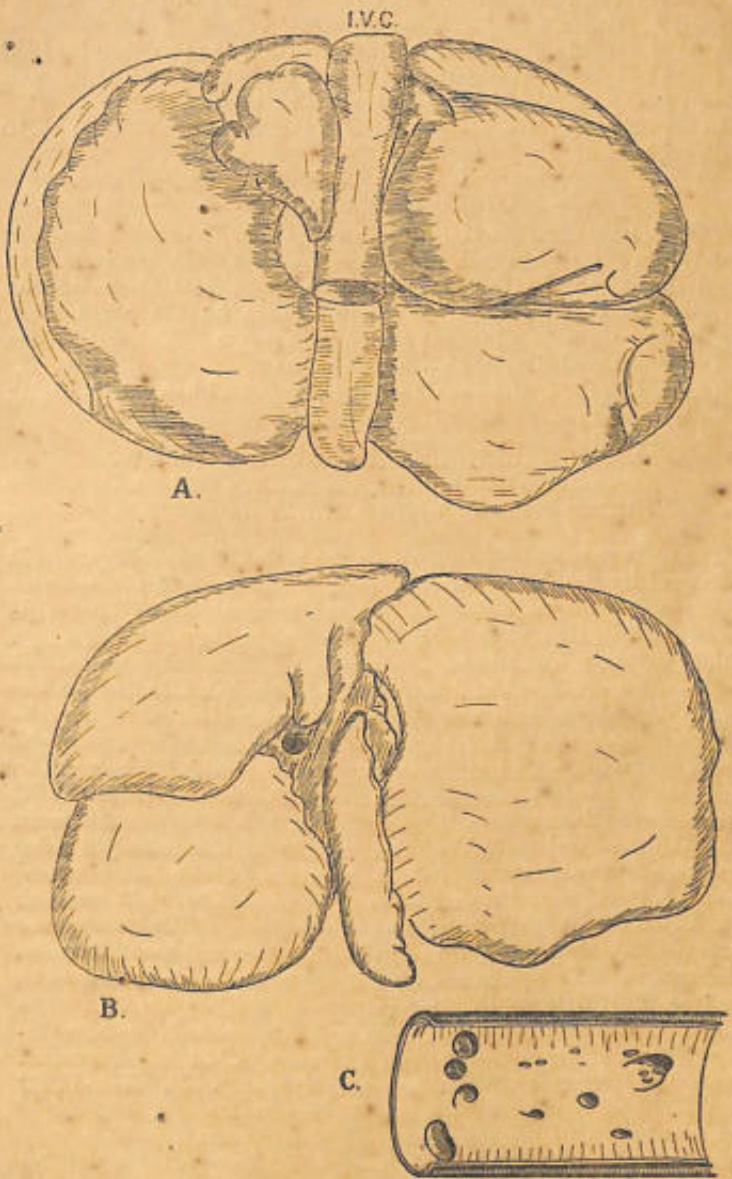
The Liver (text-fig. 24).

The liver is divided into left, right central and right lateral lobes. The *left lobe* (A.B.) is thin and flat, and extends to the left wall of the abdomen. It is connected to the right central lobe by a thin, narrow isthmus of hepatic tissue. It is in reality a left lateral lobe, for the left central and right central lobes are fused. The *right central lobe* (A.B.) is massive. It is split on its anterior aspect (ventral aspect) for about an inch to receive the ligamentum teres and falciform ligament. Slightly to the right of the umbilical fissure there is an opening in which the *fundus of the gall-bladder* (B.) is seen. At the junction of the left globe with the right central lobe the portal fissure is seen. The *right lateral lobe* (A.B.) lies both below and to the right of the right central lobe. It is connected to the right central lobe behind the portal fissure. The *caudate lobe* (A.B.) is really composed of two stumpy lateral lobules and a long intermediate process. It surrounds the vena cava inferior on its ventral, right and left surfaces. The *vena cava inferior* (I.V.C.) is completely bridged over by hepatic tissue, but the tissue is very thin on the dorsal surface and it has openings of hepatic veins from all the lobes of the liver. The gall-bladder is entirely buried in hepatic tissue except for the fundus.

The right central lobe probably includes both right and left central lobes, the line of attachment of the suspensory ligament marking out the boundary between them.

The general arrangement of the liver is similar in *Myrmecophaga*, but more of the gall-bladder is seen. Mr. Pycraft informs me, however, that the liver varies in *Orycteropus*.

Text-figure 24.



The liver from below (A) and from above and behind (B). C: the inferior vena cava opened to show the openings of the hepatic veins. I.V.C: inferior vena cava.

The liver in *Dasypus* and *Tamandua* has already been described by Flower (26). The Spigelian lobe is absent in *Dasypus* but present in *Tatusia*.

I have already figured the liver in *Bradypus tridactylus* (85) and showed that the gall-bladder is absent. And it is well known that the gall-bladder is present in *Cholœpus*.

In no Edentate are the layers of ligaments separated so as to bound a bare area

Organs of Circulation.

The *pericardium* is delicate, and is not adherent to the diaphragm; but a sheet of pleura on each side connects it to the diaphragm. In the space between the sheets there lies the azygos lobe of the right lung. In *Manis*, on the other hand, the pericardium is adherent to the diaphragm. The conditions in *Orycteropus* also exist in other Mammals.

The *heart* (Pl. I. and text-fig. 25) is large and has the following measurements:—

Length	90 mm.
Transverse width	80 mm.
Antero-posterior width	55 mm.

The apex is rounded, and lies in the fifth intercostal space. It is formed by the left ventricle alone. The long axis of the heart makes an angle of 45° with the mid-sternal line. The *right auricle* (Pl. I., R.A.) has a long, massive, triangular appendage, which passes ventral to and conceals the ascending aorta. It receives two pre-caval and one post-caval veins, all of which are large. The appendix has closely-set columnæ carneæ. The right pre-caval vein (R.P-C.V.) opens into the anterior and right corner posteriorly, and the post-caval vein (Po-C.V.) opens into the right and inferior aspect. A large Eustachian valve (E.V.) separates the latter from the orifice of the left pre-caval vein (L.P-C.V.). And only the fibrous ring of the tricuspid valve separates the valve lumen from the orifice of the left precaval vein. A few Thebesian orifices are present. The *right ventricle* (Pl. I., R.V.) is thin-walled and capacious. The moderator band (M.B.) is slender and ramifying, but several small bundles reinforce it. No pronounced papillary muscles are attached to the free ventricular wall. Several large papillary muscles arise from the inter-ventricular septum and send chordæ to the tricuspid valve. These chordæ can be arranged in three groups. The *right auriculo-ventricular valve* (text-fig. 25, R.A-V.V.) should not really be called tricuspid, for it has only two cusps, lying anteriorly and posteriorly. Both cusps are thin and membranous, and the chordæ traverse them to be attached to the fibrous ring of the valve. The chordæ are arranged in three groups, of which two go to the anterior and one to the posterior cusp. Each anterior group has a large mesial and a small lateral

sub-group, and the posterior group consists of small chordæ, some of which rise from one of the papillary muscles supplying chordæ to the right side of the anterior cusp. The *fossa ovalis* (Pl. I., F^5O_4) is well-marked, but the foramen ovale has completely closed. The *annulus ovalis* (A.O.) runs from the orifice of the right pre-caval vein above and around the fossa ovalis to the Eustachian valve. It feels dense. The *conus arteriosus* is crossed by muscle bundles, and the pulmonary valve has three small semilunar cusps.

The *left auricle* (Pl. I., L.A.) and its appendix are small anteriorly, but it deepens posteriorly. The *left ventricle* (L.V.) has thick walls and a capacious cavity. Its striking features are two enormous papillary muscles giving the chordæ tendineæ to the cusps of the mitral valve. The right papillary muscle (R.P.M.) arises by four heads from the junction of the left wall of the heart and the inter-ventricular septum. It runs upwards, and fine chordæ connect it to the left wall and septum. It supplies the chordæ tendineæ to the right half of each cusp of the mitral valve. The left papillary muscle (L.P.M.), arising from the left wall of the ventricle, supplies chordæ tendineæ to the left half of each cusp of the mitral valve. The aortic valve shows nothing peculiar.

The *inter-ventricular septum* is complete. It is 1·2 cm. thick, and many muscle bundles are attached to it. No *os cordis* exists.

Pouchet (82) has given an elaborate account of the heart in *Myrmecophaga*, and the following features are important:—

1. The heart is large.
2. The tissue of the aortic valve is continuous with the anterior cusp of the mitral valve.
3. The tricuspid valve has two cusps—anterior and posterior.
4. The right auricle has only two caval openings.
5. The Eustachian valve is double.
6. The fossa ovalis is deep.
7. The annulus ovalis is thick.

Beddard (5) has described and figured the interior of the heart in *Tamandua*, and has drawn attention to the following points:—

1. The moderator band is supplemented by a thin cord.
2. The tricuspid valve has many papillary connections to the free wall of the ventricle.
3. The papillary muscles are fleshy throughout, and are inserted into the collar of the valve as in *Ornithorhynchus*.
4. Few septal papillary muscles are connected to the tricuspid valve.

It is interesting to note how papillary muscles go to the valve

collar in *Tamandua* and how chordæ tendineæ do the same in *Orycteropus*.

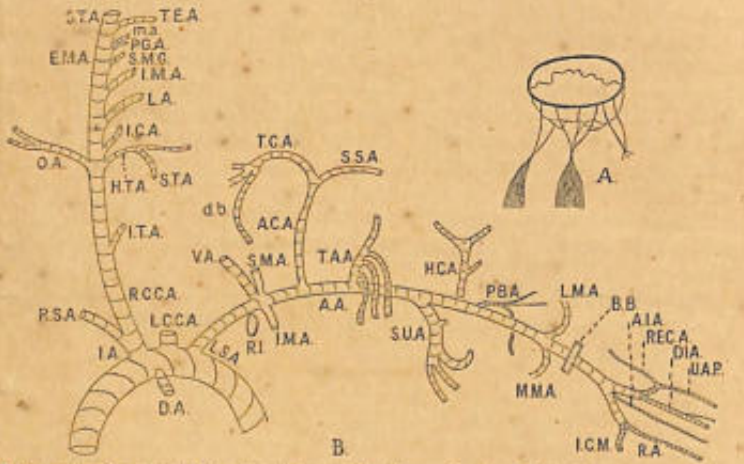
Rapp's view that the heart is small in the Anteaters is thus not always true.

In *Manis* the heart is not large for the size of the animal.

The *aorta* (text-fig. 25 B) has the usual convexity directed craniad as in all Mammals accept *Bradypus*, in which Burne (14) and I (85) have shown that it is convex ventrad.

The branches of the aortic arch are arranged in one of two ways. In *Orycteropus*, the Dasypodidæ and some specimens of *Myrmecophaga* the arch gives off the innominate left common carotid and left subclavian arteries. In *Manis*, *Bradypus*,

Text figure 25.



The tricuspid valve (A) and arteries of the thorax, head and fore-limb (B). B.B: bridge of bone forming the entepicondylar foramen; R.I: first rib. Other letters in text.

Tamandua and some specimens of *Myrmecophaga* there are only two branches—the innominate and left subclavian arteries. In *Orycteropus* alone there is an open ductus arteriosus, and in *Bradypus* alone, as in some Marsupials, the arch gives off intercostal arteries (108). The arch and its branches are closely associated with the vagus and sympathetic plexuses (86). No Edentate examined by others and by myself has any thyroidea ima. In all cases two coronary arteries arise from the beginning of the arch.

The thoracic aorta and subclavian arteries contribute to a variable extent (see below) to the nutrition of the intercostal spaces, and the abdominal part gives off its branches as shown in the subjoined table.

Coronary Arteries:—The right and left coronary arteries in *Orycteropus* arise from the corresponding sides of the ascending aorta, and no sinuses of Valsalva are present. Each vessel divides in the usual way into transverse and inter-ventricular branches. Each inter-ventricular branch is limited to one surface of the heart, and the two anastomose round the right border of the heart just short of the apex. The left and right vessels occupy the surfaces which agree in all Mammals. Each vessel supplies the adjacent parts of the two ventricles. The transverse branches also anastomose. The chambers of the heart are nourished as follows:—

A. Right Ventricle.
- *a*. Both inter-ventricular arteries.
- *b*. Trunk of right coronary.

B. Left Ventricle.
- *b*. Both inter-ventricular arteries
- *a*. Both transverse arteries.

Ductus Arteriosus (text-fig. 25, D.A.):—This vessel is patent in *Orycteropus* alone, and it has the usual relation to the left recurrent nerve. It admits a large bristle. In *Bradypus* (**85**) I observed a thick ligamentum arteriosum, but I found neither duct nor ligament in *Tamandua* and *Dasypus*.

The *Innominate Artery* (text-fig. 25, I.A.) is a short trunk, and its branches [right subclavian (R.S.A.) and right common carotid (R.C.C.A.)] have long courses to reach the first rib and neck. In *Manis* (**109**) it gives off the right subclavian, both common carotids, and thymic arteries. A tracheal branch is continued into the right bronchial artery. In *Myrmecophaga* (**82**, **109**) the branches are as in *Manis* in some specimens and as in *Orycteropus* in others. The thymic and tracheal twigs are absent. In *Dasypus* the conditions are as in *Orycteropus*. And I have already shown (**85**) that the trunk gives off the three large branches in *Bradypus*.

The thoracic parts of the left subclavian and left common carotid arteries show nothing peculiar. No *thyroidea ima* artery exists.

Intercostal Arteries:—In this animal all the intercostal arteries which enter the spaces from above and run dorso-ventrally are derived from the aorta, none coming from the subclavians. The first five spaces on each side receive a branch from a single trunk. Each of the remaining seven spaces on each side gets a separate branch from the aorta. The artery to the last space is the largest and supplies the diaphragm. The lowest arteries pass under the psoas muscle, which arises as high as the tenth rib. Hyrtl (**45**) points out that in *Manis macrura* the first space on each side receives a branch from the vertebral artery. The fifth intercostal artery gives off bronchial and œsophageal arteries. And the aorta gives off two phrenic arteries before it pierces the diaphragm. Pouchet (**82**) states that the first intercostal space on each side is supplied by a large branch of the subclavian artery in *Myrmecophaga*. Krassnig (**50**) has dealt with the intercostal and vertebral arteries

in *Bradypus*, and I have already figured intercostal arteries arising from the aortic arch in that animal (85).

The intercostal spaces also get branches from the internal mammary artery in front.

Thus it can be seen how *Orycteropus* differs from the other Edentata in its intercostal arteries. The aorta alone supplies it with dorso-ventral branches, whereas the subclavian artery gives it ventro-dorsal twigs through its internal mammary branch. In other Edentates the subclavian artery takes over the first space.

Branches of the Abdominal Aorta.

	Orycteropus.	*Manis.*	*Myrmecophaga.* (Pouchet).	(Hyrtl).	*Dasypus*	*Bradypus.*
Right phrenic	—	—	—	—	—	Phrenic inferior from common twig with suprarenals.
Left phrenic	—	—	+	—	—	
Cœliaco-mesenteric*	—	+	—	+	—	+
Cœliac axis	+	—	+	—	+	—
Superior mesenteric	+	—	+	—	+	—
Hepatic	—	—	—	+	—	—
Suprarenals	—	—	Left.	Right & left.	Right & left.	Common with phrenic.
Renals	+	+	+	+	+	+
Right spermatic	+	+	+	—	—	+
Left spermatic	+	—	+	—	—	+
Inferior mesenteric	+	+	+	+	+	+
Lumbar	6	+	...	4 pairs.	...	3
Middle sacral	+	+	+	...	—	—
Umbilical	—	—	—	—	—	+
Right common iliac	+	+	—	—	—	+
Left common iliac	+	+	—	+	+	+
Right external iliac	—	—	+	+	+	—
Left external iliac	—	—	+	—	—	—
Right internal iliac	—	—	+	+	+	—
Left internal iliac	—	—	+	—	—	—

* This vessel divides later into cœliac axis and superior mesenteric artery.

Phrenic Arteries:—There is considerable variation in the arterial supply of the diaphragm in the Edentata, as can be seen from the following list:—

Orycteropus—lower intercostal arteries.
Manis—two branches of the thoracic aorta.
Myrmecophaga—from suprarenal arteries (109); left one from aorta (82).
Dasypus—from cœliac axis.
Bradypus—from suprarenal arteries.

Cœliac Axis (text-fig, 26 A):—This vessel arises from the front of the abdominal aorta, and runs to the right. It divides into three branches:—

1. *Œsophageal Artery* (O.A.), which runs towards the cardiac end of the stomach and bifurcates. One half (T.B.) runs up into the thorax through the œsophageal opening in the diaphragm. The other half ramifies over and supplies the dorsal surface of the stomach; at the left extremity of the stomach it gives off four vasa brevia (V.B.) which anastomose with branches of the splenic artery in the hilus of the spleen.

2. *Gastro-hepatic Artery* (G-H.A.), which runs along the lesser curvature of the stomach and supplies it and the ventral gastric wall. Its branches anastomose with branches of the œsophageal artery. The parent stem is continued as a single hepatic artery into the portal fissure of the liver. The hepatic artery (H.A.) gives off a small *pancreatic artery* (P.A.), which anastomoses with a branch of the superior mesenteric artery (S.M.A.).

3. *Splenic Artery* (S.A.), which has a straight course in the gastro-splenic omentum. It breaks up into three terminal splenic vessels, which do not anastomose outside the spleen. A *gastro-epiploic* branch (G-E.B.) runs along the great gastric curvature and anastomoses with vessels on both surfaces of the stomach.

The cœliac axis gives off the following branches in other Edentata:—

A. *Manis macrura* (Hyrtl, 109).
- *a*. Hepatic.
  - 1. Hepatic.
  - 2. Right gastro-epiploic.
- *b*. Coronary.
- *c*. Splenic.
  - 1. Splenic.
  - 2. Pancreatic.
  - 3. Left gastro-epiploic.
  - 4. Vasa brevia.

B. *Dasypus* (several species).
- *a*. Two phrenic arteries.
- *b*. Coronary.
- *c*. Gastro-epiploic.
  - 1. Hepatic.
  - 2. Splenic.

C. *Myrmecophaga* (Hyrtl, 109).
- *a*. Coronary.
- *b*. Splenic.
  - 1. Vasa brevia.
  - 2. Left gastro-epiploic.
  - 3. Splenic.

D. *Myrmecophaga* (Pouchet, 82).
- *a*. Coronary.
- *b*. Pyloric.
  - 1. Right gastro-epiploic.
  - 2. Hepatic.
- *c*. Splenic.

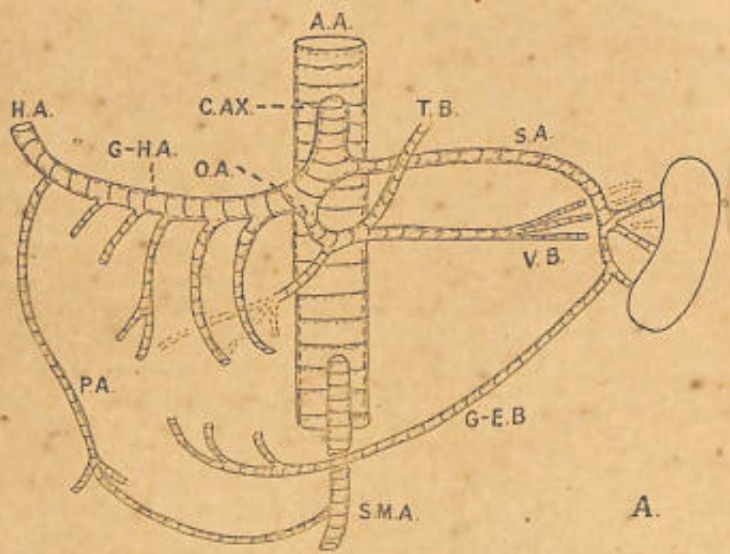
E. *Bradypus* (Hyrtl, 109).
- *a*. Inferior gastric.
- *b*. Superior gastric.
  - 1. Pancreatico-splenic.
  - 2. Gastric branches.
- *c*. Hepatic.

It is thus evident that *Manis* and *Bradypus* agree with the

condition found in other Mammals in the possession of a well-marked hepatic division of the axis. In *Orycteropus*, *Dasypus* and some specimens of *Myrmecophaga* it is a secondary branch. In other specimens of *Myrmecophaga* the hepatic artery is a branch of the aorta. The anastomoses of the arteries form an arterial circle round the stomach.

Superior Mesenteric Artery:—This vessel gives off the usual intestinal vessels, but there is no extensive series of arcades in the mesentery. A branch anastomoses with a branch of the upper half of the *inferior mesenteric artery*. The latter arises from the

Text-figure 26 A.



The coeliac axis (C.AX.) and superior mesenteric (S.M.A.) arteries arising from the abdominal aorta (A.A.). Vessels to the dorsum of the stomach are dotted. Other letters in text.

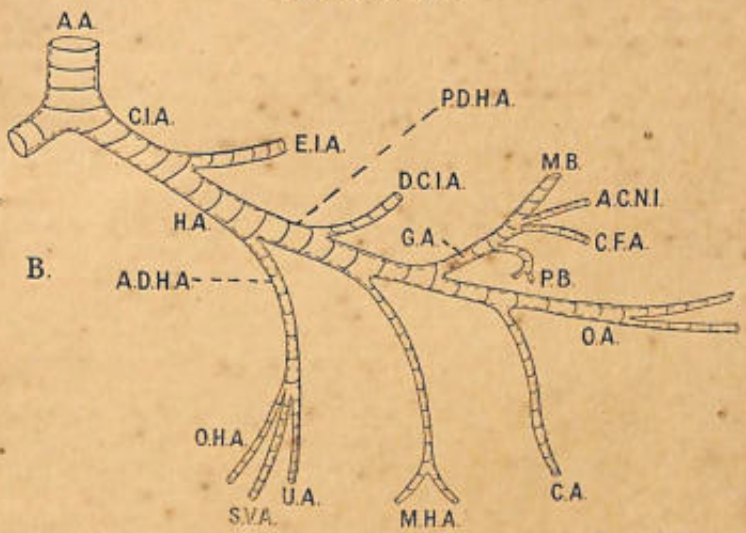
aorta an inch and a half above the bifurcation. It itself bifurcates. One half ascends and anastomoses with a branch of the superior mesenteric artery. The other half becomes the superior hæmorrhoidal artery, which descends into the pelvis, where it anastomoses with the hæmorrhoidal branch of the caudal continuation of the posterior division of the hypogastric artery (text-fig 26 B, M.H.A.).

Spermatic Arteries:—The origin in the various Edentata are shown in the table on p. 412. In *Orycteropus* (text-fig. 12) each one passes along the free edge of the common genital mesentery to the globus minor of the testis.

Renal Arteries:—The left artery arises as a small twig from the aorta. It runs outwards across the psoas muscle. About an inch from its commencement it gives off the left suprarenal artery. It breaks up into two vessels which enter the kidney. The right artery arises at a slightly higher level than the left one. An inch from the aorta it gives off the right suprarenal artery. It has two terminal renal branches. A branch runs through the connection between the renal capsule and diaphragmatic fascia. And three small vessels pass to the same fascia from the superior pole of the right adrenal body.

The number of *lumbar arteries* is shown in the table on p. 412.

Text-figure 26 B.



Pelvic and caudal arteries. C.I.A., H.A. and E.I.A: common, internal and external iliac arteries. A.A: abdominal aorta. Other letters in text.

Middle Sacral Artery:—This is a large vessel, which passes backwards on the ventral aspect of the tail muscles and supplies them.

Hypogastric Artery (text-fig. 26 B):—This vessel runs for an inch along the inner border of the psoas muscle, and divides into anterior and posterior divisions.

The anterior division (A.D.H.A.) is small. It breaks up into two terminal divisions—superior vesical and ureteric arteries. The obliterated hypogastric artery (O.H.A.), which is contained in a mesentery of its own, runs from the anterior division to the base of the anterior vesical ligament, where it is lost.

The *ureteric artery* (U.A.) lies on the outer surface of the ureter,

and gives off tortuous parietal branches, arteries to the ureter, and branches to the bladder round the ureteric entrance.

The *superior vesical artery* (S.V.A.) is small, and runs up the edge of the bladder nearly as far as the fundus.

The posterior division (P.D.H.A.) is small. It runs laterally for an inch and gives off the following branches:—

a. Deep circumflex iliac artery (D.C.I.A.).
b. Gluteal artery (G.A.).
c. Obturator (O.A.).
d. Middle hæmorrhoidal artery (M.H.A.).
e. Caudal artery (C.A.), which continues the parent stem.

The *deep circumflex iliac artery* runs dorsal to the pectineal tubercle and breaks up into numerous small branches to the iliopsoas.

The *gluteal artery* is a short trunk, which gives off parietal branches (P.B.) to the caudal muscles and is continued onwards into the gluteal region. It breaks up into vessels to the gluteal and caudal muscles (M.B.), and it gives off a small arteria comes nervi ischiadici (A.C.N.I.). A branch passes ventral to the gemellus muscles and anastomoses with the femoral artery (C.F.A.).

The *obturator artery* runs through the anterior part of the obturator foramen and breaks up into superficial and deep divisions. The former lies between the adductor mass and obturator externus, and the latter is continued dorsally to the muscles around the ischial tuberosity.

The *middle hæmorrhoidal artery* runs medially beneath the parietal peritoneum to the rectum, where it divides into ascending and descending branches.

The pudendal and inferior hæmorrhoidal arteries are absent.

The tail is supplied by the mid-sacral, gluteal, and caudal branch of the posterior division of the hypogastric artery.

In *Manis macrura* the conditions are very different (**109**). The common iliac and mid-sacral arteries supply the pelvis as follows:—

A. Common Iliac Artery.
   1. Pudendal artery to the rectum and external genitalia (this is the sole representative of the hypogastric artery).
   2. Uterine artery.
   3. Umbilical artery.
   4. Crural artery to the hind-limb.

B. Middle Sacral Artery through its rete mirabile.
   1. Gluteal twigs.
   2. Twigs to the caudal muscles.

In *Myrmecophaga*, according to Hyrtl (**109**) the branches are as follows:—

A. A rete mirabile giving off lateral sacral, gluteal and sciatic arteries.

B. Pudendal artery.
C. Inferior hæmorrhoidal artery.
D. Obturator artery.

Pouchet (82) gives the branches as follows:—

A. Obturator artery.
B. Gluteal artery.
C. Sciatic plexus.

In *Bradypus* the artery gives off plexuses as follows:—

A. Pubic plexus to the perineum and external genitalia.
B. Hæmorrhoidal plexus to the rectum.
C. Muscular plexus to the levator ani and caudal muscles.
D. Gluteal and sciatic plexus.

In *Dasypus* the artery breaks up into gluteal and obturator arteries.

It is thus evident that the conditions in *Orycteropus* differ markedly from those in the other Edentata apart from the absence of retia mirabilia. And they resemble the conditions in higher Mammals.

Arteries of the Head and Neck (text-fig. 25 B).

Common Carotid Artery (C.C.A.):—The mode of origin of the carotid arteries in the Edentata is described on p. 410. And it appears that *Manis* is the only form in which it gives off no branches other than the external and internal carotids. The branches are as follows:—

In *Orycteropus* it gives off:—

1. *Inferior thyroid artery* (I.T.A.), which enters the lower pole of the thyroid gland.
2. *Hyo-thyroid artery* (H-T.A.), which supplies the hyoid and laryngeal muscles, and gives a superior thyroid branch to the thyroid gland (S.T.A.).
3. *Occipital artery* (O.A.) to the occipital and scalp muscles, and to the auricle. It is really an occipito-auricular artery. No diploetic nor meningeal branches are given off as in *Myrmecophaga* and *Dasypus*.

At the point where the occipital artery is liberated the vessel gives off the small internal carotid artery (I.C.A.) and is continued as the large external carotid artery (E.C.A.). In all Edentates the internal carotid artery is small.

In *Myrmecophaga* it gives off the superior thyroid artery, and one to the long muscles passing from the sternum to the tongue. In *Dasypus* it gives off both superior and inferior thyroid arteries and a vessel to the muscles round the hyoid bone.

The *External Carotid Artery* ends by dividing into internal and external maxillary arteries in *Orycteropus* and *Manis*. In *Myrmecophaga* it divides into occipital, external maxillary and

temporo-maxillary arteries. In *Dasypus* it gives off many large vessels and is continued as the internal maxillary artery. In all except *Orycteropus* facial retia mirabilia are present, going to the snout and other parts. In *Myrmecophaga* alone no branches arise from the external maxillary artery before it divides. The branches in other genera are as follows:—

In *Orycteropus* the trunk gives off the *lingual artery* (L.A.). This vessel descends in close relation to the hypoglossal nerve and posterior belly of the digastric muscle, and disappears under the hypoglossus muscle, at which point it parts company with the nerve. It runs forwards under the mucous membrane of the tongue to near its tip, at which it anastomoses with its neighbour. In *Manis*, according to Hyrtl (**109**), the trunk gives off:—

1. Two vessels to the larynx and muscles.
2. Lingual artery.
3. Three vessels to the submaxillary gland.
4. Occipital-temporal artery.
   a. Temporal.
   b. Occipital.

In *Dasypus* (**109**) the trunk of the external carotid gives off the following branches:—

1. Muscular artery.
2. Pharyngeal artery.
3. Occipital artery.
   a. Muscular twig.
   b. Diploetic artery.
   c. Communicating to the vertebral artery.
4. Linguo-maxillary trunk.
   a. Lingual artery.
   b. External maxillary artery.
5. Posterior auricular artery.

The *external maxillary artery* (E.M.A.) gives off the following branches in *Orycteropus*:—

a. Artery to the submaxillary gland (S-M.G.).
b. Artery to the parotid gland (P.G.A.).
c. Muscular to the masseter (*m.a.*) and zygomatico-mandibularis.
d. Superficial temporal artery (S.T.A.) to the scalp and auricle.
e. Transverse facial artery (T.F.A.) to the panniculus, masseter and upper lip.

In *Manis* it gives off buccal and transverse facial arteries and there is a rete mirabile to the face and snout. In *Myrmecophaga* there are also a maxillary rete and small lingual and sublingual vessels. Hyrtl (**109**) points out that there is no separate lingual

artery in this animal. In *Dasypus* it breaks up into an immense number of twigs forming an extensive facial rete to the face and the side of the head below the level of the orbit. Submental twigs are also given off.

The *internal maxillary artery* (I.M.A.) in *Orycteropus* runs up on the deep aspect of the mandible. In the pterygoid region it bends forward and runs across the surface of the internal pterygoid muscle. Its whole course is visible till it disappears into the infra-orbital canal; and it is continued at the infra-orbital artery. It gives off the following branches (text-fig. 5):—

1. Submental artery (S-M.A.) to the muscles of the floor of the mouth.
2. Muscular arteries to the pterygoid muscles.
3. Inferior dental artery (I.D.A.) which enters the mandibular canal.
4. Posterior superior dental artery (P.S.D.A.) to the upper gum.
5. Communicating to the ophthalmic artery (C.O.A.).
6. Infra-orbital artery (I-O.A.). This accompanies the immense maxillary nerve. It has a long facial course, and supplies the nasal muscles and mucosa, the skin of the nose and the anterior part of the upper gum.

In *Manis* (**109**) it gives off inferior dental, pharyngeal, orbital, palatine and inferior ethmoidal arteries. In *Myrmecophaga* a temporo-maxillary trunk gives off temporal, transverse facial and internal maxillary arteries, and the latter gives off inferior dental, infra-orbital and two ethmoidal branches.

In *Dasypus* (**109**) it gives off:—

1. Transverse facial artery.
2. Communicating to the posterior auricular artery.
3. Inferior dental artery.
4. Two deep temporal vessels.
   a. Mid-meningeal artery.
   b. Diploetic artery.
5. Orbito-ethmoidal artery.
6. Two twigs to the Harderian gland.
7. Masseteric artery.
8. Pterygoid arteries.
9. Infra-orbital artery.

The *internal carotid artery* is a small vessel, giving off no branches in the neck in any Edentate. In this animal the injection material did not run well, so I was only able to study the ophthalmic artery, whose ciliary, lachrymal and central retinal arteries were well marked, particularly the first branch, which is a large posterior ciliary trunk. No anterior ciliary arteries were present.

Arteries of the Anterior Extremity.

Subclavian Arteries (text-fig. 25 B):—The right artery arises from the bifurcation of the short innominate artery, and has a long, oblique course to reach the outer border of the first rib. The left one arises from the aortic arch and passes almost straight forwards to reach the rib. It differs from many Mammals in that no scalenus anticus crosses either artery, that muscle being absent. The following branches are given off:—

1. Internal mammary artery (I.M.A.).
2. Muscular artery to the scaleni (S.M.A.).
3. Vertebral artery (V.A.).
4. Ascending cervical artery (A.C.A.).

The *internal mammary artery* is given off at the same level as the vertebral. It has the usual course, but I could not trace the communication between its superior epigastric branch and the epigastric artery.

The *vertebral artery* passes forwards and inwards to reach the foramen in the transverse process of the sixth cervical vertebra.

The *ascending cervical artery* passes forwards and onwards till it reaches a point level with the middle of the neck, and ends by dividing into the transverse cervical and suprascapular arteries.

The *transverse cervical artery* (T.C.A.) sends small branches to the prevertebral muscles and scaleni, and a descending branch (*d.b.*), which passes backwards beneath the levator scapulæ and rhomboids and ends in the muscles round the posterior angle of the scapula. The *suprascapular artery* (S-S.A.) has the usual course to and over the dorsum of the scapula.

The *Axillary Artery* (text-fig. 25, A.A.) is a large vessel. It gives off the thoracic axis and a large trunk, which divides into the subscapular and circumflex arteries. The brachial artery almost appears to be a small branch of the axillary artery.

The *thoracic axis* (T.A.A.) breaks up into pectoral and deltoid branches to the corresponding muscles. The pectoral branches are numerous and some go to the subclavius.

The *subscapular artery* (S.U.A.) runs along the axillary border of the scapula to about its middle. It then gives two branches to the latissimus dorsi, but most of the main stem turns round on to the dorsum of the scapula and ends in the infraspinatus muscle.

The *circumflex artery* (H-C.A.) is not a complete circumflex artery, but it corresponds to that vessel in higher Mammals. An anterior branch ends in the biceps and coraco-brachialis. A posterior branch turns round the humerus along with the circumflex nerve; it gives off a branch to the scapular heads of the triceps, and ends in a vessel which ascends to the shoulder joint.

In the other Edentata it is more convenient to combine the subclavian and axillary arteries, and the branches are as follows:—

Manis (109).	*Myrmecophaga* (109).	*Dasypus*.
Vertebral.	Vertebral.	Vertebral.
Internal mammary.	Internal mammary.	Internal mammary.
Combined trunk giving:	Combined trunk giving:	Superior intercostal.
ascending cervical.	ascending cervical.	Ascending cervical:
transverse cervical.	deep cervical.	spinal.
transverse scapular.	pectoral and deltoid.	pectoral.
acromial.	submaxillary gland.	anterior humeral circumflex.
Pectoral.	two anterior thoracic.	sterno-clavicular.
Long thoracic:	Combined stem giving:	prevertebral muscular.
circumflex scapular.	subscapular.	deep cervical.
3 subscapular.	superior scapular.	External anterior thoracic.
muscular to	humeral circumflex.	Arteria comes nervi ulnaris.
serratus anterior		Muscular trunk:
latissimus dorsi.		Subscapularis and teres.
		Infraspinatus, latissimus, teres.
		Posterior humeral circumflex, subscapular, long thoracic and circumflex scapular combined.

Thus it may be seen that the branches are not so combined in a few main trunks in *Orycteropus*.

Brachial Artery (text-fig. 25 B):—The brachial artery passes down the fore-limb towards the internal humeral condyle, and it runs with the median nerve through the entepicondylar foramen. It then passes deeply among the muscles on the flexor aspect of the forearm, turns medially and is continued as the ulnar artery. It gives off the following branches:—

1. Profunda artery (P.B.A.) to all heads of the triceps and the muscles round the olecranon.
2. Lateral muscular artery (L.M.A.) to biceps, brachialis anticus, coraco-brachialis and triceps.
3. Median muscular artery (M.M.A.) to the origin of the forearm flexors.
4. Anterior interosseous artery (A.I.A.) to the pronator muscles.
5. Muscular arteries to the muscles arising from the internal condyle. One of these may correspond to the radial artery (R.A.).

In the other Edentata the brachial vessels form more or less extensive retia mirabilia, and Hyrtl (109) has described in great detail the origin of the branches. The reader is referred to his papers.

Ulnar Artery (text-fig. 25 B):—This vessel is distributed to the back of the forearm and manus, but I was unable to trace the vessels in the manus as the injection material did not run well. The artery passes between the radius and ulna, and is continued as the *dorsal interosseous artery* (D.I.A.), which runs along the dorsum of the interosseous membrane and ends by dividing into two branches.

Shortly after the ulnar artery passes between the two bones of the forearm it gives off a large dorsal artery which bifurcates into:—

1. A recurrent artery (REC.A.) which runs proximally to the region of the olecranon and internal humeral condyle.
2. An artery (U.A.P.) which runs down to the manus and supplies the extensor muscles en route.

Retia mirabilia and sheafs of vessels occur in the forearm in other Edentata, and Hyrtl's work (**109**) gives the details, illustrated by beautiful coloured plates.

Arteries of the Hind Limb.

The *external iliac artery* gives off one artery on the right side and two on the left. And these vessels are destined to supply the ventral abdominal muscles, the cremaster sac and the skin of the external genitalia.

The *femoral artery* runs distally on the outer side of the femoral veins. In the interval between the adductor brevis and semimembranosus it gives off the saphenous artery and dips down to become the popliteal artery. There is no profunda artery. The following are the branches:—

1. Muscular artery to the tensor fasciæ femoris.
2. Muscular artery to the quadriceps extensor.
3. Arteria genu suprema to the muscles round the internal femoral condyle.
4. Saphenous artery, which runs down the inner side of the leg to the dorsum of the foot.
5. Muscular artery to the adductor brevis and semimembranosus.

The *popliteal artery* is two inches long. It ends by dividing into the anterior and posterior tibial arteries, and it gives off the following branches:—

1. Muscular artery to the vastus externus.
2. A trunk which divides into:—
   a. Artery to the glutei and hamstrings.
   b. Artery to gastrocnemius and soleus.
3. Small arteries to the origins of the posterior tibial vessels.
4. Articular to the back of the capsule of the knee joint.

The injection material did not run well, so I could not successfully trace the arteries among the strong tendons and fasciæ of the foot.

No retia mirabilia occur on any of the arteries of the hind-limb.

The Veins

The *anterior facial vein* (text-figs. 3 and 4, A.F.V.) begins at the inner angle of the eye. It describes a curved course over the masseter, and ascends to the interval between the parotid and submaxillary glands. There it meets the posterior facial vein to form the external jugular vein. The two anterior facial veins are connected by the vena transversa (text-fig. 8, V.T.). There is no deep facial vein. The following are the tributaries :—

1. Superior labial vein (S.L.V.) from the upper lip.
2. Inferior labial vein (I.L.V.) from the lower lip.
3. Submaxillary vein (S-M.V.) from the submaxillary gland.
4. Vena transversa.

The *posterior facial vein* (text-fig. 4, P.F.V.) begins as a vein from the orbit, nose and diploë. It courses downwards and backwards, and receives :—

1. Palpebral vein from the lower eyelid.
2. Temporal vein from the temporal region.
3. Internal maxillary vein (I.M.V.) from the pterygoid region.
4. Parotid veins.

The *external jugular vein* (text-figs. 4 and 8, E.T.V.) is concealed by the depressor auriculæ and conceals the cleido-mastoid. It crosses the inner end of the clavicle, unites with the subclavian vein and dips in behind the manubrium sterni as the innominate vein. It receives the following tributaries :—

1. Vein from the submaxillary gland.
2. Transverse scapular vein.
3. Deltoid vein.
4. Subclavian vein.

The *anterior jugular veins* are absent. The *internal jugular vein* is narrow. It ends in the innominate vein.

The *innominate veins* (Pl. I.) are formed in the usual way. They run separately to the right auricle as precaval veins, and there is no superior vena cava. No azygos vein enters the right vein, but a large one enters the left one. The left vein is encircled on its lateral and ventral aspects by a process of the left lung. A phrenic nerve courses along each innominate vein on its ventral aspect.

Azygos Veins :—Two long venous trunks course through the thorax, and the right one passes into the left one close to the spot where the latter enters the termination of the left precaval vein on the outer side of the heart.

The right trunk receives the following veins:—

1. A venous trunk draining the first five interspaces.
2–8. A vein from each of the lower seven spaces.
9–11. Three veins ascending from the abdomen.
12–13. A vein from each of the two lowest right intercostal spaces.

Of the three veins coming up from the abdomen one is the ascending lumbar vein which is the beginning of the right azygos trunk. The others enter the trunk.

The left trunk receives the following veins:—

1. A venous trunk draining the first five spaces.
2–6. A vein from each of spaces six to ten.
7. A formative ascending lumbar vein.

Beddard (4) in a study of the azygos veins points out that in *Myrmecophaga*, *Tamandua*, *Dasypus* and *Chlamydophorus* the right azygos only is present, and regards this as "an additional argument, though doubtless a small one, for the banding together of the American Edentates." As Weber (99) regards the azygos veins to be of taxonomic value, they are against a relationship of *Orycteropus* with them. Beddard also points out that "the existence of two azygos veins characterizes several Marsupials, Rodents, Insectivores and most Artiodactyla." None of Beddard's specimens show a union of the right and left trunks to form one vessel opening into one precaval vein as in my specimen of *Orycteropus*.

Veins of the Hind Limb and Pelvis.

These veins follow the course of the arteries very closely. There is no saphenous opening. The two common iliac veins unite in the usual manner to form the inferior vena cava. And there is no connection between the renal and iliac veins.

Veins of the Fore Limb.

These veins are much as the arteries, but the following points must be noted:—

1. There is no cephalic vein.
2. There is a brachial vein.

The *inferior vena cava* begins at the same level and to the right of the bifurcation of the abdominal aorta by the confluence of two common iliac veins, the left vein passing behind the right common iliac artery. It is a very capacious vessel. It passes upwards in contact with the right side of the aorta as far as the junction of the right renal vein and vena cava. There it inclines to the right, lying in contact with the right crus of the diaphragm. It passes for a short distance behind the liver, grooving its posterior surface. It is in contact posteriorly with the

tendinous fibres of the right crus of the diaphragm until it pierces the central tendon and enters the thorax. The walls of the vein are intimately blended with the central tendon. The tendon encircles the vein in a series of loops at the point of entrance. At this point the oval vein is an inch in its greatest diameter.

The vein receives the following tributaries:

1. Six lumbar veins.
2. Mid sacral vein.
3. Right spermatic vein.
4. Renal veins.
5. Inferior phrenic veins.
6. Hepatic veins.

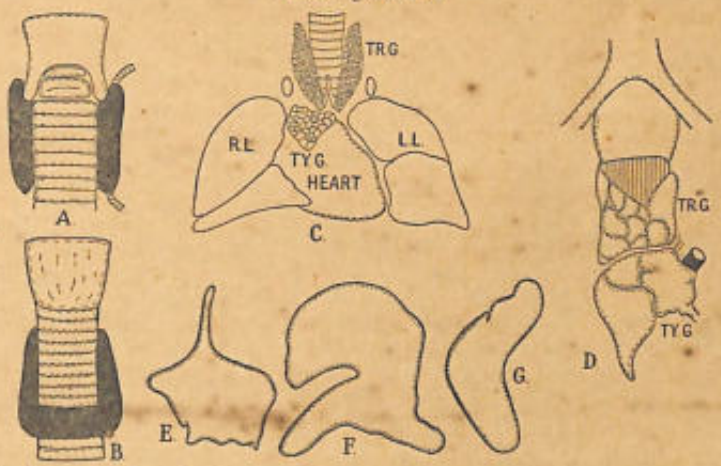
The *left spermatic vein* enters the left renal vein.

The Ductless Glands and Spleen.

Thyroid Gland (text-fig. 27).

In *Orycteropus* the gland consists of two unconnected lobes lying well down under the sterno-thyroid muscles. Each lobe is

Text-figure 27.



Ductless glands and spleen in the Edentata. A: thyroid in *Orycteropus*; B: thyroid in *Myrmecophaga*; C: ductless glands in *Dasypus*; D: ductless glands in *Tamandua*: E: spleen in *Tamandua*; F: spleen in *Dasypus*; G: spleen in *Tatusia*. R.L. and L.L: lungs; TR.G: thyroid gland; TY.G: thymus gland.

very thin and ovoid in shape. It is apposed against the lower half of the thyroid cartilage and the first nine tracheal rings. It is supplied by the superior thyroid branch of the common carotid artery. It is distant from the thymus.

In *Tamandua* the gland is more massive. It consists of a thick quadrangular body stretching across the front of the trachea, and giving off two anterior cornua, which reach the sides of the larynx. Posteriorly a narrow interval separates it from the thymus. It is coarsely lobulated.

In *Myrmecophaga* the gland is U-shaped. A thick lobulated part crosses the front of the tenth, eleventh and twelfth tracheal rings and gives off two tapering processes which nearly reach the larynx. Pouchet (**82**) describes a similar condition.

Rapp (**83**) points out that the lobes are entirely separated in *Bradypus*, *Dasypus*, *Manis* and *Orycteropus*, and the gland is simple in *Choloepus* and *Myrmecophaga*.

Thymus Gland.

Rapp (**83**) states that the thymus persists during the whole life in the Edentata, and he observed it in *Bradypus*, *Orycteropus*, *Dasypus*, *Myrmecophaga* and *Manis*. In *Orycteropus* I did not observe any trace of the gland. In *Tamandua* it is almost continuous with the thyroid gland, and its broad, lobulated anterior part sends two processes backwards over the pericardium. Of these the mesial process is the larger, and both are pointed. In a very young *Dasypus villosus* a large rudiment exists.

The Spleen (text-fig. 27).

The spleen in *Orycteropus* is a long, narrow body with slightly expanded ends. It is devoid of fissures of any kind, and the hilus is a long, narrow streak. It has the usual peritoneal connections. No accessory spleens are present.

In *Tamandua* it has a diamond-shaped body and a thin lateral piece, which is not bent upon itself. No accessory spleens are present. In *Myrmecophaga* it is a long, stocking-shaped body.

Dasypus villosus has a sagittate or bilobed spleen.

In a former paper (**85**) I described and figured the spleen in *Bradypus tridactylus*, and I pointed out that it is on the right side of the abdomen. Rapp (**83**) and others have made the same statement. In all other Edentata it lies on the left side.

The Blood.

Nuttall (**110**) pointed out that the only Mammal apart from the other Edentata, with which the blood of *Orycteropus* gives a positive reaction, is the Pig, but that is no test of affinity, for the Pig being a generalized animal gives positive reactions with animals belonging to most Orders. Gulliver (**38**) does not mention the corpuscles.

The Respiratory Organs.

Nasal Cartilage (text-fig. 3 B and C):—The cartilage is at first tubular, and is prolonged out from the interior of the nasal

cavities. It has a central dorsal spine and a vertical wall, which is continuous posteriorly with the septal cartilage. The part of the cartilage in the lateral wall on each side has a posterior part on which the compressor naris acts, and an anterior mobile portion which gives an attachment to the levator labii superioris and dilator naris.

When a vertical section is made of the skull a long respiratory tube connecting the anterior and posterior nares runs between the palate below and the maxillo-turbinal above. It corresponds to the inferior meatus of the Primates. It communicates by an orifice with an enormous fronto-maxillary excavation.

Turbinate Bones:—It has been shown by Gregory (**39**), Paulli (**72**) and others that *Orycteropus* has more turbinalia than any other Mammal, and Weber (**99**) has illustrated them. They will be considered more fully in the second part of this monograph.

Organ of Jacobson:—Broom (**11**) has made a detailed study of this structure, and he concludes that:

1. In the absence of any developments of the nasal floor cartilage to support the naso-palatine canal *Orycteropus* differs from all Eutheria except the Edentata as exemplified by *Dasypus* and the aberrant Insectivore *Macroscelides*. Its supposed Ungulate affinities must be very remote.

2. The Rodents are far remote from *Orycteropus*.

3. We must look for affinities among primitive Mammals—Edentates, Marsupials and Monotremes. It agrees with them in the absence of support for the naso-palatine canal, and in the presence of what are probably remains of the turbinal of the Organ.

4. It differs from *Dasypus*, in which the Organ opens into the nasal cavity, and it agrees with *Manis* in that the Organ opens into the naso-palatine canal.

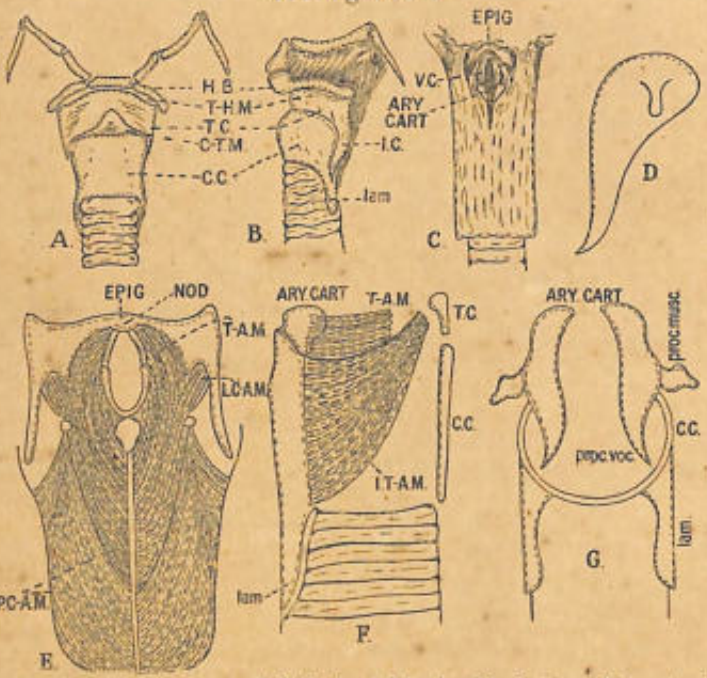
5. On the whole the Organ resembles that in Marsupials, but there are a number of differences, particularly the absence of a papillary cartilage in the palatine papilla and the absence of a support for the lower glandular ridge.

6. The evidence from the study of this region would seem to point to *Orycteropus* being descended from a line of ancestors, the early members of which were probably allied to Marsupials, whilst the later members branched off from the Eutherian stem before any of the higher Eutherian types had been specialized. If the *Orycteropus* line ever coincided with that of *Dasypus* the two must very early have diverged.

Larynx (text-fig. 28):—Some details of the anatomy are contained in the works of Rapp (**83**), Weber (**99**) and Bender (**6**). The *thyroid cartilage* (T.C.) is connected to the inner surface of the hyoid by a narrow, but powerful, thyro-hyoid membrane (T-H.M.); and it is connected to the deep surface of the upper end of the cricoid cartilage by the crico-thyroid membrane

(C-T.M.). The latter is wider in the centre than at the sides. The cartilage is narrow in the centre, but wide at the sides. It has stumpy upper cornua, which are connected by ligaments to the globular extremities of the hyoid bone (H.B.); and no triticeal cartilages exist in these ligaments. The inferior cornua (I.C.) are long. They are connected to the sides of the large cricoid cartilage by ligaments and muscles. The *cricoid cartilage* (C.C.) is very wide. It sends a long lamina (*lam.*) down on the back of the first four tracheal rings. And the body and lamina are connected to these rings by a short, strong, cricotracheal membrane. On the mid-dorsal line there is a strong

Text-figure 28.



The larynx in *Oryctéropus*. A, B, C: front, lateral and back views; D: arytenoid cartilage; E: muscles from behind; F: internal muscles; G: disposition of arytenoid cartilages. Other letters in text.

vertical ridge, which ends above in a prominent tubercle, to which the inner corners of the arytenoid cartilages are attached by fascia. The *epiglottis* (EPIG.) is only a nodule lying in the thyro-arytenoid folds of mucous membrane. It overlies a nodule (text-fig. 28 E, NOD.) on the back of the upper border of the thyroid cartilage. The *arytenoid cartilages* (text-fig. 28 G,

ARY.CART.) are pyramidal in shape, the apex of the pyramid being formed by the strong muscular process (*proc.musc.*). The vocal process (*proc.voc.*) is very long; it passes down on the inner aspect of the cricoid cartilage as far as the beginning of the lamina, and it is closely bound to the cricoid by fascia. The two processes of the cartilages are shown in text-fig. 28 G. On the under surface of the processus vocalis there is a small, convex articular facet, which operates in a wide concavity in the upper border of the cricoid cartilage. Cartilages of Santorini and Wrisberg are absent. There are no false vocal cords, and the true vocal cords are really ridges produced by the thyro-arytenoid muscles. No ventricles exist.

Text-figure 29.

The larynx in *Myrmecophaga* from the front (A) and side (B) and the larynx in *Dasypus* (C) from behind.

The *posterior crico-arytenoid muscle* (text-fig. 28, P.C-A.M.) arises from the whole of one half of the back of the cricoid lamina, and consists of two parts. The lateral part is inserted into the vocal process of the arytenoid cartilage (V.P.) The medial part runs forward over the processus muscularis, and its fibres become continuous with the thyro-arytenoid and lateral crico-arytenoid muscles. The *arytenoideus* is absent. The *lateral crico-arytenoid muscle* (L.C-A.M.) derives its origin partly from the processus muscularis and partly from the posterior muscle. It is fused posteriorly with the thyro-arytenoid muscle. The *external thyro-arytenoid muscle* (T-A.M.) arises partly from the muscular process of the arytenoid cartilage and in great part from the posterior crico-arytenoid muscle. It sweeps round the laryngeal aperture, and is blended with its neighbour. The combined mass is inserted into the back of the thyroid cartilage below the eminence. The *internal thyro-arytenoid muscle* (I.T-A.M.) arises from the outer surface and anterior border

of the long vocal process of the arytenoid muscle. The fibres converge and blend with those of the external muscle close to the insertion of the latter into the thyroid cartilage.

It is evident that the epiglottis cannot close the larynx in this animal as it is a minute nodule, but the closure is effected by the powerful thyro-arytenoid sphincter. Closure is of very great importance in this animal owing to the nature of the diet, which includes living insects.

In the other Edentata the epiglottis is not rudimentary, and it is notched in *Dasypus*. In *Myrmecophaga* the thyroid cartilage is ossified. The comparisons are shown in text-figs. 28 and 29.

The *trachea* consists of ten rings, whose cartilages are incomplete behind. The cervical rings are wide, and each splits into two parts. But the thoracic rings are narrow and entire. The first four cervical rings are firmly bound to the deep surface of the cricoid lamina.

The *bronchi* are wide. The right one runs almost straight back from the trachea to the pulmonary root, but the left one has a more transverse course. The right bronchus is also larger than the left one.

Lungs:—The left lung is thin. It is composed of two lobes, of which the upper has a long, narrow, pointed process. The right lung is massive and consists of four lobes of which one is the azygos lobe. In *Manis* the lungs have the same numbers of lobes, but the azygos lobe is completely cleft into two; there is a tendency to cleavage in *Orycteropus*. In the Armadillos the left lung may have two or three lobes, and the right one has three lobes plus an azygos appendage of the lowest lobe. In *Myrmecophaga*, according to Forbes (29), the left lung has two lobes and the right one has three, with an azygos appendage. In all these genera the lowest lobes are the largest on both sides. In *Bradypus* the lungs are undivided. In *Tamandua* I found each lung cleft, but the sulci were not deep enough to divide them into distinct lobes. In *Dasypus villosus* the right lung has three lobes and an azygos appendage, and the left one has two, of which the lower one is deeply cleft. In *Bradypus* the lungs are entire, so it is the only exceptional Edentate. The conditions in *Choloepus* are unknown to me.

The Urinary Organs.

Kidneys:—The left kidney is lower (posterior to) than the right one as in several Marsupials.

Both have four large pyramids, but only one papilla opens into the small pelvis. No fat is present in the pelvis. The cortex is a narrow strip. The capsule of the kidney strips easily, and there is no perirenal fat. The structures in the hilus have the usual relations. In *Myrmecophaga* there are no papillæ, but only a ridge. In *Dasypus villosus* there is one well-marked papilla.

The *ureters* have the usual course.

Bladder (text-fig. 23 A):—The bladder is attached to the anterior abdominal wall by an *anterior ligament* (A.L.B.), but there is no trace of the urachus. This ligament ends an inch and a half from the fundus of the bladder. The *lateral ligaments* (L.V.B.) are well marked. They stretch from the sides of the bladder outwards. Above they are continuous with the mesentery of the vas deferens. In the ligament are seen the ureter, the artery to the vas deferens and one of the vesical arteries. The *obliterated hypogastric artery* also runs in the ligament just above the ureter. This artery has a small mesentery of its own, which blends with the side wall of the bladder at the same level as the upper limit of the anterior ligament. *Posterior ligaments* are absent. The lateral ligaments are attached to the side wall of the pelvis at the level of the origin of the rectus abdominis. The anterior wall of the rectum is fused with the base of the *seminal receptacle*, and the latter is attached to the posterior surface of the bladder by a loose peritoneal sheet, thus forming a pouch. A small semilunar peritoneal fold, which appears as a prominent white ridge, stretches across between the two lateral pelvic walls across the back of the seminal receptacle.

The pyriform bladder has thin walls. The mucous membrane is thrown into many irregular and undulating longitudinal ridges on both anterior and posterior walls. The ureteric orifices do not lie on papillæ, but each one is partially encircled by a fold of mucous membrane, forming a shelf above the orifice. The urethral orifice is far from the ureteric orifices, and the longitudinal folds of the mucosa of the bladder converge on the opening. So there is no smooth area resembling a trigone. The orifice of the urethra is reduced still farther by the passage into it of these folds of the mucosa. In *Tamandua*, according to Garrod, the bladder is very muscular.

The spongy urethra is short. No uterus masculinus exists in *Tamandua*.

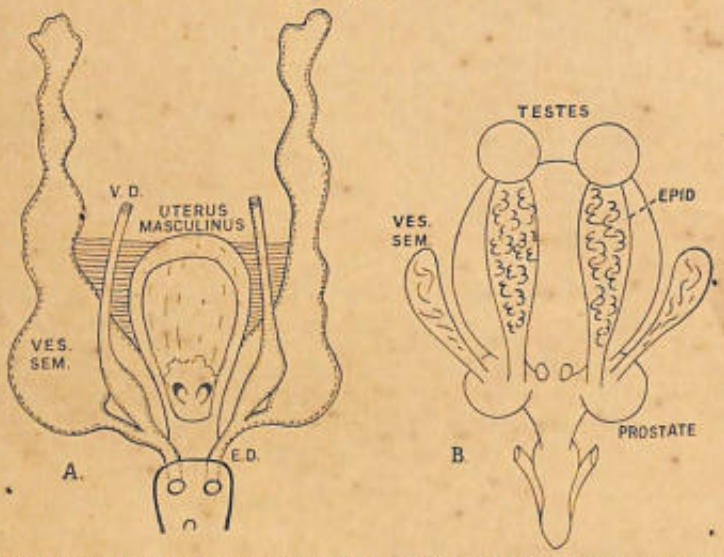
The Generative Organs.

The *testis* (text-fig. 12) is an elongated body shaped like a flattened sausage. It is contained along with the narrow epididymis between the layers of a genital mesentery; but the epididymis is separated from the testis except at the globus minor. The epididymis has a small mesentery projecting from the side of the genital mesentery. And the spermatic cord pulls away a mesentery of its own from the inner aspect of the common genital mesentery. I did not have the opportunity of examining the mesenteries in the female.

The globus major is connected by gubernacular bands to the wall of the cremaster sac and chorda gubernaculi; and the spermatic vessels are attached to the globus minor. No hydatids are present. On making a section through the testis it

is seen how the corpus Highmorianum is small, and the division into loculi by trabeculæ is poor. The tunica albuginea is thin. The vas deferens leaves the side of the epididymis and not from the end; it has the usual whipcord consistence. In this animal the testis, epididymis and parts of the genital mesentery and spermatic cord were contained within the sac-like protrusion of peritoneum through the ventral abdominal wall. The lower end of the vas has an ampullary dilatation.

Text-figure 30.



The generative organs in *Orycteropus* (A) and *Tamandua* (B). EPID: epididymis; V.D: vas deferens; VES.SEM: vesiculæ seminales.

In *Tamandua* (text-fig. 30 B) the globular testis, with its large epididymis, lies within the abdomen close to the anus. In *Myrmecophaga*, according to Rapp (**83**), the testes are contained within the abdomen, and in this they resemble the testes of the Bradypodidæ. In the Armadillos he found that the inguinal canal was so narrow that it would not contain the testis, but Macalister (**52**) observed small testes contained in the wide abdominal openings of the canals in *Chlamydophorus*. In *Manis* the general conditions are as in *Orycteropus*, but Rapp stated that the testis cannot be drawn back into the abdomen. It is extra-inguinal, but not in a scrotum.

In no Edentate is there a scrotum, but the inguinal scent-glands lying under elevations of the skin at the sides of the penis in *Orycteropus* give the appearance of a scrotum with testes. Pocock (**77**) has already dealt fully with these glands.

In the Ungulata the testes are beside the kidneys or a little behind them in *Elephas* and *Hyrax*, and they are inguinal in position in *Rhinoceros* and *Tapirus*. In the Suidæ they lie in the perineum.

Vesiculæ Seminales:—Rapp (**83**) points out that these structures are present in Sloths, Armadillos and Anteaters, and he states they are large in *Cholœpus*. In *Orycteropus* (text-fig. 30 A) each vesicle (V.S.) is a long, tapering sac with septa partly dividing up the cavity into loculi. And each has peritoneal connections, which are described below. The sac is greatly distended by masses of hard secretion, but I did not make any attempts to analyse the lumps. The thin-walled duct unites with the thicker vas deferens below its ampulla to form the ejaculatory duct, which has a circular opening into the urethra. The orfices of the two ejaculatory ducts are well marked.

The *uterus masculinus* has moderately thick walls and is capacious. On its mid-dorsal wall there are two small pits surrounded on the exterior by glandular tissue. I was unable to examine them microscopically, but the glands are either the prostate or Cowper's glands. Whatever they be, only one is present. In *Tamandua* (text-fig. 30 B) there is a prostate, but no Cowper's glands. In *Dasypus*, according to Rapp (**83**), Cowper's glands are present and large.

The *penis* is short, has a well-marked glans, and possesses a vertical meatus urinarius externus. The usual component corpora are present. The corpora cavernosa have strong walls and much erectile tissue. Anteriorly the septum between them disappears and they become one body. The corpus spongiosum has a small amount of erectile tissue surrounding the wide urethra. The striking feature is the small size of the penis, but the great size of the retro-penile parts of the corpora, and the well-developed musculature. The penis is free from the anus as in *Tamandua*.

No *os penis* is present in the Edentata.

Rapp (**83**) has given a short account of the penis in the Edentata.

Pelvic Peritoneum (text-fig. 23):—The bladder has the following connections:—

1. To the abdominal and pelvic wall by an anterior ligament.
2. To the lateral wall of the pelvis by lateral ligaments.
3. To the vas deferens.
4. To the seminal reservoir (uterus masculinus).

The *mesentery of the obliterated* hypogastric artery is connected to the lateral vesical ligaments.

The vas deferens is connected by peritoneal sheets to:—

1. The side wall of the pelvis.
2. The side of the bladder.

3. The seminal reservoir (uterus masculinus).
4. The vesiculæ seminalis.
5. The obliterated hypogastric artery.

A curved peritoneal fold crosses the pelvis and involves the backs of the seminal vesicles and seminal reservoir.

There is a peritoneal pocket between the bladder and seminal reservoir, and between the reservoir and rectum.

In a hitherto unpublished note Garrod gives the following particulars of the vesiculæ seminales:—

Tatusia peba:—vesiculæ present.
Tatusia hybrida:—vesiculæ longer than prostate.
Tatusia kappleri:—vesiculæ large.
Tolypeutes conurus:—vesiculæ absent.
Xenurus unicinctus:—No true vesiculæ for these form part of the spermatic cord, and the prostate and Cowper's glands are present.
Tamandua tetradactyla:—vesiculæ large and convoluted. Cowper's glands absent.

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EXPLANATION OF THE PLATE.

Plate I.

The heart of *Orycteropus afer*.

Fig. A. The left ventricle opened up.

Fig. B. Right auricle and right ventricle opened.

Letters in text.

18. Description of a new Genus and two new Species of Dragonflies (Odonata) belonging to the Family Gomphidæ from Tropical Asia. By F. F. Laidlaw, M.A., F.Z.S., Corresponding Member, Malayan Branch R. A. S.

[Received January 29, 1925: Read March 17, 1925.]

(Text-figures 1, 2.)

Genus Acrogomphus, nov.

Genotype, *A. fraseri*, sp. n.

A Gomphine genus with the following characters:—

1. Triangles, supra-triangles, and sub-triangles uncrossed.
2. Triangles regular in shape (*i. e.* sides approximately rectilinear).
3. Triangles of fore-wing slightly shorter than those of hind-wing.
4. No trigonal supplement.
5. No well-developed supplementary sector to Rs or M_4.
6. Cross-veins between M_{1+2} and M_4 show some indication of spacing out.
7. Pterostigma braced.
8. No basal post-costal cross-nerve.
9. Anal loop present on hind-wing.
10. Branches of Cu_1 tend to take on a pectinate arrangement.
11. Section of arculus at first parallel, then diverging.
12. Legs short; hind femora when adpressed reaching only to base of first segment of abdomen.
13. M_4 and Cu_1 parallel to level of nodus.
14. Ninth segment of abdomen shorter than eighth.

The Epigomphine genera from tropical Asia agree severally with *Acrogomphus* in the following characters:—

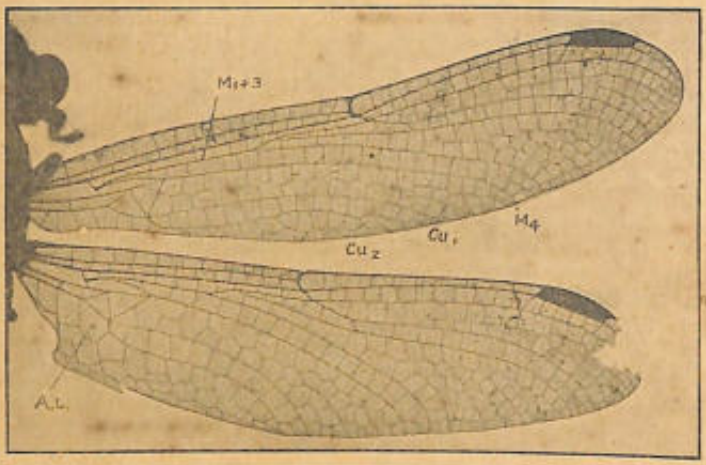
Perissogomphus	.2.3.4.5.6.7.8.9.10.11.12.14.	(1 and 6 variable in this genus.)
Macrogomphus	1.2.3.4.5. .7. .9.10.11.12.	(7 variable in this genus.)
Leptogomphus	1.2.3.4.5. .12.14.	
Heliogomphus	1.2.3.4.5. .8. .12.14.	(*H. kelantanensis* agrees in 13.)
Microgomphus	1.2.3.4.5. .8. .12.14.	

It is evident from this table that the new genus agrees more closely with *Perissogomphus* than with other Oriental genera of the series.

It shows also a closer resemblance to *Perissogomphus* in a secondary sexual character than it does to the other genera—namely, in the shape of the anal appendages of the male.

It differs from *Perissogomphus* in that the latter has always, so far as I know, at least two cross-nerves in the cubital space of all four wings, that it frequently has the triangles, especially of the hind-wings, traversed by a cross-nerve, and that the

Text-figure 1.



Wings of right side of *Acrogomphus malayanus* (♂ type).

M_{1+3}. Common trunk of branches 1 . 2 . 3 of median vein.
M_4. Fourth branch of median vein.
Cu_1. First branch of cubitus.
Cu_2. Second branch of cubitus.
A.L. Anal loop.

parallelism of M_4-Cu_1 is by no means so marked as in *Acrogomphus*.

Secondary sexual characters.

The males of the two known species of *Acrogomphus* have a *distinct exfoliation of the lateral margins of the eighth and ninth abdominal segments*; indicated also at the apex of the seventh segment.

The vesicle of the penis is not prominent and the genital hamules are small.

The two upper anal appendages are simple; tapering and slightly compressed from side to side. The valvulæ vulvæ of the female are small.

ACROGOMPHUS FRASERI, sp. n.

♂. Length of abdomen, 43·5 mm.; of hind-wing, 38·5 mm.

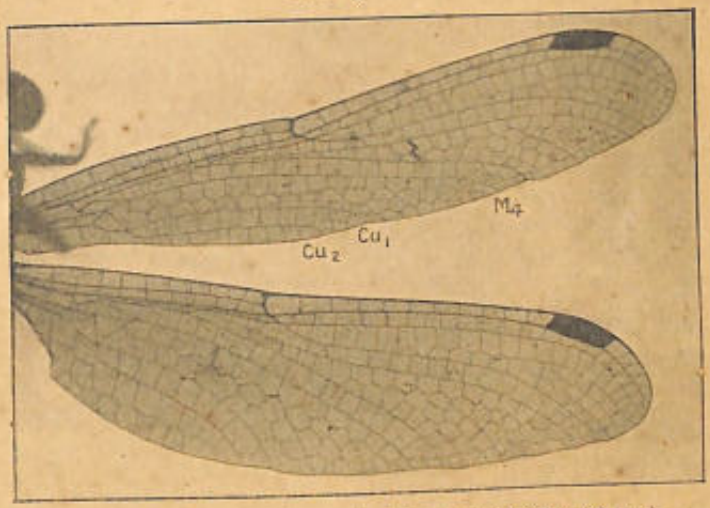
Head: Upper lip black, with a pair of round yellow spots, one on either side of the middle line. Anteclypeus and horizontal part of frons yellow; otherwise black.

Prothorax: Entirely black.

Synthorax: Black; mesothoracic collar, interrupted in the middle line, vivid yellow. A pair of small, wedge-shaped, dorsal stripes of the same colour, incomplete above and below. Each side with two broad stripes, also yellow, covering the meso- and met-epimerite.

Abdomen: Black. Sides of segments 1 . 2 with yellow marks. Segments 3–7 with apical dorsolateral spots of the same colour;

Text-figure 2.



Wings of right side of *Heliogomphus kelantanensis* Laidlaw (♂ type).
(Lettering as in text-figure 1.)

those on 7 very large, half the length of the segment, only separated dorsally by the mid-dorsal line of the segment. The others small or minute and distant from one another. Segment 8 with a rounded brownish-yellow spot on either side more ventrally placed than those of the preceding segments.

Legs: Black. Inner surface of anterior pair of femora yellow; hind femora 6·5 mm. in length; spines very small and numerous.

Anal appendages: Upper pair simple, 2·75 mm. long, slightly compressed laterally, tapering, decurved and incurved apically, black in colour. Lower appendage shorter, bifid apically, also black.

♀. Length of abdomen, 43 mm.; of hind-wing, 41 mm.

Colouring in general identical with that of the male, but it shows in addition a small spot of yellow at the upper end of the met-episternite on either side of the synthorax, which is scarcely visible in the male. The dorsolateral spots on segment 7 of the abdomen are relatively a little smaller than in the other sex.

Venation. Pterostigma 3·5 mm.

Antenodal and postnodal cross-nerves :

♂ (type) ... $\frac{11-18 \mid 18-11}{12-12 \mid 12-11}$. ♂ $\frac{11-16 \mid 16-12}{12-12 \mid 12-12}$. ♂ $\frac{9-15 \mid 16-8}{10-11 \mid 11-9}$.

♀ (allotype) $\frac{12-21 \mid 18-12}{14-15 \mid 15-13}$. ♀ $\frac{13-18 \mid 19-14}{14-14 \mid 14-14}$. ♀ $\frac{12-21 \mid 20-12}{13-15 \mid 15-14}$.

Cross-nerves between M_{1+1} and M_4:

♂ (type) ... $\frac{4 \mid 4}{2 \mid 2}$. ♂ $\frac{4 \mid 4}{3 \mid 2}$. ♂ $\frac{3 \mid 3}{2 \mid 1}$.

♀ (allotype) $\frac{3 \mid 4}{2 \mid 2}$.

In the type and allotype there are two rows of cells between M_1 and M_{1a} at the level of the distal end of the pterostigma. In one male there is but a single row on three of the wings and two rows on one front wing.

Pterostigma long, not equal to a quarter of the distance between the nodes and its distal end. Wings of both sexes slightly tinged with saffron at the base, especially in the female.

Type ♂, allotype ♀, in my collection. Sampaji Ghat, Coorg, 11. iv. 24. Coll. F. C. Fraser.

I have much pleasure in associating this species with its discoverer, Major Fraser, I.M.S., who has made so many and interesting additions to the Dragonfly fauna of India. His skill and enthusiasm as a field-naturalist, and his contributions to the literature of the Order alike entitle him to the gratitude of all specialists in Odonatology. He has given me the following notes on the habits of this species :—

"All the Indian forms of the *Epigomphus* series arboreal in their habits (I have, however, no knowledge of *Perissogomphus*)—that is to say, they rest high in the trees, the males living in forest, often far away from water, and they rarely descend to rivers except to oviposit or to drink. I have seen males fairly frequently dipping and scooping up water much the same as swallows do.

"I have seen the present species resting in trees from 12 to 100 ft. above the ground (at the latter height with the aid of field glasses). Usually they rest on a twig of a dead branch, and are thus easily picked out against the sky-line. *Macrogomphus* usually perches on twigs at lower heights, 10-20 ft., *Microgomphus* and *Heliogomphus* rest on foliage, never perch on twigs.

"The first specimen taken was a female (the allotype). I shot

the end of the abdomen off, and it fell amongst long grass and jungle debris. Examination of the wings on the spot suggested to me that it was a new species of *Macrogomphus*. I therefore searched carefully for the end of the abdomen, and finally found it. Its structure clearly showed that my capture was not a *Macrogomphus* at all.

"Two females were watched ovipositing. They hover about an inch above water, over shallows rippling over a pebbly bottom. They glide forward for about two feet, reverse rapidly in their own length and return. This manœuvre is repeated over and over again, with a long, hovering pause after each glide. Now and again they dip the abdomen and drop the eggs on the surface of the stream.

"When crossing an open space in forest, they dive low and trail the abdomen as though it were broken. Flight is slow on such occasions. Very occasionally males indulge in high, hovering flight at a level of 100–300 ft., mixing then with *Orogomphus campioni*."

ACROGOMPHUS MALAYANUS, sp. n.

♂. Length of abdomen, 33·5 mm.; of hind wing, 29 mm.

Head: Upper lip yellow, with black base and margin finely black. Anteclypeus and horizontal part of frons yellow; otherwise black.

Prothorax: Entirely black.

Synthorax: Black; mesothoracic collar, scarcely interrupted in the middle line, yellow. A pair of small wedge-shaped dorsal stripes of the same colour, incomplete above and below. Each side with two broad yellow stripes on the meso- and metepimerite.

Abdomen: Black. Sides of segments 1 . 2 with yellow marks; 2 has also a longitudinal, dorsal line of yellow. Segments 3 . 7 with apical dorsolateral spots of the same colour; those on 3 occupying more than the basal third of the segment; those on 7 more than the basal half; those on 4 . 5 . 6 about the basal quarter, each separated narrowly from its fellow of the same pair by a very fine mid-dorsal line of black. Segment 8 with a lateral basal spot also yellow.

Legs: Black. Inner surface of anterior and posterior pairs of femora marked with brownish yellow (the rest missing).

Anal appendages: Black. Upper pair simple, tapering, compressed from side to side, markedly incurved, and slightly decurved apically. Lower appendage missing.

Venation.

Antenodal and postnodal cross-nerves:

♂ (type)... $\frac{11—17 \mid 17—10}{10—12 \mid 11—9}$

Cross-nerves between M_{1+2} and M_4:

$$\frac{4\,|\,4}{3\,|\,3}.$$

Sectors of arculus show some tendency to converge at their commencement, where they are placed much closer to one another than in *A. fraseri*. Anal loop consists of one cell only.

In addition to the venational characters just mentioned, *malayanus* differs from *fraseri* in its slightly smaller size, in the smaller number of cells between Cu_2 and the anal margin of the fore-wing, and in the more extensive yellow markings of the abdomen and legs. The male of *fraseri* has a maximum of four rows of cells between Cu_2 and the anal margin of the fore-wing; it also has two rows in the postanal area, whereas *malayanus* has but a single row.

The type and only known specimen of *A. malayanus* was taken on Pulau Aor, off the east coast of Johore, 13. vi. 1912 (R. H.). It will be deposited in the British Museum.

It is possible that the Selysian species *Onychogomphus circularis* from N. Burma is closely allied here. Unfortunately I have no information as to the habits either of that species or of *A. malayanus*.

I am able, thanks to the kindness of Mr. F. W. Campion, to figure the wings of *A. malayanus*, and for comparison therewith those of *Heliogomphus kelantanensis* (Laidlaw). The latter is a true *Heliogomphus*, but differs from its congeners in the marked parallelism of M_4–Cu_1, in which character it resembles *Acrogomphus*. The figures also serve to illustrate the differences between the genera in certain of the characters enumerated above. One or two of these may be briefly discussed here.

(6) Cross-veins between M_{1+2} and M_4. The "spacing-out" is not very obvious in the specimen of *Acrogomphus* figured. The character is liable to individual variation in the two genera of Indian Epigomphines which exhibit it, viz. *Acrogomphus* and *Perissogomphus*. In the Gomphine series, on the other hand, this feature is generally exceedingly characteristic, although in certain cases, notably in the genus *Cyclogomphus*, some variability is present. On the whole, however, it is *the* character which differentiates the two series, and the small indications of spacing-out found in *Acrogomphus* and *Perissogomphus* points to a possibility of these genera occupying an intermediate position between the two series.

(9) Where the anal loop consists, as in *A. malayanus*, of a single cell, it will be noted that the anterior margin of the loop practically coincides with the anal margin of the sub-triangle. Where, as in *fraseri*, it includes two cells (and in species of other genera more than two), this loop is recognizable by the regular curve of its anal boundary.

(10) The contrast between the pectinate branching of Cu_2 of the fore-wing and its unbranched condition is fairly well shown in the two species figured. Major Fraser has pointed out to me that the occurrence of a pectinately-branched Cu_2 is often correlated with the presence of an anal loop.

19. External Characters, Skin, and Temporal Gland of a Fœtal African Elephant.

By Nellie B. Eales, B.Sc., Ph.D. (London), Lecturer in Zoology, University College, Reading.*

[Received November 6, 1924; Read March 17, 1925.]

(Plate I.; Text-figures 1–5.)

The fœtal African Elephant here described was obtained by purchase from Belgians, who brought it to this country from the Belgian Congo. Realising the importance and rarity of fœtal stages of this great mammal, they preserved it in spirit immediately after its extraction from the body of the mother. The specimen was acquired by Prof. D. M. S. Watson, of University College, London, and it is to his kindness and generosity that I am indebted for the material.

The present or Congo fœtus is the twelfth to be recorded. Five fœtuses of the Indian and seven of the African species of Elephant are known, but most of these were so indifferently preserved that anatomical investigation was not attempted. The first fœtus mentioned in the literature is the African one described by Seba as early as 1734. No measurements are given, but as the specimen was naked, it must have been less than eleven months old, according to Toldt's computation. Seba described the external anatomy and published a figure of the fœtus. In 1783 Zimmermann gave an account of a male fœtus from Ceylon, then in the possession of the Brunswick Museum. It was 13½ inches in length and had a few hairs on the tail. The next two fœtuses, both Indian, were obtained by Owen and Turner respectively. Owen's specimen, six months old, was described in 1857, and now lies in the Museum of the Royal College of Surgeons. Nine years later, Turner, in his lectures on the Comparative Anatomy of the Placenta, included an account of a half-grown fœtus, apparently about the same age as Toldt's. Lönnberg's specimen, an African one described in 1905, was less than half this size. The placenta was present in this specimen. A very small African fœtus, only 7·25 cms. long, belonging to the Berlin Museum, was described by Brauer in 1910. Another African one, twice the size of Brauer's, was recorded by Durrieux in 1912. A year after, Toldt junior† obtained an Indian fœtus of known age, viz. 11 months, and this specimen, in which certain hair-tracts are well developed,

* Communicated by Prof. D. M. S. Watson, F.R.S.

† Toldt, K., junr., "Ueber die äussere Körpergestalt eines Fötus von *Elephas maximus*." Anz. Akad. Wiss. Wien, Jg. 50, p. 302, 1913.

furnishes our only standard for the determination of the age of fœtal Elephants. We owe the most detailed account of the external anatomy and of portions of the internal anatomy to Bolk *, who described a male African fœtus, apparently slightly younger than the present one, in 1917. Unfortunately Bolk's fœtus was not sufficiently well preserved to admit of fine dissection of the soft parts. Two specimens are in the possession of the British Museum (Nat. Hist.). Through the kindness of Mr. Hinton the writer has been allowed to see these. One, the smallest yet found, is only 6·6 cms. long and came from Ceylon. The other, an African Elephant, is larger. These two fœtuses will be described by Mr. Hinton. The present (Congo) fœtus is probably older than Bolk's, but younger than that described by Toldt. As Toldt's fœtus was known to be 11 months old, the Congo specimen must be less than half term. In determining the age, measurements are misleading owing to the curvature which the body assumes while within the uterus. The only reliable factor is the development of certain structures such as the body hairs. (See description below.)

In all the accounts of fœtal Elephants mentioned above, with the exception of that by Bolk, external anatomy only is described, the specimens being either too rare or too indifferently preserved to justify internal examination. Bolk's investigations, too, as he states in his paper, were considerably hampered by maceration of the specimen, so that he confines himself almost entirely to an account of the cranial skeleton, the mouth and pharynx, and to a few general remarks on the contents of the thorax.

The fœtus here described was fortunately preserved in methylated spirit on the spot, and though its condition internally is only fair, it is good enough for macroscopic examination. The external form is seriously affected, especially in the head-region, by compression, and the brain is too soft for extraction.

When we come to the history of our knowledge of the anatomy of the Elephant as investigated by dissectors of young or adult specimens, it is not surprising to find that their statements frequently contradict one another and that omissions are numerous. Most of the organs have been described in a general way, but accurate drawings are very rare in the literature. One has only to read Blair's account † of the dissection of the carcase of an Elephant which died near Dundee to realise the enormous difficulties of the task—the hacking methods of the butchers he employed to cut up the body, the heat and its effects on the putrefaction of the carcase, the inquisitive interference of the idle public, and the utter impossibility of working out in detail any point of interest or doubt. The animal is far too large to preserve whole, and the preservation of small portions

* Bolk, L., "Anatomische Bemerkungen über einen Fetus von *Elephas africanus*." Amsterdam Verh. K. Akad. Wet 2e, Sect. 19, No. 6, pp. 1–40, 1917.

† Patrick Blair, "Osteographia Elephantica." Phil. Trans. Roy. Soc. London, vol. xxvii. p. 53, 1710.

is not very satisfactory. It appears, therefore, that a complete knowledge of the structure of the Elephant can only be gained by the dissection of well-preserved fœtuses.

Measurements and Weight.

Height when standing	22·5 cms.
Length from tip of proboscis to tip of tail over curve of back	60·5 „
Length from forehead to root of tail in a straight line	21 „
Length over curve of back	35 „
Proboscis tip to angle of mouth	16 „
Tail	9·6 „
Eye slit	1·1 „
„ bulge	2·3 × 1·7 cms.
Ear lobe	6·2 × 7·6 „
Angle of mouth to ear-opening	7·5 cms.
Fore leg	15·5 „
Hind leg to knee	12 „
Elbow to hoof	9 „
Knee to hoof	9·5 „
Circumference of fore foot	9·4 „
„ „ hind foot	8·3 „
Weight (preserved in spirit)	1864 grammes.

External Anatomy.

The fœtus is curled up in the position it occupied within the uterus (Plate I.). Externally it is well preserved, though the head is much flattened on the left side, and the thin skin is torn and stripped off in many places. All the parts of the fœtus are perfectly formed, and the characters of the species, such as the large foliate external ears, the two sub-equal prehensile lobes at the tip of the proboscis, both characters of the African Elephant, are strongly marked.

The small eyes are closed, but the curved eyelids are not fused as in many fœtal mammals. Posterior to the eye, and between it and the ear, a flattened swelling on the side of the head indicates the position of the temporal gland. The duct of the gland is visible owing to a slightly denser pigmentation of the skin in this region. No hairs are visible on the eyelids or eyebrows; a few colourless hairs, arranged in oblique rows of 3–5 hairs in each row, occur on the sides of the terminal portion of the proboscis. Bolk describes and figures two longitudinal rows of hairs on the middle third of the trunk and quotes Toldt's description, which agrees with his. In this fœtus, however, the hairs are quite definitely in paired oblique rows. These hairs on the proboscis are the only ones visible on the specimen. Hair germs, however, are developed within the dermis, as is evident from microscopic sections.

The external form of the proboscis agrees with that described by Bolk, except that the paired longitudinal furrows on the ventral side near the base are not present. The median furrow near the apex is not very deep; in fact, it is made visible chiefly on account of a less dense pigmentation of the skin along the line of the shallow groove.

The relation of the upper lip to the proboscis, the cushion-like projection near the angle of the mouth, the transverse ridges on the hard palate, and the short, thick tongue lying in the groove of the lower lip, have all been described by other observers. Some of these points will be referred to later. There are no external traces of teeth in the specimen. The small, pointed tongue protrudes from the mouth.

The limbs are well formed. The flat cushion-like sole is distinct owing to the almost complete absence of pigmentation. The sole of the fore foot is rounded in outline, with a straight posterior border. It bears five nails, which are yellow in colour and soft. The third nail is the largest; then in order 4, 2, 5, 1. The sole of the hind foot is elliptical, but is produced to a point posteriorly. Four nails are present, the third, as in the fore foot, being the largest. No nail occurs on the first digit. The fœtus has thus five nails on the fore foot and four on the hind foot—that is, the same as the adult Indian Elephant. In the adult African Elephant, however, the number is 4 and 3, so that during development one nail is lost on each foot. The relation between the circumference of the fore foot and height of the animal is in the fœtus nearly 1 : 3; in the adult this ratio becomes 1 : 2, a fact well known to elephant hunters, who judge the size of the beasts they are tracking by the footprints. This difference between the fœtus and the adult is not due entirely, as might be supposed, to an enlargement in the girth of the limbs when these are required to bear the great weight of the body, but partly to the spreading of the sole of the foot as the animal grows, the sole becoming expanded beyond the circumference of the leg on all sides. The fœtus shows the more primitive condition of the foot in this respect.

The short tapering tail has no trace of the terminal tuft of hair which occurs in the adult.

On moving the head it is seen that the neck is relatively longer and more slender in the fœtus than when the animal is full grown; in this stage it appears incapable of bearing up the bulky head.

Skin.

The skin is very loose and strips off easily. It consists of a very thin pigmented layer of a warm brown colour and an underlying colourless layer. Its thickness varies greatly in different parts of the body, being very thin over the eyes, for example, and thicker, with a spongy subcutaneous layer, at the root of the proboscis. The degree of pigmentation varies, too. The crown

of the head, the root of the proboscis and the tail are dark brown, the ventral side of the body and tip of the proboscis light brown, and the soles of the feet yellowish white. When examined with a lens the skin appears to be divided up into rounded or hexagonal areas of a brown colour, with lighter interspaces. If a portion of the skin be dehydrated, cleared, and mounted in Canada balsam, the difference in pigmentation is seen to be due, as might be expected, to differences in the arrangement of perfectly typical chromatophores, which are crowded, scattered or absent, giving dark brown, light brown, and white areas respectively. There is no suggestion of the dry, greyish, warted appearance common in the older stages.

Transverse sections of the skin reveal a stratified stratum corneum with distinct nucleated cells, the usual wavy Malpighian layer, and numerous hair follicles in various stages of development in the dermis. Sebaceous glands are not yet developed, and only those hairs mentioned above as occurring on the sides of the tip of the proboscis had penetrated the upper layers so as to emerge on the surface. Sections of the eyelids show no trace of eyelashes, though ordinary hair germs are present. No sweat-glands are to be found. This is remarkable, as the temporal gland, a much elaborated sweat-gland, is well developed.

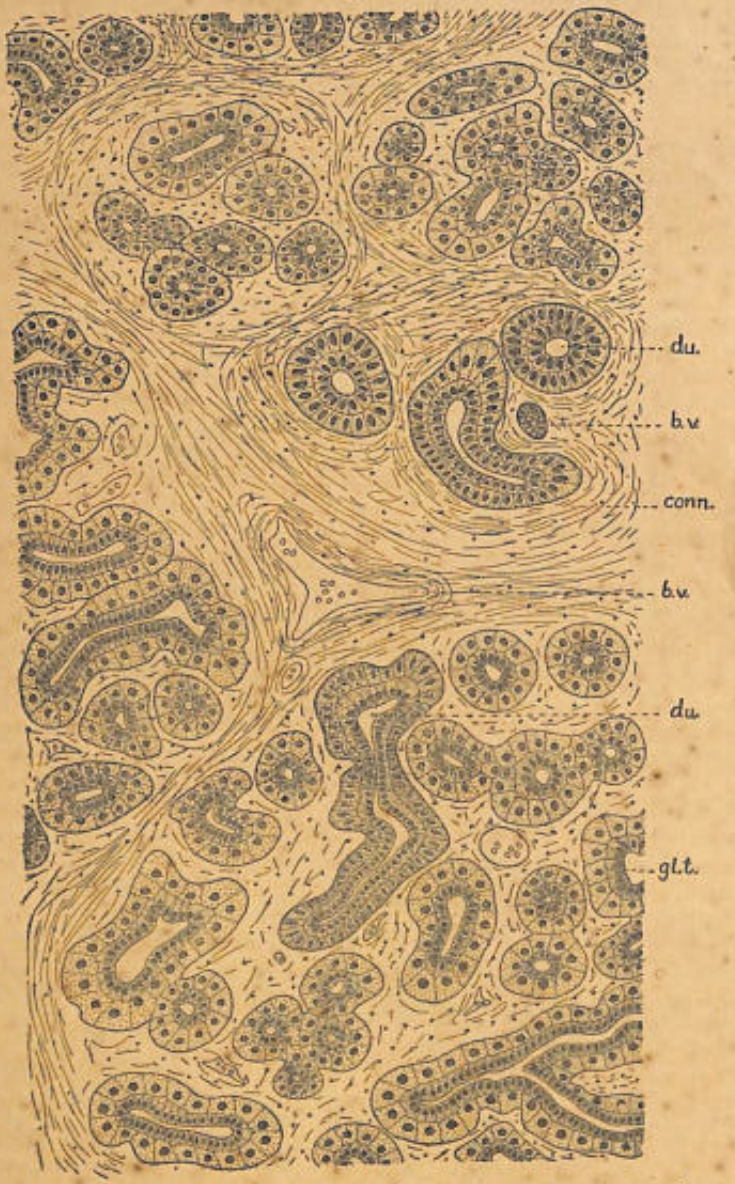
Temporal Gland. (Text-figs. 1 and 2.)

The temporal gland has been described by many dissectors of Elephants, notably by Eggeling and Cnyrim. The former* infers that the gland is a modified and complicated sweat-gland, and with his account the writer agrees. Cnyrim † gives a description of a muscle occurring in the Indian Elephant running between the eyelid and the gland, and apparently causing, by its contraction, a flow of secretion into the duct of the gland. He calls this muscle the musculus glandulæ temporalis. No trace of this muscle occurs in the African fœtus; the temporal gland is embedded in the fascia, but is unattached to any other tissue except in the region of its excentrically placed duct. The gland is a caked ovoid and flattened mass lying in a slight depression on the side of the head between the eye and the ear. It is divided into lobules fastened together by fibrous connective tissue. Each lobule contains the convoluted tubules of the gland. Sections (text-fig. 1) show that a tubule has a small lumen and a two-layered wall of columnar epithelium. Numerous tubules coalesce and merge into a common two-layered duct, and the ducts of the different tubule groups converge towards the main duct, forming a characteristic star-shaped pattern (text-fig. 2.)

* Eggeling, H., "Ueber die Schläfendrüse des Elefanten." Biol. Centralb. Bd. xxi. No. 14, pp. 443–453, 1901.

† Cnyrim, E., "Zur Schläfendrüse und zum Lidapparate des Elefanten." Anat. Anz. Bd. xlvi. pp. 273–279, 1914.

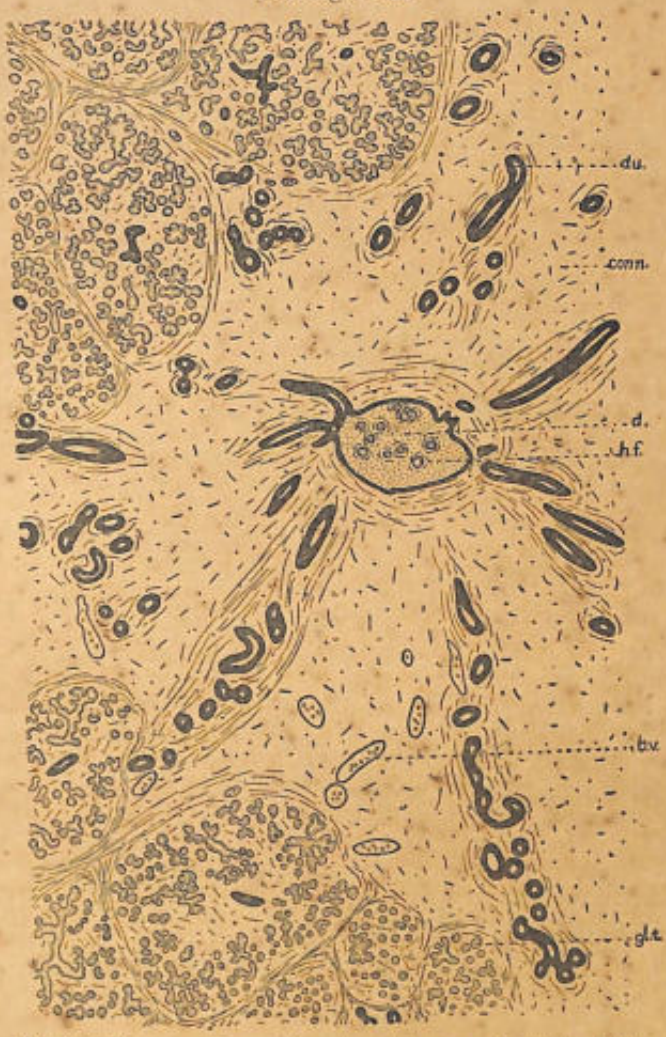
Text-figure 1



Elephas africanus. Transverse section of the temporal gland, drawn under projection apparatus and slightly diagrammatic. × 66.

b.v., blood-vessel; *conn.*, connective tissue; *du.*, ductule; *gl.t.*, gland tubule.

Text-figure 2.



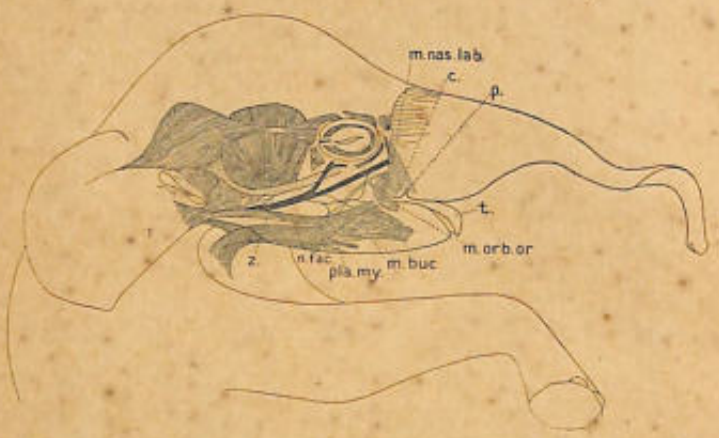
Elephas africanus. Tangential section of the temporal gland to show main duct and converging ductules. × 12·5.
Lettering as for text-fig. 1.
d., main excretory duct; *h.f.*, hair follicle.

The main duct to the exterior is undoubtedly an ectodermal invagination. In sections it is seen to be pigmented, with a cellular stratum corneum. Very young hair follicles are present in the wall of the duct. Toldt's fœtus, which was older than the

present one, exhibited hairs in this region. The duct passes obliquely ventralwards through the skin, and is densely pigmented near the surface.

The temporal gland occurs in both male and female specimens. It is said to be especially active during the period of heat, but little is known as to its function. It has been stated that the secretion is inodorous.

Text-figure 3.



Elephas africanus. Lateral view of a dissection of certain muscles of the head. × ½.

c., cushion; *m.buc.*, buccinator muscle (longitudinal portion); *m.nas.lab.*, naso-labialis muscle; *m.orb.or.*, orbicularis oris muscle (buccinator pars rimana); *n.fac.*, facial nerve; *p.*, pit; *pla.my.*, platysma myoides; *t.*, tongue; *z.*, zygoma.

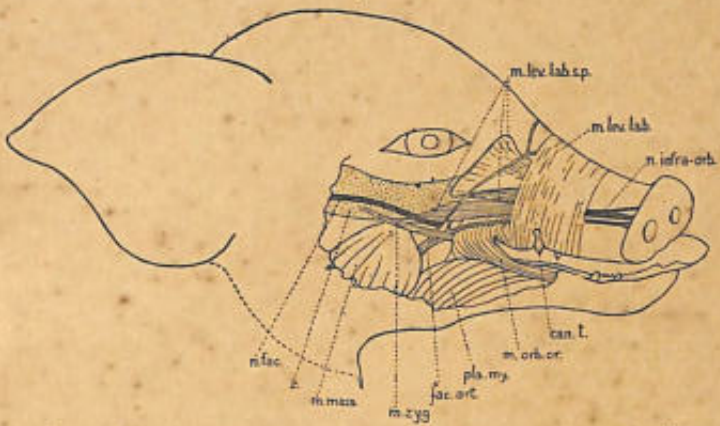
The Upper Lip.

On the upper lip of the fœtus is a structure which is partly lost during development. Toldt and Bolk both describe it in their specimens, but their interpretation of it differs, and with neither interpretation does the writer entirely agree. Close to the angle between the upper and lower lips, but lying entirely in the upper lip, the free edge of the lip forms a pendent conical cushion (text-fig. 3, *c*). In part this cushion overhangs the lower lip; inside the mouth, however, it becomes flattened owing to the pressure of the lower jaw upon it. The skin is pigmented both on the outer and the oral side of the cushion. Anterior to the cushion and still along the line of the upper lip is a somewhat crescentic opening leading to an invagination of the surface, which extends inwards for about a quarter of an inch and ends blindly. From this pit a groove ascends obliquely towards the palate to lose itself on the roof of the mouth. The skin lining

the pit is pigmented. Bolk and Toldt describe a hump arising from the projection. This is not present in the specimen under discussion.

Dissection of the side of the head reveals the fact that the cushion is largely composed of very spongy connective tissue, and that the whole structure is supplied by a muscle by whose contraction the upper lip is raised. The muscle concerned is the

Text-figure 4.



Sus scrofa. Lateral view of a dissection of certain muscles of the head of a newly-born specimen. × ½.

art.fac., facial artery; *can.t.*, canine tooth; *m.lev.lab.*, levator labii superioris alæque nasi muscle; *m.lev.lab.sp.*, levator labii superioris muscle; *m.mass.*, masseter muscle; *m.orb.or.*, orbicularis oris muscle; *m.zyg.*, musculus zygomaticus; *n.infra.orb.*, infra-orbital branch of VII.; *n.fac.*, facial nerve; *pla.my.*, platysma myoides; *z.*, zygoma.

naso-labialis of Boas and Paulli*; this appears to be the homologue of the *levator labii superioris alæque nasi*. Its origin is the connective tissue immediately beneath the skin and anterior to the eyelid slit, its course ventralwards, its insertion the cushion itself, and the upper lip immediately anterior to the cushion. The muscle is supplied by a branch of the facial nerve (temporal-facial division). The course of the muscle in the fœtus is exactly dorso-ventral; in the adult, as figured by Boas and Paulli, the elongation of the snout draws the muscle with it so that its course is more oblique. In the Pig, both in the fœtal and post-natal stages, though more markedly in the former, a somewhat similar conformation of the upper lip occurs, and in the same relative position (text-fig. 4). In the Pig the *levator labii*

* Boas, J. E. V., and Paulli, S., 'The Elephant's Head.' (Jena: G. Fischer, 1908.)

superioris is stated by Chauveau * to be absent. In the late fœtus, however, a muscle was found, lying immediately beneath the skin of the head, arising by a median longitudinal aponeurosis, passing ventralwards round the snout and inserted into the upper lip. The posterior portion of the insertion is into the cushion, the anterior into the anterior portion of the upper lip. This anterior portion is represented by only a few fibre bundles in the Elephant. A branch of the facial nerve supplies the fibres of the muscle. In the just-born Pig some of the teeth are already cut, viz. the posterior incisors and the canines. Through the gap in the upper lip anterior to the cushion it is the canine tooth that is visible, not the incisor. This tooth does not approach the groove, but projects downwards towards the mouth at this stage. In older stages of the female Pig the gap does not appear to bear any special relation to the tooth. It is a well-known fact in the Boar, however, that when irritated he bares even further his already-exposed fangs by the elevation of the upper lip, though the tooth does not actually project through the gap.

Sections of the cushion and pit in the Elephant fœtus show that large stout hairs are being developed. Neither sebaceous nor sweat-glands are as yet formed, nor are there any other glands. In a just-born Pig, sections exhibit similar large hairs, but their sebaceous glands are well developed and sweat-glands are present.

Toldt's interpretation of the pit is that it is predestined to form the point of exit for the large incisor tooth which becomes the tusk. Against this view we have the gradual disappearance, not, as might be expected, the enlargement of the pit, and the fact that many Elephants, especially the females of the Indian species, never possess a tusk. Also, in the Pig at any rate, the canine and not the incisor tooth is opposite the groove. Bolk's view is that the pit represents the primitive nostril, and he suggests that the paired furrows leading from the pit towards the present nostrils at the tip of the proboscis indicate where the snout has been elongated to form the trunk. This presupposes a very curious position for the primitive nostrils of the ancestor of the Elephant, viz. on the side of the head close to the angle of the mouth. It is, moreover, unlikely that any groove connecting the primitive nostril with the present nasal aperture would lie on the *ventral* side of the trunk. One would expect it to occur on the dorsal side.

Comparison with fœtal and postnatal stages of Ungulates suggests that the cushion and pit are inherited fold formations of the upper lip, which are similar to those of the Pig, and which disappear in the course of the development in the Elephant, partly, no doubt, because of the immobility of the upper lip, and

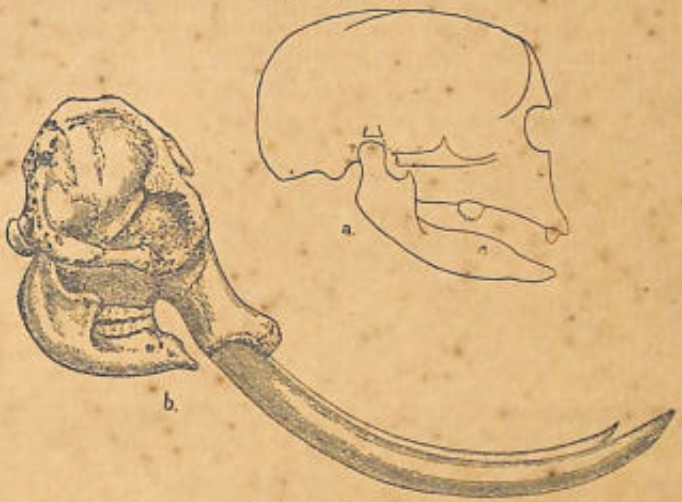
* Chauveau, A., 'Comparative Anatomy of Domesticated Animals.' Second English Edition, London, 1891.

partly because of their being no longer any necessity for baring the teeth. It is improbable that these structures bear any relation either to the nostrils or to the tusks, and they throw no light on the vexed question as to how the Elephant got his trunk*.

X-ray Photographs.

Several X-ray photographs of the fœtus were taken, one at University College, London, and others at the Royal Berks

Text-figure 5.



Elephas africanus.

(*a*) Right lateral view of head of fœtus from X-ray photograph. × ½.

(*b*) Right lateral view of skull of adult for comparison. About $\frac{1}{17}$ natural size.

Fig. 5 (*b*) is a reproduction, by permission, of fig. 31 in 'A Guide to the Elephants (Recent and Fossil),' British Museum, Nat. Hist. Second Edition, 1922.

Hospital, Reading. In general these negatives show that considerable ossification of the main bones of the skeleton has occurred. The bones of the skull, the vertebræ and ribs, limb-girdles and limbs, all are visible. Ossification of the phalanges is very pronounced.

(*a*) The general shape of the head. A comparison of fœtal and adult heads of the Elephant has been made by Bolk, but several points may be added to his account (text-fig. 5).

1. The basicranial measurement of the fœtus is greater than the vertical height of the skull. Something must be allowed for distortion here, but in the main it holds true.

* Since writing the above, Prof. Wingate Todd informs me that the inner flattened portion of the cushion persists through adult life in the Indian Elephant, the spongy connective tissue becoming tough as leather.

2. The nasal cavities face the anterior aspect and are not on the summit of the head.

3. The anterior prolongation of the premaxilla has not yet taken place.

4. The portion of the skull posterior to the mandibular articulation is relatively large; in the adult the squamosal reaches almost to the transverse plane of the occiput. Probably the air-cells at the back of the skull are not yet developed.

5. The lower jaw shows points of great interest. It is elongated and flattened, not short and right-angled as in the adult. Relatively it is much longer than when the animal is full-grown, and very closely resembles that of some fossil Proboscidean, *cf.* Mastodon, though no incisors are present. The fœtus is thus, like its ancestors of late Tertiary times, of the long chin type.

(*b*) The teeth. Six teeth are shown, embedded in the jaws. None perforates the gum. These are a pair of incisors and a pair of premolars on the upper jaw, and a pair of premolars on the lower jaw. The incisors are the milk tusks, and resemble ordinary large teeth of that type. They have not yet acquired the forward tilt of the grown tusk. The premolars are quite unlike those of an adult Elephant. Everyone knows the great crushing teeth of an Elephant, with the characteristic enamel fold pattern. Those of the fœtus show the primitive cusped condition. The upper premolars possess five cusps, the lower three. Mastodon shows the cusped condition permanently in the adult fossilized stage, but the present-day fœtal Elephant has only one tooth developed at once, not several as in Mastodon. Fossil *Elephas*, e.g. *E.* (or *Stegodon*) *clifti*, *E. insignis* possessed ridged molars, but the ridges form a linear series. The fœtal Elephant's premolar, however, has cusps which are not in a linear series, but in at least two transverse rows, one behind the other, as seen in side view. This resembles Mastodon and not *Elephas* *.

The above skeletal observations await the confirmation of dissection. X-ray interpretation of only partially-ossified structures must always be difficult and sometimes mistaken; but enough has been said to justify the hope that this rare specimen will yield many interesting points of morphology. The fœtus is being dissected under the dissecting microscope for the nerves and muscles of the head, and a detailed account of the anatomy of the head will be published later.

EXPLANATION OF THE PLATE.

Elephas africanus. The fœtus lying curled up as it was extracted from the uterus. × ½.

* Compare British Museum Guide to the Elephants (Recent and Fossil), fig. 19, p. 32 (London, 1922).

20. The Extensor Muscles of the Hinder Foot in Mammals.

By Richard H. Hunter, M.D., F.Z.S., Lecturer in Anatomy, Queen's University, Belfast.

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(Text-figures 1–12.)

This paper is a systematic study of the muscles on the extensor aspect of the hinder foot in certain groups of mammals. The anatomy of each muscle is traced through a series of types from the Monotremes to the Primates, and it is hoped by this means to arrive at some conclusions regarding the morphology of these muscles, to learn something of how much differentiation of muscles corresponds to function, and to what degree changes in form may be associated with habit and life.

The paper is divided into two parts. The first contains a simple account of the anatomy of the different muscles, and as a statement of facts observed will, I hope, be of some value. The second part is devoted to a series of summaries and generalizations founded upon the facts which these observations have furnished.

I would like to express my indebtedness to the Society's Prosector, Dr. Charles F. Sonntag, for the material used in this research; indeed, it was his suggestion that such an examination would be of practical value in the Society's Prosectorium.

The following is a list of the mammals dissected:—

Echidna hystrix.
Sarcophilus ursinus.
Dasyurus viverrinus.
Perameles obesula.
Trichosurus vulpecula.
Hypsiprymnus rufescens.
Dendrolagus bennettianus.
Phascolomys wombat.
Macropus dorsalis.
Didelphys azaræ.
Capromys pilorides.
Castor canadensis.
Cœlogenys paca.
Dipus ægyptius.
Myopotamus coypus.
Dasyprocte agouti.
Viverricula malaccensis.
Viverra civitta.

Genetta tigrina.
Felis pardalis.
Felis tigrina.
Perodicticus potto.
Ateles ater.
Cebus fatuellus.
Anthropopithecus troglodytes.

ECHIDNA HYSTRIX.

The foot has five digits. The hallux is short and stunted. In the specimen under consideration it is provided with a rounded nail covering dorsal and ventral surfaces, not confined to the dorsal region as described by Cunningham (1). The longest digit is the second—it is provided with a large curved claw. The other three digits gradually diminish in size. Each is provided with a claw.

The tibialis anterior muscle arises from the proximal fourth of the lateral aspect of the tibia. The muscular belly converges on a tendon, which passes distally to be inserted into the upper and inner aspect of the base of the first metatarsal.

Extensor hallucis longus muscle arises from the proximal fourth of the lateral aspect of the tibia, deep to the tibialis anterior, a few fibres coming from the anterior surface of the head of the fibula. The muscle converges on a tendon which passes superficially to that of tibialis anterior near the insertion of the latter, and then divides into two parts. The larger part is inserted into the upper surface of the proximal phalanx of the first digit, the smaller gains an insertion into the medial aspect of the base of the second metatarsal.

The extensor digitorum longus muscle arises from the front of the head of the fibula, from the adjacent part of the head of the tibia, the proximal half of the anterior aspect of the shaft of the fibula, the proximal third of the lateral aspect of the tibia and the interosseous membrane between these two areas. A tendon emerges from this muscular origin, which passes below two stout annular ligaments, to the dorsal aspect of the foot where it divides into two parts. One part goes to an insertion on the dorsal aspect of the base of the middle phalanx of the second digit, and one part to the middle phalanx of the third.

The extensor digitorum brevis muscle arises from the outer aspect of the head of the fibula, and from the proximal fourth of the outer aspect of the shaft of that bone. At once it splits into a superficial and a deep part. The superficial part spreads out into a broad aponeurosis which divides into three parts, one part going to the dorsal aspect of the distal phalanx of each of the second, third, and fourth digits. The deep part converges on a slender tendon, which divides into two further parts, one of which goes to the dorsal aspect of the base of the distal phalanx of the fourth digit, the other to the distal phalanx of the fifth.

The peroneal group is represented by a single muscle which arises from the outer aspect of the head of the fibula and from the proximal half of the outer aspect of its shaft. Behind the external malleolus the muscle converges on a tendon which spreads out in a fan-shaped manner at its insertion on the outer side of the base and shaft of the fifth metatarsal, to the outer surface of the calcaneus and, by some fibres which pass backwards, to the capsule of the ankle-joint.

SARCOPHILUS URSINUS.

On a superficial examination only four digits are seen, but on removing the skin a rudimentary hallux is found.

Tibialis anterior muscle arises from the proximal third of the lateral surface of the tibia, and by a few fibres from the medial aspect of the fibula. These muscular fibres so formed converge on a stout tendon deep to the annular ligament, which passes to its insertion on the under aspect of the internal cuneiform and the adjacent part of the first metatarsal.

The extensor digitorum longus muscle arises from the fronto-mesial aspect of the head of the fibula and from the proximal third of the anterior surface of its shaft. The fibres of origin are continuous with the origin of the peroneal musculature. Two slender bellies are formed which pass below the annular ligament; the medial of these passes to the dorsum of the foot, where it divides into two, one part going to join the tendon of extensor indicis proprius to form an expansion on the dorsal aspect of the base of the proximal phalanx of the second digit, the other going to form a similar expansion on the third digit. The lateral belly is the larger, on the dorsum of the foot it divides into two, one going to the fourth digit and one to the fifth. Each dorsal expansion divides into three parts: the lateral parts are inserted into the sides of the base of the proximal phalanx, the central portion passes distally to again divide at the base of the middle phalanx, where it is inserted in a similar manner, the central part passing to an insertion on the dorsal aspect of the base of the distal phalanx. These four tendons are held together by a stout vinculum.

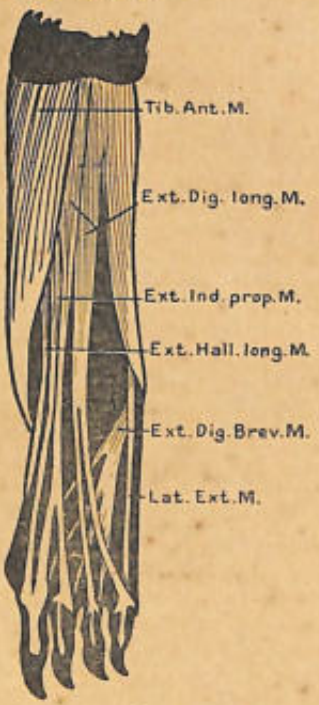
The extensor hallucis longus and the extensor indicis proprius arise by a common origin from the under aspect of the medial surface of the head of the fibula, and from the proximal fourth of the inner aspect of its shaft. Two slender muscular bellies are formed, one passing to converge on a delicate tendon which is inserted on the upper and outer aspect of the base of the proximal phalanx of the rudimentary hallux. The other converges on a fairly stout tendon which is joined by the most medial tendon of the extensor digitorum longus to form a dorsal expansion on the second digit.

Extensor digitorum brevis arises from the front of the proximal half of the shaft of the fibula. This muscular belly passes behind the external malleolus where it converges on a tendon which divides

into two parts; these pass below the malleolus to the dorsum of the foot, where they pass obliquely distally and medially, deep to the tendon of the long extensor, one part goes to join the dorsal expansion of the second digit, the other tendon again divides so that a part joins the dorsal expansion of the third digit and a part that on the fourth.

The lateral peroneal extensor muscle arises by muscular fibres from the anterior aspect of the head of the fibula and from the

Text-figure 1.



Sarcophilus ursinus. Dorsum of foot.

proximal third of the lateral surface of the shaft. A tendon emerges which passes behind the external malleolus, along the lateral margin of the foot to its insertion on the upper and outer aspect of the base of the proximal phalanx of the fifth digit, some fibres pass to the dorsal expansion of the long extensor tendon.

Peroneus brevis muscle arises from the front and lateral aspects of the head of the fibula, superficially to the extensor brevis digitorum, in continuity with the extensor digitorum longus and peroneus longus. A strong tendon emerges which passes behind the external malleolus to its insertion on the outer side of the base of the fifth metatarsal.

The peroneus longus muscle arises from the outer aspect of the head of the fibula and the proximal third of the outer aspect of its shaft, the tendon which emerges passes behind the external malleolus, along the lateral margin of the foot to the plantar aspect of the foot, then crosses obliquely in a groove to its insertion on the base of the first metatarsal and the adjacent part of the first cuneiform.

DASYURUS VIVERRINUS.

Five digits are present. The hallux is short and appears in the undissected foot as a slight protuberance on its medial margin. The outer four digits are well developed and of nearly equal size, each is provided with a sharp claw.

The tibialis anterior muscle arises from the proximal half of the outer surface of the tibia, strengthened by a few fibres from the inner aspect of the head of the fibula and from the upper and medial part of the interosseous membrane. From this muscular origin a tendon emerges which passes deep to the annular ligament to an insertion into the lower surface of the internal cuneiform, a few fibres passing to the base of the first metatarsal.

The extensor digitorum longus muscle arises from the proximal half of the anterior surface of the shaft of the fibula. In the distal third of the leg two tendons emerge; the medial of these passes distally to the dorsum of the foot where it again divides, one part of this division going to the inner side of the base of the proximal phalanx of the second digit, the other to form an expansion on the dorsal surface of the middle phalanx of this digit; the lateral fibres are inserted into the sides of the phalanx, the central part going to the distal phalanx. The lateral primary division divides into three parts, which go respectively to the third, fourth, and fifth digits where each forms a dorsal expansion, the lateral fibres being inserted into the sides of the proximal phalanx, the central to the middle phalanx at its sides, the central fibres going to the distal phalanx.

The extensor hallucis longus muscle arises as a short muscular belly from the anterior aspect of the shaft of the fibula in its middle third, from this a slender tendon emerges which passes to an insertion on the upper and inner aspect of the base of the proximal phalanx of the hallux.

The extensor digitorum brevis muscle arises from the proximal half of the shaft of the fibula, in front of the peroneus brevis. Two tendons emerge which pass behind the external malleolus to the dorsum of the foot; the medial of these tendons divides and one of these subdivisions joins the dorsal expansion of the long extensor of the second digit, the other subdivision joins the expansion on the third digit. The second tendon divides into three, one of these subdivisions going to the dorsal expansion on the third digit, one to that on the fourth, and one to that on the fifth.

The peroneus longus muscle arises from the proximal two-thirds of the lateral aspect of the shaft of the fibula. A tendon emerges which passes behind the external malleolus, then obliquely downward and medially to the plantar aspect of the foot to its insertion on the outer aspect of the internal cuneiform and adjacent part of the first metatarsal.

The peroneus brevis muscle arises from the middle third of the lateral aspect of the shaft of the fibula and by a few fibres from the proximal third of the front of the shaft. An emerging tendon passes behind the external malleolus to its insertion on the lower aspect of the base of the fifth metatarsal.

PERAMELES OBESULA.

The digits are unequal in size, the hallux is rudimentary. The bones of the second and third digits are fused except the distal phalanges, which are rudimentary. The fourth digit is strong and powerful; the fifth is also strong but less so than the fourth. Each of the lateral four digits ends in a claw.

The tibialis anterior muscle has a powerful muscular origin from the proximal third of the outer surface of the shaft of the tibia, by a few fibres from the head of both tibia and fibula, from the upper fourth of the interosseous membrane and from the deep fascia over it. It converges on a strong tendon which passes deep to the annular ligament to the dorsum of the foot, then obliquely to its insertion on the inner surface of the internal cuneiform.

The extensor hallucis longus muscle arises by a flattened tendon from the inner and lower aspect of the head of the fibula, this is joined by a few muscular fibres from the upper third of the anterior surface of the interosseous membrane. The muscular belly so formed passes distally below the annular ligament to converge on a tendon on the dorsum of the foot, then distally to its insertion on the upper aspect of the base of the rudimentary phalanx.

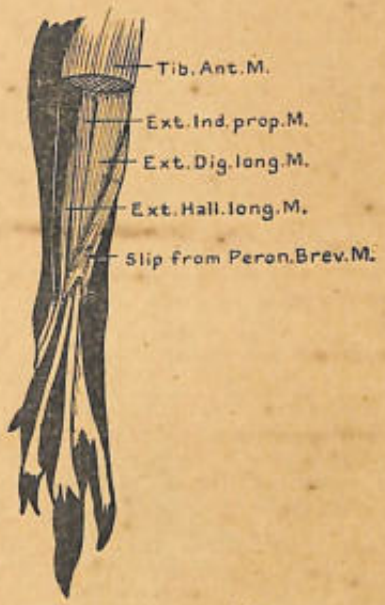
The extensor digitorum longus muscle arises from the front of the head of the fibula, the adjacent part of the head of the tibia, the upper third of the interosseous membrane, and the medial aspect of the proximal two-thirds of the shaft of the fibula. The muscle at once divides into two parts and from each a tendon emerges, which passes distally to the dorsum of the foot. The medial tendon passes to the fourth digit where it is inserted by three slips, the central slip to the upper surface of the base of the proximal phalanx, the lateral slips to the sides of the distal phalanx. The lateral tendon close to its insertion forms a broad expansion which divides into two parts, one going to an insertion on the head of the fourth metatarsal, one to the head of the fifth, a few fibres passing distally to the base of the distal phalanx of this digit.

The extensor indicis proprius muscle arises by a slender

muscular belly from the outer side of the head of the fibula, from the proximal fourth of the inner surface of the shaft of the fibula, and from the adjacent part of the interosseous membrane. The muscle rapidly converges on a thin tendon which passes below the annular ligament to the dorsum of the foot, where it divides into two parts; the larger of these is inserted into the dorsal aspect of the base of the distal phalanx of the rudimentary second and third digits. The outer slip goes to the base of the proximal phalanx of the fourth digit.

The lateral peroneal extensor muscle arises from the outer surface of the head of the fibula, the capsule of the knee-joint

Text-figure 2.



Perameles obesula. Dorsum of foot.

just above it, and from the proximal two-thirds at the outer surface of the shaft of the fibula. It passes distally behind the external malleolus, then along the outer side of the foot, perforating the tendon of the peroneus brevis on its way to its insertion into the dorso-lateral aspect of the head of the fifth metatarsal bone and adjacent part of the proximal phalanx of the fifth digit.

The peroneus brevis muscle arises from the middle two-thirds of the outer surface of the shaft of the fibula. It converges on a tendon behind the external malleolus which broadens out as the lateral extensor perforates it, and is inserted on the lateral aspect of the base of the fifth metatarsal.

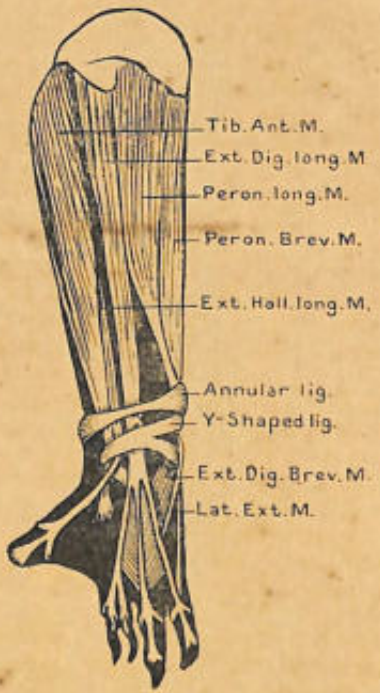
There is no indication of a peroneus longus muscle.

A thin band of muscular fibres passes from the anterior border of the peroneus brevis distally and medially to the dorsum of the foot, where it splits to form an arch below which the extensor digitorum longus passes. The muscular fibres are inserted on the upper aspect of the anterior end of the calcaneus.

TRICHOSURUS VULPECULA.

Five digits are present. The hallux is well developed and opposable, the second and third are rudimentary, the fourth is the

Text-figure 3.



Trichosurus vulpecula. Dorsum of foot.

strongest, the fifth is also strong. The hallux carries a nail on its extremity. Each of the lateral four digits has a claw.

The tibialis anterior muscle arises from the proximal half of the lateral surface and the anterior margin of the shaft of the tibia and from the outer side of its head. The muscle converges on a stout tendon that passes deep to the annular ligament to its insertion on the upper and medial aspect of the base of the second metatarsal bone. The tendon passes through a looped ligament

which has a bifid origin from the anterior margins of the external malleolus, and an insertion on the upper and inner aspect of the base of the fourth metatarsal.

The extensor digitorum longus muscle arises from the proximal three-fourths of the anterior surface of the shaft of the fibula and from the front of its head. It passes distally through the looped ligament to the dorsum of the foot where it divides into three parts, these are held together by a strong vinculum as far as the metatarso-phalangeal joint. The most medial of these tendons splits into two so as to give a slip to the second and third digits. The lateral tendon passes to the fifth digit, the central part going to the fourth digit. Each tendon forms a dorsal expansion, the lateral parts of which are inserted into the sides of the base of the middle phalanx of its own digit, the central part going to the dorsum of the base of the distal phalanx.

The extensor hallucis longus muscle arises from the outer aspect of the head of the fibula and from the proximal half of the anterior surface of the shaft of that bone. It converges on a slender tendon which passes below the annular and looped ligaments to its insertion on the dorsum of the hallux. The lateral fibres of the expansion are inserted into the sides of the base of the proximal phalanx, the central fibres to the dorsum of the distal phalanx.

The extensor digitorum brevis muscle arises as a slender muscular belly from the lower extremity of the fibula and from the upper part of the calcaneus below. The muscle passes obliquely forward and medially, deep to the tendons of the long extensor, and divides into two parts, from each of which a tendon emerges. One of these goes to form a dorsal expansion which divides so as to give a small tendon to the base of the proximal phalanx of the second and third rudimentary digits, the other part goes to the proximal phalanx of the fourth digit.

The peroneal muscles are represented at their origin by a single muscular mass from the proximal three-fourths of the outer surface of the shaft of the fibula and from the adjacent part of its head. In the distal third of the leg the muscle divides into three unequal parts which pass behind the external malleolus. The smallest part converges on a tendon which is inserted on the dorso-lateral aspect of the base of the proximal phalanx of the fourth digit. The next in size passes along the outer border of the foot to its insertion on the base of the proximal phalanx of the fifth digit, piercing the tendon of the largest part of the muscle which is passing to its insertion in a fan-shaped manner, the anterior part going to the outer side of the fifth metatarsal, the posterior to the lower and outer side of the cuboid.

HYPSIPRYMNUS RUFESCENS.

The hallux is entirely suppressed. The second and third digits

are rudimentary, the fourth is strong and powerful, the fifth is strong but less powerfully developed than the fourth. Each carries a claw.

The tibialis anterior muscle arises from the proximal half of the lateral surface of the tibia and from the fronto-mesial aspect of the head of the fibula. The emerging tendon passes to the side of, and superficial to, the annular ligament. Passing through the

Text-figure 4.

Hypsiprymnus rufescens. Dorsum of foo

looped ligament the tendon courses obliquely downward and forward to an insertion on the lower part of the medial aspect of the internal cuneiform.

The extensor digitorum longus muscle is represented by two separate muscular bellies, one associated with the second and third digits, the other with the fourth and fifth. The first is a slender muscular belly arising from the fronto-mesial aspect of the head of the fibula and at once converges on a delicate tendon, which

passes deep to both the annular and the looped ligaments (but not through the latter) to the dorsum of the foot to be inserted on the bases of the proximal phalanges of the rudimentary second and third digits. The main part of the muscle arises from the proximal third of the anterior and lateral aspects of the shaft and head of the fibula and the proximal half of the lateral surface of the tibia. Four parts separate from this, and the largest part converges on a tendon which passes to the dorsum of the foot, where it splits into a superficial and a deep part; the superficial part spreads over the metatarso-phalangeal joint of the fourth digit and is attached to the sides of the capsule and base of the proximal phalanx, the central part of the tendon passes forward to the sides of the middle phalanx, where the central fibres pass forward to the dorsum of the distal phalanx. The deep part of the tendon divides into two, the medial part going to the fourth expansion, the lateral part to the fifth to be inserted in the same manner as the superficial part is to the fourth. The other muscles separating from this common origin pass behind the external malleolus as three delicate tendons. The middle tendon passes to the outer aspect of the base of the fifth metatarsal. The anterior tendon passes along the outer border of the foot to the upper aspect of the base of the proximal phalanx of the fifth digit. The dorsally placed tendon passes to the plantar aspect of the foot to be inserted on the under aspect of the fourth metatarsal.

DENDROLAGUS BENNETTIANUS.

The hallux is suppressed. The second and third digits are rudimentary and fused except at their terminal phalanges. The fourth is well-developed, as is the fifth, though less so. Each is armed with a sharp claw.

The tibialis anterior muscle arises from the proximal third of the lateral aspect of the shaft of the tibia, the adjacent part of its head, and from the interosseous membrane. A powerful tendon emerges which passes to an insertion on the inner aspect of the internal cuneiform.

The extensor digitorum longus muscle arises from the proximal half of the anterior surface of the shaft of the fibula, from the interosseous membrane, and from the head of the fibula. A broad tendon emerges in the lower third of the leg which passes deep to a stout ligament on the upper aspect of the calcaneus. This splits into three parts, the medial part passing to the medial side of the foot to give a slip to each of the rudimentary second and third digits. The lateral tendon passes to give slips to the base of the proximal phalanx of the fourth and fifth digits. The central part of each passes to the distal phalanges as in *Hypsiprymnus*.

The extensor digitorum brevis muscle arises from the middle third of the lateral surface of the shaft of the fibula. Its tendon

passes behind the external malleolus between those of peroneus longus and brevis, then distally and forward to the outer side of the base of the proximal phalanx of the fourth digit.

The peroneus longus muscle arises from the proximal two-thirds of the outer surface of the shaft of the fibula behind the extensor digitorum brevis, and from the outer side of the head of that bone, passing behind the external malleolus it gains the outer side of the foot, then bends below to the plantar aspect to its insertion on the under aspect of the fused second and third metatarsals.

The peroneus brevis muscle arises from almost the whole length of the outer surface of the shaft of the fibula. Its tendon after passing behind the external malleolus is inserted on the upper aspect of the base of the proximal phalanx of the fifth digit.

PHASCOLOMYS WOMBAT.

The foot of this animal is inverted. There are five digits present. The hallux is short though broad. The second, third, and fourth digits are nearly equal in size, the fifth is the shortest. The lateral four digits each carry a claw.

The tibialis anterior muscle arises from the proximal half of the lateral surface of the shaft of the tibia. In front of the ankle-joint a tendon emerges which passes below the stout ring-like ligament on the upper surface of the calcaneus. This tendon bends medially and divides into two parts which are inserted on the medial side of the internal cuneiform, and the upper aspect of the base of the phalanx of the first digit respectively.

The extensor hallucis longus muscle arises from the outer aspect of the distal fourth of the shaft of the fibula, the tendon which emerges is inserted on the hallux with the tendon of the tibialis anterior.

The extensor digitorum longus muscle arises by four separate muscular bellies from the proximal two-thirds of the lateral surface of the tibia, deep to the origin of tibialis anterior, and from the adjacent part of the interosseous membrane. Each of these bellies converges on a tendon, the lowest of these is inserted on the upper and outer aspect of the head of the fifth metatarsal bone, the next to the upper and outer aspect of the proximal phalanx of the fifth digit, the next part is inserted on the upper aspect of the middle phalanx of the same digit. The upper belly of all divides into two parts, one going to the fourth digit and the other to again divide so as to give a slip to the third and second digits. Each of these three tendons is inserted into its own digit in the same manner as the tendon of the fourth digit in *Hypsiprymnus*.

The extensor digitorum brevis muscle is rudimentary. It arises as a thin muscular sheet from the upper surface of the calcaneus. Its tendon of insertion passes to the proximal phalanx of the

third digit, sending fibres to the sides of the phalanges of the adjacent second and fourth digits.

The peroneal muscles arise by a common origin from the proximal three-fourths of the outer surface of the shaft of the fibula. Three tendons emerge from this muscular origin which pass behind the external malleolus; the strongest is inserted on the under and outer aspect of the base of the fifth metatarsal, the smallest passes along the outer border of the foot to the base of the proximal phalanx of the fifth digit. The remaining tendon

Text-figure 5.

Phascolomys wombat. Dorsum of foot.

is inserted on the under and outer sides of the base of the first metatarsal, passing in a groove on the plantar aspect of the foot.

MACROPUS DORSALIS.

The foot consists of a greatly enlarged fourth digit, with a small fifth and a rudimentary second and third, the latter fused except at the distal phalanges. The hallux is completely suppressed.

The tibialis anterior muscle arises from the proximal three-fourths of the lateral surface of the shaft of the tibia, from the front of the head of the fibula and the capsule of the knee-joint. Midway down the leg a tendon emerges which passes below a stout annular ligament in front of the ankle-joint, gaining the dorsum of the foot it turns medially to an insertion on the infra-medial aspect of the second metatarsal.

The extensor digitorum longus muscle has a short muscular origin from the outer aspect of the head of the fibula and from the capsule of the knee-joint. A tendon emerges which passes below the annular ligament to the dorsum of the foot to its insertion on the sides and dorsal aspect of the base, and of the proximal phalanx and metatarso-phalangeal joint of the fourth digit, the central fibres passing distally to an insertion as in *Hypsiprymnus*.

The extensor digitorum brevis muscle arises from the outer surface of the head and shaft of the fibula. A tendon emerges which passes with the long extensor to the dorsum of the foot, where it is inserted partly with the latter on the fourth digit and partly into the phalanges of the fused second and third digits and to the fifth digit.

There are no peroneal muscles present.

DIDELPHYS AZARÆ.

The foot has five digits. The hallux is opposable and carries a nail. The four outer digits each carry a claw. They are nearly uniform in length, the fifth being the smallest and the fourth the longest.

The tibialis anterior muscle arises from the proximal third of the lateral surface of the shaft of the tibia, the adjacent part of the head of the capsule of the knee-joint. It converges on a tendon which passes deep to the annular ligament, in a groove on the anterior aspect of the distal end of the tibia, then passes obliquely to its insertion on the medial surface of the internal cuneiform.

The extensor digitorum longus muscle arises from the proximal fourth of the fronto-medial aspect of the fibula and from its head. This long muscular belly converges on a tendon which passes below the annular ligament to the dorsum of the foot where it divides into four slips, one going to each of the four lateral digits, each tendon is inserted on its own digit in the same manner as that on the fourth digit in *Hypsiprymnus*.

The peroneal group consists of the following five separate muscles, all form tendons which pass behind the external malleolus.

The extensor hallucis longus muscle arises from the proximal two-thirds of the fronto-medial aspect of the shaft of the fibula deep to the long extensor. Behind the annular ligament it

converges on a tendon which passes to the dorsum of the foot to its insertion on the phalanges of the hallux in the same manner as the long extensor.

The peroneus longus muscle arises from the proximal half of the outer surface of the shaft of the fibula and from the groove on the fronto-mesial aspect of the head of the bone. A stout tendon emerges which passes obliquely over the lateral side of the foot to the plantar aspect to its insertion on the base of the first metatarsal.

The peroneus brevis muscle arises from the proximal third of the fronto-lateral border of the shaft of the fibula. The tendon from this muscle is inserted on the outer aspect of the base of the fifth metatarsal.

The lateral peroneal extensor muscle arises from the groove on the fronto-lateral aspect of the head of the fibula and from the adjacent part of the head of the tibia. The tendon from this passes to an insertion on the dorsal expansion of the long extensor on the fifth digit.

The remaining two muscles arise together from the middle third of the fronto-medial border of the shaft of the fibula. A tendon emerges from each of these slender bellies, one going to the base of the fifth metatarsal and one to the base of the fourth.

CAPROMYS PILORIDES.

Each foot has five digits, each digit carrying a claw. The hallux is the smallest.

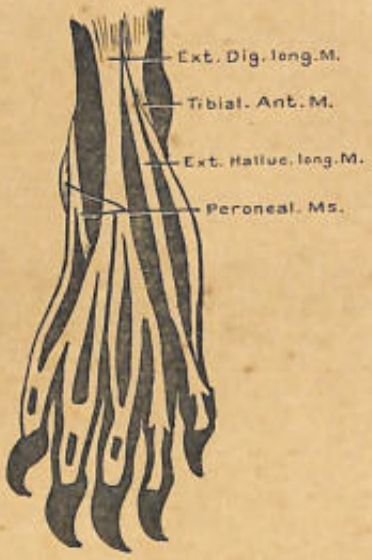
The tibialis anterior muscle arises by two heads, one from the proximal fourth of the lateral surface of the shaft of the tibia and by a few fibres from the head of the tibia and fibula, the other part arises from the proximal third of the fronto-medial border of the shaft of the fibula. These two heads meet to form a single muscular belly which converges on a tendon below the annular ligament, the latter then passes obliquely to an insertion on the inner side of the base of the first metatarsal, fibres spread out from the front of this insertion to gain a secondary insertion on the whole of the medial side of the shaft of this bone.

The extensor digitorum longus muscle arises from the fronto-mesial aspect of the head of the fibula and by a tendon from the front of the external condyle of the femur. A long slender muscular belly emerges which passes behind the annular ligament and the looped ligament where it forms a tendon which divides into three parts. The outer of these primary divisions again divides, one joining the lateral extensor to form a dorsal expansion on the fifth digit, the other two parts join to form an expansion on the fourth digit. The inner primary division goes to form an expansion on the second, on its way giving off a slip to join the middle primary division to form with it an expansion on the third digit. Each tendon forms a dorsal expansion over the metatarso-phalangeal joint; the central part of

each expansion is inserted on the upper aspect of the base of the middle digit, the lateral parts passing onward to meet and form an expansion which is inserted on the base of the distal phalanx.

The extensor hallucis longus muscle arises in line with the fibular origin of the tibialis anterior on the middle third of the fronto-medial border of the fibula. The slender belly converges on a tendon as it passes deep to the annular ligament and passing deep to the looped ligament, to an insertion on the inner side of the base of the proximal phalanx of the hallux, the central part of this ligament passing distally to an insertion on the dorsal aspect of the base of the distal phalanx.

Text-figure 6.



Capromys pilorides. Dorsum of foot.

The peroneus longus muscle arises from the outer side of the postero-lateral border of the shaft of the fibula. It passes distally in a groove behind the external malleolus on its way to the plantar aspect of the foot, where it is inserted into the outer side of the base of the first metatarsal.

The peroneus brevis muscle arises by two heads from the head of the fibula, one head arising from in front of the origin of the peroneus longus, and one head behind. The two parts soon come together and are joined by some deep fibres from the outer surface of the shaft of the fibula in its proximal half. A stout tendon emerges which passes over a groove on the superficial aspect of the external malleolus, then forward to its insertion on the outer

aspect of the base of the fifth metatarsal bone. Fibular origin of the extensor digitorum brevis muscle arises from the postero-lateral border of the proximal two-thirds of the shaft of the fibula. It converges on a slender tendon behind the external malleolus with the peroneus longus and then divides into two parts, one to pass forward to join the extensor tendon of the fifth digit, the other to join the extensor tendon of the fourth digit. The calcanean head of extensor digitorum brevis muscle arises from the upper surface of the calcaneus and from the capsule of the ankle-joint. It separates into two parts, and each part forms a tendon, one of which is inserted into the extensor tendon on the second digit and one into that on the third digit.

DASYPROCTA AGOUTI.

There is a long narrow foot of three digits, the second, third, and fourth, the hallux is suppressed as is the fifth digit.

The tibialis anterior muscle arises from the lateral side of the head of the tibia, from the proximal fourth of the lateral surface of the shaft of the tibia, and from the capsule of the knee-joint. The emerging tendon passes deep to the annular and looped ligaments to its insertion on the lower part of the medial surface of the second metatarsal.

The extensor digitorum longus muscle arises by a tendon from the front of the external condyle of the femur and by a few muscular fibres from the head of the fibula. A muscular belly is formed which again becomes a tendon as it passes below the annular and looped ligaments, gaining the dorsum of the foot it divides into three parts (held together by a vinculum) forming a tendon for each of the three digits present, each is inserted in the same manner as the extensor tendon of *Capromys pilorides*.

The extensor digitorum brevis muscle arises by two heads, one from the front of the proximal third of the shaft of the fibula, the other from the upper aspect of the calcaneus. The fibular part forms a tendon which joins the long extensor tendon going to the second digit, the calcanean divides into two and passes to the extensor tendons of the third and fourth digits.

The peroneus longus muscle arises from the outer aspect of the head of the fibula and through a thickened band from the outer side of the capsule of the knee-joint to the outer side of the condyle of the femur. The emerging tendon passes in a deep groove on the posterior margin of the external malleolus, then over the side of the foot to the plantar aspect to its insertion on the lateral side of the base of the second metatarsal.

The peroneus brevis muscle arises in common with the lateral extensor from the lateral aspect of the head of the fibula, the proximal fourth of the outer side of the shaft of the fibula, and from the proximal three-fourths of the anterior surface of that bone. A tendon emerges which passes in a deep groove on

Text-figure 7.

Dasyprocta agouti. Dorsum of foot.

the posterior surface of the external malleolus, then along the outer side of the foot to join the long extensor on the fourth digit.

DIPUS ÆGYPTIUS.

There is a long narrow foot formed by the fusion of the second, third, and fourth metatarsals. The corresponding phalanges are elongated and separate as three digits.

The tibialis anterior muscle arises from the lateral side of the head of the tibia and from the anterior half of the proximal fourth of the lateral surface of the shaft of the tibia. A tendon emerges which is inserted on the base and shaft of the middle metatarsal.

The extensor digitorum longus muscle arises from the front of the external condyle of the femur by a stout tendon, this forms a muscular belly which in turn forms a tendon towards its insertion. The tendon splits into a superficial and a deep part, the deep part going to the metatarso-phalangeal joint, the superficial part dividing into three to give one slip to each of the digits present. The insertion is as in *Capromys pilgrides*.

The peroneus longus muscle is present as a slender muscle belly arising from the lateral side of the head of the tibia and the adjacent part of the rudimentary fibula. The tendon of

insertion passes to the under aspect of the base of the fused metatarsals.

The peroneus brevis muscle is small; it arises from the outer side of the shaft of the rudimentary fibula and is inserted on to the cuboid.

CŒLOGENYS PACA.

Five digits are present, of which only the second, third, and fourth are well developed; the hallux and fifth digits are rudimentary.

The tibialis anterior muscle arises from the head of the fibula and from a triangular area on the proximal third of the outer surface of the shaft of the tibia. This powerful muscle converges on a tendon which passes below the annular ligament, then passes obliquely to its insertion on the upper and inner sides of the base of the first metatarsal and the adjacent part of the internal cuneiform.

The extensor digitorum longus muscle arises from the front of the head of the fibula and from the proximal half of the anterior surface of the shaft. This converges on a flattened tendon which gives off a slip from either side which pass to form expansions on the dorsum of the second and fourth digits. The central part forms the dorsal expansion on the middle digit.

The extensor hallucis longus muscle is very slender. It arises from the inner and under aspects of the head of the fibula. It converges on a delicate tendon which passes deep to the annular ligament and on gaining the dorsum of the foot divides into two parts, the most medial part going to the base of the proximal phalanx of the hallux, the lateral part to join the dorsal expansion of the long extensor on the second digit.

The peroneus longus muscle arises from the outer surface of the head of the fibula and from the proximal half of the outer surface of the shaft. It passes behind the external malleolus to an insertion on the base of the second metatarsal.

The peroneus brevis muscle arises from the middle two-thirds of the outer surface of the shaft of the fibula. Its tendon passes behind the external malleolus to its insertion on the outer side of the shaft of the fifth metatarsal.

The extensor digitorum brevis muscle has four separate slips of origin: (*a*) From the middle third of the outer surface of the shaft of the fibula, its tendon passing behind the external malleolus to the base of the proximal phalanx of the fifth digit. (*b*) From the middle half of the postero-lateral border of the shaft of the fibula. Its tendon passes behind the external malleolus to its insertion on the upper aspect of the base of the proximal phalanx of the fourth digit. (*c*) From the distal third of the inner surface of the shaft of the fibula. Its tendon passes deep to an annular ligament to its insertion on the base of the second digit. (*d*) From

the upper surface of the calcaneus by a muscular belly which soon divides into two parts, one part is inserted on the dorsal surface of the shaft of the third metatarsal, the other to the fourth metatarsal.

MYOPOTAMUS COYPUS.

Five digits are present, each carrying a nail. The foot is webbed.

Tibialis anterior muscle arises from the front of the capsule of the knee-joint and the anterior half of the proximal third of the lateral surface of the tibia. This powerful muscle converges on a tendon which passes below the annular ligaments to its insertion on the inner and under aspect of the internal cuneiform.

The extensor digitorum longus muscle arises as a broad tendon from the outer part of the front of the external condyle of the femur. It soon forms a muscular belly which below the annular ligament converges on a tendon and then divides into three parts. The outer gives a slender slip to the base of the fifth digit, the main part passing to form a dorsal expansion on the dorsal aspect of the base of the proximal phalanx of the fourth digit. The second tendon gives a slip to the expansion of the fourth digit, its main part passing to form the dorsal expansion on the base of the third digit. The last part of the tendon forms the expansion for the second digit, sending a slip to the expansion on the third. Each expansion gives off fibres to be attached to the sides of its own proximal phalanx, the central part passing to again expand on the proximal inter-phalangeal joint and give fibres to the sides of the second phalanx, the central part going to the dorsum of the distal phalanx.

The extensor hallucis longus muscle arises from the front of the lower part of the free portion of the fibula and from the upper part of the portion fused to the tibia. Its emerging tendon passes deep of the annular ligaments to the dorsum of the foot, giving off a slip to join the dorsal expansion of the second digit, the main part going to the hallux where it is inserted in the same manner as the extensor tendons to the other digits.

The extensor digitorum brevis arises by three separate parts, two from the fibula and one from the calcaneus. The upper part arises from the back of the expanded head of the fibula. It rapidly forms a tendon which passes behind the external malleolus to the dorsum of the foot to an insertion on the base of the fifth metatarsal. The next part arises from the postero-lateral border of the free part of the fibula; it passes with the upper portion of the short extensor tendon to the dorsum of the foot to an insertion on the proximal phalanx of the fourth digit, part joining the dorsal expansion of the long extensor tendon. The lower part of this muscle arises from the upper part of the calcaneus and at once divides into two parts from each of which a tendon emerges, one tendon going to join the dorsal expansion on the third digit and one to the expansion on the second digit.

The peroneus longus muscle arises from the proximal third of the outer surface of the shaft of the fibula, its tendon passes behind the external malleolus over the side of the foot to the plantar aspect to gain an insertion on the base of the first metatarsal.

The peroneus brevis muscle arises from the middle two-fourths of the outer surface of the shaft of the fibula, its tendon passes with that of the peroneus longus behind the external malleolus to its insertion on the outer and under aspects of the fifth metatarsal.

CASTOR CANADENSIS.

Five webbed digits are present. The fifth is rudimentary, the fourth is the strongest, the third, second, and first gradually becoming smaller.

The tibialis anterior muscle arises from the front of the head of the tibia where it is continuous with the origin of the extensor digitorum longus, the capsule of the knee-joint, and the proximal two-thirds of the lateral surface of the tibia. The emerging tendon is strong and passes deep to the annular ligaments to its insertion on the inner aspect of the base of the first metatarsal.

The extensor digitorum longus muscle arises by two bellies, one from the fibula, in common with the tibialis anterior, and the proximal third of the lateral aspect of the tibia. Two tendons emerge, one of which passes to the dorsal expansion of the third digit giving a slip of communication to the tendon going to the second digit, the other part goes to the dorsal expansion of the second digit giving slips to the tendons of third and first digits; the other division of the main tendon also divides, one part going to the base of the proximal phalanx of the fourth digit and one part to the base of the middle phalanx sending fibres to the base of the distal phalanx. The second part of the muscle arises from the middle third of the interosseous membrane. The superficial part of the muscle becomes tendinous and divides into two parts, one forming the dorsal expansion of the first digit, the other joining the tendon of the tibial part of the muscle going to the second digit. Before the interosseous part divides it gives off a strong transverse slip to the tendons of the second, third, and fourth digits. The deep part of the interosseous head remains muscular, and after inserting some of its fibres on to the capsule of the ankle-joint converges on a tendon which passes to the upper and medial aspect of the base of the proximal phalanx of the third digit.

The peroneus longus muscle arises from the outer aspect of the external condyle of the femur by a stout ligamentous origin, this is joined by muscular fibres from the proximal half of the outer surface of the shaft of the free portion of the fibula. The emerging tendon passes behind the external malleolus, over the side of the foot to the plantar aspect to its insertion on the under aspect of the base of the first metatarsal.

The peroneus brevis muscle arises from the lower half of the outer surface of the shaft of the fibula in its free portion and from the upper half of the fused portion of that bone to the tibia. Its

Text-figure 8.

Castor canadensis. Dorsum of foot.

tendon passes behind the external malleolus to the side of the foot, where it is inserted on to the under aspect of the base of the fifth metatarsal.

FELIS TIGRINA.

Four digits are present. The second, third, fourth, and fifth each carries a sharp claw.

The tibialis anterior muscle arises from the front of the head of the fibula, from the lateral side of the head of the tibia, from the proximal fourth of the lateral surface of the shaft of the tibia and the adjacent part of the interosseous membrane. A powerful ligament emerges which passes behind the annular ligament to its insertion on the inner and under aspect of the base of the fifth metatarsal bone.

The extensor digitorum longus muscle arises as a stout tendon from the front of the lateral surface of the external condyle of the femur. Beyond the knee it becomes muscular, and behind the annular ligament it again becomes a tendon which expands

and then divides into four parts, one tendon going to each of the four digits present, though held together by vincula. Each tendon close to its insertion forms an expansion, and from the sides of each fibres are given off to be inserted into the sides of the base of the proximal phalanx, the central part passing onward to again divide giving fibres of insertion into the base of the middle phalanx, the central fibres passing to an insertion on the upper aspect of the distal interphalangeal joint.

The extensor digitorum brevis muscle arises from the upper surface of the calcaneus. It at once divides into five parts. The

Text-fig. 9.

Felis tigrina. Dorsum of foot.

most medial forms a tendon which passes to be inserted on the inner side of the base of the proximal phalanx of the second digit. The other four slips form tendons which pass to join the dorsal expansion of each of the four digits.

The peroneus longus muscle arises from the anterior surface of the head of the fibula, tendinous fibres are continued upwards to the capsule of the knee-joint and so are indirectly attached to the femur. A long muscular belly emerges which converges on

a tendon which passes over the superfical aspect of the external malleolus behind a well-marked spur on the outer side of the calcaneus to its insertion on the under aspect of the base of the second metatarsal bone.

The peroneus brevis muscle arises from the back part of the outer surface of the head of the fibula and the proximal third of its shaft below. Its tendon passes behind the external malleolus then in a groove over the spur of the calcaneus to its insertion on the outer side of the base of the fifth metatarsal.

Lateral peroneal extensor muscle arises from the proximal third of the front of the shaft of the fibula. This slender muscular origin converges on a tendon which passes behind the external malleolus to the side of the foot, where it is inserted on the upper and outer surface of the fifth metatarsal.

FELIS PARDALIS.

Four digits only are present. The second, third, fourth, and fifth each carries a sharp claw.

The tibialis anterior muscle arises from the front of the head of the fibula, the capsule of the knee-joint, the proximal third of the lateral surface of the tibia and the adjacent part of the anterior border. The emerging tendon passes below two powerful annular ligaments to the dorsum of the foot to its insertion on the inner side of the internal cuneiform and the adjacent part of the second metatarsal.

The extensor digitorum longus muscle arises as a stout rounded tendon from the lower part of the front of the external condyle of the femur. Below the knee-joint it spreads out into a muscular belly strengthened by some muscular fibres arising from the proximal two-thirds of the medial aspect of the fibula. Deep to the annular ligament it again becomes tendinous, and passing below the looped ligament it divides into four parts, one part going to each digit to be inserted as in *Felis tigrina*.

The extensor digitorum brevis muscle arises by two heads, one from the side of the looped ligament and the side of the talo-calcaneo-interosseous ligament, the other from the upper and outer aspect of the calcaneus. The first part converges on a tendon which passes to a dorsal expansion on the second digit, the other part separates into three from each of which a tendon emerges, which go to the second, third, and fourth digits (there is no tendon to the fifth digit).

The peroneus longus muscle arises from the front margin of the lateral aspect of the head of the fibula. A tendon emerges which passes over the superficial aspect of the external malleolus, then over the cuboid to the plantar aspect of the foot to its insertion on the under aspect of the base of the second metatarsal.

The peroneus brevis muscle arises from the middle two-fourths of the shaft of the fibula. A powerful tendon emerges which

passes behind the external malleolus to an insertion on the outer and under aspect of the fifth metatarsal.

The lateral extensor muscle arises from the proximal half of the

Text-figure 10.

Felis paradalis. Dorsum of foot.

outer aspect of the fibula. It passes behind the external malleolus to its insertion on the dorsal expansion of the long extensor of the fifth digit.

GENETTA TIGRINA.

The hallux is rudimentary, the outer digits are well developed, each carrying a claw.

The tibialis anterior muscle arises from the front of the head of the fibula and from the proximal two-thirds of the anterior border of the shaft of the tibia. The muscle glides over the lateral surface of the shaft of the tibia but is not attached to it. Behind the annular ligament it converges on a tendon which passes obliquely to its insertion on the under surface of the base of the first metatarsal.

The extensor digitorum longus muscle arises by a tendon from the front of the lateral surface of the external condyle of the femur. Below the level of the knee-joint this tendon converges on a slender muscular belly which below the annular ligament forms a tendon. This tendon passes through the looped stem of a typically Y-shaped ligament to the dorsum of the foot where it forms four tendons, one for each of the four lateral digits to be inserted as in *Felis tigrina*.

The extensor digitorum brevis muscle arises from the upper aspect of the calcaneus. The muscle of origin at once divides into four slips, one for each of the four lateral digits to assist in the formation of the dorsal expansions. The most medial tendon gives a slip to the rudimentary hallux.

The peroneus longus muscle arises from the lateral side of the head of the fibula, its superficial fibres being continued upwards over the capsule of the knee-joint to the outer side of the femur. In the distal quarter of the leg a tendon emerges which passes in a groove on the superficial aspect of the external malleolus, then obliquely to its insertion on the plantar aspect of the foot on the base of the second metatarsal.

The peroneus brevis muscle arises from the front of the shaft of the fibula on its entire extent and from an oblique line in front of the proximal third of the shaft. It converges on a stout tendon which passes behind the external malleolus over the upper aspect of a deep groove on the lateral spur of the calcaneus to its insertion on the outer and under aspects of the base of the fifth metatarsal.

The lateral extensor muscle arises from the outer side of the head of the fibula and from the posterior half of the proximal third of the outer surface of the shaft of the fibula. The slender muscular belly converges on a tendon which passes behind the external malleolus to the outer border of the foot to its insertion on the outer side of the base of the proximal phalanx of the fifth digit.

Viverricula malaccensis.

Five digits are present. The hallux is rudimentary, the lateral four are well developed, and each carries a sharp claw.

The tibialis anterior muscle arises from the capsule of the knee-joint, the lateral side of the head of the fibula and from the proximal fourth of the lateral surface of the shaft. The emerging tendon passes deep to the annular ligament to its insertion on the inner and under aspects of the base of the first metatarsal.

The extensor digitorum longus muscle arises by two heads, one from the front of the lateral side of the external condyle of the femur by a tendon, and one from the inner border of the front of the shaft of the fibula just below the head, by a few muscular fibres. These muscular fibres join the tendinous origin and the two parts pass as a muscular belly behind the annular ligament,

where a tendon emerges which passes through the loop of the Y-shaped ligament to the dorsum of the foot where it divides into four parts, the four parts being held together by a strong vinculum. One of these tendinous parts goes to each of the four lateral digits to be inserted as in *Felis tigrina*.

The extensor digitorum brevis muscle arises as a slender muscular belly from the upper aspect of the calcaneus and from the capsule of the talo-calcaneo joint. It at once separates into three parts and from each a tendon emerges. The three tendons so formed pass to the second, third, and fourth digits to join the dorsal expansion of the long extensor on each.

The peroneus longus muscle arises from the outer side of the head of the fibula, rapidly converges on a tendon which passes in a groove on the posterior part of the external malleolus, then below the lateral spur of the calcaneus to the plantar aspect of the foot to its insertion on the base of the first metatarsal.

The peroneus brevis muscle arises from the proximal third of the fronto-lateral border of the shaft of the fibula and from the middle two-thirds of the outer surface of the shaft. It converges on a tendon which passes behind the external malleolus, then in groove above the lateral spur on the calcaneus to an insertion on the outer surface of the base of the fifth metatarsal.

The lateral peroneal extensor muscle arises from the proximal fourth of the outer surface of the shaft of the fibula as a slender muscular belly, which converges on a tendon, passes behind the external malleolus, bends forward between the tendons of peroneus longus and brevis along the outer margin of the foot to its insertion on the outer aspect of the base of the proximal phalanx of the fifth digit.

VIVERRA CIVITTA.

Five digits are present. The four lateral are of nearly equal size, the hallux is rudimentary.

The tibialis anterior muscle arises from the front of the outer head of the fibula, from the outer side of the head of the tibia, and from the proximal fourth of the lateral side of the shaft of the tibia. An emerging tendon passes below the annular ligament, then passes obliquely and to the medial side to its insertion on inner side of the base of the first metatarsal.

The extensor hallucis longus muscle arises as a slender belly from the middle half of the antero-medial border of the shaft of the fibula. The muscle passes deep to the annular ligament, then through the loop of the stem of the Y-shaped ligament towards its insertion on the base of the proximal phalanx of the hallux, sending fibres from the central part of the insertion to the base of the distal phalanx.

The extensor digitorum longus muscle arises as a flattened tendon from the front of the lateral surface of the external condyle of the femur. This soon forms a muscular belly which

passes below the annular ligament, then again becomes tendinous and passes through the looped portion of the Y-shaped ligament to its insertion by four tendons, one going to each of the four lateral digits to be inserted as in *Genetta tigrina*.

The extensor digitorum brevis arises from the upper aspect of the calcaneus by muscular fibres, this soon divides into three parts which become tendons and pass to the second, third, and fourth digits. The third slip gives off a few fibres to the adjacent part of the fifth digit. Each tendon at its insertion joins the dorsal expansion of its own digit.

The peroneus longus muscle arises from the lateral side of the head of the fibula. It converges on a tendon which passes in a groove on the superficial aspect of the external malleolus, then distally below the spur on the lateral side of the calcaneus to the plantar aspect of the foot, to its insertion on the base of the first metatarsal.

The peroneus brevis muscle arises from the proximal half of the front of the shaft of the fibula and the middle half of the front of the outer surface of that bone. The emerging tendon passes behind the external malleolus, then forward to its insertion on the outer side of the base of the fifth metatarsal.

The lateral peroneal extensor muscle arises from the proximal fourth of the outer surface of the shaft of the fibula. The emerging tendon passes behind the external malleolus, then forward along the side of the foot to its insertion on the outer side of the base of the fifth metatarsal.

PERODICTICUS POTTO.

Five well-developed digits are present. The hallux is strong and opposable, the second digit carries a claw, the third, fourth, and fifth like the hallux carry a nail each.

The tibialis anterior muscle arises from the anterior half of the proximal three-fourths of the outer surface of the shaft of the tibia. It passes behind the annular ligament as a stout tendon to its insertion on the inner and plantar aspects of the first cuneiform.

The extensor hallucis longus muscle arises by a narrow origin from the outer side of the head of the tibia and the outer side of the proximal half of the shaft of that bone, deep to the origin of tibialis anterior. It passes deep to the annular ligament, but not to the looped ligament, then to its insertion on the dorsum of the hallux and on the sides of the base of the proximal phalanx, the central parts passing the base of the distal phalanx.

The extensor digitorum longus muscle arises from the front of the head of the fibula and by a long narrow line from the fronto-medial side of the shaft of that bone. Its emerging tendon passes deep to the annular ligament and through the looped ligament to the dorsum of the foot where it divides into three slips. The central slip is the strongest and passes to the fourth digit.

The lateral slip goes to the fifth digit and the medial slip to the third. There is no slip to the second. Each is inserted on the base of the proximal phalanx of its own digit giving fibres to the sides, while the central parts go to the base of the next phalanx and again central fibres passing to the distal phalanx.

The extensor digitorum brevis muscle arises from the dorsal aspect of the calcaneus. It divides into three parts. The medial belly forms a tendon which is inserted on the medial side of the dorsal surface of the base of the proximal phalanx of the hallux.

Text-figure 11.

Perodicticus potto. Dorsum of foot.

The lateral part is inserted by a tendon on the lateral side of the base of the proximal phalanx of the fifth digit. The central part divides further into two, one part going to the proximal phalanx of the second digit, the other to the proximal phalanx of the fourth digit.

The peroneus longus muscle arises from the front and lateral aspects of the head of the fibula and from the proximal half of the lateral postero-lateral border of the shaft of the fibula. Its tendon passes behind the external malleolus, then bends sharply forward and medially to the plantar aspect of the foot to its insertion on the outer aspect of the base of the first metatarsal.

Peroneus brevis muscle arises from an oblique area on the front and lateral aspects of the middle two-thirds of the shaft of

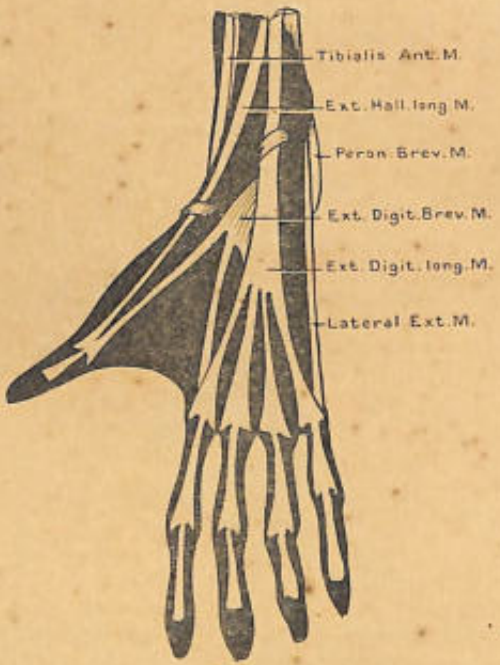
the fibula. It converges on a tendon which passes behind the external malleolus, then forward to its insertion on the lateral aspect of the base of the fifth metatarsal.

CEBUS FATUELLUS.

There is a long foot with five digits. The hallux is opposable; the outer digits are of nearly equal length, the fifth being the smallest.

The tibialis anterior muscle arises by two heads, the stronger of which arises from the outer side of the head of the tibia,

Text-figure 12.



Cebus fatuellus. Dorsum of foot.

from the proximal fourth of the outer surface of its shaft, and from the fronto-medial border of the shaft of the fibula. A stout tendon emerges which is inserted on the medial and under aspects of the internal cuneiform. The slender secondary tendon arises from the lateral aspect of the head of the tibia and from the front of the head of the fibula. This long slender muscle converges on a tendon which passes to an insertion on medial aspect of the base of the first metatarsal.

The extensor hallucis longus muscle arises from the proximal third of the fronto-medial border of the fibula. The emerging tendon passes with the tibialis anterior below the annular ligament, then along the side of the foot, held down at the base of the first metatarsal by a stout pulley-like ligament, and is inserted as a dorsal expansion as in man.

The extensor digitorum muscle arises from the front of the head of the fibula and from the proximal two-thirds of the front of the shaft. A tendon emerges which passes through the stem of the looped Y-shaped ligament to the dorsum of the foot where it divides into four tendons, one going to each of the four lateral digits, each forming a dorsal expansion and inserted as in man.

The extensor digitorum brevis muscle arises from the upper aspect of the calcaneus. It at once divides into four bellies, and from each a tendon is formed, each tendon goes to take part in the formation of a dorsal expansion with the long extensor. These tendons pass to the hallux, second, third, and fourth digits.

The peroneous longus muscle arises from the lateral side of the head of the fibula and the proximal half of the outer surface of the shaft of the fibula. Its tendon passes behind the external malleolus, grooves the outer side of the cuboid and passes to the plantar aspect of the foot to its insertion on the lateral side of the first metatarsal and the internal cuneiform beside it.

The peroneus brevis muscle arises from the middle third of the outer aspect of the shaft of the fibula. Its emerging tendon passes behind the external malleolus, then obliquely forward to its insertion on the outer aspect of the base of the fifth metatarsal.

The lateral peroneal extensor muscle is very slender. It arises from the muscular fibres of the peroneus brevis. It soon converges on a tendon which passes behind the external malleolus, then along the lateral border of the foot to be inserted on the outer side of the base of the fifth digit sending fibres to join the dorsal expansion over the proximal interphalangeal joint.

ATELES ATER.

There is a long narrow foot. The hallux is opposable, the fifth digit is considerably smaller than the middle three.

The tibialis anterior muscle arises from the proximal half of the outer surface and anterior border of the shaft of the tibia, a few fibres coming from the front of the head of the fibula and from the adjacent part of the head of the tibia: this continuous muscular origin at once splits into two separate bellies, which converge on tendons which pass below the annular ligament, then obliquely downwards and medially to their insertion on the inner side of the foot. The tendon inserted on the inner surface of the first cuneiform is the larger, the other tendon is inserted on the medial surface of the base of the first metatarsal.

The extensor hallucis longis muscle arises from the middle two-thirds of the inner surface of the shaft of the fibula. This is a long flattened muscle which passes in close contact with the tibialis anterior as far as its insertion, the tendon of the extensor hallucis then passes through a pulley-like ligament which passes from the navicular over the tendons of tibialis anterior, then splits its attachment to the base of the first metatarsal, the tendon then courses along the side of the foot to gain its insertion on the side and dorsal aspect of the hallux in the same manner as the tendon of *Cebus fatuellus*.

The extensor digitorum longus muscle arises from the front of the head of the fibula, receiving a few fibres from the adjacent part of the head of the tibia. In the middle third of the leg the muscle receives a further set of muscular fibres from the middle third of the anterior border of the shaft of the fibula. A tendon emerges as the muscle approaches the ankle-joint, which passes first deep to the annular ligament, then through the loop of the stem of the Y-shaped ligament, reaching the dorsum of the foot it expands and then divides into four parts making a tendon for each of the four outer digits, each tendon forming a dorsal expansion as in *Perodicticus potto*.

The extensor brevis digitorum muscle is a triangular-shaped muscle arising at its apex from the upper aspect of the calcaneus. This muscle at once gives off a part which converges on a tendon passing to the dorsal expansion on the fourth digit. The remaining part of the muscle passes forward, and divides into three parts: these form tendons, one to pass to an insertion on the dorsal aspect of the base of the proximal phalanx of the hallux, the other two pass to the dorsal expansions on the second and third digits.

The peroneal muscles arise as a single muscular mass from the proximal half of the anterior surface of the shaft of the fibula and from the adjacent part of the head, additional fibres arise from the middle third of the lateral side of the shaft of that bone. Three muscles separate from this origin, the peroneus longus and brevis and the lateral peroneal extensor. The converging tendon of the peroneus longus passes behind the external malleolus, over the side of the foot to its insertion on the outer side of the base of the first metatarsal and adjacent part of the internal cuneiform. The peroneus brevis tendon passes behind the external malleolus to its insertion on the under and outer side of the base of the fifth metatarsal fibres passing from the front part of the tendon to an insertion on the side of the shaft of this metatarsal. The lateral extensor tendon also passes behind the external malleolus, then passes along the outer side of the foot to its insertion partly into the dorsal expansion of the long extensor and partly on to the outer side of the base of the proximal phalanx of the fifth digit.

ANTHROPOPITHECUS TROGLODYTES.

The foot has five digits and closely resembles the hand of man. The hallux, however, is much more powerful than the thumb in man.

The tibialis anterior muscle is present as two separate muscles, one placed superficially to the other. The superficial part arises from the inner and under aspect of the head of the fibula, the adjacent part of the head of the tibia, and from a short area on the anterior border of the shaft; the deep part arises from the outer aspect of the head of the tibia and from the proximal half of the outer surface of the shaft. The superficial tendon passes distally deep to the annular ligament and then to the inner side of the foot to its insertion on the mesial surface of the base of the first metatarsal, the deep part of the muscle converges on a tendon which soon passes behind the tendon of the superficial part to its insertion on the inner surface of the base of the first cuneiform.

The extensor digitorum longus muscle arises from the anterior aspect of the head of the fibula, the adjacent part of the head of the tibia, and almost the whole length of the antero-medial surface of the shaft of the fibula. The converging tendon passes deep to the annular ligament, then through the loop of the stem of the Y-shaped ligament to the dorsum of the foot where it divides into four parts, forming one tendon for each of the four lateral digits. The second of these tendons is very slender. The first tendon divides into two parts, the medial part going to the second digit, the lateral part to the second tendon to the third digit, the third and fourth go to the third and fourth digits respectively. Each tendon forms a dorsal expansion and is inserted in the manner described for *Perodicticus potto*.

Extensor hallucis longus muscle arises from the middle third of the antero-medial surface of the shaft of the fibula. It converges on a tendon which passes deep to the annular ligament, then through the loop of the naviculo-metatarsal ligament, then distally to the dorsum of the metatarso-phalangeal joint, where it forms a dorsal expansion and is inserted in the same manner as the long extensors.

The peroneus longus muscle arises from the outer surface of the head of the fibula and from the whole length of the outer surface of the shaft. Its tendon passes behind the external malleolus to the side of the foot, grooves the cuboid and gains the plantar aspect to pass to its insertion on the under surface of the base of the first metatarsal and to the proximal half of the shaft. There is no attachment to the internal cuneiform.

The peroneus brevis muscle arises from the lower half of the outer surface of the shaft of the fibula. Its tendon passes behind the external malleolus to the outer side of the foot to its insertion on the lateral aspect of the projecting base of the fifth metatarsal.

Conclusion.

It is now left to consider what may be learned concerning the morphology of these muscles, to see if variation and attachment would serve for purposes of classification. Each muscle will be considered separately.

The most noticeable feature of the tibialis anterior muscle is the constancy of its attachment as a strong muscular mass to the shaft of the tibia. It is only in the Primates that any great variation occurs. In some mammals the tendon of insertion is attached to the base of the most medially placed metatarsal, in others to the base of the internal cuneiform. In *Perodicticus potto*, as in the Rodents and Marsupials generally, there is a single tendon of insertion, but in the case of *Perodicticus* the insertion is on the plantar aspect of the internal cuneiform, not on the medial surface as in the other forms. In *Ateles ater* the tendon is double, the smaller part passing to the internal cuneiform and the larger to the first metatarsal. In *Cebus fatuellus* and in *Anthropopithecus troglodytes* the tibialis anterior is represented by two muscles, one passing to the internal cuneiform, the other to the first metatarsal. These observations agree with Macalister (2), Hepburn (3), Champneys (4), and Sonntag (5). It was pointed out by Wilder (6) that the double insertion is in accord with the use of the hallux as a thumb. The insertion on the plantar aspect in *Perodicticus* is in keeping with the tendency for inversion of the hinder foot in the Lemuroid group.

The origin of the extensor digitorum longus muscle to the fibula varies as well as the insertion. In *Echidna hystrix*, *Sarcophilus ursinus*, *Dasyurus viverrinus*, and *Perameles obesula* the tendon divides into two parts, these in turn dividing to give rise to four tendons, one for each of the four lateral digits. In *Trichosurus vulpecula* and in *Dendrolagus bennettianus* the main tendon divides into three parts, the outer again dividing, and so again are formed a tendon for each of the four outer digits. In *Hypsiprymnus rufescens* it is represented by two separate muscles; in *Phascolomys wombat* by four separate muscles. In *Didelphys azaræ* the single muscle of origin converges on a tendon which divides into four parts. In *Capromys pilorides*, *Dasyprocta agoûti*, and *Myopotamus* the origin is from the front of the external condyle of the femur, the tendon of insertion dividing into three, the lateral portion again dividing to form tendons for the fourth and fifth digits. In *Dipus ægypytius* the origin is from the femur alone, its tendon of insertion being modified to suit the reduced number of digits present. In *Castor canadensis* there is a double origin, one part arising from the tibia and one part from the fibula. Here again is a marked modification to suit the swimming habits of this creature. In *Felis tigrina*, *Felis pardalis*, *Genetta tigrina*, and *Viverra civetta* the extensor digitorum longus muscle arises from the femur, its tendon of insertion dividing into four parts. In *Viverricula malaccensis*

the origin is from the fibula with an indirect attachment to the femur through the capsule of the knee-joint. In the Primates the origin is from the fibula. In *Ateles ater*, *Cebus fatuellus*, and *Anthropopithecus troglodytes* the tendon divides to give a part to each of the lateral digits, but in *Perodicticus potto* the medial tendon passes to the hallux, the other tendons to the three outer digits. The second digit receives a tendon from the extensor digitorum brevis only. This arrangement is not universal in the Lemuroids, the usual arrangement is as in the other Primates.

According to Windle and Parsons (7) the typical mammalian arrangement of the extensor digitorum longus muscle is to have its tendon of origin attached to the "front of the outer condyle of the femur." The present series of dissections would appear to show that this is not so. In none of the Monotremes, Marsupials, or Primates is there any indication of a femoral attachment. In the Rodents the muscle arises as a rule from the external condyle of the femur, but in *Cœlogenys paca* the muscle arises from the fibula alone. In *Dasyprocta agouti* the femoral origin is strengthened by fibres from the head of the fibula. Parsons (8) describes the muscle arising from the femur alone in the Rodents except in *Mus barbarus*, *Sphingurus*, and *Dipus*, which have accessory fibres from the head of the fibula. In *Viverricula malaccensis* the attachment is mainly to the fibula, the attachment to the femur is an indirect one through the capsule of the knee-joint. Macalister (9) describes only fibular attachments in Marsupials. Hepburn (3) and Sonntag (10) find only a fibular origin in the Primates.

The exact origin of the extensor hallucis longus muscle shows considerable variation. In *Echidna hystrix* it arises from the tibia. In *Cœlogenys paca* it arises from the head of the fibula only. In *Myopotamus coypus* it arises from the lower part of the shaft of the fibula. The average attachment is to the middle of the inner surface of that bone. Parsons states (8) that the extensor hallucis longus muscle is always present in the Rodents, but no trace of it is present in either of the specimens dissected of *Dipus ægyptius*, or *Dasyprocta agouti*. In *Castor canadensis* it is fused at its origin with extensor digitorum longus. The muscle is absent in *Viverricula malaccensis*, *Felis pardalis*, and *Felis tigrina*. It is present as a slender structure in *Viverra civetta*, where it is closely associated with tibialis anterior. The muscle is usually inserted by a tendon to the dorsum of the phalanges of the hallux. In *Sarcophilus ursinus*, *Cœlogenys paca*, and *Myopotamus coypus* there is a double insertion, one part going to the hallux, the other to join the dorsal expansion on the second digit. In the Primates the tendon passes to the side of the foot through a looped ligament, called by Sonntag (10) the "naviculo-metatarsal trochlea," to an insertion on the proximal phalanx of the hallux. The tendon is so placed that it can act

in a double capacity as an extensor and as an abductor. This double movement can be associated with the great mobility of the hallux among the Primates.

The extensor digitorum brevis muscle is first seen to arise from the fibula and gradually slips distally to the upper aspect of the calcaneus. In *Echidna hystrix* it is attached to the head and proximal part of the shaft of the fibula. In *Sarcophilus ursinus* it arises from the proximal half of the shaft of the fibula, in *Perameles obesula* it has slipped down to the middle third, in *Trichosurus vulpecula* it is partly attached to the lower end of the fibula and partly to the upper aspect of the calcaneus; in *Phascolomys wombat* it has lost its fibular attachment and is confined to the calcaneus. In *Didelphys azaræ* it arises as a series of muscular slips from the fibula, each tendon passing as a separate structure to its own digit. Among the Rodents there is almost always a double attachment, one from the fibula and one from the calcaneus. The muscle is absent in *Dipus ægyptius*. In the Carnivores the attachment is to the calcaneus and to the ligaments in the immediate neighbourhood. In the Primates the origin is as in the human subject, and it is here for the first time that the first tendon is attached to the phalanx of the hallux, the lateral tendons going to the dorsal expansions of the outer digits. In the lower forms the insertion of the first tendon passes to the dorsal expansion of the extensor to the hallux.

The peroneus longus muscle is a constant structure throughout the mammals dissected. In most cases it exists as a separate muscle though its origin varies. In *Echidna hystrix*, *Trichosurus vulpecula*, and *Phascolomys wombat* it arises with the peroneus brevis and the lateral peroneal extensor by a common muscular mass. In *Dipus ægyptius*, *Felis pardalis*, *Viverricula malaccensis*, and *Viverra civetta* its origin is from the head of the fibula alone. In *Dasyprocta agouti*, *Felis tigrina*, and *Genetta tigrina* it arises from the head of the fibula and from a thickened band of fibres in the capsule of the knee-joint leading to the outer side of the external condyle of the femur. In all the other forms the muscle arises from the head and the shaft of the fibula. The femoral attachment agrees with the observations of Ruge (11), who states that in certain carnivores the peroneus longus arises from the femur. Windle and Parsons (8) failed to find any femoral origin. The tendon of the muscle passes in a groove on the outer surface of the external malleolus towards its insertion except in the Primates, where it passes behind the malleolus. The insertion is confined in many cases to the base of the first metatarsal, and in some cases to the internal cuneiform. In other cases it has a double insertion to both these bones. Hepburn (12) states that its insertion is limited to the metatarsal in the Primates. This is denied by Sonntag (10), Sommer (13), and Fick (14). In the Primates dissected in the

preparation of this paper, the insertion is partly to the metatarsal and partly to the internal cuneiform except in *Anthropopithecus troglodytes*, where the insertion is confined to the metatarsal.

The peroneus brevis muscle is present in some form in all the mammals dissected except in *Echidna hystrix* and *Macropus dorsalis*. Macalister (9) describes its presence in the former, but no trace was found in the present dissection. In *Trichosurus vulpecula* and *Phascolomys* the three peroneal muscles arise from a common origin. In *Sarcophilus ursinus* it arises from the shaft of the fibula in continuity with the fibres of the extensor digitorum longus. In *Dasyurus viverrinus* it is attached to both front and lateral aspects of the shaft of the fibula. In *Perameles obesula* the attachment is to the lateral surface, the position in most Rodents, Carnivores, and Primates. Among the latter in *Ateles ater* the peroneus brevis muscle arises from a common origin with the other peroneus muscles. The insertion of this muscle in the different groups is uniformly to the base of the fifth metatarsal, where it can act in many forms as a powerful abductor of the fifth digit. Some writers state that the tendon of insertion gives a slip to the dorsal expansion on the proximal phalanx of the digit in *Anthropopithecus troglodytes*, but there was no slip seen in the present specimen.

The presence of the lateral peroneal extensor muscle varies greatly within members of the different groups. It is not found in *Dasyurus viverrinus* or *Dendrolagus bennettianus*, neither is it present in any of the Rodents dissected, nor in *Perodicticus potto* or in *Anthropopithecus troglodytes*. It is present in *Sarcophilus ursinus*, *Perameles obesula*, *Didelphys azaræ*, *Cebus fatuellus*, *Ateles ater*, and in all the Carnivores. Its attachment varies. In those animals where the peroneus longus muscle arises only from the head of the fibula, the lateral extensor has an attachment to the shaft of that bone close to the head, and the external popliteal nerve passes between the two muscles, but as the peroneus longus gains an attachment to the shaft of the fibula and the lateral extensor recedes distally the nerve is seen to apparently pierce the longus muscle.

In considering these details of muscular attachment it is easy to pick out points of similarity between animals of the same group, but how far these should be allowed to influence ideas of classification is seen to be of great doubt. If a comparison be made of the stout digging foot of *Phascolomys wombat* with the powerful springing foot of *Hypsiprymnus rufescens*, or the swimming foot of *Castor canadensis* with the springing foot of *Dipus ægyptius*, it will at once be admitted that function is an important if not the chief consideration in determining muscular arrangement.

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21. The Mammals obtained by Mr. Herbert Stevens on the Sladen-Godman Expedition to Tonkin. By Oldfield Thomas, F.R.S., F.Z.S.

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By the combined generosity of the Trustees of the Percy Sladen and Godman Exploration Funds, Mr. Herbert Stevens, who had previously had experience in collecting near Darjiling, was sent to Tonkin, a country from which our National Museum had almost no mammals, and one from which much of novelty might be expected, its Mammalogy being exceedingly little known.

Mr. Stevens left Darjiling, where he was living, on September 3rd, 1923, and, going by way of Calcutta, Rangoon, Penang, Saigon, and Haiphong, reached Hanoi, Tonkin, on October 8th. After interviews with various Forest officials, of whom several were most helpful to him, he proceeded inland to Bao-Ha and Thaï-Niên in the forest country of the Red River, where he stayed until April 2nd, making collections of all sorts. Unfortunately, the natives proved to be not only unhelpful, but actively troublesome and insolent, which added greatly to his difficulties.

He then moved on to the highest part of Tonkin, to a place called Ngai-Tio, at an elevation of 4800 feet, just beyond the Col des Nuages, where he worked with considerable success until July. He next proposed to ascend the Clear River towards the eastern part of Tonkin, to get into a different Forest area, but most unfortunately, on the 20th July, the river-steamer in which he was travelling was upset, and he and his wife barely escaped with their lives, one European and 25 natives being drowned, and the whole of Mr. Stevens's equipment being lost. This put an end to the possibility of any further work, and he therefore came home to England, having, however, stayed quite as long in Tonkin as had originally been expected, in view of the bad summer climate. Fortunately, before this accident, Mr. Stevens had already dispatched home all the specimens he had so far collected, none of these being lost.

Besides specimens belonging to other groups of the animal kingdom, on which papers will be contributed by the specialists concerned, the mammal collection consists of about 200 examples, belonging to 35 species and subspecies, and of these I have had occasion to describe seven as new, thus showing a considerable degree of difference between the mammal fauna of Tonkin and that of the neighbouring countries. Several of the novelties are markedly distinct from their nearest allies, but nothing further has turned up equal in peculiarity to the remarkable *Chrotogale*

owstoni, described in 1912 from a young specimen, of which we had hoped Mr. Stevens would have obtained an adult skull showing the permanent dentition. But, unfortunately, the only part of it he was able to get was a native skin without skull.

Perhaps the most interesting accession in the collection is the very handsome climbing Rat, on which I have founded the new genus *Chiromyscus*, the species having been described as a "*Mus*" as long ago as 1891, but of which the British Museum had not previously possessed a specimen.

Altogether, the collection has proved of great value and interest, and we have reason to be most grateful to the donors of the funds with which Mr. Stevens was enabled to carry out his trip. Tonkin had previously formed a marked lacuna in our knowledge of Asiatic Mammalogy, and the expedition has therefore been of decided value to science, so that its abrupt conclusion is greatly to be regretted.

The three localities at which Mr. Stevens collected are all in the area of the Song-Koi or Red River, Bao-Ha, and Thaï-Niên, on the river itself, respectively at 250 and 300 feet altitude, while Ngai-Tio is high up in the hills at 4800 feet, approximately at 22° 40′ N., 103° 30′ E., some fifty miles south of Möng-tsze.

1. Nycticebus pygmæus Bonh.

♂. 112. Thaï-Niên, Fleuve Rouge. 300′.

Closely agrees with adult topotypes of Bonhote's species, of which the type was not by any means so fully adult as he supposed.

2–3. Rhinolophus spp.

♂. 164. ♀. 165. Ngai-Tio. 4800′.

Two species, not now determinable with the material available.

4. Hipposideros armiger Hodgs.

♂. 172 (immature). Ngai-Tio. 4800′.

5. Pipistrellus sp.—coromandra group.

♂. 4, 20. ♀. 40, 41, 42, 45.

10 in spirit. Thaï-Niên.

6. Tylonycteris pachypus Temm.

♀. 1. Bao-Ha. 250′.

♀ in spirit. Ngai-Tio. 4800′.

7. Miniopterus schreibersi Kuhl.

♂. 168, 169. ♀. 167 and four in spirit. Ngai-Tio. 4800′.

One of the dark Eastern forms of this widely spread bat, whose different races need further working out. Possibly the same as *blepotis* Temm.

8. HYLOMYS SUILLUS MICROTINUS, subsp. n.

♀. 39. Bao-Ha. 250'.
♀. 62. Thaï-Niên. 300'. 2 March, 1924. *Type*. B.M. No. 25.1.1.16.

Size and skull as usual. Colour lined greyish brown, nearly exactly as in ordinary brown Voles, such as *Microtus agrestis* and allied species; lighter than in the Malay *suillus* and darker than in *siamensis*.

Dimensions of the type:—

Head and body 129 mm.; tail 26·5; hind foot 21·5; ear 16.

Skull: greatest length 34 mm.; condylo-basal length 33; zygomatic breadth 18; combined length of ms^{1-3} 5·5.

Hab. and *Type* as above.

The rare insectivores of the genus *Hylomys* are all very closely allied in their essential characters, but there seem to be several local colour-races. The present one, which represents the furthest locality recorded to the north-eastwards, is decidedly darker than *siamensis*, and lighter than the Malayan forms.

9. TUPAIA BELANGERI TONQUINIA, subsp. n.

♀. 12, 14. Bao-Ha. 250'.
♀. 72. Thaï-Niên. 300'.
♂. 114, 121 (yg.). ♀. 159. Ngai-Tio. 4800'.

Most nearly allied to *T. belangeri modesta* (as I should call Allen's *T. modesta*) of Hainan, with which it agrees in the ochraceous colour of the ends of the hairs below, but with blacker tail. Tail almost wholly grizzled blackish, each hair with a much broader subterminal black band than in *modesta*. Characters otherwise the same, or the general colour a little darker. The neighbouring *T. b. yunalis* of Yunnan has the under surface washed with yellowish, not ochraceous.

Skull with rather more robust teeth than in most forms of *belangeri*.

Dimensions of the type:—

Head and body 168 mm.; tail 147; hind foot 45; ear 16.

Skull: greatest length 48 mm.; condylo-basal length 46; front of p^4 to back of m^2 9·5.

Type. Adult female. B.M. No. 25.1.1.22. Original number 12. Collected 22 November, 1923.

The Ngai-Tio specimens from the highlands are less typical, but still have the ochraceous under surface which distinguishes both *tonquinia* and *modesta* from *yunalis*.

I owe to the kindness of the New York Museum the loan of representative specimens of the Hainan *modesta*, the British Museum not as yet containing any examples of the island form. The Annam *T. concolor* is a decidedly larger animal than either *modesta* or *tonquinia*.

10. Crocidura sp.

♀. 163, 179, 186. Ngai-Tio. 4800'.

Skull about 24 mm. in length.

11. Crocidura sp.

♀. 88. Thaï-Niên. 300'.

♂. 161. ♀. 185. Ngai-Tio. 4800'.

A small species, its skull about 17 mm. in length.

12. Felis bengalensis Kerr.

♀. 180. Ngai-Tio. 4800'.

13. Felis temminckii Vig. & Horsf.

♀. 35. Bao-Ha. 300'.

Quite a kitten.

14. Viverra zibetha Linn.

♂. 31. Bao-Ha. 250'.

15. Viverricula malaccensis Gmel.

♂. 154. ♀. 152, 153. Ngai-Tio. 4800'.

Mere kittens.

16. Pardictis (g. n.) pardicolor Hodgs.

♂. 17. Bao-Ha. 250'.

Agrees fairly closely with representative examples of *pardicolor* from Nepal.

While studying this and the next succeeding specimen, my attention has been attracted by the cranial and other characters which distinguish the two species commonly referred to the genus *Prionodon*—*P. gracilis*, the genotype, and *P. pardicolor*, its Himalayan ally,—and I have come to the conclusion that these differences are of more than specific value; equally in distribution, in colour-pattern, and in skull the two are distinguished in ways which have analogies in other groups, and it seems suitable to separate them.

The new genus, which may be called *Pardictis*, is northern in range, from Nepal to Tonkin, instead of Malayan—Peninsula and Islands. The pattern of marking consists of spots arranged more or less longitudinally, instead of broad transverse bands, and in the skull the following differences are observable. The palatal tube is shorter and more parallel-sided, with the ectopterygoids not swollen and expanded as they are in *Prionodon*. The bullæ, instead of being composed almost wholly of the posterior inflated part, with the anterior tympanic portion reduced and the meatus small, as in *Prionodon*, have the two

portions more nearly equal in extent, the annular anterior part swollen, with large meatus, and the posterior part comparatively small and less inflated.

The genotype of *Pardictis* would be *Prionodon pardicolor*, *P. gracilis* being that of both *Prionodon* and *Linsang*.

17. PARDICTIS PARDICOLOR PRESINA, subsp. n.

♂. 174. Ngai-Tio. Alt. 4800'. B.M. No. 25.1.1.33. *Type*.

A larger race of *Pardictis pardicolor*, of paler colour.

Size appreciably greater than in true *pardicolor*, as judged by the skull. Markings essentially as in that animal, though the lines tend to be slightly narrower and the spots smaller than the average in *pardicolor*. Ground-colour of a distinctly paler buff, both above and below, the difference well marked as compared with every example of *pardicolor*, of which the Museum contains more than a dozen. Below especially the colour is far paler, creamy-buff, with no trace of the ochraceous so often present in old males of *pardicolor*. Tail with the dark rings less developed in proportion, not broader than the pale ones, as they usually are in *pardicolor*, and more evidently tending to be broken in the middle line below. Other characters as in *pardicolor*.

Skull essentially as in *pardicolor*, but decidedly larger in all dimensions.

Dimensions of the type:—

Head and body 380 mm.; tail 350; hind foot 68; ear 38.

Skull: greatest length 76 mm.; condylo-basal length 74; zygomatic breadth 36; interorbital breadth 12·5; breadth of brain-case 25; mastoid breadth 23·5; palatal length 34; front of canine to back of p^4 25; breadth between outer corners of p^4 20·5; length of bulla 14·5; p^4, length on outer edge 68.

While the lowland *Pardictis* closely agrees with true Nepalese *pardicolor*, this highland specimen shows such differences that I think it ought to be considered as representing a special subspecies, characterised by its paler colour and larger size.

18. CHROTOGALE OWSTONI Thos.

♂. 86 A. Skin without skull. Thaï-Niên. 300'.

Of all the Tonkin animals which it was desirable that examples, adult, with skulls, should be obtained, this remarkable carnivore takes the leading place, but fortune did not smile on Mr. Stevens's efforts, for the above native skin, with no skull, was the only specimen of it that he could procure, and I am therefore unable to furnish any further information about its cranial and dental characters. The genus and species were described * from a young specimen with milk-dentition, and from the very peculiar characters shown by this it is clear that much interest will attach to the adult when found.

* P.Z.S. 1912, p. 490.

But, none the less, this skin is of value, for it shows the coloration to be even more striking than was previously evident from the badly-prepared immature type, the face having a series of black and white stripes corresponding in position to those of *Hemigalus*, but narrower and more sharply contrasted, those above and behind the eye particularly clear and distinct. The nape-hairs, as in the type, are directed backwards, while in *Hemigalus* they slant forwards. The two black bands running down the sides of the nape are broad, black, and strongly contrasted, while the transverse dorsal bands are apparently one less than in *Hemigalus*, four on the back and one on the base of the tail, but these are probably variable in both animals. The fur throughout is longer and coarser than in *Hemigalus*, and the ground-colour lighter, so that all the markings are more strikingly contrasted.

19. Helictis taxilla, sp. n.

♂. 187 (3100'). ♀. 123 a (4000'). Ngai-Tio.

Smaller than *H. moschata*, the skull with low narrow brain-case and more slender muzzle.

Size, as gauged by skull, decidedly less than in *moschata* and *millsi*. Fur fairly well provided with underfur. General colour dark purplish grey, about as in *millsi*, but how far the drabby tone of the original specimens of *moschata* is due to bleaching, I am not at present in a position to say. Head-markings about as in *moschata*, but as usual widely variable. Under surface more fully whitish than in the allied species, with scarcely any darker tone at the bases of the hairs. Tail with its median area below definitely more whitish or buffy.

Skull small, narrow, less high throughout than in *moschata*, the brain-case especially low, narrow, and little inflated. Rostrum narrower than in the allied forms. Female skull equally with narrow rostrum, but the brain-case is more inflated. Bones of zygomata very slender; anteorbital foramina low. Posterior palatal tube markedly narrower than in *moschata*. Bullæ little inflated.

Teeth very small throughout, carnassial and molar decidedly smaller than in *moschata*, and still smaller than in *millsi*.

Dimensions of the type:—

Head and body 310 mm.; tail 148; hind foot 55; ear 30.

Skull: greatest median length 77·7 mm.; condylo-basal length 74; zygomatic breadth 40; breadth of muzzle across canines 12; interorbital breadth 18; breadth across postorbital projections 20; intertemporal breadth 16·5; breadth of brain-case 31; mastoid breadth 34; palatal length 33; breadth outside p^4 17·7; posterior palatal breadth 7·4; maxillary tooth-row 21·5; p^4 on outer edge 5·5.

The female skull is 69 mm. in condylo-basal length, and 32 mm. across the brain-case.

Hab. As above.

Type. Old male with well-marked ridges. B.M. No. 25.1.1.36. Original number 187. Collected 3 July, 1924.

The Ferret-badger of Tonquin seems to be fairly distinguishable from those of Assam and South-West China respectively by the small size and other characters of the skull above detailed. That of Eastern China (*ferreogrisea*) is the largest of all.

20. Petaurista lylei badiatus, subsp. n.

♂. 173. ♀. 123, 160. Ngai-Tio.

Essentially similar to true *lylei* of N. Siam, but the hoary character of the upper surface less developed, the general colour more strongly suffused with chestnut-rufous, and the parachute, especially posteriorly, almost wholly rufous. Other characters, and skull, as in *lylei*.

Dimensions of the type:—

Head and body 510 mm.; tail (imperfect, another specimen 435); hind foot 88; ear 51.

Skull: condylo-incisive length 74 mm.

Hab. Central Tonkin; type from Ngai-Tio.

Type. Adult female. B.M. No. 25.1.1.42. Original number 123. Collected 7 May, 1924.

Apparently constantly more rufous than the hoary typical form of this splendid Squirrel. The long ears with their ochraceous proectotes are as in *lylei*, in which connection I may note that this character is not observable in youth, two half-grown examples of *lylei*, one from N. Siam (Lyle) and one from near Raheng (Stockley), differing from adults by having brown proectotes, and also much more rufous wrists and parachute edges, and a greyer tail.

21. Belomys sp.

♂. 16. Bao-Ha. 250′ (without skull).

22. Callosciurus castaneoventris castaneoventris Gr.

♂. 50, 66. ♀. 60, 61. Thaï-Niên.

♂. 13, 25, 26, 34. ♀. 9, 10, 27. Bao-Ha.

In their valuable "List of Sciuridæ of the Oriental Region," 1918, Messrs. Robinson and Kloss pointed out that the type of Gray's *castaneoventris* (B.M. No. 72*a*) agreed (after a washing of its tail) with the form from Hainan, named by Allen *Sciurus erythræus insularis**, and deduced from this, not only that *insularis* was a synonym of *castaneoventris*, but that the type-locality of the latter was the island of Hainan.

Now, however, the discovery by Mr. Stevens of a similar Squirrel on the mainland invalidates the latter conclusion, and I have no doubt that Reeves's specimen, like his other mammals, came from the mainland of S.W. China, more or less in the region of Canton.

* Bull. Am. Mus. xxii. p. 473 (1906).

Fortunately, the British Museum contains examples from Hainan representing *insularis*, and, since there does not appear to be the slightest difference between these and the Tonkin specimens, the identification of *insularis* with *castaneoventris* is now confirmed.

Mr. Stevens's specimens form, therefore, a very acceptable addition to the Museum collection, as helping to clear up this doubtful question.

23. Callosciurus imitator, sp. n.

♂. 57, 59. Thaï-Niên. 300'.

A member of the *caniceps-epomophorus-concolor* group, very similar to *concolor*, but widely separated geographically.

Size as in *concolor*. General colour as in the warmer-tinted members of that species, e. g., *C. c. telibius*. Whole upper surface a warm ochraceous-cinnamon, the face and crown like the back, not greyer, as it usually is in *concolor*. Sides greyer, less cinnamon. Under surface blue-grey, as in *Tomeutes stevensi*, with scarcely a trace of the faint median darker stripe present in *concolor*. Ears like crown. Hands and feet grizzled grey, not becoming yellow terminally. Tail finely grizzled black and buffy, the hairs of the end forming a black, but not sharply-defined tassel, of which many of the hairs are ringed terminally with whitish. Skull about as in *concolor*, or even more broadly built, quite different from the comparatively delicate skull of *Tomeutes stevensi*. Nasals particularly broadly expanded anteriorly.

Dimensions of the type:—

Head and body 218 mm.; tail 195; hind foot 45; ear 19.

Skull: greatest length 52 mm.; condylo-incisive length 47; zygomatic breadth 31; nasals 17 × 9; upper cheek-tooth series exclusive of p^3 9·5.

Hab. as above.

Type. Adult male. B.M. No. 25.1.1.68. Original number 59. Collected 26 February, 1924.

This Squirrel presents a most remarkable and interesting problem when viewed in conjunction with the features of the *caniceps-concolor* group, indicated in the paper on them by Mr. H. C. Robinson and myself in 1921*. For the forms of that group were considered to be best sorted into three species, each with various subspecies, *caniceps* from north of 13°, *epomophorus* from between 13° and 7°, and *concolor* from south of 7°, all down the Malayan Peninsula and its adjacent islands. But here we have, in about N. latitude 22°, a Squirrel not like the nearer ones from north (and only a short way north) of 13°, but one so like *concolor* from the southern and most distant part of the chain, south of 7°, 15 degrees distant, with the whole of Siam between, as to be hardly distinguishable from it. Indeed, had the present animal come from the Malay Peninsula, one would

* Ann. & Mag. Nat. Hist. (9) vii. p. 118.

have had to go into very close details to show reason for separating it at all, while it has no resemblance whatever to *canicaps* and *epomophorus*, the allied forms geographically nearer. In addition, its superficial resemblance to the Assam *Tomeutes stevensi* is most striking, the two being barely distinguishable, except by the characters of the skull.

24. Dremomys rufigenis ornatus Thos.

♀. 24. Bao-Ha. 250'.
♂. 166. Ngai-Tio. 4800'.

The Ngai-Tio specimen is precisely like the type, believed to be from Möng-tze; the other is a little more saturate, tending to approach the subspecies *belfieldi*. A specimen of the same form was obtained by Mr. Kingdon Ward, at Chü-tun in Northern Yunnan in 1921, the range being therefore fairly considerable.

25. Tamiops inconstans Thos.

♂, 2, 8, 15, 18, 19, 22. ♀. 3, 5, 23. Bao-Ha.
♂. 53, 54. ♀. 55, 63. Thaï-Niên.

Quite agreeing with the typical specimens from Southern Yunnan.

26. Rattus edwardsi Thos.

♂. 150, 176. ♀. 147, 182, 183. Ngai-Tio. 4800'.

Agreeing nearly with Assamese specimens referred to *R. listeri*, but these giant Rats vary so much, and are so closely allied, that I propose to use the older name for the Tonkin specimens.

27. Rattus bowersi And.

♂. 131 (young), 132 (young). 181. Ngai-Tio. 4800'.

28. Rattus—R. rattus group.

Forty specimens from all three localities, apparently belonging to more than one race, but not at present determinable with certainty.

29. Chiromyscus (g. n.) chiropus Thos.

♂. 33. Bao-Ha. 300'.

This is a most valuable and interesting accession, as the "*Mus*" *chiropus*, which I described in 1891 * from a specimen obtained in the Karin Hills by L. Fea for the Genoa Museum, has never turned up since, and its characters were such as to render highly probable its generic distinction from other Rats.

* Ann. Mus. Genov. (2) x. pp. 884 and 935, pl. xi. figs. 4–7 (1891-92).

Thanks to the kindness of Dr. Gestro and Dr. de Beaux, I have now been enabled to have the loan of the original specimen, and find that Mr. Stevens's Tonkin example is unquestionably of the same species.

The study of the two specimens, one in spirit and the other in skin, confirms my supposition that the animal should be distinguished as a special genus, to which I would give the above name, and would diagnose as follows:—

General essential characters as in *Rattus*, but the feet specialized for climbing, the claws very short, surpassed by the pads, and the hallux widely opposable to the rest of the foot, so as to render the hind foot a "hand." Number of mammæ not known.

Skull as in *Dacnomys*, *Lenomys*, *Diplothrix*, and allied genera, with the supraorbital ridges much developed, overhanging the orbits, and forming distinct angular postorbital projections. Zygomatic plate little projected forwards.

Teeth not strongly zig-zagged as in *Dacnomys* and *Lenomys*, about as in *Diplothrix*, and therefore not very materially different from those of some members of *Rattus*, as is indicated in the description of the Liu Kiu animal *.

Genotype: *Chiromyscus chiropus* (*Mus chiropus* Thos.).

Apparently this genus is allied to *Diplothrix*, but is distinguishable by its more normal rat-like form, its reduced claws, and highly specialized opposable hallux.

Now that a well-prepared skin is available, I am able to record that the colour and general appearance are much more striking than was evident on the typical spirit-specimen. For not only is the dorsal colour a warm lined buffy, with the ochraceous lateral band originally mentioned, but the whole side of the cheeks is bright ochraceous, the ochraceous area passing up beyond and behind the ears, forming a bright-coloured patch almost unique in Muridæ, and reminiscent of some of the species of *Dremomys*. A rather darker ring around the orbit. Ears short-haired, flesh coloured. The rump, hips, and base of tail are also, like the ear-patches, rich ochraceous.

30. Mus dubius Hodgs.

♂. 97. ♀. 73, 78, 79, 108. Thaï-Niên. 300'.

31. Leggada pahari Thos.

♂. 127. Ngai-Tio. 4800'.

32. Micromys minutus Pall.

♂. 175. ♀. 142, 151. Ngai-Tio. 4800'.

33. Vandeleura dumeticola Hodgs.

♀. 96, 113. Thaï-Niên. 300'.

* J. Bomb. Soc. xxiv. p. 401 (1916).

34. Rhizomys senex Thos.

6 from Bao Ha. 300'.
18 from Ngai-Tio. 4800'.

The fine series of skulls contained in Mr. Stevens's collection is of interest as showing the degree of cranial variability that occurs in these animals. As a matter of fact, the variability is but slight, if care be taken to compare specimens of corresponding age; the condition of wear of m^3, rather than m^1, should be taken as the criterion of age. As usual with these animals, there is no sexual difference in size or other characters; the largest skull, that of a female, attains 71·3 mm. in condylo-incisive length, and the next, a male, 70.

All agree in their superiority in size over *R. pruinosus*, while the cranial differences which have induced the descriptions of the other members of the restricted group, *latouchei* and *pannosus*, appear to hold throughout, although *senex* is no doubt very closely allied to *latouchei*. *R. sinensis*, similar in size, appears to belong to another group, which also contains *R. vestitus*, *wardi*, and *davidi*. In addition to other characters, the vertically slender zygomata of *sinensis* readily distinguish it from all members of the *pruinosus* group, and show its alliance with the non-hoary Chinese species.

35. Atherurus stevensi, sp. n.

♀. 156. Ngai-Tio. 4800'. 8 June, 1924. B. M. No. 25.1.1.93. *Type*.

Distinguished by lighter belly, whitish wool-hairs on back, and by various skull-characters.

Size as in *macrourus*. General colour above about as in *A. macrourus*, or a little lighter; below very much whiter, the majority of the spines and hairs nearly white. Upper surface with much greater development of the close coat of wool-hairs beneath the spines, and these wool-hairs are almost completely white. In *macrourus* there are only a few brownish wool-hairs, and in *assamensis*, although there are more than in *macrourus*, they are still less than in *stevensi*.

Skull not of the peculiar narrow build of that of *A. assamensis*, its length and breadth about as in *macrourus*. It is, however, distinguishable from that by a number of slight but apparently constant characters, as follows:—Upper profile from crown to nasal tip quite straight, not convex or inflated. Muzzle more slender, the lateral profile slightly concave opposite the hinder end of the nasals. Nasal bones longer and narrower, less square, their posterior breadth less, their hinder edge projecting decidedly behind the premaxillary frontal processes; the latter tapering posteriorly, much narrower than in *macrourus*. Supraorbital edges parallel, without trace of postorbital processes. Malar

with less marked ascending postorbital angle. Palatal foramina divergent, longer, reaching back to the transverse suture. Posterior palate less cut out, the palation level with the junction of m^2 and m^3, instead of to the middle of m^2. Hamular processes large and sickle-shaped. Bullæ as in *macrourus*.

Incisors more proodont, their index in the type 93°. Molars apparently more bulky, but in the varying stages of wear this is difficult to be sure of.

Dimensions of the type:—

Head and body 525 mm.; tail 228; hind foot 75; ear 36.

Skull: greatest length 102 mm.; condylo-incisive length 95; zygomatic breadth 50; breadth of muzzle on premaxillary suture 21; nasals, greatest length 29·5, breadth anteriorly 15·5, in posterior third 12·5; hinder breadth of premaxillary processes 3; intertemporal breadth 29; mastoid breadth 34·7; palatilar length 44·4; palatal foramina 7; upper cheek-teeth 17·8.

Hab. and *Type* as above.

This Brush-tailed Porcupine is evidently quite a distinct species, its whitish belly, peculiar whitish wool-hairs at the base of the spines, and the various skull-characters above detailed readily distinguishing it from its two allies, *A. macrourus* and *assamensis*. The skull has been compared with that of the type of *A. assamensis* and with five good skulls of *A. macrourus* from Penang and the Malay Peninsula.

I have much pleasure in naming the species after its discoverer, Mr. Stevens, who has taken very great pains and interest in making the collection, and was much distressed at the abrupt and compulsory termination of his expedition.

22. The Development and Neuromery of the Mid-Brain and the Hind-Brain in *Sphenodon punctatus*.

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(Text-figures 1–21.)

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1. Introduction.

This paper records the results of an investigation of the development and neuromery of the mid-brain and hind-brain of *Sphenodon punctatus*. The same methods and material have been employed as in an earlier paper on the fore-brain of this reptile (Wyeth, 1924, *b*), in which I concluded that the fore-brain comprised a single primary neuromere from which three secondary definitive neuromeres were ultimately developed. No comprehensive account of the development of the brain of *Sphenodon* has yet been published, although that of certain isolated cerebral structures has been described by Osawa (1897–8), Dendy (1899, 1910), Gisi (1907), Elliot Smith (1919), Hines (1923), and in my own earlier papers. Gisi alone deals with the mid-brain and hind-brain, and she describes nothing earlier than Stage Q, and confines herself almost entirely to Stages S, T, and adult *Sphenodon*. Much has been written respecting the development and neuromery of the mid-brain and hind-brain in other vertebrates, but there appears to be no recent and complete account of the development of these structures from the time of their first appearance until they assume the adult condition. Most writers agree in dividing the mid-brain into two neuromeres (Orr, Hoffman, McClure, Locy, Hill, Johnston, Waters, Herrick, Reese, Warren, Bartlemez). Neal (in *Acanthias*), Froriep (in the Mole), and Zimmermann (in *Mustelus*, Chick, and Rabbit) find three mid-brain neuromeres, doubtless because they include the synencephalon, which is really a fore-brain structure. It is generally accepted that the hind-brain of Reptiles (Orr, Hoffmann, McClure), Birds (McClure), and Mammals (Zimmermann, Bartlemez) contains seven neuromeres. There is, however, considerable divergence of opinion as to the exact meaning to be attached to the term "neuromere," and also as to the segmental value of these structures. It seems desirable to indicate the significance of the terminology employed in this paper. Goodrich (1918) and de Beer (1922, 1924) have recently reviewed the evidence respecting the segmentation of the vertebrate head. The mid-brain and hind-brain region appears to comprise five head-segments, which are termed the premandibular, mandibular, hyoid, first post-hyoid, and second post-hyoid respectively. It appears that in *Sphenodon* and the Chick the head-region containing the fore-brain and lying in front of the premandibular head-segment is to be regarded as a prostomium, or acromerite (Brachet, 1921). A primary neuromere is regarded as the cerebral component of a head-segment, and may ultimately divide into two or more secondary neuromeres. The ultimate or definitive neuromeres may thus be either primary or secondary, and are numbered rostrocaudally as neuromeres I–XII. The fore-brain consists of a single primary neuromere, the prosencephalon, which divides into three secondary neuromeres. These are neuromeres I–III, and are termed respectively telencephalon, diencephalon, and

synencephalon (Wyeth, 1924, *b*). The single primary neuromere of the mid-brain divides into two secondary neuromeres. These are neuromeres IV and V, and are called the first and second mesencephalic neuromeres. The hind-brain appears to comprise four primary neuromeres, which in this paper are termed neuromeres A, B, C, and D. In an earlier paper (Wyeth, 1924, *b*), in order to avoid premature implications they were called "segments." In the youngest embryo examined neuromere D is only faintly indicated, and although this phenomenon may be peculiar to the individual specimen, it is to be observed that Bartlemez (1923) notes a similar feature in a two-somite human embryo. Neuromere A divides into three secondary definitive neuromeres (neuromeres VI, VII, VIII). Neuromere B, which remains undivided, is readily identified as the otic neuromere, which is therefore both primary and definitive (neuromere IX). Neuromere C divides into two secondary definitive neuromeres (neuromeres X, XI), while neuromere D remaining undivided is primary and definitive, and is identified as neuromere XII.

I desire here to record my gratitude to Professor Dendy, in whose laboratory this work has been carried out, for his valuable advice and criticism; also to Mr. C. Biddolph, of the Zoological Department of King's College, London, who prepared photographs of many of my models, which have been reproduced in the figures accompanying this paper.

2. The Development of the Mid-Brain and the Hind-Brain.

Stage D.

Embryo 58 was examined and modelled (text-fig. 1).

Mid-brain.—The mid-brain rudiment first appears as a large, oval, transversely-elongated, and somewhat shallow dilatation of the widely-open neural groove. The neural folds which ultimately form its lateral walls are very low and hardly distinguishable, and its rostral and caudal boundaries are indicated by two low transverse ridges, which separate it from the fore-brain and hind-brain rudiment respectively.

Hind-brain.—This region exhibits a series of three shallow transversely elongated oval dilatations, with faint indications of a smaller and caudalmost fourth, which are regarded as rudiments of primary neuromeres. Neuromere A is short and broad, neuromere B is considerably larger and deeper, and is the most conspicuous member of the series. Neuromere C is small, and neuromere D almost indistinguishable. Caudad of this the neural groove is much narrower, and two pairs of rudimentary somites are distinguishable, the whole embryo exhibiting a marked similarity to the two-somite human embryo described and figured by Bartlemez (1923, fig. 1).

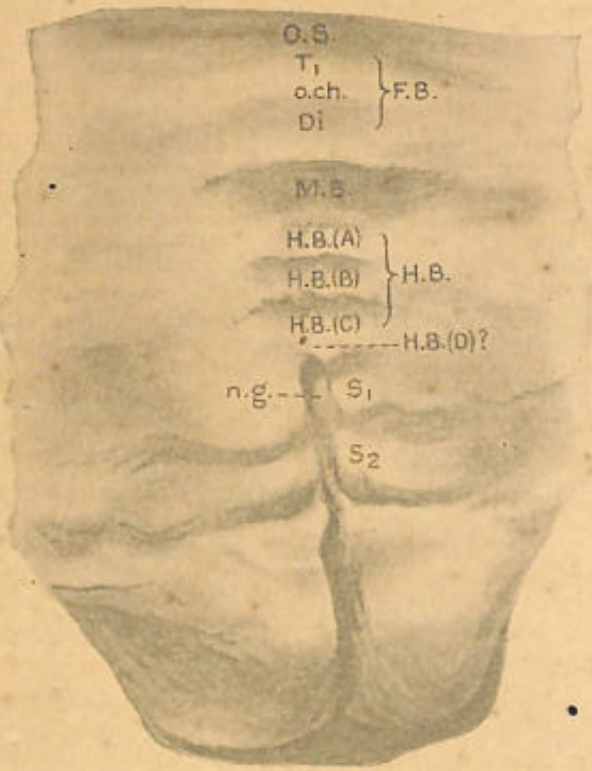
Stage E.

Embryos 56 and 64 were examined and modelled (text-figs. 2 and 3).

The dorsal growth of the lateral neural folds has caused the neural groove to become much deeper, and it is now open by only a narrow dorsal slit.

The *Mid-brain* is a large rounded vesicle, its caudal boundary

Text-figure 1.



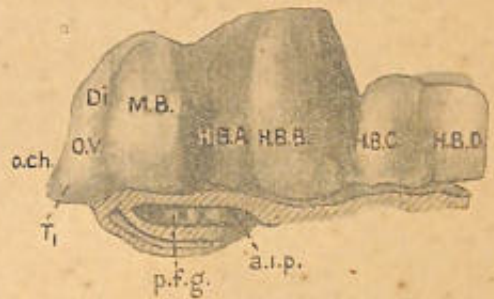
Sphenodon, Stage D, Embryo 58. Model, dorsal view (×100).

being indicated by a conspicuous internal ridge and corresponding external groove separating it from the hind-brain. The rostral boundary is similarly but less clearly indicated.

Hind-brain.—The rudiment of neuromere A is deep, but narrower than the mid-brain, its lateral walls being less convex and the cross-section of its cavity being U-shaped. Neuromeric

rudiment B is very conspicuous, deep, boldly convex laterally, and its neural folds are strongly developed. In the mid dorso-lateral region of the wall of this neuromere, in the angle included between the wall of the neuromere and the head epiblast, the otic primordium is visible as a low, inconspicuous, caudally-elongated

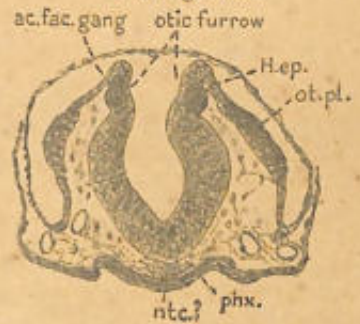
Text-figure 2.



Sphenodon, Stage E, Embryo 56. Model, left side of brain (red. to × 50).

thickening. The primordium of the otic disc appears as an ill-defined thickening of the head-epiblast in the same region, and extends somewhat further caudad. These structures have been identified in young human embryos by Wilson (1914) and Bartlemez (1922). The rudiments of neuromeres C and D are

Text-figure 3.



Sphenodon, Stage E, Embryo 56. Transverse section of hind-brain to show otic primordium and otic plate.

considerably smaller than the preceding, somewhat less clearly differentiated, and less boldly convex laterally (text-fig. 2).

Stage F.

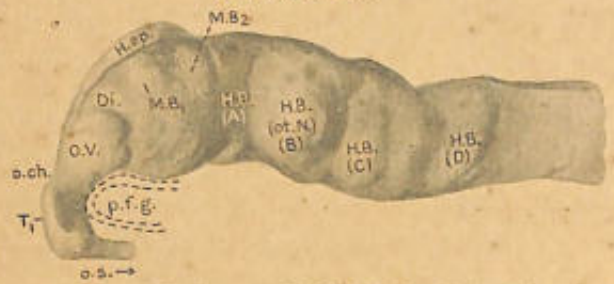
Embryos 61 and 72 were examined and modelled (text-fig. 4).

A cranial flexure has developed which involves and slightly distorts the mid-brain and the rostral half of the hind-brain.

The identification of the mid-brain and hind-brain regions is confirmed by the position of the apex of the cranial flexure, the rostral extremity of the pharynx, and the anterior portal aperture (Bartlemez, 1923).

Mid brain.—This is considerably larger and more spherical than in Stage E. In embryo 72 the boldly convex lateral walls of the mid-brain just fail to meet in the mid-dorsal line in the rostral region, but caudad of this they fuse dorsally, thus completing the mesencephalic roof. In the slightly older embryo 61 the roofing of the mid-brain is complete. The presence in the latter embryo of a low internal ridge crossing the middle of the floor of the mid-brain, and of a corresponding but less conspicuous external ventro-lateral groove, indicates the impending appearance of two approximately equal secondary neuromeres in the mid-brain.

Text-figure 4.



Sphenodon, Stage F, Embryo 61. Model, left side of brain (red. to × 50).

Hind-brain.—This is considerably elongated and approximately pyriform, tapering caudally into the narrow post-cephalic neural tube. Neuromere A is still short and cylindrical; neuromeres B and C are large and rounded, the former being the wider and more laterally convex. The otic primordium (acustico-facialis anlage) is now a well-marked eminence and extends throughout the whole length of neuromere B, and on the dorso-medial surface of the wall of the same region is a fairly wide ventricular groove, the otic sulcus, the whole appearance of this region being strikingly similar to that of the eight-somite human embryo described and figured by Bartlemez (1922, fig. 5). Neuromere D is short and cylindrical and less conspicuous than neuromere C. The inter-neuromeric grooves are now conspicuous.

Stage G.

Embryo 59 was examined and modelled (text-fig. 5).

The peculiar lateral and dorsi-ventral flexure of this embryo has previously been noted and figured (Wyeth, 1924, *b*).

Mid-brain.—Owing to the above-mentioned flexures this has

become somewhat wedge-shaped, with an elongated dorsal and shortened ventral surface. Two secondary neuromeres are now evident, these being rudiments of neuromeres IV and V.

Hind-brain.—The very strong cranial flexure has resulted in a shortening of neuromere A. Neuromere B is very conspicuous, and is separated from neuromere C by a well-defined inter-neuromeric groove. Neuromere C is large, rounded, and shows signs

Text-figure 5.

Sphenodon, Stage G, Embryo 59. Model, left side of brain (red. to × 50).

of impending division into a slightly larger rostral and a shorter and smaller caudal portion. These ultimately become neuromeres X and XI respectively (text-fig. 5, HBC_1, HBC_2). Neuromere D is larger and more rounded than it was during Stage F.

Stage H.

Embryo 78 was examined, but it differs so little from the specimen just described that any further reference to it is unnecessary, save to note that the otic disc is now slightly hollowed to form an incipient otic cup.

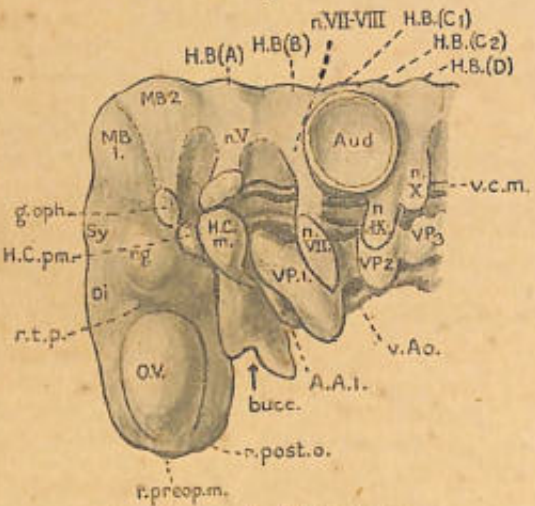
Early Stage J.

Embryos 44 and 46 were examined, and the former was modelled (text-fig. 6).

Mesencephalon.—This is very large and conspicuous, its roof forming a hemispherical dome, but owing to the very strong cranial flexure, the floor is short and inconspicuous, the neuromere thus being distinctly wedge-shaped. The syn-mesencephalic and rhombo-mesencephalic grooves are wide and deep. A shallow external groove, and a low internal ridge corresponding thereto, traverse the roof and sides of the mesencephalon, incompletely dividing it into two nearly equal portions. These are ultimately found to be two secondary definitive neuromeres, the first and second mesencephalic neuromeres, *i.e.* neuromeres IV and V, and for the sake of brevity they will so be termed. The roof and

walls of the mesencephalon are somewhat thickened, while its floor is relatively thin, but none of them as yet exhibits any histological differentiation. In the loose axial mesenchyme laterad of the floor of the mesencephalon appears the small oval premandibular head-cavity, and immediately morphologically dorso-laterad of this is a small oval mass of dense tissue, confluent laterally with an oval-thickened patch of head-epiblast. Comparison of this embryo with those of late Stage J and Stage K (text-fig. 7) indicates that these structures are the rudiments of a mesencephalic ganglion and placode respectively. A wide, but laterally flattened, strand of thickened periaxial tissue unites the ganglionic rudiment with the dorsal region of the mesencephalon.

Text-figure 6.



Sphenodon, Stage early J, Embryo 44. Model, left side of brain (red. to × 50).

This strand is evidently the primary cerebral connexion of the mesencephalic ganglion, and may be interpreted as the rudimentary ophthalmicus profundus neurencytium. Proximally it appears to be continuous caudally with the periaxial tissue of the neural crest of the rhombencephalon, and extends latero-ventrally to the mid-level of the brain-wall, its dorsal border being included within the angle between the brain-wall and the head-epiblast. It is very difficult to determine the exact extent of this periaxial tissue, but it can generally be distinguished from the looser axial mesenchyme around it by the more regular arrangement of its component cells. Both the ganglionic rudiment and the placode are much more clearly defined in the embryos of late Stages J and K.

Rhombencephalon.—Neuromere A is large and clearly defined, its roof and lateral walls being boldly convex and its somewhat shorter floor considerably less so. In the mesenchyme laterad of its floor occurs the conspicuous pyriform mandibular head-cavity (text-figs. 6, 7, 8). This is bounded by a single layer of flattened cells, and around it is the somewhat dense rudiment of mesoblastic somite 2. This is rather more conspicuous than the rudimentary mesoblastic somite 1, which is similarly situated relatively to the premandibular head-cavity noted above, from which cavity the mandibular head-cavity, owing to the habenular flexure, is separated by only a thin layer of mesoblast. Immediately dorsad of the mandibular head-cavity the head-epiblast exhibits an oval thickening and a thickened mass of periaxial tissue underlying it, and from the latter a thick sheet of periaxial tissue runs dorsally to terminate in the neural crest of the neuromere. These structures are more conspicuous than those previously described in the mesencephalic region, and evidently constitute the rudiments of the trigeminal placode, ganglion, and nerve-trunk. At the mid-level of the brain-wall the trigeminal primordium is continuous rostrally with the mesencephalic neural crest, and caudally with the less conspicuous neural crest of neuromere B.

Neuromere B is slightly larger than neuromere A, its floor being more conspicuous than that of the latter, and its walls and roof slightly more convex. This neuromere does not now, or subsequently, show any signs of differentiation into secondary neuromeres. It is evidently both primary and definitive, and is to be identified as neuromere IX—the otic neuromere. From its rudimentary neural crest, which is low, thick, and somewhat laterally situated, there extends a stout laterally-flattened strand of dense periaxial tissue. The middle portion of the caudal region of this tissue is in contact with the rostral border of the auditory pit, and its ventro-lateral portion terminates in contact with a well-defined thickened patch of head-epiblast, the ventral border of which is in contact with the extreme latero-dorsal border of the first visceral pouch (text-fig. 6). This epiblastic patch is evidently the rudimentary facial placode, and the strand of periaxial tissue is the rudimentary acustico-facialis neurencytium, the dorso caudal portion of which extends caudally into the rostral region of neuromere C, forming a mass of rudimentary auditory neurencytium included between the brain-wall, the head-epiblast, and the dorso-medial surface of the auditory pit. The neural crest in this region is reduced to a very thin layer of periaxial cells which never rises dorsally above the level of the general surface of the neuromere.

Neuromere C is clearly differentiated into two secondary definitive neuromeres—neuromeres X and XI, the walls of these being moderately convex, and the former is slightly longer than the latter neuromere. Neuromere D is short and cylindrical, and never shows any sign of division into secondary neuromeres.

It is therefore both primary and definitive, and is identified as neuromere XII. The neural crest throughout neuromeres XI and XII is fairly conspicuous, and is continuous with the less developed crest of neuromere X.

'In neuromere XI it gives off latero-ventrally a somewhat ill-defined periaxial strand, which terminates distally in contact with the extreme dorso-lateral border of the rudimentary second visceral pouch; and although the head-epiblast in this region appears to be slightly thickened, there is as yet no definite placode. The dorso-caudal border of the periaxial strand is in contact with a less clearly-defined and shorter extension of the neural crest of neuromere XII (text-fig. 6). Examination of older embryos makes it evident that the periaxial tissue of neuromere XI must be identified as the rudiment of the glosso-pharyngeal, and that of neuromere XII as the vagus neurencytium; but as the strands are confluent, the exact boundaries of these neurencytia cannot be determined at this stage of development.

Late Stage J.

Embryo 79 was examined and modelled, but it differs so little from that last described that only the following points need be noted :—

Mesencephalon.—Neuromeres IV and V are more clearly differentiated and dorso-laterally convex, the general configuration of the fore-brain and mid-brain of this embryo suggesting that considerable rostral development has occurred. The mesencephalic neural crest and periaxial tissue have considerably diminished; and although the mesencephalic placode and ganglionic rudiment are more conspicuous, and the latter appears to have undergone slight caudal elongation towards the trigeminal ganglion, the periaxial strand connecting the mesencephalic ganglion with the mesencephalic neural crest has almost disappeared, the appearance suggesting that it has been reduced in a rostro-caudal direction. The periaxial tissue and neural crest between the mesencephalic and rhombencephalic regions have been much reduced.

Rhombencephalon.—Neuromere A now shows traces of impending division into three secondary definitive neuromeres, and in Stage K these are clearly differentiated, and can be identified as neuromeres VI, VII, and VIII. The trigeminal neurencytium is conspicuous, and can be clearly distinguished from the surrounding mesenchyme, the cells of which are sparsely scattered and fusiform, while those on the neurencytium are much more closely packed, with conspicuous oval nuclei and scanty cytoplasm. These cells are evidently similar to the "α-neuroblasts" of Cameron and Milligan (1910). The acustico-facialis neurencytium is clearly defined, and the glosso-pharyngeal rudiment is well developed. Possibly owing to the commencing development

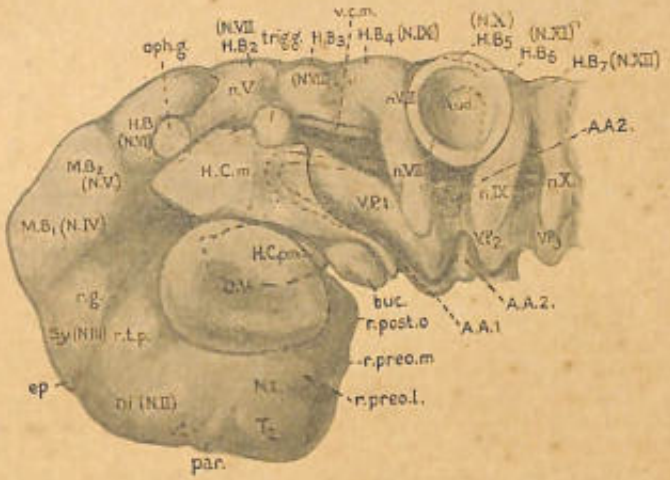
of the third visceral pouch, the ventro-lateral and caudal part of the vagus neurencytium is more developed than was the case in the younger embryo, and has thickened laterally so that a distinct groove appears between its distal extremity and that of the glossopharyngeal neurencytium, from which, however, it is not yet separated.

Stage K.

Embryo 39 was examined and modelled (text-fig. 7).

It is considered that the structure of this embryo is sufficiently indicated in the figure; no general account of it seems necessary. The mesencephalic ganglion has lost its original connexion with the neural crest, which has now entirely disappeared from the

Text-figure 7.



Sphenodon, Stage K, Embryo 39. Model, left side of brain (red. to × 50).

mesencephalic region, and the ganglion has acquired a secondary cerebral connexion by uniting caudally with the rostral border of the trigeminal neurencytium. The stout cylindrical neuroblastic strand by which these two structures are united is evidently to be identified as the rudiment of the ramus ophthalmicus profundus, which persists in adult *Sphenodon*. The second visceral pouch is well developed, the third somewhat less so, and the glossopharyngeal and vagus neurencytia are separated distally, each forming a stout elongated cylindrical neuroblastic mass, the proximal parts of which are still united.

During the subsequent stages of development the cranial nerves will be figured, but only briefly noted, as the development of some of them has been described in an earlier paper (Wyeth, 1924, *a*; nerves VII–XII), and that of the others is discussed in Section 3 below.

Stage L.

Embryo 50 was examined and modelled (text-fig. 8).

A comparison of text-fig. 8 with those preceding and following it shows that the definitive neuromeres of the mid-brain and the hind-brain are more clearly differentiated than they are during any other stage of development, and that between early Stage J

Text-figure 8.

Sphenodon, Stage L, Embryo 50. Model, left side of brain (red. to × 50).

and late Stage N the general proportions and contours of the mid- and hind-brain regions undergo little modification. In the mesencephalic region the oculomotor nerve appears as a stout neuroblastic strand issuing from the floor of the mid-brain just laterad of the middle line, and passing laterad of the pre-mandibular head-cavity and mesoblastic somite 1 appears to enter a ciliary ganglionic rudiment, and immediately disappears in the adjacent mesenchyme. The ophthalmic (mesencephalic) ganglion lies dorsomedial of the mandibular head-cavity and mesoblastic somite 2, and from it pass two rostrally-directed neuroblastic strands which almost immediately disappear in the mesenchyme.

The Gasserian (trigeminal) ganglion gives off latero-ventrally, and laterad of the mandibular head-cavity, two trigeminal nerve-trunk rudiments, the more caudal of which can be traced into the mandibular arch. The acustico-facialis neurencytium has differentiated into a large proximal auditory ganglion and a smaller distal facial or geniculate ganglion, the ventral surface of the latter lying against the dorso-lateral border of the 1st visceral pouch, and from it are given off short pre-trematic and post-trematic nerve rudiments. Nerves VII–X have been fully described in an earlier paper (Wyeth, 1924, *a*).

Stages N and O.

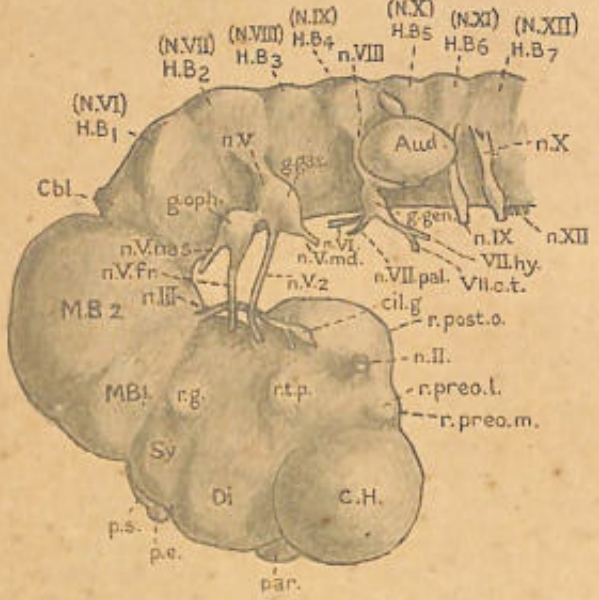
These stages of development may conveniently be considered together, since during the period included within them the development and growth of the mid-brain and hind-brain make little progress.

Stage N, Embryo 14 *a* and **Stage N–O**, Embryo 24 *a* were examined. The former was modelled, and is shown in text-figs. 9 and 10, and the latter is figured by Dendy (1910, text-fig. 1).

The *Mesencephalon* is ovoid in shape, its more bluntly convex surface being caudally situated, while along the mid-dorsal line the two lateral surfaces meet to form a sharp roof-ridge, which is characteristic of this period of development, the roof along this line being much thinner than are the walls of the remainder of the mesencephalon, these having undergone considerable thickening since Stage L. The second mesencephalic neuromere (neuromere V) is about twice as long and wide as neuromere IV. In the mesencephalic floor the pedunculi mesencephali appear, having apparently been formed by a caudal extension of the pars ventralis thalami. The rudiment of the oculomotor nucleus can be distinguished as an oval mass of dense tissue in the mesencephalic floor just laterad of the middle line, and immediately caudad of it appears the caudally elongated ansulate commissure. The inter-mesencephalic boundary is less conspicuous than in Stage L, and the very pronounced habenular flexure has caused the first mesencephalic neuromere (neuromere IV) to become wedge-shaped, with a dorsally convex roof and much shorter floor. In the rostral part of its roof, immediately above the ependyma, appear the developing fibres of the posterior commissure (text-fig. 10). In sagittal section the commissure is seen to be composed of a larger oval caudal portion, the lamina commissuralis mesencephali—the rostral border of which forms the syn-mesencephalic boundary in this region—and a flatter and smaller rostral portion, the lamina commissuralis synencephali, which lies in the roof of the synencephalon.

The large second mesencephalic neuromere is similar in shape to that previously described, but its walls and roof are somewhat thicker and more convex. It is divided from the rhombencephalon by the wide and deep transverse mesen-rhombencephalic

Text-figure 9.



Sphenodon, Stage N, Embryo 14 *a*. Model, left side of brain (red. to × 20).

Text-figure 10.

Internal view of same (red. to × 20)

fold. The roof and walls of the mesencephalon consist of a layer of tall, narrow, columnar, ependymal epithelial cells, external to which lie a number of closely-packed cells with scanty cytoplasm and conspicuous oval nuclei, the arrangement of which suggests that the wall consists of four or five layers of somewhat narrow and radially-elongated cells.

Rhombencephlon.—The cerebellum now appears as a dorsal and lateral expansion of the first neuromere of the hind-brain (neuromere VI), and is set almost at right angles to the longitudinal axis of the hind-brain, its walls being of similar structure to, and almost as thick as those of the mid-brain. The rhombencephalic roof consists of a single layer of flattened epithelial cells, and is flattened and thrown into a number of low irregular folds which appear to be artifacts. The rhombencephalon is approximately rectangular, its length being about two and half times its depth and width, and its cross-section is nearly circular, but its cavity is pyriform in cross-section owing to a thickening of the latero-ventral walls. The neuromeric segmentation is much less distinct than it was during Stage L, but it is still just to be discerned in the dorso-lateral zone. The roots and proximal portions of the cranial nerves are shown in text-fig. 9. Nerve VI now appears for the first time, and a group of nerve-rootlets which are evidently the rudiments of nerves XI and XII can be seen. It is to be noted that, with the exception of nerves III, VI, and XI–XII, the nerve-roots are still dorsal in position, although the ventral displacement, which is a feature of their ontogeny, has already begun, especially as regards nerves V, VII–VIII, and IX.

Stages P, P–Q, and Q.

The period between Stages N–O and P is one during which the mid-brain and hind-brain have undergone very considerable growth and development. After Stage P, until Stage R is reached, there is little increase in the dimension of these structures and little progress in their development. The chief phenomena occuring during the period included between Stages N–O and R are:—

1. The dimensions of the second mesencephalic neuromere are doubled, while those of the first mesencephalic neuromere remain practically unchanged.
2. First appearance of the rudiment of the sub-commissural organ as a pair of bilaterally-arranged dorsal evaginations of the central cavity of the first mesencephalic neuromere. These ultimately become a pair of longitudinal grooves on the inner surface of the rostral part of neuromere, and are situated just laterad of middle line.
3. Rapidly increasing histological differentiation within the brain-wall, and appearance of main fibre-tracts and nuclei of the cranial nerves.

4. First appearance of the trochlear nerve.
5. Rapid development of the cerebellum, epencephalon, and choroid plexus of the fourth ventricle.

For the sake of brevity, and because the conditions are so similar during Stages P, PQ, and Q, a few details only of Stages P and Q are given, but the mid-brain and hind-brain of Stage PQ, Embryo 51 *a*, which may be considered to be typical of the whole period, are described in detail.

Stage P.

Embryo 45 *a* was examined and modelled (Wyeth, 1924, *b*, text-fig. 20).

The first mesencephalic neuromere is less conspicuous than formerly, and now occupies only the rostral fifth of the mid-brain, appearing as an inconspicuous wedge-shaped segment with a low convex roof. The second mesencephalic neuromere is about twice as long and wide as it was during Stages N–O, and its rostro-lateral surface is more convex and is slightly extending forward to encroach upon the caudo-lateral region of the first mesencephalic neuromere. The roof-ridge is still prominent, although distinctly less so than it was during Stages N–O, while the caudal part of the neuromere is elongated slightly to overhang the deep mesen-rhombencephalic fold. In this region the roof-ridge has disappeared, but the differentiation of the neuromere into the two optic lobes is not yet apparent. The cerebellum is considerably developed dorsally, and in the middle part of the tectum rhombencephali appears a shallow transverse fold—the rudimentary infold of the choroid plexus of the fourth ventricle. In other respects this embryo differs little from that next to be described.

Stage PQ.

Embryo 51 *a* was examined and modelled (text-figs. 11 and 12).

Mesencephalon.—There has been a further rostro-lateral extension of the second mesencephalic neuromere, its encroachment upon the first mesencephalic neuromere masking the caudo-lateral surface of the latter and practically obliterating the external mesencephalic groove in this region. In, and immediately laterad of, the mid-dorsal line the rostral development of the second mesencephalic neuromere has caused a rostro-caudal compression of the roof of the first mesencephalic neuromere, the dorsal surface of which becomes more convex. The inter-mesencephalic groove is visible externally in only the dorsal and dorso-lateral regions, but the internal inter-mesencephalic ridge is still conspicuous, especially in the roof- and floor-regions (text-fig. 12). The first mesencephalic neuromere is about one-fourth as long and two-fifths as wide as the second mesencephalic neuromere, and its roof and lateral walls are somewhat thickened, possibly owing to the rostral

pressure exerted by the rapidly-extending second mesencephalic neuromere. In text-fig. 11 the rostral extremity of the model of this embryo has been slightly rotated laterad, in order fully to expose the lateral wall of the first mesencephalic neuromere, much of which would otherwise have been hidden by the rostro-lateral convexity of the second mesencephalic neuromere. The posterior commissure has considerably thickened since Stage N–O, and is extending both caudally and rostrally. The lamina commissuralis mesencephali is thicker and larger than the lamina commissuralis synencephali, and the rostral

Text-figure 11.

Sphenodon. Stage PQ. Embryo 51 *a*. Model, left side of brain (red. to × 20).

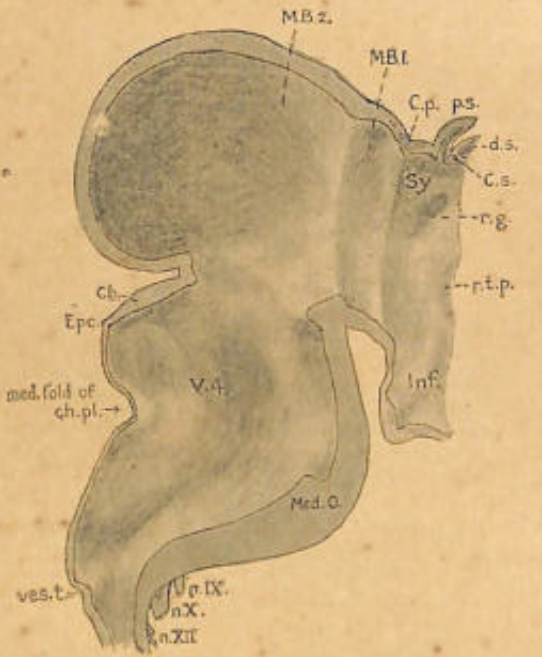
extremity of the latter is now joined by the nerve-fibres of the tractus pinealis, while a caudal extension of the lamina commissuralis mesencephali almost reaches the inter-mesencephalic boundary.

The *Subcommissural Organ* is now a pair of rather wide shallow longitudinal grooves on the internal surface of the roof of the first mesencephalic neuromere, each being situated just laterad of the middle line and traversing nearly the whole length of the neuromere. The walls of the grooves are lined by columnar epithelial cells somewhat taller than those of the adjacent regions.

During Stages PQ and Q the grooves are very obviously paired rostro-caudally elongated dorsal evaginations of the central cavity of the first mesencephalic neuromere, and appear to be serially homologous with the members of the dorsal series of paired diverticula of the central cavity of the fore-brain (Wyeth 1924, *b*). The question of this apparent serial homology is fully discussed in Section 4 (B) below.

Rhombencephalon.—The form and extent of this is indicated in text-figs. 11 and 12. The boundary between the mesencephalon

Text-figure 12.



Internal view of same (red. to × 20).

and the rostro-lateral border of the cerebellum is marked by a low, rounded, transverse ridge which almost disappears in the middle line. This is the fold of the velum medullare anterius (text-fig. 11), within which have developed the fibres of the trochlear nerve, while slightly caudad of these are the fibres of the decussatio veli. Gisi (1907, fig. R) shows in an embryo which she assigns to Stage Q (*cf.* fig. 13) a wide lumen included between the tall walls of this fold, the apex of which is nearly level with the apex of the cerebellum. In none of the embryos I have examined have I found this lumen, nor is the

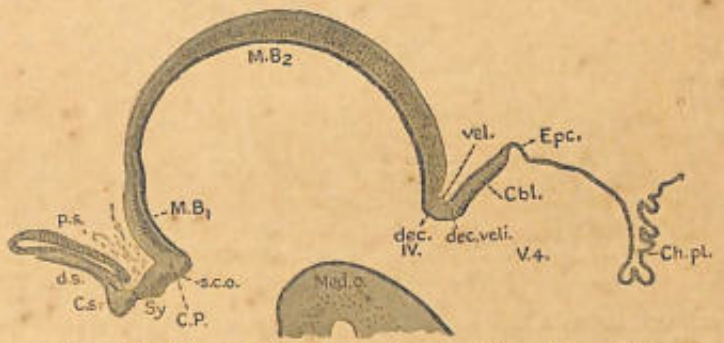
ridge very conspicuous. In Stage P it is hardly visible, and in Stage R it has almost disappeared. The cerebellum is still small, better developed laterally than dorsally, its rostral surface somewhat convex, its lateral angle prominent, and its dorsal border nearly disappearing in the middle line. The central portion of its wall is much thickened, but thins rapidly towards the periphery. The tegmentum rhombencephali is dorsally convex, and a transverse epencephalic fold slightly overhangs the dorsal border of the cerebellum. Immediately laterad of the transverse median fold of the choroid plexus the rudimentary lateral fold bulges into the cavity of the fourth ventricle. On the external surface of the lateral wall of the rhombencephalon a low rounded tuberculum trigemini and a similar but less conspicuous tuberculum acustici appear just dorsad of the roots of nerves V and VII–VIII respectively.

Stage Q.

Embryo 52 *a* was examined and modelled.

There has been little developmental progress since Stage PQ. The roof of the first mesencephalic neuromere is somewhat less extensive and less convex, and the inter-mesencephalic groove is less distinct. The posterior commissure is thicker, has extended

Text-figure 13.

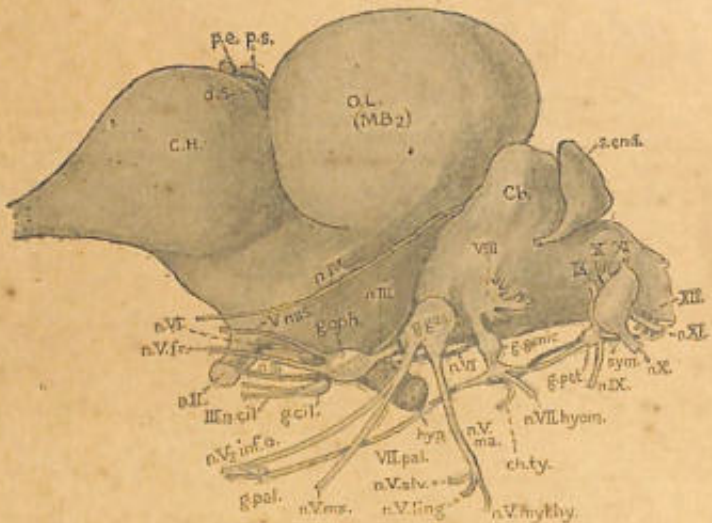


Sphenodon, Stage Q, Embryo 52 *a*. Approximately median sagittal section of mid-brain region.

further both rostrally and caudally, and bulges ventrally into the mesencephalic cavity. The subcommissural organ is more clearly defined, its characteristic epithelial cells being taller and the limits of their distribution being more clearly visible (text-fig. 13). The thickening of the epithelium has not yet obliterated the traces of the original bilateral and evaginated character of the organ. The second mesencephalic neuromere is somewhat more spherical, its total wall-surface being slightly increased.

The medial sagittal constriction which defines the medial surface of the optic lobes during the closing stages of development has now begun to operate, and this, together with the continued growth and increasing convexity of the walls of the neuromere, has caused the dorso-lateral surface of the neuromere to rise on each side of the mid-dorsal line to a level slightly above that of the now inconspicuous roof-ridge. The brain-wall is slightly thicker and its histologically differentiated layers are more distinct. Gisi (1907) gives an account of the histological features of the walls of the mid-brain and hind-brain in adult *Sphenodon*, and of the distribution of the chief cranial nuclei

Text-figure 14.



Sphenodon, Stage R, Embryo 142. Model, left side of mid-brain and hind-brain (red. to × 20).

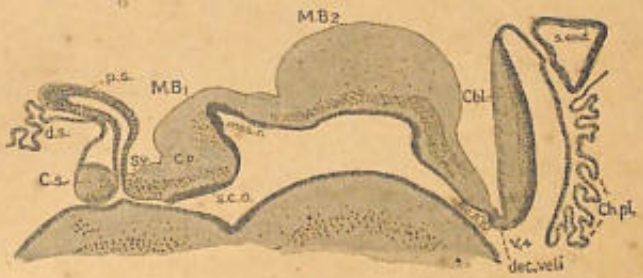
and nerve-tracts therein. Unless otherwise stated in the later sections of this paper, my observations concerning these structures agree with hers, and further description is unnecessary. The results obtained are in general agreement with those described by Kappers (1921, p. 857, and fig. 448, p. 841). The corpora posteriora, cerebellum, and epencephalon are better developed than in Stage PQ. In the walls of the choroid plexus a number of secondary folds, radiating medially, rostrally and caudally from the main lateral fold, give to the plexus a characteristic fan-like appearance. Caudad of the plexus the rhombencephalic cavity slightly dilates to form a pyriform vesica terminalis, the caudal apex of which slightly overhangs dorsally the rostral extremity of the myelencephalon.

Stages R, S, and Adult *Sphenodon*.

Stage R.

Embryos 142 and 162 were examined and the former was modelled (text-figs. 14 and 15).

Text-figure 15.



Sphenodon, Stage R, Embryo 142. Medial sagittal section, mid-brain (red. to × 25).

Stage S.

Embryos 9 *a* and 11 were examined and the latter was modelled (text-fig. 16).

Adult *Sphenodon*.

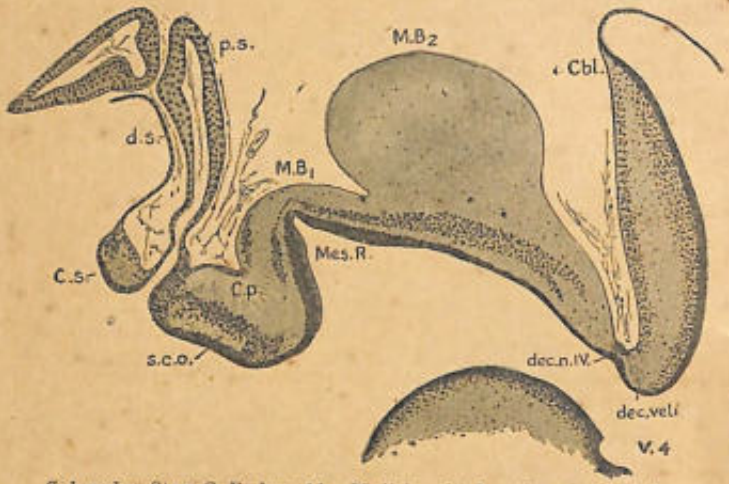
The head and neck of a specimen were dissected, and sections of Nos. I and V were examined (text-figs. 20 and 21).

For the purpose of the present paper the general morphology of the mid-brain and hind-brain during the closing stages of development does not exhibit any features of great importance. Gisi (1907, Sect. III) has given an account of the general morphology of the brain of *Sphenodon* during Stages R, S, and adult condition. Dendy (1910) has described the pineal region and the subcommissural organ, and I have described (Wyeth, 1924, *a*) the development of the auditory region and associated structure. Any additional account of these structures would therefore appear to be unnecessary. Only those features which have not been previously described, or which are germane to the question of the neuromery of this region, will therefore be noted.

The long axis of the mid- and hind-brain region still retains its somewhat open S-shaped flexure, so that the rostral portion of the hind-brain is overlapped dorsally by the caudal part of the mid-brain. The rostral part of the optic lobes overlie the first mesencephalic neuromere; but if the former be removed, the dome-shaped roof of the latter can be clearly distinguished.

In sagittal sections of Stages R, S, and adult *Sphenodon* (text-figs. 15, 16, and 17) the inter-neuromeric boundary is conspicuous, and in Stage S, owing to the straightening out of this region, the

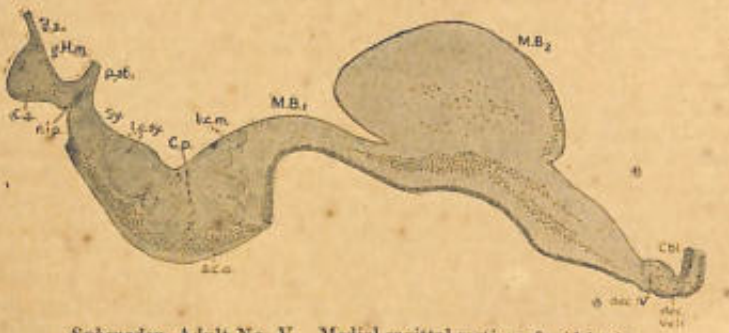
Text-figure 16.



Sphenodon, Stage S, Embryo 11. Medial sagittal section of mid-brain.

length of the first neuromere is approximately equal to that of the sagittal or stalk region of the optic lobes. The division of the mesencephalon into two secondary definitive neuromeres is thus distinguishable even in the adult condition; but practically

Text-figure 17.



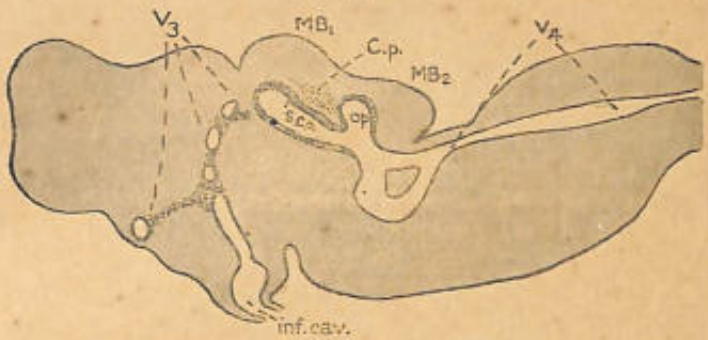
Sphenodon, Adult No. V. Medial sagittal section of mid-brain.

all external traces of the neuromeric segmentation of the hind-brain have disappeared after Stage R, in which the condition of this region is essentially similar to that obtaining in adult *Sphenodon*.

3. The Development, Distribution, and Nuclei of the Cranial Nerves of the Mid-Brain and the Hind-Brain.

The distribution of the cranial nerves in *Sphenodon* has been briefly described by Osawa (1898), and some of them by Schauinsland (1900), while Gisi (1907) describes nuclei and nerves in embryos of Stages S and T, and in adult *Sphenodon*.

Text-figure 18.



Myxine glutinosa. Medial sagittal section of brain.

I am able generally to confirm the observations of these authors, and in an earlier paper (Wyeth, 1924, *a*) I have described the development and distribution of nerves VII–XII. The present

Text-figure 19.

Bdellostoma stouti. Medial sagittal section of brain.

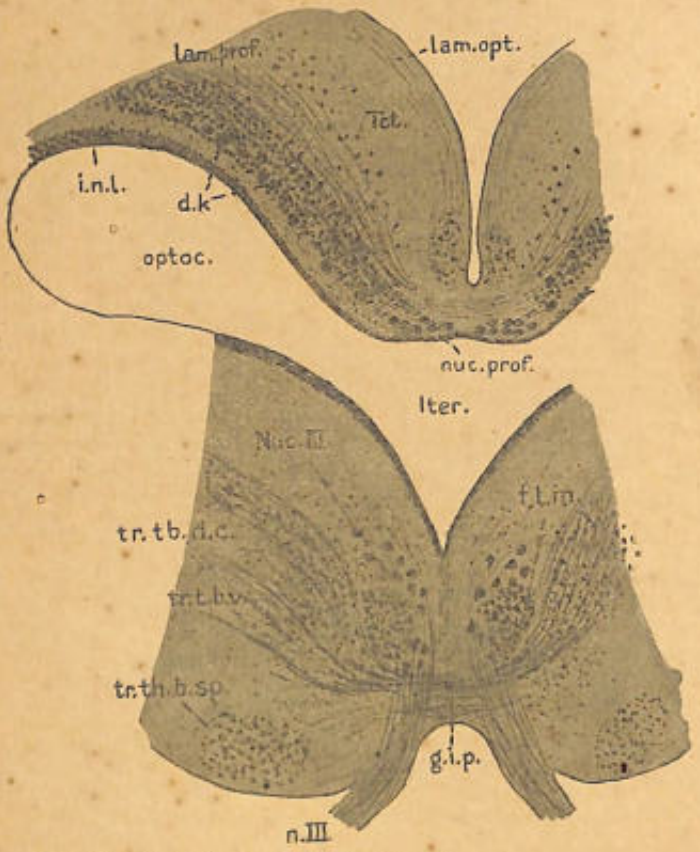
section therefore deals only with the development and distribution of nerves III–VI and their nuclei, and with the palatine branch of nerve VII.

Nerve III. (*Oculomotor nerve*).

The first appearance of this nerve as a stout neuroblastic strand springing from the mesencephalic floor and dividing into a very short lateral branch which enters the rudimentary ciliary ganglion,

and into a medial branch which disappears in the adjacent mesenchyme, has already been noted (p. 518), as has also the first appearance of the oculomotor nucleus in Stage N (p. 519). From the ventral surface of the nucleus the developing nerve-trunk, which now contains a number of nerve-fibres, passes latero-ventrally to emerge from the ventral surface of the mesencephalon.

Text-figure 20.



Sphenodon, Adult No. I. Transverse section through mid-brain to show profundus nucleus, dachkern, oculomotor nucleus, and roots (× 20).

It passes ventrally and slightly laterally; then continuing medially and rostrally, it passes mediad of the developing rami nasalis and frontalis ophthalmici, and of the second or infra-orbital branch of the trigeminus, which lies considerably laterad of the preceding rami. It then bears laterally on a short branch

(the ciliary ganglion), and its main trunk runs rostro-dorsally to a point slightly caudad and ventrad of the optic stalk, where it disappears in the surrounding mesoblast, from which the eye-muscles of the premandibular head-segment are ultimately formed. From the latero-dorsal surface of the rostral portion of the ciliary ganglion emerges a fine nerve-twig, which passes dorsally and slightly laterally and almost immediately disappears. This is the rudiment of the ramus ciliaris of the oculomotor nerve. The general condition and relationships of the nerve during Stage PQ, which are typically of the conditions obtaining during Stages P, PQ, and Q, are sufficiently indicated in text-fig. 11, and do not appear to need description. During and after Stage Q the oculomotor ganglion is conspicuous, becomes somewhat laterally flattened, and is situated immediately mediad and dorsad of the fasciculus longitudinalis medialis (text-fig. 20). In Stage S, and in adult *Sphenodon*, it consists of two laterally-flattened oval groups of large multipolar ganglion cells, a smaller dorso-rostral and a larger ventro-caudal group, the two groups being connected by a narrow intermediate tract of cells. From the nucleus the oculomotor fibres run ventrally and slightly rostrally near the middle line, curve slightly laterad as they cross the decussating fibres of the tractus tecto-bulbaris, and then leave the brain-floor as a strong rostrally and latero-ventrally directed nerve-trunk. The conspicuous ganglion inter-pedunculare separates the oculomotor nerve root from its fellow of the opposite side. The emergent fibres leave the brain-floor at the level of the rostral third of the nucleus. From the caudal part of the nucleus a number of fibres cross the middle line at the ventral border of the decussatio tecto-bulbaris, and enter the oculomotor root of the opposite side, as already noted by Gisi (*op. cit.*). The oculomotor nerve passes mediad of the ophthalmic ganglion from a position dorso-mediad to ventro-rostrad of this ganglion and then bifurcates (text-fig. 14), a laterally-directed and rather short ramus ciliaris oculomotorius passing into the ovoid ciliary ganglion. In the adult this ganglion is rostro-caudally elongated and club-shaped. The ramus ciliaris leaves the latero-rostral surface of the ganglion, and runs rostrally and somewhat laterally to a point immediately caudad and ventrad of the junction of the optic nerve with the eyeball. Here it divides into two fine branches, one of which turns abruptly laterad to pierce the sclerotic coat of the eyeball, while the other passes immediately ventrad of the optic nerve, and then turns laterad to pierce the sclerotic coat immediately rostrad of the optic nerve. The main oculomotor trunk passes rostrally and medially, remaining near the middle line. Just before reaching the optic nerve it divides into three branches. The most dorsad of these branches runs dorsally and laterally, and is distributed to the superior rectus muscle. The second branch passes medio-ventral to the first, passes ventrad of the optic nerve, and divides into two branches, of which the

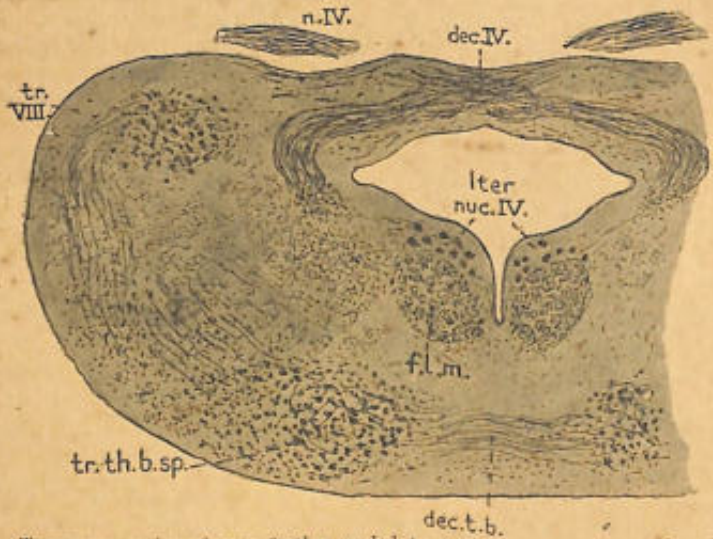
dorsal is distributed to the rectus internus muscle, and the ventral to the inferior rectus muscle. The third or most ventral of the original rami bends laterad of the second, passes between the rectus internus and rectus inferior muscles, and is distributed to the inferior oblique muscle.

In her plate i. fig. 3, Gisi (1907) shows the oculomotor nerve and ciliary ganglion lying dorsad of the ophthalmic ganglion in an embryo of Stage S, but in her fig. 2 of an adult specimen the ciliary ganglion lies ventrad of the ophthalmic ganglion and nerve, and the ciliary branch from the latter enters the dorsal surface of the ciliary ganglion. In all the specimens of Stages R, S, and adult *Sphenodon* which I have examined, the ciliary ganglion is thus ventrally placed, and the ciliary branch from the ophthalamic nerve enters the latero-dorsal surface of the ciliary ganglion. The difference of relative position in Stage S and adult *Sphenodon* shown by Gisi did not exist in these specimens.

NERVE IV. (*Trochlear nerve*). (Text-figs. 11, 14, 21.)

This nerve first appears during a late stage of development (Stage O–P) as a fine strand of neuroblastic tissue, somewhat

Text-figure 21.



Transverse section of same, further caudad, to show nucleus and decussation of trochlear nerve (× 20).

laterally compressed and issuing from the surface of the velum medullare anterius slightly laterad of the middle line; it curves laterally and slightly caudally, and then passes laterad and ventrad

of the mesoblast of the mandibular somite, and continuing its rostral course, passes laterad of the oculomotor nerve-trunk almost immediately after the latter emerges from the floor of the mid-brain. During Stage PQ, nerve-fibres appear in the trochlear trunk, and the decussation of the pair of nerves can be distinguished. The trochlear nucleus is first clearly distinguishable during early Stage R, during which and subsequent stages of development the nerve-fibres can readily be traced from the decussation into the nucleus, which extends slightly rostrad of the level of the root exit. The nucleus consists of a small compact rounded group of large multipolar ganglion cells, ten to fifteen of which appear in a cross-section (text-fig. 21). The nucleus lies immediately dorsad of the fasciculus longitudinalis, and between it and the wall of the iter, the cavity of which in this region is prolonged to form a pronounced ventral sagittal fissure separating the nucleus and fasciculus from their fellows of the opposite side. From the caudal extremity of the nucleus the trochlear nerve-fibres emerge ventro-laterally, but meeting the medial surface of the tractus tecto-bulbaris, they somewhat abruptly change direction, and curve dorso-laterally and slightly caudally around the ventricular cavity to decussate in the roof of the brain (text-fig. 21). After decussation the nerve runs laterally around the caudal surface of the base of optic lobe (text-figs. 11 and 14), then bends rostrally and ventrally to a point slightly laterad of the oculomotor root. It then proceeds rostrally, pursuing a course along the middle level of the inner surface of the cranial wall, slightly ventrad of the ventral surface of the caudal portion of the cerebral hemisphere, to a point level with the rostral border of the ciliary ganglion. Here it turns laterad, passes through a foramen in the cranial wall, penetrates the investing membrane, and in Stages P and Q it then disappears in the adjacent mesoblast; but in later embryos and in adult specimens the nerve passes immediately laterad of the internasal cartilage, dorsad of the optic nerve, and immediately dorsad of the superior rectus muscle, and is distributed to the middle of the caudal surface of the superior oblique muscle.

The Ramus Ophthalmicus Profundus. (Text-figs. 6, 7, 8, 9, 11, 14, 20.)

The first appearance of a mesencephalic ganglion rudiment connected with the mesencephalic neural crest region by means of a laterally-flattened sheet of periaxal tissue during Stages H–J has been described in Section 2 above (pp. 514–516), and these structures are shown in text-fig. 6. During the interval between late Stage J and Stage K the direct connexion between the mesencephalon and the mesencephalic ganglion disappears, and during and after Stage K (text-fig. 7) the mesencephalic ganglion is connected to the trigeminal rudiment by a thick strand of neuroblastic tissue, which ultimately persists in the adult condition as the ramus ophthalmicus trigemini. Thus the mesencephalic

or ophthalmic ganglion having lost its primary central connexion with the mid-brain, has acquired a persistent secondary cerebral connexion *via* the trigeminal nerve-root (text-figs. 7, 8, 9, 11, 14). The epiblastic placode and that part of the original periaxial tissue strand lying between it and the mesencephalic ganglion rudiment now disappear, and in Stage L the ophthalmic nerve-rudiment and ganglion appear as a tract of neuroblasts extending rostrally and slightly laterally and ventrally from the rostro-ventral surface of the trigeminal neurencytium, passing medio-dorsad of the mandibular head-cavity and swelling into a ganglionic mass lying dorso-mediad of the rudimentary ciliary ganglion. From the rostral part of this ophthalmic ganglion rudiment the neuroblast strand runs rostrally, and almost immediately disappears in the adjacent mesoblast of the pre-mandibular somite. During Stages N–Q, nerve-fibres develop in the proximal part of the ophthalmic nerve-rudiment, and the ophthalmic ganglion becomes large and ovoid (text-fig. 9). Owing to the pronounced cranial flexure, the ophthalmic ganglion lies closely dorsad and laterad of the ciliary ganglion during Stage N, and the ramus connecting the former with the trigeminal root is very stout and short. During Stages P and Q the ciliary ganglion is considerably more rostrad of the ophthalmic ganglion, and lies immediately ventrad and laterad of the proximal part of the ramus nasalis. The rami nasalis and frontalis have appeared since Stage L, and can be traced almost to those regions to which they are ultimately distributed as described below. The proximal part of the ramus ophthalmicus profundus uniting the ophthalmic ganglion with the trigeminal root is still short and thick, but between Stages Q and R it undergoes very marked elongation and becomes a moderately stout cylindrical nerve-trunk (text-fig. 14). The profundus nucleus can first be distinguished during Stage R, in approximately that region of the mid-brain dorsad of which the mesencephalic neural crest was formerly present. The nucleus of each side consists of a laterally-elongated somewhat diffuse group of large and usually multipolar nerve-cells situated in the roof of the optic lobe immediately laterad of the mid-dorsal furrow separating the lobes, and mediad of the lamina profundus of the tectum mesencephali. The nucleus extends to the middle line, no clear interval dividing it from its fellow of the opposite side, and it extends from a point slightly caudad of the rostral convexity of the mid-brain to nearly the level of the caudal border of the lateral cornu of the optocœle, *i. e.* in practically the same vertical transverse plane as the caudal border of the oculomotor nucleus. The fibres uniting the nucleus with the ophthalmic or mesencephalic root of the trigeminal nerve curve caudally and laterally with the fibres of the deep medullated lamina of the tectum, and pass caudally and ventrally into the floor of the mid-brain as described in *Chelone* by Van Valkenburg (1911) and in *Damonia* by Black (1920). Thence they pass

caudally into the floor of the rhombencephalon immediately mediad of the area acustica alba, and turning ventrad of this, they leave the mid-lateral surface of the brain-floor immediately ventrad and rostrad of the mandibular root and dorsad of the ventral or motor trigeminal root, and passing ventrad and mediad of the gasserian ganglion continue rostrad as the ophthalmic trunk.

Laterad of the profundus nucleus lies the main "Dachkern" group, a layer of slightly larger nerve-cells, extending from a point slightly laterad of the former to the vertex of the optocœle. The two cell-groups are not very clearly separated. Passing caudally from the level of the middle of the optic lobe the cells diminish in number, the more lateral cells disappearing slightly more rapidly than those more centrally placed. The maximum number of cells in a single cross-section was 65, the average number in the widest part of the groups being about 50.

In embryos of Stages R and S, and in adult *Sphenodon*, the ramus ophthalmicus profundus is a stout cylindrical nerve leaving the rostro-ventral border of the trigeminal root-complex; it does not enter the gasserian ganglion, but passes ventrally and rostrally, lying in a shallow groove in the lateral surface of the cartilaginous cranial floor. It closely approaches the oculomotor nerve, the cranial wall at this point being very thin (and mostly membranous during Stage R), and enters the large ovoid ophthalmic ganglion which lies immediately laterad of the ophthalmic nerve. From the rostro-lateral surface of the ganglion emerges the stout ramus frontalis of the ophthalmic nerve. This runs laterally and rostrally, and crosses dorsally the optic nerve and immediately divides into two branches. The larger of these passes laterad of the superior oblique muscle, and is distributed to the upper eyelid and adjacent regions, and the other branch passes between the rectus superior and superior oblique muscles, then ventrad of the latter to the inner angle of the upper eyelid. The ramus nasalis leaves the medio-dorsal surface of the rostral extremity of the ophthalmic ganglion, gives off ventro-laterally a fine ramus ciliaris to the dorsal surface of the ciliary ganglion, and then curves medially and dorsally, crosses dorsad the optic nerve, ventrad of the rectus superior and superior oblique muscles, and passes into the nasal region (text-fig. 14).

Nerve V. (*Trigeminal nerve*). (Text-figs. 6, 7, 8, 9, 11, 14.)

The appearance of the trigeminal neural crest, its latero-ventral periaxial extension, ganglionic rudiment, and epiblastic placode in Stage J, and the development of the trigeminal neurencytium dorsad of the mandibular head-cavity and mesoblast during Stage K have already been described in Section 2 above. In Stage L the trigeminal ganglion is a large, slightly bilobed, and nearly spherical mass of neuroblasts united with the third

definitive neuromere of the hind-brain, and lies medio-dorsad of the mandibular head-cavity. Two fairly stout but rapidly tapering strands of neuroblasts leave the lateral surface of the neurencytium. The first of these runs ventrally and rostrally, passes dorsad and slightly laterad of the premandibular head-cavity, and then considerably laterad and slightly ventrad of the oculomotor rudiment, to disappear in the mesenchyme immediately ventrad and caudad of the optic vesicle. This strand is evidently the anlage of the second or combined infra-orbital and maxillary ramus of the trigeminal nerve. The second branch leaves the latero-caudad surface of the neurencytium, runs laterally and ventrally, passing laterad of the caudal part of the mandibular head-cavity, traverses the mesenchyme of the mandibular arch, near the middle level of which structure it disappears. This strand is the anlage of the third or mandibular ramus of the trigeminal nerve. In Stages N, O, P the trigeminal root is short and stout, soon swelling out into the large dorso-ventrally elongated ovoid gasserian ganglion, which during and after Stage P is divided into a proximal rostro-dorsal ovoid and a latero-ventral and caudally-situated distal lobe. From the ventro-medial surface of the former lobe passes the ramus ophthalmicus profundus as already described. Almost at right angles laterally from the rostro-ventral surface of the distal lobe of the gasserian ganglion springs the second ramus of the trigeminal nerve, which runs laterad of the ophthalmic ganglion and immediately ventral to the developing auditory capsule, and passes rostrally, curving laterad until it reaches a point immediately ventral to the rostral extremity of the auditory capsule, and passes ventrad below the centre of the under surface of the eyeball. Its ultimate distribution can be clearly distinguished in Stages R and S, and in adult *Sphenodon*, in which it divides into two rami just rostrad of the auditory capsule, the bifurcation taking place slightly more caudally in Stage R. The smaller and more lateral of these rami passes along the inner surface of the upper jaw between the two rows of teeth, to which it is distributed, and to the palate. This is the ramus maxillo-palatinus. The larger or infra-orbital ramus curves dorsally and medially, and at the level of the optic nerve it receives on its medial side a laterally-directed nerve, merging from a laterally-elongated ovoid ganglion situated in the angle between the roof of the mouth and the inner surface of the upper jaw. This ganglion is the palatine ganglion, and the nerve passing from it to the trigeminal ramus is the palatine branch of the facial nerve. From the caudal extremity of the gasserian ganglion a laterally- and ventrally-directed nerve passes down the mandibular arch, and in Stages N–P enters the dense mesoblastic tissue from which Meckel's cartilage is developed, and within which it pursues a rostral course. In and after Stage R this nerve, the mandibular ramus of the trigeminal nerve, gives off a number

of small nerve-twigs to the external pterygoid and temporo-massetericus muscles, between which it passes, and divides into three rami at a point immediately mediad of the ventral angle of the mandible. One ramus, the main mandibular ramus trigemini, passes through the mandibular foramen into the mandible and runs rostrally therein, ventral to the teeth of the lower jaw, to which it gives off numerous nervi dentales. The second nerve-branch runs between the external and internal pterygoid muscles, turns dorso-medially, and then runs rostrally in the loose tissue immediately ventrad of the angle included between the latero-ventral border of the tongue and the inner surface of the lower jaw. It is distributed by the hyoglossus muscle, and also gives off a number of minute branches to the latero-ventral part of the tongue. This nerve is the ramus lingualis trigemini. The third branch of the ramus mandibularis is the nervus alveolaris inferior, and is distributed to the lateral surface of the lower jaw. The trigeminal nucleus is described by Gisi (1907), and my observations are in agreement with hers.

Nerve VI. (*Abducens nerve*). (Text-figs. 9, 11, 14.)

This nerve first appears during Stage N (text-fig. 9) as a slender cylindrical nerve, leaving the latero-ventral surface of the rostral portion of the hind-brain just caudad of the cerebellum. The point of exit of the nerve is situated ventro-mediad of the caudal third of the acustico-facialis nerve-root at the level of the vestige of the second arterial arch, between the vena capitis medialis and the mid-ventral line. The nerve leaves the brain-surface almost at right angles, turns rostrad and slightly laterad, and almost immediately disappears in the dense mesenchyme from which the external rectus muscle is ultimately developed, below the floor of the brain. It is similar in Stage O. During and after Stage P its proximal portion is composed of a longitudinal series of five fine rootlets, the most rostral of which is somewhat separated from the others. These immediately unite to form a single root, leaving the latero-ventral surface of the brain ventro-mediad of the caudal portion of the acustico-facialis nerve-root, and immediately caudad of the arteria medullaris posterior and laterad of the arteria basilaris. The exact position of this nerve-root is important, since it is additional evidence of the primitive nature of *Sphenodon* (see also Davidson Black, 1920). The nerve turns rostrad, crossing ventrally the former artery, runs ventrally and laterally, crosses ventrally the arteria carotis interior, passes through a foramen in the basi-sphenoid bone, crosses the lateral surface of the retractor oculi muscle, and is distributed to the external rectus muscle. The abducens nucleus consists of four or five groups of rather small nerve-cells, forming a rostro-caudally elongated oval nucleus lying immediately laterad of the fasciculus longitudinalis and immediately ventrad of the ascending motor facialis fibres. From the nucleus

the nerve-fibres pass ventrally and slightly caudally and laterally to their point of exit. Gisi (1907, p. 108) states that the nucleus lies immediately mediad of the trigeminus motor nucleus. This is incorrect. As might be expected in so primitive a reptile as *Sphenodon*, the abducens nucleus lies considerably caudad of the trigeminal nucleus, and the exit-level of the abducens root is somewhat caudad of that of the acustico-facialis root.

The Palatine Ramus of the Facial Nerve.

A rudimentary pre-trematic extension of the distal portion of the facialis neurencytium is given off along the rostro-dorsal surface of the first visceral pouch in an embryo of Stage K, and during Stages M and N this develops into a short cylindrical nerve-trunk. In Stage N it is a well-developed conical extension of the rostro-ventral portion of the geniculate ganglion, and can be recognized as the rudiment of the ramus palatinus facialis. During and after Stage P the ramus palatinus becomes a fairly stout nerve-trunk, leaving the geniculate ganglion and passing rostrally and slightly ventrally of the arteria carotis interna (Wyeth, 1924, *a*, figs. 7, 9–11, 14, 17, 26, 28, 32, and 41). It lies close to the lateral surface of the arteria palatina and, accompanying this vessel in a rostro-ventral direction, leaves the auditory region. It passes ventro-mediad of the extra-columella, crosses the dorsal surface of the pterygoid, and enters the orbital region, where it bears the conspicuous ovoid palatine ganglion, situated ventrad and immediately caudad of the middle of the optic nerve. Laterally the ganglion communicates by a slender nerve-twig with the ramus infra-orbitalis trigemini. Leaving the rostral border of the ganglion palatinus, the ramus palatinus runs rostrally and slightly medially, passes ventrad of the superior rectus and superior oblique muscles, and is distributed to the region of the nares and to the rostral portion of the palate.

4. The Neuromery of the Mid-Brain, and the Morphological Value of its Chief Derivatives.

(A) *The Neuromery of the Mid-Brain.*

Although a number of authors have previously asserted the presence of two neuromeres in the mid-brain of Vertebrates, recent literature appears to contain no detailed account of the complete course of development of these structures, and in the case of *Sphenodon* no neuromeric analysis of the mid-brain has yet been attempted. The present investigation shows that in *Sphenodon* during Stages D–F a single mesencephalic rudiment is present, the caudo-rostrally proceeding dorsal closure of the dilated neural groove in this region completing the mesencephalic roof during late Stage F. A subdivision of the primary mesencephalon into two definitive neuromeres is indicated with increasing clearness during Stages late F to late J, and a completely

encircling inter-mesencephalic groove appears during Stage K. During Stage J the mesencephalic neural crest develops and gives off a latero-ventral strand of periaxial tissue, the primordium of the nervus ophthalmicus, which terminates distally in a mesencephalic ganglion. This process has been noted in a large number of vertebrate embryos by a long series of writers from Beard (1888), in the Chick, to Veit and Esch (1922) and Bartlemez (1923), in human embryos. The mesencephalic ganglion loses its mesencephalic connexion, and becomes secondarily connected with the trigeminal complex (Stage K). Johnston (1905) notes that this transference of cerebral connexion is a typical vertebrate characteristic. The premandibular head-cavity and somite 1 have now appeared in the axial mesenchyme ventrad of the floor of the mesencephalon (Wyeth, 1924, *a*). Until Stage K is reached, the two neuromeric rudiments have developed with approximately equal and increasing rapidity. The first mesencephalic neuromere continues to increase in size, but more slowly, until Stage S is reached, and then becomes approximately doubled in attaining the adult condition. From Stage K to Stage PQ the second mesencephalic neuromere increases very rapidly, each of its axes being about three times as long as that of the first neuromere. At this juncture the medial longitudinal constriction between the developing optic lobes begins to appear, but the lobes increase enormously and ultimately become the most conspicuous features of the adult mid-brain and hind-brain region. After Stage N the inter-mesencephalic boundary becomes less conspicuous, and its visible portion becomes increasingly limited to the regions immediately laterad of the mid-dorsal line, although even in Stages R, S, and in the adult it is still visible in sagittal sections or if the optic lobes be removed (text-figs. 12, 15, 16, 17). The existence of the inter-mesencephalic boundary during the later stages of development has not previously been noted, probably owing to the fact that unless a considerable number of sagittal sections, and of models made from serial transverse sections through a close series of embryonic stages, be examined, its invariable presence would not be detected. Any slight infolding of the mesencephalic wall that might be noted in isolated specimens would perhaps be regarded as an artifact. Gisi (1907, fig. R) gives a sagittal section of a *Sphenodon* embryo which she assigns to Stage Q and in which she shows a constriction of the mesencephalic cavity, this being due to the presence of the inter-mesencephalic groove, although she does not so describe it. She says, however (p. 137):—"Das frontal Dritteil der dorso-medianen Mittelhirnzone bildet eine dorsal- und frontalwarts gerichtete Ausstulpung. Sie uberwolbt den Eingang zu den lateralen Hornern des Mittelhirnventrikels. Sie erhebt sich fast bis zur Hohe des Pineal-organs und drongt frontal die Lobi Optici seitwarts. Ventral wird die mediane Ausstulpung teilweise

durch die caudalwarts gebogene Commissura posterior abgeschlossen." This description evidently applies to the cavity of the structure that I have identified as the first mesencephalic neuromere, and is in almost exact agreement with its condition in Stage PQ (Embryo 51 *a*), to which stage of development Gisi's fig. R suggests that her embryo should be referred. From a consideration of the facts detailed above, as well as of some additional developmental features which will be described below, it is concluded that the mesencephalon is at first a primary neuromere, and that it afterwards divides into two definite secondary neuromeres. That some inter-neuromeric grooves appear earlier than others has been observed in *Lacerta* and *Chrysemys* by Warren (1911), in *Cryptobranchus* by Smith (1912), and in the human embryo by Bartlemez (1923), who, after summarizing the results obtained by earlier investigators, concludes that the primitive neuromeres alike are "expressions of the same fundamental metamerism."

In Section 2 of this paper the development of the *first mesencephalic neuromere* has been traced from the time of its first appearance as a small ovoid vesicle during Stage F until it assumes its adult form as a wedge-shaped segment with a dorsally domed roof, lying almost hidden below and between the rostro-medial portion of the optic lobes. During the period of most rapid growth of the second mesencephalic neuromere (Stages N to R) the roof of the first mesencephalic neuromere becomes more dorsally arched and its walls somewhat thicker than those of the second mesencephalic neuromere. This is doubtless due to the pressure resulting from the great rostral growth of the second neuromere. For the same reason the posterior commissure and the sub-commissural organ bulge downwards into the mesencephalic cavity. When subsequently the constriction between the optic lobes increases, the pressure diminishes, and a straightening out of the first mesencephalic region results. In the next sub-section of this paper it is pointed out that, like each of the three fore brain neuromeres, the first mesencephalic neuromere possesses a pair of bilateral dorsal evaginations of its central cavity, these evaginations constituting the cavity of the sub-commissural organ. Contiguous to this organ occurs the lamina commissuralis mesencephali; and although no nervous connexion between the organ and the commissure has yet been demonstrated, it is possible that such may once have existed, and may have disappeared during phylogeny. The existence of such a commissure in the dorsal inter-mesencephalic boundary zone might be expected, since in the roof of the fore-brain the boundaries of the neuromeres are defined by a series of transverse commissures. Thus the commissura aberrans indicates the boundary between the telencephalon and the diencephalon, the commissura superior separates the diencephalon and the synencephalon, and the lamina commissuralis synencephali separates the

synencephalon and the first mesencephalic neuromere. It is true that in adult *Sphenodon* the commissura aberrans lies caudad of the rostral wall of the dorsal sac, and is therefore entirely within the diencephalon, but Dendy (1910) has shown that the original position of the commissure was on the rostral surface of the wall of the dorsal sac, that a change of relative position of the commissure occurs during ontology, and that it is really an inter-neuromeric structure. Similar ventral boundaries between the telencephalon, the diencephalon, and the synencephalon are formed by the optic chiasma and the commissura retro-infundibularis respectively. No similar nerve commissure appears to separate the mid-ventral portions of the synencephalon and the first mesencephalic neuromere. It seems probable that the absence of a commissure in this region may be due to the great pressure in the brain-floor which results from the strong habenular flexure which is at its maximum just at that period when the nerve commissures are developing. A ventral commissure between the synencephalon and the first mesencephalic neuromere may therefore have been suppressed, or it may have been caudally displaced and incorporated with the rostral part of the ansulate commissure which lies in the mesencephalic floor immediately caudad of this region. It may be noted that the development of the emergent roots of the oculomotor nerve, which occur at this time and in this region, may possibly assist such caudal displacement, and, further, that the ansulate commissure possesses a partly-detached rostral segment lying immediately caudad of these roots.

As regards the *second mesencephalic neuromere*, it need only be noted that the optic lobes are universally regarded as paired dorso-lateral evaginations of the mesencephalon. Their development and structure have been described in Section 2 above; and if the rostral part of the mid-brain has been correctly identified as the first mesencephalic neuromere, it is evident that the optic lobes and their peduncles must be referred to the second mesencephalic neuromere. The floor of this neuromere is separated from that of the first mesencephalic neuromere by the caudal segment of the ansulate commissure. The presence of a definite dorsal nerve commissure in the brain-roof forming the boundary between the two mesencephalic neuromeres is uncertain. The caudalmost fibres of the posterior commissure unite the bilaterally-placed nuclei of the commissure in this region, but it cannot definitely be stated that any of these fibres actually lie as far caudad as the inter-neuromeric boundary. Gisi describes a pair of small and somewhat diffuse ganglia laterales mesencephali lying in the mesencephalic roof laterad and dorsad of the sub-commissural organ and caudad of the nuclei of the posterior commissure. Certain tectal fibres appear to leave these ganglia, but it is impossible to affirm that they constitute a definite commissure. If they did, such a commissure would almost

certainly lie in the inter-mesencephalic boundary. Nicholls (1912) notes that in the Lamprey the axons of certain cells which occupy a position similar to those just described, but which he appears to regard as part of the "Dachkern," "appear to pass to that side of the brain remote from the cells from which they arise," and it seems possible that these cells are those referred to by Gisi. I am inclined, therefore, to regard Gisi's ganglia laterales mesencephali as being serially homologous with the nuclei of the posterior commissure and the habenular ganglia, and to conclude that if there be found to exist or if there ever existed in the phylogeny of *Sphenodon* any nerve commissure connecting the ganglia laterales mesencephali, this commissure would be an inter-neuromeric structure serially homologous with the commissura aberrans, the superior commissure, and the posterior commissure. Caudally the second mesencephalic neuromere is separated mid-dorsally from the rhombencephalon by the decussatio veli, and mid-ventrally by the decussating fibres of the tractus habenulo-peduncularis.

In Sub-section E below it will be suggested that the single mesencephalic vesicle of the earlier stages of development is the primary mesencephalic neuromere situated in the premandibular head-segment. From the evidence reviewed above, and that to be given in Sub-section E, it appears that the mid-brain of *Sphenodon* ultimately comprises two definitive and secondary neuromeres, both of which lie in the premandibular head-segment.

(B) *The Serial Homology of the Sub-Commissural Organ.*

In Section 2 above it has been shown that the sub-commissural organ in *Sphenodon* appears as a paired evagination of the rostral portion of the roof of the first mesencepalic neuromere, and that each of its constituent parts lies immediately laterad of the mid-dorsal line. The account of its development and structure given by Dendy (1910) has been confirmed and somewhat amplified. During the closing stages of development the thickening of the epithelium of the walls of the organ ultimately obliterates the cavities of the paired grooves and converts these structures into two thickened bands, the ventral surfaces of which become convex instead of concave, and therefore bulge into the mesencephalic cavity. It is to be observed, however, that the original bilateral and evaginated form of the sub-commissural organ persists, and can be clearly distinguished in the adult brain of *Petromyzon* and *Esox*, while it is somewhat less evident in *Sphenodon* embryos of Stage R (Nicholls, 1912, figs. 1, 4, and 6). In *Sphenodon* embryos of Stages P, Q, and R, and in adult specimens of *Bdellostoma*, *Myxine*, and *Petromyzon*, the original form and bilateral structure of the organ are clearly evident. In *Geotria* and in the higher Vertebrates the two halves of the organ become united in the middle

line to form a single structure with a horseshoe-shaped cross-section, the internal cavity of which may be partly obliterated owing to the internal extension of the much thickened epithelium of its walls, as in *Microtus* and *Lepus* (Nicholls, *op. cit.* figs. 8 and 9). In Mouse, Cat, Chimpanzee, and Man, and especially in adult specimens of the two latter types, the bilateral evaginated origin of the organ is practically unrecognizable (Dendy and Nicholls, 1910, figs. 1–3 and text-figs. 1–9).

These two authors have also shown the existence of a small mesocœlic recess in the brain of *Sphenodon*, Chimpanzee, and Man. The present investigation confirms their statement that the mesocœlic recess in *Sphenodon* is really a tucked-in portion of the original cavity of the sub-commissural organ. This, then, like the mesocœlic recess in Petromyzontidæ and the Myxinoideæ, must be regarded as a part of the rostro-dorsal region of the central cavity of the first mesencephalic neuromere. In the adult brain the main part of the sub-commissural organ lies ventral to the lamina commissuralis mesencephali; and the position of the caudal part of the organ, the cavity of which has been termed the mesocœlic recess, and which in *Sphenodon*, *Rana*, and *Scyllium* lies dorsad of the posterior commissure, is probably secondary and due to transverse folding in this region. It appears later during development, and must not be confused with the dorsal position now to be referred to. The extent and state of development of the posterior commissure at the time of the first appearance of the rudiments of the sub-commisural organ make it almost certain that the portion of the mesencephalic cavity from which the sub-commissural organ is evaginated *originally lay entirely caudad and dorsad of the posterior commissure* (Stages N–PQ). It is obvious, therefore, that had the evagination of the paired rudiments of the organ progressed to the extent that it has done in the cases of the cerebral hemispheres, the primary optic vesicles, and the pineal outgrowths, the originally paired condition of the organ would have been evident, and that its final position would have been dorsad of the posterior commissure.

Dendy (1910) describes a number of cells situated between and dorsal to the bases of the columnar epithelial cells of the sub-commissural organ, and he suggests that they may be nerve-cells which, as a result of further investigation, may ultimately prove to be connected with the epithelial cells of the organ. Owing to lack of suitably stained material it has been impossible to prove the presence or otherwise of axones proceeding from these cells, which appear to me to be typical "amacrine" cells, similar to those occurring in the retina and the olfactory bulb, in which situations they are also found in many birds. If they be such, no axones are to be expected. The presence of amacrine cells would support the homology I suggest between the primary optic vesicles and the sub-commisural organ. The latter would therefore be assigned to the series of dorsal paired diverticula of the

central cavity of the brain, of which series the fore-brain components of which are the cerebral, the primary optic, and the pineal evaginations. Like the cavities of the primary optic and pineal vesicles, the cavity of the sub-commisural organ is lined with modified epithelium, possibly sensory in character (Dendy, Nicholls). The epithelial lining of the members of the corresponding lateral series of paired diverticula (Wyeth, 1924, *b*) is not similarly modified. This fact appears to give additional support to the homology suggested above.

The existence of nervous connexion between the lamina commissuralis synencephali and the pineal complex *via* the pineal tract has been demonstrated in *Sphenodon* by Dendy (1910) and in the Chick by Cameron (1903–4), and it has been noted in Section 2 that simultaneously with the development of the sub-commissural organ the posterior commissure extends rostrally into the roof of the synencephalon and establishes nervous connexion with the pineal complex (Dendy). At the same time, the commissure undergoes a similar caudal extension within the roof of the first mesencephalic neuromere. In addition, in all stages of development subsequent to Stage P, the commissure is incompletely constricted into a smaller rostral lamina commissuralis synencephali and a larger caudal lamina commissuralis mesencephali. With the thin rostral extremity of the former the pineal nerve-fibres are connected. A similar but possibly more complete segmentation of the posterior commissure is found in some other reptiles. Warren (1911) found that in embryos of *Lacerta* and *Chrysemys* the constriction of the commissure is so marked that he is not certain that there are not in these reptiles two separate commissures, an earlier anterior one in the roof of the synencephalon and a later caudal one in the roof of the mesencephalon. Alternatively he suggests that a single commissure has been folded on itself, thus producing a transverse median constriction. Such a folded appearance is found in nearly adult *Sphenodon* embryos, but in adult specimens this is much less marked. Since, then, the rostral segment of the posterior commissure lies in the roof of the synencephalon and has nervous connexion with the pineal complex, while the caudal segment of the commissure lies in the roof of the first mesencephalic neuromere, of which the sub-commissural organ is a derivative, and since there have been demonstrated so many other homologies between the pineal and sub-commissural evaginations, it would seem that only the demonstration of nervous connexion between the caudal portion of the posterior commissure and the sub-commissural organ is required in order fully to establish the suggested serial homology between the pineal evaginations and the sub-commissural organ.

From a consideration of all the above-mentioned facts and inferences, I am therefore inclined to homologize the sub-commissural organ with the members of the dorsal series of paired diverticula of the cavity of the fore-brain. These were fully described in an earlier paper (Wyeth, 1924, *b*).

(C) *The Morphological Value of the Oculomotor Nerve.*

It is generally believed that the oculomotor nerve is the ventral, and the ramus ophthalmicus profundus the dorsal, root of the segmental nerve of the neuromere which belongs to the premandibular head-segment. That these nerves innervate the group of eye-muscles believed to be developed from the mesoblast of this head-segment is universally accepted. Nicholls (1915) found a ganglionic rudiment of the oculomotor roots in *Scyllium* and *Rana*, and he suggests that the oculomotor nerve is sensori-motor, and that it really represents a complete segmental nerve of which the dorsal and ventral roots have fused. He notes that Gast (1909) states that in certain Selachians a transient dorsal root related to the oculomotor appears during development, and that in these embryos there exists a root ganglion, the cells of which are of medullary origin, upon the oculomotor nerve. Nicholls argues that since the dorsal roots of the cranial nerves practically always shift somewhat ventrally from their primitive positions during the course of development, this ventral dislocation might easily have resulted in a confluence of the dorsal and ventral roots into a single structure. In support of his suggestion he quotes the conclusions of Sherrington (1894–7), who believes that the oculomotor nerve might prove to be sensori-motor; of Carpenter (1906), who believes that the ciliary ganglion is partly derived from cells which have migrated along the oculomotor nerve; and of Tozer (1912), who found ganglion cells on or near the oculomotor roots in *Macacus*, *Gadus*, and *Columba*. Nicholls further points out that in those forms in which the oculomotor retains its ganglion the ophthalmicus profundus is little developed, and is said to be absent in the adult. He admits that in many vertebrates which have been carefully examined no oculomotor ganglion has been found, and that this can hardly be due to its having been overlooked. He suggests that in such forms the cells of the oculomotor ganglion have migrated into the neighbourhood of, or may have fused with, the ciliary ganglion. As regards the development of *Sphenodon*, it must be observed that at no stage of its ontogeny is there any sign of the existence of an oculomotor ganglion or of a dorsal root. It is true that in this reptile the ventral displacement of the dorsal roots of the cranial nerves during the course of development is very conspicuous, but the oculomotor nerve does not exhibit any such shifting. From the time of its first appearance during Stage L until the adult condition is reached it appears to be a typical ventral root, nor does an oculomotor ganglion ever appear to be present.

Johnston (1905) accepts the usual segmental interpretation of this nerve, and assigns both the oculomotor and ophthalmicus profundus nerves to the second mid-brain neuromere, which he calls neuromere V. He admits that the point of exit of the oculomotor root is actually located in the first mid-brain neuromere (neuromere IV), but he regards this as the result of a

rostral displacement due to pressure exerted by the developing ansulate commissure. The paths of the nerve-fibres leaving the oculomotor nucleus and their position relative to the ansulate commissure in *Sphenodon* seem to me to afford some support to this suggestion, but further evidence would appear to be necessary in order to justify Johnston's assignment of the oculomotor nerve to the second mid-brain neuromere. Johnston appears to consider each of the mid-brain neuromeres to be a primary neuromere, and he assigns neuromere V to the premandibular head-segment. This renders it necessary either to assign the oculomotor nerve to the second mid-brain neuromere in spite of the fact that its point of exit is located in the first mid-brain neuromere, or to reject the generally-accepted view which assigns both the oculomotor and ophthalmicus profundus nerves to the same neuromere, *i.e.* to neuromere V, which Johnston regards as the neuromere of the premandibular head-segment. The present investigation suggests a solution which avoids both of these difficulties. It appears that Johnston is wrong in considering neuromeres IV and V to be primary. As I suggest in Sub-section E below, it appears that in *Sphenodon* the whole mid-brain constitutes a slight primary neuromere which lies in the premandibular head-segment. From this neuromere they ultimately develop neuromeres IV and V, which are definite and *secondary* neuromeres, both lying in the premandibular head-segment. The oculomotor nerve is situated in neuromere IV, and the ophthalmicus in neuromere V, but *obviously belong to a single primary neuromere.*

This interpretation of these nerves is in accordance with the generally-accepted view of their segmental value (Neal, 1914; Goodrich, 1918; de Beer, 1922–4) (see Sub-section E below).

(D) *The Morphological Value of the Nervus Ophthalmicus Profundus.*

The relationships of this nerve in adult *Sphenodon* are such as to suggest that it is part of the trigeminal complex, and as such to be referred to neuromere A of the hind-brain. The development of the nerve is described in Section 3 above. Osawa (1897) found no ophthalmic ganglion in adult *Sphenodon*, but it has been described in embryos of Stages S and T and in the adult reptile by Gisi (1907, pp. 114–5, and shown in pl. i. figs. 2 and 3). The present account of the nerve and ganglion generally confirms and considerably supplements these results. In Section 2 of this paper it is clearly shown that the anlagen of the profundus nerve and ganglion possess a primary direct mesencephalic connexion which is lost between Stages J and K, and is replaced by a secondary and persistent cerebral connexion by means of the trigeminal root. The conditions obtaining during Stage J are similar to those described in *Scyllium* by Goodrich

(1918) and shown in his figs. 2 and 3, while those in Stage K are similar to those shown in his figs. 5 and 7. Between Stages O and P the ophthalmicus nerve acquires a connexion with the ciliary ganglion by means of a fine ramus ciliaris, and at this period the condition persisting in adult *Sphenodon* is attained. During and after Stage Q the ophthalmicus profundus nucleus can be distinguished, and appears to be connected by a nerve-tract with the mesencephalic trigeminal nerve-roots, the general structure and relationships of the nucleus and fibres being similar to those described in *Chelone* by Van Valkenburg (1911), in *Damonia* by Davidson Black (1920), and very briefly in *Sphenodon* by Gisi (1907).

There evidently exists evidence sufficient to permit the identification of the ramus ophthalmicus profundus as the dorsal nerve-root of the primary mesencephalic neuromere, and this interpretation of the segmental value of the nerve is in agreement with the generally-accepted view of its nature (Neal, 1898, 1914; Johnston, 1905; Goodrich, 1918; and de Beer, 1922).

(E) *The Segmental Value of the Primary Mesencephalic Neuromere.*

It has been shown in the earlier sections of this paper that the mid-brain of *Sphenodon* consists at first of a single neuromere, and that the oculomotor nerve is the ventral, and the ophthalmicus profundus is the dorsal, nerve of this neuromere. It has also been suggested that this single mesencephalic neuromere is primary, and is to be assigned to the premandibular head-segment.

During Stages J–L there is present in the mesoblast laterad of this neuromere a cavity which on purely topographical grounds I have in an earlier paper (Wyeth, 1924. *a*) called the premandibular head-cavity. It apparently represents a mesocoele, while the layer of dense mesoblast immediately surrounding it appears to be a vestige of the premandibular mesoblastic somite (somite 1). The present investigation indicates that from this mesoblast is developed the group of eye-muscles innervated by the oculomotor and ophthalmicus profundus nerves. During Stages J–L the premandibular head-cavity communicates with its fellow of the opposite side by means of a narrow tubular canal which passes transversely immediately rostrad of the rostral extremity of the notochord and Seessel's pouch. A similar head-cavity was found in the American Alligator by Reese (1910) and in *Scyllium* by Goodrich (1918). The present interpretation of the cavity and the surrounding mesoblast agrees with that given by the latter writer. The ramus ophthalmicus profundus passes mediad of mesoblastic somite 2 and laterad of mesoblastic somite 1, and apparently constitutes the dorsal or somatic sensory-nerve component of the mesencephalic neuromere, while the oculomotor is the ventral or somatic motor, and the ciliary

nerve and ganglia are the splanchnic sensory components of the neuromere. I have already suggested that the subcommissural organ is to be regarded as a serial homologue of the primary optic vesicles and the pineal evaginations, and is therefore probably a special sense component of this neuromere (*cf.* Johnston, 1905, Table B). In an earlier paper (Wyeth, 1924, *a*) I have suggested that the arteria maxillaris and the arteria lingualis are probably to be regarded as premandibular vestiges of the dorsal and ventral aortæ respectively, and the presence of these arteries may perhaps suggest that a premandibular arterial arch may have existed in some remote ancestral vertebrate type. It will be observed that the present interpretation of the neuromery of the mid-brain involves the assumption that two secondary definite neuromeres are found in the premandibular head-segment of *Sphenodon*. It is evident, as already observed by Locy (1895), that the appearance of the primitive neuromeric segmentation precedes that of the mesoblastic segmentation in this region, and Von Kupffer (1903) expresses the same opinion. Neal (1898) concludes that it is the primary neuromere of the mid-brain which affords evidence of the segmentation of this part of the head, and the evidence obtained during the present research confirms this conclusion. Froriep (1892) doubts the segmental value of the definitive neuromeres of the mid-brain, and appears to regard them as the expression of varying degrees of pressure exerted upon the brain by the surrounding structures, and de Beer (1922) also appears to doubt their segmental value.

In view of the facts now recorded, there appears to be some reason to doubt the segmental value of the individual definitive secondary neuromeres of the mid-brain in *Sphenodon*. It seems evident that the undivided primitive mesencephalon must be identified as a primary neuromere, that it must be assigned to the premandibular head-segment, and that the two definitive mesencephalic neuromeres are secondary. The secondary character of the definitive neuromeres of the mid-brain has previously been asserted by Neal (1898), Hill (1899–1900), Von Kupffer (1903), and Warren (1911), while de Beer (1922) and Kingsley and Adelmann (1924) appear to doubt that all neuromeres possess equivalent morphological value. Johnston (1905) believes the definitive neuromeres to be primary, and attempts to correlate them with the head-segments. The present investigation appears to show that these definitive mid-brain neuromeres are secondary and cannot be so correlated.

Not only does the foregoing interpretation of the segmental value of the neuromeres of the mid-brain appear to be in accordance with the observed facts of development, but it seems to introduce no new difficulties, while it certainly disposes of certain old ones.

5. The Neuromery of the Hind-Brain.

(A) *The Morphological Value of the Trochlear Nerve.*

This nerve is generally considered to be the ventral nerve of the neuromere which is situated in the mandibular head-segment, and it innervates the superior oblique muscle, which is the only one of the eye-muscles to be developed from the mesoblast of the mandibular head-segment. The trigeminus is regarded as its corresponding dorsal nerve. This is the conclusion arrived at by a long line of investigators (v. Wijhe, 1882; Neal, 1896; Johnston, 1905; Goodrich, 1918; de Beer, 1922). Johnston suggests that the dorsal exit of the trochlear nerve may be due to the inability of its fibres on leaving the nucleus to pass latero-ventrally owing to the presence of certain fibre-tracts which have already developed in the brain-floor laterad and ventrad of the nucleus. He thinks that the presence of these tracts causes the developing trochlear fibres to be deflected dorsally, and that when they emerge from the surface of the brain they do so from the dorsal surface, their path being such as to cause them to decussate. This explanation appears to be in agreement with the observed facts of the development of this nerve in *Sphenodon*, in which, owing to the late development of the trochlear nucleus and nerve (Stage PQ), a number of fibre-tracts lying laterad and ventrad of the point of origin of the nerve on the ventral surface of the nucleus have already been developed. These tracts, the fasciculus longitudinalis medialis, the tractus thalamo-bulbaris et spinalis, and the decussatio tecto-bulbaris, are among the earliest to appear in this region. The trochlear fibres, instead of penetrating these tracts and emerging from the ventral surface of the rostral portion of the floor of the hind-brain, take a path of less resistance, and eventually emerge from the dorsal surface of the velum medullare anterior. Further, it may be argued that the presence of the dense tissue of the thick roof of the cerebellum immediately caudad of the path of the developing trochlear fibres prevents their exit at the normal level, so that this factor, together with the influence considered above, combine to cause a rostral as well as a dorsal displacement at the point of exit of the nerve. In respect of its point of exit, the nerve therefore assumes a mesencephalic instead of a post-velar rhombencephalic character. Its distribution to the superior oblique muscle, however, supports the generally-accepted view that the nerve must be assigned to the neuromere of the mandibular head-segment, *i. e.* to the first primary neuromere (neuromere A), of the hind-brain, although this neuromere has differentiated into three definitive secondary neuromeres (neuromeres VI, VII, and VIII) before the nerve actually appears, and the latter appears to belong to neuromere VI.

(B) *The Segmental Value of Neuromeres* A *and* B.

As regards the segmentation of the preotic head-region caudad of the premandibular head-segment, the following conclusions are generally accepted by recent writers, *e. g.* Balfour (1876), v. Wijhe (1882), Neal (1898), Koltzoff (1898), Ziegler (1908), Goodrich (1918), and de Beer (1922–24) :—

(*a*) Two head-segments, the mandibular and hyoid, are present.

(*b*) The mandibular head-segment possesses a dorsal nerve (the trigeminal), a ventral nerve (the trochlear), mesoblastic somite 2 with its mesocœle (the mandibular head-cavity), and a lateral mesoblastic branchiomere, the mandibular arch, in which is situated the first or mandibular arterial arch.

(*c*) The hyoid head-segment possesses a dorsal nerve (facialis), a ventral nerve (abducens), mesoblastic somite 3, and occasionally a hyoid head-cavity, the hyoid arch and the second, or hyoidean, arterial arch.

If it be supposed that neuromeres possess a segmental value, it would seem reasonable to expect the presence of one neuromere in each of these head-segments, whereas most observers (Orr, Hoffmann, Neal, McClure, Locy, Hill, Zimmermann) find that there are ultimately four definitive neuromeres present in this region of the hind-brain. These are usually assumed to be neuromeres VI–IX. Johnston (1905) assumes that these are primary, and he assigns one to each of four head-segments; whereas Froriep and de Beer appear to doubt the segmental value of these neuromeres, and Kingsley and Adelmann doubt whether all of them are of equal segmental value. In the morphological section of this paper, I have indicated that in these two head-segments in *Sphenodon* and the Chick there are at first neuromeres A and B, and that the former of these ultimately differentiates into three definitive secondary neuromeres (neuromeres VI–VIII), while the latter remains undifferentiated and is the otic neuromere (neuromere IX). It would therefore appear that the definitive neuromeres are not all of equal segmental value, and that neuromeres A and B are primary neuromeres each of which corresponds to a single head-segment. This view is adopted because it is in accordance with the ascertained facts of development, and because it appears to be preferable to either of the alternative conclusions which have sometimes been adopted, viz. :—

(*a*) That the four definitive neuromeres are primary, and that there has been a phylogenetic suppression of two branchiomeres and other head-segment components. This assumption has been generally rejected (Koltzoff, Johnston, Goodrich).

(*b*) That the four definitive neuromeres are primary, but that a considerable shifting or dislocation of nerves and other components and a suppression of some of them has occurred. This view is adopted by Johnston, who argues it at some length. It does not remove all difficulties, nor does the evidence in its favour appear to be conclusive.

It will be necessary separately to consider neuromeres A and B; and as the case of the latter appears to be somewhat simpler, and because at all stages of development it can be very clearly distinguished by its characteristic form, the behaviour of the periaxial tissue, and its relation to the optic plate (Bartlemez, 1922–3), this neuromere will first be considered.

(i.) *The Neuromery and Segmental Value of Neuromere* B.

From the time of first appearance of any traces of segmentation in very early embryos of *Sphenodon*, Chick, and Man (Bartlemez) this is the most conspicuous of the hind-brain neuromeres, and it remains so until a late stage of development. The otic primordium and otic plate also appear early during development (*Sphenodon* Stage E, and human embryo of two somites). The ultimate development of the otic neuromere, otic primordium, and otic plate have been traced in *Sphenodon* in the present paper, and in an earlier paper (Wyeth, 1924, *a*), and in human embryos by Wilson (1914) and Bartlemez (1922, 1923). In both cases it is evident that the neuromere undergoes no further segmentation, and it is evidently both primary and definitive, and to be identified as the otic neuromere (neuromere IX). The head-segment in which it is situated is universally agreed to be the hyoid segment, and in *Sphenodon*, as in other types, it contains the hyoid arch, mesoblastic somite 3, the second arterial arch, and is innervated by the facial and abducens nerves. The post-trematic ramus of the facial nerve passes into the hyoid arch (Stage M), and the acustico facialis neurencytium is obviously attached to the neuromere. The lateral mesoblastic plate is perforated by the visceral pouch and cleft in such a way that the clefts alternate with the mesoblastic somites, and the latter come to lie over each arch, but extend forward over the pouch in front. These facts agree with the results obtained in embryos of *Scyllium* (Goodrich, 1918), *Squalus* (de Beer, 1922), and *Heterodontus* (de Beer, 1924). The abducens nerve innervates the external muscle, which is universally considered to be derived from the mesoblast of the hyoid head-segment. As Goodrich points out, the rostral position of this muscle is due to rostral displacement during ontogeny; and this causes the abducens nerve, which belongs to head-segment 3, to emerge from the skull somewhat rostrad of the mandibular ramus of the trigeminal nerve, which belongs to head-segment 2. The abducens nerve arises late during development (Stage N), and therefore the exact position of its point of

exit on the brain-floor relative to the inter-neuromeric groove is difficult exactly to determine. In *Sphenodon* it is somewhat caudad of the rostral border of that of the facial root. This might be expected in so primitive a reptile, as it is the usual condition in the lower Vertebrates and in Reptiles, except *Boa* and *Varanus* (Davidson Black, 1920). Neal and Dohrn believe that the abducens nerve consists of the fused ventrals of the nerves of several head-segments; but this appears to be very doubtful, and receives no support from the conditions observed during the development of *Sphenodon*. Johnston (1905, pp. 214–215), having assumed the primary nature of the definitive neuromeres and having assigned neuromere VI to the mandibular head-segment, proceeds to assign neuromere VII to the hyoid head-segment. Since the facial nerve is generally assigned to the neuromere situated in the hyoid head-segment, he has to explain the attachment of the nerve to neuromere IX by assuming that it has shifted caudally from neuromere VII. He is also compelled to separate the abducens nerve from the facial nerve, and to assign the former to neuromere VII, although both nerves admittedly belong to the same neuromere, *i. e.* to the neuromere of the hyoid head-segment. In *Sphenodon* it has been shown that the facial, and so far as can be ascertained the abducens also, both arise in connexion with neuromere B, *i.e.* neuromere IX, and that this neuromere is situated in the hyoid head-segment. It will be observed that this conclusion reconciles the observed neuromery of the brain of *Sphenodon* with the generally-accepted view of the segmentation of the Vertebrate head, without necessitating the assumption of a suppression or dislocation of any head components.

(ii.) *The Neuromery and Segmental Value of Neuromere* A.

From the time of its first appearance in Stage D until early Stage J this structure appears to be a single neuromere, and its relationship to the head-segment in which it lies suggests that it is also primary. Before it differentiates into three definitive neuromeres (neuromeres VI, VII, and VIII) there have appeared in the region of the head latero-ventrad of the undivided neuromere a conspicuous mandibular head-cavity and the mesoblast around it, which evidently represents the second or mandibular somite, of which the mandibular head-cavity is the mesocœle. The caudo-ventral mandibular canal has extended into the mandibular arch, in which also is present the first arterial arch, while the trigeminal primordium has developed in connexion with the dorso-lateral surface of the neuromere. The conditions observed during Stage J (text-fig. 6) entirely agree with those described and figured in two 11-mm. embryo of *Heterodontus* by de Beer (1924) and in a *Scyllium* embryo by Goodrich (1918, figs. 2 and 3). During Stages K–P the position of the trigeminal ganglion dorsad of the

somite, and the penetration of the mesoblast of the mandibular arch by the developing ramus mandibularis trigemini, which lies laterad of the mandibular canal (Stages J–L), entirely agree with the observations of the investigators who have examined similar embryos of other vertebrate types. Mesoblastic somite 2 extends dorsad and lies laterad of the ramus ophthalmicus profundus, and the superior oblique muscle, which is developed from the mesoblast of this somite, lies dorsad of the same nerve. The relative positions and relationships of all these structures in *Sphenodon* are identical with those exhibited in embryos of corresponding stages of development in *Scyllium* (Goodrich, 1918), *Squalus* (de Beer, 1922), and *Heterodontus* (de Beer, 1924). After Stage J the primary neuromere differentiates into neuromeres VI, VII, and VIII, the mandibular head-cavity shows signs of corresponding segmentation, and the trigeminal nerve-root appears to be situated on the latero-dorsal surface of neuromere VII. In *Sphenodon*, as in Man, neuromere VIII appears to be differentiated somewhat earlier than neuromeres VI and VII. Johnston (1905) regards them as primary neuromeres, and assigns neuromere VI, together with the trochlear nerve, the trigeminal nerve, mesoblastic somite 2, and the mandibular arch, to the mandibular head-segment. He finds, however, that the trigeminal nerve is actually united with neuromere VII, and therefore assumes that the nerve has undergone a caudal displacement. It is only thus that he is able to reconcile the generally-accepted view that this nerve is the dorsal nerve of the mandibular head-segment with the fact of its position in neuromere VII. In *Sphenodon* there seems to be no trace of such shifting of the trigeminal nerve, but Johnston (p. 208) states that such has been observed in Selachian embryos by Zimmermann and Neal. The more recent work of Goodrich and de Beer does not appear to confirm this statement; and it seems possible that what was really seen was the disappearance of the rostral portion of the periaxial tissue of the rudiment of the ophthalmicus profundus which takes place in *Sphenodon* (Stage J). If, as I now suggest, the whole of neuromere A constitutes the primary neuromere of the mandibular head-segment, then the trochlear and trigeminal nerves being connected with this neuromere belong, as they are generally assumed to do, to the neuromere of the mandibular head-segment. Thus no shifting of the trigeminal nerve need be assumed in order to account for its position in neuromere VII. It also avoids the supposition of the suppression of a branchial segment, which Johnston's view of the primary nature of the definitive neuromeres requires as an alternative if his suggested shifting of the trigeminal nerve be not accepted. The work of Goodrich, de Beer, Kingsley and Adelmann, Bartlemez, and the results now recorded, appear seriously to conflict with Johnston's assumption that all neuromeres are primary and of equal

morphological value; and it appears justifiable to hold that in Selachians, *Sphenodon*, Chick, and Man there is at first a single primary neuromere in the mandibular head-segment, that the trochlear and the trigeminal are its ventral and dorsal nerves respectively, and that neuromeres VI, VII, and VIII arise later during ontogeny and are secondary structures. These latter structures appear to have no individual segmental value, and may be the product of stresses set up owing to the presence of a strong cranial flexure.

(C) *The Neuromery and Segmental Value of Neuromere* C.

The first appearance of neuromere C during Stage D, its first sign of impending differentiation into two "segments" (C_1 and C_2) in Stage G, and the ultimate identification of these as definitive neuromeres in Stage J (text-fig. 6) have already been described in Section 2 of this paper. Between Stages E and J the otic plate is converted into an otic pit, and extends into the rostral region of the head-segment in which neuromere C is situated. Visceral pouch 2 develops at a level between neuromere B (otic neuromere or neuromere IX) and neuromere C during Stage J, and during Stage K the second arterial arch (text-fig. 7) begins to appear ventrad of the rostral division (C_1) of neuromere C, while the glossopharyngeal neurencytium has developed on the dorso-lateral surface of the caudal portion (C_2) of neuromere C. The development of the auditory organ has been accompanied by a considerable elongation of C_1. Mesoblastic somite 4 appears caudo-ventrad of the auditory organ and is partly obliterated by it (Stage K). From these facts it would appear that neuromere C must be identified as the primary neuromere situated in the first post-hyoid head-segment (head-segment 4). The differentiated portions (C_1 and C_2) of this neuromere are therefore identified as secondary and definitive neuromeres, viz. neuromeres X and XI. These are clearly differentiated from early Stage J until Stage M. That neuromere C is a primary neuromere lying in head-segment 4 is indicated by its position relative to the other components of this head-segment, *i.e.* the auditory organ, mesoblastic somite 4, visceral arch 3 lying between visceral pouches 2 and 3, and the dorsally situated glossopharyngeal nerve which crosses lateral somite 4, as described in *Scyllium* by Goodrich (1918), while during Stage L the roots of the hypoglossal nerve appear, and the most rostral of these appear to be the ventral nerve of neuromere C.

(D) *The Neuromery and Segmental Value of Neuromere* D.

This neuromere is only faintly indicated during Stage D, but is clearly visible although considerably smaller than neuromeres B or C in Stage E. It increases considerably in size during Stages F and G. During Stage J visceral pouch 3 is

developed latero-ventrad of and between neuromeres C and D, and the vagus neurencytium appears on the latero-dorsal surface of the latter. The rostral border of this neurencytium is at first continuous with the caudal portion of the glossopharyngeal neurencytium, but is clearly differentiated in Stage K and quite separated from it in Stage L. The third visceral pouch is perforated by a cleft in Stage M, and the vagus root now bifurcates, its rostral portion lying dorsad and caudad of the third visceral pouch, *i.e.* in the fourth visceral arch, and its caudal portion ultimately extends caudad of neuromere D. In Stage N the serially-arranged rootlets of the hypoglossal nerve appear, emerging from the brain-floor ventrad of the vagus root. Somite 5 lies ventrad of the latter nerve-root, and as in *Scyllium*, it appears to form no distinct myotome (Stages K–M). By the time the hypoglossal nerve-roots appear the inter-neuromeric grooves have nearly disappeared, but the position of the roots suggest that the more caudal of them constitute the ventral nerve of neuromere D. This neuromere shows no signs of further differentiation, and its position and relationship to the other head components suggest that it is to be identified as neuromere XII, and that it is the primary neuromere situated in the fifth head-segment (second post-otic). This head-segment contains also the fourth visceral and arterial arches, mesoblastic somite 5, the rostral portion of the vagus nerve, and the hypoglossal nerve. This agrees with the generally-accepted view as to the contents of the fifth head-segment.

6. Summary.

1. The fore-brain in *Sphenodon* appears to comprise one primary neuromere, the prosencephalon, which ultimately divides into three secondary definitive neuromeres. These are the telencephalon, the diencephalon, and the synencephalon (neuromeres I, II, and III; Wyeth, 1924, *b*).

2. The mid-brain comprises one primary neuromere, which lies in the premandibular head-segment. This segment contains also the following paired structures:—the premandibular head-cavity, mesoblastic somite 1, and the arteriæ lingualis and maxillaris. These arteries are possibly the ventral and dorsal vestiges respectively of an ancestral (premandibular) arterial arch. The oculomotor is the ventral, and the ophthalmicus profundus is the dorsal, nerve of this neuromere.

3. The primary neuromere of the mid-brain divides into two secondary definitive neuromeres, neuromeres IV and V, which at first are of approximately equal size. Ultimately neuromere V develops dorsally a pair of massive optic lobes, which overlie and partly obscure the inconspicuous neuromere IV.

4. Neuromere IV develops a pair of dorsal diverticula of its central cavity, which ultimately coalesce to form the sub-commissural organ. These diverticula are serially homologous with the

pair of dorsal diverticula possessed by each of the three secondary neuromeres of the fore-brain (Wyeth, 1924, *b*).

5. The hind-brain comprises four primary neuromeres, here termed neuromeres A, B, C, and D. As in human embryos, the caudalmost of these (neuromere D) is at first somewhat less conspicuous than the others, while neuromere B (the otic neuromere) is easily recognizable during all stages of development.

6. Neuromere A lies in the 2nd or mandible head-segment. Its ventral nerve is the trochlear and its dorsal nerve is the trigeminus. This head-segment also contains the following paired structures:—The mandibular head-cavity, the 2nd mesoblastic somite, and the 1st or mandibular arterial arch.

7. Neuromere A divides into three secondary definitive neuromeres (neuromeres VI, VII, and VIII).

8. Neuromere B does not subdivide, and is therefore primary and definitive (neuromere IX). It lies in the 3rd or hyoidean head-segment, which contains also the paired 3rd mesoblastic somites and the 2nd or hyoidean arterial arches. The facial is the dorsal, and the abducens is the ventral, nerve of this neuromere. On the dorso-lateral surface of each side of the neuromere develops the otic primordium, and the otic plate develops from the head-epiblast of the same region, but soon extends caudad into the region of the next head-segment.

9. Neuromere C is the primary neuromere of the 4th or first post-hyoid head-segment. The glossopharyngeal is the dorsal, and the rostral root of the hypoglossal appears to be the ventral, nerve of this neuromere. This head-segment contains the auditory organ (which has invaded it from in front), mesoblastic somite 4 (which ultimately breaks up into mesenchyme), and the 3rd (first branchial) arterial arch.

10. Neuromere C divides into two secondary definitive neuromeres (neuromeres X and XI). The rapid and extensive development of the auditory organ lying laterad of neuromere X appears to push back the other segment components enumerated above into neuromere XI.

11. Neuromere D lies in the 5th or second post-hyoid head-segment. This neuromere does not subdivide, and is therefore primary and definitive (neuromere XII). The vagus (rostral root) is the dorsal, and the hypoglossal is the ventral, nerve of this neuromere. The head-segment contains also the following paired structures:—The 4th (or second branchial), arterial arch, and mesoblastic somite 5, the caudal portion of this latter structure appearing to give rise to a few muscle-fibres, although the first definitive myotome appears to arise from the mesoblastic somite of the next caudal head-segment.

12. The primary neuromeres, some of which persist as definitive neuromeres, appear to possess a definitive and equal segmental value. The secondary neuromeres appear to possess no segmental value. They arise in regions, and during periods, characterised by rapid extension, and may be merely expressions of mechanical stresses.

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List of Reference Letters to Figures.

A.A. 1–6, arterial arches; *ac.fac.gang.*, acustico-facialis ganglion; *a.i.p.*, anterior intestinal portal; *Ao.*, aorta; *Aud.*, auditory pit or vesicle; *bucc.*, buccal cavity; *Cbl.*, cerebellum; *C.H.*, cerebral hemisphere; *ch.pl.*, choroid plexus; *ch.ty.*, chorda tympani; *C.p.*, posterior commissure; *C.s.*, superior commissure; *dec.* IV, decussation of 4th nerve; *dec.veli*, decussatio veli; *d.end.*, ductus endolymphaticus; *Di.*, diencephalon; *dk.*, dachkern; *d.s.*, dorsal sac; *ep.*, epiphysis; *epe.*, epencephalon; *F.B.*, fore-brain; *f.l.m.*, fasciculus longitudinalis; *g.cil.*, ciliary ganglion; *g.gas.* or *trig.g.*, gasserian or trigeminal ganglion; *g.genic.*, geniculate ganglion; *g.H.m.*, habenular ganglion; *g.i.p.*, ganglion inter-pedunculare; *g.pal.*, palatine ganglion; *g.pet.*, ganglion petrosum; *H.B.A*, *H.B.B*, *H.B.C*, *H.B.D*, primary neuromeres of hind-brain; *HB.*1–7, definitive neuromeres of hind-brain; *H.C.m.*, mandibular head-cavity; *H.C.pm.*, premandibular head-cavity; *H.ep.*, head-epiblast; *lam.opt.*, layer of opticus fibres; *lam.prof.*, deep layer of medullated fibres; *l.c.m.*, lamina commissuralis mesencephali; *l.c.sy.*, lamina commissuralis synencephali; *M.B.*1, *M.B.*2, secondary neuromeres of mid-brain; *Med.O.*, medulla oblongata; *mes.r.*, mesocœlic recess; *m.f.ch.pl.*, median fold of choroid plexus; *N.*I–XII, definitive neuromeres of brain; *n.*II–XII, cranial nerves; *n.*III.*cil.*, ramus ciliaris oculomotorius;

n.V.alv., ramus alveolaris inferior; *n.V.fr.*, ramus frontalis; *n.V.alv.*, ramus alveolaris inferior; *n.V.fr.*, ramus frontalis; *n.V.inf.o.*, ramus infraorbitalis; *n.ling.*, ramus lingualis; *n.V.md.*, ramus mandibularis; *n.V.mx.*, ramus maxillo-palatinus; *n.V.myl.hy.*, ramus mylohyoideus; *n.V.nas.*, ramus nasalis; *n.V.oph.*, ramus ophthalmicus profundus; *n.VII.hy.*, ramus hyomandibularis; *n.VII.pal.*, ramus palatinus; *n.VII.r.c.e.*, ramus communicans externus; *n.VII.r.c.i.*, ramus communicans internus; *n.g.*, neural groove; *Nuc.III*, nucleus oculomotorius; *nuc. prof.*, nucleus profundus; *o.ch.*, optic chiasma or its rudiment; *O.L.*, optic lobes; *optoc.*, optocoele; *o.s.*, oral sinus; *ot.N.*, otic neuromere; *ot.pl.*, otic plate or disc; *O.V.*, primitive optic vesicle; *par.*, paraphysis or its rudiment; *p.e.*, pineal eye or its rudiment; *p.f.g.*, primitive fore-gut; *phx.*, pharynx; *p.s.*, pineal sac; *p.st.*, pineal stalk; *r.g.*, recessus geniculi; *r.i.p.*, recessus infrapinealis; *r.post.o.*, recessus postopticus; *r.preo.l.*, recessus preopticus lateralis; *r.preo.m.*, recessus preopticus medius; *r.t.p.*, recessus thalami præneuclearis; *S.1*, *S.2*, etc., mesoblastic somites; *s.c.o.*, subcommissural organ; *s.end.*, saccus endolymphaticus; *Sy.*, synencephalon; *sym.*, sympathetic nerve-trunk; T_1, primary, and T_2, secondary telencephalon; *Tct.*, tectum mesencephali; *tr.t.b.dc.*, dorsal arcuate fibres of tractus thalamo-bulbaris; *tr.t.b.v.*, tractus thalamo-bulbaris ventralis; *tr.th.b.sp.*, tractus thalamo-bulbaris et spinalis; *V.3*, *V.4*, 3rd and 4th ventricles of brain; *v.c.m.*, vena capitis medialis; *vel.*, velum medullare anterior; *ves.t.*, vesica terminalis; *V.P.* 1–4, visceral pouches 1–4; *v.t.*, velum transversum.

23. On the Skull of *Tupaia*.

By W. E. Le Gros Clark, F.R.C.S., F.Z.S.

[Received February 3, 1925 : Read April 7, 1925.]

(Text-figures 1–6.)

The literature dealing with the cranial characters of the Tupaiidæ is far from scanty, and it is unnecessary here to enter into a systematic description of the skull. During the course of an investigation of the Tupaiidæ, I have made a careful study of the skull, in order, in the first place, to confirm the results of other authors. The present paper serves to record the observations which extend or modify the results of previous researches, and concludes with a brief summary of the features of the skull, which may throw light on the classification of the Tree-Shrews.

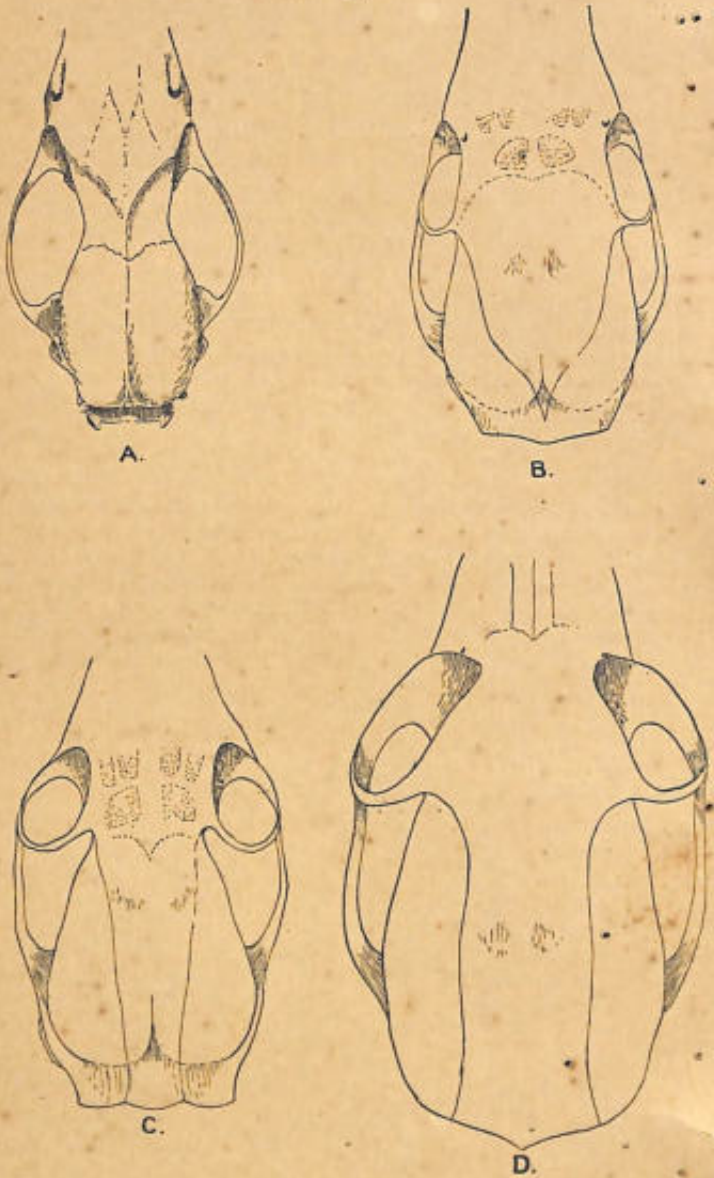
The material for this investigation consisted of a number of specimens of *T. minor* and *T. ferruginea* preserved in formalin; the partially disarticulated skull of *T. montana*, for the loan of which I have to thank Prof. D. M. S. Watson; a set of serial sections through the complete head of *Tupaia* (species uncertain), prepared and kindly lent by Dr. H. H. Woollard; and the rich collection of *Tupaia* and other skulls in the British Museum, for the opportunity of studying which I am greatly indebted to Mr. Oldfield Thomas.

In general form, as Gregory (4) has described, the brain-case of *Tupaia* is large and well-rounded, the frontal region being especially conspicuous for its relative breadth. This is shown in text-fig. 1, which represents the norma verticalis of the skull of *Tupaia minor* compared with the skull of *Gymnura*, *Ptilocercus*, and *Lemur*.

In *Tupaia* the development of the frontal region has led to a divergence of the temporal crests anteriorly. In *Ptilocercus* this condition is carried further so that, as in *Lemur*, the temporal crests do not meet at all on the vertex. It may be noticed, also, that in *Ptilocercus* the orbits are rotated forwards and approximated to each other so that the posterior end of the nasal cavities occupy much more of an interorbital position and the frontal poles of the brain, to a corresponding degree, do not extend so far anteriorly in relation to the orbits. In this respect *Ptilocercus* serves to link up *Tupaia* with *Lemur*.

The angle made by the antero-posterior plane of the orbital margin with the mesial plane has been measured in a number of

Text-figure 1.



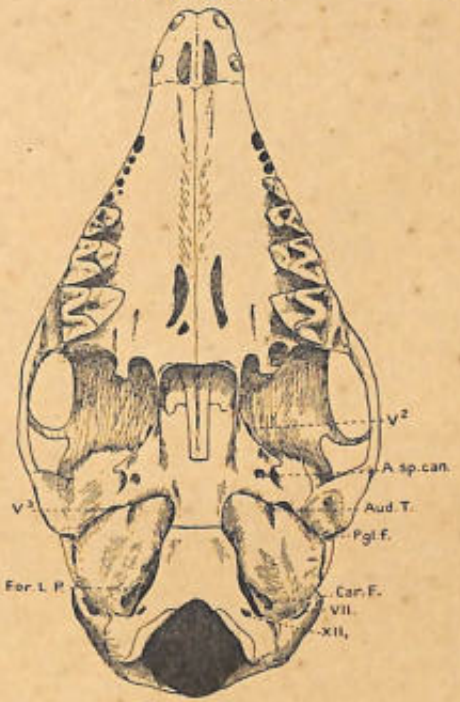
Norma verticalis of the skull of (A) *Gymnura*?; (B) *Tupaia minor*; (C) *Ptilocercus*; (D) *Lemur catta*.

skulls, and the average results of these measurements are as follows:—

Tupaia	17°
Ptilocercus	37°
Lemur catta	41°

The reduction of the olfactory bulbs is accompanied by alterations in the ethmoidal region of the basis cranii, leading to a

Text-figure 2.



Basal view of skull of *Tupaia montana* (immature specimen).

Asp.can. Alisphenoid canal.
Aud.T. Auditory tube.
Car.F. Carotid foramen.
For.L.P. Foramen lacerum posterius.
Pgl.f. Postglenoid foramen.
V². Foramen rotundum. } (Rendered conspicuous in this figure for clearness.)
V³. Foramen ovale. }
VII. Stylomastoid foramen.
XII. Hypoglossal canal.

partial flexion of the face on the basicranial axis which has been noted by Gregory. Similar changes have been initiated in the occipital region where the development of the occipital poles

of the brain is associated with a depression of the plane of the foramen magnum from a vertical position.

The basal aspect of the immature skull of *T. montana* is shown in text-fig. 2. The arrangement of the various foramina in this region is here shown. It is important to note the degree of differentiation and separation of these foramina.

The carotid foramen (through which the internal carotid artery enters the bulla) is quite distinct from the stylomastoid foramen. To the medial side of the former lies the elongated foramen lacerum posterius. The Eustachian tube leaves by a slit-like opening on the anterior aspect of the bulla. The foramen ovale is hidden from view by the greatly expanded bulla. The posterior opening of the alisphenoid canal can be seen in the pterygoid region, and the anterior opening is, in the majority of instances, separate from and immediately to the lateral side of the foramen rotundum. The latter is quite distinct from the sphenoidal fissure, which, again, is separated from the optic foramen by a bony spicule.

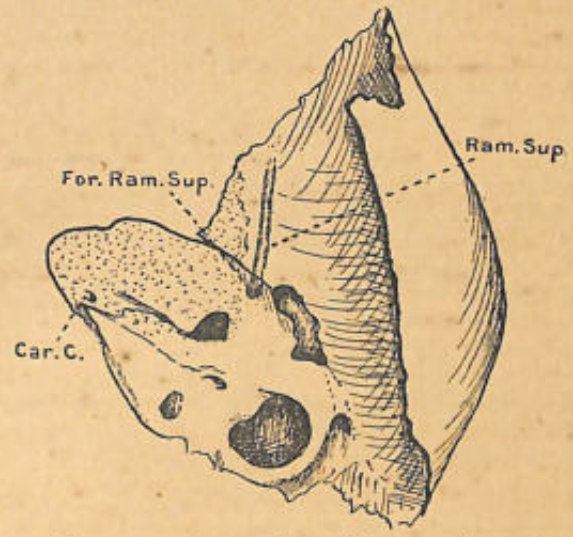
Tympanic Region.

This has been dealt with in considerable detail by van Kampen (8), who has pointed out that in the construction of the tympanic bulla, the position of the ectotympanic and the course of the entocarotid artery through the tympanic cavity, *Tupaia* differs widely from the Lipotyphla and resembles the Lemurs of Madagascar. I propose to deal in some detail with the course of the entocarotid and its branches in this region, as my observations are not in agreement with a statement made by Gregory (6). This author, in reference to the branches of the art. stapedia, relying on Hyrtl's (7) work, says that the "ramus inferior is large and issues from the tympanic cavity anteriorly as in *Erinaceus*."

An examination of the tympanic region from below reveals no foramen for this branch (ramus inferior) as in *Erinaceus* and other Lipotyphla, and herein there is agreement with the illustrations given by van Kampen on page 451 of his monograph. The actual state of affairs, as shown by dissection and corroborated by serial sections, is as follows:—

The entocarotid pierces the tympanic bulla at its posterior end, close to the foramen lacerum posterius. After a short course (about 1 mm. in *T. minor*) in an osseous canal on the medial wall of the tympanic cavity, the stapedial branch is given off. The latter runs upwards to the roof of the cavity, piercing the stapes on its way. It then passes forwards and pierces the os petrosum close to its junction with the squamous bone at the lateral margin of the alisphenoid (for.ram.sup., text-fig. 3). The vessel now forms the arteria mening. med., and runs forwards in a groove in the middle fossa of the skull, eventually to enter the orbital cavity and effect an anastomosis with the ophthalmic artery.

Text-figure 3.

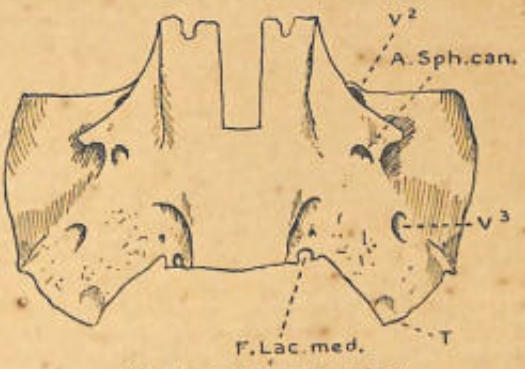


Upper aspect of temporal bone of *Tupaia montana*.

Car.C. Opening of carotid canal.
Ram.Sup. Groove for ramus superior of art. stapedia.
For.Ram.Sup. Foramen for ramus superior.

(The stippled area indicates the surface covered by the alisphenoid.)

Text-figure 4.



Alisphenoid of *Tupaia montana*.

A.sph.can. Alisphenoid canal.
F.Lac.med. Notch or foramen for internal carotid artery.
T. Tympanic process.
V^2. Foramen rotundum.
V^3. Foramen ovale.

The entocarotid (which is much smaller in calibre than the art. stapedia) runs forwards and medially, pierces the upper surface of the petrous bone close to its apex (car.c., text-fig. 3), and enters the cranial cavity by passing through a notch or foramen at the posterior border of the junction of the alisphenoid and basisphenoid (for.lac.med., text-fig. 4).

A careful scrutiny of serial sections of the head of an immature individual shows, on one side only, one or two minute twigs given off by the art. stapedia as it enters the intracranial cavity, and which appear to run down through the suture between the bulla and the alisphenoid. These can hardly be called a ramus inferior, though it is possible that they may represent the remains of this vascular connection with the internal maxillary artery.

It is therefore clear that in the course of the entocarotid and its branches, and in the relative sizes of the entocarotid and stapedial arteries, there is complete agreement with the condition found by Tandler (10) in *Lemur varius*, and a corresponding divergence from the Lipotyphla.

The Turbinals.

By means of dissections and serial sections, I have been able to confirm the results of Paulli's investigations (9) with reference to *Tupaia*. The Tree-Shrew resembles the Lipotyphla and Lemuroidea in the possesion of four endoturbinals (including, it should be noted, the naso-turbinal). Of these, the second endoturbinal divides to form two olfactory scrolls, so that altogether there are five of these scrolls. *Tupaia* agrees with *Lemur* and differs from all the Lipotyphla examined by Paulli (*Erinaceus*, *Talpa*, *Sorex*, and *Centetes*) in having two ectoturbinals only. The reduction of the ectoturbinals associated with a general simplicity in the architecture of the turbinated bones parallels the evidence derived from the brain, in which the olfactory regions are relatively diminished (2).

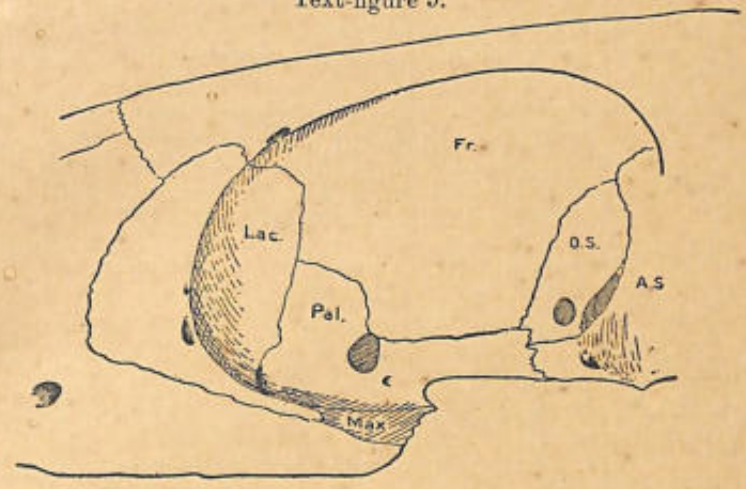
The Orbits.

The construction of the bony orbit has been made clear by a study of young skulls and confirmed by the serial sections. The bones entering into the formation of the orbital walls are shown in text-fig. 5, where it will be seen that they are arranged as has been shown to be the case in *Lemur* by Wood-Jones (11).

The palatine bone extends forwards to articulate with the lachrymal, and the ethmoid does not appear. This is what might be expected, for the forward extension of the palatine bone would seem to be determined by the position of the naso-palatine foramen, and this, in turn, depends upon the position of the nasal cavities relative to the orbits. In those Prosimiæ which show a recession of the nose between the eyes the orbital plate of the palate becomes correspondingly abbreviated, and the ethmoid begins to take a part in the formation of the medial wall of the orbit.

Carlsson (1) thinks that the ethmoid appears in the orbit in a 38-mm. fœtal specimen of *Tupaia*, but expresses uncertainty on the point.

Text-figure 5.

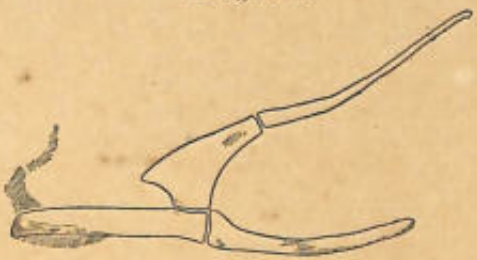


Orbit of *Tupaia* (zygomatic arch removed).

The lachrymal foramen lies immediately outside the orbital margin.

The supraorbital foramen (sometimes a notch), which is present in *Tupaia*, is absent in *Ptilocercus*, and text-fig. 1 seems to indicate that this is associated with the forward and inward rotation of the orbits in this animal as in Lemurs.

Text-figure 6.



Hyoid bone of *Tupaia ferruginea*.
(Anterolateral view from left.)

Hyoid Bone.

The hyoid bone of *Tupaia* has not, so far as I am aware, hitherto been described. The basihyal is a simple attenuated bar

of bone, slightly flattened antero-posteriorly, and strongly curved to form a complete semicircle. The thyrohyal is simple, and shows a slight caudal convexity.

The ceratohyal is a flattened triangular piece of bone, somewhat convex anteriorly and concave posteriorly, and articulates with the basihyal by a synovial joint.

Extending from the upper end of the ceratohyal up to the bulla is a slender epihyal.

The dimensions in *T. ferruginea* are as follows:—

Basihyal.....	5 mm.
Thyrohyal	5·5 ,,
Ceratohyal	3·5 ,,
Epihyal	6·25 ,,

The general simplicity of the hyoid bone is to be noted.

Conclusion.

A study of the skull of *Tupaia* reveals a combination of primitive or metatheroid features with characters that can be paralleled only among the Primates, and this conclusion is in conformity with the condition of the brain, genital system, etc. Primitive characters are evidenced in the tympanic wing of the alisphenoid, palatal vacuities, alisphenoid canal, and the dentition (Gregory).

The primitive and generalized status of *Tupaia* among the Mammalia is evident. The important question is to assess the value of the characters which appear to ally *Tupaia* with the Primates.

Taken alone, the relatively-expanded brain-case might be regarded as a character acquired in correlation with arboreal habits, and of no taxonomic value. Similarly, the reduction of the olfactory apparatus may be directly associated with this mode of life. With regard to the latter, however, the fact that the Squirrel shows no reduction as compared with terrestrial rodents (the Squirrel and the Rabbit both possess four ecto-turbinals, according to Paulli) is worthy of note, especially as the Squirrel bears such a remarkable resemblance to the Tree-Shrew in its activities and superficial appearance.

The following points, however, can hardly be regarded in this light:—

a. The differentiation of the vascular and nervous foramina in the base of the skull.
b. The construction of the tympanic bulla.
c. The shape and position of the ectotympanic.
d. The course of the carotid artery through the bulla.
e. The absence of a ramus inferior of the stapedial artery (a branch which is present in the Lipotyphla and typically absent in the Lemurs).

f. The tympanic ossicles, which approach in their form those of Lemurs and higher Primates (Doran, 3) and depart widely from the Lipotyphlous type.

g. The form of the ectopterygoid fossæ suggesting a Lemuroid condition (Gregory).

h. The presence of malar foramina.

i. The well-developed postorbital bars.

These features, combined with the general characters of the skull of *Tupaia*, are very significant, and seem to lead to a conclusion which is irresistible—this is, that *Tupaia* is a representative of a very generalized group of insectivorous mammals which was an offshoot from the stem of the Primate phylum after the latter had become definitely differentiated from other mammalian phyla.

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24. On a new Species of *Temnocephala* (*T. chæropsis*) (Trematoda) from West Australia.

By MARY L. HETT, B.Sc., F.Z.S., Junior Lecturer in Zoology, Bedford College.

[Received December 11, 1924: Read March 3, 1925.]

(Text-figures 1–8.)

TEMNOCEPHALA CHÆROPSIS, sp. n. Host: *Chærops preissi*. Habitat: West Australia. 2 mm. long. Five tentacles present. Sucker rather small, provided with well-marked circular ridges on its outer surface. A pair of posterior glandular organs present. Four accessory pouches at the base of the receptaculum vitelli.

The specimens on which this investigation was made were collected in West Australia and kindly placed at my disposal by the late Professor Dendy. The work was carried out in the Zoological Department of University College, Gower Street.

A number of individuals were taken from a stream in the neighbourhood of the Mammoth Cave, W.A., where they occurred as parasites of *Chærops preissi*. This *Temnocephala* differs from other species of the genus in several respects, notably in the possession of a pair of posterior glandular organs and in the structure of the sucker.

External Features (text-figs. 1 & 2).

The body is oval in shape and about 2 mm. long. There are five tentacles, which are no doubt contracted in the preserved specimens, but, even allowing for this, they are relatively short.

The sucker, which is very muscular, has a diameter equal to about half the width of the body. The margin of the cup is crenated, and the epidermis of the outer surface is raised into a number of circular ridges with rounded outline. There is also a series of ridges encircling the stalk of the sucker, but here the margin of each ridge is produced to form a narrow projecting rim with a sharp edge (text-fig. 3). The peripheral region of the concavity of the sucker is marked off from the central area by a groove-like depression; in surface-view the sucker appears to consist of an inner darker portion, with a pit at the centre, and a lighter peripheral portion with a wavy margin (text-fig. 1).

The specimens having been for some time in spirit, there was no evidence of pigment on examination of the entire animal, but

Text-figure 1.

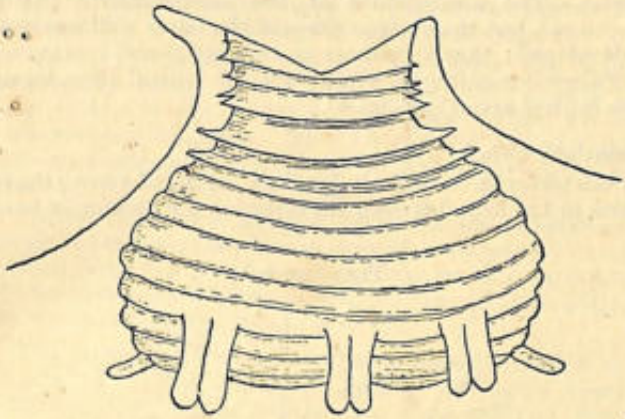
External features of *Temnocephala charopsis*. Ventral view.

Text-figure 2.

External features of *Temnocephala charopsis*. Lateral view.

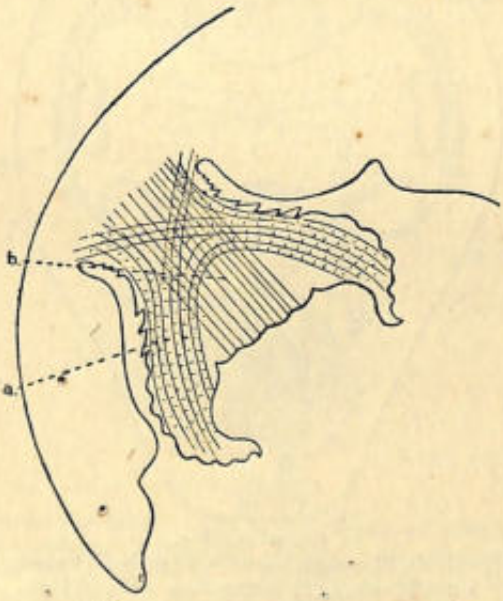
sections showed that there were a number of pigment-cells present below the epidermis on the dorsal side of the body

Text-figure 3.



Sucker. Lateral view.

Text-figure 4.



Sucker. Median longitudinal section.
(*a*) oblique fibres; (*b*) dorso-ventral fibres.

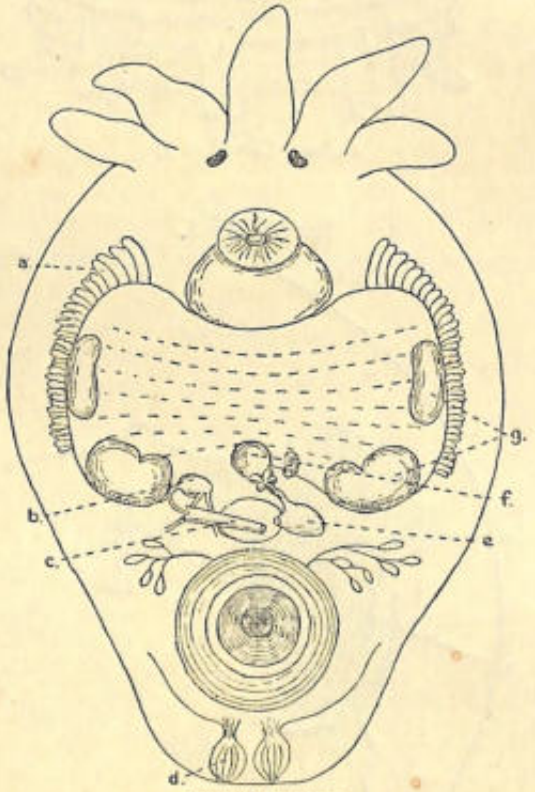
Internal Anatomy.

Sucker.—The musculature of the sucker shows the usual arrangement, but the oblique fibres of the outer wall are specially well developed: they terminate on the peripheral portion of the sucker already mentioned, while the dorso-ventral fibres terminate on the central area (text-fig. 4).

Alimentary Canal.

In the pharynx the unicellular glands situated among the radial muscles in the area between the anterior and posterior bands of

Text-figure 5.



General anatomy.

(*a*) rhabdite glands, (*b*) vesicula seminalis, (*c*) penis, (*d*) posterior glandular organ, (*e*) ootype, (*f*) receptaculum vitelli, (*g*) testes.

circular muscles are very conspicuous. The intestine has seven or eight partitions.

The Excretory and Nervous Systems are of the usual type.

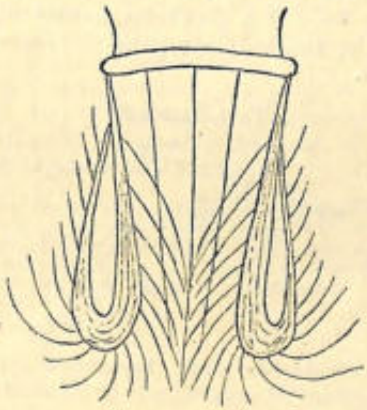
The Reproductive System (text-fig. 5) resembles that of *T. fasciata*, but differs from it in the following particulars:—

1. Testes: The anterior pair are oval with the long axis parallel to the length of the body. They lie opposite to the anterior portion of the intestine. The posterior pair are bilobed and transversely elongated. They lie entirely behind the intestine or at its extreme posterior end on either side of the genital aperture.

2. The penis, which is straight, has no terminal dilatation; the introvert is lined with numerous rows of small spines. A narrow duct leads from the proximal end of the penis to a small oval vesiculum seminalis, which receives the paired vasa deferentia. There is no distinct ejaculatory sac.

3. The receptaculum vitelli is remarkable in possessing four small pouch-like diverticula at its base just before it passes into the oviduct. From their position, and from the fact that they contain sperms but no yoke, they are probably to be regarded as receptacula seminales. The walls are thick and muscular and quite different in character from that of the receptaculum vitelli (text-fig. 7). These pouches do not appear to have been described for other species of *Temnocephala*.

Text-figure 6.

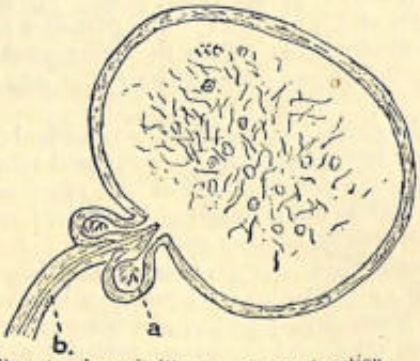


Introvert of penis.

Integumentary Glands.—The usual types of integumentary glands are present. "Prostate glands" occur throughout the body in close juxtaposition to the rhabdite glands, which are very large and numerous. Connected with the rhabdite glands are a curious pair of organs behind the sucker. The posterior edge of the body projects a certain distance beyond the sucker, owing to

the relatively small size of the latter; the organs in question lie one on either side of the middle line in the flattened area posterior to the sucker. In surface-view they have the appearance

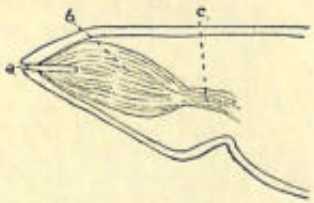
Text-figure 7.



Receptaculum vitelli. Longitudinal section.
(*a*) receptaculum seminis, (*b*) oviduct.

of an oval bundle of cigar-shaped bodies connected at their upper ends to a strand of tissue, while their lower ends are close to the posterior edge of the body (text-fig. 5). On examining these organs by means of transverse and longitudinal sections it became evident that they were of a glandular nature and bore a close resemblance to the tentacular organs in some Trematodes—e. g., *Gyrodactylus*.

Text-figure 8.



Posterior glandular organ. Longitudinal section.
(*a*) aperture, (*b*) elongated cells, (*c*) fibrous strand.

Each organ was made up of a group of cigar-shaped structures arranged to form a solid oval or spindle-shaped cone. The cigar-shaped elements had the appearance of cells, although nuclei could not be detected, and the cytoplasm contained longitudinal fibrillæ. The whole organ was enclosed in a membranous sheath, which opened to the exterior by a minute pore at the posterior edge of the body (text-fig. 8). At their proximal ends the elongated cells were continuous with a number of fibrous strands, and

these in their turn were connected with a band of curious fibrous-looking tissue which ran forwards in a slightly lateral direction till it passed into a group of rhabdite cells lying on the outer side of the testes. At first sight it seemed possible that the fibrous tissue might represent a small nerve-strand, but on close examination it became obvious: (1) that the fibrous tissue differed from that of the nerves, since it contained a lightly staining cytoplasm, whereas the contents of the nerve-tubes are practically colourless; (2) that this tissue is almost identical in structure with that of the rhabdite cells when free from secretion *.

These observations, together with the fact that strands of tissue passing off from the organs under discussion can be definitely traced to a group of rhabdite cells, leave, I think, no room for doubt as to the glandular nature of the whole of the apparatus, and this conclusion is supported by the resemblance in appearance and general arrangement to the tentacular organs of *Gyrodactylus*. It would appear to be a locally specialised and concentrated arrangement for the pouring out of the gelatinous secretion which adds to the adhesive power of the body. As in other species of *Temnocephala*, there are two main groups of ducts carrying the secretion of the rhabdite glands to the exterior, one group passing to the tentacles, the other opening on the inner surface of the sucker. In *T. chæropsis*, however, the glandular organs described above must form an additional channel for the outward passage of the secretion from the rhabdite cells posterior to the intestine. Presumably here the posterior rim of the body forms a further point of adhesion, a condition which would be facilitated by the fact that this region projects beyond the sucker. It is to be noted that the sucker also is a more powerful organ of attachment than usual. Possibly the habit of life necessitates a closer adherence to the host.

* Haswell describes the cytoplasm of these cells as sometimes presenting an open network of fine branching threads. This structure is obscured when the cells are full of the minute rod-like bodies which they secrete, and, indeed, the appearance is so different in the two cases that the identity of the cells with and without secretion might easily be overlooked on a superficial examination.

25. On the Structure of the External Genitalia in Dipodidæ and Zapodidæ (Rodentia) as a Classificatory Character.

By B. S. Vinogradov, Curator-Assistant, Zool. Mus. Russ. Acad. Sc.*

[Received December 4, 1924; Read March 3, 1925.]

(Plates I.–V.)

In the present paper I intend to apply some characters of external male genitalia and os penis to the classification of two interesting families of rodents, the Dipodidæ and Zapodidæ. Some peculiarities of these organs were observed by Tullberg†, Lataste‡, Sonnini §, and other authors. Such characters have been used in the classification of *Sicistinæ* by L. v. Méhely ‖, and in the classification of Dipodidæ by R. I. Pocock ¶.

Rich material in the collections of the Zoological Museum of the Russian Academy of Science enabled me to examine a considerable number of forms, and among them some rare species as *Euchoreutes naso* Scl., *Salpingotus kozlovi* Vinogr., *Pygeretmus platyurus* Licht., *Eozapus setchuanus* Pouss., etc. I am not inclined to form a classification exclusively on the basis of the characters of the genitalia; and it seems to me that a rationally constructed system must be based on a complex of different anatomical and external characters. But a study of the genitalia allows one to suppose that their modifications are usually correlated or coincide with many essential modifications in the structure of the skull, teeth, skeleton of hind-foot, etc.; and therefore it seems to me indubitable that the modifications of the genitalia furnish important classificatory characters in Zapodidæ and Dipodidæ, as has indeed been shown already by Méhely and Pocock (*l. c.*). As the result of my study I have thought it necessary to make some changes in the classification of Dipodidæ, and in another paper I shall try to prove that such changes are based not only on the characters of genitalia, but on many other morphological peculiarities.

To shorten the descriptions I have reduced them to analytic keys, and illustrated them with schematized but exact figures, prepared with the drawing apparatus of Abbé Zeiss.

The morphology of the penis of Rodents is not known satisfactorily. L. v. Méhely showed that the so-called glans penis of

* Communicated by Martin A. C. Hinton, F.Z.S.

† Tullberg, 'Ueber das System der Nagethiere' (Upsala, 1899).

‡ Lataste, "Mammifères de Barbarie," Act. Soc. Linn. Bordeaux, vol. xxxi. p. 56 (1885).

§ Sonnini, 'Voy. en Egypte,' 1800, pp. 173–174.

‖ L. Méhely, Ann. Mus. Nat. Hung. vol. xi. (1913).

¶ R. I. Pocock, Proc. Zool. Soc. Lond. pt. iii. pp. 675–678 (1922).

Sicistinæ is not homologous with the human glans penis. In the following description, under the name penis I suppose only its terminal part freed from its tegument.

A study of the structure of the external genitalia of Dipodoidea enables us to distinguish easily not only most of the species and genera, but also some of the subfamilies, as will be shown below; but it is very difficult to find any constant and sharp characters in the structure of the genitalia characteristic of the whole superfamily Dipodoidea and both its families—Zapodidæ and Dipodidæ. Therefore, I cannot give a diagnosis of Dipodoidea on the basis of the structure of genitalia, and the diagnosis of the families will be only as follows:—

Os penis always present; its basal part without a median prominent crest ..... Fam. ZAPODIDÆ. (Pl. V. figs. 1–6.)

Os penis not always present; but when present its basal part has always a median prominent crest. Fam. DIPODIDÆ. (Pl. III. figs. 1–6.)

Family DIPODIDÆ.

I think the family Dipodidæ after more detailed study will be separated in four or five natural groups which I consider here provisionally as subfamilies—*Alactaginæ*, *Dipodinæ*, *Euchoretinæ*, *Salpingotinæ*, and perhaps *Cardiocraniinæ*. Such a proposition is based not only on the structure of genitalia, but also on many osteological and anatomical characters. Now I give here only some distinguishing characters of genitalia:—

Penis (viewed from above) stout, with well-developed horny spines or scales directed mostly backwards.

Os penis absent. The tip of penis simple, without lateral folds ("pouches"); on the lower surface of penis no deep longitudinal furrow Penis ovate, cordate or lanceolate, covered with small spines (long spikes always absent).
Subf. ALACTAGINÆ. (Pl. I. figs. 1–9.)

Os penis present. The tip of penis mostly provided with deep folds ("pouches") on each side of external orifice of urethra; on the lower surface of penis a deep longitudinal crease always present; on each side of it may be another shorter crease. Penis ovate or parallel-sided. In addition to the small spines a pair of long styliform spikes mostly present. A naked, mostly well-defined area on the dorsum of penis present (such an area situated on the level of the median ridge of os penis).
Subf. DIPODINÆ. (Pl. II. figs. 1–4; Pl. III. figs. 1–5.)

Penis (viewed from above) thin, gradually becomes thinner to the tip, or flattened laterally and not covered with perceptible spines or scales (on its surface may be seen only very minute grains).

Os penis present; its tip, covered with epithelium, strongly curved above. Penis flattened laterally.
Subf. EUCHORETINÆ. (Pl. II. fig. 6; Pl. III. fig. 6.)

Os penis absent. Penis thin, gradually becomes thinner to the tip and somewhat flattened laterally near the tip.
Subf. SALPINGOTINÆ*. (Pl. II. fig. 5.)

* This subfamily seems to be nearly related to *Cardiocraniinæ*, but unfortunately I had only a skin of *Cardiocranius* and a spirit specimen of a female, and therefore could not introduce this species in the present analytical key.

Subfamily ALACTAGINÆ.

Spines on the upper surface of penis all directed backwards; such spines occupy almost the whole upper surface.
A longitudinal furrow on the upper surface absent. Penis ovate or barrel-shaped.
Spines minute and pointed. *Alactaga mongolica* (Radde). (Pl. I. fig. 3.)
Spines coarser and blunt... *A. suschkini* Sat. (Pl. I. fig. 4.)
A longitudinal furrow on the upper surface present. Penis cordate, with pointed or blunted tip.
Penis 6·3 mm. or more. The longitudinal furrow reaches only to the middle of penis or a little further and divides in two divergent furrows.
Upper surface of penis with about sixty spines. The basal swollen portion of penis is very large. Penis mostly about 7·3 mm. in length.
A. saliens (Gmel.). (Pl. I. fig. 1.)
Upper surface of penis with about forty spines. The basal swollen portion of penis is moderate. Penis about 6·3 mm. in length .. *A. severtzovi*, sp. n.* (Pl. I. fig. 2.)
Penis less than 6·3 mm. Longitudinal furrow reaches to the tip and only sometimes divides in slightly divergent furrows near the tip.
Basal third or quarter of penis without spines. Longitudinal furrow well-marked, slightly divergent near the base and near the tip. The tip is pointed.
A. elater (Licht.). (Pl. I. fig. 5.)
Basal part of penis covered with spines. Longitudinal furrow less plainly marked, sometimes interrupted in the middle, but mostly reaching to the tip. The tip is mostly truncated ... *A. williamsi* Thos. (Pl. I. fig. 6.)
Spines of the upper surface of penis near its base curved inwards. A well-marked naked area (without spines) is present in the basal portion of the upper surface.
In the middle of upper surface two weak longitudinal depressions present. The spines near the base slightly curved inwards. Penis relatively large, lanceolate.
Alactagulus acontion (Licht.). (Pl. I. fig. 7.)
In the middle of upper surface a sharply-marked, narrow, deep longitudinal depression present. The spines near the base curved very strongly inwards. Penis relatively small, cordate.
Pygeretmus platyurus (Licht.). (Pl. I. fig. 8.)

(The penis of *Scarturus tetradactylus* (Pl. I. fig. 9) is very similar to that of other *Alactaginæ*, as one may judge from the description and figure given by Mr. Pocock (*l. c.*). Unfortunately I have had no opportunity of examining this animal, therefore I have not introduced it in the present analytical key.)

Subfamily DIPODINÆ.

Median crest of os penis situated on basal plate; antero-external angles of basal plate sharply marked, acute. On the lower surface of os penis a deep longitudinal crease present, which rises from the basal portion of penis; on each side of it may be only shallow furrows ..... Gen. SCIRTOPODA Brandt. (Pl. II. figs. 1, 3, 4; Pl. III. figs. 1, 3-5.)

* For diagnosis of this species see below.

Two long spikes on the penis present. The surface of penis covered with well-developed short spines; such spines are longest near the base of the enormous spikes. A naked area is sharply marked, covered with many furrows and wrinkles. Penis is broad, somewhat flattened dorso-ventrally, oval (viewed from above). Median crest on the basal plate of os penis is very sharply prominent.
The style of os penis is transformed into a thin broad plate, separated from the basal plate by a well-marked narrowing. The median crest on the base of os penis from the side view with a broad rounded border. Penis about 13 mm. in length. Two spikes very long (8·5 mm.), far overtopping the tip of penis (in adult specimens), lying in a weak median depression of the upper surface of penis. *Sc. mauritanica* Duvern. (Pl. II. fig. 1; Pl. III. figs. 3–4.)

The style of os penis normal, not broadened, not separated from the basal plate by a narrowing. The median crest on the base of os penis (from the side view) with an acute-angled border. Penis about 8 mm. in length. Two spikes of moderate length, not overtopping the tip of penis (2·8 mm.), not lying in a weak median recess of the upper surface. *Sc. telum* Licht. (Pl. II. fig. 3; Pl. III. fig. 1.)

Two long spikes on the penis absent. The surface of penis covered by very minute scales or spines, somewhat stronger on the distal portion of the upper surface. Penis mostly cylindrical in form, parallel-sided. Median crest on the basal plate is feebly prominent ..... *Sc. jaculus* L. (Pl. II. fig. 4; Pl. III. fig. 5.)

Median crest of os penis situated on the style (on its basal portion). Antero-external angles of the basal plate not marked, rounded. On the lower surface of penis a deep longitudinal fissure rises only from the middle of penis; on each side of it two other deep fissures present, which rise from the base of penis and extend almost to the tip. (Other external characters essentially as in *Sc. mauritanica*—two long spikes, pouches on each side of external aperture of urethra, etc.) Gen. DIPUS (based on *Dipus sagitta*). (Pl. II. fig. 2; Pl. III. fig. 2.)

The subfamily *Euchoreutinæ* (Pl. II. fig. 6; Pl. III. fig. 6) has only one genus and species (*Euchoreutes naso* Sel.). Subfamily *Salpingotinæ* (Pl. II. fig. 5) has one genus with two species (*S. kozlovi* and *S. crassicauda* Vinogr.); the penis of the first-named species is described above, but that of *S. crassicauda* is unknown. The penis of the single representative of the subfamily *Cardiocraniinæ*—*Cardiocranius paradoxus* Sat.—is also unknown.

Family ZAPODIDÆ.

On the upper surface of distal portion of penis a longitudinal, mostly very deep, slit present ("Samenfalte" of Méhely); in the end of it is seen a prominent tubercle, which is formed by the tip of the os penis. The whole surface of penis covered with minute horny spines or scales. Os penis more or less bow-shaped. Subf. SICISTINÆ. (Pls. IV.–V.)

In addition to the minute spines and scales, there are on the penis one or two more robust spines situated on the strictly fixed points. The base of the os penis forms an enlarged plate. On each side of longitudinal slit ("Samenfalte") rises an oblique slit, which is united with the median one.

In the bottom of the deep median slit one or two relatively long spines present (only partly seen at the exterior). On the basal and lower part of penis no long spines. Os penis considerably bow-shaped.

The longest spine only one in number; before its base is situated one separate concave horny scale of variable shape. Two lateral slits, rising from the median slit, divergent Λ-shaped, not passing into the lateral surface. Penis is not divided in two lobes. The basal plate of os penis nearly triangular, not much enlarged; the style relatively long, provided with a thin lamellar border. On the tip of os penis no canalicular widening.

Sic. nordmanni Keys. & Blas. (=*S. loriger* Nath.). (Pl. IV. fig. 1; Pl. V. fig. 1.)

The longest spines two in number; before its base are situated only minute numerous horny scales. Two lateral slits, rising from the median slit, divergent W-shaped, passing on to the lateral surface and dividing the penis into two lobes (superior and inferior). The basal plate of os penis rhomboidal, much enlarged; the style relatively short, without lamellar border. On the tip of os penis a canaliculate widening present.

Sic. montana Méh. (Pls. IV.–V. fig. 2.)

In the bottom of the deep median slit no long spines, but externally on the lateral surface of penis two large rather stout spines present; the lower surface of penis armed with less enlarged spines; six of them, more prominent, are situated nearly in two longitudinal rows.

Sic. napæa Holl. (Pls. IV.–V. fig. 3.)

In addition to the minute spines and scales there are on the penis no separate spines and scales. The base of os penis feebly enlarged. On each side of the longitudinal slit of penis no oblique slits.

Penis thin and long, slightly clavate, covered with thin pointed spines directed backwards. Longitudinal slit occupies about a third of total length of penis. The base of os penis very feebly enlarged, rather convex and gradually passing into the style ..... *Sic. caucasica*, sp. n.* (Pls. IV.–V. fig. 4.)

Penis rather stout and short, slightly enlarged to the tip, covered with blunt, rounded, horny plates. Longitudinal slit occupies about a half of total length of penis. The base of os penis somewhat more enlarged, rather concave, and more abruptly separated from the style.

Sic. caudata Thos. (Pls. IV.–V. fig. 5.)

On the upper surface of distal portion of os penis no longitudinal slit. A prominent tubercle, formed by the tip of the os penis, projects from the campanulate end of the penis. The surface of penis (except that of its basal portion) covered with soft oval prominent tubercles. Os penis is bowed very feebly and in reverse direction as compared with *Sicistinæ*; only the tip of penis bowed upwards, as in *Sicistinæ*.

Subf. ZAPODINÆ (based on *Eozapus setchuanus* Pous.). (Pls. IV.–V. fig. 6.)

CONCLUSIONS.

The brief description of some peculiarities of the external genitalia of Jerboas and Jumping-mice in the foregoing pages enables me to make some remarks on the classification of Dipodoidea.

* For diagnosis of this new species see below.

In the present paper I adopt the following classification of Dipodoidea:—

I. Family ZAPODIDÆ.
  1. Subfamily SICISTINÆ.
  2. „ ZAPODINÆ.

II. Family DIPODIDÆ.
  1. Subfamily ALACTAGINÆ (*Alactaga, Alactagulus, Pygeretmus, Scarturus*).
  2. „ DIPODINÆ (*Dipus, Scirtopoda*).
  3. „ EUCHOREUTINÆ (*Euchoreutes naso* Sel.).
  4. „ SALPINGOTINÆ (*Salpingotus, kozlovi, S. crassicauda* Vinogr.)
  5. „ CARDIOCRANIINÆ (*Cardiocranius paradoxus* Satun.).

This system is based on the classifiication of M. Lyon*, but I have separated the group of *Alactaga* and its allies from the *Dipus* group, and established also two new subfamilies for *Salpingotus* and *Cardiocranius*.

The subfamily *Alactaginæ* is sharply separated from *Dipodinæ* not only by the absence of os penis, but also by many important characters in the structure of the hind-foot, skull, upper incisors, etc. *Scarturus tetradactylus* was mentioned as an intermediate form between the *Alactaga* and *Dipus* groups, but it seems to be only an aberrant member of *Alactaginæ*, which has no hallux on the hind-foot. *Pygeretmus platyurus* is very closely related to the genus *Alactagulus*, as shown already by Nehring†; such resemblance exists also in the characters of the external genitalia, as is shown above. The genus *Alactagulus* differs from *Alactaga* not only by the number of the cheek-teeth and their structure, but also by some peculiarities of the penis.

The group of *Dipodinæ*, which I consider here as a subfamily, seems to me quite natural and distinctly separated from *Alactaginæ*, but the arrangement of the genera and subgenera in this group is not quite clear now. However, it is possible to affirm now that *Dipus sagitta* with its near relations (*D. loftusi* Blanf., *D. sowerbyi* Thos.) must be considered as members of the separate genus *Dipus*, which may be characterized by the structure of the tympanic and mastoid part of the skull, the dental characters, and also by some peculiarities of the genitalia, as shown above.

The Asiatic *Scirtopoda telum* Licht. is more like the African Three-toed Jerboas than the Asiatic *Dipus sagitta*, as observed already by Brandt‡, who put *S. telum* and the African Three-toed Jerboas into the subgenus *Scirtopoda* and *Dipus sagitta* into the subgenus *Dipus*. Now both groups may be considered as separate genera. Perhaps the genus *Scirtopoda* may be divided into

* M. Lyon, Proc. U.S. Nat. Mus. xiii. (1901).
† Nehring, Zool. Anz. 1900.
‡ Brandt, Bull. cl. phys.-math. Acad. Imp. Sc. St. Petersburg, vol. ii. nos. 14, 15 (1843).

several subgenera, as was partly done by Brandt and Pocock (*loc. cit.*), but I think it will be possible to do that only after more detailed study of the anatomical characters of the members of this group.

The subfamily *Euchoreutinæ* is a very isolated group (only the structure of the skeleton of the hind-foot is quite the same as in *Alactaginæ*). It is a very interesting fact that the structure of genitalia in *Euchoreutes* is also quite peculiar, sharply distinguishing it from all other *Dipodidæ*.

A very aberrant subfamily *Salpingotinæ* has also a quite peculiar structure of the genitalia, as shown above.

The subfamily *Cardiocraniinæ*, which seems to be near to *Salpingotinæ*, has, however, many important distinguishing characters (five not ankylosed metatarsals, the structure of the zygomatic arch, etc.). The genitalia of *Cardiocranius paradoxus* unfortunately are not known.

The structure of the penis of some *Sicistinæ* was described by L. v. Méhely *. He described the penis of *S. montana* Méh. and *S. nordmanni* Keys. & Blas. (*S. loriger* Nath.). The penis of *S. caucasica* (= *S. concolor* Ognev, Satunin; not Büchner) was briefly described by S. I. Ognev †. The genitalia of *S. napæa* and *S. caudata*, so far as I am aware, have not been known before.

S. caudata and *S. caucasica* belong to the *concolor* group, and have also similar characters of the genitalia. *S. napæa*, coloured nearly as the members of the *concolor* group, has many characters which separate it from the group of *S. concolor* (the structure and dimensions of the hind-foot, the length of the tail, etc.); in full accordance with these the genitalia of *S. napæa* are sharply distinguished from these organs in the *concolor* group.

ALACTAGA SEVERTZOVI, sp. n.

Type. From Tomar-Utkul, distr. of Kopal, prov. Semiretschensk, Russ. Turkestan. Collected by V. N. Shnitnikov, 20. viii. 1916. Coll. of Zool. Mus. Russ. Acad. Sc. No. 308—1916. 16.

Specimens examined.—Seven from the following localities:—Semiretschensk Province (see above), Ferghana (Kara-tau, Mussulm-kul), and Buchara (Karshi).

Diagnosis.—A member of the *A. saliens* group, easily distinguished from the true *A. saliens* by smaller size, the distribution of the white and black colour on the lower surface of the tuft of tail, and by the structure of the penis (see Pl. I. fig. 2).

Colour similar to that of *A. rückbeili*, paler and greyer than in *A. saliens*. Hairs of the back on its base neutral grey, or deep neutral grey of Ridgway; on the middle they are cinnamon-buff (17″ *b*) and on the tips army-brown, or natal-brown (13‴ *i-k*).

* Méhely, Ann. Mus. Nat. Hung. vol. xi. (1913).

† S. I. Ognev, Proc. of Simpheropol Nat. Hist. Soc. vol. v. p. 52, pl. ii. fig. 7 (1916).

Head above light cinnamon-drab (13'''' *b*). Tail with the white ring before the black one absent; the black ring interrupted below along the vertebræ, which are covered with white hairs.

Skull like that of *A. saliens* in shape, with nearly perpendicular rami superiores of zygomatic processes of maxillary bones; the last molar relatively large (not so small as in the *A. mongolica* group). Skull considerably smaller than in *A. saliens*.

A. severtzovi is distinguished from *A. rückbeili* Thos. and other members of the *mongolica* group by the absence of the white ring before the black one on the tail, by having perpendicular rami superiores of zygomatic processes of maxillary bones (instead of oblique ones), and by the relatively large last molar.

Measurements (of type-specimen).—Head and body 162 mm.; tail 227; hind-foot 80; ear 60; condylo-incisive length 40·7; zygomatic breadth 29·3; nasalia 17; interorbital constriction 11·4; breadth of brain-case 21; palatilar length 25; foramina incisiva 9·3; maxillary tooth-row (without præmolar) 7·3.

(All measurements, as one may see, considerably smaller than in *A. saliens*.)

I have named this Jerboa in honour of N. A. Severtzov, a famous explorator of the Turkestan fauna, who presented the first specimens of this species to the Zoological Museum of the Russian Academy of Science.

SICISTA CAUCASICA, sp. n.

Sminthus concolor (not Büchner), Satunin, Bull. of Caucasus sect. of Russ. Geogr. Soc. vol. xxiv. p. 60 (1903).

Sicista concolor Ognev, Proc. of Simpheropol Nat. Hist. Soc. vol. v. p. 52 (1916).

Type. From distr. of Maikop, province of Kuban, Northern Caucasus, alt. 7000–9000 ft. Collected by F. O. Kratky. Coll. of Zool. Mus. Russ. Acad. Sc. No. 7514 (skin and skull).

Diagnosis.—A member of *S. concolor* group, which is distinguished from *S. concolor* by its brighter dorsal colour, shorter ears, shorter rostrum and nasalia.

Upper parts tawny of Ridgway (13' *i*); head, cheeks and sides brighter (about Ridgway's 13' *b*). Underparts light ochraceous-buff (15' *d*). On the upper surface of tail there is a narrow strip of black hairs. On the base of ear a rufous spot is present.

Skull with considerably shorter and shallower rostrum than in *S. concolor*; nasalia are longer.

Measurements (of type).—Head and body 54 mm.; tail 105; hind-foot 17·7; ear 11·2; condylo-basal length of skull 19·5; zygomatic breadth 9·3; interorbital constriction 3·8; occipital breadth 9·1; occipital depth 6·4; nasalia 7·8; diastema 5·1; maxillary tooth-row 3·2.

S. caucasica is distinguished from *S. concolor* by its brighter colour, shorter ears, shorter rostrum and nasalia. (I was unable to compare *S. caucasica* directly with the type-specimen of *S. concolor* Büchn.)

EXPLANATION OF THE PLATES.

Plate I.

External view of penis.

Fig.
1. *Alactaga saliens* Gmel.
2. „ *severtzovi*, sp. n.
3. „ *mongolica* Radde.
4. „ *suschkini* Sat.
5. „ *elater* Licht.
6. „ *williamsi* Thos.

Fig.
7. *Alactagulus acontion* Licht.
8. *Pygeretmus platyurus* Licht.
9. *Scarturus tetradactylus* (from Pocock, Proc. Zool. Soc. 1922, p. 676, fig. K).

Plate II.

External view of penis.

Fig.
1. *Scirtopoda mauritanica* Duv.
2. *Dipus sagitta* Pall.
3. *Scirtopoda telum* Licht.
4. „ *jaculus* L.

Fig.
5. *Salpingotus kozlovi* Vinogr. (*a*, upper view; *b*, side view).
6. *Euchoreutes naso* Schl. (*a*, upper view; *b*, side view).

Plate III.

Os penis.

(*a*, upper view; *b*, side view.)

Fig.
1. *Scirtopoda telum* Licht.
2. *Dipus sagitta* Pall.
3. *Scirtopoda mauritanica* Duv. (sub-adult specimen).

Fig.
4. *Scirtopoda mauritanica* Duv. (adult specimen).
5. *Scirtopoda jaculus* L.
6. *Euchoreutes naso* Sel.

Plate IV.

Penis of *Sicista* and *Zapus*.

Fig.
1. *Sicista nordmanni* Keys. & Blas.
2. „ *montana* Méh.
3. „ *napæa* Hollist (*a*, upper view; *b*, side view).

Fig.
4. *Sicista caucasica*, sp. n.
5. „ *caudata* Thos.
6. *Eozapus setchuanus* Pous.

Plate V.

Os penis of *Sicista* and *Zapus*.

(*a*, upper view; *b*, side view.)

Fig.
1. *Sicista nordmanni* Keys. & Blas.
2. „ *montana* Méh.
3. „ *napæa* Hollist.

Fig.
4. *Sicista caucasica*, sp. n.
5. „ *caudata* Thos.
6. *Eozapus setchuanus* Pous.

26. On a new Genus of the Family Engystomatidæ (Batrachia).

By C. R. Narayan Rao, M.A., and B. S. Ramanna, B.Sc. (Department of Zoology, Central College, Bangalore) *.

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(Text-figures 1–9.)

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(2) A brief account of the Habits of the Species, *Ramanella symbiotica*	589
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(1) Introduction.

While looking for material of Engystomatidæ locally, we met with a Frog which was identified as representing a new genus of that group. On forwarding two specimens to Miss J. B. Procter, who was then in charge of the Reptile Department in the British Museum, for the purpose of comparison with the series of collections in that institution, she informed us very kindly that the examples sent to her were really a new genus, and added that they were also examined by Dr. Boulenger, who happened to be there at the time. I take this opportunity of thanking Miss Procter for the numerous acts of kindness and courtesy I have received from her from time to time, and also Dr. Boulenger for confirming the identification.

Family Engystomatidæ.

Genus Ramanella, nov.

Pupil vertical; tongue oblong, notched behind: the palatine bones form a slight ridge, only occasionally denticulate, across the palate in front of the œsophagus. No other folds are present on the roof of the buccal cavity; tympanum hidden; fingers and toes free; tips of fingers dilated; those of toes blunt, not dilated; outer metatarsal united; no pre-coracoid; no omosternum; diapophyses of sacral vertebra broadly dilated. Terminal phalanges triangular.

I have associated this genus with the name of my old pupil, Mr. B. S. Ramanna, who has shown great zeal in collecting

* Communicated by Miss J. B. Procter, F.Z.S.

research material for cytological and embryological work. Of the three genera of Engystomatidæ recorded from S. India, *Callula* approaches this genus far more closely, as is evidenced by the anatomical and osteological characters.

RAMANELLA SYMBIOTICA, gen. et sp. nov.

Head far broader than long; snout short, obtuse, longer than the diameter of the eye, projecting beyond the mouth and obliquely truncated; interorbital space perfectly flat, twice as broad as the upper eyelid; loreal region oblique, slightly concave; nostrils nearer to the tip of the snout than to the eye.

Fingers rather long, with moderately-developed terminal discs: first shorter than the second; second equals the width of interorbital space, but only slightly shorter than the fourth; subarticular tubercles moderate, prominent; two large, fleshy, oval prominences at the base of the first and fourth fingers. The fore-limb (without manus) is slightly less than three-fourths the length of the hind-limb (without foot). Upper-arm as long as the fore-arm.

Hind-limb short, the tibio-tarsal articulation reaching the axilla or only slightly beyond it; the heels just touch each other when the limbs are folded at right angles to the body; tibia slightly more than twice as long as and about a quarter of the length from snout to vent and longer than the fore-arm by about a third. Toes perfectly free, slender, with blunt tips, which are not dilated into discs. Two metatarsal tubercles: the outer very small, conical; the inner comparatively larger, oval, about half the length of the 2nd or 5th toe and slightly less than the 1st. Sub-articular tubercles feebly prominent.

Skin on both surfaces smooth. Colour on the dorsal surface brown with yellow marbling. On the sides yellow dots. The upper surfaces of limbs marbled. Ventral surface white, immaculate.

Male with a median bronze-coloured vocal sac.

Habitat. Bangalore (Mysore), 3000 ft., S. India.

Remarks. Only eight specimens were obtained, and the type-specimen has had to be anatomically dealt with for the purpose of studying the structure of the brain, in consequence of the distribution at an earlier date of some of the specimens to the British Museum and Natural History Museum, Bangkok, Siam, while others have been used for the preparation of the skeleton.

Measurements in millimetres.

From snout to vent	34
Length of head	5½
Width of head (across tympanic region)	8½
Snout	3
Eye	2

Interorbital width	4
Upper eyelid	2
Arm	6½
Fore-arm	6½
First finger	3
Second finger	4
Third finger	5½
Fourth finger	4½
Length of thigh	11
Length of tibia	8½
First toe (free portion)	2
Second toe	3
Third toe	4½
Fourth toe	7½
Fifth toe	3
Tarsals	7
Inter-metatarsal tubercle	1½

(2) The Habits of the Species.

This little Engystomatid Frog is an extremely interesting species, both from the natural history and anatomical points of view. It affects practically dry situations, sharing the burrows of the Black Scorpions (*Palamneus fulvipes*) under heavy stones and boulders. When uncovered it remains quietly until disturbed, when it runs about briskly, toppling over the scorpions unmolested. When the scorpions crawl over the Frog, the latter crouches flat on the ground, absolutely motionless. In captivity, which it stands for months, it burrows if given soft earth. It remains in the burrow with the snout projecting over the surface, and does not appear to be such a deep digger as *Cacopus*. Termites are the staple food and small beetles are not refused. When the pot or tray containing the earth in which the specimens had burrowed was introduced into a glass aquarium, strange to say the Frogs left the tray and remained in water among stones which were heaped round the vessel. If driven to the deeper parts of the water, the Frogs assume a characteristic vertical posture, while under similar circumstances their aquatic congeners would float perfectly horizontally on the surface. For weeks, extending almost to months, the Frogs would remain in the water, squatting on the stones which they, however, leave and enter the tray on the introduction of termites, which they greedily swallow. When the males are held under the axilla, they show no symptoms of alarm nor utter any cries, and when allowed to sit on the palm of one's hand, they would remain perfectly quiet without struggling to jump off. We have not succeeded in inducing these Frogs to breed in the aquarium, and their breeding-habits must doubtless be very interesting. On irritation the skin pours out a thick milky secretion, which also exudes when the animals are chloroformed. The poison dissolves

in nothing except boiling water, which dissolves it only slightly. This habit of throwing out a dense mass of poison when killed is common among most members of Engystomatidæ like *Cacopus* and *Callula*, and is meagre only in *Microhyla*. This cutaneous secretion—which in colour and consistency resembles bufonin—gives the Frog a measure of immunity, which it enjoys in the midst of the pugnacious scorpions. The Frog is capable of climbing the vertical glass surfaces, and on two occasions one of the specimens was found to have escaped from the glass bell-jar, and on looking round was discovered squatting under the tap in the laboratory.

(3) Remarks on the General Anatomy.

The anatomical characters of this little Engystomatid are peculiar in certain respects, and a few brief remarks are worthy of putting on record.

Skeleton.

The Vertebral Column.—In the case of the vertebral column there is a very marked overlap of each neural arch dorsally upon that immediately posterior to it, so that the centra are not

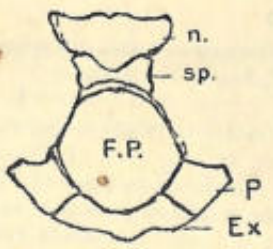
Text-figure 1.

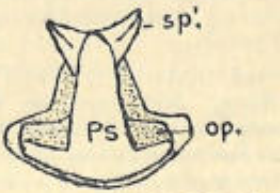
Vertebral column showing the imbricate nature of the neural arches.—*ep.*, epiphyses of sacral diapophyses; *ten.*, tendinous extension of epiphyses meeting the coccyx behind.

visible from this aspect. This character the present species shares with the other members of the Engystomatidæ, such as *Cacopus*, *Microhyla*, and *Callula*, which have also been examined. In this imbricate condition of the vertebral column—due to the centra being slightly shorter than the neural arches—the Engystomatidæ retain a primitive character which is met with in the families Discoglossidæ and Pelobatidæ. In addition to the longer neural arches, the broader articular surfaces, pre- and post-zygapophyses, contribute to shut out the view of the centra

from the dorsal aspect. Though the centra are very feebly developed, being only almost as thick as the arches themselves, the vertebræ are not acentrous. The spinous processes are almost obsolete throughout the vertebral axis. The transverse process of the third vertebra, slightly directed headwards, is nearly 1½ times broader than the one anterior and twice that posterior to it. Those belonging to vertebræ 5–8 are progressively shorter, and are directed anteriorly as in *Discoglossus* and *Pelobates*, and in this respect they differ from Ranidæ, in which family the diapophyses are perfectly horizontal. The only pair of transverse processes which are directed in some measure posteriorly are those belonging to the 4th vertebra, and no doubt the anterior deflection of the transverse processes of the trunk vertebræ must be considered one of the many archaic characters presented by the vertebral column of this and other members of Engystomatidæ. The sacral diapophyses are broad and wing-like, and the marginal epiphysial cartilage, so noticeable in *Cacopus*, is reduced in this species, but produced in a filamentous form posteriorly to a considerable length, becoming attached to the coccyx. The urostyle is cylindrical, and equals the length of the last seven vertebræ in this species, but is shorter in the other genera, and the terminal cartilage is less broad than in *Cacopus*. The transverse processes are absent, but the canals (*Canalis vertebralis*, *Canalis coccygei*) are well developed. The absence of the dorsal ridge or blade from the urostyle suggests the problem whether the caudal vertebral elements in the family Engystomatidæ are homologous with the trunk vertebræ. This subject is still under investigation.

Text-figures 2 and 3.





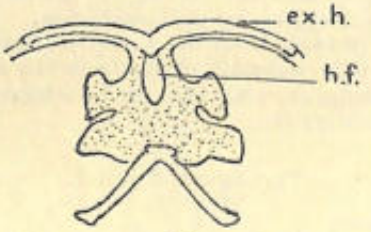
The dorsal and ventral aspects of the cranium.—*Ex.*, exoccipital; *F.P.*, fronto-parietal; *n.*, nasal; *op.*, opisthotic region; *P.*, pro-otic; *sp.*, sphenethmoid; *sp'.*, bony processes of the sphenethmoid underlying the nasals.

Skull.—The comparative shortness of the skull of this species is a character which it shares with the other members of Engystomatidæ, and the narrow mouth is accounted for—as in *Cacopus*, in which this particular feature has already been noticed—by the forward deflection and the greatly reduced nature

of the pterygoids, quadrato-jugals, and squamosal. The zygomatic process of the latter is wanting. The fronto-parietals are perfectly oval, and their length equals their width across the middle line. The pro-otic is completely uncovered, and the suture between it and the exoccipitals is distinct and intimate. On account of the shortness of the fronto-parietals, the sphen-ethmoid is exposed, and its anterior lateral margins are produced into two partly-ossified processes, which in *Rana* remain perfectly cartilaginous and form the outer wall of the nasal chamber. The posterior limb of the parasphenoid is perfectly non-existent owing to the transverse arms arising from the hindermost extremity of this bone. In front of the transverse arms and partly covered by them are ossified regions which are distinct from the pro-otic elements, probably representing the opisthotic. Such ossified regions are not present in *Cacopus* and *Rana hexadactyla*. The other palate bones are incompletely ossified, and are soonest affected by the process of maceration.

Hyoid.—The anterior cornu of the hyoid on each side bears on its anterior border an accessory bar of cartilage meeting mid-ventrally, these are supposed to be "extrahyals," but are better

Text-figure 4.



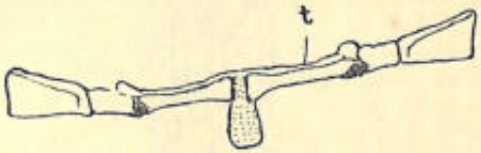
Hyoid.—*ex.h.*, anterior processes of the anterior cornu, having united into a transverse bar of cartilage; *h.f.*, hyoglossal foramen.

termed "anterior processes" in conformity with the terminology of *Rana*. Ridewood has worked out, in the case of *Pelodytes punctatum*, the development of these anterior processes and how, after fusion with the ceratohyals, they touch one another in the antero-median line so as to convert the hyoglossal sinus into a foramen. A similar fusion of the anterior hyoid processes with the anterior cornua has been noticed by Beddard in *Breviceps* and *Hemisus*, and in these genera the anterior cornua meet so that the hyoglossus muscle actually passes through a foramen. Dr. Devanesen, in his paper on *Cacopus*, refers to the broadly-expanded nature of the anterior hyoid processes, which, however, do not meet; consequently the hyoglossal sinus remains broad and deep. This condition has been noticed by the present

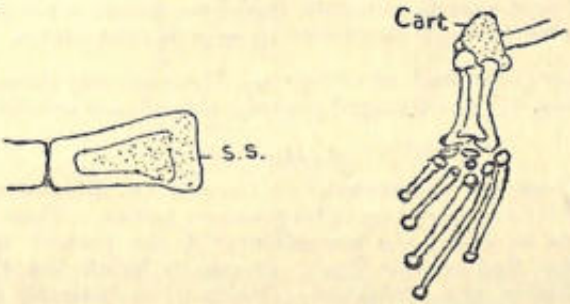
writers in *Microhyla rubra* and *M. ornata* and *Callula obscura*. But the features of the hyoid skeleton of *R. symbiotica* would, however, appear to depart widely from these genera and approximate more nearly the condition of *Pelodytes* rather than *Breviceps* and *Hemisus*.

Pectoral Girdle and Anterior Limb.—As in the case of all the members of Engystomatidæ, the place of the sternum is taken by a plate of median cartilage which in this species is less broad than in *Cacopus*. The suprascapula is ossified only on the

Text-figure 5.



Text-figures 6 and 7.



Pectoral girdles of the new Frog, the suprascapula of *Cacopus*, and the heel of the new Frog.—*cart.*, heel cartilage; *s.s.*, suprascapula showing the ossification in the anterior and posterior borders, the dotted portion representing the cartilage; *t.*, tendon which perhaps represents the clavicle.

anterior margin, while in the latter genus only the central portion remains cartilaginous. There is a slender ligament connecting the scapula and the median anterior border of the coracoid, representing perhaps the vestiges of clavicles.

In the anterior limb the terminal phalangeal bone is Y-shaped, and the number of carpalia is normal with os capitato-hamatum as the largest.

Pelvic Girdle and the Hind-Limb.—The ilia are cylindrical, and anteriorly bear two ligamentous processes which extend beyond the diapophyses of the sacral vertebra on to those of the eighth. Both pubis and ischia are ossified. There is a wide, oval

cartilaginous flap over the cruro-metatarsal joint, and the astragalus and calcaneum exhibit imperfect fusion at the epiphysial

Text-figure 8.

The sacral vertebra and the pelvic girdle, showing the cartilaginous bars in front of the ilia extending to the transverse process of the eighth vertebra.

points where they touch one another. There are only three other tarsal bones, and the terminal phalangeal bones are pointed.

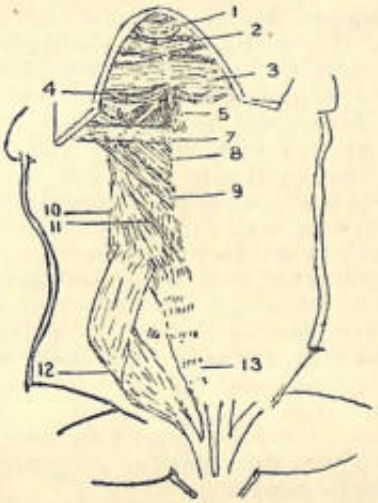
Muscles.

In his paper on the anatomy of *Cacopus* Dr. Devanesen has given a detailed description of its muscular system. There are a few points in which the musculature of the present species differs from that of this Toad. Practically in all the Indian Engystomatidæ the *subhyoideus* (Beddard) is distinctly larger than its anterior division, *submaxillaris*; and in some measure the two muscles by their powerful contraction press the soft food (termites) against the convex surface of the parasphenoid, though no doubt the former muscle in the case of male examples must help in the expansion of the single gular sac.

The muscles of the abdomen are extremely delicate, and the fibres are so sparsely disposed that without much teasing they can be microscopically examined for the details of their structure. The *rectus abdominis* muscles arise by two tendons from the posterior border of the pubes, and in the pelvic region divide into an inner and outer division. The inner ramus of the tendon immediately expands into the inner portion of the *rectus abdominis*, which, on account of the extreme thinness, does not develop the *inscriptio tendinea* to any degree. The outer portion of the *rectus* muscle is more strongly developed, and attached to the skin along a greater part of its course, passing anteriorly into the *portio abdominalis* of the *pectoralis* muscle. There is

thus produced a considerable lymphatic space between the external and internal divisions of the *rectus abdominis* on the one hand, and on the other the lateral borders of the *obliquus abdominis externus* muscle. This space, which is fairly wide, is limited both above and below by special connections between the muscles referred to. A similar arrangement of parts is met with in *Microhyla*, while in *Rana breviceps* the external divisions of the *rectus abdominis* are more strongly developed, and are attached

Text-figure 9.



The muscles of the abdomen, chest, and throat of the new Frog.—1, submentalis; 2, submaxillaris; 3, subhyoideus; 4, petrohyoidei; 5, hyoglossus and geniohyoideus; 6, all the three sternohyoidei; 7, sterno-radialis; 8, 9, 10, 11, the anterior and posterior abdominal portions to pectoralis; 12, 13, external and internal divisions of the rectus abdominis; 14, lymph-space between 12 and 13.

to the skin from the source of their origin almost over half the abdominal length. On account of the excessive thickness of both the divisions of the *rectus abdominis*, the lymphatic space described in the members of Engystomatidæ does not occur in this species of *Rana*, but the proportionately large development of *portio abdominis* of the pectoral muscle is a noticeable feature in this burrowing *Rana*.

In the present species of Engystomatidæ the *cutaneus pectoris* muscles are remarkably thin and transparent, and may be mistaken for pectoral septum. Each is more or less triangular and, arising from the external oblique muscle, is attached to the skin.

Dorsally the *obliquus externus* muscle extends as far as the

shoulder-blade, and the *portio omo-abdominalis* is not recognizable as a separate muscle. Both form a continuous muscular sheet. In *R. breviceps* the muscles in the region of the dorsum and axilla are so heavily loaded with fat that it is not easy to make out whether the *portio omo-abdominalis* is or is not distinct. But in species like *Rana tigrina* it is a small strip of muscle from the hinder margin of the scapula, and becomes continuous with the larger *obliquus externus* near the axilla.

We have already drawn attention to the fact that the cartilage complex of the hyoid approaches the condition met with in *Pelodytes* and *Breviceps*, owing to the conversion of the *hyoglossus* sinus into a foramen by the fusion of the processes of the anterior cornua. The musculature of the hyoid presents certain features which resemble those of *Breviceps* and *Cacopus*, both described already in greater detail. The *geniohyoideus* muscle does not differ from *Rana tigrina* except for the fact that in *Ramanella*, in common with *Microhyla* and *Callula*, the two inner divisions fuse together so as to hide the *hyoglossus* more markedly. The posterior offshoots of *geniohyoideus* referred to by Dr. Devanesen also occur, having similar insertions.

The *sternohyoid* is in two parts as in *Cacopus* and in other genera like *Microhyla* and *Callula*, and the fibres of *hyoglossus* are comparatively coarse and aggregated over the body of the hyoid. Some of the new muscles (*cornuoideus posterior* and *sterno-cornuoideus*) which Dr. Devanesen has recorded in *Cacopus* are not made out in the present species, whose musculature is in general feebly developed.

The *petrohyoid* muscles are present in normal number, and their insertions on the thyrohyal bar are precisely as has been described to occur in *Cacopus*.

The muscles of the chest are generally feeble in this species, and even *portio sternalis-anterior* and *portio abdominalis* exhibit a similar tendency. The *deltoideus* muscle is practically degenerate in this species, but fairly conspicuous in *R. breviceps*.

The muscles of the hind-limb resemble those of *Cacopus*.

The temporal muscle is compact, more or less wedge-shaped, and, situated immediately behind the eyes, arises from the lower border of the *fronto-parietals*. It receives fibres from the anterior border of the *annulus tympanicus*, but none from the squamosal, whose anterior cornu is suppressed in this and other Engystomatid Frogs. No fibres arise even from the inferior cornu of the squamosal to be inserted into the tendon of the temporal muscle, which converges towards the cornual process of the mandible.

Lymphatic System.

The outstanding facts of the lymphatic system of this Frog and *Cacopus* are that the septal sinuses of the pectoral and lateral septa are enlarged and are separate. The dorsal and ventral septa are coalescent, and the latter is almost lateral in position,

and therefore separates the dorsal and ventral subcutaneous spaces. On the dorsal aspect the inguinal septum gives off a slip, to which the superior and intermediate femoral septa are attached. Thus a secondary subcutaneous space, very spacious in *Cacopus*, is produced on the dorsal surface of the root of the thigh. The lateral septum does not join the inguinal as in *Rana*, but stops short posteriorly at the inguinal level, thus permitting a wide communication between the dorsal and ventral lymph-spaces.

The decidedly spherical shape of *Cacopus*, and of a similar tendency to obesity on the part of the Engystomatidæ in general, must be due to these causes. The subcutaneous lymph in the triangular space on the dorsal surface of the root of the thigh, and the very broad cavity in the region communicating the dorsal and ventral lymph-chambers, will cause a general bulging out of the skin in these regions, thus producing a shortness of appearance of the thighs, which, on exposure of these cavities, show a proportion of parts common among the other related batrachia.

Anteriorly the confluence of the dorsal and ventral lymph-chambers in the superior axillary region gives rise to a secondary space which perhaps represents the remains of the lateral lymph-space, which ventrally opens by a broad sinus into the thoracic lymph-cavities, an arrangement of anatomical parts which gives rise to the roundness of the body in this region also.

The ventral septum does not extend over the arm dorsally as in *Rana*.

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27. The Relation between the Feeding-habits and the Structure of the Mouth-parts in the Asilidæ (Diptera).

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(Plates I., II.; Text-figures 1–15.)

The mouth-parts of the Diptera have long been the subject of a great deal of research, and much valuable work has been done upon them, but until recently it has been exceedingly difficult to homologize and correlate the extraordinary variations and developments of the various parts of the Dipterous mouth. Peterson (1916), however, has solved this problem, and has homologized the mouth-parts throughout the Diptera. The work of many investigators has enabled us to understand the structure and function of many of the more interesting types, but the mouth-parts in the Diptera undergo such amazing modifications and specialization of structure that one might almost say that until every family had been worked down to genera, and the mouth-parts in each thoroughly worked out, our understanding of the structure of the Dipterous mouth were incomplete. It is but a question of time before a complete knowledge of the structure is obtained; we have yet to understand, however, the meaning of this extraordinary development of the Dipterous mouth, what function some of the highly specialized structures fulfil and what bearing upon the feeding-habits of the insects the various degrees of development have.

It is significant that in cases where the explanation of complicated and highly specialized structures is forthcoming, it is invariably a study of the feeding-habits in conjunction with a study of the mouth-parts that has eventually cleared up any misconceptions and wrong interpretations. Such examples are, however, with the exception of the blood-sucking Diptera and certain other species, few and far between, and the real function and working of the mouth-parts is in the majority of cases unknown.

There is one factor which has stood in the way of any further advance being made in this direction, namely an almost universal lack of knowledge of the feeding-habits of the Diptera; and no matter how carefully the structure of a certain species, or type, may be worked out, a complete understanding of the function of the various parts, and the meaning of the various modifications which occur, is impossible without an exhaustive study of the feeding-habits of the insect or insects in question. We have but

* Communicated by Prof. H. M. Lefroy, F.Z.S.

to compare the other orders of insects to see how true this is. In the Orthoptera, Odonata, Coleoptera, Neuroptera, Rhynchota, and Hymenoptera the structure of the mouth-parts bears a direct relation to the feeding-habits of the insects. In the first four orders mentioned the relation between habit and structure is perfectly clear. The insects in these orders possess mandibular type mouths and their feeding-habits range from purely plant-feeding through omnivorous to purely predaceous types; the structure of the mouth-parts varies accordingly, the plant-feeding types being furnished with broad, blunt mandibles and maxillæ and many of the predaceous species possessing sharp-pointed, lance-like mandibles and maxillæ, and between these two types every grade is found. In the Rhynchota, although the mouth-parts have become modified to form a piercing rostrum, the same relation between habits and structure may be traced; here again the insects range from purely plant-feeding to predaceous forms, without, however, passing through any omnivorous or scavenging stage. The relation is equally obvious, plant-feeding Rhynchota having long, thin rostrums suitable for piercing the outer tissues of their food-plants and reaching the phloem, etc., while the predaceous species are furnished with very short, curved powerful rostrums, suitable for plunging into the body of struggling prey. In the last-mentioned order, the Hymenoptera, a rather different state of affairs is found, as the structure of the mouth-parts varies not only with feeding-habits but with other habits as well, such as are found amongst different types of nest-building insects, Mason-bees, Carpenter-bees, etc.; nevertheless, the relation between structure and habit is also plainly visible, and aids in no small way the interpretation and understanding of the mouth-parts.

Among the above-mentioned orders, it is a common thing to be able to tell the feeding-habits of the insect by an examination of the mouth-parts. So far, this has not been possible with the majority of Diptera. The latter order present a somewhat different problem to the other orders of the Insecta, and beyond a certain point no amount of study of the mouth-parts will indicate the feeding-habits of the insects. A certain number of species have been worked out and are fully understood, but these belong almost entirely to two distinct classes:—

A. Those Diptera which have come under man's notice on account of their medical importance; these, of course, include the blood-sucking Diptera, and others such as the House-fly which are hardly less important as carriers of disease.

B. Those Diptera which have come under man's notice on account of exaggerated or peculiar mouth structures, which have been so noticeable or interesting as to draw attention to themselves, e.g. *Corizoneura* (*Pangonia*) etc.

Minute and accurate descriptions of the actual methods of feeding have only been made by other authors in the above-mentioned cases; the habits of a few flower-feeding types, mostly inaccurately however, have also been described. It will be seen, then, that the Diptera, with the above exceptions, require a considerable amount of study before a really satisfactory understanding of their mouth-parts is obtained.

The original aim of this research was to determine, as far as was possible, the relation between the structure and habit in the mouth-parts of Diptera; circumstances, however, curtailed the work, and it was only found possible to complete the Asilidæ; it is hoped, however, that in due course the Empidæ may also be dealt with in a similar manner.

Methods.

In order that sufficient data might be acquired on the feeding-habits, the whole of the spring and summer of 1924 and much of 1923, from the beginning of April to the end of October, was spent in the field in observing the living insects. This was done in two ways. The greater part of the work was performed in the field, where, by the aid of a series of pocket-lenses, it was found possible to obtain excellent data on the living insects, and to get some exceptionally close studies of species, the habits of which have hitherto scarcely been investigated at all. In many cases, however, this was found to be not quite accurate enough for the purpose of this research, so observation in the laboratory under more advantageous conditions was resorted to.

The flies were brought in alive, together with a large supply of their food material—prey, flowers, dung, fruit etc.,—and were placed in large glass cylinders which were covered at the top with muslin. The flies fed readily when thus confined, and no difficulty was experienced in observing their habits, were they predaceous or flower-feeding. A high-power binocular dissecting microscope was used for observation purposes; it was mounted on an adjustable arm, enabling every movement of the insect to be followed irrespective of its position in the cylinder. In this manner, most accurate and minute observations were found to be possible, and every species that was worked on was observed thus as well as in the field.

When sufficient data had been amassed as regards feeding-habits, the insects were killed and immersed in Carnoy's Fixative (No. 2 formula) for 24 hours, and then preserved in 70 per cent. alcohol, so that by October 1924 a very considerable amount of fixed material was available for examination. Use was also made, in certain cases, of dried specimens from the collections in the Entomological Department of the Imperial College of Science.

In the examination of the structure of the mouth-parts about equal use was made of the dissecting needles and the microtome,

it being impossible to determine correctly the exact structure without both methods. Use was also made of preparations *in toto*, which were found to be extremely useful in some cases for examining parts *in situ*. Preparations were made from fresh and Carnoyed material, and from material which had been cleared in a 10 per cent. solution of potassium hydroxide; it was found best to soak the object for a few days in cold potash, rather than to boil it, as all risk of distorting or fracturing the more delicately chitinized parts was thus eliminated. The cleared preparations were stained in Acid Fuchsin, Light Green, Orange G., and a mixture of Acid Fuchsin and Light Green. Where possible, paraffin-wax of a melting-point of 58° C. was used as a medium for embedding specimens for sectioning, but recourse had, in many cases, to be made to Celloidin-wax embedding, which, although somewhat complicated, was found to be the only means of obtaining reliable sections of many of the harder species. The sections were stained in Ehrlich's Acid Hæmatoxylin. All dissections were made under the same binocular microscope that was used for the living insects during the summer.

ACKNOWLEDGMENTS.

This research was carried out in the Entomological Laboratories of the Imperial College of Science and Technology, under the supervision of Professor H. Maxwell Lefroy, to whom I am very greatly indebted for the great interest, encouragement and assistance which he has at all times been so ready to extend. I am also greatly indebted to Major E. E. Austen, D.S.O., of the British Museum, for the identification of the majority of the material worked on and for much valuable advice and assistance, to Mr. Barnett for the identification of several species of Sciomyzidæ, Sepsidæ, and Anthomyiidæ, to Dr. Waterston for the identification of certain Hymenopterous prey of the Asilidæ, to Mr. D. E. Kimmins for much useful material and for a great deal of valuable information and assistance regarding the habits of many of the Diptera, and to Mr. S. S. Light for the photomicrographs of the proboscis of *Machimus atricapillus*, for much very valuable advice and assistance and also for the great help he rendered me in reading over the manuscript and proofs. I am also extremely grateful to Prof. E. B. Poulton, F.R.S., for the interest he has taken and much useful information he has given me regarding the predaceous Diptera, and to Mr. L. N. Staniland for the help and advice he has tendered me regarding the technique of much of the microtome work. Finally, I should like to express my admiration and gratitude for the very great help which has been tendered to me by the Imperial Bureau of Entomology in finding most of the literature upon the subject.

MATERIAL.

The scope of this research was limited to the number of species which it was possible to observe accurately during the summer,

and for the same reason it was impossible to choose the species to work upon. Consideration had to be taken of two things: (1) to work upon those species of which there were a sufficient number to observe accurately and to preserve for examination; (2) to work upon those species which best showed a relation between habit and structure,—in other words, not to confine the study to flies of the same habit.

As has already been mentioned, it was only found possible to complete the work upon the Asilidæ, but very detailed information as to the feeding-habits was obtained upon the following families:—

DIPTERA.

ORTHORRHAPHA.

NEMOCERA.

Tipulidæ.
Psychodidæ.
Bibionidæ.

BRACHYCERA.

Leptidæ.
Stratiomyidæ.
Asilidæ.
Bombyliidæ.
Empidæ.
Dolichopodidæ.

CYCLORRHAPHA.

ASCHIZA.

Pipunculidæ.
Syrphidæ.

SCHIZOPHORA.

ACALYPTRATÆ.

Conopidæ.
Ortalidæ.
Drosophilidæ.
Sepsidæ.
Sciomyzidæ.
Cordyluridæ.

CALYPTRATÆ.

Anthomyiidæ.
Muscidæ.
Sarcophagidæ.
Tachinidæ.
Dexiidæ.

THE FEEDING-HABITS OF THE DIPTERA.

From the point of view of feeding-habits the Diptera may be divided into the following classes:—

1. Blood-sucking.
2. Predaceous.
3. Flower Feeding.
4. Surface Feeding.
5. General Feeding and Scavengers.
6. Non-feeding.

On the first class, Blood-sucking, so much work has been done that I do not propose to touch upon them beyond pointing out that their mouth-parts are developed to pierce thick hides and skins, and that it is among the blood-sucking types that the only mandibulate Diptera are found.

The Predaceous Diptera.

The predaceous Diptera are somewhat more complicated than the blood-sucking types, in that they vary considerably and very little work has been done on their habits. Among the British families, only one is entirely predaceous, the Asilidæ, so that this family forms an excellent basis with which to compare all other types.

The ASILIDÆ.

Throughout the Asilidæ, both the feeding-habits and the general structure of the mouth-parts remain the same. The feeding-habits are of a nature entirely predaceous upon other insects and the mouth-parts are adapted and modified to enable the fly to kill its prey as quickly as possible.

The work done upon the Asilidæ may, from the point of view of the mouth-parts and feeding-habits, be divided roughly into two classes.

1. Morphological.
2. Bionomical.

Of the writers on the former class, but two are of any great importance, Meinert (1881) and Hansen (1883); both these authors have gone very thoroughly into the structure and musculature of the Asilid mouth, but they were hampered both by inferior technical equipment and by lack of knowledge of the feeding-habits of the Asilidæ. To the latter class, which consists in the main of lists of prey, many writers have contributed, the most important being Aaron (1894), Marshall (1902), Poulton (1906), Lundbeck (1908), Bromley (1914), and Melin (1923). Of these, Marshall, Poulton, and Bromley have tabulated lists of the prey of many different species of Asilidæ, and Lundbeck also gives the prey known to have been taken by the species which he deals with. Aaron has been the only writer, with the exception of Melin, who has described in detail the method of attack of the Asilidæ. Melin has investigated, very thoroughly indeed, the biology, morphology, and metamorphosis of the family, and he is the only author who has attempted to correlate the structure of the mouth-parts with the feeding-habits of the flies. No one, however, has definitely set out to study the feeding-habits, and then, in the light of what has thus been discovered, to investigate the structure and function of the mouth-parts.

As has already been pointed out, the Asilidæ are entirely predaceous, the nature of their prey varying from the largest and most formidable of Hymenoptera and Coleoptera, to the smallest and softest of Diptera and Rhynchota. The first point that comes to one's notice, on studying the feeding-habits of the

Asilidæ, is the fact that the main object of the flies is to kill their prey as quickly as possible. There can be no doubt that in the case of an Asilid attacking a stinging Hymenopter, a Cicindelid, a Reduviid or some such formidable insect, if it did not immediately put its prey *hors de combat*, it would very often be itself the victim. In view of the rapidity with which such prey are overcome, it seems to me that a proper understanding of the method and mechanism by which this is effected is the first step towards a complete understanding of the mouth-parts. Such observers as Le Conte (1850), Edwards (1883), Girschner (1898), Hoemke (1899), Poulton (1906), Bell (1907), and Melin (1923), have all testified to very rapid death or paralysis of the victims of the Asilidæ, and, as I have already mentioned, I considered the primary point of investigation, from the point of view of this research, was the why and the wherefore of the Asilids' killing power. In doing this research my ultimate aim has been of finding the relation between habit and structure, and with this aim in view I have divided my investigations into the following sections :—

1. **The Nature of the Prey.**
2. **Method of Attack, and the Position of Insertion of the Hypopharynx.**

A. *The Time from the Insertion of the Hypopharynx to the Death of its Prey, which I shall designate as the Pre-Mortem Period.*

B. *The Relation between the Method of Attack etc. and the Pre-Mortem Period.*

1. The Nature of the Prey of the Asilidæ.

The main object in investigating the nature of the prey is to have as many data as possible of the type of insect which is attacked by the different species of Asilidæ, so that some conclusion may be reached in the relation of the type of prey with the structure of the mouth-parts for each species. With this end in view I have placed the results of former workers first and my own results afterwards, so that a comprehensive study may be made of the habits of the Asilidæ in this respect.

I have worked on the following species :—

Leptogaster cylindrica De G.
Dioctria rufipes De G.
Dioctria atricapilla Mg.
Dioctria baumhaueri Mg.
Asilus crabroniformis L.
Machimus atricapillus Fln.

1. LEPTOGASTER CYLINDRICA De G.

Melin (1923) is the only writer, so far as I know, who has made any observations on this species. As prey he has noted down flies, plant lice and Cicadidæ of different kinds, a little parasitic Hymenopter, and a small spider.

I have recorded the following:—

Sex of Predator.	Prey.	Locality and Date.
1. ♂	*Phora* sp.	Heston, 15. 6. 24.
2. ♂	*Rhyphus punctatus* F., ♀.	Streatley-on-Thames, 12. 8. 24.
3. ♀	*Culex pipiens* L., ♀.	Beckenham, 19. 6. 24.
4. ♀	*Culex pipiens* L., ♀.	,, 19. 6. 24.
5. ♀	A small Tipulid.	,, 11. 7. 24.
6. ♀	A small Chironomid.	,, 11. 7. 24.

2. DIOCTRIA RUFIPES De G.

Poulton (see Marshall) (1902) gives as prey to a ♀ the Tenthredinid *Blennocampa assimilis* Fln. ♀, erroneously called an Ichneumon. See also Poulton (1906). Poulton (1906) gives as prey to a ♀ the Syrphid *Sphegina clunipes* Fln. ♀, and as prey to a ♂? the Empid *Empis pennipes* L. ♀. Lundbeck (1908) gives a *Sphecodes* as prey. Melin (1923) gives different parasitic Hymenoptera such as *Alysia* sp. and *Cratocryptus* sp., *Microcryptus basizonius*, *Ischnus nigricollis*, *Hypamblys transfuga*, and *Hypomecus quadrimaculatus*.

I have recorded the following:—

Sex of Predator.	Prey.	Locality and Date.
1. ♂	Very small *Tipula oleracea* L.	Heston, 12. 6. 24.
2. ♂	*Miris calceratus* Fln.	Burnham Beeches, 27. 6. 24.
3. ♀	*Bibio pomonæ* F., ♂.	Heston, 30. 6. 24.
4. ♀	*Musca domestica* L., ♀.	,, 8. 7. 24.
5. ♀?	*Borborus equinus* F.	,, 12. 7. 24.
6. ♀?	*Chloromyia formosa* Scop., ♀.	,, 12. 7. 24.
7. ♀?	An Ichneumonid minus abdomen.	,, 14. 7. 24.

3. DIOCTRIA ATRICAPILLA Mg.

Poulton (see Marshall) (1902) gives as prey to a ♀ an Ichneumon. See Poulton (1906). Poulton (1906) gives as prey

to a ♀ the Ichneumon *Meloboris rufiventris* Grav. ♂. Lundbeck (1908) gives *Homalomyia scalaris* Fabr.

I have recorded the following:—

Sex of Predator.	Prey.	Locality and Date.
1. ♂	*Bibio pomonæ* F., ♀.	Heston, 2.6.24.
2. ♂	*Bibio pomonæ* F., ♂.	„ 18.6.24.
3. ♂	*Scatophaga stercoraria* L., ♀.	„ 20.6.24.
4. ♀	*Bibio pomonæ* F., ♀.	„ 4.6.24.
5. ♀	*Empis pennipes* L., ♂.	„ 6.6.24.
6. ♀	*Lucilia cæsar* L., ♂.	Burnham Beeches, 14.6.24.
7. ♀	*Capsus lanarius* L.	„ „ 14.6.24.
8. ♀	A small Braconid.	Osterley, 9.7.24.
9. ♀	*Lissonota sulphurifera* Grav., ♀.	„ 9.7.24.

4. Dioctria baumhaueri Mg.

Poulton (1906) records as prey to a ♀ the Ichneumon *Microcryptus galactinus* Grav. ♂.

I have recorded the following:—

Sex of Predator.	Prey.	Locality and Date.
1. ♂	A parasitic Hymenopteron which it dropped.	Heston, 4.6.24.
2. ♀	A Chironomid *.	„ 4.6.24.
3. ♀	*Hybos* sp.	„ 7.6.24.
4. ♀	*Syrphus corollæ* F., ♀.	„ 6.7.24.
5. ♀	*Halictus fulvicornis* Kirb., ♀.	„ 14.7.24.
6. ♀	*Lissonota sulphurifera* Grav., ♀†.	„ 14.7.24.
7. ♀	„ „ „ ♀†.	„ 14.7.24.
8. ♀	„ „ „ ♀†.	„ 14.7.24.

* The Chironomid was in a very bad condition, being covered with saliva and much crushed, so that further identification was impossible.

† The Ichneumons, of which there were a great many, were being extensively preyed upon by *D. baumhaueri*, but I was only able to record definitely the above three instances.

5. Asilus crabroniformis L.

Poulton (1906) gives as prey to females:—The grasshopper *Stenobothrus viridulus* L. ♀; *Lucilia cæsar* L. ♂; the grasshopper, *Gomphocerus maculatus* Thunb. ♂; and as prey to ♂ or ♀:—The beetle *Sermyla halensis* L., *Sarcophaga carnaria* L., *Sericomyia borealis* Fln., a smaller Asilid, probably *Machimus*

atricapillus Fln., the grasshopper *Mecosthus grossus* L. ♀. Verrall (1909) records *Sericomyia borealis* Fln. and *Sarcophaga carnaria* L. Melin (1923) gives as prey:—The grasshoppers *Stenobothrus* sp. and *Gomphocerus* sp., the beetles *Aphodius contaminatus*, *A. fimetarius*, *A. fœtans*, and *Philonthus splendens*.

I have recorded the following:—

Sex of Predator.	Prey.	Sex of Predator.	Prey.
1. ♂	*Mesembrina meridiana* L., ♂.	17. ♀	*Calliphora erythrocephala* L., ♀.
2. ♂	*Eristalis tenax* L., ♂.	18. ♀ ?	„ „ „ ♀.
3. ♂	*Volucella pellucens* L., ♀.	19. ♀ ?	*Sarcophaga carnaria* L. ?
4. ♂	*Calliphora erythrocephala* L.	20. ♀ ?	*Tachina fera* L., ♀.
5. ♂	*Apis mellifica* L., ☿.	21. ♀ ?	*Phaonia erratica* Fln., ♂.
6. ♀	*Empis livida* L., ♀.	22. ♀ ?	„ „ „ ♀.
7. ♀	*Machimus atricapillus* Fln., ♂.	23. ♀ ?	*Apis mellifica* L., ☿.
8. ♀	„ „ „ ♀.	24. ♀ ?	*Andrena fulva* Schr., ♀.
9. ♀	„ „ „ ♀.	25. ♀	*Vespa germanica* F., ♀.
10. ♀	*Eristalis tenax* L., ♀.	26. ♀	*Aphodius rufipes* L., ♂.
11. ♀	„ „ „ ♀.	27. ?	*Vespa germanica* F., ☿.
12. ♀	*Volucella pellucens* L., ♂.	28. ?	*Aphodius rufipes* L., ♂.
13. ♀	*Calliphora* sp.	29. ?	*Telephorus rusticus* Fln. ?
14. ☿	*Mesembrina meridiana* L., ♂.	30. ♀	*Stenobothrus bicolor* Charp., ♀.
15. ♀	„ „ „ ♀.	31. ?	„ „ „ ♀.
16. ♀	„ „ „ ?	32. ?	„ „ „ ?

The locality was Streatley-on-Thames. ♂s were observed from the 8th of August to the 29th of August. ♀s from 6th August to 17th September, 1923–24.

6. Machimus atricapillus Fln.

Poulton (see Marshall) (1902) gives as prey the Dipteron *Chrysops cœcutiens* L. ♂. See also Poulton (1906). Poulton (1906) gives as prey to females:—*Melanostoma scalare* F. ♀, *Dolichopus ungulatus* L. ♀, *Sarcophaga* sp. ? (*melayura* Mg.) ♀, and a ♂ and ♀ Asilid in cop., the ♀ with a Cercopid of genus *Athysanus* as prey, and as prey to a ♂ *Hylemyia* sp. (headless). Lundbeck (1908) gives as prey: *Homalomyia scalaris*. Melin (1923) gives as prey:—The fungus gnats *Leptis lineola*, *Chrysogaster*, *Melanostoma* and *Pipunculus* sp., a Phorid, *Psila gracilis*, *Hydrochæta pupillata*, Tachinids, *Rhinophora melania*, Anthomyiids, *Lasiops hirsutula*, *Hydrothæa irritans* and *Chortophila floralis*, *Stomoxys calcitrans*, *Musca domestica* and *M. tempestiva*, various kinds of Cicadidæ and plant lice, *Lasius niger* and *Myrmica rubra*, *Alysia* sp., a moth butterfly and *Aphodius* sp.

I have recorded the following:—

Sex of Predator.	Prey.	Locality and Date.
1. ♂	*Musca domestica* L., ♀.	Streatley-on-Thames, 4.8.24.
2. ♂	*Lucilia cæsar* L., ♂.	„ „ „ 9.8.24.
3. ♂	*Sicus ferrugineus* L., ♂.	„ „ „ 9.8.24.
4. ♂	*Tipula oleracea* L., ♀.	„ „ „ 6.8.23.
5. ♂	*Aphodius contaminatus* Helst., ♂.	„ „ „ 6.8.23.
6. ♂	*Nabis major* Cost., ♂.	„ „ „ 12.8.24.
7. ♂	*Odynerus trifasciatus* Oliv., ♀.	„ „ „ 7.9.23.
8. ♂	„ „ „ ♀.	„ „ „ 19.8.24.
9. ♀	*Anthomyia pluvialis* L.	Heston, 22.7.24.
10. ♀	*Scatophaga stercoraria* L., ♀.	„ 26.7.24.
11. ♀	*Stomoxys calcitrans* L., ♂.	„ 26.7.24.
12. ♀	„ „ „ ♀.	Streatley-on-Thames, 9.9.23.
13. ♀	*Lucilia cæsar* L.	„ „ „ 13.8.23.
14. ♀	„ „ „ ♀.	„ „ „ 7.9.24.
15. ♀	*Sarcophaga carnaria* L.	„ „ „ 15.9.24.
16. ♀	*Rhyphus punctatus* F., ♂.	„ „ „ 28.8.24
17. ♀	„ „ „ ♀.	„ „ „ 28.8.24.
18. ♂ ?	„ „ „ ♀.	„ „ „ 28.8.24.
19. ♂ ?	„ „ „ ?	„ „ „ 28.8.24.
20. ♂ ?	„ „ „ ?	„ „ „ 30.8.24.
21. ?	A small Tipulid.	„ „ „ 17.8.23.
22. ?	*Empis livida* L., ♂.	„ „ „ 11.9.23.
23. ?	*Mydaea impuncta* Fln.	„ „ „ 16.8.23.
24. ?	*Halictus smeathmanellus* Kirb., ♀.	„ „ „ 30.8.23.

A study of the foregoing records of the prey of the Asilidæ, as represented by the six species worked on, will at once indicate that Melin (1923) was undoubtedly correct in his statement that the size and strength of the prey was in proportion, among other factors, to the size and strength of the hypopharynx in particular and proboscis in general. It is also significant that the prey ranges from one of the largest and most dangerous insects that could be attacked (in England), the Vespid queen, to such small and soft insects as Chironomids, plant lice, etc.

In the case of *Leptogaster cylindrica*, the prey includes Rhynchota, Diptera, Hymenoptera, and a Spider. The Diptera predominate over all other orders, and consist of small flies in the main. The only case of prey being attacked which was at all formidable is given by Melin (1923). He witnessed an encounter between *L. cylindrica* and a small spider. He says:

"The spider tried to save its life by always trying to keep on the opposite side of the grass stem; but in the end the fly struck its prey. When it was frightened away, the spider, at any rate, appeared to be quite crippled." Melin also says, in discussing the prey of the family in general, "It is pretty probable, therefore, that the Arachnids also form a serviceable prey, although the sedentary life and poisoning capacity of spiders are unfavourable factors for the flies."

In view of these facts, it would seem that in the case of the spider, the Asilid injected some sort of poison, in order to have such a crippling effect on its prey: also, if it had not killed its prey very quickly it might have been bitten, and would have itself become the prey, and the spider the victor.

In the next species, *Dioctria rufipes*, the prey consists about equally of Diptera and Hymenoptera, on the whole somewhat larger and more powerful than the prey of *Leptogaster*. The only case where trouble might have ensued for the Asilid, if it had not killed its prey very rapidly, is given by Lundbeck (1908), who records a *Sphecodes*. On the other hand, however, the majority of cases are of powerful, vigorous insects that would most certainly struggle very violently and would prove very awkward for the fly, unless rendered inactive.

In the list of prey for *Dioctria atricapilla*, the most formidable is probably *Scatophaga stercoraria* (3), which, although not actually dangerous to its captor, might very possibly manage to inflict some damage in the prolonged struggle which would undoubtedly occur unless it were killed at once. Here, again, the prey is composed of Hymenoptera and Diptera in about equal proportions, and one Capsid.

Dioctria baumhaueri furnishes us with similar results, the Hymenoptera, however, preponderating over the Diptera, the only instance of an insect at all dangerous being *Halictus fulvicornis* (5).

In the above four species of Asilidæ, although very little evidence has been obtained pointing to a poison injected by the Asilid, yet in view of the vigorous nature of some of the prey, it would seem probable that some means of silencing them would be employed, other than mere puncturing the cuticle and sucking the juices.

In the next two species, however, ample evidence, in the shape of really dangerous prey, is forthcoming, pointing to an absolute necessity for the injection of some poison, if the Asilid were going to come off the conqueror.

Asilus crabroniformis is no respecter of insects, and Diptera, Hymenoptera, Coleoptera, and Orthoptera all contribute to furnish it with prey. The most vigorous of insects are overcome, such beetles as *Aphodius rufipes* (28), *Telephorus rusticus* (29), and Acridians as *Stenobothrus bicolor* (30, 31, 32), and *S. viridulus* being overpowered with the greatest of ease. Among the

Diptera it attacks even its own family, and has more than once been recorded as preying on *Machimus atricapillus* (7, 8, 9). It is among the Hymenoptera, however, that we find cases of really formidable insects being attacked,—*Apis mellifica* (5, 23), *Andrena fulva* (24), and *Vespa germanica* (25, 27) all being powerful and well-armed opponents which would most certainly have killed their enemy unless immediately deprived of the power of doing so; this is especially true in the case of the queen *Vespa germanica* (25), which could have destroyed the *Asilus* in a very short time if the latter had not managed to kill it instantaneously.

Finally, in the recorded prey of *Machimus atricapillus* we again get complete indiscrimination in its choice of victims, although Diptera are rather more in evidence than any other order. Among them we find the Reduviid *Nabis major* (6), the Eumenid *Odynerus trifasciatus* (7, 8), and *Empis livida* (22), all of which would be capable of destroying their captor, if they could manage to get at grips with it.

We see, then, that neither size nor offensive power in their victims has much effect upon the Asilidæ, and that they will not hesitate to attack insects considerably more formidable than themselves, relying always upon the factor of surprise, and thus getting the first blow in. The fact that no second blow is needed points to some means, other than mere insertion of the proboscis into their prey, for the production of death in so short a time.

The relatively few "dangerous" insects among the prey of the first four species is easily accounted for, by the fact that their mouth-parts are probably not powerful enough to pierce the hard chitinous integument of most formidable species. In the latter two cases, *A. crabroniformis* and *M. atricapillus*, the mouth-parts of the flies are very much more powerful, and capable of piercing extremely hard and thick chitin, also the insects themselves are distinctly more active, and better built for attacking vigorous and "dangerous prey."

2. The Method of Attack, and the Position of Insertion of the Hypopharynx.

The foregoing lists are the records of every Asilid that I have seen with prey, and that I could determine with accuracy. In many cases I was only able to observe them long enough to record the species of predator accurately, others I was fortunate enough to capture, and was able to dissect the prey for evidence of damage and injury inflicted upon them. My chief aim, however, was to study the feeding-habits of the Asilidæ as closely as possible, and in a considerable number of cases I was able to notice at least the position of insertion of the hypopharynx, while in some cases I watched the entire drama through, from start to finish. [Continue on p. 614.]

Method of Attack; Position of the Insertion of the Hypopharynx; Pre-Mortem Period.

Asilid.	Prey.	Position of Insertion of Hypopharynx and Method of Attack.	Pre-Mortem Period.
*2. *Leptogaster cylindrica* De G., ♂.	*Rhyphus punctatus* F., ♀.	The back of the head at the insertion of the neck.	Died instantaneously.
3. „ „ ♀.	*Culex pipiens* L., ♀.	„ „ „ „ „ „ „ „	„ „
6. „ „ ♀	*Chironomus* sp.	The Chironomid was fixed by the thorax upon the proboscis of its captor.	Was still moving feebly.
2. *Dioctria rufipes* De G., ♂.	*Miris calceratus* Fln.	The prey was seized by the first two pairs of legs, and the hypopharynx of the Asilid driven right in between the eyes at the top of the head.	Died instantaneously.
3. „ „ ♀.	*Bibio pomonæ* F., ♂.	The Bibionid was on a grass stem, and as it was flying off the Asilid attacked it, leaping upon its back and driving its proboscis deep into the back of the head of its victim.	„ „
6. „ „ ♀ ♀	*Chloromyia formosa* Scop., ♀.	The Asilid settled on a leaf, and a moment later *C. formosa* also alighted on the same leaf; the Asilid immediately attacked it, jumping sideways and driving its proboscis into the thorax right between the wings.	Prey struggled violently for a short time, and then suddenly expired.
3. *Dioctria atricapilla* Mg., ♂.	*Scatophaga stercoraria* L., ♀.	Caught its prey upon a flower-head of Umbelliferæ, jumped sideways at it and drove its proboscis through the right eye.	Died instantaneously.
4. „ „ ♀.	*Bibio pomonæ* F., ♀.	Prey was stuck on the proboscis of the Asilid by the prothorax.	Still struggling feebly.
5. „ „ ♀.	*Empis pennipes* L., ♂.	Hypopharynx of Asilid was thrust clean through thorax of the Empid.	Died instantaneously.
7. „ „ ♀.	*Capsus lanarius* L.	Caught while flying and pierced at base of pronotum.	„ „
3. *Dioctria baumhaueri* Mg., ♀.	*Hybos* sp.	Prey was pierced at the side of the neck, just behind right eye.	Died instantaneously.
4. „ „ ♀.	*Syrphus corollæ* F., ♀.	The back of the head, through the neck.	„ „
7. „ „ ♀.	*Lissonota sulphurifera* Grav., ♀.	At the back of the thorax.	Struggled feebly for about half a minute.

1. *Asilus crabroniformis* L., ♂.	*Mesembrina meridiana* L., ♂.	The back of the head just above the insertion of the neck.	Died instantaneously.
4. „ „ ♂.	*Callipliora erythrocephala* L.	The back of the head a little to the left, and below the insertion of the neck.	„ „
5. „ „ ♂.	*Apis mellifica* L., ☿.	Through the centre of the thorax, between the fore-wings.	Struggled violently for half a minute, but was held with apparent ease by the Asilid. Died quite suddenly at the end of half a minute.
6. „ „ ♀	*Empis livida* L., ♀.	Thrust right into thorax, just under left wing, pointing downwards.	Died instantaneously.
14. „ „ ♀.	*Mesembrina meridiana* L., ♂.	Asilid seized prey, and thrust proboscis into abdomen. After sucking for some time, changed position and thrust it into side of thorax.	Struggled for at least four minutes, and was still moving after 12 minutes.
10. „ „ ♀.	*Eristalis tenax* L., ♀.	Through top of head just between eyes.	Died instantaneously.
20. „ „ ♀.	*Tachina fera* L., ♀.	Back of head, above neck.	„ „
26. „ „ ♀.	*Aphodius rufipes* L., ♂.	Through neck into head.	„ „
30. „ „ ♀.	*Stenobothrus bicolor* Chp., ♀.	Through back of the head.	„ „
24. „ „ ♀ ♀	*Andrena fulva* Schrank.	Back of head, above the neck.	„ „
25. „ „ ♀.	*Vespa germanica* F., ♀.	Through top of neck into head.	„ „
29. „ „ ♀.	*Telephorus rusticus* Fln., ♀.	Through left elytron.	„ „
3. *Machimus atricapillus* Fln., ♂.	*Sicus ferrugineus* L., ♂.	Through side of thorax under left wing.	Died almost instantaneously.
6. „ „ ♂.	*Nabis major* Cost., ♂.	Through centre of pronotum.	„ „ „
10. „ „ ♀.	*Scatophaga stercoraria* L., ♀.	Through back of head.	Died instantaneously.
14. „ „ ♀.	*Lucilia cæsar* L., ♀.	The Asilid flew on to a fence, with prey impaled upon its proboscis by the abdomen.	Still struggling when seen; went on for about ¾ minute
16. „ „ ♀.	*Rhyphus punctatus* F., ♂.	Through thorax at the base of the right wing.	Died instantaneously.
17. „ „ ♀.	„ „ ♀.	Through back of the head.	„ „
22. „ „ ♀	*Empis livida* L., ♂.	Through back of the head.	„ „
24. „ „ ♀	*Halictus smeathmanellus* Kirb., ♀.	Through back of the thorax, above petiole.	„ „

(* The figures refer to those in the tables on pages 606-609.

A. The Pre-Mortem Period.

The observation of the time in which the prey succumbed after being struck is naturally involved with the method of attack and the position of the insertion of the hypopharynx, it being obviously impossible for the time to be ascertained unless the actual attack was witnessed. I have therefore tabulated my results, their significance being better realised in that way (pp. 612–613).

An analysis of the foregoing results shows that out of 33 observations 26 were cases where the prey died instantaneously, or almost instantaneously, and 7 were cases where the prey struggled, violently or feebly, but took a short time to die.

Of the 26 cases of instantaneous death, the hypopharynx of the Asilid was inserted in the head in 18 cases, and through the thorax in 8 cases. Of the 18 cases where it was inserted in the head, 14 were pierced at the back of the head just above the neck.

Among the 7 cases where the prey did not die at once, they were pierced in the thorax in five instances, and in the abdomen in two.

Two significant facts stand out from these figures:—

1. That of the total number of instances where a detailed study could be made of the attack, over 75 per cent. were cases where the prey was killed instantaneously.

2. That of these cases of instantaneous death, over 75 per cent. of the prey were pierced at the back of the head.

B. The Relation between the Method of Attack and the Pre-Mortem Period.

It would seem from the above results that the Asilidæ attack, when possible, the back of the head, especially in the cases of large and formidable insects, there being not one record of prey that had been pierced in the head that had not died instantaneously. This is, of course, only to be expected, as the head of an insect is undoubtedly the most vulnerable part of its anatomy, and the back of the head offers a considerably easier passage for a sharp instrument such as the hypopharynx of the Asilids, than does the thorax, for instance. In fact, going upon the results, one might be tempted to come to the somewhat natural conclusion that the secret of the Asilids' killing power lay in accuracy of aim, and that the hypopharynx piercing the brain of the prey was sufficient to cause instantaneous death. This is not the case, however, for Le Conte (1850) made an extremely interesting experiment with Cicindelid beetles and a pin, and he found that even inserting the pin into the head of the beetle and twisting it round did not cause immediate death. I myself carried out a series of experiments upon the same lines, with similar results; before, however, going into this point with any detail, I shall discuss the results and observations of earlier writers.

Very few workers mention the method of attack of the Asilidæ, and still fewer the position and method of insertion of the hypopharynx.

Robineau-Desvoidy (1836) says, with reference to *Selidopogon diadema* Fabr. catching bees:—"L'asile, au moment où il avait saisit l'abeille, lui avait enfoncé dans la tête son suçoir garni de larmes tranchantes et probablement couvertes d'une salive empoisonnée."

Le Conte (1850), referring to *Promachus vertebratus* capturing Cicindelids, states that the latter were always killed before the Asilid could be driven off, and that vital action appeared to cease instantly.

Fitch (1865) does not mention where the Asilid pierces its prey, but states that the latter often sting and attack their captors, both bees and hornets stinging them without effect. He also states that an "Asilid will live for an hour with a pin dipped in Cyanuret of Potassium piercing it."

Todd (1881) gives an instance of an *Asilus* attacking a dragon-fly. The *Asilus* was clinging to the Odonate under its right fore-wing, and was sucking its prey in that position.

Edwards (1883), in describing the attack of an Asilid upon the Geometrid *Aspilates dissimilaria* Guen., states: "I captured some of the *Asilus* the moment the moth was seized, but in all cases death appeared to have ensued at once, the point of attack being the thorax of the *Aspilates*."

Aaron (1894) has paid more attention to the actual method of attack; he states that the "Robber-fly always pounces upon the back of its victims," and he describes an encounter between an Asilid and a grasshopper: "An *Asilus* has been seen to seize a grasshopper, and the powerful Acridian did everything for a few moments to dislodge its captor, the first few springs rolling them both over in the grass; the robber keeping its hold, and remaining on the grasshopper's back, while the latter tried to scrape the fly off with his long hind legs. In a moment the sword proboscis was thrust away into the back of the hopper's head, and with a few convulsive kicks the Acridian expired, literally bereft of his brains or what part of them the fly could make a meal of." He also says "the keen and sword-like proboscis is easily thrust through the hard coat of mail of a wasp, hornet, certain beetles and all other softer insects, and will stop their struggles in a few seconds."

Poulton (1906) mentions one case of *Laphria gibbosa* which was sucking a Buprestid *Ancylocheira flavomaculata* and had its proboscis thrust through the cephalothoracic articulation. He says: "Dr. Chapman has pointed out to me that if the beetle had not already been killed, or killed the instant of insertion, it could have crushed the Asilid's proboscis with ease. When an Asilid is captured and held by the wings it often extrudes, as if in defence, a frothy liquid from the end of its proboscis; and it is probable that this is the poison."

Melin (1923) describes how *Dioctria hyalipennis* attacked a Hymenopter, and pierced it under the right eye, throwing it on its back in so doing; it did not, however, kill it immediately. But in alluding to *Laphria flava*, he says: "its booty is usually seized from behind, and as far as I have observed is fixed on to the proboscis even during the flight." But when describing the actual process of suction he says: "As regards the process of suction, this is carried out in the following way. After the fly has brought its prey near the proboscis by means of its front pairs of legs, the proboscis is pressed against some suitable point after careful examination: and after this the hypopharynx is shot out and pierces the skin of the victim."

It will be seen from the above quotations that the only writers to devote any attention to the insertions of the hypopharynx are Aaron and Melin, while Edwards has observed an instance of a species of Asilidæ attacking a moth, when it always inserted its proboscis in the thorax. Aaron comes to the conclusion that the general position for attack is the back of the insect, and in his description of the attack of an Asilid the back of the head of the prey was the spot. Melin does not seem to have made any definite observations on this point, except that he considers that the Asilid chooses its spot with considerable care, apparently involving some little time in the doing so; at least it is difficult to see how the fly could manage to strike instantaneously, which it would certainly have to do in many instances, and at the same time choose its position of attack with care. On one point, however, practically every authority is agreed: that the Asilids kill their prey with extreme swiftness, often instantaneously.

From my own observations, as has already been pointed out, it will be seen that the favourite place of attack is the back of the head, and one might be tempted to think that the mere fact of anything being inserted in such a position would kill an insect. Le Conte (1850) proved that this was not so, and a report of an address which he gave to the American Association on "Some curious Habits of a Species of Asilus," states, referring to *Promachus vertebratus* capturing Cicindelids, "they were always killed before the Asilid could be driven off," and that "vital action appeared to cease instantly, and this was evidently caused by a very virulent poison, as the insect attacked was always found in a completely relaxed state, nor did the ligaments become stiff again until the specimen was dried. This was not owing to the sudden introduction of a sharp-pointed instrument (such as the beak of the *Asilus*) into the vital parts of the insect, for Dr. Le Conte had taken a larger pin and introduced it between the head and thorax of Cicindelæ, and even moved it about, without producing any apparent effect, and even when the insect finally did die, the limbs were not relaxed."

As already mentioned, I carried out experiments similar to those of Le Conte, on a larger scale, and obtained similar results;

the insects I used for this purpose were the following:—*Vespa germanica* ☿, *Stenobothrus bicolor*, *Eristalis tenax*, *Calliphora erythrocephala*, and *Musca domestica*. In the case of *Vespa germanica* the insertion of a pin into the head appeared to have no immediate effect on the wasp at all; even when it was moved about freely, completely destroying the brain and internal organs of the head, no immediate effects were visible on the insect. The wasp flew off when released and settled on the window pane, moving about rapidly for some time, and finally flying about the laboratory with every apparent sign of vigour; at length it settled once more upon the window, and after remaining motionless for a few moments, relaxed its hold and fell on to the bench, dead. The time from the insertion of the pin to death was 28½ minutes. The same thing happened with every insect experimented upon, the time varying with the physical strength of the individuals; the wasps seemed to be the most resistant, a fact which lends significance to Fitch's statement that the Asilidæ are very resistant to wounds and stings, both the Asilidæ and the Vespidæ being predaceous insects.

The results are tabulated in order of resistance:—

Vespa germanica, ☿	30 minutes.
,, ,, ☿	28½ ,,
,, ,, ☿	26 ,,
Stenobothrus bicolor, ♂	24 ,,
,, ,, ♀	22½ ,,
Calliphora erythrocephala, ♀	19 ,,
Stenobothrus bicolor, ♀	18 ,,
Eristalis tenax, ♂	16 ,,
,, ,, ♀	15 ,,
Calliphora erythrocephala, ♂	14 ,,
,, ,, ♀	10 ,,
Musca domestica, ♂	7 ,,
,, ,, ♀	5 ,,
,, ,, ♂	4 ,,

The above results are from insects pierced in the head, the most vulnerable part of an insect's body; when pierced in the thorax or abdomen, in every case the victims lived considerably longer. A familiar experience to collectors, at any rate when they start collecting, is the insufficiently poisoned specimen, which although pinned through the thorax on to a setting board, yet survives and manages to destroy itself by its struggles.

It is evident then that the Asilid must do something more than merely pierce its prey,—it must eject some sort of poisonous saliva. Melin (1923), referring to the salivary secretion, "on the strength of Le Conte's experiments, and all other observations," considers that "it is pretty certain that the secretion acts as a poison," but he goes on to point out that the effects are

very different, varying with the amount of use and the nature of the weather. "If, for instance, a fly has caught a number of victims in rapid succession, it often seems as if the victims last caught were not properly paralysed, but move their antennæ and legs for a more or less long time. In cold and rainy weather also the victims are apt to be inadequately paralysed. Thus, for instance, the weather was chilly and wet when I observed the *Dysmachus* female mentioned in the first chapter which had taken possession of a large Tipulid. Although the fly had been sucking at its victim for a considerable time, yet the latter flew away suddenly without any sign of discomfort."

It is a pity that Melin does not mention where the *Dysmachus* inserted its proboscis; I should hardly think that it was in the back of the head. In the single case of *Asilus crabroniformis* feeding upon *Mesembrina meridiana* (pp. 608, 613, no. 14), and not killing its victim instantaneously, the victim did not die for a considerable time, but apparently as the *Asilus* could hold it with ease, and also had nothing to fear from a sting, it did not trouble to inject any poison; the weather incidentally happened to be very fine at that particular moment, and the whole day had been very hot.

Melin goes on to say: "Instead of this the primary function of the secretion is to be found in quite other physiological reactions, such as the prevention of the coagulation of the nutritive liquid, and as in the *Dytiscus* larvæ and other insects, to bring about a dissolution of the nutriment outside the intestines."

This seems plausible, but how to account for the killing power of the flies? It is not usual in nature for one salivary secretion to function both as a poison and as a solvent: a separate secretion for poisoning prey and for salivary purposes is found in snakes, spiders, scorpions, and wasps and bees,—why not in the Asilidæ? The following accounts of instances where I observed the entire process of attack and feeding of Asilidæ illustrate this point; I proved beyond any doubt, to my own satisfaction, that the Asilidæ possess two separate secretions with an outlet in the proboscis. Subsequent examination of the mouth-parts revealed the sources of both.

The following are accounts of the entire process of attack and feeding of various Asilidæ, three cases being observed in the field by the aid, at times, of a hand-lens, and two cases being in the laboratory under a powerful dissecting binocular.

Taking the field observations first:—

1. *Dioctria baumhaueri* ♀ attacked the Syrphid *Syrphus corollæ* ♀ (p. 612, no. 4).

The Syrphid was feeding on a buttercup, and after a short time flew up and hovered over another one. *D. baumhaueri* was on the head of a short Umbellifer about 4 inches distant and a little higher; it immediately saw the Syrphid and turned round facing

it. As the latter hovered lower almost touching the flower preparatory to settling, the Asilid leapt and landed squarely upon the back of its prey. It seized it by the two fore pairs of legs, imprisoning the right wing and fore legs of its victim, at the same time thrusting its proboscis deep into the back of its head, forcing it forward and so exposing the neck. The hypopharynx was plunged into the head just above the neck, and almost instantly the Syrphid relaxed its struggles—apparently dead.

The process of feeding was not so easy to observe accurately, as the Asilid continually turned its prey over and inserted its hypopharynx in a fresh place. The most notable point was that a copious quantity of saliva was secreted, and even when the hypopharynx was embedded in the victim, saliva continued to exude over the exterior of the prey, coming apparently from the interior of the proboscis. This fact astonished me considerably, as the only outlet of the salivary duct is at the apex of the hypopharynx, but in all subsequent observations the same phenomenon was observed, and in some cases more accurately.

The second case was of *Asilus crabroniformis* ♀ attacking *Stenobothrus bicolor* ♂ (p. 613, no. 30).

A. crabroniformis was seated upon a large patch of cow-dung, and had been there for some time when a large female *S. bicolor* alighted from a short flight on the bottom leaf of a thistle plant which was only about 9 inches from the Asilid. As in the first case, the latter turned to face its prey, and started creeping towards it; when the Asilid had reached the edge of the patch of dung, the Acridiid walked off the leaf on to the grass, and started to approach the fly. Immediately the latter sprang into the air and landed squarely upon the back of its victim; it at once thrust its proboscis hard against the back of the head of the *Stenobothrus*, forcing it slightly forward so as to expose the region just above the neck. The hypopharnyx was inserted in this region, and almost immediately the struggles of the Acridiid ceased. The Asilid remained where it was for some time, sucking its prey, and so still was it that I was able to examine in detail the process of feeding. In this case there was no doubt about the matter, saliva being exuded from some orifice other than the hypopharynx (unless by some chance the saliva from the hypopharynx was welling up along the outside of the blade, and so looked as if it were coming from the proboscis; this, however, was extremely unlikely). After a time the Asilid withdrew its hypopharynx and inserted it in the thorax of its victim, and I was again enabled to see the process of insertion. The proboscis was pressed against the side of the thorax, and the hypopharynx, thrust out, piercing, with apparent ease, the thick chitin; once more a heavy salivary secretion was noticed making the area around the wound excessively sticky. After the Asilid had finished its meal I examined the prey and found that the entire contents of the head and much of the thorax had been consumed.

The third case was extremely interesting:—

A ♀ *Asilus crabroniformis* attacked a queen *Vespa germanica* (p. 613, no. 25).

The *Asilus* was seated upon a patch of cow-dung when the Vespid flew past, very low and quite slowly, making a great buzzing; it circled round once more and then flew off. The *Asilus* had evidently noticed it, as it had raised itself upon its legs and was standing in an alert attitude of watch. In a few moments the Vespid returned and once again flew round the cow-dung on to a thistle flower which had been broken off the parent plant and was lying among the grass. The *Asilus* had turned and was facing it, remaining in a watchful attitude while the Vespid moved about on the flower-head. In a short time the latter flew off, and as it did so the *Asilus* made its spring, catching its prey in the air as it flew above it, and landing clean upon its back; it thrust its proboscis between the head and thorax, inserting its hypopharynx in the back of the head. Almost immediately the wasp fell to the ground, and after a few convulsive struggles relaxed and lay still.

On my making a movement the *Asilus* flew off, but I was able to obtain its prey, and on examination found it to be in an apparently paralysed condition, but whether it was really paralysed or whether it was dead I was unable to determine. On dissecting it the wound was found to be immediately above the entrance of the neck into the head, but there was no sign of any displacement of the internal organs of the head. The only means of telling that the wasp had not died a natural death was the relaxed state of the limbs and the very small puncture behind the head which could be easily seen under a pocket-lens.

In captivity the Asilidæ did not feed at all readily. I was successful, however, in observing two *Dioctria* attack and feed upon a Cordylurid and an Empid.

These observations were made in the laboratory by means of the apparatus described on page 601.

In the first case (p. 612, no. 3) both the insects were upon a flower-head of Umbelliferæ. The Cordylurid *Scatophaga stercoraria* ♀ was feeding upon the juices of the exposed nectaries of the flowers. The Asilid, which was *Dioctria atricapilla* ♂, was seated motionless upon the same flower-head, apparently taking no notice at all of the *Scatophaga*. For some time the same state of affairs continued, the *Scatophaga* often wandering right in front of the Asilid without the slightest effect. Suddenly, however, the would-be victim in its searching for food contrived to come up alongside its dangerous companion. Directly it drew level, the *Dioctria* made a jump sideways, and catching its prey by the head drove its hypopharnyx clean into the right eye. The effect was startling, for almost instantaneously the fiercely-struggling *Scatophaga* crumpled up and in about six seconds was completely still. The Asilid commenced feeding immediately, and removing

its hypopharynx from the eye of its prey, inserted it in the thorax. Through the binoculars this was very easy to follow, and I was fortunate enough to notice, and so confirm my suspicions of what I had seen in the field. The proboscis was pressed tightly against the side of the thorax, and the hypopharynx shot out, puncturing the chitin, as in the case of *A. crabroniformis* and *Stenobothrus*, with the greatest apparent ease; at the same time great quantities of saliva were secreted, covering the region of the thorax where the hypopharynx had been inserted. After a time the apices of the labium were drawn tighter together, and the blunt instrument thus formed was driven further into the prey, making a considerably larger wound, thus giving the hypopharynx much more freedom of movement. I was consequently able to see somewhat better, and could occasionally observe the tip of the hypopharynx as it was shot in and out; after a time the Asilid changed its position once more, and withdrawing its hypopharynx from the thorax proceeded to insert it in the abdomen. Before inserting it again, however, it remained still over its prey, cleaning its head, and at the same time exuding great quantities of frothy liquid from its proboscis, evidently identical with that observed by Poulton (1906), (p. 615). This fluid not come from the hypopharynx but from the proboscis itself; there was no doubt whatever upon this point, as occasionally the hypopharynx was extruded beyond the liquid, and the apex remained quite clear of any secretion. It then once more inserted its proboscis, this time in the abdomen of its prey, but owing to the change of position I was unable to see as clearly as before, and in a few moments it left its meal and flew off to another flower-head, where after cleaning its head and proboscis it remained motionless.

The second case was of *Dioctria atricapilla* ♀ attacking *Empis pennipes* ♂ (p. 612, no. 5).

The Asilid was seated on the edge of the Florence flask containing the flowers, and there were, among other Diptera, several *E. pennipes* in the cylinder. One of them flew right up in front of the Asilid, which immediately attacked it, seizing it with the front two pairs of legs, and thrusting its hypopharynx clean through the thorax. The prey was held quite easily upon the hypopharynx alone, and during the entire process of feeding was never once moved. The only movement noticeable was the extension and retraction of the hypopharynx, bringing the prey away from and close to the proboscis, respectively. Saliva was again secreted, covering the entire body of the Empid, but it was not produced in such great quantities as in the previous case. It was perfectly clear that it was not emerging from the hypopharynx, but from the proboscis, the apex of which could be clearly seen under the binocular. In about eleven minutes the Asilid, using its first pair of legs, scraped the Empid off its hypopharynx and flew off round the cylinder.

The above records all point to an auxiliary secretion, apparently salivary, in the proboscis of the Asilidæ. Auxiliary glands exist in the Diptera in the Syrphidæ, Muscidæ, and Tabanidæ; these glands are labial, and are situated at the fork of the labella, but as far as I know glands of such a nature have never been recorded in any other Diptera.

On examining the mouth-parts of the Asilidæ, I discovered a pair of glands situated in, and opening on to, the inner wall of the labium. Their structure I shall deal with under Mouth-parts. As regards their function, it is fairly certain that they could not be the means of poisoning the prey as the hypopharynx is the only portion of the proboscis which actually pierces the victims when they are seized. The logical explanation is that the thoracic salivary glands which open into the hypopharynx are the means of poisoning the prey, while the labial glands fulfil the function of liquefying the thick body-cavity fluid, and to a certain extent digesting externally the more solid portions of the internal anatomy of the fly's victims, which is ordinarily carried out by the thoracic glands.

Summary of the Feeding-habits, and Conclusions drawn from Experiments.

In brief the feeding-habits of the Asilidæ, as represented by the six species worked on, are:—

1. They are entirely predaceous.

2. They will attack insects considerably larger than themselves, —such dangerous creatures as Vespids, Cicindelids, Spiders, and Reduviids being attacked.

3. They kill their prey instantaneously, unless it is weak enough for them to ignore its struggles,—a feat only possible by means of some poisonous secretion, and they attack, when possible, the back of the head of their victims.

4. They consume a considerable part of the more solid portions of their victims,—a feat only possible by means of a powerful digestive saliva.

It is, I think, obvious that unless one secretion can do the work of both poison and digestive fluid, there must be two secretions utilized in killing and feeding upon the prey. Examination in the field and under the binoculars revealed a secretion evidently not of the usual origin, and investigation has shown there to be a pair of labial glands.

In view of these facts, a reasonable conclusion is that the Asilidæ kill their prey by means of a virulent poison, acting probably upon the cephalic, or, in the cases where the prey were pierced in the thorax, upon the thoracic ganglia; the fact that when pierced in the abdomen, death frequently does not occur till much later, tends to point to the nervous system as being the tissue most vulnerable to the poison.

A study of the structure of the mouth-parts elucidates much that is doubtful concerning the functions of the various parts of the proboscis, and confirms beyond any doubt the deductions I have drawn from my observations on the feeding-habits of the flies, and the experiments I have performed in this connection.

The Structure of the Mouth-parts in the Asilidæ.

Three writers only have investigated the mouth-parts of the Asilidæ really thoroughly,—Meinert (1881), Hansen (1883), and Melin (1923). The two earlier writers, especially Hansen, go very thoroughly into the structure of the mouth-parts; but, unfortunately, owing to the lack of up-to-date technical equipment they were unable to avoid certain morphological errors. Melin redescribes the mouth-parts and gives excellent figures; on certain points, however, he is inaccurate, and he has not described the muscular system of the mouth-parts in any detail, relying for his information upon Hansen. The latter certainly went very thoroughly into the musculature of the mouth-parts, but his

Text-figure 1.

Hypopharynx of *Machimus atricapillus* Fln. × 53.
Sd.=Salivary duct. Lh.=Ledge of Hypopharynx.

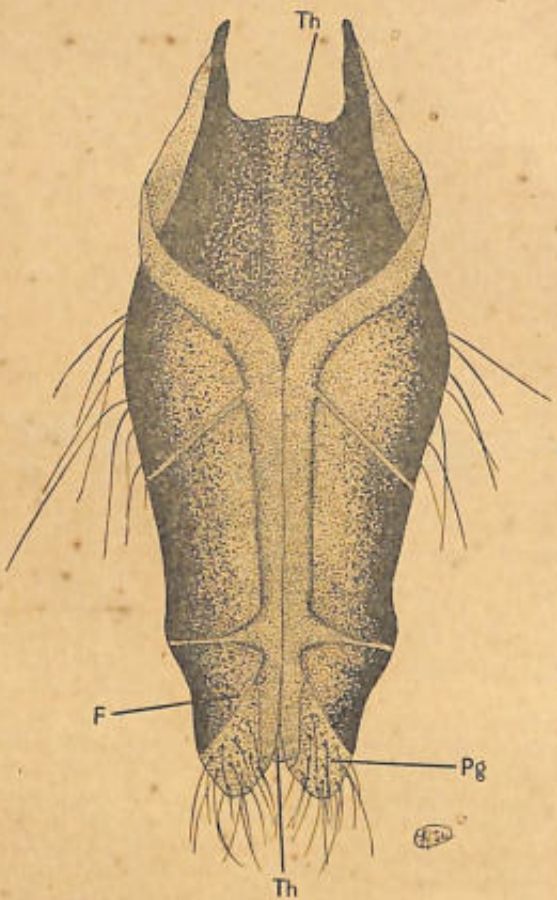
figures are somewhat inadequate from the point of view of this research, and in some cases they are inaccurate. I shall therefore redescribe both the mouth-parts and their musculature; in describing the mouth-parts I have followed Peterson's (1916) nomenclature.

The mouth-parts of the Diptera consist in their complete form of a labrum-epipharynx, mandibles, maxillæ, hypopharynx, and labium; this complete form is, however, only found among the blood-sucking Diptera, in all others the mandibles being absent. The parts are of two types, those which belong to the fixed parts of the head, and those which belong to the movable parts of the head. The former type consists only of the labrum-epipharynx, all the remaining mouth-parts being movable.

The mouth-parts of the Asilidæ, which are the same in both sexes, consist of a longish, stout proboscis, extremely hard and strongly chitinized, in which slides the hypopharynx, somewhat upon the principle of a hypodermic needle; and the structure of the remainder of the mouth-parts, which consist of labrum-epipharynx and maxillæ, is modified to form an adequate slide, or support, for the hypopharynx.

The hypopharynx (text-fig. 1) is a long and extremely powerful piercing organ, in shape like a stout needle, very heavily chitinized and more or less open on the upper surface; it varies from being quite straight to being slightly upcurved similar to

Text-figure 2.

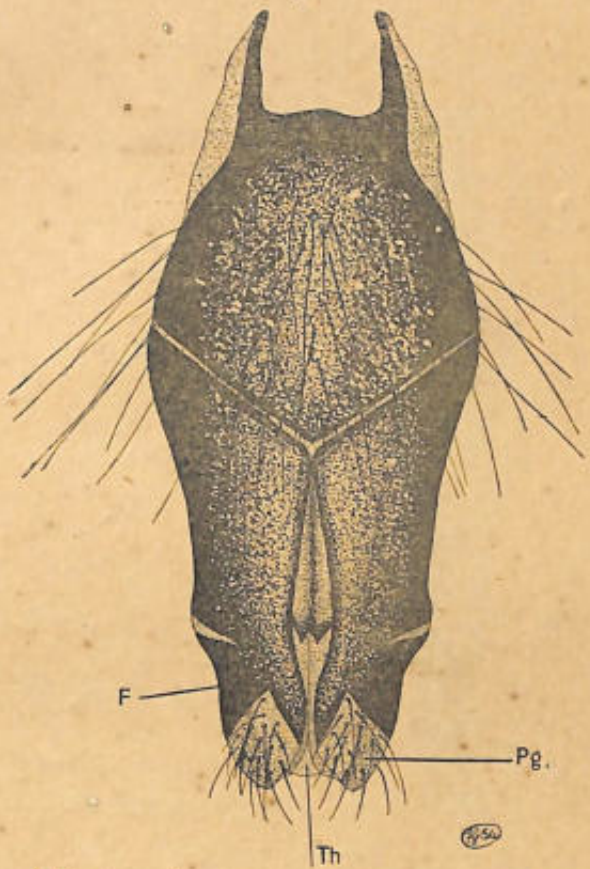


Labium (dorsal aspect) of *Machimus atricapillus* Fln. ×181.
F.=Furca. Th.=Theca.
Pg.=Paraglossa.

a sabre. Upon the under surface runs a ledge or keel, which was discovered by Melin (1923), appearing a short distance from the apex and broadening out rapidly, but contracting towards the base until the hypopharynx forms a 'T' in cross-section.

At the apex is situated a thick dorso-lateral, bristly covering, extending from a third to over half the length of the hypopharynx; the bristles are arranged in transverse rows and bend inwards and backwards, partly covering the lance-shaped dorsal opening of the hypopharynx, their probable function being to

Text-figure 3.

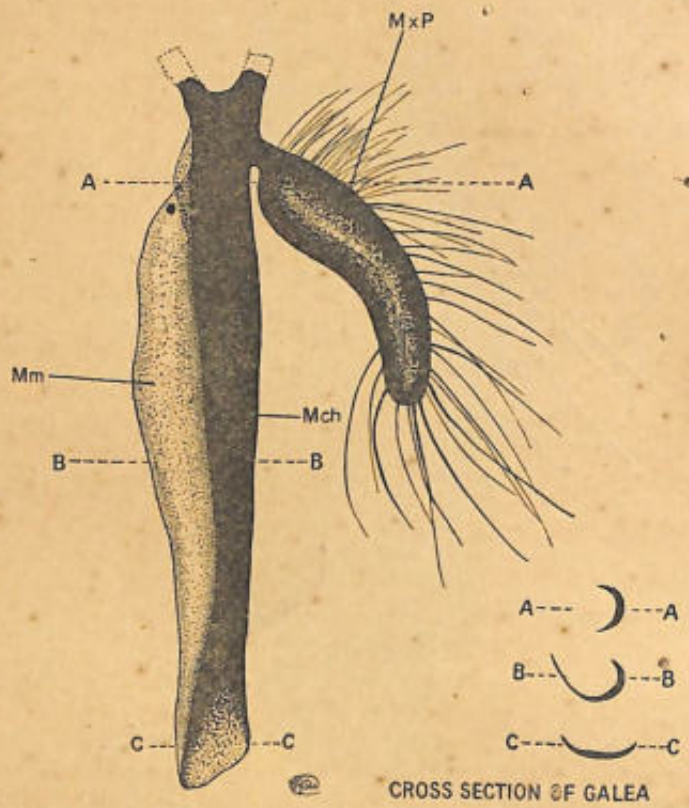


Labium (ventral aspect) of *Machimus atricapillus*. × 81.
F.=Furca. Th.=Theca.
Pg.=Paraglossa.

assist in obtaining a grip upon the prey (see pp. 612–613), and to act as a sifting apparatus. Inside along the base runs a salivary duct which opens at the apex; this duct is connected to the thoracic glands, and at the base of the hypopharynx is situated a salivary pump which forces the saliva from the glands, through the duct in the hypopharynx, into the prey.

The hypopharynx being the sole means by which the Asilidæ pierce their prey, it is therefore natural that it should be heavily chitinized and strong, but however strongly chitinized it might be it would be inadequate for piercing the thick and hard integument of many insects unless it had adequate support to

Text-figure 4



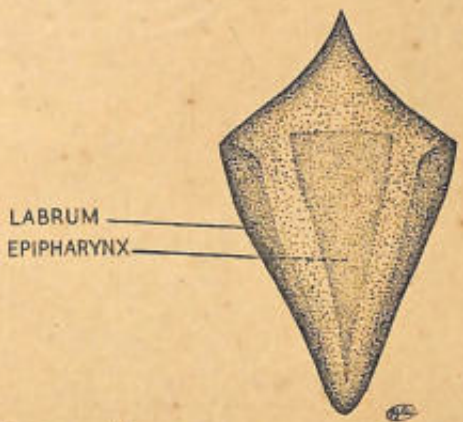
Left maxilla of *Machimus atricapillus* Fln. × 92.
Mch.=Heavily chitinized portion of galea.
Mm.=Membranous portion of galea.
MxP.=Maxillary palp.

prevent it from buckling or breaking; this support is provided by the remainder of the mouth-parts.

The labium (text-figs. 2, 3), which is extremely strong and hard, forms a tube, open above towards the base, in which are encased the remainder of the mouth-parts; it is wide at

the base, to which are attached retractor muscles (text-fig. 15) enabling it to be moved in a vertical plane, a fact which Melin pointed out, narrowing towards the apex, and is divided into three parts by slight joints which correspond to the basi-proboscis, mediproboscis, and distiproboscis of other Diptera. The basiproboscis, which attains well over half the total length of the labium, is covered upon its under surface with long bristly hairs; the apical portions consist of the furca and paraglossæ; the latter are provided with somewhat shorter bristles than are on the basiproboscis and which are probably sensory in nature. The labium is provided inside with three pairs of muscles, the best illustration of which is given by Hansen (1883). The functions of these three pairs of muscles are to relax or contract the labium,

Text-figure 5.

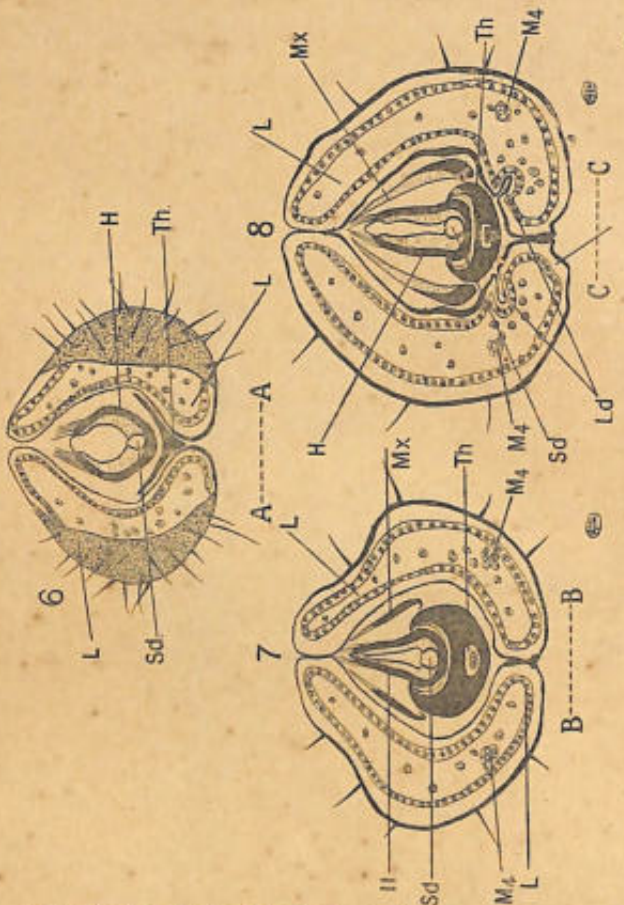


Labrum-epipharynx of *Machimus atricapillus* Fln. × 61

making it a compact, hard tube round the hypopharynx, or allowing it to open slightly, thus giving the maxillæ more room for cleaning purposes, etc.

The inner surface or floor of the tube formed by the labium consists of the theca (text-figs. 6–10 & 15), a distinctly chitinized area throughout the Diptera, but which, in the case of the Asilidæ, has been very highly developed to form a slide for the hypopharynx. No writer seems to have discovered the true nature and shape of the theca, and although Melin figures it, he has evidently not realized its true significance, and his figure does not give any idea of its real shape. At the base of the labium the theca is merely a thinly chitinized membrane, but towards the centre it assumes a thicker and more sturdy aspect, at the same time altering in shape to form a channel with smaller channel-shaped edges; Melin has figured it thus, and he

Text-figures 6, 7 & 8.



Series of cross sections of the Proboscis of *M. atricapillus* Fln.

The letters A.....A, etc., refer to the positions on th proboscis of the cross sections (see fig. 15).

Magnifications are as follows:—

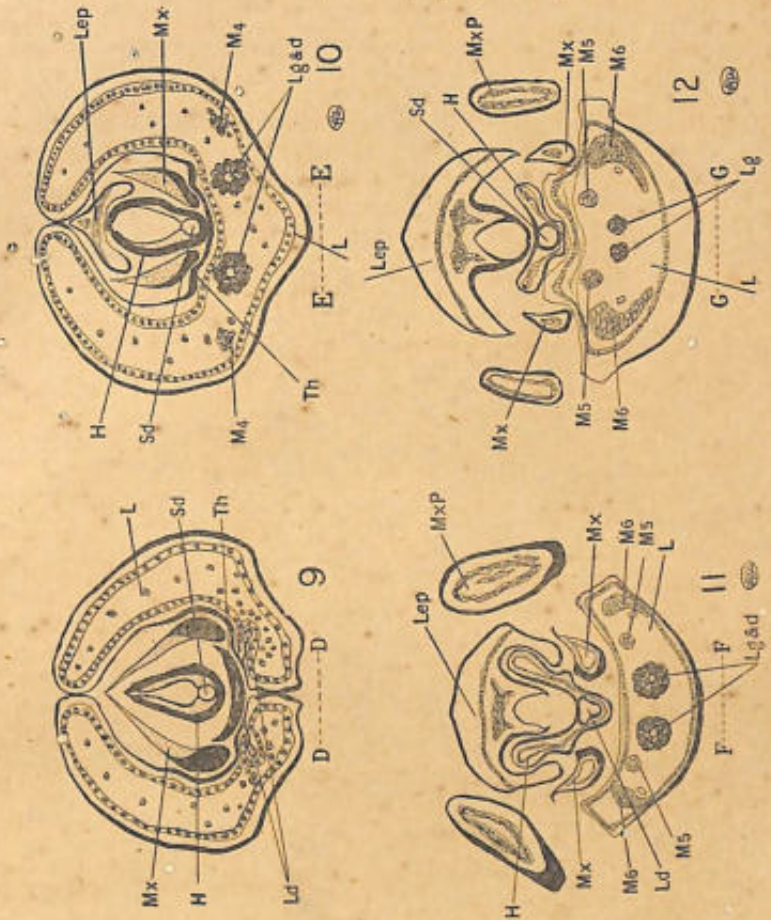
Fig. 6 × 216. Fig. 7 × 166. Fig. 8 × 160.

H.=Hypopharynx.
L.=Labium.
Ld.=Labial duct.
Lep.=Labrum-epipharynx.
Lg.=Labial gland.
Mx.=Maxilla, galea of.
MxP.=Maxillary palp.
Sd.=Salivary duct.
Th.=Theca.
M4.=1st labial muscles.
M5.=2nd " "

apparently does not realize that it develops still more as it nears the apex, the ledges curling over and forming a crescent-shaped,

thickly chitinized, and immensely strong tube open towards the upper surface, in which slides the hypopharynx. Here it breaks

(Text-figures 9, 10, 11 & 12.)



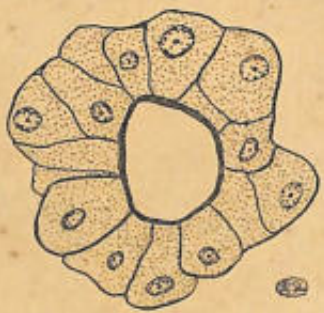
Series of cross sections of the Proboscis of *M. atricapillus* Fln.
The letters D.....D, etc., refer to the positions on the proboscis of the cross sections (see fig. 15).
Magnifications are as follows:—
Fig. 9 × 175. Fig. 10 × 163. Fig. 11 × 93. Fig. 12 × 110.
For explanation of lettering see figs. 6–8.

right away from the floor of the labium, which joins up underneath it so that it has the appearance of a tongue lying in the

labium. It is here that the purpose of the keel of the hypopharynx is apparent, as the incurved edges of the theca close over and fit exactly upon the edges of the keel, thus not only forming a slide for the hypopharynx, but gripping it firmly, almost approaching in efficiency the piston and cross-head guides of a steam-engine.

It will be seen that the theca forming such a support for the hypopharynx gives the latter enormously increased strength and efficiency, an illustration of which can be found in an ordinary pin; if one takes a pin and attempts to pierce the elytra of such an insect as a large Buprestid, considerable difficulty will be experienced, the pin often being bent. If, however, the pin be slid in a very small bore glass tube, short enough to enable the pin to be moved up and down, much less difficulty will be experienced, and there will be no danger of the pin bending.

Text-figure 13.



Cross section of Labial Gland and Duct of *M. atricapillus* Fln. × 777.

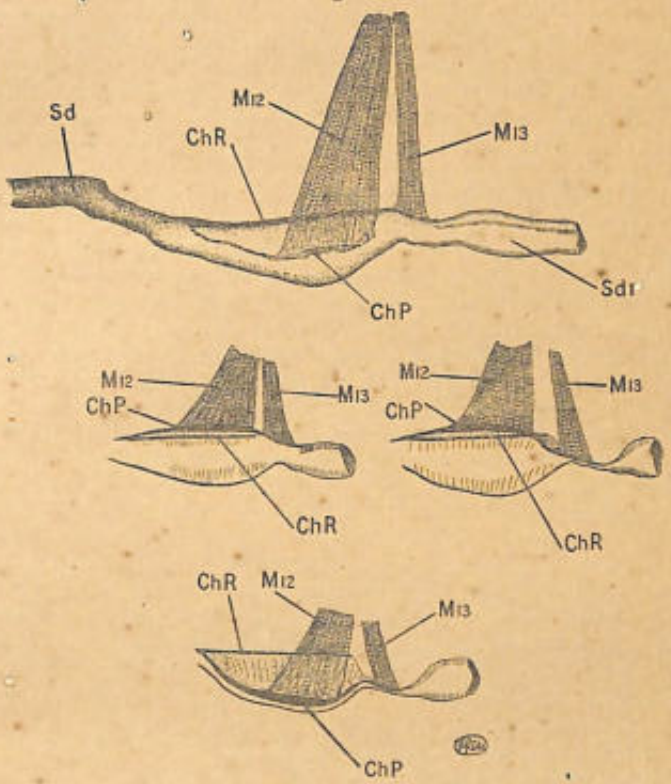
A similar function is performed by the theca for the hypopharynx, the limits of the latter's piercing power being set only by the strength of the muscles working it.

The maxillæ (text-fig. 4) also play their part in the mechanical efficiency of the hypopharynx as a piercing organ; in the Asilidæ they consist of stipites, galeæ, and palpi; the stipites are embedded in the membranous area ventrad of the occipital foramen; the galeæ and palpi are free appendages, the latter lying outside the labium close to the head. The galeæ are concavo-convex in cross-section and are covered with hair on their inner surfaces, they are more or less heavily chitinized on their lower edges, the upper edges being membranous; they lie inside the labium along the ledges of the theca, their membranous upper edges folding one over the other, forming a sheathing for the hypopharynx and closing over its dorsal opening. Muscles (fig. 15) are attached to them enabling them to be moved freely inside the labium, thus probably assisting in keeping the interior

free from food and other impedimenta. The labium forms a protective covering for the whole, and at its base, which is open, is covered by the labrum-epipharynx (text-figs. 5, 10–12, 15).

The labrum is triangular in shape, the apex being rounded off in some cases, and in others produced to a blunt point; it is

Text-figure 14.



Salivary pump of *Machimus atricapillus* Fln. × 148.
ChP. = Chitinous plate, forming attachment for muscle.
ChR. = Chitinous ring framework of pump.
M 12 = 1st Expansor muscle.
M 13 = 2nd " "
Sd = Salivary duct in hypopharynx.
Sd1 = " " from thoracic salivary glands.

recurved at the sides, more so at the base than the apex; the epipharynx is situated on the under surface between the recurved sides of the labium, forming a half tube diminishing towards the apex where it merges into the labrum, but increasing in size and circumference towards the base, until it finally joins right up and forms a complete tube.

The hypopharynx at about half-way begins to broaden out, and instead of being a tube becomes a channel, while the epipharynx, as has been pointed out, from being merely a roof to the hypopharynx, begins to join up and form a tube inside the channel of the latter (text-figs. 10–12); thus the hypopharynx is the means of conveying the nutriment until the epipharynx takes on that function, and owing to the firmness with which the former is held by the theca, its extrusion or retraction makes no difference to its relative position with the epipharynx. The labrum-epipharynx is held in position in relation to the hypopharynx by the incurving upper edges of the base of the labium, so that, however much the hypopharynx be thrust out, there is always a continuous food-channel to the sucking basipharynx (text-fig. 15).

The labrum-epipharynx, as has been previously noted, takes on the function of the hypopharynx as a food-channel, and leads into the basipharynx; Melin's statement that the latter leads towards the hypopharynx is inaccurate, for the hypopharynx is merely hinged to its lower surface, and the basipharynx forms a continuous tube with the epipharynx until at least a quarter the way down the hypopharynx, which then takes on the function of the alimentary passage. The basipharynx is heavily chitinized at its side edges, which are drawn out at their bases to two disc-like formations, the cornu, to which are attached retractor and extensor muscles; the cephalic surface of the basipharynx is membranous, and is actuated by a pair of powerful expansor muscles, thus forming a sucking pharynx. Neither Meinert nor Hansen has figured these expansor muscles quite accurately, in both cases the muscles of the basipharynx being figured as working only the membrane of that organ; actually however, at the dorsal end of the basipharynx, between the cornu, where the œsophageal pump leads into it, the sphincter muscle of the pump merges gradually into the two expansor muscles, thus forming an automatic control of the swallowing process, as will be explained in detail later.

At the dorsal end of the basipharynx is situated the œsophageal pump (text-fig. 15), a funnel-shaped organ roofed over with a stout diaphragm, which is operated by a powerful expansor muscle. The funnel is actuated by a sphincter muscle, which in conjunction with the diaphragm renders it a very powerful sucking organ. The œsophageal pump leads into the œsophagus, and the prolonged chitinous framework of the funnel and diaphragm are actuated by four adductor muscles (text-fig. 15), so controlling the passage of food from the pump to the œsophagus.

Attached to the cornu are, as has already been pointed out, powerful retractor and extensor muscles (text-fig. 15). These muscles, by working on the basipharynx, are the means of extruding and retracting the hypopharynx, the fact that the

latter is hinged to the basipharynx being counteracted by the firm seating which the theca provides for it.

Situated in the labium and opening out on its inner wall beneath the theca, where the latter is beginning to get thicker, are two glands (text-figs. 10, 11, 13 & Pl. I.), probably salivary in nature, which I have already mentioned in discussing the feeding-habits. They are considerably larger than any other labial glands found in the Diptera, and extend nearly the whole way up the labium, tailing off just where the latter joins the head. They consist of large nucleated single cells clustered round a common duct which extends right up to the base of the labium. So far as I know, these glands have never been seen before, which, unless the proboscis had been sectioned, is not to be wondered at, as they are extremely difficult to dissect out owing to the brittleness of the labium; unfortunately, owing to an accident, much of the material was destroyed, and I was only able to detect their presence in *Machimus atricapillus* and in *Asilus crabroniformis*; it is hoped, however, to get a great deal more material next summer, and to examine many more species for these glands.

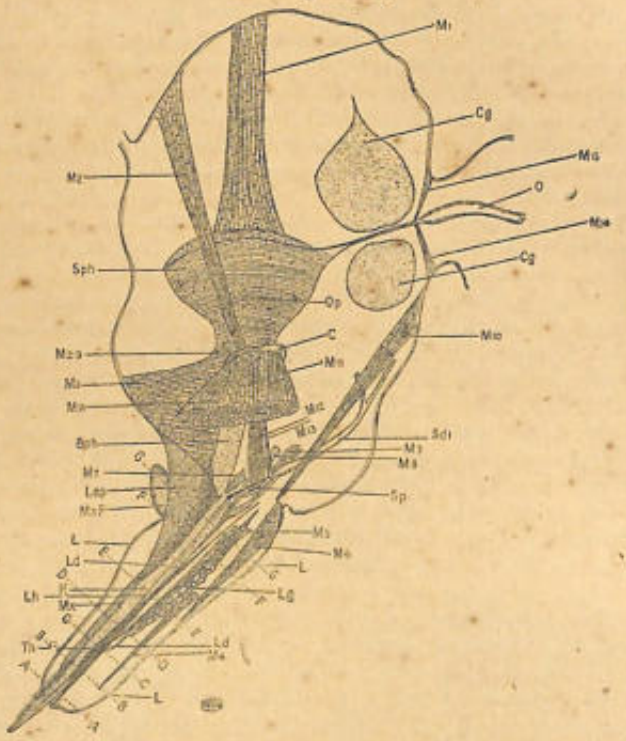
The thoracic salivary glands lead by means of two ducts to a common duct in the head, which leads into a salivary pump (text-figs. 14, 15) attached to the base of the hypopharynx. The salivary pump consists of a chitinous framework in the shape of a horseshoe, from which is suspended a stout chitinous sac; lying on top of this sac is another sac in the centre of which is a thick plate of chitin to which is attached an expansor muscle, The portion of the duct immediately behind the upper sac has a chitinized area upon its dorsal surface, a continuation of the thick chitinous plate which is situated in the sac; this area is stretched between the ends of the arms of the horseshoe and is operated by a second expansor muscle. This latter muscle when relaxed allows the chitinous patch between the two arms to contract, thus closing the duct into the pump; upon the contraction of the muscle the duct is opened. The larger muscle operating the upper sac is then contracted, stretching the sac away from the lower one, and so forming a receptacle into which is sucked the saliva from the duct; the first mussle is then relaxed, so closing the bag from behind and allowing the saliva only one egress—through the duct in the hypopharynx. The larger muscle is then relaxed, forcing the saliva through the hypopharynx into the prey.

The presence of two pairs of glands, both opening into the proboscis, tends to point to a poisonous function for one or the other pair, a fact, which in view of the flies' habits, is more than probable. The position of the duct openings of the labial glands at once precludes them from this function, as the labium is never inserted into the prey at the moment of capture, and is only rarely used as a means of enlarging the wound originally made by the hypopharynx. The latter, on the other hand, is

the only part of the mouth that is inserted for the purpose of killing the prey, and, coupled with the powerful pump, it would seem extremely likely that the thoracic salivary glands have taken on the function of secreting a virulent poison, which is injected into the prey the moment the hypopharynx is inserted.

This would account for the presence of the labial glands, for, situated as they are, and opening where they do, inside the labium, the saliva which they presumably secrete would be employed to its fullest advantage, performing the double function

Text-figure 15.



Schematic diagram of musculature and mechanism of the Mouth-parts of *M. atricapillus* Fln.

The letters A.....A, etc., refer to the cross sections of proboscis in figs. 6–12.

Bph.=Basipharynx.
C.=Cornu of basipharynx.
Cg.=Cephalic ganglia.
H.=Hypopharynx.
L.=Labium.
Ld.=Labial duct (right).
Lep.=Labrum-epipharynx.
Lg.=Labial gland (right).
Lh.=Ledge of hypopharynx.
Mx.=Maxilla, galea of.
MxP.=Maxillary palp.
Op.=Œsophageal pump.
Sd 1=Salivary duct from thoracic salivary glands.
Sp.=Salivary pump.
Th.=Theca.

of lubricating the interior of the proboscis and of thinning the juices and dissolving the tissues of the prey; in short, taking on the function which the thoracic glands have discarded.

A glance at fig. 15 will at once indicate how the mouth-parts operate. The Asilid pounces upon its prey, the proboscis is thrust against the back of its head, and the muscles (M 4, M 5, M 6) tighten it up making a rigid and efficient cylinder for the hypopharynx; the extensor muscles (M 11) of the basipharynx are then contracted, thrusting out the hypopharynx which pierces the prey and sinks deep into its head, at the same time the salivary pump injects, through the hypopharynx, a jet of extremely poisonous saliva which kills the prey instantaneously, and the process of feeding commences.

The process of suction is as follows:—the labial glands first of all secrete copious quantities of (presumably) saliva which not only lubricates the interior of the proboscis, but facilitates generally the process of feeding by liquefying and dissolving the contents of the prey; at the same time the maxillæ, moving up and down inside the proboscis, help to keep it clear from undesirable material and by being pressed tightly against the hypopharynx form a roof over it and thus considerably increase the power of the suction.

The actual sucking is performed by the basipharynx and the œsophageal pump; the expansor muscles (M 3) of the basipharynx contract, allowing it to fill with nutriment. At the same time the sphincter muscle (Sph.) of the œsophageal pump is relaxed, and as the expansors of the basipharynx merge into it, their contraction automatically opens the base of the funnel. The expansor muscle (M 1) of the pump now contracts and the pharynx muscles relax, so filling the œsophageal pump. The expansor muscles (M 13, M 14) contract, allowing a free passage into the œsophagus, the sphincter contracts and the expansor (M 1) relaxes, so forcing the food into the alimentary canal.

Explanation of Muscles.

(right) or (left) after a muscle means that there is a pair, and indicates which one is figured.

M 1 = Expansor Muscle of œsophageal pump.
M 2 = Retractor Muscle of basipharynx (left).
M 3 = Expansor Muscle of basipharynx (left).
M 2-3 = Fusion of M 2 and M 3.
M 4 = 1st Labial Muscle. } (right).
M 5 = 2nd " " }
M 6 = 3rd " " }
M 7, M 8, M 9 = Retractor Muscles actuating maxilla (right).
M 10 = Retractor Muscle of labium (right).
M 11 = Extensor Muscle of basipharynx (left).
M 12, M 13 = Expansor Muscles of salivary pump.
M 14 = Inferior Adductor Muscle (right) } of œsophageal pump.
M 15 = Superior Adductor Muscle (right) }
Sph = Sphincter Muscle of œsophageal pump.

Summary.

Both in habit and structure, the Asilidæ represent the highest point of development in the predaceous Diptera, in fact it would be difficult to find a type of insect which shows such modifications of structure for the purpose of attacking other insects. Throughout the Diptera the labium is generally the most highly developed and most important part of the mouth, although it varies greatly in shape and function; among the predaceous Diptera, however, it tends to lose its importance, and to become an auxiliary to the labrum-epipharynx, as in the Empidæ. In the Asilidæ the hypopharynx assumes the chief position of importance among the mouth-parts, the remainder of the mouth-parts becoming modified to assist in its efficient working. In fact, the hypopharynx in the Asilidæ has taken upon itself the function of the sting of the Hymenoptera. The thoracic salivary glands have similarly assumed the function of poison glands, while to replace them we find a well-developed pair of labial glands. So specialized are the Asilidæ, that they form an excellent starting point from which to compare all other types of Dipterous mouth-parts, and they furnish, possibly, the best example of a close relation between habit and structure to be met with in the Diptera; for, with the exception of certain Empidæ, they are the only British Diptera whose food consists entirely of prey, even the blood-sucking forms frequently feeding upon the nectar and juices of flowers.

It is hoped that a closer study of the labial glands in the Asilidæ will be possible in the near future, and it is intended to examine many more species for the presence and function of these glands. As has already been mentioned, a very large amount of data has been amassed regarding the feeding-habits of many families of Diptera, and it is hoped that it will be possible to publish a similar paper on the Empidæ before very long, and possibly in the near future to complete the work of correlating habit with structure throughout the predaceous Diptera.

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EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. Photomicrograph of T.S. proboscis of *Machimus atricapillus*, showing hypopharynx, theca, labial ducts, etc.

Fig. 2. Photomicrograph of T.S. proboscis near head of *M. atricapillus*, showing labrum-epipharynx, hypopharynx, and labial glands and ducts.

Fig. 3. Photomicrograph of L.S. proboscis of *M. atricapillus*, showing labial gland and duct.

PLATE II.

Fig. 1. Photograph of head of *Leptogaster cylindrica*, showing hypopharynx extruded. (Highly magnified.)

Fig. 2. Photograph of *Asilus crabroniformis*, showing :—

1. Proboscis.
2. Claws and bristles on legs. } × 2.

28. A Study on Parasitism in the Cuckoos. By the Rev. F. C. R. Jourdain, M.A., M.B.O.U., H.F.A.O.U., etc.*

[Received March 17, 1925; Read March 17, 1925.]

(Plates I.–V.)

Introduction.

"There are two essentially different kinds of ornithology: systematic or scientific, and popular. The former deals with the structure and classification of birds, their synonymies and technical descriptions. The latter treats of their habits, songs, nesting and other facts pertaining to their life-histories.... But systematic ornithology being a component part of biology—the science of life—is the more instructive and therefore more important."

R. Ridgway, 'Birds of North and Middle America,' p. 1.

These words occur in the opening lines of what is perhaps the greatest work produced by any American ornithologist, 'The Birds of North and Middle America,' which comes almost in the same category as Dr. Hartert's 'Die Vögel der Palaärktischen Fauna' on this side of the Atlantic. It represents with perhaps more frankness than usual what most anatomists and taxonomists feel with regard to the study of other aspects of Bird-Life, and discloses some of the weaknesses of present day ornithology. For at the present time there is too great a tendency to work in "water-tight compartments," if one may be allowed to use such a term. The Comparative Anatomist has no knowledge of the bird in life, although every structural development must be closely related to the life-habits of the animals: serious work on classification and nomenclature can only be carried on by specialists in our great museums where vast series of skins are available for comparison and extensive libraries are at hand; so that it tends to become more and more the preserve of a close corporation, who regard the naming of subspecific forms as the aim and end of all ornithology, and spend their time in immortalizing one another. All are, however, agreed on one point, and that is the somewhat contemptuous toleration with which all other branches of "Popular" ornithology are regarded. The study of the life-history of the bird from the egg to its death, its social ceremonies, its breeding-habits, its migrations, its distribution—these are comparatively trivial matters which can be left to the egg collector, the bird photographer, and the bird watcher. Yet a wider and less narrow-minded view of the whole field may induce some qualms as to whether there may not be something to be said on the other side. Possibly the man who by weeks of patient

* Communicated by the Secretary.

field-work establishes beyond cavil some new law in the history of a species is after all doing quite as good work as a man who pulls out a drawer with 100 skins in it, and after spending an hour or two in arranging them geographically, finds that the northern birds have a slightly yellower tinge on the mantle (invisible of course by artificial light, but perceptible in about 70 per cent. of the specimens by bright daylight).

In the present paper I propose to deal with a single episode in Bird-Life, the "Brut-Parasitismus"—a convenient compound word which defines Parasitism which is restricted to the nestling period alone. In the list of literature of the Palæarctic and Indian Cuckoos alone appended to this paper over 100 titles are mentioned of papers, all dating within the last 150 years, yet quite double this number of notes of varying length have been omitted as bearing solely on special branches of this subject which are not investigated here in detail. The mere study of this list, the slow accumulation of facts, the gradual elimination of the unreliable evidence and the untenable theories, and the interesting side-lights which come out when one re-reads the old records in the light of later observations, form a task of enthralling interest.

Perhaps it will make the matter clearer if I indicate the principal facts that have already been established with regard to the Common Cuckoo and their authors. It has, of course, been known from very early times that the European Cuckoo (*Cuculus canorus*) lays eggs of widely different types, usually one in a nest, making use of various fosterers. That some similarity existed between the eggs of the Cuckoo and the fosterer was hinted at by Salerne in 1767. Lottinger carried out a series of experiments by placing eggs in the nests of various birds, in most cases causing them to desert, though this was not the case with the Cuckoos' eggs desposited by the bird itself (1775 and 1795). Jenner in 1788 showed from personal observation that the young Cuckoos ejected the young or eggs of the fosterer, and this was subsequently confirmed by personal observations made by Montagu (1802), Blackwall (1824), Mrs. Blackburn (1872), John Hancock (1886), and others; though Waterton (1838) flatly denied and even Seebohm (as late as 1884) discredited the story *.

Baldamus (1853–4) was the first to investigate the problems of the eggs on scientific lines, and satisfied himself that each hen Cuckoo laid eggs of the same type, and that as a rule this type corresponded with the eggs of the fosterer in whose nests the eggs were laid. He believed that the eggs were laid on the ground and afterwards inserted by means of the bill, and offered no satisfactory explanation as to how the correspondence between the eggs of the Cuckoo and the fosterer came about. On the other hand, his evidence tends to show that both male and female

* Still more astonishing is "Le Testament d'un Ornithologiste" by X. Raspail (Rev. Franç. d'Orn. 1925, p. 88) in which Jenner's observations are contemptuously dismissed as a 'Légende absurde'!

have definite territories. When the work of Baldamus became known in England, much incredulity was expressed with regard to the genuineness of some of the more striking cases of mimicry reported, especially in the case of the blue type. This was not unnatural, in view of the fact that the Hedge-Sparrow (*Prunella modularis*) habitually accepts and broods eggs which bear no resemblance to its own blue eggs, while blue eggs of the Cuckoo are unknown here. As the Hedge-Sparrow is a common fosterer in the South of England, it is not surprising that those familiar with the striking contrast between the eggs of the fosterer and its host should be incredulous of anything more than accidental mimicry.

There is little doubt that Brehm's investigations of the habits of the Great Spotted Cuckoo, which appeared almost at the same time as the paper of Baldamus, gave additional support to this theory of mimicry.

In 1871 Rey published his first paper on Cuckoos' eggs, marking a new era in research of this kind—a combination of keen and persevering field-work together with accurate recording and cautious inferences. In 1876 Walter also began serious work in the same field—he suggested that the Cuckoo laid twice weekly—and in view of a recent controversy on the subject, it is interesting to note that he records at this date two breeding nests of Wren (*Troglodytes troglodytes*), each containing a Cuckoo's egg, deserted owing to the Cuckoo having torn the opening by forcing its way into the nest, and that in these cases the egg was not introduced by the bill. He still maintains, however, that the latter method is sometimes used.

Previous lists of recorded fosterers being very incomplete, Bidwell compiled a nominal list of recorded British fosterers in 1883, followed by more complete general lists by Rey (1892), Bidwell and Bladen (1896), Rey (1901), and Jourdain (1911 and 1923), the last referring to British records only *. The supposed case of a Cuckoo incubating was completely discredited by Walter (1889), though occasionally quoted by English naturalists at a much later date.

Rey's collected observations in 'Altes und Neues' (1892) established so many new facts that this work deserves a special paragraph. Besides fixing the criteria for distinguishing Cuckoos' eggs, in itself a notable achievement, he pointed out that in the case of some fosterers mimicry is exceedingly close in practically every case, in others less close and not invariable, while in the third category it does not exist. The number of eggs laid in a season by one female Cuckoo might reach about twenty, laid on alternate days. Though strong evidence was adduced on behalf of this last proposition, it was not demonstrated beyond doubt till Chance's observations (1919–1923). Many

* Of these lists all but Jourdain (1911) are merely lists of species: the list in question gives references to the original records on which their presence rests.

other points already noticed were confirmed, such as the restricted territory of the hen Cuckoo, the general rule that each individual is parasitic on one species and that she lays eggs of similar type throughout her life, the removal of (usually) one of the fosterer's eggs, etc. No light is thrown on the questions of how mimicry has been attained, or the method of deposition, but it was then generally believed, as suggested by Baldamus, that the similarity in colouring was due to the food of nestling parasite and host being alike. On the whole, Rey's 17 propositions have stood the test of time well, although one or two of them require slight modifications.

Čapek (1896) followed with a careful series of observations on similar lines, but even more detailed. As in one season alone no fewer than 65 eggs were collected, these notes are of extreme interest. In many cases they confirm the results of Rey and in others modify them. Thus males as well as females have definite territories, but their limits do not coincide. The average laying season is 48 days for the species, but for individual females 40 days is the longest record.

Čapek was of opinion that the eggs were laid in two clutches, with a pause or interval between them. Chance's researches have shown us that these pauses are due to lack of suitable fosterer's nests. Perhaps the most valuable feature in Čapek's paper is the detailed information as to the proportion of deserted nests and similar points, which can only be gleaned laboriously from other writers, but are here collated and tabulated.

J. H. Gurney (1898) gave fairly conclusive evidence, subsequently confirmed by Milburn, Headley, Jourdain, etc., that the Cuckoo occasionally destroys nests with young, in order to create opportunities for oviposition. O. H. Latter (1901) brought out an entirely new point when he showed that careful measurements of large series showed a distinct though small approximation in size of the Cuckoo's egg to that of the fosterer's *. J. A. Link's posthumous paper (1903) contains full historical notes on several points in the economy of the Cuckoo, but not much original matter.

A series of notes by J. H. Owen (1912-21) showed the extremely high rate of mortality among young Cuckoos during the nestling stage, proving that selection is still at work; and E. C. S. Baker's paper (1913) is noteworthy from the fact that he enunciates distinctly the proposition that perfect adaptation is attained by the gradual elimination of contrasting eggs on the part of the fosterers. Perhaps too much stress is laid on the general inability of fosterers to notice discrepancies in size (p. 386), and the theory that the oldest forms of parasite can be detected by the closeness of adaptation of their eggs alone is

* It must be remembered that the authenticity of some of the material used by Latter is not beyond suspicion. Possibly research on a more carefully selected series might result in even stronger evidence of adaptation in size to the fosterer's eggs.

obviously open to criticism, as will be referred to later. There are some interesting notes on rejection, but the importance of the study of this phase is underestimated. Swynnerton (1918) returned to the experimental methods of Lottinger, Leverkühn, and Pralle, but in a much more thorough way.

The results of E. Chance's intensive work began to appear in 1919. To him we owe the conclusive evidence of several facts already surmised and partially proved: the territorial limits of the female and consequent struggles for the mastery with intruders, her general adherence to one fosterer, the laying on alternate days and usually abstracting a single egg at the same time; but also others that were entirely new, such as the fact that, given a succession of available fosterers' nests, the clutch might extend to 26 and that the eggs were *laid in* the nests in all the cases observed and not inserted with the bill, while the closeness of the observation enabled the laying to be forecasted, witnessed from a hide, photographed, and even filmed—these are entirely new facts, for which we are deeply indebted to him. Von Lucanus (1921), from an examination of the material in the Berlin Museum (728 cases), comes to the conclusion that 78 per cent. resemble the fosterers, while only 22 per cent. are unlike, while other writers had previously given estimates varying from 10 to 50 per cent. Later I propose to show that all these figures are quite misleading. For the present it is enough to note that in his detailed account of the eggs examined he gives no indication of their place of origin, though it is evident from one case at any rate that the eggs cannot all belong to *C. canorus canorus*, as the fosterers breed in Japan!

He also attributes the close resemblance between the eggs of *Clamator glandarius*, *C. jacobinus*, etc., and their fosterers to choice on the part of the Cuckoos of fosterers with similarly coloured eggs to their own—*i. e.*, selection by the parasite instead of by the fosterer. On the other hand, he recognizes the theory already enunciated by Baker that selection on the part of the fosterers is responsible for the development of mimicry in the case of the Common Cuckoo.

E. C. S. Baker's paper in the P. Z. S. (1923) is noteworthy from the fact that he clearly demonstrates that the local or geographic variation in the eggs of the Crows is faithfully imitated by the parasite. This is shown in a wonderful way by the remarkable plate (II.) of Crows' eggs and parasitic Koels. Baker's inferences as to the respective ages of the different groups of parasites derived from a consideration of the perfection attained in mimicry are, I think, untenable, and some of the flaws in his argument have already been pointed out by Stresemann (1924).

Recently a somewhat heated controversy has taken place between those who hold that many Cuckoo's eggs must, from the exigencies of the site, be inserted by the bill, and those who hold with Chance that the egg is always laid into the nest, though in

some cases probably while clinging to the side of the nest. B. Rensch (1924), returning to experimental methods, proves that the addition of striking colour to one of the fosterer's eggs, frequently leads to its expulsion or desertion, though not necessarily at once.

So far as to our present state of knowledge with regard to the habits of these birds. Much still remains to be done; but many erroneous theories have now been disproved, and one by one a whole series of facts has gradually emerged from the obscurity of 150 years ago. If we can carry on the process a step or two further we shall have at any rate achieved something.

Firstly as to the origin of this Breeding Parasitism. It seems hardly to be realized that this is not a unique phenomenon, but that at the present time we have in the bird world every stage between complete Breeding Parasitism, as exemplified in the Cuckoos, Cow-Birds, Honey-Guides, etc., and its most elementary form as shown by the habitual use of some old nest of another species for breeding purposes, as in the case of the Falcons.

Let us take a few examples in natural order. The Sparrow-Hawk builds a large nest, but generally uses as a foundation the scanty weathered remains of some old nest or accumulation of leaves and twigs. The true Falcons breed as a rule on ledges of rock without a vestige of a nest, but in open wooded country, though food is plentiful, there are no breeding-sites of this kind, so the old nests of Ravens, Carrion-Crows, Magpies, Rooks, and Herons are used to supply the lack. Again, some species like the Pied Wagtail (*Motacilla alba*), Spotted Flycatcher (*Muscicapa striata*), and Great Tit (*Parus major*) can and do build perfect nests of their own, but also at times place them inside the nests of some other species. These may be classed together as representing different degrees of the first stage in the evolution of parasitism.

The second stage is reached when the eggs are dropped in the occupied nest of another species. In South Spain, having put a Raven (*Corvus corax hispanus*) off a nest in a pine, I was much surprised to find, besides the five eggs of the Raven, a fresh Kestrel's egg. The Kestrel had taken possession of an old nest, but had been dispossessed by the Ravens, but the egg was not removed or destroyed by them. If that egg had been hatched out and reared by the Ravens, would it not be within the grounds of possibility that the bird, if a female, might attempt to drop her eggs into the nests of Ravens like that in which she herself had been reared? As a matter of fact there is a natural obstacle in the way of this development. The incubation period of the Hawk is roughly four weeks, that of the Raven three weeks, so that the young Ravens would be hatched a week earlier than the Kestrel, which would be at a great disadvantage as compared with its companions even if it survived the last week of incubation. A similar fate would befall young Starlings (*Sturnus vulgaris*) hatched in Jackdaws' nests, and probably also

the young Rollers (*Coracias garrulus*) hatched from eggs laid in Pigeons' nests would starve to death. (Game-birds, being kept under artificial conditions, often lay their eggs in other birds' nests, but these we need not now consider.) Among Ducks, where the feeding-habits of the young are more or less similar and they can to a great extent fend for themselves, parasitism has progressed, and in South America there is little doubt that one species at any rate (*Heteronetta atricapilla*) is regularly parasitic on *Coscoroba*, *Chauna*, *Larus*, etc. * Much information on this subject will be found in Leverkühn's 'Fremde Eier im Neste,' to which the student is referred.

That the boundary between this stage and regular parasitism is a somewhat fine one is, I think, shown clearly by the study of the breeding habits of the South American Molothri. Here, in the same genus, we have closely allied species, some of which incubate their own eggs though frequently annexing the nests of other species for breeding purposes; other species are habitually parasitic on their congeners, and have abandoned both the habit of nest-building and also that of incubation †.

The third stage of regular parasitism has been attained in the Palæarctic Region by the Cuculi alone; in the Nearctic and Neogean Regions the Cow-Birds (*Molothri*) have achieved the same result; while in India various genera of Cuculi (*Cuculus*, *Hierococcyx*, *Cacomantis*, *Penthoceryx*, *Chalcococcyx*, *Surniculus*, *Clamator*, and *Eudynamis*), and in the Æthiopian Region the Indicatoridæ, Cuculidæ, and certain Finches have also reached this degree; while in Middle and South America we have strange and abnormal breeding habits in some genera (*Crotophaga* and *Guira*) but not parasitism, except in the case of certain Molothri, and the Duck (*Heteronetta*), already referred to.

I do not think that anyone would seriously maintain that the Falconidæ, which have adopted the habit of annexing the nests of other species, sometimes new as well as old, are therefore of more recent origin than the Indicatoridæ or the Cuculidæ. But in his paper in the P. Z. S. (1923) Mr. Baker points out that, judging from the closeness of the mimicry between the egg of the parasite and its host in some genera and species, evolution is at its earliest stages, while in others it has progressed much further and in certain cases has reached finality. As examples of perfected evolution he gives the eggs of *Clamator jacobinus* and *Hierococcyx varius*. Both these Cuckoos lay pure blue eggs without markings, which, except for shape and texture, agree closely with those of their fosterers. He explains the differences in the degree of evolution by the hypothesis that Cuckoos are a modern "creation," and that even among them the habit of partial

* Mr. E. S. Steward informs me that during a recent visit to Myvatn, where vast numbers of Ducks of many species breed regularly, a very large proportion of nests examined proved to contain eggs of more than one species.

† See some interesting notes on this subject by C. H. Smyth in the 'Oologists' Record,' v. pp. 6-8 (1925).

parasitism is more recent than the bird, and that among those which have acquired the habit, some have taken to it more lately than others.

This is, of course, partly true. An examination of any collection of Cuckoos' eggs with those of their foster parents will show cases of almost perfect approximation, partial resemblance, and striking differentiation. Here I may state the reason why the published estimates of the percentage of eggs which show mimicry are valueless, *unless drawn from one district*. Rey's figures are useless because he included in his tables eggs from Leipzig and also from Herefordshire, etc. Von Lucanus also took all the eggs in the Berlin Museum as his material, and the result is equally valueless. As mimicry has been produced by the selective agency of the fosterers, and as the normal fosterers vary according to locality, so does the standard required by them.

Thus in the thickly-wooded districts of Southern Finland the normal fosterer is the Redstart (*Phœnicurus phœnicurus*), which lays pale blue eggs. Whinchats (*Saxicola rubetra*) are also occasionally victimized, but their eggs conform to the same type of colouring. Here practically the only type of Cuckoo's egg which has survived the ordeal of selection is the blue egg. In the great local collection of Herr E. Wasenius at Helsingfors, which I had the pleasure of viewing in June 1924, was a series of between forty and fifty locally taken Cuckoos' eggs. Of these all but about four were of the blue type; so that it is impossible to ascribe this state of things to the fact that "a few individual Cuckoos have reached a very high degree of evolution in this respect, while the great majority are still only in its earliest stages" (P. Z. S. 1923, p. 290).

According to Mr. Baker's theory, therefore, the Finnish Cuckoo, indistinguishable from our own bird, is an example of perfect evolution, like the more ancient *Clamator jacobinus*! At Leipzig, Rey obtained 127 Cuckoos' eggs out of a total of 147 from nests of *Lanius collurio*. In the case of this species the resemblance is not as a rule at all striking; so that for this district we must put the date of the acquisition of the parasitic habit at considerably later in time. On the other hand, at Oslawan, in Mähren (Moravia), Čapek found that out of 247 eggs laid by Cuckoos, 92 were found in nests of Redbreasts (*Erithacus rubecula*) and 88 in those of *Phœnicurus phœnicurus*. Here, in the same district, the Cuckoos were laying two types of eggs—the one blue for the Redstart in the wooded region, indicating an ancient strain, while the other, laid in Redbreast's nests in more open country, showed only partial approximation, and therefore should be of far more recent origin!

Of our British Cuckoo it is very generally stated that the resemblance to the fosterers is slight, but this is only partially true.

In the Southern and Midland counties it is true that *Prunella modularis* is one of the ordinary fosterers, and between the eggs

of the two the contrast is very striking. This ought to mean its recent adoption as a fosterer on Mr. Baker's hypothesis, though in my opinion it has no such significance, but simply shows that *Prunella* has no eye for colour and in consequence has exercised no influence by selection on the colour of the Cuckoos' eggs. But a point which is generally overlooked is the fact that all over the hilly districts and moorlands of the North of England, as well as locally in the South and in Scotland, the normal fosterer is the Meadow-Pipit (*Anthus pratensis*)*.

From these districts eggs are comparatively rarely found, being scattered over vast expanses of moorland and rough pasture, so that the number in collections bears no reference to the actual number laid annually. But from a study of those which we have, it is evident that the mimicry is close. On these wastes for many miles all the Cuckoos are parasitic on the same host, and as long as the different *gentes* (to use Newton's expression) can be kept apart, it is easy to ensure the stabilization of one type of egg. There are, however, certain districts in England, more especially in the South, where several common fosterers, whose eggs differ widely, such as the Pied Wagtail (*Motacilla a. yarrellii*), the Hedge-Sparrow (*Prunella modularis*), the Robin (*Erithacus r. melophilus*), and the Reed-Warbler (*Acrocephalus scirpaceus*), are found breeding close to one another. I think there is reason to believe that the Cuckoos parasitic on the Reed-Warblers, both male and female, may keep to one particular kind of territory, and so remain untainted by interbreeding with other strains. But that interbreeding does sometimes take place between Wagtail-, Robin-, and Hedge-Sparrow-Cuckoos seems extremely probable, and while the Hedge-Sparrow gens would not be adversely affected, it is almost certain that the standard of mimicry in the Robin gens is lower in England than abroad, and to that extent the popular belief that mimicry in British Cuckoos is in a low state of development is true.

It seems incredible that the inheritance of the characteristics which appear on the egg should be entirely unaffected by the influence of the male; yet, on the other hand, it is equally unreasonable to suppose that pairing never takes place between a male Cuckoo belonging to a Wagtail clan and, let us say, a female belonging to a Robin clan in a district where both species are common fosterers. Judging from the evidence of the eggs, this is exactly what does take place. In some districts of Mähren where Capek worked, the Robin (*Erithacus r. rubecula*) was almost the only regular fosterer, and a comparison of Cuckoos' eggs from this region and other parts of the Continent with British-taken Robin-Cuckoos' eggs shows that a far higher

* An amusing case of theorizing on insufficient data is furnished by Dr. Gloger (J. f. O. 1854, p. 240). He believes that blue eggs of Cuckoos are most numerous in hilly districts, as being the usual breeding place of the Hedge-Sparrow; so are probably to be found in greater numbers in the British Isles than in any other part of Europe!

degree of assimilation has been reached there than in our own southern counties, where a mixed type is very prevalent and where one frequently finds a Cuckoo's egg in a Robin's nest which would be more appropriately placed in that of a Pipit or Wagtail. Still, even here it seems possible that just as the Reed-Warblers return annually to their restricted breeding haunts, so do little parties of male and female Reed-Warbler-Cuckoos arrive and parcel out their hunting-grounds between them, irrespective of the Hedge-Sparrow-, Robin-, and Wagtail-Cuckoos which breed close at hand. Two more examples quoted by Rey are worth notice as showing the local distribution of a particular gens. Out of thirty-one Cuckoos' eggs taken in one district of Pommern, no fewer than twenty-six were found in Wrens' nests, and bore not the slightest resemblance to those of the host! while forty-five out of fifty-seven from Brandenburg were in the nests of *Motacilla alba*, where the mimicry was close. Mr. J. J. Baldwin Young also informs me that in some of the forest districts of West Prussia practically no fosterers were available except the Wren and Leaf-Warblers (*Phylloscopi*).

If the presence in varying degrees or absence of mimicry is no test as to the antiquity of the parasitic habit, have we then any means by which we can ascertain whether the process of selection and the gradual elimination of certain types of eggs is still proceeding? I think we have, but it is a point which has not been sufficiently investigated, though a certain amount of evidence is fortunately available.

Most field-workers occasionally come across cases in which either the nests are deserted by the fosterer after the Cuckoo's egg has been deposited, or sometimes the Cuckoo's egg is ejected, and in that case is no doubt very frequently overlooked. Another plan is for the fosterer to build over the original nest and to bury the intruding egg in the foundations.

One of the most remarkable instances of this kind is that recorded by the Rev. J. R. Hale. On June 15, 1893, he found a bulky Reed-Warbler's (*Acrocephalus scirpaceus*) nest with four fresh eggs. On taking these out, a Cuckoo's egg was just visible embedded in the lining. When this was removed, a Reed-Warbler's egg was found, and still lower a sixth Reed-Warbler's egg: below this again was a seventh Warbler's egg with another egg of the Cuckoo. Carefully taken to pieces, the structure proved to consist of three or, more exactly, two and a half nests built one over the other, the uppermost being merely a new rim with a slight lining. The Cuckoo's eggs were not of the same type. (A similar case of an American Warbler (*Dendræca æstiva*) building a three-storied nest in order to avert the attentions of a Cow-bird is given in the Ann. Rep. of the Field Museum of Chicago, U.S.A., and quoted in the 'Field,' July 1906.)

This is a case of a very determined fosterer rejecting the egg of the intruder twice in succession. A careful study of published

material, together with my own notes and others furnished by friends, has shown that rejections by the fosterers do occur from time to time in varying proportions.

For instance, Mr. E. Chance informs me that on June 1st, 1923, a Spotted Flycatcher's nest (*Muscicapa striata*) was reported to him as containing two eggs and one of a Cuckoo. At 10 A.M. on the following day the Cuckoo's egg was lying broken on the ground beneath the nest. On June 11th in the same district another Flycatcher's nest was found with three eggs and a Cuckoo's. On the 13th, fragments of the Cuckoo's egg were lying below the nest, and the Flycatcher was sitting on three eggs. It will be noticed that in both cases the parasite's egg was not ejected at once, but after some consideration. In later finds of Cuckoos' eggs from this hen the eggs were removed at once before the fosterer had an opportunity of ejecting them.

It is hardly necessary to remark that if all the eggs had been removed when found, or had been examined only at a later stage, most probably the action of the fosterer would never have been suspected. Rey gives details of 14 cases in which Cuckoos' eggs were thrown out, eaten, broken in the nest or built into it, in every case but two by *Lanius collurio*, but also twice by *Sylvia borin*. The most striking results, however, are those obtained by Walter by observation on *Troglodytes troglodytes* and the Phylloscopi. Out of 44 cases in which Cuckoos' eggs were found in nests of the former, the fosterer deserted in about 16 cases; at least one nest was not occupied, and, what is very significant, four Cuckoos' eggs were discovered lying on the ground below the entrance to the Wrens' nests. In the case of *Phylloscopus collybita* details are given of five cases in every one of which the fosterer deserted, and Walter adds that this was the case in every instance in which the Cuckoo victimized this fosterer.

Čapek fortunately goes more deeply into the question, and gives exact figures as to the numbers of cases in which desertion has resulted. Out of the total of 240 Cuckoos' eggs found, 33 were laid in nests already forsaken. Excluding these there were 39 instances (*i. e.* 16 per cent. of the total) in which the fosterers deserted the nest.

In the case of *Phœnicurus phœnicurus*, where mimicry is so close that it may be classed as "complete evolution," only 5 out of 88 eggs were forsaken (6 per cent.); in *Motacilla alba* one out of 10 (10 per cent.); in *Lanius collurio* 4 out of 40 (10 per cent.); in *Erithacus rubecula* 13 out of 92 (14 per cent.); while 13 out of 17 of *Phylloscopus sibilatrix* (77 per cent.) were deserted.

From my friend Pastor Kristen Barfod, of Denmark, who has himself found no fewer than 200 Cuckoos' eggs since 1886, I have also received some interesting information on this point.

Thus on eight occasions, between the years 1902 and 1924, he found nests of the Whitethroat (*Sylvia communis*) containing a Cuckoo's egg only. All the nests were revisited, but no Whitethroats' eggs were laid, and it was evident that in every case the nest was forsaken. In another instance the same fosterer had built over a Cuckoo's egg, which was just visible at the bottom of the nest and had not been affected by the incubation of the other eggs. In a tenth case the Cuckoo's egg was fixed in the nest-lining, the pointed end downwards, and in this case also was not incubated. With the exception of one instance in which a Yellow Bunting (*Emberiza citrinella*) had built over a Cuckoo's egg and subsequently deserted the nest, no other cases of desertion or building in came under Pastor Barfod's notice, so that in his district the selection by the Whitethroat was obviously more severe than with the other normal fosterers.

In addition to the above evidence I have collected a number of isolated instances from my own experience and other sources. For example, out of three Wrens' nests with Cuckoos' eggs found by Messrs. Musselwhite and Ware in England, two were deserted and the third was unoccupied. Other cases of desertion or rejection which have come to my knowledge chiefly relate to the rarer fosterers, such as the Chaffinch, Chiff-Chaff, Yellow Bunting, Marsh-Warbler, Tree-Pipit, Garden-Warbler, and Thrush; while the works of Rey, Čapek, Ziemer, A. von Homeyer, Walter, L. Schuster, C. Jex, etc., contain references to a number of other cases mostly referring to the rarer foster parents (Chiff-Chaff, Blackcap, Lesser Whitethroat, Garden-Warbler, Linnet, Yellow Bunting, Wren, etc.).

Baker also states that in India he sometimes found deserted nests with Cuckoos' eggs, and that in such cases the contrast between the eggs of parasite and host was striking. He instances various species of *Suya*, *Cisticola*, *Horornis*, *Garrulax*, *Mesia*, *Leiothrix*, *Anthus*, and *Lanius*, and notes that in the case of the last-named both the Shrike's and the Cuckoo's eggs had been smashed by a bird's bill, perhaps the fosterer, in a fit of fury at the attempted deception.

In considering the above evidence it is obvious that many cases of rejection may escape notice altogether.

Thus, if the nest is built high up in a hedge or bush and the Cuckoo's egg is ejected, it is almost impossible to find traces of it except by accident. Probably many cases of "built-in" eggs also escape notice, and only an infinitesimal fraction of nests is ever critically examined by ornithologists; but when it is remembered that the rarer fosterers only occur in a small proportion of the Cuckoos' eggs found, and yet records of rejection on the part of the rarer fosterers far outweigh all recorded cases in which selection has been exercised by the common ones, one is here faced with evidence that cannot be

ignored. It is the negative influence that turns the scale: the hundreds of finds with the standard or normal fosterers and only occasional evidence of selection on the part of individuals. Out of some 25 instances in which eggs have been laid in Hedge-Sparrows' nests which have come under my own observation, there has been no evidence of desertion or rejection by the fosterer in a single case.

Yet this is according to Mr. Baker's classification a case of evolution in its earliest stage, though to my mind it is just as final as the case of *Clamator jacobinus*, because there is now practically no selection on the part of the fosterer to produce further development. The Reed-Warbler is another common fosterer in the Thames Valley, yet I only know of two or three cases which indicate selection on its part. It is interesting also to note in the case of *L. collurio* the percentage of desertions and rejections from the figures given by Rey and Čapek works out in both cases to the same figure, *i. e.* about 10 per cent. of the total finds, while in *Erithacus* we have reliable figures from Čapek which show 14 per cent. of rejections, perhaps the highest proportion among the common fosterers.

When we leave the regular fosterers and take the cases of the rarer ones, which cannot be claimed as "accidental" because there are obviously hen Cuckoos which confine themselves partly or wholly to these species, the percentage rises so rapidly that it becomes quite evident that drastic selection is still going on. For some reason the Cuckoo seems to be struggling to establish itself as a parasite on what at first sight seems quite an unsuitable fosterer in the Wren.

The proportion of failures is still extremely high, and probably will continue to be so until a type of egg has been evolved which assimilates more closely to that of the fosterer, though perhaps the difficulties caused by the formation of the Wren's nest have something to do with the frequency of desertion. It is not easy from Walter's records to ascertain the proportion of cases in which the parasite's egg was accepted by the host, because in most cases the eggs were taken when found; but it is certainly less than 50 per cent., and in all probability the percentage of rejections, desertions, and failures on the part of the parasite amount to at least 50 or 60 per cent.* It must also be high in the case of the Spotted Flycatcher (*M. striata*), while among the Phylloscopi only the Willow-Warbler (*Ph. trochilus*) appears to be unable to discriminate between the eggs of the parasite and her own.

* The statement in the 'Ibis,' 1917, p. 202, that according to Walter the Wren invariably deserts nests in which Cuckoos' eggs are laid, is obviously quite incorrect, as he recorded instances in which the fosterers laid eggs subsequently, and continued to brood, and on at least one occasion found a young Cuckoo in a Wren's nest. Rey also found a young Cuckoo in a Wren's nest. The statement that Willow-Wrens also invariably forsake is equally incorrect, though it is approximately true of the Chiff-Chaff (*Ph. collybita*).

In four cases which came under Čapek's notice the Cuckoo's egg was adopted each time by Willow-Warblers, though out of 17 cases where nests of Wood-Warbler (*Ph. sibilatrix*) were victimized, the very high proportion of 13 were deserted, giving an average of 77 per cent. of rejections. With the Chiff-Chaff (*Ph. collybita*), the proportion is probably even higher, for in every case of which we have details desertions took place, but in this species recorded instances are few.

As a rule, with the single exeption of the Brambling in the far north, Finches are not often victimized by the Cuckoos in Europe, though a fair number of instances are on record. Many of these are undoubtedly "accidental," *i. e.* due to birds that have failed to find a suitable nest of the normal fosterer. But that even in Europe some females will devote themselves to Buntings, is proved by Mr. Chance's record of 14 eggs from Yellow Buntings' nests, all laid by one female. In this series one nest was apparently deserted, another was certainly deserted, and in a third case the Cuckoo's egg lay broken in two halves outside the Bunting's nest.

There is also evidence from two other sources of the ejection of Cuckoos' eggs from nests of this species, so that the elimination of unsuitable eggs is evidently a serious obstacle in the way of the increase of the use of this fosterer. It must also be remembered that in the British Isles alone Cuckoos' eggs have been found in no fewer than 14 species of Fringillidæ; and even if we exclude the Yellow Bunting and Linnet from consideration as not being among the rarest fosterers, there still remain 12 species of which there are altogether not less than 90 recorded instances of parasitism from Great Britain. There is also evidence that parasitism is sometimes at any rate successful, as young Cuckoos have been met with in the nests of Bullfinch, Chaffinch, House-Sparrow, and Reed-Bunting, though in some cases the young fail to reach maturity.

Before proceeding further it may be as well to emphasize the more important results of the investigation. Firstly, the proportion of rejections by the fosterer either by desertion or rejection varies enormously. In some species the percentage falls to as low as 5 per cent. or less, while in others it rises to nearly 80 per cent., and perhaps in some cases almost to 100 per cent. Secondly, these rates are not necessarily connected with the closeness of the mimicry or the reverse. If the parasite is to hold its own it must reach a certain level to satisfy the discrimination of the host, but that level may be a low one or a high one, and varies according to the fosterer in question. Therefore it is not the closeness of the mimicry or the reverse, as Baker suggests, which gives us the key to the age of the practice, but the activity of selection by the fosterer or its indifference. Where stability has been attained and selection has practically ceased, we cannot draw any inference as to the antiquity of the

habit, whether the mimicry is close or not. There remains still another point which requires further elucidation, and that is what constitutes "perfect evolution." We are all agreed that there are degrees in mimicry:—Elementary, where there is some rough approximation in size but little or no resemblance in colouring (though even in size there are often startling discrepancies, as in Wren-Cuckoo and Willow-Warbler-Cuckoo eggs); advanced, where there is distinct approximation in size and colour, and Perfected or Complete where the host and fosterer are only distinguishable by slight differences in size, texture of shell, or colouring. In Mr. Baker's paper these three stages are referred to as degrees of "evolution." This, I venture to think, is a somewhat deceptive term, for the Hedge-Sparrow-Cuckoo's eggs must fall under Category I.; yet it is obvious that selection has ceased to operate equally with the Redstart-Cuckoo eggs, which would fall under Category III. Surely, if we are to classify Cuckoos' eggs from the evolutionary standpoint, we must place in the lowest category those which almost always fail to satisfy the host and are rejected (*e.g.* Wood-Warbler- and Chiff-Chaff-Cuckoos). These show wide differences in size or colour or both. Category II. should contain those cases in which some considerable proportion of the parasite's eggs are accepted by the host but selection is still in an active state and many are rejected, and here approximation is often met with.

Category III. includes those cases where a great majority of the Cuckoos' eggs are accepted, sometimes showing extraordinarily close resemblance to the host, but in others (such as Hedge-Sparrow-Cuckoos) wide differences. Even where the resemblance is so close that careful examination is necessary to detect the parasite's egg, and selection has ceased, there are still great differences in the degree of achievement, and the Orphean Warbler-Cuckoo, Great Reed-Warbler-Cuckoo, or Brambling-Cuckoo represents a far more advanced type than the plain blue eggs of *Clamator jacobinus* and *Hierococcyx varius*, which are selected by Mr. Baker as types of perfected evolution.

In order to appreciate the point it is necessary to go into the question of the colouring of birds' eggs. Accepting the theory that birds' eggs were originally white, let us first investigate the stages by which the extraordinary range of variation in colour and markings has been reached.

The simplest and most primitive type of coloured egg is that in which the ground-colour is some shade of blue or green without markings. This is in most cases the first stage of colouring, and, unlike the last-applied pigments, it must be the result of liquid or semi-liquid matter in the oviduct, almost certainly derived from bile products; and as it is the first application, it is probable that the shell is in a softer and more absorbent condition than at a later period. Sometimes there is a tinge of yellow, in which case we have a green ground. The

second stage comes with the secretion of red or brown pigment, almost certainly derived from the blood, sometimes in the form of innumerable fine stipples, in this case obscuring the blue ground and producing the almost uniform olive of the Nightingale's egg, but more frequently appearing in the form of blotches or spots, often in the form of a zone or cap at the large end.

It is evident that this colour is exuded from ducts, which are situated near the lower end of the oviduct, shortly before the extrusion of the egg. At first the colour shows a tendency to soak into the shell and to spread. This produces the ashy-violet blotches so frequently found together with the "surface" markings, which represent the latest exudations when the shell is hard and no absorption takes place. A rotary movement sometimes takes place while the egg is on its way down the oviduct, and to this is due the remarkable series of spiral smears which are conspicuous on Terns' eggs.

If the shell is hard and colour exudes from a small opening and dries rapidly, streaks are produced. In some genera the movement of the egg down the oviduct is apparently not accompanied by rotation, and in this case we get the longitudinal smears which are noticeable in Birds-of-Paradise eggs. Rounded blotches of colour also suggest that the egg is at rest while the colour is being secreted, and much of the difference between deep black and pale red or brown is simply a question of depth of colour. Probably erythristic eggs merely represent the absence (normally or owing to some defect) of the liquid biliary matter deposited while the egg is in the upper part of the oviduct.

This, I believe, represents the normal way in which a coloured egg is produced. I have not gone into details as to the exceptional cases, such as the eggs of the Tinamous with their extraordinary gloss and bizarre colouring, the Guira Cuckoos, or the Cormorants with their surface deposits of lime, but it will be seen that it furnishes a working hypothesis on which almost every type of egg can be accounted for satisfactorily. What is more, it derives strong confirmation from the study of defective eggs in which for some reason or other the colouring is abnormal.

Taking first the non-parasitic Cuckoos in which no selective agency has been at work, we find that the great majority lay white eggs. There are certain species which lay coloured eggs, and these, as might be expected, have the most primitive type of colouring, viz. the uniform blue ground (*Coccyzus*). In others the blue ground is more or less hidden by superimposed deposits of white chalky matter sometimes almost completely concealing the ground (*Crotophaga*), though readily removed by wear, and in other cases consisting of a raised network of chalky matter (*Guira*).

Now, if we take a series of parasitic Cuckoos' eggs from all parts of the world in which, as far as our present state of knowledge admits, we believe that a majority of the eggs are

accepted by their normal fosterers and in which their evolution is complete or nearly so, the simplest and most primitive type is the white egg laid among the white eggs of the fosterer. It is, I think, not generally known (except among South African oologists) how common this is in the Æthiopian region. Curiously enough, a common African fosterer, the Bulbul (*Pycnonotus*), has the same lack of colour perception as our Hedge-Sparrow, so that white eggs of African Cuckoos are found not only in nests of species which also lay white eggs, such as the Barbets, but also in cases where the contrast is very striking.

Mr. Swynnerton's experiments confirm what the eggs of the parasite suggest, that the Bulbul is the "fool" of the South African Passeres.

Next to the white eggs I should place the blue eggs of Cuckoos which lay in nests of fosterers also laying blue eggs, such as *Clamator jacobinus* and *coromandus*, *Hierococcyx varius*, and *Cuculus c. canorus* (from Finland)*. Among these blue Cuckoos' eggs a certain proportion will be found to show distinct traces of yellowish or brownish spots. A higher type of mimicry is found when we have the secondary colour deposits well developed. Here the blue ground is present, but is almost hidden by subsequent deposits of some shade of brown or red. Just as in certain fosterers we find a tendency to erythrism, caused by the absence of the primary colour deposits, so do we meet with similar variation in the case of the parasite. Of course, it must be remembered that in some species among the smaller Passeres, which are victimized by the Cuckoo, the range of variation is very great in individual birds. In such cases a "mixed type" showing the general characteristics of the species is all that it is possible for the parasite to produce, since each hen must always produce the same type of egg, and undue specialization would only result in greater incongruity in most cases.

It is true that *Clamator jacobinus* or *Cuculus poliocephalus* with their extraordinary blue and red eggs present us with wonderful and striking instances of colour adaptation. But, after all, these results are comparatively simply obtained, and far more wonderful is the adaptation of the Cuckoo's egg to those of *Acrocephalus arundinaceus*, *Fringilla montifringilla*, and *Sylvia hortensis*, or perhaps most marvellous of all, that of the egg of *C. canorus telephonus* to that of *Emberiza cioides ciopsis*. This case is also remarkable from another point of view, for, in the Western Palæarctic Cuckoos, the favourite fosterers are to be found among the soft-billed insect-eating birds, such as the Motacillidæ, the Muscicapidæ (in its widest sense), and the Prunellidæ. What is the cause, then, of this extraordinary development in the case of a Fringilline fosterer in Japan? This is, I think, an interesting problem. Some years ago the late Alan

* It is significant that while all the known eggs of *Clamator jacobinus* from India are blue, those recorded from South Africa are white.

Owston sent over for sale to England the whole of his great collection of eggs made in Japan by Japanese collectors. On looking over the catalogue of this wonderful series, one could not fail to be struck by the extraordinary number and variety of Buntings' eggs. In our own British ornis, which one might expect to correspond fairly closely to that of Japan, we have only one really common and widely-distributed species of Bunting and two others which are fairly common locally. But it was quite evident from the numbers of eggs collected in Japan that at least four species must be plentiful there. On the other hand, the Sylviidæ, which form such a prominent feature of our summer bird-life, are either absent or represented only by certain aberrant genera such as *Cettia*, which lays a wonderful red egg and has a special parasitic Cuckoo (*C. poliocephalus*), which also lays similarly coloured eggs. So that, if we exclude the Finches and Shrikes, there remain only about a dozen common species of soft-billed birds which might possibly act as fosterers, and nearly all lay eggs which differ widely from one another in size and colour, e. g. *Saxicola*, *Muscicapa*, *Hypsipetes*, *Zosterops*, *Phylloscopus*, *Acrocephalus*, *Motacilla*, and *Anthus*. Evidently the Cuckoo has imposed herself on what appear to be the most common and widely-distributed species. We know that in England the Yellow Bunting is very critical of parasitic eggs which do not closely resemble her own, and we may make a similar inference with regard to the Brambling (*Fringilla montifringilla*). Judging from results, the Japanese Buntings have pursued a very drastic policy of selection, with the result that it is difficult to believe that the eggs of the Cuckoo which has survived the ordeal are not merely abnormally large and possibly double-yolked specimens of the fosterer. They have all the characteristics of Buntings' eggs except size. The network of irregular streaks and spots, especially towards the large end, is reproduced with marvellous exactitude in the Cuckoo's egg; and were it not for the fact that a whole series of these eggs is in existence, taken from the fosterers' nests, and that microscopic examination by R. Schlegel and others confirms their identification, we should be strongly inclined to doubt their authenticity. Double-yolked eggs do actually occur in Buntings' nests, but they are of exceedingly rare occurrence—in fact of such a common species as *Emb. calandra* I only know of one example,—and it would be impossible to get together a series of this abnormality. Moreover, such eggs are thin-shelled and light as compared with normal eggs *, whereas in the abnormally thick shell of the Cuckoo's egg we have, I think, an indication, confirmed by Mr. Latter's paper already referred to, that a reduction in size has taken place by a process of selection.

Another small item of confirmatory evidence is furnished by a

* *Cf.* M. Schönwetter, 'Beiträge zur Fortpflanzungsbiologie der Vögel,' i. pp. 49–52 (1924).

clutch of *Saxicola torquata stejnegeri* eggs with one of *Culculus c. telephonus*. Here the Cuckoo's egg harmonizes very closely with that of the host in colour, but close examination shows that, instead of the fine stippling of red-brown which is characteristic of *Saxicola* eggs, we have plainly visible a network of faint Bunting-like streaks, inconspicuous owing to their suffused and cloudy nature, yet similar in type to the bolder markings found in the Cuckoo's eggs when laid in Buntings' nests.

There is another point in the life-history of certain Cuckoos which seems to have received less attention than it deserves. In the case of *Cuculus canorus*, while some degree of resemblance in the eggs of the parasite is enforced by the great majority of fosterers, when once the young Cuckoo is hatched, all necessity for concealment is at an end. Nothing more unlike the nestling of most of the ordinary fosterers can well be imagined than the great brown bird with huge orange gape and stumpy tail which sits on the crushed remains of what was once a nest and keeps up its penetrating food call, which, by the way, is quite unlike the ordinary notes of their young. Yet at this stage rejections are almost unknown, and it is a fact that other birds beside the actual fosterers will respond to the insistent demands for food on the part of the young parasite. When, however, the life-history of other genera is investigated, it becomes evident that this state of things is not universal. The Great Spotted Cuckoo (*Clamator glandarius*) is a common parasite, chiefly on the Magpie (*Pica pica melanotus*) in some parts of Spain, and also in other countries on the Hooded Crow (*Corvus cornix*). The females usually remove an egg of the fosterer when laying their own, though sometimes a particularly vigilant Magpie manages to keep her clutch intact. When the young Cuckoos are hatched they make no attempt to eject their foster brothers, and all live peaceably together. The first glance at a nest with fledged young of both species shows that the juvenile Cuckoo is quite a different looking bird to the adult. As it lies crouching at the bottom of the nest, one is struck by its black crown and dark back, totally different to the ashy grey of the adult, but bearing a superficial likeness to the young Magpies by its side.

In the Indian *C. jacobinus* and *C. coromandus* exactly the reverse is the case. Here the adults have glossy greenish-black crowns, while the juveniles are brownish, approaching in appearance their ordinary fosterers. In the Koel (*Eudynamis scolopaceus*) the young are first black (in which stage they bear some resemblance to young Crows), but soon afterwards adopt a plumage not unlike that of the brown female Koel.

The natural explanation of this extraordinary state of things seems to be that the Crows and Pies, with their superior intelligence, have enforced, by a process of selection, a certain degree of mimicry on the part of the young parasite in addition to extremely close resemblance in the egg; while the smaller Passeres, with their lower brain power, respond to the stimulus

of the widely-opened mouth and the insistent hunger cry instinctively, even in some cases when they are not the actual fosterers.

There is one more point to which I should like to make reference, viz. the way in which the Cuckoo's egg is deposited in the nest of the host. Most of the earlier observers took it for granted that the egg was laid on the ground and picked up in the bill to be deposited in the nest by the Cuckoo, though at the same time there was clear evidence by Naumann and others that occasionally, at any rate, the egg was laid direct into the nest. Mainly as the result of Mr. E. Chance's systematic observations, it is now demonstrated that in the case of the Meadow-Pipit (*Anthus pratensis*), and probably in all the ground-building birds, the egg is laid in the nest even when the Cuckoo has considerable difficulty in forcing herself into position. There is also very definite evidence of similar procedure in the case of several other species, such as Reed-Warbler, Pied Wagtail, Hedge-Sparrow, etc. On the other hand, there are many cases where this seems at first to be a physical impossibility, as, for example, when the nest is built inside a hole in a tree, with an entrance too small to admit of the passage of the Cuckoo. In such cases it has been assumed, perhaps too rashly, that the egg must be inserted by means of the bill. Apparent confirmation of this is furnished by the sight of the Cuckoo clinging precariously to the side of the nest and peering into the opening. The observed facts are, however, capable of another interpretation. The Cuckoo may glance into the nest and attempt, with or without success, to remove one of the fosterer's eggs with her bill. She may then, while still clinging to the side of the nest, bring the mouth of the oviduct up to the nest entrance and actually lay her egg into the nest or on to the edge of it. Without rashly asserting this to be invariably the case, it is at any rate a possible solution of the facts which has received confirmation of a remarkable kind from various sources.

In the case of the Wren (*Troglodytes troglodytes*) and the Leaf-Warblers (*Phylloscopi*), which build their nests of moss and similar soft materials, there is strong evidence, some of it dating back for fifty years, that the Cuckoo makes every effort to force an entrance into the nest, even though she partly destroys it in the process. Walter, who had perhaps more experience of Cuckoos parasitic on Wrens than any one else, makes repeated references to this habit. He believed, however, that in some cases the egg was inserted by means of the bill, and instances one occasion where the Wren's nest was built on an upright twig at the top of a juniper-bush, so that the Cuckoo could only cling to it with difficulty, and the egg proved to be broken when subsequently examined. In the light of later theories this seems to be a case where the evidence might tell equally for the other side.

Then there are also numerous cases where the Cuckoo's egg has been found lying on the ground beneath the entrance to the nest (see Walter Coll. Nos. 29, 35, 40, 43, and 44) or left lying at the entrance. If these eggs were deposited by means of the bill, there seems no adequate reason why they should have fallen outside; and though there are many cases of ejection by the fosterer, one would hesitate to believe that it was the work of a Wren without some confirmatory evidence, especially in the case of deserted nests.

In this connexion I may call attention to a remarkable letter which appeared in 'British Birds,' xvii. p. 215. The writer had an opportunity of watching the actual laying of an egg by a Cuckoo through a window within a few inches of the bird. He describes the tail-feathers as raised and flattened against the glass. When the Cuckoo raised herself to lay, the body "appeared to elongate and to become almost pointed. The point was bent downwards . . . and it almost seemed as though it felt about for the edge of the nest, for it moved from side to side. As soon as it touched the side of the nest, the egg began to be extruded, and when it finally left the bird it rolled to its place by the side of the other two eggs."

Side by side with this let me quote an "undesigned coincidence," in my opinion the strongest kind of confirmatory evidence, though in this case indirect. The South African Honey-Guides (Indicatoridæ) are parasitic like the Cuckoos, and frequently deposit their eggs in the nests of Barbets, which are hole-breeders.

Mr. R. H. Ivy (Ibis, 1901, pp. 21–22) watched for some time a Honey-Guide (*Indicator minor*) attempting to enter the hole of a Barbet, but hustled away by the owners of the nest. He shot all three birds, and on picking up the Honey-Guide, found that it had an egg "protruding from the vent, being covered with skin, probably an evaginated portion of the lower part of the oviduct." The egg was still unbroken when the bird was picked up.

It is at least possible that the remarkable appearance recorded by Fr. Horne may have been due to a similar state of things to that recorded by Mr. Ivy in the case of the Honey-Guide, which would naturally facilitate the deposition of an egg in a hole by a bird clinging to the side of the nest.

Lastly, a few words may be added in explanation of the coloured plates. Plate I. represents some typical eggs of non-parasitic Cuckoos. The majority of these eggs are white: all the known eggs of the Musophagidæ (Plantain-eaters) are white: so are also the eggs of the large family of Coucals (*Centropodinæ*) (though the eggs of this group often show nest stains on their chalky surface), the Sirkeers and Malkohas (*Phænicophaïnæ*) and the Road-Runners of the New World (*Geococcyx*). On the other hand, in America we find that most species of the genus *Coccyzus*

lay bluish or greenish eggs, though even here we have a significant exception in the case of *C. cinereus* (Argentina), which lays a plain white egg (fig. 2), while its allies (*C. erythrophthalmus* and *C. americanus*) lay bluish-green eggs (figs. 1 and 3). The Crotophagidæ present some extraordinary characteristics, not only in their breeding habits, but also in their eggs. These are blue, but are usually covered with a partial or complete deposit of lime, so that in many cases they appear to be white. In the case of *Crotophaga ani*, eggs are occasionally but rarely met with entirely lacking the superficial chalky deposit (fig. 6). Normally they are covered with a thin deposit of lime, but this is soft, and scratches from the beak and claws of the birds reveal the blue colouring beneath. The results are seen in figs. 4 and 9. A similar state of things occurs in the much larger *C. major* (fig. 8). The Guira Cuckoos lay eggs which are quite unique. The ground-colour is deep blue, but over the surface is a tracery of white chalky matter. Through the openings in this network the blue ground is seen, the deposit standing out in high relief.

In Plate II. we pass on to the consideration of the eggs of parasitic Cuckoos. It has not been thought necessary to figure more than two eggs of those Cuckoos which lay pure white eggs. Figs. 1 and 3 represent two parasitic species (*Cuculus serratus* and *C. clamosus*), both of South African origin, whose eggs were found together in a nest of *Andropadus importunus*. This is apparently a case like that of our own Hedge-Sparrow (*Prunella modularis*), where practically no selective action is taken by the fosterer in spite of the great contrast in the appearance of the eggs. From what we have already seen of the eggs of the non-parasitic Cuckoos, we should expect to find eggs with a pure blue ground occurring in Parasitic birds also, and this results in many cases in almost perfect mimicry. Several examples of this are illustrated from the Palæarctic and Indian regions. From India are figured eggs of *Clamator jacobinus* (fig. 5) with the similarly coloured *Argya* egg: *C. coromandus* (fig. 7) with that of *Garrulax*: also *Hierococcyx varius* (fig. 9) and *H. sparveroides* (fig. 11) with their respective fosterers. From Japan is shown the egg of *H. fugax nisicolor* (fig. 13) with that of *Luscinia cyane*, and from Finland an egg of our common *Cuculus c. canorus* (fig. 15) with that of the Redstart (*Phœnicurus*).

Plate III. illustrates rather more advanced stages of mimicry. In Finland, where practically all the Cuckoos' eggs are blue, some are laid in the nests of the Bramblin3 (*Fringilla montifringilla*). As a blue type also occurs in the Finch, this occasionally results in close similarity (figs. 1 and 2), but in some cases still closer imitation has been effected, and both in markings and ground-colour a close approximation has been attained (figs. 7 and 8). The Indian *C. canorus bakeri* (fig. 6) and *Cacomantis merulinus querulus* both lay eggs with a few

brown markings on a blue ground in eggs of fosterers of similar type.

The remaining figures illustrate a considerable advance from the plain blue egg or blue egg with brown spots. The extraordinarily close imitations of the eggs of the Great Reed-Warbler (*Acrocephalus a. arundinaceus*) in Hungary, the Orphean Warbler (*Sylvia h. hortensis*) in S. Spain, the Pied Wagtail (*Motacilla a. yarrellii*), the Meadow-Pipit (*Anthus pratensis*), and the Whitethroat (*Sylvia c. communis*) in the British Isles (figs. 10, 12, 14, 16, 20, and 18) can only be attained by close adaptation of the ground-colour, and characters as well as colour of both surface and suffused markings.

Plate IV. also illustrates advanced development due to selective agencies. Fig. 3 represents the Great Spotted Cuckoo's egg (*Clamator glandarius*), which is parasitic on the Corvidæ in the Palæarctic Region and lays an egg quite different in appearance to that of its Indian congeners. (It is interesting to note that though the Indian *C. jacobinus* always lays blue eggs, in S. Africa it has been recorded as laying white eggs!)

The wonderful eggs of *Cuculus c. telephonus* (figs. 1 and 4) from Japan, which show such remarkable similarity in colour and type of markings to those of the fosterers, may be specially noted on account of the way in which the characteristic interlacing lines, which are characteristic of the Buntings, have been imitated. Traces of these characters can also be detected, though obscurely, in fig. 7. The chocolate-red and olive eggs, though in some respects more striking, are achieved by simpler means. In the case of red eggs (figs. 16, 17, 18) this result is attained by the elimination of the first deposits of blue ground-colour and a close uniform deposit of the later surface pigment. Perhaps the olive ground (fig. 10) is obtained by the mixture of the primary (blue) and the secondary (red or brown) deposits.

Plate V. Here it must be remembered that *in the nest* the only conspicuous parts of the young bird are the crown of the head, and perhaps the back, though this is often hidden by the heads of other nestlings. In the figures the throat colouring is conspicuous, but this is not the case when the young are crowded together in the nest.

Figs. 1 and 4 represent the adult and nestling of *Clamator glandarius*. The dark crown of the nestling shows a close approximation in colouring to that of the young Magpie (*Pica p. melanotus*), or for that matter to the young Hooded Crows and Ravens, with which it is brought up, but is very strikingly different to the grey crown of the adult bird. The adult *Clamator jacobinus*, on the other hand, is reversely coloured, and has a green-glossed black crown and cheeks. Yet the nestling shows no sign of this dark colouring, but approaches far more nearly to the type of the young *Argya* or *Crateropus* with which it lives. The adult male Koel (*Eudynamis scolopaceus*) has a

black head, but the female is a brown bird. The nestling is also black-headed like the young Crows, but the extraordinary fact remains that it moults into a brown plumage (not unlike the adult female) after leaving the nest.

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EXPLANATION OF THE PLATES.

Plate I.

Eggs of Non-Parasitic Cuckoos.

Fig.
1. *Coccyzus erythrophthalmus* (U.S.A.)
2. „ *cinereus* (Argentina).
3. „ *americanus* (U.S.A.).
4. *Crotophaga ani* (Paraguay).
5. *Centropus sinensis* (Sind).
6. *Crotophaga ani* (Paraguay).

Fig.
7. *Coccyzus minor* (Jamaica).
8. *Crotophaga major* (Brazil).
9. „ *ani* (Paraguay).
10. *Coua reynaudi* (Madagascar).
11. *Guira guira* (Argentina).
12. *Taccocua leschenaulti* (India).

Plate II.

Eggs of Parasitic Cuckoos (elementary stages).

1. *Cuculus serratus*.—2. *Andropadus importunus*.—3. *Cuculus clamosus* (Cape Province).
4. *Argya malcolmi*.—5. *Clamator jacobinus* (India).
6. *Garrulax pectoralis*.—7. *Clamator coromandus* (India).
8. *Crateropus canorus*.—9. *Hierococcyx varius* (India).
10. *Trochalopterum chrysopterum*.—11. *Hierococcyx sparveroides* (India).
12. *Luscinia cyane*.—13. *Hierococcyx fugax nisicolor* (Japan).
14. *Phœnicurus ph. phœnicurus*.—15. *Cuculus c. canorus* (Finland).

Plate III.

Eggs of Parasitic Cuckoos (advanced stages).

1. *Fringilla montifringilla*.—2. *Cuculus c. canorus* (Finland).
3. *Orthotomus sutorius*.—4. *Cacomantis merulinus querulus* (S. China).
5. *Liothrix lutea*.—6. *Cuculus c. bakeri* (Khasia Hills).
7. *Fringilla montifringilla*.—8. *Cuculus c. canorus* (Lapland).
9. *Acrocephalus a. arundinaceus*.—10. *Cuculus c. canorus* (Hungary).
11. *Acrocephalus g. arundinaceus*.—12. *Cuculus c. canorus* (Hungary).
13. *Sylvia h. hortensis*.—14. *Cuculus c. canorus* (Spain).
15. *Motacilla a. yarrellii*.—16. *Cuculus c. canorus* (S. Wales).
17. *Sylvia c. communis*.—18. *Cuculus c. canorus* (Essex).
19. *Anthus pratensis*.—20. *Cuculus c. canorus* (Hants).

PLATE IV.

Eggs of Parasitic Cuckoos (advanced stages).

1. *Cuculus c. telephonus.* 4. *Cuculus c. telephonus.*
5. *Emberiza fucata* (Japan). 8. *Emberiza c. ciopsis* (Japan).
2. *Pica pica melanotus.*—3. *Clamator glandarius* (Spain).
6. *Saxicola t. stejnegeri.*—7. *Cuculus c. telephonus* (Japan).
9. *Arachnothera magna.*—10. *Hierococcyx sparveroides* (Khasia Hills).
11. *Cyornis rubeculoides.*—12. *Hierococcyx f. nisicolor* (Japan).
13. *Lanius collurio*—14. *Cuculus c. canorus* (Germany).
14. *Erithacus r. rubecula.*—15. *Cuculus c. canorus* (Mähren).
16. *Cuculus p. poliocephalus.* 17. *Cuculus p. poliocephalus.* 18. *Cuculus p. poliocephalus.*
19. *Prinia flavirostris* (Khasia Hills). 20. *Horornis fortipes* (Khasia Hills). 21. *Cettia cantans* (Japan).

PLATE V.

Mimicry in Nestlings of Parasitic Cuckoos.

1. *Clamator glandarius* (ad.). 2. *Eudynamis s. scolopaceus* (ad. ♀).
3. *Clamator jacobinus* (ad.).
4. *Clamator glandarius* (juv.). 5. *Eudynamis s. scolopaceus* (juv.).
6. *Clamator jacobinus* (juv.).
7. *Pica pica melanotus* (juv.) (Spain). 8. *Corvus splendens splendens* (juv.) (India).
9. *Argya malcolmi* (juv.) (India).

LITERATURE.

The following references to some of the principal papers on the habits of the Cuckoos and other parasitic birds may, it is hoped, prove useful to other students of the subject. Records of the rarer fosterers (of which many have appeared in the 'Zoologist' and 'British Birds') and of habits as observed in confinement are not included in this list.

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29. The External Characters of the Lagomorph Rodents.

By R. I. Pocock, F.R.S., F.Z.S.

[Received March 2, 1925: Read April 21, 1925.]

(Text-figures 13–30.)

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Introduction.

Exotic hares and rabbits are seldom imported for exhibition in our Zoological Gardens, and the only examples that I was able to examine in a fresh state in the Society's Prosectorium were a specimen of *Lepus senegalensis* from Senegambia, presented by H.E. Capt. C. H. Armytage, and one of *Sylvilagus superciliaris* from Colombia, presented by Mr. W. K. Pomeroy. I have, however, procured and examined many specimens of both sexes of the common rabbit caught at all seasons of the year, one or two specimens of both sexes of the English hare, and a pair of Scots hares very kindly shot for me at Thornhill, Dumfriesshire, by Mr. H. S Gladstone. In addition to these I have seen spirit-preserved material of *Lepus peguensis* from Moulmein, of *Lepus omanensis* from Oman, and of *Macrotolagus callotis* from Zacatecas, Mexico, preserved in the Natural History Museum; and I have relaxed and examined the feet and the ears of dried skins of several species in that collection, including representatives of all the type species of genera or subgenera that were available, that is to say, of *Pronolagus crassicaudatus* from Natal, *Caprolagus hispidus* from N. India, *Nesolagus netscheri*

from Sumatra, *Pentalagus furnessi* from Liu-Kiu, and of such American forms as *Lepus americanus*, the type of *Pœcilolagus*, *L. arcticus*, the type of *Lagos*, *Sylvilagus floridanus*, *Limnolagus aquaticus* and *palustris*, *Tapeti brasiliensis* and *Romerolagus nelsoni*. *Brachylagus* and *Boreolepus* I have not seen.

I may here add that of the American forms *Macrotolagus* is admitted by Nelson and Miller as a subgenus of *Lepus*, *Pœcilolagus* and *Lagos* are regarded as synonyms of *Lepus*, and *Tapeti*, of which *Limnolagus* is a synonym, is a subgenus of *Sylvilagus*.

Of the Ochotonidæ I have seen spirit-preserved material of species identified in the British Museum as *O. curzoniæ* from Lhasa, *O. melanostoma* from Central Asia, *O. bedfordi* from Shansi, and of an unidentified form from the Thian Shan collected by Prejevalsky; and also the splendid collection of dried skins *.

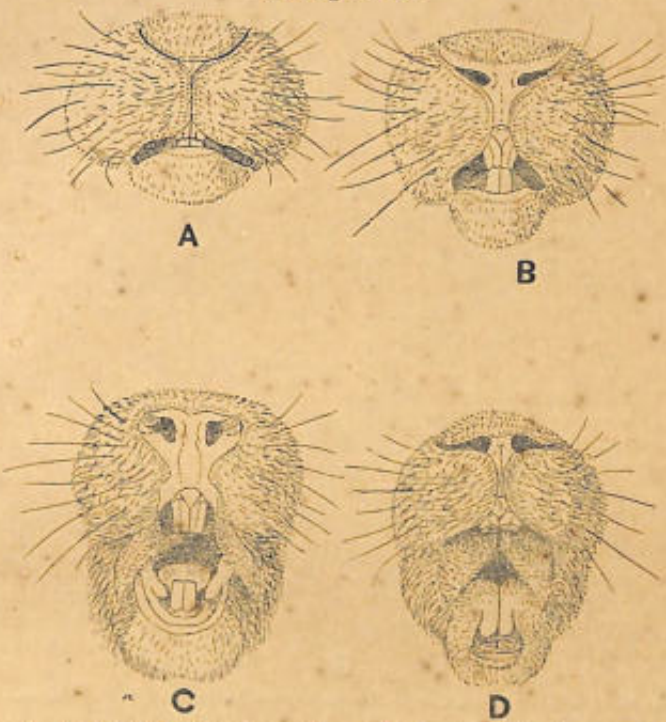
In 1899 (Trans. Linn. Soc., Zool. vii. pt. 2, pp. 433–520), Forsyth Major reviewed the attempted classifications of the Leporidæ down to that date, and it is needless to repeat what he said. Basing his opinions entirely upon osteology and dentition, he divided the family into two main sections—the Caprolagine, the so-called rabbits, including *Oryctolagus*, in which he included the South African species *crassicaudatus*, subsequently separated by Lyon as a distinct genus *Pronolagus*, *Caprolagus*, *Nesolagus*, and *Sylvilagus*: and the Leporine section or hares proper, containing all the remaining forms referred to the genus *Lepus*, which differ from the rabbits in the inflation of the nasal chambers, the size of the mesopterygoid fossa, and other characters subservient to the intake of a greater volume of air necessitated by speed and endurance in running.

In 1904 Lyon (Smiths. Misc. Coll. vol. 45, no. 1456, pp. 321–445) monographed the Lagomorpha (Leporidæ and Ochotonidæ) on the osteological lines adopted by Major in his classical work, giving the distinctive characters of the genera as supplied by different parts of the skeleton; and in 1909, Nelson (U.S. Dept. of Agriculture—North American Fauna, no. 29) monographed the North American species. Miller did the same for the species of Europe, excluding Russia, in 1912 (Cat. Mamm. Western Europe); and the same author in 1924 issued a nominal list of the North American forms (Bull. U.S. Nat. Mus. no. 128, pp. 449–480). No similar attempts have been made to deal as a whole with the species of Asia and Africa, although the Indian species were described by Blanford in 1891 ('Fauna of British India') and later by Wroughton (Journ. Bombay Nat. Hist. Soc. xxvii. pp. 66–71, 1920), and the South African species in 1901 by W. L. Sclater ('Fauna of South Africa: Mammals,'

* The nature of the material examined is not without importance. Fresh specimens are better than those preserved in spirit and the latter are better than dried skins. In the dried skin, for instance, I found that the feet would not in all cases relax absolutely satisfactorily, and it is possible that the effects of shrinkage, especially perhaps of the webs, could not be altogether counteracted.

vol. ii.). The rest of the literature consists mainly of isolated papers dealing with new genera or subgenera, species or subspecies. Since the only external characters hitherto used by systematists are the coat and its colours, and the relative lengths of the ears, feet, and tail, it seemed that an attempt to discover if a more detailed study of the feet, ears, and other organs on the lines followed in my previous papers on Mammals might be both interesting and useful.

Text-figure 13.



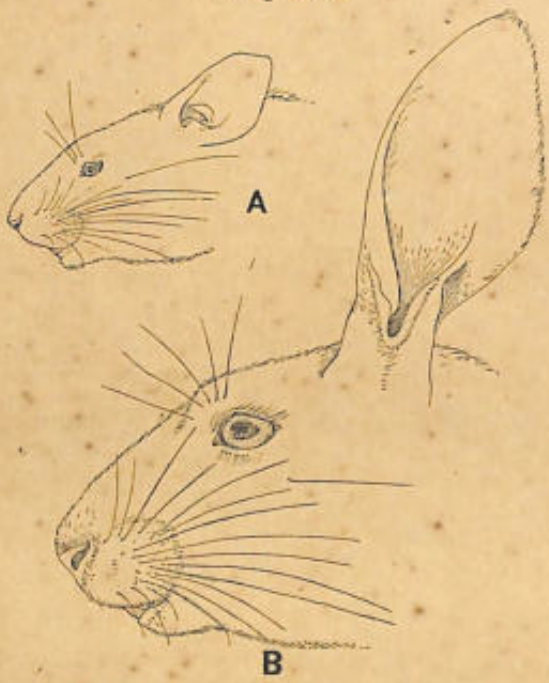
A. Muzzle of *Lepus timidus* with nostrils closed and rhinarium concealed by the skin of the nose and lips.
B. The same with rhinarium and nostrils partially exposed.
C. The same with the nostrils dilated, the rhinarium entirely exposed, and the mouth open.
D. The same with the teeth cut short and tongue removed to show the flaps of hairy skin in the mouth.

The Head and its Organs.

The Rhinarium.—The nostrils, which are normally constructed, the orifice being narrowed posteriorly and laterally and expanded

internally and anteriorly, the latter portion looking forwards, are surrounded by a rim of naked skin. The strip above them is narrow, the skin of the summit of the nose being covered with short hair and capable of being depressed like a hood over the nostrils so as to close them. Similarly the skin on each side of the upper lip, which is deeply and widely cleft by a philtrum, can be drawn upwards so as to close the nostrils from below and inwards and meet in the middle line above the upper incisor

Text-figure 14.



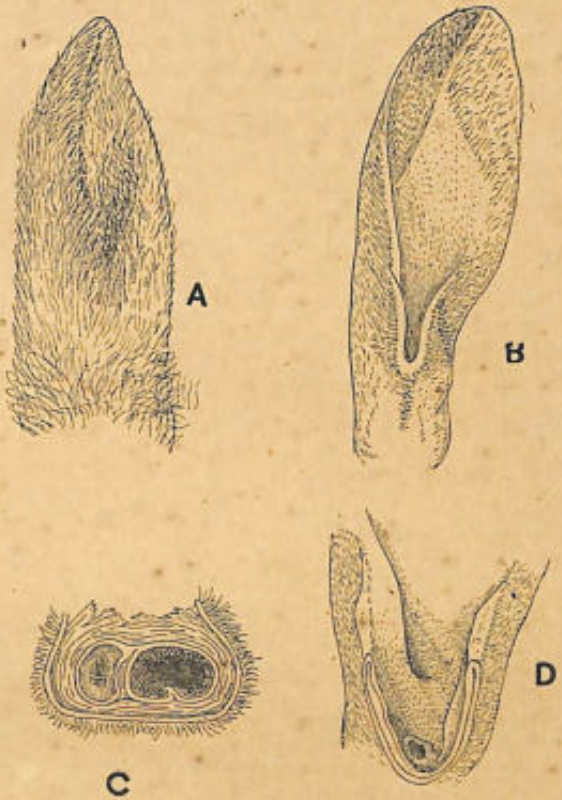
A. Head of *Ochotona* sp. from Thian Shan showing the facial vibrissæ. (Spirit specimen.)

B. The same of *Lepus senegalensis*. (Fresh specimen.)

teeth. When thus closed the nostrils appear as a continuous crescentic crease with its concavity opening upwards, and the philtrum is reduced to a median vertical crease running downwards from the middle of the convexity of the crescent. In this condition the moist naked skin of the rhinarium is entirely hidden. The internarial septum is moderately broad, but although narrower than the naked area below, which extends downwards to the gum of the incisors, is not otherwise differentiated from it. (Text-fig. 13, p. 671.)

The Mouth.—The buccal margin of each upper lip is provided with a lobe, covered with short hair, andthese lobes are capable of meeting in the middle line over the palate behind the upper

Text-figure 15.



A. Ear of *Lepus timidus* with the hair intact.
B. The same with the hair cut short.
C. Transverse section of the base of the ear of the same, showing the two cavities, the posterior to the right being the larger and deeper and showing inferiorly the crest passing from the antitragus to the neighbourhood of the orifice.
D. Base of the ear of the same cut open showing the tragus turned forwards to the left, the large anterior crest ceasing above the auditory orifice at the bottom and the small crest descending from the antitragus.

incisors. In addition to this there is on each side a strip of hairy skin extending inside the mouth along the cheek on a level approximately with the molar teeth. The lower lip is similarly

provided on each side with a lobe of skin which is capable of meeting its fellow of the opposite side behind the lower incisor teeth beneath the tongue. The lower lobes, however, are much smaller than the upper and are naked. I have found no noticeable variation in the structure of the rhinarium and mouth in all the species of Leporidæ examined; and the Ochotonidæ resemble the Leporidæ in these particulars. (Text-fig. 13, p. 671.)

Facial Vibrissæ.—In both the families of Lagomorpha the mystacial vibrissæ are always numerous and generally long; and the superciliary tuft is represented by a series of three or four vibrissæ over the anterior half of the eye. The genal tuft is usually represented by a single vibrissa, very rarely by two, rising a little below the posterior angle of the eye. This vibrissa, or pair of vibrissæ, is presumably of little importance when the length and number of the mystacials is taken into consideration. In a considerable number of skins they are not perceptible; but their absence may in some cases at least be due to moulting. In no species either of Leporidæ or Ochotonidæ did I discover a trace of the interramal tuft. (Text-fig. 14, p. 672.)

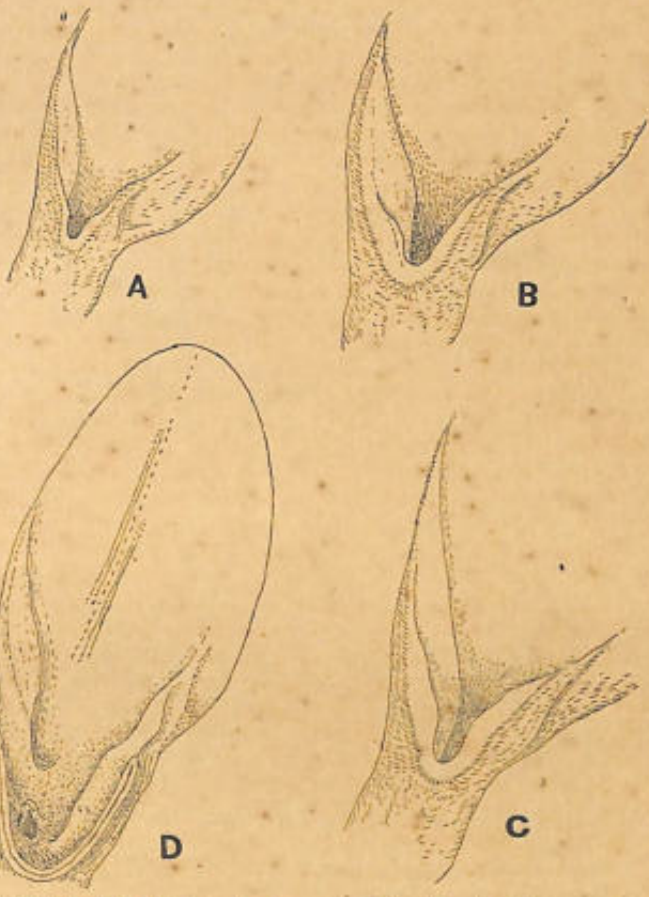
The Ears.—In the Leporidæ* the ears differ considerably in length, width, and hairiness according to the genus or species; but within the limits of the family present no marked structural variations.

The basal portion, which is highly mobile, consists of a deep cartilaginous tube or cup at the bottom of which lies the auditory orifice surrounded by soft membrane (text-fig. 15, C, D, p. 673). This cup is divided by a vertical transverse partition into an anterior smaller and shallower portion and a posterior larger and deeper portion. The latter, containing the orifice, is partially subdivided externally by a vertical ridge or crest which descends from the inner surface of the antitragal ridge, ceasing on the bottom of the cup on the outer side of the auditory orifice. The summit of the posterior wall of the anterior division of the cup passes upwards externally into a long high crest, convex below, which, becoming attenuated in its course, ascends and blends with the anterior edge of the pinna. This crest projects into the cavity of the pinna, and the half-tube it defines behind is continuous with the cavity of the anterior division of the cup. At its base externally there is usually a soft flap of skin which may be called the tragus, and between this and the large injutting crest there is a more or less well-developed, low cartilaginous rod continuous above with the edge of the pinna. Corresponding to the tragus there is a well-developed sublobate antitragal crest which is continued above as a ridge forming the inferior edge of the hollow of the pinna behind. Usually the tragus, antitragus, and an area of skin below the intertragal notch, where they meet, is conspicuously naked. The

* The ear of *Lepus europæus* and of *Oryctolagus cuniculus* has been described and figured by Boas (Die Ohrknorpel etc., 1912).

pinna is capable of being folded longitudinally along a crease which runs from its summit along its inner wall, and it is sufficiently rigid in its basal portion to dispense with the

Text-figure 16.

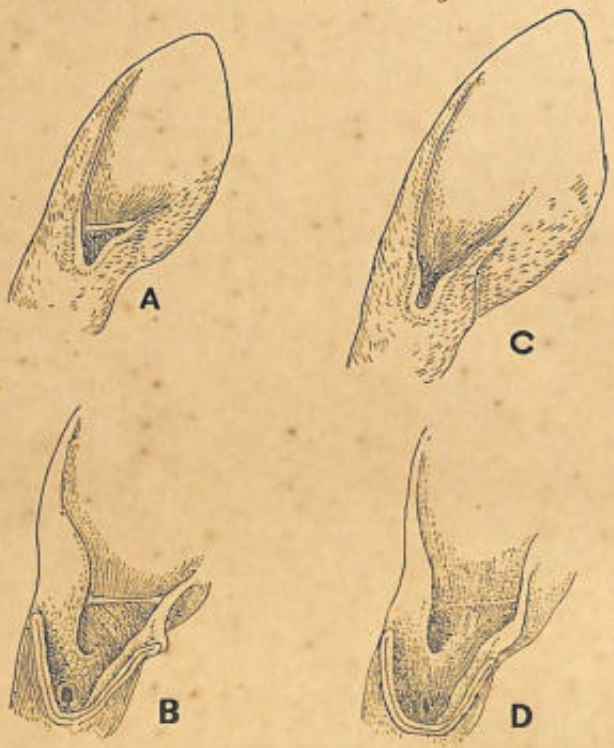


A. Base of ear of *Sylvilagus floridanus*, with the hair cut short.
B. The same of *Pronalagus crassicaudatus*.
C. The same of *Lepus omanensis*.
D. The entire ear of *Lepus brachyurus* cut open and spread to show the fine ridges adjoining the crease along which the pinna folds.

vertical cartilaginous ridges developed in many long-eared mammals like the Artiodactyla, for example. The only exception I have found to this occurs in the Japanese hare, *L. brachyurus*,

where there is on each side of the longitudinal crease a very fine cartilaginous rod (text-fig. 16, D, p. 675). The very general absence of all trace of the supratragus, or *plica principalis*, as a noticeable feature; but some of the short-eared forms, often called rabbits, possess it as a narrow longitudinal crest running along the inner wall of the cup from a point within the antitragus to

Text-figure 17.

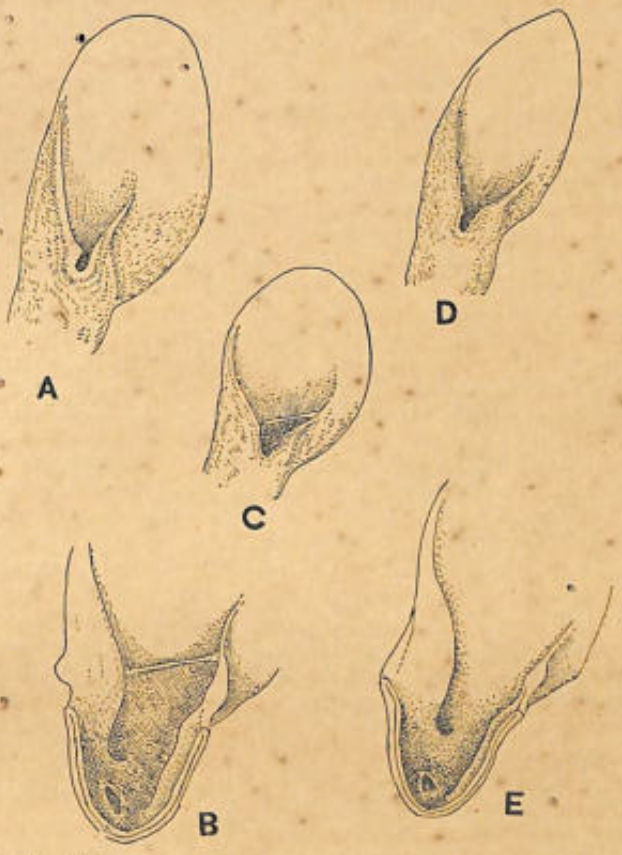


A. Ear of *Nesolagus netscheri* showing the supratragus and the reduced tragus.
B. Base of ear of the same cut open.
C. Ear of *Limnolagus palustris*.
D. Base of ear of same showing reduced supratragus.

the vertical crease within the anterior infolded crest. This supratragus is comparatively well developed in *Caprolagus*, *Nesolagus*, and *Romerolagus*, weak in *Limnolagus palustris*, and just perceptible by touch rather than by sight in *Oryctolagus*. I did not find a trace of it in *Pentalagus*, *Pronolagus Tapeti brasiliensis*, or in *Sylvilagus floridanus*. (Text-figs. 17 & 18, pp. 676–677.)

The anterior infolded crest varies considerably in width. In some forms of *Lepus*, like *L. omanensis*, *senegalensis*, and also in *Pronolagus*, it is wider than in *L. timidus* or *Oryctolagus*, which

Text-figure 18.



A. Ear of *Caprolagus hispidus* showing the lobate tragus and the wide area of the pinna behind the antitragus.
B. Base of ear of the same showing also the well developed anterior and posterior ridges.
C. Ear of *Romerolagus nelsoni*, with supratragus.
D. Ear of *Pentalagus furnessi*, without supratragus.
E. Base of ear of the same showing large anterior and small posterior ridge.

have shorter and narrower ears; but in some short-eared forms like *Caprolagus*, *Nesolagus*, and *Pentalagus* it is exceptionally deep. In *Romerolagus*, however, it is much narrower than in

the last named. It is moderately well developed in *Limnolagus palustris* and *Sylvilagus floridanus*.

The tragus is also variable. In *Lepus timidus*, *europæus*, and *Oryctolagus* it is a low, elongated ridge of integument. In *L. omanensis* it is much better developed both in length and depth. In *Pronolagus* it is shorter. In *Caprolagus* it forms a very definite stiff semicircular lobe; but in *Nesolagus* it is not at all prominent; nor is it in *Romerolagus*. In these and other small-eared forms—e. g., *Pentalagus*, *Romerolagus*—scarcely a trace remains of the naked area around the intertragal notch so noticeable in the larger hares.

The antitragus is less variable than the tragus, consisting of a softish flap of skin continuous above with a stiff ridge. This ridge is exceptionally strong in *Caprolagus*, in which the area of the pinna behind it is exceptionally wide (text-fig. 18, A, p. 677).

The range in actual size of the ears is shown in some of the figures, those of *Nesolagus* and *Romerolagus*, the most diminutive members of the family, being the smallest, and those of *Macrotolagus* or some of the tropical species of *Lepus* of the Old World the largest. On the other hand, relatively the smallest ears are found in *Pentalagus* or, perhaps, *Lepus americanus*, and relatively the largest perhaps in the little Arabian hare, *L. omanensis*.

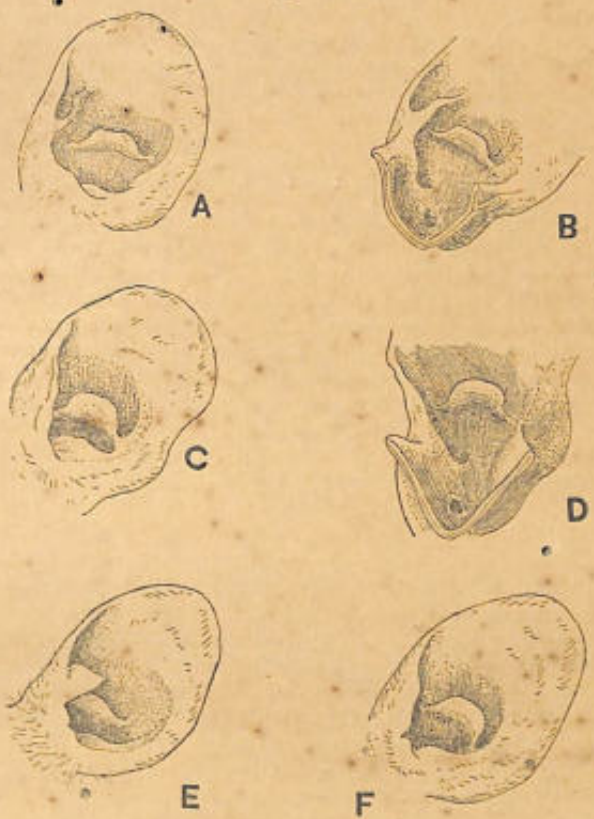
In the Ochotonidæ the ear is on the average considerably shorter, wider, and less tubular than in the Leporidæ, although it is not much, if at all, shorter relatively than in some of the short-eared hares, like *Pentalagus*. It is, however, less freely jointed to the head, to which it is attached by a comparatively wide base. It varies a good deal in size, shape, and structure within the family, but always apparently differs from that of the Leporidæ in the following structural points:—(1) The supratragus is retained as a large, nearly semicircular valvular flap, generally upturned but susceptible of being depressed to act as a lid to the basal tube of the ear; (2) the posterior crest, which in the Leporidæ descends from within the antitragus to the bottom of the basal tube, is absent; (3) the antitragus, varying much in size, being sometimes large and valvular, sometimes very small, is nearly horizontal; and (4) the tragus is produced backwards so that it overlaps externally at least the anterior portion of the antitragus. (Text-fig. 19, p. 679.)

For the rest the ear varies structurally in different species to a very noticeable degree; but only a few of the more striking variations can here be dealt with. Boas * has shown that the ears of *O. roylei* and *O. alpina* differ in one very remarkable particular. In *O. roylei* the anterior crest which, as in the Leporidæ, descends into the basal tube to cease a little distance above the auditory orifice, where it forms the edge of the aperture of the anterior pit of the tube, passes upwards and ends simply in a point on the anterior edge of the pinna within the well-developed tragal ridge (text-fig. 19, C–F, p. 679). In *O. alpina*,

* Die Ohrknorpel der Säug.

on the contrary, the upper portion of this ridge divides, giving off a lamina which passes into the cavity of the ear and forms the posterior wall of a very definite pit just within the margin of the ear in front (text-fig. 19, A, B, p. 679). A precisely similar

Text-figure 19.



A. Ear of *Ochotona alpina*.
B. Base of ear of the same cut open.
C. Ear of *Ochotona roylei*.
D. Base of ear of the same cut open.
E. Ear of *Ochotona syrinx*.
F. Ear of *Ochotona saccana*.

modification may be seen in *O. hyperborea*, *sushkini*, *hamica*, and a few more Asiatic species as well as in *O. princeps* from the Rocky Mountains. The more primitive and simpler arrangement

observed in *O. roylei* is, however, of commoner occurrence, and no trace of this submarginal pit is to be seen in *O. ladacensis*, *dauurica*, *rufescens*, *rutila*, and others *. But within this section there are other modifications of interest. For instance, in *O. rutila* and *O. wardi* the anterior crest is long and wide; in *O. ladacensis*, *saccana*, *rufescens* and others it is much shorter and narrower; in *O. dauurica* it is almost suppressed; in *O. syrinx* it is also scarcely perceptible. But the most remarkable structural variation in *O. syrinx* is the development on the anterior rim of the pinna above the tragus of a conspicuous triangular lamina which juts into the cavity and forms a supplementary valve (text-fig. 19, E, p. 679).

The Feet of the Leporidæ.

The feet of the Lagomorpha are characterized by the replacement of the plantar pads and the metatarsal pads, and the carpal pads as well, by long hairs constituting a mat, covering the portion of the sole that rests on the ground, whether the animal be squatting or running. The peculiarity of this modification depends upon its persistence with comparatively slight variations in the typical hares, irrespective of habitat. It is found in Arctic and tropical species occurring in the mountains or plains, in sandy deserts, woodland, marshland, or snow. But in some of the more aberrant types of the family it is much less pronounced. In *Romerolagus*, for example, the woolly padding of the feet is scarcely more developed than in the typical Ochotonidæ.

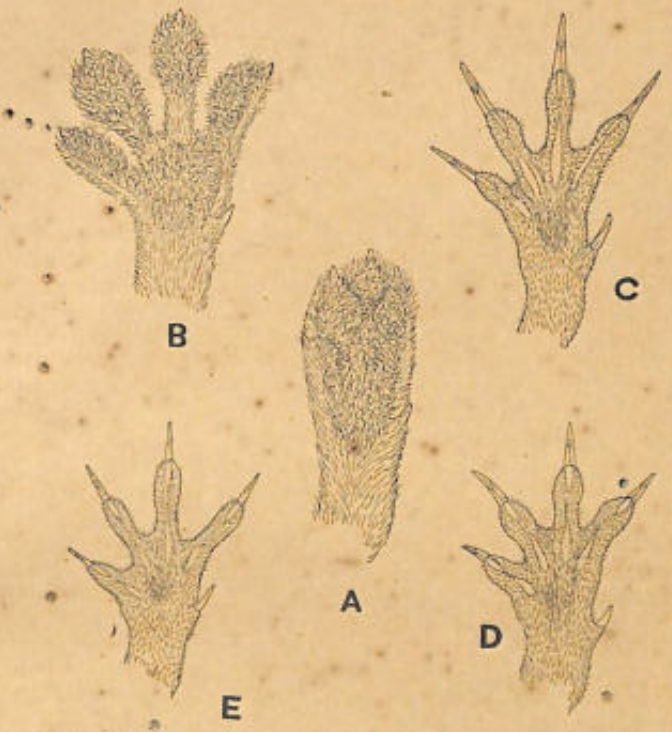
The *Fore feet* are tolerably uniform in structure throughout the group, and are pentadactyle and perissodactyle, the 3rd digit being the longest of the series, set in the middle line, and flanked on each side by the 2nd and 4th, which are subequal. The 5th digit is much shorter than the 4th, but hardly so widely separable from it as the 4th is from the 3rd; but the 1st is represented externally merely by its claw, which projects from the skin of the inner side of the foot a considerable distance above the 2nd.

In the Leporidæ the hairy mat, consisting mainly of coiled woolly hair, covers the sole approximately as far back as the point of emergence of the 1st digit, whence it extends to the tips of the digits. When the digits are in contact the mat is continuous

* A study of the ears on fresh or spirit-preserved material of this group is likely to yield useful systematic characters. By the character mentioned above, for instance, the Ochotonidæ are divisible into two sharply defined genera. The first, containing the ear-pocket, must apparently be called *Pika* because *alpina*, the type of *Pika* according to Thomas (Proc. Zool. Soc. 1908, p. 982), possesses that character. The second must take the name *Ochotona* because *dauurica*, the type of *Ochotona* according to Thomas, is without it, and since *roylei*, the type of the genus *Conothoa*, is also without it, *Conothoa*, in default of other generic characters to distinguish *roylei* from *dauurica*, will fall as a synonym of *Ochotona* as Thomas, for other reasons, maintained. I must add that I have accepted, without looking into the matter, the specific names attached to the specimens in the Natural History Museum.

and appears to be undivided; but when the digits are separated it may be seen to be composed roughly of five constituents, the largest, the plantar mat, growing on the sole of the foot and overlapping distally the bases of the digits, and four smaller ones, the digital mats, which are thickest and longest upon the extremities of the digits where they conceal the digital pads. On the 2nd and 5th digits, the digital mats are continuous more

Text-figure 20.



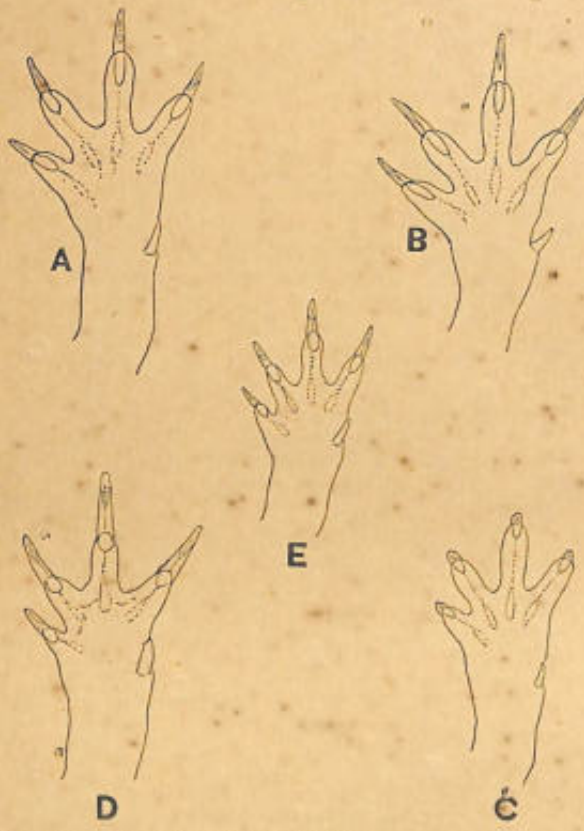
A. Right fore foot of *Lepus timidus scoticus*.
B. The same with the digits spread to show the disposition of the hair-mats the anterior hairs of the plantar mat turned back.
C. The same with the hairs cut short.
D. The same of *Lepus europæus occidentalis*.
E. The same of *L. americanus* from Fort Simpson (relaxed on dried skin).

or less with the plantar mat; on the 4th digit it is more clearly differentiated from the plantar mat, and on the 3rd, which has the smallest digital mat, it is restricted to the distal half of the

digit. The tips of the hairs of the digital mats extend to the ends of the claws. (Text-fig. 20, A, B, p. 681.)

In *Lepus timidus*, when the hairs of the feet are clipped short, the 2nd, 3rd, and 4th digits are seen to be long, evenly spaced, and united by a narrow web extending about half-way along the

Text-figure 21.



A. Right fore foot of *Macrotolagus callotis*.
B. The same of *Oryctolagus cuniculus*.
C. The same of *Pronolagus crassicaudatus*.
D. The same of *Pentalagus furnessi*.
E. The same of *Caprolagus hispidus*. With the exception of B these figures are drawn from relaxed feet on dried skin.

first or proximal phalanx bone. Proximally their margins are lightly concave, the distal end is expanded and ovate, carries a long pointed claw and bears beneath a very narrow strip of

naked skin representing the digital pad *. Behind this pad there is a narrow strip of naked skin which extends backwards on to the fore part of the plantar area which is elsewhere closely covered with hair. When placed together the convexity of the inner distal edges of the 2nd and 4th fit into the concavities of the proximal edges of the 3rd, and their tips reach about half-way along the expanded distal portion of the latter. The 5th digit is similar in shape to the others but much shorter. It fits similarly against the outer side of the 4th but extends barely half-way along it.

There is no trace of plantar or carpal pads; and the carpal vibrissæ are also suppressed. (Text-fig. 20, A–C, p. 681.)

The form of the fore feet in a few selected types is shown in text-figs. 20, 21, pp. 681–682. In *Lepus europæus* it is very like that of *L. timidus*, but in the fresh specimen examined is a little shorter in the digits, which also carry shorter claws. The relaxed foot on a dried skin of *L. americanus* from Fort Simpson is also very similar to that of *L. timidus*, except that the 1st digit is not so high above the 2nd and the 5th is more widely separable from the 4th, the 1st and 5th being consequently more nearly on a level. The claws also are thinner. In *Macrotolagus callotis* the digits are a little shorter than in *L. timidus* but are similarly placed, except the 1st, which is higher above the base of the 2nd, a modification correlated with the longer foot as indicated by the position of the wrist.

Oryctolagus cuniculus has a short foot with the 5th digit long and the 1st set low down as compared with *L. timidus*. *Caprolagus* is also short-footed, but the 5th digit is much smaller than in *Oryctolagus*. In *Pentalagus* the foot is short and broad, with short digits armed with exceptionally long and strong claws. In *Pronolagas* the foot, measured to the wrist, is much longer than in *Oryctolagus*, the 1st digit is set higher up, and the 5th is much smaller; and the claws on digits 2 to 5 are very short and blunt.

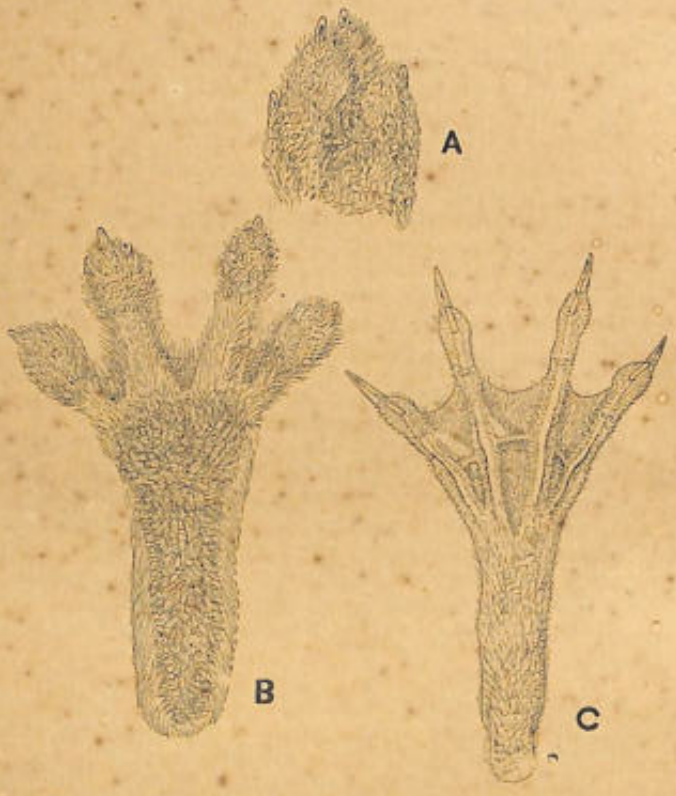
The *Hind feet* are similar to the fore feet in their hairy padding, but the mat is continued over the metatarsal and tarsal areas to the tip of the calcaneum; and the digital pads are the only pads retained. There are, moreover, only four digits, the first or hallux being suppressed, and the foot is typically almost† artiodactyle, the digits, described below respectively as the 2nd, 3rd, 4th, and 5th, being symmetrically or subsymmetrically paired, the middle line of the foot passing between the 3rd and 4th.

* The inconspicuousness of the digital pads is not a seasonal character in the Scots hare. In a specimen in summer pelage shot by Mr. Gladstone in August and preserved in the Natural History Museum, they are no larger than in the example described above.

† But not quite, the axis of the tarso-metatarsus passing nearer to the 3rd than to the 4th digit when the two are separated.

In *Lepus timidus scoticus* the digits are long as compared with the tarso-metatarsal area, the 3rd measured from the transverse ligament, attaching it proximally to the 4th, to the tip of the digital pad being nearly half the length of the tarso-metatarsus measured from that ligament to the end of the calcaneum.

Text-figure 22.



A. Toes of right hind foot of *Lepus timidus*.
B. Right hind foot of the same with digits spread and anterior hairs of plantar mat turned back to show position of digital mats.
C. The same with the hairs cut short.

Their lengths in descending order are 3, 4, 2, 5, the 3rd being noticeably, but not much, longer than the 4th. The 2nd reaches about half-way along the second or middle phalanx of the 3rd, whereas the 5th barely surpasses the distal end of the first phalanx of the 4th. They are tolerably widely separable, the

distance between the 3rd and 4th being only a little greater than that between the 2nd and 3rd or the 4th and 5th. They are joined together by deep wide webs. The web between the 3rd and 4th reaches at the sides almost up to the joint between their proximal and middle phalanges, being a little lower on the 3rd than on the 4th. The webs between the 2nd and 3rd and the 4th and 5th extend externally up to the terminal swelling of the 2nd and 5th digits, considerably in advance of the joints between their proximal and middle phalanges. Proximally, the four digits are securely tied together where they articulate with the metatarsus by three strong transverse elastic ligaments, the median ligament between the 3rd and 4th being longer than those between the 2nd and 3rd and the 4th and 5th, which are also more oblique. Behind or proximally to these ligaments the distal ends of the metatarsi are separable and are united by webs similar to those joining the digits, and not by a mass of muscular tissue such as is found in the hind feet of most mammals.

The *claws* are moderately long, stout, and pointed, and the digital pads are very narrow strips of naked skin *. Behind the pads the lower side of each digit has a narrow median area of naked skin, which is continued proximally on to the distal ends of the metatarsi. But normally this naked strip is concealed from view by being overlapped by the hairy skin at its sides; and at the proximal ends of the digits and at the distal ends of the metatarsi the overlapping skin on the outer side of each digit, away from the middle line, is thickened and raised into a thickly haired ridge. The tendons also are thickly haired, so that this area of the foot, upon which the hare rests when on the move, is more padded than the rest of the digits and metatarsus. (Text-fig. 22, p. 684.)

The hind feet of the common English hare, *Lepus europæus occidentalis*, is very similar in every respect to that of the Scots hare, *L. timidus scoticus*, except that the webs are a little shallower, and in the Irish hare, *L. hibernicus*, belonging in cranial characters to the same category as the Scots hare, the feet are apparently quite like those of the English hare, although in a relaxed foot of the dried skin examined the digits were not quite so widely separable. This difference may, however, have been due to shrinkage.

The hind feet of the peculiar short-tailed, short-eared Japanese hare, *L. brachyurus*, are tolerably similar to those of *L. europæus*, but the webs are considerably shallower, more particularly the lateral webs in their extension along the inner edges of the 2nd and 5th digits, which are distally free to a much greater extent than in *L. europæus*. Correlated with this difference is a wider span of the digits, suggesting that this hare lives habitually on

* These pads are equally narrow in the summer, there being no seasonal change in their width.

softer, possibly more marshy ground, than our species. (Text-fig. 23, A, B.)

Text-figure 23.

A. Right hind foot of *Lepus europæus*, clipped.
B. The same of *Lepus brachyurus*.
C. Distal end of the same of *L. campestris* from Oregon. A from a fresh specimen, B & C relaxed on dried skins.

I have examined the feet, mostly on dried skins, of a considerable number of African and Asiatic species without finding any very marked structural differences except a certain amount

of variation in the length of the digits and of the tarso-metatarsus and in the depth of the webs. It is beyond my present purpose to discuss these differences, but it may be added that the webs are always shallower than in *L. timidus* and *L. europæus*. The foot of an example probably of *L. senegalensis* from the Gambia (*Dr. Hopkinson*) will serve to illustrate this difference (text-fig. 25, A, p. 689). The shallowness of the webs as compared with those of *L. timidus* and *L. europæus*, above referred to, may in some cases be due to incomplete relaxation after shrinkage from drying. But this is certainly not always the explanation, as is shown by spirit-preserved material of *L. senegalensis* and *L. peguensis*.

There is one tropical species, however, which calls for notice as differing in the structure of its foot from the other species of *Lepus* examined. This is the little South Arabian hare, *L. omanensis*, from Oman, the smallest known species of the genus (text-fig. 25, B, p. 689). In this hare the 2nd and 5th digits, especially the 5th, are longer as compared with the 3rd and 4th, which are subequal, than in other species. The interdigital webs, moreover, are very unequal in development. The median web joining the 3rd and 4th digits is exceedingly shallow, extending only a very short distance beyond the elastic tendon. The web between the 2nd and 3rd is markedly deeper and of average dimensions for the majority of species; but the web between the 4th and 5th digits is considerably deeper, relatively as deep, indeed, as in *L. europæus*, and it ties these digits closer together than the 4th is to the 3rd or the 3rd to the 2nd. The tarso-metatarsal area is comparatively short, being about twice the length of the 3rd digit; but it is capable of being widely expanded distally at the base of the digits, giving a wide area of support no doubt as an adaptation to the sandy soil on which the hare moves. A further adaptation to this habitat is seen in the development of the mats of hair on the digits and plantar area both of the fore and hind feet *.

Turning to the American species, I find that the hind foot of an immature example of *L. americanus* † from Fort Simpson (*B. E. Ross*) differs in some respects from that of the European species described above. The tarso-metatarsus is shorter, the 3rd digit being more than half its length, the claws are thinner, longer, and sharper, and the interdigital webs are much shallower and consequently narrower, leaving a larger extent of the digits, especially of the 2nd and 5th, free from web (text-fig. 24, A, p. 688).

The foot of an American Arctic hare, *L. arcticus* ‡, from the

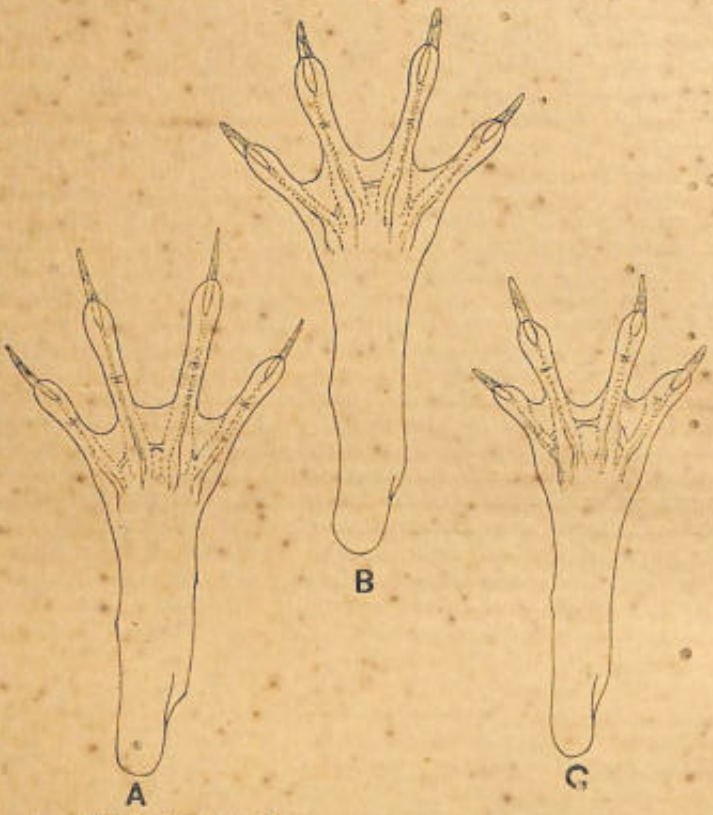
* Since writing this description of the foot of *L. omanensis*, I have examined the hind foot of *L. arabicus* from the neighbourhood of Aden and found it to be very similar.

† Type of the genus *Pœcilolagus* Lyon not admitted even as a subgenus by Nelson and Miller.

‡ Type of *Lagus* Palmer, which is not admitted by Nelson and Miller. Of the Greenland hare, *Borcolepus*, admitted as a subgenus of *Lepus* by Nelson and Miller, I have seen no specimen. The species is said to have long, heavy claws.

Arctic Regions (*Commdr. Markham*) has webs a little narrower and shallower than in *L. americanus*, and the digits are much shorter as compared with the tarso-metatarsus, which is about twice and a half times the length of the 3rd digit. The claws also are shorter, stouter, and blunter (text-fig. 24, B).

Text-figure 24.



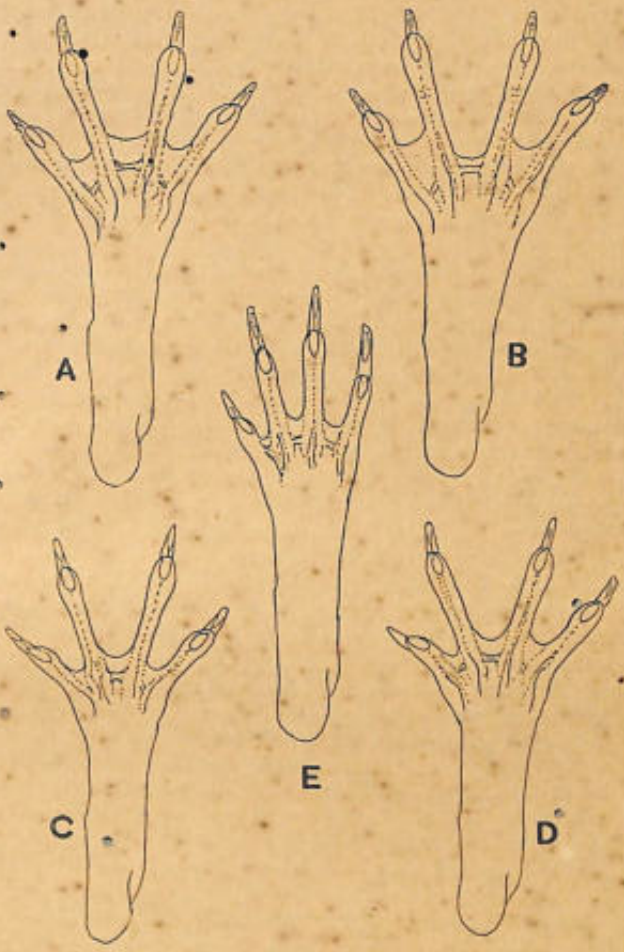
A. Right hind foot of *Lepus americanus*.
B. The same of *L. arcticus*.
C. The same of *Macrotolagus callotis*. All relaxed on dried skins

In *Lepus campestris* * the foot of an example from Oregon is of the same general type as that of *L. europæus*, although the webs are not quite so deep, a longer portion of the distal end of the digits being free. The digits are tolerably long, the 3rd being about half the length of the tarso-metatarsus. As compared

* One of the American White-tailed Jack Rabbits.

with *L. americanus*, the claws are thicker, the 5th digit is much more fully webbed on the inner side and the tarso-metatarsus is longer. The claws are like those of *L. arcticus*, but the digits

Text-figure 25.



A. Right hind foot of *Lepus senegalensis*, clipped.
B. The same of *Lepus omanensis*.
C. The same of *Sylvilagus floridanus*.
D. The same of *Tapeti brasiliensis*.
E. The same of *Limnolagus aquaticus*. All relaxed on dried skins.

are longer as compared with the tarso-metatarsus and the webs are deeper, especially the web between the 4th and 5th. (Text-fig. 23, C, p. 686.)

The foot of *Macrotolagus* * *callotis*, from Zacatecas, Mexico, is very different from that of *L. americanus* in the length of its tarso-metatarsus, the shortness of the digits, and the shallowness of the webs. The foot of *L. arcticus* is almost intermediate in these respects; but in *M. callotis* the tarso-metatarsus is more than two and a half times the length of the 3rd digit. The 4th is about equal to the 3rd. The 2nd and 5th are short, and the webs on their inner sides extend up to the proximal end of the swollen distal portion and hold these digits tolerably closely to the 3rd and 4th respectively, so that, with the shortness of the digits, the foot is comparatively narrow. The webs are about as deep as in *L. arcticus*, but the median is slightly shallower than the lateral. The foot of this hare, with its short compact digits and long tarso-metatarsus, seems especially adapted for swift running. (Text-fig. 24, C, p. 688.)

In *Sylvilagus* † *floridanus*, from Florida (text-fig. 25, C, p. 689), the digits are joined basally by shallow webs and are widely separable; but the 2nd and 5th, particularly the 5th, are shorter as compared with the 3rd and 4th than in typical *Lepus*. The 3rd digit is nearly half the length of the metatarsus. The foot of this species differs very markedly in its proportions from that of *Macrotolagus callotis*. It also differs, though to a less extent, from the feet of *L. americanus* and *L. arcticus*.

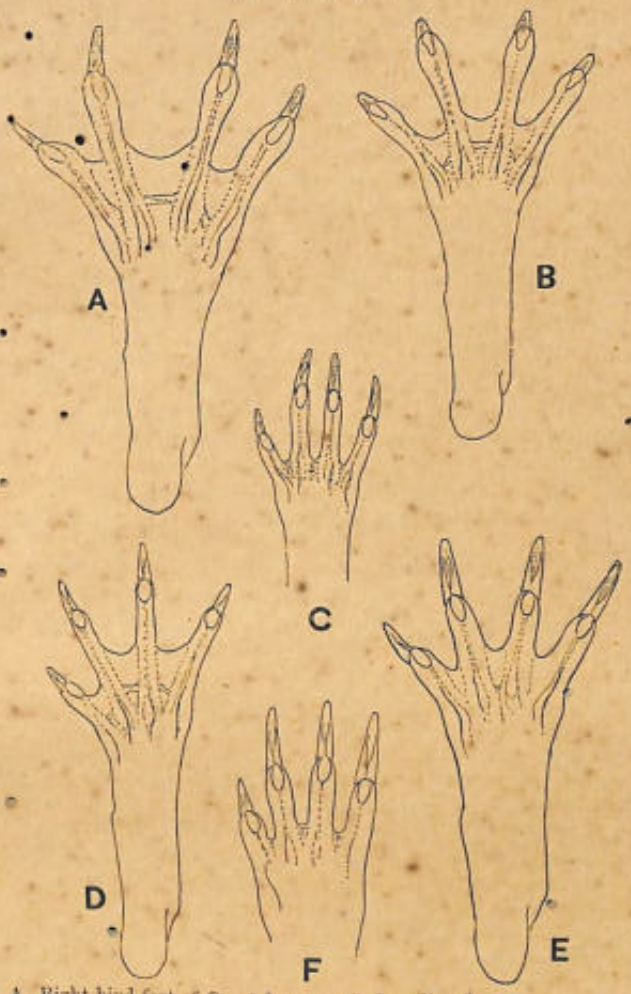
The hind foot of *Tapeti* ‡ *brasiliensis* (text-fig. 25, D, p. 689) hardly differs at all from that of *Sylvilagus floridanus*, although in the specimens examined the 2nd digit of the former is a little longer and the 5th a little shorter.

In *Limnolagus* § *aquaticus* (text-fig. 25, E, p. 689) the digits are a little shorter as compared with the tarso-metatarsus than in *Sylvilagus floridanus*, the 5th is greatly reduced in length and the claws are more powerful, especially that of the 2nd which is exceptionally long and strong. There seems also to be a tendency towards the assumption of perissodactylism, the 3rd digit apparently taking naturally a position more in the middle of the foot between the 2nd and 4th, instead of pairing with the latter. This I also notice in *L. palustris*, a related species, the foot of which resembles that of *L. aquaticus*, except that there is not quite the same inequality in length between the 2nd and 4th digits. These species may be advantageously compared in this connection with *Caprolagus*, described below.

There is nothing particularly remarkable about the foot of the diminutive rabbit *Romerolagus*, from Mount Popocatapetl. The webs are basal and very shallow. The 2nd digit is longer than in *Sylvilagus* and the 4th is if anything longer than the 3rd, but both are comparatively short. The claws are powerful. (Text-fig. 26, C, p. 691).

* The American Black-tailed Jack Rabbits.
† The American Cotton-tails.
‡ Admitted as a subgenus of *Sylvilagus* by Nelson and Miller.
§ Regarded by Nelson and Miller as a synonym of *Tapeti*. These are the Swamp Rabbits of the States.

Text-figure 26.



A. Right hind foot of *Oryctolagus cuniculus*, clipped.
B. The same of *Pronolagus crassicaudatus*.
C. Distal end of the same of *Romerolagus nelsoni*.
D. Entire foot of *Caprolagus hispidus*.
E. The same of *Pentalagus furnessi*.
F. Distal end of the same with toes less spread. Except A, all relaxed on dried skins.

In the common Rabbit, *Oryctolagus cuniculus*, the foot does not differ very greatly from that of *L. europæus*, but the 2nd

digit is relatively longer, reaching to the middle of the terminal thickening of the 3rd. It is also a little more closely tied to the 3rd, the interdigital web being narrower distally, where it reaches approximately to the joint between the second and third phalanges of the 2nd digit. The 5th digit is also relatively a little longer and is much more closely tied to the 4th by the narrowness of the web distally. The interdigital webs are tolerably deep, deeper than in *Lepus arcticus*, *L. americanus*, *Macrotolagus callotis*, *Sylvilagus floridanus*, *Tapeti palustris*, and *Pronolagus crassicaudatus*. The 3rd digit is almost half the length of the metatarsus. (Text-fig. 26, A, p. 691.)

In the relative lengths of its digits the foot of *Pronolagus crassicaudatus* is tolerably like that of *Oryctolagus*; but the tarso-metatarsus is longer as compared with the 3rd digit, the claws are very short and blunt, the pads are small, and all the digits are widely separable, the 5th being as widely separable from the 4th as the 4th is from the 3rd and more widely than the 3rd is from the 2nd. The webs are basal and shallow and of approximately equal depth, digits 2 and 5 on account of their length being free from web to an exceptional extent. This hare is said to frequent rocky situations at high altitudes in South Africa. Hence it may be inferred that the shortness and bluntness of its claws are adaptations to that habitat. Certain resemblances between the skulls of this species and of *Oryctolagus* induced Forsyth Major to regard them as congeneric. But the differences in the feet, let alone other structural points, hardly admit the adoption of that view. (Text-fig. 26, B, p. 691.)

Caprolagus hispidus, the North Indian coarse-coated hare, has a foot recalling in many respects that of *Limnolagus*. It is perissodactyle. The 2nd digit is as long as the 4th and much longer and stronger than the 5th, which is relatively a little shorter even than in *T. palustris* and it is closely tied to the 4th by a deeper web. The webs between the 2nd and 3rd and the 3rd and the 4th are also much deeper and wider than in *T. palustris* and better developed than in most species of the Leporidæ. The pads are large and the claws moderately long and strong. The tarso-metatarsus is long as in *T. palustris*, being considerably more than twice the length of the 3rd digit. (Text-fig. 26, D, p. 691.)

Of the little Sumatran hare, *Nesolagus netscheri*, I have not been able to examine the feet, the bones having been extracted from the skins in the only examples available. *Nesolagus* is supposed to be related to *Caprolagus*, but the resemblance between the skulls is not very close.

The peculiar short-eared, short-tailed hare, *Pentalagus furnessi*, from Liu Kiu, has also a very peculiar hind foot. It is artiodactyle as in typical Leporidæ, but the digits are short and stout and provided with very long stout claws and well-developed

rounded pads. The 3rd and 4th digits are subequal and the 2nd is not much shorter, and the 5th is well developed, although considerably shorter than the 2nd. The three interdigital webs are tolerably equal, moderately deep but narrow so that the digits are not very widely separable. The tarso-metatarsus is wide and, owing to the shortness of the 3rd digit, is over three times its length. (Text-fig. 26, E, F, p. 691.)

The Feet of the Ochotonidæ.

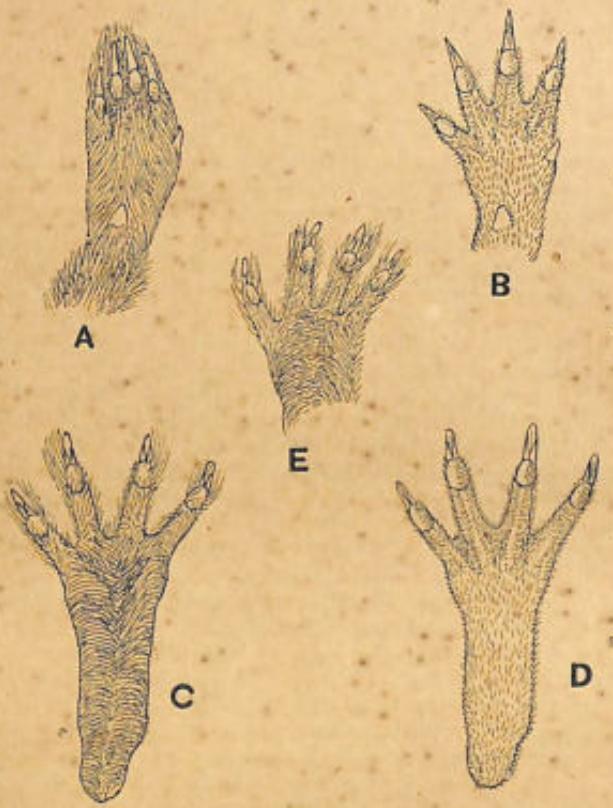
The *Fore feet* of a species of *Ochotona* of the *roylei*-group, from Thian Shan, differ from those of the Leporidæ in retaining a distinct conical carpal pad and in being without the mat of woolly hairs on the under side of the digits and plantar area, the entire sole from the carpus forwards and the lower side of the digits being covered with long hairs which project inwards and forwards from the margins towards the middle line. The claws of the four main digits are long and pointed and overlapped above by long hairs from the upper side of the digits. The pads are conspicuous and well developed, although overlapped behind by the hairs of the under sides of the digits. The 1st digit or pollex is short and situated as in the Leporidæ towards the middle of the inner edge of the foot, where it is represented by a claw only, there being no trace of pad. The sole is broader and the digits are shorter than in typical Leporidæ; but the arrangement and relative lengths of the digits are the same as in that family, the foot being perissodactyle, with the 3rd digit in the middle line and flanked by the 2nd and 4th, which are subequal and a little shorter than the 3rd. The 5th is as well developed as in typical Leporidæ; and the basal webs are all narrow and shallow. (Text-fig. 27, A, B, p. 694.)

The *Hind foot* is artiodactyle as in typical Leporidæ. It is short as compared with most of the species of that family, although not much shorter than in *Oryctolagus*. It is clothed beneath with long hairs, which on the tarso-metatarsal area project transversely inwards from the margins to the middle line where they meet; and the plantar area immediately above the base of the digits is padded by longish hairs directed obliquely backwards and inwards from the proximal ends of the digits. On the tips of the digits above them are long hairs overlapping the claws. The pads are well developed, as in the fore feet. The digits are moderately long and separable, being united only at the base with shallow, narrow webs. The 3rd and 4th are subequal and the 2nd is very nearly as long as the 3rd. The 5th also is long, relatively longer than in any of the Leporidæ, and widely separable from the 4th. (Text-fig 27, C, D, E, p. 694.)

In spite of the differences above recorded between the feet of the Ochotonidæ and those of the typical Leporidæ, it can hardly be claimed that they differ from the latter more than do the feet

of such a form as *Pentalagus*—and within the limits of the Ochotonidæ there is much variation in the hairiness of the sole. The digital pads are sometimes almost as concealed as in typical Leporidæ, whereas sometimes, as in *O. ladacensis*, they are entirely

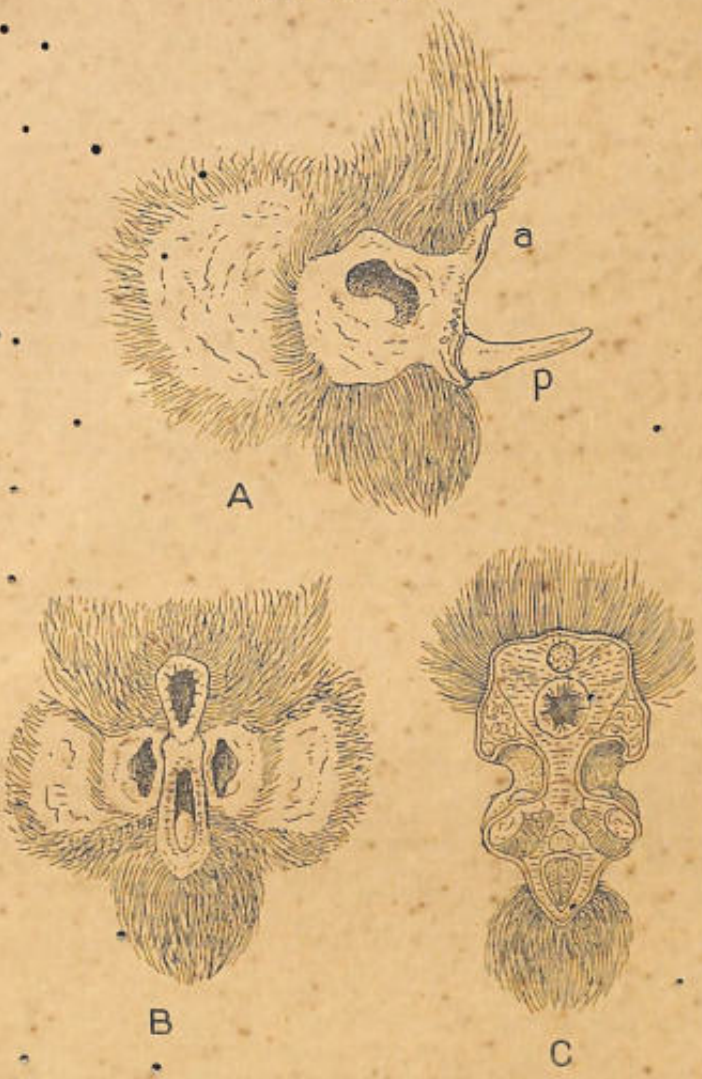
Text-figure 27.



A. Right fore foot of *Ochotona* from Thian Shan.
B. The same with hairs cut short and digits spread.
C. Right hind foot of the same with digits spread.
D. The same with hairs cut short.
E. Digital end of the same showing position of digits when partially spread.
All from spirit specimens.

exposed and appear like thick leathery cushions. Even in the case of the fore feet the carpal pad is sometimes hardly detectable on dried skins and may be perhaps altogether suppressed.

Text-figure 28.



A. Lateral view of anal and genital area of male *Lepus timidus*, showing the anus (*a*) with tail raised above it, the penis (*p*) extended to its fullest extent, the perinæal gland with its sac and, to the left, the naked tract of skin on the thigh.

B. Posterior view of the same of the female, showing the anus and vulva in the middle line and the glandular perinæal area and naked tract of skin, the two last foreshortened, on each side.

C. Vertical transverse section through the same region in male *Lepus europæus*, showing a caudal vertebra and the rectum above, the glandular pit in the middle on each side, and the glands and penis lower down.

The Anal and Genital Area.

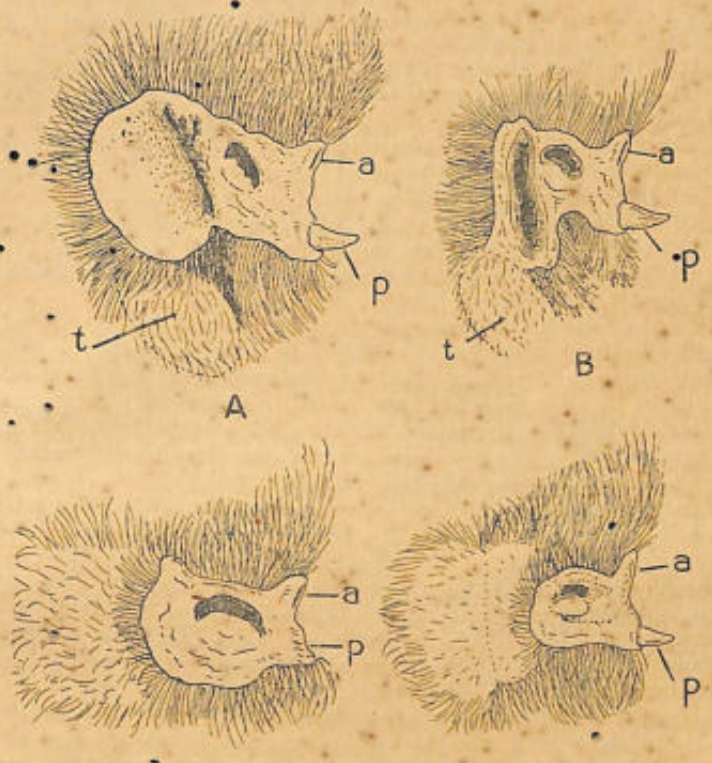
Perineal Glands.—These glands, briefly described in the case of the Rabbit in many students' text-books *, are present in all the fresh or spirit-preserved specimens of the Leporidæ I have seen and differ in no points of great importance in the different species. They are as well developed in the female as in the male; and although I have examined them in rabbits caught in spring, summer, autumn and winter, I have not succeeded in finding any seasonal variation in their size or activity. They are situated on each side and in front of the naked perineal strip of skin running between the anus and the generative orifice (text-fig. 28, p. 695). The glandular area is a conspicuous field of naked skin, somewhat longer than deep and stretching forwards from the region between the anus and the genital aperture, and sharply defined above by the long hairs at the sides of the root of the tail and below by the similar long hairs of the inguinal region in front of the penis or vulva. In front and externally it is bordered by a narrow fringe of long hairs which separates it from a large area of nearly naked skin covering the side of the pelvis and the adjoining part of the inner surface of the thigh. The glandular area is marked above by a distinct pouch or pocket with a wide, generally crescentic, mouth opening downwards, and at the lower edge of the orifice there is an oval or rounded elevation marking the position of the cutaneous gland, the source of the secretion with which the pouch is commonly to a large extent filled (text-fig. 28, A, p. 695.)

When the hind limbs are in their natural position the naked or nearly naked area of skin in front of and external to the glandular area and situated on the inner surface of the base of the thigh is opposed to and in contact with the glandular area; and the crease or fold formed by the junction of the skin of the thigh with that of the perinæum lies just in front of the delicate fringe of hair defining the glandular area anteriorly. The variations observed do not affect the glandular area itself but the area of nearly naked skin on the inner side of the thigh externally to it. As a rule this area is not very sharply defined marginally and is variable in the extent of its hairy clothing. In *L. peguensis*, for example, it is scarcely differentiated from the rest of the skin of the thigh, being merely a little less thickly hairy (text-fig. 29, C, p. 697). But in *Lepus callotis* it differs from that of all the other species examined. It is somewhat reduced in size and is as sharply defined marginally by the abrupt cessation of the hairs surrounding it as is the glandular area itself, and there is no fringe of hairs between it and the glandular area. It acts, moreover, as a pouch for the storage of the secretion which collects in some quantity along the deep part of the crease formed when the thigh lies alongside the perinæum. (Text-fig. 29, A, B, p. 697.)

* *Cf.* 'Practical Zoology' by Marshall and Hurst, ed. 2, p. 306, 1888; and also in subsequent editions.

Since these glands are equally well developed in both sexes, there is no reason to suppose they have a special sexual significance. They probably help the individuals of the species to follow and find each other. From their position it may be inferred that their secretion scents the grass when the rabbit or

Text-figure 29.



A. Lateral view of anal and genital area of male *Macrotolagus callotis*, showing the deep crease between the perineal gland and the naked skin on the thigh.

B. The same showing how the crease forms a pouch for the storage of secretion.

C. The same of female *Lepus peguensis*.

D. The same of male *Oryctolagus cuniculus*. *a* anus, *p* genital orifice, *t* testis.

hare is squatting in the attitude habitual to these animals. It may be noticed, moreover, that when the tail of these animals is depressed, the whole perineal area is, as it were, closed; but

when the tail is raised, as it always is during flight, the glandular areas are exposed and must, it may be presumed, scent the air with their odorous secretion. It is commonly believed that the exposure of the white under side of the tail of a rabbit or hare in flight acts as a guiding signal to other individuals, perhaps more particularly to the young. If we accept that as the explanation of the instinct to carry the tail upcurled, it seems to me that the wafting of the scent on the air probably serves the same end and may have been a factor almost or quite as important in fostering the behaviour in question.

It is the scent of these glands, it may be added, which gives hares and rabbits their peculiar odour somewhat resembling that of human perspiration.

The Anus and External Genitalia.—The Leporidæ and Ochotonidæ differ profoundly with respect to these organs, the Leporidæ being the more primitive of the two.

In this family the anal orifice surrounded by a narrow rim of naked skin is separated from the genital orifice by a definite but short and narrow perinæal area which is naked and studded with apparently glandular papillæ.

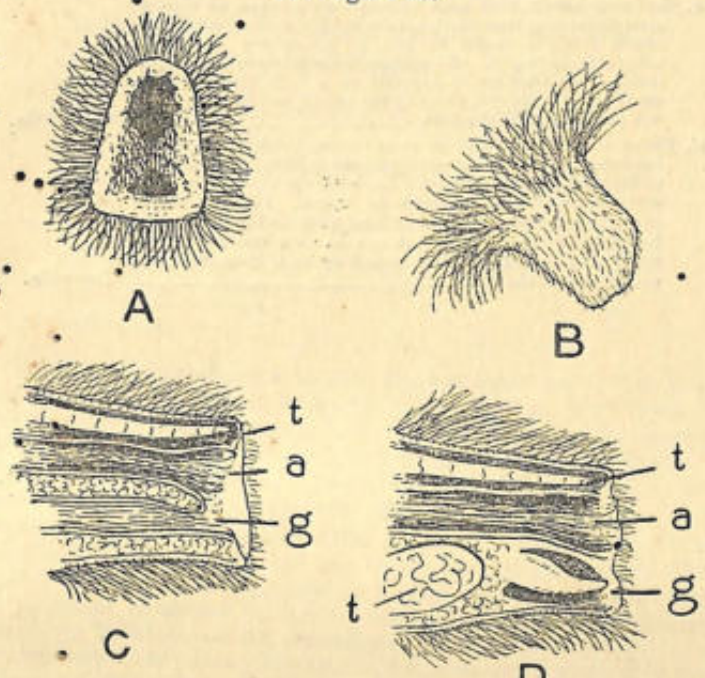
In the *female* the perinæum is quite short and the genital orifice below it opens in the middle of a naked papillate area continuous at the sides with the perinæum and of the same width as it. The orifice is narrow and is provided inferiorly or anteriorly with a linguiform clitoris. Below the genital area there is a swelling covered with long hair and recalling a scrotum in shape and position. (Text-fig. 28, B, p. 695.)

In the *male* the condition is very similar, except that the soft elastic perinæum is longer. The penis, which is comparatively short, evenly tapering to a point and simple in structure, is normally retracted and entirely concealed from view, the preputial orifice recalling the genital orifice of the female, so that the two sexes are not easy to distinguish upon superficial examination. Beneath and at the sides of the naked area upon which the penis opens there is a hairy scrotum-like swelling similar to that of the female. But there is no scrotum, the two testes being perceptible beneath the skin of the inguinal region, each being some distance from the middle line approximately in a transverse line with the preputial orifice.

The anus and external genitalia of the Mouse-hares (Ochotonidæ) differ from those of the Leporidæ in that the anal and genital orifices are enclosed by a common sphincter, so that superficially there appears to be a single aperture only at the end of the body; and this aperture is situated at the tip of a stout cylindrical hairy prominence projecting posteriorly, like a short truncated tail. This prominence is movable and is strengthened and supported in its upper part by a rod formed from the slender attenuated vertebræ of the abbreviated tail. (Text-fig. 30, A, B, p. 699.)

Within the sphincter lie the anus above and the genital or preputial orifice immediately beneath, the perinæum being reduced to a minimum. In the case of the male the orifice beneath the anus is the prepuce and within it lies a small short, simple, pointed penis, shaped very like that of the Leporidæ, and

Text-figure 30.



A. Posterior view of anal and genital area of female *Ochotona* from Thian Shan, the anus above and the vulva below, the two embraced by a common sphincter.
B. The tail-like anal and genital prominence of the same from the side with the hair cut short.
C. Longitudinal vertical section of the same.
D. The same of the male. *t.*, tail; *a.*, anus; *g.*, genital orifice, the latter in D containing the penis to the right and the testis to the left.

in front of the penis and of the base of the prominence are situated the testes. In the female the orifice beneath the anus is the vulva leading to the vagina which traverses the prominence beneath the rectum. (Text-fig. 30, C, D.)

The loss of all trace of the external tail and the substitution for it of the ano-genital prominence is a remarkable morphological feature in the Ochotonidæ.

Conclusion.

So far as the characters described in this paper are concerned the only organs which present constant differences between the Leporidæ and the Ochotonidæ are found in the ears and the region of the anus and external genitalia. They may be summarised as follows:—

a. Ears more sessile, with large valvular supratragus, no vertical crest descending from antitragus to auditory orifice; antitragus nearly at right angles to axis of pinna and overlapped anteriorly by tragus. No perinæal glands; anus and genital orifice close together at the end of a cylindrical tail-like prominence supported above by the caudal vertebræ which do not project beyond the anus ..... *Ochotonidæ.*

a'. Ears stalked, supratragus at most represented by a thin cartilaginous ridge, a crest descending from antitragus to auditory orifice; antitragus nearly in a line with the axis of the pinna and not overlapped in front by tragus. Perinæal glands present; perinæum moderately long, anus and genital orifice tolerably widely separated, not carried on a tail-like prominence, the caudal vertebræ projecting to a greater or less extent beyond the anus ..... *Leporidæ.*

30. The Comparative Anatomy of the Tongues of the Mammalia.—XII. Summary, Classification and Phylogeny.

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(Text-figures 31–45.)

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During the examination of the tongues described in the preceding papers of this series two main objects were kept in view. In the first place, attempts were made to discover characters which can be added to those which are employed in classification. The success which followed my efforts in this direction varied considerably, as is shown on pp. 729–733. In the second place, data were accumulated for phylogenetic purposes. Many hundreds of tongues were examined, and my own observations, coupled with those of other anatomists, gave me a good knowledge of the range of variation exhibited by the lingual structures in many species. Very few genera were not represented in my own material.

I attempted to give explanations of the meaning of the features which were observed, but I was unable to explain the significance of many conditions, for our knowledge of the comparative embryology of the tongue and mouth is very poor. So many of the features which I described must remain as recorded facts only till we know more about the development of the tongue.

A. Summary of Anatomical and Physiological Characters.

The tongue fills the mouth in all Mammals except some of the adult Odontoceti, Rodentia and *Ornithorhynchus*. In some Rodents it is excluded from the front of the mouth by inward prolongations of the hair-clad lips through the diastemata. In the young *Ornithorhynchus* the tongue reaches the end of the mandible to permit of suckling, but it lies far back in the adult because of the growth of the bill. In all Odontoceti in which I examined the parts *in situ* the tongue lay far back, but its tip overlaps the symphysis menti in the fœtus.

In many Mammals the tongue so fills the mouth that its dorsum bears the imprint of the palatal rugæ, and one must be careful not to mistake these marks for natural lingual structures. In all Anteaters except *Orycteropus* and *Manis* inwardly-projecting folds of mucous membrane derived from the gums and cheeks form a sheath for the long vermiform tongue.

Colour of the Tongue:—In several Primates and Ungulata the tongue is pigmented in whole or in part, and the colour may form a definite pattern on the dorsum or inferior surface. Sometimes the gustatory papillæ alone are pigmented. The colour varies, sometimes very considerably, in each species, so it is of no taxonomic value. In my paper on the Cebidæ (4), I figured several pigmentary patterns, and I pointed out that the colours vary in their resistance to the bleaching action of preserving fluids.

Sometimes the colour of the tongue is similar to that of the hairs and epidermis, the most striking illustration being the tongue of *Cercopithecus patas*. The pigment cells or granules lie in that part of the epithelium which corresponds to the stratum Malpighii of the epidermis. Sometimes the pigment cells are branched.

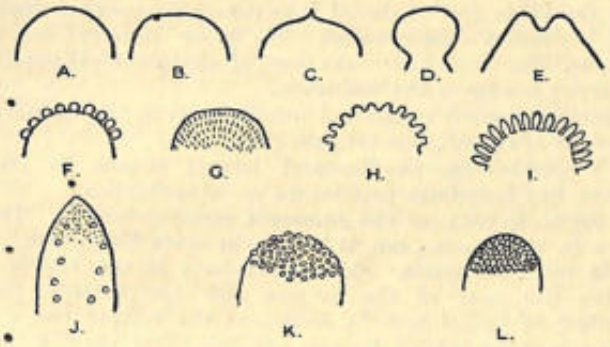
Shape of the Tongue:—The tongue is tapering, spatulate, rectangular or vermiform, the latter being the only adaptation for a particular kind of diet, namely living ants. It is thin in the Polyprotodont Marsupialia and in the Carnivora. And it is thick in the Bradypodidæ, Rodentia and Mystacoceti. In the other Orders the thickness is not unduly small or great. In the Felidæ the apex is very frequently gripped tightly by the incisor teeth after death.

Divisions of the Tongue:—The upper surface of the tongue is divided into oral and pharyngeal parts, the division between them being the circumvallate papillary area; and the lengths of these parts vary considerably. Thus the pharyngeal part or base is short in the Rodentia, Chiroptera and Hapalidæ, so that the circumvallate papillæ lie close to the epiglottis. The base is long in *Manis*, and there is a long tract of mucous membrane between the tongue and epiglottis in the Lion and Jaguar, an arrangement which is supposed to be associated with their roaring habits. In many Mammals the posterior part of the oral division is raised up to form an intermolar eminence.

When no circumvallate papillæ are present, as is the case in many of the Cetacea, it is impossible to distinguish the two parts of the tongue; so it is only by a study of development that one can observe them. In other Mammals the histological structure without any macroscopic examination will help us, because the base is glandular and the oral part is not. In many Cetacea (7) most of the tongue is very glandular, so histology does not help us at all, and will mislead us unless we know very accurately from what part of the tongue sections have been taken. Again,

the oral part of the tongue has conical and fungiform papillæ which are distinctive, but many Odontoceti do not possess these structures. Hence one can see that a study of development is frequently the only means of distinguishing between the two primary divisions in the Cetacea. There is no other Mammalian Order to which this condition applies, for all have characteristic papillæ on the oral part of the tongue.

Text-figure 31.



The apex of the tongue in various Mammals. A, *Homo* and *Simia*; B, Monkeys; C, *Physeter macrocephalus* (fœtus); D, Myrmecophagidæ and *Manis*; E, many Pinnipedia; F, *Tupaia minor*; G, Sirenia; H, many Odontoceti; I, some species of *Sus*; J, *Giraffa*; K, Cercopithecidæ; L, *Ornithorhynchus*.

The oral part in Man is developed from the first branchial arch, and the pharyngeal part or base springs from the second and third arches. It is probable that the same rule holds good in other Mammals. The relative proportions of these parts to one another vary greatly. The base is very short, thus bringing the circumvallate papillæ close to the epiglottis in the Rodentia, Chiroptera and Hapalidæ; the base is long in *Manis*; and there is a long stretch of mucous membrane between the tongue and epiglottis in the Lion and Jaguar, the large space at the back of the mouth being associated with the roaring habits of these animals. In many Mammals the posterior part of the oral division of the tongue is greatly thickened to form the intermolar eminence.

The *intermolar eminence* is present in *Ornithorhynchus*, *Hyrax*, and many Sirenia, Mystacoceti, Ungulata and Rodentia; and it is absent in all Marsupialia, Insectivora, Chiroptera, Edentata, Carnivora and Primates. Relatively to the size of the tongue it is largest in *Ornithorhynchus* and some Rodents. It is not a character of primary importance in classification. It is supposed to raise the food up to the level of the grinding teeth. In the

Mystacoceti it helps to expel the water containing the small Pteropods and other animals on which the Whales feed through the baleen plates. The eminence may be as wide as the tongue as in many Rodents and *Ornithorhynchus*, or it may be in the centre of the dorsum only.

The surface of the eminence is smooth, or covered with papillæ of different kinds; and it has markedly pointed structures in *Ornithorhynchus* and *Cavia cobaya*. In the former there are two strong, pointed horny structures called lingual teeth on the anterior border of the eminence; and these are supposed to direct insects and other food material into the cheek-pouches when the animal is feeding under water. No other Mammal has these structures. In *Cavia* there are rows of sharp conical papillæ on the anterior border of the eminence.

I described several individual peculiarities in the eminence in my account of the Murine tongues (10).

The circumvallate papillæ and lateral organs lie on the eminence, but fungiform papillæ are variable thereon.

The region in front of the eminence varies in length. Thus it is short in the Beaver, but it is long in some Ungulates. It is divisible into two parts. Most anteriorly is the tactile area including the apex of the tongue, and the posterior part is mechanical in function. In *Zaglossus* the tongue has a solid posterior part on which lie the circumvallate papillæ, lateral organs and dense spines, and a long, cylindrical, very mobile anterior part; and I believe that the posterior part corresponds to the intermolar elevation.

The *apex of the tongue* varies in shape, being rounded, truncated, pointed or globular (text-fig. 31). Sometimes it has a small notch, but it is deeply cleft in the Pinnipedia. In a fœtal *Physeter macrocephalus* it had a very pronounced median process, but I did not have the opportunity of examining an adult animal to see whether it is present or not. It certainly does not exist in any other Cetacean tongue examined by myself.

In human development the tuberculum impar, derived from the mandibular arches, becomes buried by two laminæ which fuse to form the oral part of the dorsum. Sometimes the laminæ do not unite anteriorly, so the apex of the tongue becomes cleft, resembling in a slight degree the condition which exists in Lizards and Snakes. This occasional occurrence in Man is the rule in all Pinnipedia. It must have some physiological significance, but it is not apparent to me.

The apex is bound down to the floor of the mouth in all Odontoceti, but it was free in a very young fœtus of *Physeter macrocephalus*. It has been suggested that the tongue is not very mobile in the Odontoceti because of the binding down to the floor of the mouth. Such a condition alone is not conclusive, for the tongue of the Elephant, which is mobile, has no free anterior part. When the Elephant masticates, a piece of the dorsum

becomes converted into an apex. The reason for the poor mobility in the Odontoceti lies in the condition of the muscles. In the Sirenia the mobility is slight, but I suggested (7) that the hard, retroverted apical papillæ enable it to exert its maximum mechanical action when the animals crop the vegetation on which they subsist.

The apex and the dorsum behind it may be destitute of obvious structures, but the following appearances are noteworthy:—

1. There is a marginal row of fungiform papillæ in *Metachirus opossum*, *Marmosa elegans*, *Tupaia minor* and *Cercopithecus tantalus*.

2. There is a thick cluster of fungiform papillæ in the Simiidæ, Cercopithecidæ, some Cebidæ, Lemuridæ and Ungulata. These papillæ have taste-buds and tactile nerve-endings.

3. There is a thick cluster of large conical papillæ in the Sirenia, Pinnipedia, Ungulata and *Ornithorhynchus*.

4. There are marginal lobules in *Galeopithecus* and some Cetacea. In *Tursiops tursio* there is a large blunt median lobule, corresponding perhaps to the long median process in the fœtal *Physeter macrocephalus* mentioned above.

5. There are long, pointed or club-shaped papillæ in some species of *Sus* and *Ursus*.

The apical part of the tongue is prehensile, tactile or gustatory in function, or it may perform two or all these functions, but the chief and most widespread use is no doubt touch. Nerve-endings of various kinds have been detected, and it is possible that certain types, which only occur in Man, are associated with speech. The tactile function probably reaches a high degree of perfection in the Anteaters, whose tongues are really glutinous, exploring and prehensile organs. But there are differences in the apex in various Anteaters. Thus the apex is pointed in *Zaglossus* and *Oryeteropus*, but it is globular in *Myrmecophaga*, *Tamandua* and *Manis*.

The prehensile function of the tongue for solids is great in the Monotrematous and Edentate Anteaters, the Giraffe and some Bats. Owen points out that the apical papillæ in the Bat *Monophyllus* are employed for probing night-blowing flowers for insects. All these animals have very mobile tongues, but the Rodentia, Odontoceti and Sirenia have the least protrusible tongues. It will be shown later that there is a relation between the prehensile function of the tongue and the characters of the lower incisor teeth. In Mammals which drink the tongue plays an important part in the process, and it is used either for lapping or for suction. In the Primates we find that the Lemuroidea, which have cleft upper lips adhering to the gum, drink by lapping, whereas the Anthropoidea, which have entire, non-adherent upper lips, drink by suction. The degree of mobility varies in each Order, and the differences may be very striking, as can be seen by comparing the tongue of *Ornithorhynchus* with those of *Zaglossus* and *Acanthoglossus*.

In *Dasypus peba* there are two pointed structures under the apex of the tongue. Muscle fibres pass to their bases, and Mayer suggested that they are useful for killing insects.

Sulci:—The dorsum of the tongue may have a median longitudinal sulcus on its anterior part, on its base or on both parts, but there is never a complete sulcus extending from the apex right back to the epiglottis. The circumvallate papillæ interrupt the sulcus in its complete form. When an intermolar eminence is present there is never a sulcus on it. These sulci may be regarded as traces of bilateral origin of both the oral and pharyngeal parts of the tongue. In the Lemuridæ and Simiidæ there is a Y-shaped group of circumvallate papillæ, and the vertical limb of the Y lies over the position of the median dorsal sulcus on the base of the tongue.

There is frequently a median ventral sulcus; indeed, it is more often present than the median dorsal sulcus. It receives the lingual attachment of the frenum linguæ in its posterior part. In *Cœlogenys paca* alone the median dorsal and median ventral sulci are continuous round the apex of the tongue.

Permanent transverse sulci radiate from the median dorsal sulcus in *Mustela erminea*; they indent the mucous membrane, so they cannot be mistaken for the shallow, wide grooves, which are formed by the palatal rugæ. Permanent transverse ventral sulci exist in *Cœlogenys paca* and *Galeopithecus volans*. In *Manis* and *Zaglossus* there is a deep groove or tunnel on the anterior part of the tongue, and the walls are formed by the upward folding of the sides of the dorsum; in the former the floor of the groove is smooth, but it has long spines in the latter. No trace of the tunnel exists in *Myrmecophaga*, *Tamandua* or *Orycteropus*. It may act as a trap for insects. The presence or absence of sulci is of little value in classification.

Median ventral ridges occur in many Mammals. In some cases they are undoubtedly artefacts produced by the action of preserving fluids. In other cases they are vestigial structures, being remnants of the lytta or sublingua.

The *lateral borders of the tongue* are thin or massive, and they lodge the foliate papillæ or lateral organs at their posterior extremities when these organs are present (see p. 714). They have conical and fungiform papillæ, and they have lobules anteriorly in *Galeopithecus* and some Cetacea. When the apex of the tongue is fixed the lateral borders may be quite mobile. Thus the apex is bound down to the mandibular symphysis in *Platanista gangetica*, but the edges are free and mobile. The animal is blind, and burrows in mud at the bottom of rivers for small fishes and crustacea, which constitute its diet. And the sensitive edges of the tongue may be organs of exploration. The lateral lobules in the adult Cetacea are not present in some fœtuses which have been described.

Lingual Papillæ:—The mucous membrane of the mouth and

tongue is in reality the modified skin of the stomodæum, so a comparison between the cutaneous and lingual papillæ is important. There is, moreover, as far as I can ascertain, no definite account of the difference to be found anywhere. In the general skin surface the papillæ are all buried beneath the surface of the smooth epidermis. Some papillæ have blood-vessels arranged in loops, and others have sensory end-organs, but papillæ with blood-vessels have no end-organs. Nerves pass into the epidermis, but none of these have a more complicated mode of termination than a small varicosity. The sudorific and sebaceous glands do not end in close association with the special end-organs. In some special tactile areas such as the skin of the bill of *Ornithorhynchus* and the snout of the Mole there are special end-organs near the surface. In the tongue, particularly on the base, a few papillæ are buried, but most stand up prominently on the surface of the mucous membrane. The corium centres have both vessels and nerves, but all the special sense-organs lie in the epithelium. The serous glands open alongside the gustatory organs, and are never found anywhere except in close relation to these structures. Their degree of development corresponds more or less to that of the gustatory papillæ, and there is a theory that the lateral organs were evolved from serous glands. No cutaneous papillæ carry out any mechanical function. These notes show that the adequate stimuli demand that the lingual papillæ should be elevated, and have their sense-organs near the surface; in the skin that is not necessary.

From the physiological point of view the papillæ fall into two great groups as follows:—

A. Mechanical papillæ.
B. Gustatory papillæ.
   a. Fungiform papillæ.
   b. Circumvallate papillæ.
   c. Lateral organs.

Of these the mechanical and fungiform papillæ occur in several classes of Vertebrates, but the circumvallate papillæ and lateral organs are only found in Mammals. It is interesting to note that the mechanical papillæ remain, whereas the gustatory papillæ are absent or strangely modified in the Cetacea in which the tongue has degenerated.

The papillæ may be described in any order, but I have begun here with the fungiform papillæ, as they represent early stages in the evolution of the circumvallate papillæ.

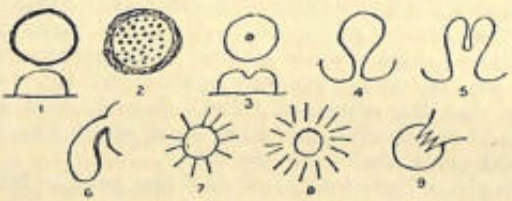
The Fungiform Papillæ (text-fig. 32).

The fungiform papillæ are bright in colour in the living tongue, but they are dead white in preserved ones; and the dead-white colour is of importance in enabling us to detect them when they

are very small, as they are in primitive Mammals. They vary in appearance, number and arrangement. They are hemispherical, globular or pedunculated bodies standing on the flat surface of the tongue, or contained within pockets in the mucous membrane. Those which lie in pockets near the junction of the oral and pharyngeal parts of the tongue are apt to be mistaken for circumvallate papillæ, and histological examination may be necessary to determine the true nature of a particular papilla. The surface is smooth, granular or umbilicated, the granules being formed by secondary papillæ.

The different forms are not characteristic of particular Orders. Thus the hemispheral form occurs in all Orders, and pedunculated forms are found in *Homo*, the Simiidæ, *Cercocebus*, *Nasua*, and the small group of Felidæ containing the Domestic, Wild and Caffre Cats, the Lynx and the Caracal. In that group of Felidæ pedunculated papillæ with taste-buds lie in the positions of the

Text-figure 32.



Types of fungiform papillæ. 1, hemispherical on plan and section; 2, granulation by secondary papillæ; 3, umbilicated papilla; 4, clavate type; 5, umbilicated clavate type; 6, depending papilla; 7–9, relations to conical papillæ.

lateral organs, and I suggested the name of papillæ clavatæ for them (8). Their value in classification is described on pages 729–733. It may be difficult or impossible to detect papillæ macroscopically, either because they are very minute, or they are concealed by overhanging conical papillæ. I could not detect them even with a powerful lens in *Galeopithecus*, some Canidæ and the Monotremata. In the Arctic Fox there are individual variations, some specimens having minute, but visible, papillæ, whereas others have none visible macroscopically. The converse condition is observable in some Rodents, the small fungiform papillæ being thrown into prominence by the small size of the conical papillæ around.

Papillæ are present on the oral part of the dorsum, the lateral borders and a greater or less extent of the periphery of the inferior surface. As none are found behind the circumvallate papillæ, they are limited to the part of the tongue which is formed from the first pair of branchial arches.

On the oral part of the dorsum the papillæ may cover the entire surface from before backwards and from side to side, but in many specimens they are absent from the central part. They may or may not exist on the intermolar eminence. The extent of the surface containing them varies with age in Man. Thus the infant has them all over the dorsum, but the adult has not. These observations on the age-changes in Man have not been supplemented by observations on other Mammals. In lower Orders the papillæ may cover the dorsum.

The central area of the dorsum which is free from fungiform papillæ may extend back into the area of the circumvallate papillæ; or it may be shut off by a posterior cluster or rows of papillæ. And the presence or absence of these groups is of value in classification.

The papillæ on and behind the apex may be sparse, or they may be irregularly grouped in a cluster of variable size. In the lower Orders the cluster is very small or absent, but in higher Orders it is small or large. Moreover, in some of the higher Orders the more primitive animals have smaller clusters than the specialized ones. These statements are illustrated in the subjoined table. On the dorsum behind the apex the papillæ are arranged in rows of varying degrees of obliquity; and they increase in size, and perhaps in number, as we proceed from the lower Orders to the higher. On the lateral borders of the tongue they are numerous or scanty, and are disposed in one or more rows.

On the bounding zone on the inferior surface of the tongue the fungiform papillæ may be scanty or numerous. They may be irregularly disposed, or they may be arranged in one or two rows. Of these rows both may have papillæ of equal size, as in the Gorilla, or the inner row may contain larger elements than the outer one. There may be a thick cluster of papillæ beneath the apex of the tongue, and this group is largest in the higher Primates.

When the papillæ in the various Orders are compared, one sees that they vary in numbers, in size, and in concentration on various parts of the tongue. Of special interest is the size of the apical cluster. The arrangements are shown in the following table, which deals with all Orders except the Chiroptera, of which too few specimens were available to enable me to draw any conclusions of value.

From a study of the subjoined table the following conclusions can be drawn:—

1. In the lower Orders the papillæ are relatively fewer and smaller than those in the higher ones.

2. As we proceed from the lower Orders to the higher ones we notice a concentration of papillæ at the apex of the tongue. The apical cluster is largest in the Cervidæ and Catarrhine Primates.

3. In some Orders the fungiform papillæ have vanished, but the tongue has otherwise undergone specialization. In *Ornitho-*

Order.	*Apical* cluster.*	*Lateral dorsal papillæ.*	*Remarks.*
Monotremata	absent.	absent.	
Marsupialia.			
a. Didelphyidæ	"	few.	Papillæ all minute.
b. Dasyuridæ	"	numerous.	Papillæ larger than in *a*.
c. Perameliдæ	slight.	"	Papillæ larger than in *a* and *b*.
d. Phalangeridæ	absent.	"	Papillæ all very small.
e. Phascolarctidæ	"	"	" " "
f. Macropodidæ	"	"	" " "
Edentata.			
a. Dasypodidæ	"	a few.	
b. Bradypodidæ	moderate.	"	Papillæ larger than in *a*.
c. Myrmecophagidæ	absent.	absent.	
d. Manidæ	"	"	
e. Orycteropodidæ	"	a few.	Papillæ larger and more than in *a*.
Insectivora	"	"	Papillæ very small.
Dermoptera	"	absent.	
Rodentia	small or absent.	variable.	Papillæ always small.
Carnivora.			
a. Felidæ	small or moderate.	"	Papillæ small or of medium size.
b. Viverridæ	small when present.	"	" " " " "
c. Protelidæ	not large.	"	Size moderate.
d. Hyænidæ	" "	a few.	
e. Canidæ	small or absent.	"	Papillæ usually very small.
f. Mustelidæ	small.	numerous.	" " " "
g. Procyonidæ	good.	"	Papillæ small.
h. Ursidæ	"	variable.	Size moderate.
Cetacea	absent.	small or absent.	Papillæ always small when present.
Ungulata.			
a. Perissodactyla	small.	numerous.	Size moderate.
b. Suina	"	"	" "
c. Tylopoda	"	not numerous.	" "
d. Cervidæ	large.	" "	Papillæ large.
e. Bovidæ	absent.	numerous.	" "
f. Tragulidæ	small.	"	Size moderate.
Sirenia	absent.	very few.	Papillæ very small.
Primates.			
a. Tarsiidæ	minute.	scanty.	Papillæ of moderate size or large.
b. Chiromyidæ	"	"	" " " "
c. Lorisidæ	"	variable.	" " " "
d. Galagidæ	"	"	" " " "
e. Lemuridæ	moderate.	numerous.	" " " "
f. Hapalidæ	"	scanty.	" " " "
g. Cebidæ	"	numerous.	" " " "
h. Cercopithecidæ	large.	"	" " " "
i. Simiidæ	"	"	" " " "
j. Hominidæ	"	"	" " " "

* Small and slight mean that an occasional papilla occurs here and there.

rhynchus the conical papillæ have become highly developed; in the Monotrematous and Edentate Anteaters, except *Orycteropus*, the tongue is mainly a prehensile, exploring organ and the fungiform papillæ have vanished; in the Cetacea the reduction in or complete loss of the papillæ is part of a degenerative process, which has involved the lingual structures.

When the papillæ are examined histologically it is seen how many have secondary papillæ composed of epithelium alone, or of epithelium and corium. Taste-buds are present in animals belonging to most of the Mammalian Orders, and the nerves may be large and provided with ganglia. The taste-buds have fewer gustatory cells than the buds in the circumvallate papillæ, and are nearer the surface. No glands are connected to the fungiform papillæ. In lower Vertebrata the epithelium may consist of a single layer of columnar cells, or it may be stratified as in the Mammalia. In Oppel's 'Text-book of Microscopic Anatomy' many buds and papillæ have been figured.

The Circumvallate Papillæ (text-fig. 33).

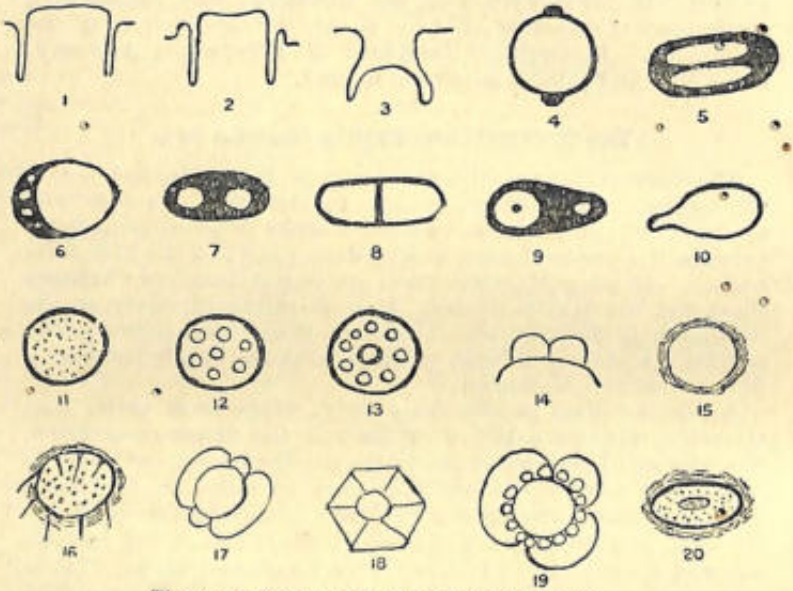
The circumvallate papillæ occur only in Mammals, but not in all species. They differ greatly in structure, number and arrangement; and there is a complete series of transitional forms between the various forms, and between them and the fungiform papillæ. In many Mammals there are transitional forms between them and the lateral organs. It is therefore necessary in the first place to describe the characters of a typical circumvallate papilla. And the papilla in question must not be selected from a Monotreme or a Marsupial.

A circumvallate papilla has a body, whose form varies considerably, lying in a hollow or fossa in the mucous membrane. The mucosa of the tongue covers the papillary body and lines the fossa. The outer wall of the fossa may be raised up to form a ridge or vallum. Serous glands always open into the depths of the fossa, and the presence of these glands is one of the features which distinguishes the papilla from a fungiform papilla. Taste-buds lie in the epithelium of both sides of the fossa, whereas they are never in the angle between the body and the tongue surface in the fungiform papillæ. It is sometimes stated that taste-buds are on the upper surface of the fungiform papillæ, but are not there in the circumvallate papillæ. That is, however, not true, for authors have described or figured them on the upper surface of the circumvallate papillæ in *Ornithorhynchus*, *Capra*, *Mus*, *Ovis*, *Talpa*, *Meles*, *Felis*, *Canis*, *Mustela* and in the new-born child. These buds are more numerous at birth than in adult life, so their diminution is one of the age-changes which occur in the tongue. The dermis component of the papillæ contains connective-tissue, blood-vessels and nerves, and the nerves may be plexiform or provided with large ganglia.

The vallate papillæ mark the boundary between the part of the tongue developed from the first arch and that arising from the second and third arches. In the higher Primates the bilateral origin of the latter may be indicated by the vertical stem of the Y-shaped group of papillæ.

The papillæ may stand up higher than, be flush with, or be recessed below the surrounding dorsum of the tongue, but the protruding form is commonest. When it is recessed, as in the Monotremata, the object attained is protection. It must, however, be noted that preserving fluids may make the papillæ contract into a smaller volume and shrink down into the vallum.

Text-figure 33.



The macroscopic characters of circumvallate papillæ.

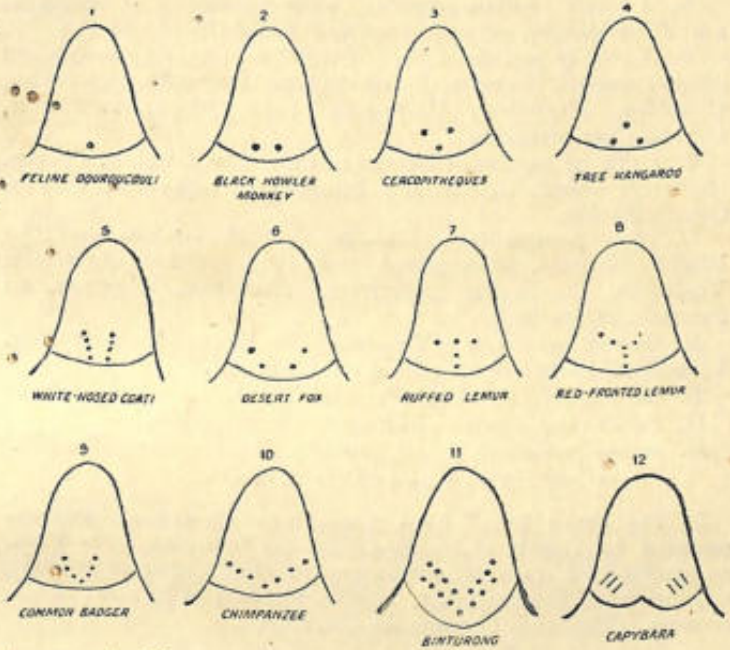
The papillary body may be hemispherical, as in *Ornithorhynchus*, globular as in *Vespertilio*, *Meles*, and *Macacus*, cylindrical or conical. In conical types the apex or base may be attached to the tongue. The fossa is shaped according to the form of the body, as it undermines the papillary body when the latter is conical with the apex attached. These forms are shown in text-fig. 33. It will be shown later that a series of phylogenetic stages includes several of these forms.

The fossa usually appears as a slit around the papillary body, but it is sometimes very patulous in tongues removed immediately after the death of the animal. And this would seem to show that variations in the fossa may accompany the act of mastication.

In *Macacus rhesus* and *M. fascicularis* the fossæ have patulous recesses at the anterior and posterior papillary poles, but these close up when the tongue is immersed in preserving fluids.

Each fossa may contain more than one papilla, and these papillæ may be completely separate, or they may be lobes of one large papilla. The two may be of the same dimensions, or the sizes may differ. These must not be regarded, however, as stages in the extra-uterine division of a papilla, for such a phenomenon

Text-figure 34.



Arrangements of the vallate papillæ. On p. 739, which deals with phylogeny, these are grouped as follows—3 = A; 2 = B; 1 = C; 9 = D; 5 = E; 1 = F; 7 = G.

does not take place. They represent the end of some process which took place in development. Probably one of the divisions is a greatly enlarged secondary papilla, and it is analogous to the long pointed summit of the papilla in *Dasyurus*.

The surface of the papillary body is smooth, polished and glistening, or it is granulated by secondary papillæ. In many Marsupials it is drawn out into a long point. Sometimes the centre is umbilicated. Secondary papillæ are very well marked on the sunken papillæ in *Manis*.

The vallum may not be raised, but when it is it is smooth and entire, or divided up into one or more concentric circles of lobules, which are circular, oval, reniform or quadrangular.

The greatest numbers of papillæ are found in the Giraffe, which has 50, and in *Antilope americana*, which has 52. On the contrary *Hyrax* and some Cetacea and Pinnipedia have none at all.

The papillæ are slit-like in *Moschus*, the Caviidæ and some Cetacea; and they are sac-like in the Sirenia and some Cetacea. The other arrangements are:—

A. *A single median papilla*:—some specimens of *Macropus* and *Phascolarctos*, some specimens of *Aotus*, the Muridæ.

B. *A pair of papillæ*:—New World Edentata, Lagomorph and Hystricomorph Rodents, Perissodactyla, Tragulidæ, Ailuroidea, Cynoidea, Mustelidæ, Chiroptera entomophaga, Lemuridæ, Cebidæ, Cercopithecidæ.

C. *Pairs of papillæ in chevron*:—Camelidæ, Cervidæ, Bovidæ, Carnivora except Ursidæ and Pinnipedia, Lemuridæ, Cebidæ, Cercopithecidæ.

D. *Three papillæ in a triangle*:—all Marsupialia and Old World Edentata, Sciuromorph Rodents, Dipodidæ, Spalacidæ, Viverridæ, Pinnipedia, Insectivora, *Chiroptera frugivora*, all Primates except Man.

E. *Several papillæ in a* V:—Tapiridæ, Pinnipedia, Arctoidea, Viverridæ, Anthropoidea except the Hapalidæ.

F. *Papillæ in line*:—Tapiridæ, *Tarsius*.

G. *Papillæ in clusters*:—Rhinocerotidæ, Giraffidæ.

H. *Several papillæ in* T:—Lemuridæ, Cebidæ, Cercopithecidæ.

I. *Several papillæ in* Y:—Lemuridæ, Simiidæ.

In the above list I have taken into account all patterns recorded by myself and others. In the following table PO= no papillæ; PI, a single median papilla; PP, a pair of papillæ; CH, pairs in chevron; LI, papillæ in line; PS, slits; PCL, clusters. The lateral organs are also shown.

	Y.	T.	V.	Δ.	CH.	PP.	LI.	PS.	PCL.	PI.	PO.	*Lateral organs.*
Order MONOTREMATA	–	–	–	–	–	+	–	–	–	–	–	+
Order MARSUPIALIA	–											
Didelphyidæ	–	–	–	+	–	–	–	–	–	–	–	–
Dasyuridæ	–	–	+	+	–	–	–	–	–	–	–	–
Peramelidæ	–	–	–	+	–	–	–	–	–	–	–	–
Phalangeridæ	–	–	–	+	–	–	–	–	–	–	–	+
Macropodidæ	–	–	–	+	–	–	–	–	–	+	–	+
Phascolarctidæ	–	–	–	+	–	–	–	–	–	+	–	+
Order EDENTATA.												
Dasypodidæ	–	–	–	–	–	+	–	–	–	–	–	variable.
Bradypodidæ	–	–	–	–	–	+	–	–	–	–	–	–
Myrmecophagidæ	–	–	–	–	–	+	–	–	–	–	–	variable.
Manidæ	–	–	–	+	–	–	–	–	–	–	–	
Orycteropodidæ	–	–	–	+	–	–	–	–	–	–	–	variable.

	Y.	T.	V.	Δ.	CH.	PP.	LI.	PS.	PCL.	PI.	PO.	*Lateral organs.*
Order INSECTIVORA.												
Erinaceidæ	−	−	−	+	−	+	−	−	−	−	−	+
Centetidæ	−	−	−	+	−	−	−	−	−	−	−	+
Solenodontidæ	−	−	−	+	−	−	−	−	−	−	−	−
Potamogalidæ	−	−	−	+	−	−	−	−	−	−	−	−
Chrysochloridæ	−	−	−	+	−	−	−	−	−	−	−	−
Soricidæ	−	−	−	+	−	+	−	−	−	−	−	−
Talpidæ	−	−	−	−	−	+	−	−	−	−	−	−
Tupaiidæ	−	−	−	+	−	−	−	−	−	−	−	−
Order DERMOPTERA	−	−	−	−	−	+	−	−	−	−	−	+
Order RODENTIA.												
Sciuridæ	−	−	−	+	−	−	−	−	−	−	−	+
Castoridæ	−	−	−	+	−	−	−	−	−	−	−	+
Myoxidæ	−	−	−	+	−	−	−	−	−	−	−	+
Muridæ	−	−	−	+	−	−	−	−	−	+	−	variable.
Spalacidæ	−	−	−	+	−	−	−	−	−	−	−	+
Dipodidæ	−	−	−	+	−	−	−	−	−	−	−	−
Octodontidæ	−	−	−	−	−	+	−	−	−	−	−	+
Hystricidæ	−	−	−	−	−	+	−	−	−	−	−	variable.
Chinchillidæ	−	−	−	−	−	+	−	−	−	−	−	−
Dasyproctidæ	−	−	−	−	−	+	−	−	−	−	−	+
Caviidæ	−	−	−	−	−	−	−	+	−	−	−	+
Leporidæ	−	−	−	−	−	+	−	−	−	−	−	+
Order CARNIVORA.												
Felidæ	−	−	−	−	+	+	−	−	−	−	−	variable.
Viverridæ	−	−	+	+	+	+	−	−	−	−	−	variable.
Hyænidæ	−	−	−	−	+	+	−	−	−	−	−	+
Protelidæ	−	−	−	−	+	+	−	−	−	−	−	+
Canidæ	−	−	−	−	+	+	−	−	−	−	−	variable.
Mustelidæ	−	−	+	−	+	+	−	−	−	−	−	variable.
Procyonidæ	−	−	+	−	+	−	−	−	−	−	−	variable.
Ursidæ	−	−	+	−	−	−	−	−	−	−	−	variable.
Pinnipedia	−	−	+	+	−	−	−	−	−	−	+	variable.
Order CETACEA	−	−	+	−	−	−	+	+	−	−	+	−
Order UNGULATA.												
Equidæ	−	−	−	−	−	+	−	−	−	−	−	−
Tapiridæ	−	−	+	−	−	−	+	−	−	−	−	variable.
Rhinocerotidæ	−	−	−	−	−	−	−	−	+	−	−	−
Suidæ	−	−	−	−	−	+	−	−	−	−	−	variable.
Phacochœridæ	−	−	−	−	−	+	−	−	−	−	−	+
Tragulidæ	−	−	−	−	−	+	−	−	−	−	−	+
Camelidæ	−	−	−	−	+	−	−	−	−	−	−	−
Bovidæ	−	−	−	−	+	−	−	+	−	−	−	−
Giraffidæ	−	−	−	−	−	−	−	−	+	−	−	+
Order PROBOSCIDEA	−	−	−	−	+	−	−	−	−	−	−	+
Order HYRACOIDEA	−	−	−	−	−	−	−	−	−	−	+	+
Order SIRENIA	−	−	−	−	−	−	−	+	−	−	−	variable.
Order PRIMATES.												
Lemuridæ	+	+	−	+	+	−	−	−	−	−	−	+
Lorisidæ	−	−	−	+	−	−	−	−	−	−	−	−
Galagidæ	−	−	−	+	−	+	−	−	−	−	−	−
Chiromyidæ	−	−	−	+	−	+	−	−	−	−	−	−
Tarsiidæ	−	−	−	+	−	−	+	−	−	−	−	−
Cebidæ	−	−	+	+	+	+	−	−	−	+	−	+
Hapalidæ	−	−	−	+	+	−	−	−	−	−	−	+
Cercopithecidæ	−	+	+	+	+	+	−	−	−	−	−	+
Hylobatidæ	+	+	−	+	−	−	−	−	−	−	−	+
Simiidæ	+	+	+	+	−	−	−	−	−	−	−	+
Hominidæ	−	−	+	−	−	−	−	−	−	−	−	+

The following table contains observations of Tuckerman and myself relative to the number of taste-buds in the vallate papillæ and lateral organs :—

	Number of vallate papillæ.	*Number of buds in the papillæ.*	*Number of buds in the lateral organs.*
Perameles nasuta	3	2,160	no organs.
Didelphys virginiana ...	3	2,900	" "
Phascolomys wombat	3	3,500	
Phascolarctos cinereus ...	3	4,200	
Dasypus peba	2	2,400	organs variable.
Dasypus villosus	2	2,500	" "
Fiber zibethicus	1	520	800
Lepus cuniculus	2	2,400	14,500
Lepus campestris	2	1,200	16,800
Cynomys ludovicianus ...	2	1,100	
Tamias striatus	3	750	
Vespertilio subulatus.....	2	800	
Pteropus pselaphon	3	3,500	
Sus scrofa	2	10,760	4,800
Ovis aries.....	24	9,600	organs absent.
Calf	24	35,200	" "
Capra hircus	12	15,400	" "
Antilocapra americana ...	52	48,000	" "
Felis domestica	6	600	
Canis vulpes.....	4	9,500	
Canis familiaris.....	4–7	8,000	
Canis lupus	2	2,900	
Canis latrans	7	5,000	
Mephitis mephitica	2	4,000	
Putorius vison.....	4–5	2,000	
Lutra canadensis	7–8	2,400	
Macacus cynomolgus	4	4,000	
Macacus rhesus	3	1,800	
Homo sapiens	9	6,000	3,000

A series of observations was made to determine whether the members of an Order, which are primitive or specialized in other features of bodily structure have differences in the patterns of the vallate papillæ, and the following table contains the results of the investigation. The examples selected were those chosen by Pocock in his studies of the relations of the various tactile arrangements in the Mammalia. I have omitted the Cheiroptera, for the material at my disposal was scanty, and I have left out the Cetacea, in which the papillæ have been lost as the result of degenerative processes.

Order.	A. *Primitive species.*	B. *Specialized species.*	*Remarks.*
Marsupialia	*Trichosurus.*	*Dendrolagus.*	Patterns identical in A & B.
Edentata	*Dasypus.*	*Tamandua.*	" " "
	"	*Bradypus.*	" " "
Insectivora	*Centetes.*	*Sorex.*	B has more patterns than A.
Rodentia	*Atherura.*	*Erethizon.*	Patterns identical in A & B.
Carnivora	Viverridæ.	Felidæ.	A has more patterns than B.
	Ptocyonidæ.	Ursidæ.	" " "
	Canidæ.	"	" " "
Ungulata	*Tajassu.*	*Hippopotamus.*	Both have one pattern.
	Tragulus.	Pecora.	" " " "
	Tapiridæ.	Equidæ.	A has more patterns than B.
	"	*Rhinoceros.*	" " "
Primates	*Tarsius.*	Lemuridæ.	A has fewer patterns than B.

In the above selected forms of Marsupials, Edentates and Rodents the number of papillæ is identical in each Order. But in the Ungulata the single pattern and the number of papillæ in each varies.

There are transitional types between the fungiform and circumvallate papillæ.

The conclusions regarding the circumvallate papillæ are given on page 718.

The Lateral Organs (1, text-fig. 16).

Like the circumvallate papillæ these gustatory organs are found only in Mammals, but not in all species. They vary in appearance and development. They are found at the posterior extremities of the lateral borders of the tongue or on the sides of the intermolar eminence. Sometimes they are replaced by rows of club-shaped fungiform papillæ containing taste-buds.

In the table on page 714 it is seen how lateral organs are absent in all Polyprotodont Marsupials, the vast majority of Lipotyphlous Insectivora, some Rodents and Ungulates, the Cetacea, the Tarsioidea and the Lorisiform Lemuroidea. They show individual variations in most of the animals formerly grouped in the Edentata, the Carnivora and some of the Ungulata. They are invariably present, though differing in type in the Monotremata, Diprotodont Marsupials, most Rodents, Hyracoidea, Proboscidea, Lemuriform Lemuroidea and Anthropoidea.

In some Marsupials (e. g. *Halmaturus* and *Macropus*) there appears on each side of the tongue at the posterior extremity of each lateral border a row or rows of small orifices like the mouths of the ducts of glands, and the row may be straight or curved.

Some of these orifices are glandular, but others represent the lateral organs. The organs are arched over by a fringe of long filiform papillæ. When sections are made through the tongue it is seen how each duct receives ductules and has taste-buds in its wall. Poulton points out that horizonial sections show that the narrow ducts, which open into the circular depressions on the surface of the tongue, are really slit-like. The taste-buds are in tiers, and nerves approach them from the sides; and the nerves have small ganglion cells. The secreting alveoli are of the serous type. The gland-ducts which receive the secretions of alveoli of the mucous type have no taste-buds. In *Macropus* the organs are more like depressions than gland-ducts. In *Trichosurus vulpecula* the organ is a row of slits, but none of the tongue in or around the organ is elevated. Taste-buds are on each side of the slits, and serous glands open into the bases. The slits are not absolutely regular as in higher Mammals The Marsupial forms are shown in P. Z. S. 1921, p. 556, text-fig. 58.

In the higher Mammals the organs may be identical, or one may be larger than the other. They consist of fissures separating laminæ of varying degrees of prominence. In a former paper (1) I called these sulci primary fissures for they separate laminæ, and I named fissures partially cleaving the laminæ secondary fissures. The primary fissures are disposed in a straight line or in an arc. The laminæ may be long and narrow, or they may be small oval bodies. Finally the whole organ may be raised up to form a body of an oval, crescentic or wedge shape. These forms occur as follows:—

A. Laminæ not elevated—*Colugenys, Simia, Gorilla.*
B. Laminæ elevated—most Mammals.
C. Lateral organs elevated in toto—*Lemur, Lepus.*

The form of the organs is of value for purposes of classification, as is shown in section 2 of this paper.

The slits may have no diverticula from them, or there may be several recesses, which, as they are lined by bulb-containing epithelium, extend the surface available for the performance of the gustatory function. These are very well marked in the Racoon.

In all adult animals the taste-buds lie down in the laminæ bounding the sulci. In the new-born child they also occur on the summits of the laminæ (11, and text-fig. 36), but they diminish as age advances. So we have here another example of the degenerative changes which occur with advancing years in the human tongue. It probably occurs in other Mammals as well.

In the Caviidæ the vallate papillæ and lateral organs resemble one another macroscopically.

The following conclusions can be drawn from a study of the circumvallate papillæ and lateral organs:—

1. The commonest pattern is three vallate papillæ in a triangle with the apex directed backwards. These have been termed the

central or apical papilla and the basal or lateral papillæ. This type is present in members of all Orders except the Monotremata and Ungulata, and it is the primitive type. Next in frequency is a pair of papillæ, the central papilla being absent. The type in which the central papilla alone is present is not very widely distributed, for it only occurs in the Muridæ and in some examples of *Macropus*, *Phascolarctos* and *Aotus*. The remaining types of most frequent occurrence are the V and several pairs of papillæ in a chevron. These can be derived from the triangle by filling in of the side limbs by papillæ, thus giving the V-type, and by loss of the apical papillæ of the V, thus forming the chevron.

2. In the lower Orders the number of patterns is small, whereas it is large in the higher ones, as can be seen by comparing the Monotremata, Marsupialia, Insectivora and Edentata with the Carnivora, Ungulata and Primates. Not only so, but the species in the lower Orders have a smaller range of individual variation than those in the higher ones.

3. When a group of animals has one fixed papillary pattern, the number of papillæ may vary in individuals.

4. It is impossible to correlate the papillary pattern with the type of food, as can be seen from the following examples:—

a. Man consumes a more varied diet than any other Mammal, and he never has any other pattern than a V; the only variations which he exhibits is the number of papillæ in the V.

b. Animals which consume one kind of diet may have several patterns.

c. The same pattern exists in frugivorous, phyllophagous, carnivorous or insectivorous animals. And that type is usually the primitive triangle.

5. There is no fixed relation between the papillary pattern and the degree of specialization of the species in each Order. Thus a primitive species may have more patterns than a specialized one, or *vice versa*; or the type may be the same in all species. In the Marsupialia, Edentata and Rodentia the primitive species have the same patterns as the specialized ones; in the Carnivora there is no fixed rule; in the Insectivora and Primates the primitive species have fewer patterns than the more advanced forms; and in the Ungulata the variations affect only the number of papillæ.

6. In the Marsupialia the pattern is constant, but the papillæ themselves show grades of specialization. Some papillæ are of the low Marsupial type, but others approximate to those in the higher Mammalia.

7. The Y and T types occur only in the Lemuridæ and Simiidæ.

8. The number of taste-buds in the vallate papillæ and lateral organs have been counted in many animals, but no generalizations can be made from the figures given.

9. There is no relation between the number of vallate papillæ and the presence or absence of lateral organs. Many species have

both structures, some have vallate papillæ and no organs, and *Hyrax* has organs and no papillæ. Nor can one associate the presence or absence of organs with particular kinds of diet.

10. The taste-buds in the human lateral organs diminish as age advances.

11. From the above it will be seen that there is no relation between the arrangement, presence or absence of, the main gustatory organs (vallate papillæ and lateral organs) and diet, but there are varying degrees of persistence of primitive features.

12. There are probably, though we do not know them, differences in the physiological conditions of the taste-buds in animals consuming different kinds of diet.

The Conical Papillæ.

These papillæ are present in members of all Vertebrate Classes, and they are the most numerous of all lingual papillæ in the Mammalia. From the physiological point of view they are tactile or mechanical, but never gustatory in function. They vary in size, character, and arrangement. They occur on the oral part of the dorsum in all Mammals except the Cetacea, which have none. Sometimes they occur on the base of the tongue and on a bounding zone of the inferior surface.

Arrangement:—In most Mammals the papillæ are aggregated in a cluster of variable size on and behind the apex of the tongue; they are disposed in transverse rows on the middle of the dorsum; and they are in oblique chains posteriorly. They are thus disposed in a manner very similar to that exhibited by the fungiform papillæ, but they are also present on the centre. In *Pteropus* they are all in transverse rows, in *Mustela erminea* all the rows are oblique, and in *Cercopithecus æthiops* there are no regular rows. In the Primates, Sirenia and many Ungulata the apical cluster is large. On the base of the tongue there may be no definite arrangement or the papillæ may be in oblique chains.

Size:—There are various groupings according to size, and these are of value in classification. This matter is more fully considered in section 2 of this paper, so only a list of the types is given here:—

1. There is a steady increase in size from the apex of the tongue to the base and from the edges to the middle line. This is the commonest form.

2. The papillæ are small all over.

3. The papillæ on the oral part of the dorsum are small and those on the base are large.

4. The papillæ on the oral part are large, but those on the base are small or absent.

5. There are no papillæ.

6. The largest papillæ form a central patch on the oral part of the dorsum or on the apex of the tongue.

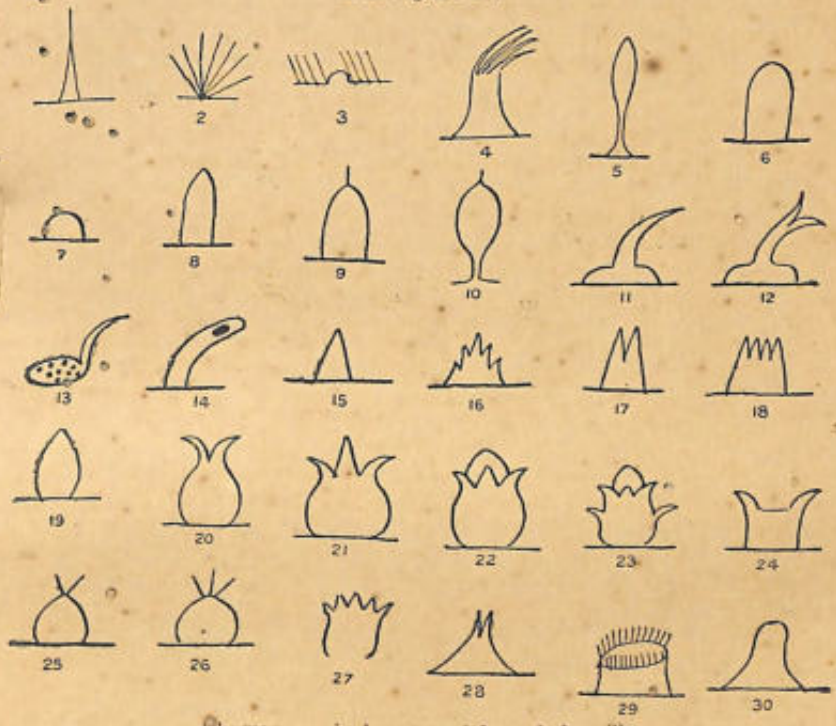
7. There is a gradual decrease from before backwards.

8. Papillæ may be present or absent on an intermolar eminence.

The grouping of papillæ on the sides and inferior surface of the tongue has no taxonomic value.

Cornification:—The conical papillæ are cornified to a variable extent, and confer a rough feeling on the dorsum. One side alone may be strongly cornified, or the whole papilla may be surrounded

Text-figure 35.



The macroscopic characters of the conical papillæ.

by a horny sheath, and the sheet is frequently thickest on its posterior aspect (e.g. *Ornithorhynchus*, *Canis*, *Erinaceus*). In *Eringeus* there is also a horny septum passing down into the epithelium from the back of the papilla, and a smaller one descends from in front. Oppel reproduces Carlier's illustration showing the relation of the keratin sheath to the eleidin-containing cells in the deeper part of the epithelium. I have been unable to discover an account of the transformation of the eleidin into the keratin in the tongue.

Form of the Papillæ:—Numerous kinds of papillæ exist, but no form is characteristic of any Order, and transitional forms occur. Each group has simple and compound types, the latter possessing secondary papillæ.

Group. I. Filiform Papillæ.

Division A. Simple Papillæ (text-fig. 35):—

a. *Hair-like papillæ* (1). They taper from base to apex. A number may radiate from a single fixed point on the dorsum (2). They occur in several Orders. They help to distinguish *Halmaturus*, *Macropus*, *Petrogale* and *Dasyurus* from other Marsupials.

b. *Papillæ spinosæ* (11–13) in which horny spines project from an elevated base. Seen in *Didelphys* and Ailuroid Carnivora.

Division B. Compound Papillæ.

The stout papillary body is surmounted by a bunch of hair-like papillæ (fasciculate type) (4) or by a ring of hairs—the *coronate form* (29).

Group II. Cylindrical and Fusiform Papillæ.

Body cylindrical or fusiform and may have no secondary papillæ—simple type (5–8), or an apical hair may be present—the compound type (9, 10).

Group III. Globular Papillæ.

Only compound forms exist (20–23).

Group IV. Triangular Papillæ (15–18).

Simple forms have no secondary papillæ, but compound types have these papillæ or a divided apex.

In most Mammals the points of the papillæ are directed backwards, or backwards and inwards. But in many Ruminants there is an area on the back of the tongue in which the papillæ point in all directions.

The relations between the epithelium and the connective-tissue core of the papillæ vary in complexity. They are considered fully in section 3 of this paper.

When we consider the papillæ in the various Orders some interesting conclusions can be made. Thus:—

1. The lower Orders have simpler papillæ and a smaller range of types than the higher ones.

2. The increase in the complexity follows the same rules as the vallate and fungiform papillæ.

3. In some of the higher Orders the primitive species have simpler papillæ and a smaller range of types than the higher ones. This can be demonstrated as follows in the Primates:—

1. Lorises and Galagos have a less complex arrangement than the Lemuridæ.
2. The Platyrrhini are less complex than the Catarrhini.
3. The Lemuroidea are less complex than the Anthropoidea.

On the inferior surface of the tongue the following structures demand consideration :—

1. Bounding papillary zone.
2. Frenal lamella.
3. Sublingua.
4. Plicæ fimbriatæ.
5. Isingual combs.

The *bounding papillary zone* is best marked in the Primates. It varies in extent and in its degree of development beneath the apex of the tongue. It has conical papillæ in every case, but fungiform papillæ may be absent. The arrangement of the fungiform papillæ, when these are present, has been described above (see p. 709). Sometimes the zone is pigmented.

The *frenal lamella* is present in all Primates except Man and some specimens of Orang. And it is absent in all other Mammalia. It is a triangular or complicated fold of mucous membrane which is set astride the frenum, and Wharton's ducts traverse it to open on its anterior border upper surface or under surface. The apex is frequently cleft and one salivary duct opens on each half. It is not to be mistaken for the sublingua, and some authors including Burmeister have made that mistake. In *Nycticebus* there are supplementary lamellæ. Pocock points out that the lamellæ overlie the ducts of the submaxillary and sublingual glands, but I passed bristles through the ducts and lamellæ in many Primates.

I suggest that the occurrence of the lamellæ in the Lemuroidea, Tarsioidea and Anthropoidea links these animals together as divisions of the Order Primates, and is against the view that the Lemuroidea and Tarsioidea form a separate order Prosimiæ. And this observation is to be added to existing observations on the brain and fœtal membranes which led anatomists to a similar conclusion.

The lamella is formed partly from the mucosa of the tongue and partly from the mucosa of the floor of the mouth. It is not a remnant of the sublingua, for it is present in a well-developed form in the Lemuroidea, which have the best sublingua. I am unable to explain its true nature, for we do not possess a good knowledge of the comparative embryology and comparative physiology of the Mammalian mouth. It is, however, certain that there is no structure in lower Vertebrata with which it can be homologized. It is probably connected in some way with the development of the salivary apparatus. In Man and the Orang it may have been absorbed into the floor of the mouth, leaving only the points projecting as the salivary papillæ.

Sublingua:—On the under surface of the tongue in some Marsupials, Rodents and Primates there are to be found complete structures representing a complete sublingua or remnants thereof. They are of great importance, for they help us to understand

the phylogeny of the tongue. In the present section only the anatomical data are considered, the phylogenetic aspect being described later (p. 744).

The sublingual structures are as follows:—

1. A sublingual plate which is large or small.
2. A central ridge and plicæ fimbriatæ.
3. Plicæ alone.
4. A ridge alone.

All these varieties are really stages in the degeneration of the sublingua, and the stages can be seen in members of families, and at different periods in the age of individuals.

In the Marsupialia the sublingua is soft, and its apex is bound down to the under surface of the tongue. It shows various degrees of reduction even in genera of the same family. In the Didelphyidæ it is complete in all genera except *Philander*; its apex reaches as far forwards as the apex of the tongue, and it is split up into processes; on the ventral surface there is a median keel, and the edges are free posteriorly. In *Philander* the median keel alone exists. In the Peramelidæ the keel reaches the apex of the tongue, and the lateral parts are slightly reduced. The Dasyuridæ have a median keel reaching the apex of the tongue, and the lateral parts are reduced, but not as much as in the Peramelidæ; but the reduction is greater in *Sarcophilus* than in *Dasyurus*. It is thus evident that the reduction of the sublingua in the Polyprotodontia proceeds in the order Didelphyidæ, Dasyuridæ and Peramelidæ. It will, however, be shown later that, taking all characters of the tongue into consideration, the Dasyuridæ have more primitive tongues than other Polyprotodontia. In no forms is the reduction such that plicæ fimbriatæ are present, so the reduction involves the lateral parts of the sublingua, leaving the central parts alone.

In the Diprotodontia the sublingua presents greater variations than that in the Polyprotodontia. In *Cœnolestes* and the Phalangeridæ the conditions are most primitive, there being a good central keel and lateral flanges. In the Macropodidæ the keel is present and the lateral parts are greatly reduced. In *Phascolomys* there is no keel, the central part of the sublingua is thin and the lateral parts are exceedingly thick. And in *Phascolarctos* there are merely diminutive plicæ fimbriatæ. Hence *Phascolomys*, and to a greater extent *Phascolarctos*, make a nearer approach to the Primates than to other Marsupialia in the characters of the sublingua.

In no Marsupial does the sublingua perform any function. It has no gustatory organs, and although muscle fibres pass into it in some species it is immobile. So we must regard it as entirely vestigial.

Gegenbaur did not observe any trace of the sublingua in the Insectivora, but Vogt and Yung saw it in several species. In

Talpa and *Rhynchocyon* there is a median ventral ridge which may be a remnant. Owen and Garrod described sublingual structures in *Tupaia*, and I found that it had a mixture of Lemuroid and Tarsioid features. Owen described plicæ fimbriatæ, but Garrod described a complete sublingua similar to that in *Chiromys*. Possibly *Tupaia* shows variations dependent on age.

Gregory stated that the sublingua in *Galeopithecus* is similar to that in *Tupaia*, but I did not see any trace of it in young or adult animals.

In all Chiroptera examined by myself there is no trace of the sublingua or its rudiments.

In the Rodentia I observed a sublingua in the Dormice alone, and this is the first occasion that the sublingua has been seen in this Order. In characters it resembles that in the Marsupialia, particularly *Phascolomys*. That is to say, it is a thick, soft, adherent, immobile plate without a median ventral keel.

The Edentata and Sirenia have no trace of the sublingua or of plicæ fimbriatæ.

In the Cetacea the sublingua is absent in the adult animal, but Schulte described a small triangular plate in the fœtus of *Balænoptera borealis*. In the young fœtus of *Physeter macrocephalus* examined by myself there were two ridges of mucous membrane which may represent plicæ fimbriatæ.

No sublingua nor plicæ fimbriatæ have been seen in the adult Carnivora, but Nussbaum observed plicæ in fœtal dogs measuring 4–5 cm.

In the Primates there is a great range of variation in the characters and degree of reduction of the sublingua.

In the Lemuroidea it is a structure which has become specialized for the purpose of cleaning the backs of the procumbent lower incisor teeth, which are used for combing the fur, the nails being useless for this action. It is consequently better developed than that in other Mammals, in which it is purely a vestigial structure. It is a strong, horny plate of a lyrate or quadrangular shape, whose apex anterior border is divided up into a variable number of strong, pointed denticles, which fit in between the teeth. On one or both of its upper and lower surfaces there is a ridge. In *Chiromys* the anterior border is smooth, but there is in its centre a strong hooked process. In many species it is quite free from the tongue, but in the others it adheres to it by its central part. The anterior part is always free. The consistence of the plate and the freedom of the anterior part distinguish it from the sublingua in the Marsupialia. The Lemurs can be distinguished from the Lorises, Galagos and *Chiromys* by the characters of the sublingua. In the fœtal *Chiromys* the sublingua is well developed, but its characters differ from those in the adult; they resemble the less specialized state in the Lemurs. The anterior border is serrated, and the strong hook is replaced by a soft, straight point.

When a section is made through the sublingua in the Lemuroidea it is seen how the stratum corneum is greatly thickened on the under surface of the sublingua, particularly in the median keel or keels. Muscle fibres pass into the sublingua. In *Stenops* and *Chiromys* there is an internal cartilaginous rod, but in *Lemur* that structure is absent.

In the Tarsioidea the lower incisor teeth are not procumbent, nor are they entirely used for combing the fur as in the Lemuroidea. The sublingua is reduced, soft, and only delimited laterally from the under surface of the tongue by a groove on each side. Anteriorly it has no denticles, but there is a small knob or blunt point lying in the position of the hook in *Chiromys*.

In none of the Platyrrhini examined by me was there any trace of the sublingua or its remnants. As regards the Cercopithecidæ I only saw plicæ fimbriatæ in one young *Cercopithecus patas* which still had its milk dentition. The Gibbons have neither a sublingua nor plicæ in the post-natal state, but Deniker saw a sublingua in the fœtus.

In all other Simiidæ and in the Hominidæ there is a well-marked sublingua or there are plicæ fimbriatæ, and these structures are better marked in youth than in adult life. In the Hominidæ they are better marked in the lower than in the higher races. In the child they have taste-buds, but these organs disappear, and that is one of the reasons why the child has a more acute gustatory sense than the adult. When the sublingua is reduced the central parts suffer more than the lateral parts, and a median ventral keel is usually absent.

The part played by the sublingua in evolution will be described later (p. 744).

From the above remarks the following conclusions can be drawn:—

1. The sublingua is functionless in the Marsupialia.

2. In the Lemuroidea it is functional throughout life.

3. In Man it is a gustatory organ in the early years.

4. Sufficient observations have been made to show that it is present in the fœtus in animals born without any trace of it. In existing works on the tongue one gets a disjointed view, for it is only described in Marsupials and Primates, as these observations make things more harmonious.

5. In the Marsupialia and Primates the primitive species have larger sublinguæ than the specialized ones.

6. The lower human races have larger sublinguæ than the higher ones.

7. Diminution in the sublingua is, therefore, a sign of specialization; and the degradation involves the central or lateral parts of the plate.

8. The Monotremes, in having no sublingua, are specialized animals.

Sublingual Combs.—In the Lemuroidea the sublingual plate has its apex or anterior border divided up into a variable number of sharp denticles, which fit into the interstices below the postero-superior aspects of the procumbent lower incisor teeth. And it appears, from the writings of Flower and Pocock, that their function is to free the teeth, which are employed for combing the fur, from scurf and other foreign material.

In many Ungulata there is a denticulated fold of mucous membrane on each side under the tongue. It is formed from the mucosa of the tongue and floor of the mouth. The processes into which the free edge is divided fit into the grooves between the backs of the incisor teeth. The processes are triangular in the Tylopoda and Tragulidæ, but they are long, sharp, spiny processes in the Bovidæ and Cervidæ. These folds are absent in the Perissodactyla, Suina, Proboscidea and Hyracoidea. So they exist in ruminating Ungulates.

Lingual Glands:—Three glandular masses may occur in the Mammalian tongue:—

1. Basal serous glands (Ebner's glands).
2. Basal mucous glands.
3. Apical gland of Nuhn or Blandin.

Serous glands, it is said, are related to the papillæ which bear taste-buds. But it is only in relation to the circumvallate papillæ and lateral organs that they are found. There are none connected to the fungiform papillæ. This is probably related to the position of the taste-buds. The buds in the fungiform papillæ come into close relation to the food while it lies on the surface of the tongue, but the constituents of the food can only excite the deeply-placed buds in the vallate papillæ and lateral organs after they have been dissolved in the glandular secretions. The glands open into the bases or outer sides of the fossæ of the vallate papillæ and into the bases of the sulci in the foliate papillæ. In a very few animals the glands are found up in the bodies of the papillæ. Their cells have large nuclei. Podwisotzky regarded them as salivary glands, but Ranvier considered them to be sensory rather than salivary in function. Flemming detected a granular structure in the cells, which he likened to appearances in the pancreatic cells.

Ranvier detected serous glands which have no relation to gustatory organs.

The *mucous glands* are found on the base of the tongue. Their cells have small nuclei and a thick basement membrane. They are modified tubular glands, whereas the serous glands are of the acinous type.

In many animals glandular orifices and pits are visible to the naked eye on the base of the tongue. And the following list shows some examples drawn from various Orders:—

Order Primates:—A few pits are present in the Hominidæ and

Simiidæ. They are numerous in the Cercopithecidæ, and they may be large or small, diffused all over or concentrated close to the tonsils and faucial pillars. They are particularly large in the Langurs and Guerezas. No pits are present in the Platyrrhini nor in the Lemuroidea and Tarsioidea.

Order Ungulata:—The Perissodactyla have numerous pits, but the Artiodactyla, Hyracoidea and Proboscidea have few or none.

Order Sirenia:—Dorsum has orifices singly or in pairs. None on inferior surface.

Order Cetacea:—Orifices more numerous than in any other Order. They are present all over the dorsum.

Order Carnivora:—Orifices numerous, scanty or absent.

Order Edentata:—Orifices only seen in *Bradypus*.

Rodents, Insectivores, Marsupials and Monotremes have few or no orifices.

It must, however, be emphasized that orifices do not demonstrate the true extent of lingual glands.

The Lytta.

Under this heading authors have included a number of more or less supporting structures, which have different origins and structure. They are present in very many, but not in all Mammals. They can be arranged in three groups:—

1. Lyttæ which are only specialized portions of the mucous membrane of the dorsum of the tongue—Horse.
2. Lyttæ which are differentiated parts of the septum of the tongue—Mole.
3. Lyttæ which are remnants of the os entoglossum of lower vertebrates. It is the only group which should really be termed the lytta. They are of two kinds:—

   a. Lyttæ of the tongue.
   b. Lyttæ of the sublingua.

The structural elements contained in the lytta are variable, for they include in each case one or more of the following—muscle, fat, fibrous tissue and cartilage.

The following list shows the presence or absence of lyttæ of the third group in the tongues of Mammals:—

Monotremata—Lytta present.
Marsupialia—Lytta absent.
Edentata—Lytta only present in *Manis*.
Rodentia—Lytta absent.
Carnivora—
Ailuroidea:—Small lytta lying in the anterior third of the tongue.
Cynoidea:—Large lytta may have a thread running back to the hyoid bone.

Arctoidea:—Lytta very large in *Cercoleptes* (*Potos*).
Pinnipedia:—Lytta absent.

Cetacea—Lytta absent.
Ungulata—No lytta of the third group. First type in Horse.
Hyracoidea and *Proboscidea*—No lytta.
Sirenia—No lytta.
Insectivora—Lytta of second type present in *Talpa*.
Primates—*Chiromys* has lingual and sublingual lyttæ.
Stenops has a sublingual lytta.
Tarsius has two lingual cartilage rudiments. None in sublingua.
Lyttæ absent in Lemuridæ and Anthropoidea.

B. The Value of the Tongue in Classification.

It must be strongly emphasized at the outset that lingual characters must not be used alone for purposes of classification. And any system which, based on them alone, would be suspect, especially if it differed from one which was drawn up after organs chosen from many parts of the body had been examined.

Several animals have such characteristic tongues that they can be recognized at a glance. And it is a curious fact that these animals are of particular interest from other points of view. They are *Ornithorhynchus*, *Phascolomys*, *Manis*, *Orycteropus*, *Hydrochærus*, *Castor*, any Cetacean and Sirenian, *Hyrax*, *Proteles*, *Hyæna*, *Galeopithecus*, *Tarsius*, *Tupaia*, *Chiromys* and *Homo*.

Order Primates.

With the exception of *Homo* and some specimens of Orang all Primates have well-marked frenal lamellæ, and there are other points in which the tongue of the Orang is most similar to that in Man (2). If one finds in a given tongue that there are many fungiform papillæ at the tip, no papillæ at all on the base, several vallate papillæ in a V, presence of lateral organs and traces of a soft sublingua one can decide that it belongs to *Homo* or *Simia*. And one distinguishes between them by the characters of the lateral organs (2). If one gets an Orang tongue with frenal lamellæ the distinction is still further emphasized.

The other Primates from *Lemur* up to *Gorilla* have well-marked frenal lamellæ.

The Lemuroidea differ from the Tarsioidea and Anthropoidea in the characters of the sublingua as follows:—

Lemuroidea—sublingua functional, is free and has a variable number of processes on its anterior border.

Tarsioidea—sublingua not functional, is fixed and has one process.

Anthropoidea—sublingua not functional, is absent or only in traces.

The Lemuridæ can be distinguished in several ways from the Lorisidæ, Galagidæ and Chiromyidæ (5). But I am unable, from lack of material, to say anything about the Indrisidæ.

It is difficult, and in the case of some specimens, apart from the characters of the sublingua, to distinguish the tongues of the Lorisidæ and Galagidæ from that of *Tarsius*.

As regards the Anthropoidea the tongues fall into four groups:—

1. Platyrrhini.
2. Cercopithecidæ.
3. Hylobatidæ.
4. Gorilla and Chimpanzee.

The separation of the Gibbons is not in accordance with text-book teaching, but many anatomists believe that the Gibbons should form a separate family.

The Platyrrhini, Cercopithecidæ and Gibbons have no sublingua whatsoever. The Platyrrhini are distinguished from the Cercopithecidæ by the characters of the lateral organs and the absence of a thick apical cluster of fungiform papillæ. The Cercopithecidæ are distinguished from the Gibbons by the characters of the lateral organs, and by the fact that the Gibbons have their vallate papillæ in a Y, a form unknown in the Cercopithecidæ. The genera of the Platyrrhini and Cercopithecidæ have special lingual differences (3, 4), but one cannot distinguish the species of the first three groups by lingual characters.

The Y type of vallate papillæ occurs in both Hylobatidæ and the Simiidæ except *Simia satyrus*.

The tongues of the Gorilla and Chimpanzee can be distinguished from one another by the characters of the lateral organs (2).

It is thus evident that the lingual characters support other views on the divisions of the Order Primates, and they are of value for distinguishing the genera of Monkeys from one another.

Anatomists have drawn attention to the resemblances between *Tupaia* and the Lemurs. On examining the tongues one finds that the characters present are a mixture of those in the Lemuroidea and *Tarsius*, together with some of those in the primitive Mammalian tongue.

Order **Insectivora**.

Of the suborder Menotyphla I could only examine the tongue of *Tupaia*, and I found that the good sublingua distinguishes it from the tongues of the Lipotyphla. As regards the Lipotyphla the tongues are not sufficiently distinctive for taxonomic purposes. Some structures are constant, but others vary; and I found that classifications of the tongues conflicted with those based on skeletal characters. The only forms which stand out prominently are *Erinaceus* and *Chrysochloris*.

Order Chiroptera.

Insufficient material was available for me to draw any conclusions of value.

Order Dermoptera.

Galeopithecus has Insectivore and Primate characters in the tongue, the Insectivore which it resembles being *Tupaia*.

Order Carnivora.

The value of the tongue in the classification of the Ailuroidea, Cynoidea, Arctoidea and Pinnipedia varies considerably (8).

In the Ailuroidea the tongue is of great value in classification. Indeed, it is of greater value in the classification of these animals than of any other Mammalian group. It enables us to distinguish the families from one another. In the Felidæ it enables us to arrange the large number of species in a number of groups. The most striking feature is the separation of the Domestic and Wild Cats, the Lynxes and the Caracal from the others. The grouping of the species by their lingual characters is almost identical to that drawn up by Pocock as the result of the examination of external and craniological characters.

In the Cynoidea the tongues present such homogeneous features that they are quite useless for classification. In the Arctoidea it is possible to distinguish the families from one another; it is possible to distinguish between the subfamilies; and it is possible to group the genera in each subfamily. The genera of the Pinnipedia have definite lingual characters, and these mark off *Trichechus* from the others.

Thus it can be seen that the value of the tongue in the classification of the Carnivora is considerable, and it agrees with classifications based on external and skeletal characters.

Order Cetacea.

It is only possible to distinguish the Mystacoceti from the Odontoceti by lingual characters, for the tongue gives no assistance in the characterization of families and genera.

Orders Sirenia, Hyracoidea and Proboscidea.

As regards the tongues the Sirenia and Hyracoidea have some features in common, but the Proboscidea differ entirely from the others. In fact, *Elephas* has peculiarities not found in other Mammals (7). The Sirenia have characteristic tongues, and one can distinguish that of the Manatee from that of the Dugong.

Order Ungulata.

It is a simple matter to distinguish between the tongues of the Perissodactyla and those of the Artiodactyla.

Of the Perissodactyla the Rhinocerotidæ have lingual characters which differ from those of the Equidæ and Tapiridæ.

And although the two last-mentioned families have certain characters in common their tongues are quite distinctive.

As regards the Artiodactyla, I had no tongue of *Hippopotamus*, but the tongues of the Suidæ were found to differ from all the others, and formed one large group. The remaining forms, or Ruminantia, fall into the following groups according to the characters of the tongue:—

1. The Tragulidæ.
2. The Camelidæ.
3. The Bovidæ and Cervidæ.

It is also possible to distinguish between the tongues of the Bovidæ and those of the Cervidæ. Thus it can be seen that the division of the Ungulata according to lingual characters agrees with a classification based on other anatomical and on external characters.

When the tongues of the different families are examined the following conclusions can be drawn:—

1. Family Suidæ:—*Sus* differs from the other genera, but all the others can be distinguished from one another.

2. Family Tragulidæ:—*Tragulus* can be distinguished from *Hyomoschus*.

3. Family Camelidæ:—Genera not definitely distinguishable from one another.

4. Family Cervidæ—Tongues fairly uniform, and not useful for distinguishing between the different animals.

5. Family Bovidæ:—From the material at my disposal it was possible to arrange the tongues in groups (7), but I had not enough specimens to make anything like a full classification.

Order Rodentia.

As regards the characters of the tongues, the Rodents fall into three great groups:—

1. Sciuromorpha.
2. Myomorpha.
3. Hystricomorpha and Lagomorpha.

The Hystricomorpha can easily be distinguished from the Lagomorpha although they have some lingual features in common. Of these groups the families all have distinctive characters and, with the exception of the Sciuridæ, the genera also have their own peculiar characters. Full details were tabulated formerly (10).

The Spalacidæ and Dipodidæ have features present in both the Sciuromorpha and Myomorpha, and the Myoxidæ have a sublingua not present in the other Rodents.

Order Edentata.

Although the Order is now broken up into three the old term is employed for convenience here.

The New-World forms agree with each other and differ from the Old World species, which agree with one another in the number of circumvallate papillæ. The tongues of the Dasypodidæ, Myrmecophagidæ and Bradypodide can all be distinguished from one another, but the genera and species of each family cannot be distinguished. The tongues of the Manidæ differ from those of the Orycteropodidæ in that they alone have a lytta.

Order **Marsupialia.**

In my paper on the tongues of these animals I showed that it is not possible to distinguish the tongues of the Polyprotodontia from those of the Diprotodontia. But the lingual characters are of value in distinguishing between the genera when other characters have been employed in separating the two suborders.

Order **Monotremata.**

It is exceedingly simple to distinguish the tongue of *Ornithorhynchus* from those of the Echidnidæ, for they represent widely-different adaptive characters; and it is equally simple to differentiate between the tongues of the Echidnidæ and those of the insectivorous Edentates, though all have undergone similar adaptive changes.

From the above analysis of my papers on the tongues one can see that the lingual characters are frequently very useful additions to the characters at present in use in classification. They will assist other internal structures in defining the main groups, leaving external characters to distinguish between the species.

C. Evolution of the Tongue.

Under this heading three studies are included:—

1. Evolution of the papillæ, muscles and glands.
2. The origin and characters of the primitive Mammalian tongue.
3. The conversion of that primitive tongue into the types found in the various Orders. Here we pay special attention to the sublingua and lytta. Thus study helps to throw light on the evolution of the Mammalia.

Evolution of the Papillæ.

In lower Vertebrates conical and fungiform papillæ are found, but Mammals alone have circumvallate papillæ and lateral organs.

Conical Papillæ (text-fig. 36):—It is possible to arrange the various forms in a series of stages which are marked by an increasing degree of complexity. They are as follows:—

Stage 1: The epithelium has no papillary elevations on its outer surface, but its deep surface is penetrated by processes of the connective tissue of the corium. This is seen in all Vertebrates.

Stage 2: On the outer surface of the epithelium there is a cellular projection which is situated over or slightly to the side of the connective-tissue process, but the process does not penetrate it. This occurs in all kinds of Vertebrates.

Stage 3: The epithelial papilla is traversed by a connective-tissue core. This is seen in all kinds of Vertebrates.

Stage 4: Here the series of stages hitherto described recommences again. The simple connective-tissue process develops secondary processes, but the epithelium does not yet show renewed activities. This enlargement of the corium leads to an expansion of the papilla. This stage occurs in Reptiles and Mammals.

Stage 5: The epithelium develops secondary papillæ which may not or may receive processes of connective tissue. This stage is seen in Mammals, but I am not prepared to say whether it does or does not occur in the Reptilia, although I have not seen them there.

Stage 6: The corium grows up into the secondary papillæ.

In Mammals one finds that all these stages may occur in any single tongue, particularly in the higher Orders.

The Amphibia must be excluded from this phylogenetic study, for the epithelium covering the papillæ is of a totally different character from that in other Vertebrates. Still the general structure in the first three stages is present in them.

When these five stages are examined it is seen how the corium begins the process of papillary formation before the epithelium takes part. And after the epithelium has participated, its development is at first on simple lines. Later on the epithelium shows complexities, but no specialization is possible until the corium has undergone renewed activities. In other words, *the corium regulates the activities of the epithelium*. This I regard as one of my most important conclusions.

The conditions shown in stage 1 (text-fig. 36A) are widely distributed in Vertebrate tongues, and I regard parts of the tongue containing it as potential papillary areas. It is common on the base of the Mammalian tongue; and there is no part of the Mammalian tongue which varies so much in the presence or absence, and in the degree of development of papillæ.

The stimulus for papillary growth may come from without or from within, or from both directions. Stimulation from without consists of mechanical action on the food or against the palate, and stimuli from within are the active circulation of blood resulting from the movements of the muscles of the tongue. This matter has not received any serious attention hitherto. I believe that external stimuli play a part, but the greatest effect results from muscular activity. Of course, in some regions the papillæ rise up to elevate tactile nerve-endings.

When a stimulus, no matter how slight, is applied to the surface of the skin, changes are induced in the cutaneous blood-vessels by reflex action, and it may be that the stimulus of food

on the tongue reflexly increases the circulation in the corium projections into the epithelium. These papillæ have vascular loops or sheafs of blood-vessels and nerves, and the nerves may be vaso-motor as well as tactile in function.

Text-figure 36.

Evolution of the papillæ and relations of epithelium and corium are shown in the upper group (A–J), and the likeness between the fungiform papillæ and some circumvallate papillæ is seen in the lower group (A–D). In the upper group A–F are stages in the evolution of conical papillæ, G is a fungiform papilla, H and I are different complexities of vallate papillæ, and J shows roots of secondary papillæ on transverse section.

Some years ago I made a number of observations on the effects of stimuli of different kinds and intensities on the human skin, and I noticed that mild and moderate stimuli, unless applied to wide areas of the skin, were followed by vaso-constriction which sooner or later gave way to vaso-dilatation. So I suggest, on

analogy with the skin, that the repeated stimulus by food and by contact with the palate in mastication or any other form of feeding, as in Reptiles, produce a series of vaso-constrictions and vaso-dilatations. The result would be that the circulation in the tongue will show rhythmic activities which are felt in the papillary processes of the corium.

There is evidence, both positive and negative, that the action of the muscles must play an important part in the formation of papillæ, particularly the types shown in stages 4 and 5. In the non-muscular tongues of Fishes the papillæ are simple and never or rarely advance to stage 3; and their main function is touch. The stimuli come entirely from without. And in toothed and baleen Whales the musculature is reduced, with resulting poor mobility, especially in the case of Odontoceti. We see in them a great loss of papillæ, and the interesting facts concerning the degeneration are described later. In the mobile Reptilian and Mammalian tongues, stages 4 and 5 are present along with the earlier stages.

The papillæ have a variable degree of keratinization of their superficial parts in Fishes, Reptilia and Mammals, and in some Fishes and Mammals the papillæ are dense and very sharply pointed. Specially dense forms are known as lingual teeth, as in Fishes and *Ornithorhynchus*, or papillæ spinosæ, as in *Didelphys* and the Felidæ. Keratinization is also controlled by the corium.

When a number of papillæ are examined after sections have been specially stained, one can see that the epithelium undergoes wear and tear like the skin. But that might be expected, for the mucous membrane of the mouth and tongue is really modified skin.

Many sections show desquamation of the superficial horny cells, and special stains reveal eleidin granules in the deeper cells from which the keratin is renewed.

In the systematic papers of this series I figured many different kinds of papillæ, and it was shown that species of higher Orders have a larger range of forms than those of lower ones. And it is a very simple matter to tell what stage of evolution is present in each type.

An important conclusion which can be drawn from these systematic accounts is that the higher Mammals have a much greater aggregation of papillæ on the apex of the tongue than the lower ones; and the importance of this aggregation will be shown when we come to study the evolution of the tongue in the Primates. The presence or absence of large papillæ on the base of the tongue is also very important in that connection.

Fungiform papillæ are present in Amphibia, Reptilia and Mammalia, so they appear early in evolution, but later than do the conical papillæ. They may have a smooth surface, or secondary papillæ may be present; but the latter are not very frequent. The connective-tissue core is divided up at its periphery, so the usual fungiform papilla corresponds to stage 4.

of the conical series, as shown in text-fig. 36. In many lower Vertebrata the epithelium is not stratified.

In Mammals some fungiform papillæ are gustatory in function and others are tactile. And Oppel suggests that the circumvallate papillæ and lateral organs have taken away much of their gustatory function.

In ontogenetic development of the conical and fungiform papillæ the corium grows up into the epithelium, which then proliferates, as in the series shown in text-fig. 36. The epithelium between the future papillæ then desquamates, leaving them all exposed. The fungiform papillæ do not assume their globular shape till well on in development, and some may develop secondary papillæ. Hence in ontogeny the fungiform papillæ pass through stages similar to the phylogenetic evolution of the conical papillæ.

I have already shown (p. 710) that there is a concentration of fungiform papillæ at the apex of the tongue as we ascend the animal scale.

Circumvallate Papillæ:—As regards the relations of the corium and epithelium, all six stages shown in text-fig. 36 can be seen. When secondary epithelial papillæ are present the whole papilla has a granular surface; and it is evident that the corium also controls the epithelium as in the case of mechanical papillæ.

Some years ago Poulton (P. Z. S. 1883) propounded the following theory to explain the arrangements which he had observed in animals from *Ornithorhynchus* upwards.

1. Food first stimulates sub-epithelial tactile nerve-endings.

2. Papillary processes of the corium rise up and push these endings towards the surface.

3. Serous glands are developed from mucous glands. The ducts probably surrounded a circular or oval area containing the endings.

4. The organs and processes grew up so far that the epithelium was perforated and the organs were exposed.

5. Tactile nerve-endings became converted into gustatory endings.

6. The margins of the gustatory area were folded over to protect the endings, and the organs were exposed.

7. Sub-epithelial end organs vanish and taste-buds appear in the interpapillary processes of epithelium.

8. The papillæ become less protected, and the buds sink down into the edges of the sulcus round the papillary body. In *Ornithorhynchus*, which retains good protection, they remain all over the surface.

The following points are against Poulton's views:—

1. Oppel has shown in the third volume of his Comparative Histology that taste-buds are not present on the summits of the papillæ, but only in the sulcus in both Monotremata.

2. In many Mammals the papillæ are quite as well protected

at the bottom of a pit as in *Ornithorhynchus*, but no buds are on the free surface (text-fig. 33, no 3).

A second theory, which has several adherents, is that the circumvallate papillæ are simply large fungiform papillæ surrounded by a ridge.

An examination of the naked-eyed appearances of the papillæ in the vallate area in many animals would certainly support that view; but it is in that area only, for we know that vallate papillæ are never present on the anterior two-thirds of the tongue, whereas fungiform papillæ are. There is a complete series of transitions between fungiform and vallate papillæ (text-fig. 36).

In many tongues (A) the fungiform papillæ lie in hollows of the mucous membrane, and taste-buds are present on their upper surfaces. But no glands open into the hollow in which the papilla lies.

In some animals, as for example the Badger (B), the vallate papillary body and hollow are as in A. A few buds occur on the upper surface, but many occur deep down; and serous glands open into the fossæ.

In many new-born animals, if not in all, taste-buds occur on the whole papilla, but those on the upper surface disappear as age advances (C).

In the Macaque Monkeys (D) the globular papillæ have buds only on the deep aspect, and serous glands open into the fossæ. The fossæ are deeper than the hollows in A.

As regards the macroscopic appearances, it is thus difficult or impossible to distinguish between some fungiform and vallate papillæ, but microscopic examination shows the essential differences, for no fungiform papilla has glands connected to it, and it has no taste-buds on its under surface. Vallate papillæ have associated glands; and taste-buds are present deep down, although some occur on the upper surface in a number of cases.

To convert a fungiform papilla into a vallate papilla the following changes must take place:—

1. The papilla would have to enlarge and sometimes change its shape.

2. The hollow under the papilla would have to deepen, or a fossa would appear.

3 Taste-buds must form deep down on the sides of the fossa.

4. Glands must pass into the fossa.

We shall see later that the developing human papillæ undergo some of these changes.

The changes necessary to convert a fungiform papilla into a vallate papilla are not so complex as those which take place in Poulton's evolutionary stages.

There is, I think, no doubt that the primitive papillary pattern was three papillæ in a triangle, with the apex directed backwards. Whether they were completely evolved vallate forms, or transitions between fungiform and vallate papillæ, on the primitive

Mammalian tongue cannot be absolutely settled; but, for reasons given on p. 744, it is probable that they were proper vallate papillæ. This primitive form has persisted in animals belonging to all Orders, as is shown in the table on p. 714. The most complex type is the Y form, and Münch has named the papillæ as in text-fig. 34. It is a simple matter to convert one type into another by adding or subtracting papillæ. The additional papillæ were probably not developed from existing ones, but are new formations out of fungiform papillæ. The types could arise as follows (text-fig. 34):—

1. Three papillæ in a triangle—the primitive type (A).
2. Loss of the papillæ centralis—the single pair (B).
3. Loss of the basal papillæ—the single papilla type (C).
4. Filling in the side limbs—the V-type (D).
5. Filling in the limbs and then loss of the apical papilla—the chevron type (E).
6. Filling in the side limbs and addition of papillæ behind—the Y-type (F).
7. As in No. 6, plus flattening out of the angle—the T-type (G).
8. Loss of the central papilla and multiplication of the number of basal papillæ as in some Ungulates (H).

Lateral Organs (text-fig. 37):—If one connected two poles of a circumvallate papilla across the fossa to the rest of the mucosa of the tongue, and then stretched the whole structure, one would produce a condition like a single lamina of the organ with its sulci. And I have already shown (10) that the vallate papillæ in *Hydrochærus*, *Dolichotis* and *Cavia* have this appearance. There is, in fact, no essential difference structurally between the vallate papillæ of these animals and the lateral organs. In fact in all Mammals the lateral organs resemble long vallate papillæ in all essential details. And the question arises whether they have arisen in the same way. Poulton (P. Z. S. 1883) describes a totally different mode of origin for the two structures. His views on the origin of the vallate papillæ have already been mentioned (p. 737). The lateral organs in his opinion begin as a row of gland-ducts with taste-buds in their walls, and these ducts eventually open into newly-formed depressions in more evolved types. The new depressions correspond to the sulci of the lateral organs. Poulton thinks that the term foliate papillæ is objectionable because it focusses attention on the laminæ of the organ instead of on the sulci which appear first.

In favour of the view that the lateral organs are modified descendants of fungiform papillæ the following evidence is available.

1. In many different kinds of Mammals there are no lateral organs, but rows of fungiform papillæ are present in their position. These have taste-buds arranged on the top as in the normal way for fungiform papillæ.

2. In the new-born child a cross-section of a lamina has the identical shape of that of a vallate papilla, and taste-buds are numerous on the free upper surface. They are in fact relatively more numerous than those on the side of the sulcus.

3. A series of sections of the human tongue at different ages show the following stages:—

1. No buds on the free surface, but many opening into the upper part of the sulcus.
2. Buds open into the middle of the sulcus.
3. Buds open into the fundus of the sulcus.

These stages could be explained in one of two ways:—

1. The buds have moved downwards.
2. Buds have disappeared, but fresh ones have formed in different parts as the result of changes in the cells induced by nerve-fibres; for it is known that nerves will induce cells to become gustatory cells.

In the ontogenetic development of the human vallate papillæ there are at first two ridges arranged in V-formation, and each ridge consists of a ridge of corium with an epithelial covering. This epithelium grows down and breaks the ridges up into separate areas. Eventually slits appear in the epithelial growths and fuse to form the fossæ. So we have here a stage similar to that of a fungiform papilla. Buds grow out from the epithelial downgrowths and give rise to glands and their ducts. Nerves reach the epithelium early, and under their influence cells form taste-buds. Hence vallate papillæ pass through stages which resemble fungiform papillæ, but it is wrong to say that they were first large fungiform papillæ which sank down. The vallum is a secondary upgrowth of epithelium. Hence we may conclude that a vallate papilla is a fungiform papilla surrounded by a ridge and serous glands have become added. The nerve-endings and taste-buds have become displaced downwards. And the relations of the epithelium and corium are similar in vallate and fungiform papillæ and in the fourth, fifth and sixth stages of the conical series (text-fig. 36).

The comparative embryology of Mammalian tongues is very slightly known, so we cannot determine whether the various patterns are produced by isolated action of the epithelium in different spots, or whether there are ridges which become cut up into vallate papillæ as in Man.

In the ontogenetic development of the human tongue fungiform and conical papillæ appear simultaneously, and the lateral organs are the last to form. Moreover, it has been shown above that lateral organs appear lost in evolution, so we see that ontogeny and phylogeny agree in this respect, that lateral organs are the latest papillæ. It will be shown in the studies of the evolution of the tongue, that in the Cetacea with degenerate tongues the lateral organs are always absent though other papillæ are present.

Musculature of the Tongue.

In the Frog there are both intrinsic and extrinsic muscles, and the complete series is as follows:—1. Hyoglossus; 2. Genioglossus; 3. Transversus; 4. Longitudinalis lying beneath the mucosa on the dorsum of the tongue. The longitudinalis was formed from the hyoglossus and genioglossus. The transversus gets no attachment to a septum linguæ.

In Reptiles the same muscles are present, with the addition in some cases of the verticales and longitudinalis inferior. In the lower part of the tongue lies the os entoglossum.

In Mammals the musculature becomes greater than in lower Vertebrates, and it presents differences in various Orders. It consists of extrinsic and intrinsic muscles:—

Extrinsic—hyoglossus, genioglossus, styloglossus, chondroglossus, palatoglossus.

Intrinsic—transversus, verticalis, longitudinalis superior and inferior.

The *transversus linguæ* is attached mesially to the septum lingua. In Anteaters it forms a ring musculature. And in several Mammals some fibres are not related to the septum, and form the cruciate muscle.

The *longitudinales muscles* differ from those in Reptiles in the great development of the inferior part. As the latter increases it pushes down and compresses the os entoglossum and the surrounding tissues. And these lower parts become the lytta and sublingua. In some animals there is a musculus longitudinalis impar lying above the septum.

Conclusions.

1. The gustatory apparatus is better developed in herbivorous and frugivorous animals than it is in carnivorous and insectivorous species.

2. In many Mammals the papillary structures as a whole are well developed; but there are numerous species in which the papillæ on the apex of the tongue—mechanical, tactile or gustatory—are better developed than those on the remainder. They may be larger or more numerous. These animals with specialized apices fall into two groups—those with peculiarities in the incisor teeth, and those which employ their hands in feeding. Some animals belong to both groups. And in studying these animals one must not omit to take into account the first conclusion, mentioned above.

In the Edentata, incisor teeth are entirely absent. In the Bradypodidæ, which live on vegetable matters, the apex of the tongue comes into ready contact with food, and the apex has large mechanical papillæ. In the insectivorous forms the tongue is really a viscid finger, and its apical papillæ are absent. But the apex forms an expanded tactile organ in several species. The Armadillos have good apical conical papillæ, which are tactile.

In the ruminating Ungulates the upper incisor teeth are

missing, and these animals have better apical papillæ than all other Mammals except the Primates. The apex of the tongue comes in contact with the food, and the tongue is frequently prehensile. Prehensility is accompanied by the development of numerous conical papillæ, but the fungiform papillæ are not increased at the same time. A good example is seen in the tongue of the Giraffe, which is very prehensile; the conical papillæ on the apex are numerous, but fungiform papillæ are almost absent therefrom. Conical papillæ would make the grip of the tongue secure, just as papillary ridges help to secure the grip of the hand. The papillæ fungiformes are numerous over a large area of the tongue, so we have no special cluster *on the apex* as in the Primates.

In *Tupaia* and the Lemuroidea the lower incisor teeth are more or less procumbent, and the animals use their hands for holding food while they are eating it. *Tupaia* eats fruits and insects and the Lemuridæ consume insects, fruit and small animals. But if a captive Lemur is given a diet of meat and vegetable matters it selects a greater portion of the latter. *Tupaia* has a fringe of large fungiform papillæ round the apex of the tongue (text-fig. 31), and the Lemuridæ (text-fig. 31) have a cluster of large fungiform papillæ in the apical region. In the Lorises the apical papillæ are not as specialized as those in the Lemuridæ, probably because of the high proportion of insects in the diet (see conclusion No. 1).

Many animals employ their hands in feeding, either by holding food in the paws while they nibble with the teeth, as in the case of the Squirrels and *Tupaia*, or by conveying food to the mouth in the hands. *Tarsius* crams insects into its mouth by its hands (Le Gros Clark), but its apical and other gustatory papillæ are poor owing to its insectivorous diet. Le Gros Clark could only feed it on grasshoppers and milk.

The Anthropoidea consume fruits, shoots, leaves, eggs, insects, nestlings, etc., and they convey the food to their mouths by means of their hands. The anterior part of the dorsum including the apex of the tongue shows an increase in the size and number of the papillæ, due in all probablity to a combination of the mode of feeding and nature of the diet.

The influence of the mode of feeding on the apical part of the tongue can be understood by a small experiment. If one fixes a piece of food to a plate and employs one's teeth to secure pieces of it, one can observe how the apex of the tongue is retracted away and does not touch the morsel. If, now one conveys the food to the mouth by hand, the apex of the tongue at once touches the morsel as soon as it passes between the incisor teeth. The frequent stimulation of the apex of the tongue resulting during feeding is one of the factors which lead to the specialization of its papillæ *.

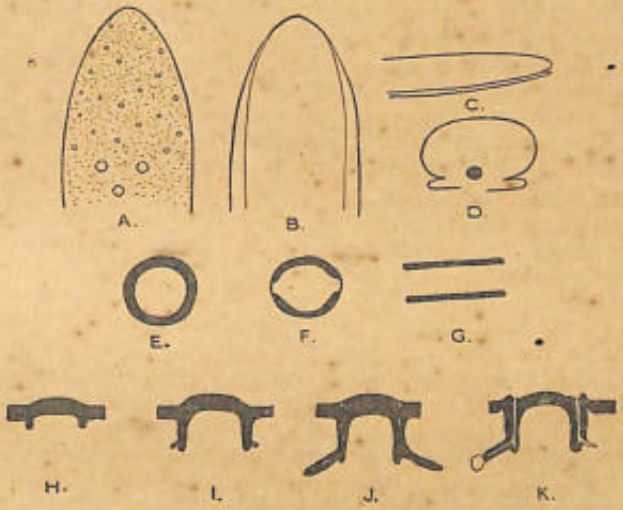
* See, however, the section on the sense-organs (p. 758).

Origin and Characters of the Primitive Mammalian Tongue.

Mammals differ from lower Vertebrates in their mastication and insalivation, and in their licking powers. They also differ from them in sucking, for the Mammalian sucking differs from the action of the mouth in Cyclostomes. The movements involved in these actions have led to the emergence of the Mammalian tongue and to its further development after it had evolved. Of these functions mastication came first, and it is important at the outset to compare the features present in most Mammals with those present in Whales, which do not masticate or insalivate.

A complete Mammalian tongue possesses lateral organs, circumvallate, fungiform and conical papillæ, muscles and glands. No Cetacea have lateral organs, but this may be explained in one of

Text-figure 37.



A–D, upper, lower, side and section views of the primitive Mammalian tongue; E–G, transition between vallate papillæ (E) and lateral organs (G); H–K, development of human vallate papillæ after Grefberg.

two ways—they had not yet evolved in the Creodont ancestors of the Cetacea, or they have degenerated in the latter. Thus the last structure to appear in evolution is absent. Circumvallate and fungiform papillæ are very frequently absent, the best vallate papillæ being present in species with very mobile tongues. Conical papillæ are present in a few cases. But most Cetacean tongues are quite smooth. Hence Cetacea have a very degenerate papillary apparatus. During suckling the little Whale does not do much, for the mother's mammary muscles force the milk into its mouth. Licking does not occur in the Odontoceti, but the tongue helps to remove food particles from the baleen plates in

the Mystacoceti. The muscles are poor in the Odontoceti, but better developed in the Mystacoceti. And the lingual glands are secondarily increased, possibly to provide a protective substance for the surface of the tongue (7). Hence the loss of mastication and insalivation, and the slight efforts in lactation have reduced the Cetacean tongue almost to that of Fish and Crocodiles.

As it is now generally accepted that Mammals have arisen from a group of Cynodont Reptiles, it is obvious that the evolutionary history of the tongue must be traced back to these creatures. But as some of the later Cynodonts masticated, they probably had, in a slight or moderate degree of development, some of the characters of the primitive Mammalian tongue. Hence we must go still farther back to be sure of getting a tongue uncomplicated by Mammalian features. Of course we do not possess any fossil tongues, so we must deduce the characters from a wide view of tongues of Vertebrates. I suggest that such a tongue would be a simple plate traversed near its lower surface by an os entoglossum. The musculature would be simple. The mucous membrane would have mucous glands or gland cells, and the nerve-endings would be tactile in function. The papillæ would not be prominent and would be mainly conical. Fungiform papillæ would be scanty, but neither vallate papillæ nor fungiform papillæ would be present.

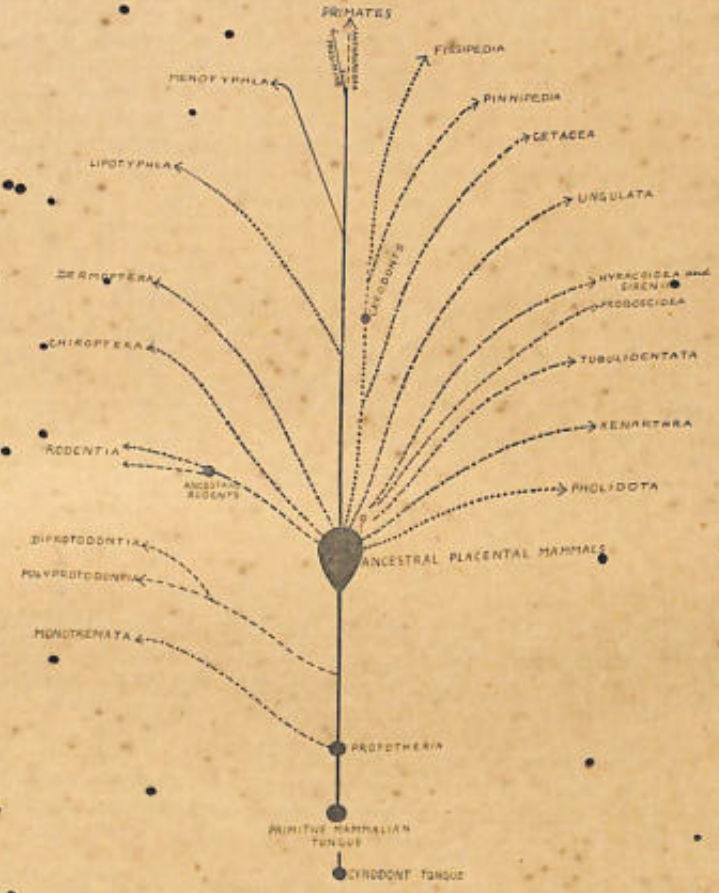
The Mammalian tongue was evolved out of the Reptilian tongue by an increase in its musculature and papillary structures. The increased musculature thickened the tongue between the dorsum and the os entoglossum, the most marked changes being the increase in the genioglossus and lingualis inferior. The os entoglossum and the lower part of the Reptilian tongue became the lytta and sublingua. These structures proceeded to disappear in various Orders. Some Orders retained both, others retained the sublingua or lytta, and others again eliminated both. The lytta became absorbed into the septum linguæ, and the sublingua was absorbed into the under surface of the tongue. In many Orders there is no trace, as a rule, of the sublingua in the adult, but its occurrence in the fœtus, and the very occasional appearance of remnants in young animals, shows a condition that once was. The arrangements in the Orders are as follows:—

Lytta and sublingua present.	*Lytta lost.*	*Sublingua lost.*	*Lytta and sublingua lost.*
Primates.	Marsupialia.	Fissipedia.	Pinnipedia.
Menotyphla.		Lipotyphla.	Chiroptera.
		Pholidota.	Dermoptera.
			Cetacea.
			Ungulata.
			Hyracoidea.
			Sirenia.
			Proboscidea.
			Xenarthra.
			Tubulidentata.
			Rodentia.
			Monotremata.

The primitive Mammalian tongue (text-fig. 37) would have the following characters:—

1. It was small in size.
2. There were three circumvallate papillæ in a triangle with

Text-figure 38.



Evolution of the tongue in the Mammalian Orders. The characters shown by different kinds of lines are: ——— lytta and sublingua present; — — — sublingua present, lytta absent; ● ● ● lytta present, sublingua absent; — ● — ● — ● lytta and sublingua absent.

the apex directed backwards. This character has persisted in members of most Orders.

3. Lateral organs had not developed.

4. Fungiform papillæ were small and scanty, and were not aggregated in an apical cluster.

5. The conical papillæ were not aggregated into a large cluster on the apex of the tongue.

6. The lytta was present.

7. The sublingua was present, but its anterior border was not cut up into denticles (a condition hereafter described as specialization of the sublingua).

It will be shown later that these features persisted almost unchanged in the ancestral placental Mammals, so they occurred along the line which gave off the Monotremes and Marsupials.

In the descriptions of the evolution of the tongue in the Orders, stress is laid on the presence or absence of the lytta and sublingua, for I employ these as the main features running through the whole series of tongues. Specializations of the papillary apparatus are secondary characters, which are useful in breaking up the Orders into smaller groups.

Evolution of the Tongue in Monotremata.

The Monotreme tongues have departed far from the primitive type. They have lost the heritages from the Reptilian tongue (lytta and sublingua) and the dorsum has become highly specialized. Lateral organs are well developed and the apical circumvallate papilla has disappeared. The conical papillæ have become highly specialized. In *Echidna* the tongue has become elongated as in the placental Anteaters, and in *Ornithorhynchus* a large intermolar eminence has developed as in Rodents, Ungulates, Sirenians, etc.

Evolution of the Tongue in Marsupialia (text-fig. 39).

The tongues have not departed as far from the primitive type as have those of the Monotremata. Indeed, the only real point of difference between the primitive Mammalian tongue and the most primitive Marsupial tongue is the loss of the lytta in the latter.

The generalized Marsupial tongue had the primitive dorsum and large sublingua, but neither lateral organs nor lytta existed. And that type is seen only in *Marmosa*. The subfingua remains large, but there is a specialization of conical papillæ to form a spinous patch in *Didelphys*.

The Dasyuridæ have a reduced sublingua like the Peramelidæ, but they differ from them in having large conical papillæ on the base of the tongue. In the possession of these large papillæ the Dasyuridæ differ also from the Didelphyidæ. The vallate papillæ have pointed processes.

The progressive reduction in the sublingua goes on in the Diprotodonts; and lateral organs make their appearance and become increasingly complex. There are also degrees of specialization of the circumvallate papillæ, although the primitive

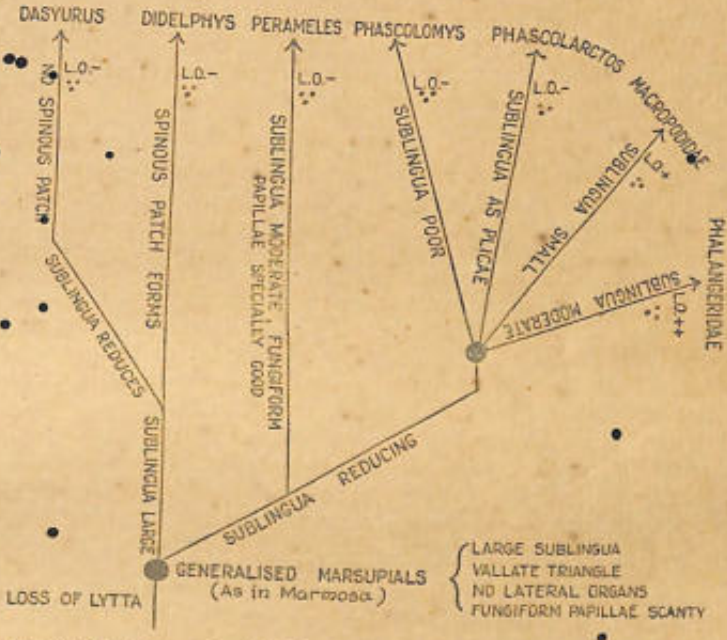
triangle is retained as in the Polyprotodonts. But the specialization of the lateral organs is not proportional to that of the vallate papillæ in *Phascolomys*.

The characters on the lines shown in text-fig. 39 are as follows:—

1. *Cynolestes*—No lateral organs. All vallate papillæ elevated, and have triangular prolongations as in *Dasyurus*.

2. *Tarsipes*—No lateral organs.

Text-figure 39.



Evolution of the tongue in the Marsupialia. L.O., lateral organs, whose development is indicated by signs; ○○, ○○, ●●, indicate degrees of progressive evolution of the circumvallate papillæ.

3. *Phascolomys*—No lateral organs. All vallate papillæ as in higher Mammals.

4. *Phascolarctos*—No lateral organs. Posterior vallate papillæ as in higher Mammals; anterior papillæ transitional.

5. *Phalangeridæ*—Lateral organs approaching, or as good as those in higher Mammals. Vallate papillæ as in *Phascolarctos*.

6. *Macropodidæ*—Lateral organs increase in complexity, as do the vallate papillæ.

The tongues of the placental Mammals can be arranged in five groups as follows:—

1. Tongues with the primitive dorsum, sublingua and lytta.
2. Tongues with the primitive dorsum and lytta, but no sublingua.
3. Tongues with the primitive dorsum, but neither lytta nor sublingua.
4. Tongues with a specialized dorsum and lytta, but no sublingua.
5. Tongues with a specialized dorsum and neither lytta nor sublingua.

When the lines representing these radiations are traced backwards, they meet in a tongue which has all the characters of the primitive Mammalian tongue; so the primitive form was retained in the ancestral placental Mammals.

Evolution of the Tongue in the Edentata (text-fig. 38).

The tongues of the animals formerly united in the Order Edentata show three distinct evolutionary lines. One is represented by the Xenarthra, the second by the Pholidota and the third by the Tubulidentata.

The tongues of the Pholidota have a mixture of primitive and specialized features, but the primitive features are more marked than in the other Edentata. The specialized features are the elongation of the tongue, the specialization of the tactile apex and the atrophy of the fungiform and conical papillæ. The primitive features are the vallate triangle, the absence of lateral organs and the large lytta. The sublingua has vanished as in other Edentata.

The Xenarthra have proceeded farther than the Pholidota and Tubulidentata in the elimination of primitive features, for they have lost the lytta and sublingua and the apical vallate papilla. The Dasypodidæ sometimes possess lateral organs, and the conical papillæ are highly developed; their lingual apex has a thick cluster of conical papillæ, but no fungiform papillæ. The Bradypodidæ have shortened tongues, with well-developed conical papillæ; there is a concentration of fungiform papillæ at the apex of the tongue, but lateral organs are absent. The Myrmecophagidæ have elongated tongues; but conical and fungiform papillæ have atrophied, and lateral organs have not developed.

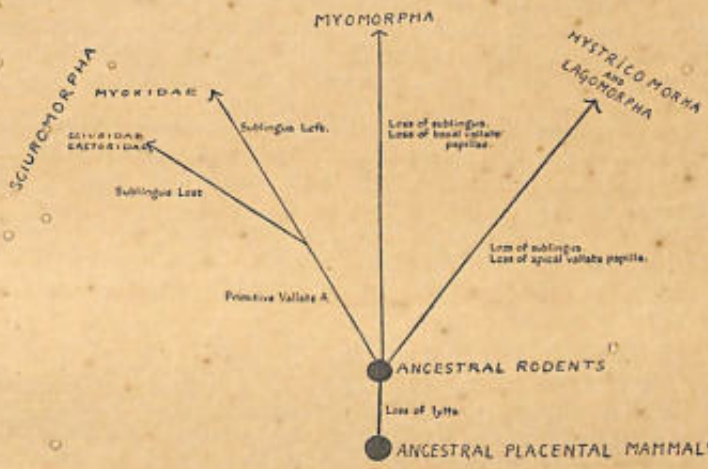
The tongues of the Pholidota and Myrmecophagidæ have elongated to act as prehensile fingers for obtaining the insects upon which they thrive.

The Tubulidentata have long, triangular tongues retaining the primitive vallate triangle, but neither lytta, sublingua nor lateral organs are present. Conical and fungiform papillæ have increased, but are not aggregated into a thick cluster on the apex of the tongue.

Evolution of the Tongue in the Rodentia (text-fig. 40).

The tongues of the Rodents have advanced beyond those of the primitive placental Mammals in the loss of the lytta; and the sublingua has disappeared in all except the Myoxidæ. Lateral organs are frequently well developed, but they are slight or absent in many species. An intermolar eminence has developed in all except some of the primitive Sciuromorpha. Fungiform and conical papillæ have become more numerous, but they do not form large apical clusters in the vast majority of species. The circumvallate papillæ show various degrees of departure from the primitive triangle, but the latter is retained in some species.

Text-figure 40.



Evolution of the tongue in the Rodentia.

When we trace the various forms back, they meet in an ancestral Rodent tongue which only differed from the tongue of the primitive placental Mammal in the loss of the lytta; so it is easily derived from the latter.

The most primitive conditions are retained in the Sciuromorpha, particularly the Myoxidæ. The Sciuridæ are less advanced than the Castoridæ; and these degrees are shown as follows:—

Myoxidæ.	*Sciuridæ.*	*Castoridæ.*
Vallate triangle.	Vallate triangle.	Vallate triangle.
No intermolar eminence.	No eminence.	Large eminence.
Lateral organs absent or small.	Lateral organs moderate.	Lateral organs immense.
Fungiform and conical papillæ progressively increase.		
Sublingua present.	No sublingua.	No sublingua.

The Spalacidæ and Dipodidæ are intermediate in complexity between the Castoridæ and Sciuridæ, for they have intermolar eminences and small lateral organs.

The tongues of the Myomorpha, Hystricomorpha and Lagomorpha have undergone some identical changes, but the Myomorpha differ from the Hystricomorpha and Lagomorpha in the changes which have taken place in the circumvallate papillæ. The common changes have been:—

1. Loss of the sublingua.
2. Formation of an intermolar eminence.
3. Increased development of mechanical papillæ.

The Lagomorpha and Hystricomorpha have increased their lateral organs, and they have lost the apical circumvallate papilla, leaving the basal pair; but these papillæ take various forms, some being like ordinary vallate papillæ, whereas others are merely slits. The Caviidæ and Leporidæ have slits, but all others have typical papillæ. Some of the Hystricidæ have developed special plates on the apex of the tongue. The Chinchillidæ have no lateral organs.

The Myomorpha have small lateral organs, or lateral organs may be missing; and they have lost the basal vallate papillæ, but retained the apical one, which is of large size. This a high degree of change.

The vallate papillary pattern in the Myomorpha and that in the Lagomorpha and Hystricomorpha are not derivable from one another, but both can arise from the primitive triangle, such as occurs in the Sciuromorpha.

Evolution of the Tongue in the Carnivora (text-fig. 41).

In all Carnivora the sublingua has disappeared, but it has been seen in the fœtus. The lytta has persisted in all Fissipedia, but has disappeared in the Pinnipedia; and its dimensions vary considerably. Lateral organs may or may not be present, and the fungiform and conical papillæ exhibit various degrees of specialization. It is, however, in few cases only that these papillæ form a large cluster on the apex of the tongue. The circumvallate papillæ form a V or chevron, so they have specialized, in most cases, but a number of Viverridæ retain the primitive triangle.

In many Ailuroidea the conical papillæ enlarge and form a spinous patch on the oral part of the dorsum, but that structure is absent in some Viverridæ, the Cynoidea, Arctoidea and Pinnipedia.

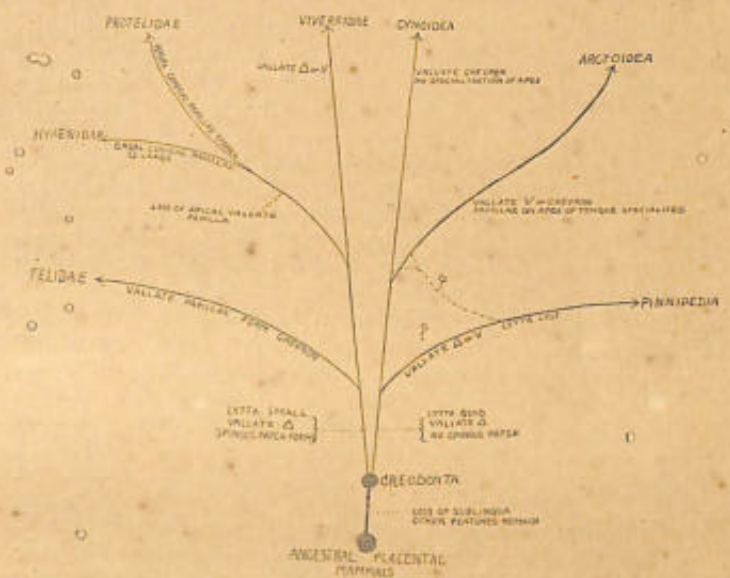
When the various types of tongue are traced backwards, they meet in a tongue which had the following characters:—

1. Three vallate papillæ in a triangle.
2. Fungiform papillæ scanty and not concentrated at apex of tongue.

3. Conical papillæ simple, and not specialized to form a spinous patch.
4. No lateral organs.
5. Lytta present.
6. Sublingua reducing or absent.

These would be the characters of the Creodont tongue, and they are practically identical to those of the primitive placental Mammals. And it is evident that the Rodents showed a different kind of change, for they lost the lytta. It will be shown later

Text-figure 41.



Evolution of the tongue in the Carnivora. ?? indicates that the Pinnipede tongue could arise in either direction

that the Lipotyphla experienced the lingual changes which went on in the Creodonta, but the Menotyphla did not, for they followed the changes in the Prosimiæ.

The Viverrine Section of the Viverridæ (i. e. *Nandinia, Civettictis, Viverra, Paradoxurus, Viverricula, Genetta, Arctictis*) underwent comparatively few changes, for they exhibit the following characters:—

1. Vallate papillæ in a triangle or V.
2. Spinous patch absent or poor.
3. Lytta small.
4. Lateral organs small or absent.

The Herpestine Section of the Viverridæ (i. e. *Cynictis,*

Mungos, Atilax, Crossarchus, Suricata) have advanced more than the previous group in the development of the spinous patch; but the other features are similar.

In most Viverridæ the vallate triangle is present. Some genera always possess it, whilst in others the triangle is occasionally present.

In the Hyænidæ and Protelidæ the apical vallate papilla is absent, leaving the basal pair, the lytta is small and no lateral organs are present. In the former the basal conical papillæ are large; but they are small in the latter. The Protelidæ are more specialized than the Hyænidæ in the characters of the spinous patch.

The Felidæ have advanced beyond all other Ailuroidea in the development of the spinous patch. Their vallate papillæ form a chevron by loss of the apical papilla of a vallate V; and this type is unknown in the other Ailuroidea. The lytta is small, and lateral organs are small or absent.

In the Cynoidea the lytta is relatively larger than in all other Carnivora. The vallate papillæ form a chevron, but lateral organs are small or absent. The fungiform papillæ are scanty and insignificant, and there is no spinous patch. The tongues, in fact, are more primitive than those in the Ailuroidea when the conditions of the vallate papillæ are excluded.

The Arctoidea, like the Cynoidea, have a good lytta. The vallate papillæ form a V or chevron, and the lateral organs are small. No papillæ spinosæ are present. They have, however, advanced beyond the Cynoidea in the specialization of the papillæ on the apex of the tongue; and I showed in my paper on the tongues of the Carnivora (8) that the Mustelidæ, Ailuridæ, Procyonidæ and Ursidæ have developed their papillæ in different ways.

The Pinnipedia have their vallate papillæ in a triangle or V, or they may have none at all. And the lateral organs are well-developed or absent. The lytta is absent and there is no spinous patch.

It is thus evident that the Carnivora show two radiations in their lingual characters. One of these is represented by the Ailuroidea, which develop the spinous patch. The other, represented by the Cynoidea, Arctoidea and Pinnipedia, do not develop the patch. It is impossible to state exactly whether the tongues of the Pinnipedia arise from the tongues of the Arctoidea or not, but the occurrence of vallate papillæ in a triangle in some examples might suggest that they arose from the combined stem of the Cynoidea and Arctoidea rather than from the Arctoid branch. The loss of the lytta does not settle that problem.

Evolution of the Tongue in the Ungulata.

It is impossible to give in detail the evolution of the tongue in the Ungulata, because the characters are so mixed in the

Perissodactyl and Artiodactyl suborders. The tongues of the Artiodactyla, particularly the Cervidæ, are, however, more specialized than those of the Perissodactyla. It is impossible to decide whether they had totally different origins, as many zoologists believe. The sublingua is absent, and there is a lytta in many species; but the lytta is not a remnant of the os entoglossum as it is in the Carnivora and Primates. Hence we

Text-figure 42.

Evolution of the tongue in the Insectivora.

cannot employ it as we have done with the lyttal remnants of the os entoglossum in other organs. Consequently we must show that the Ungulata are among the Orders which have lost both the lytta and sublingua. The Hyracoidea, Proboscidea, Sirenia and Tubulidentata have also lost both. The Hyracoidea, Sirenia and Proboscidea have some lingual features in common, but they differ in the characters of their lateral organs and circumvallate papillæ.

Evolution of the Tongue in the Insectivora (text-fig. 42).

The tongues of the Insectivora represent two radiations corresponding to the Lipotyphla and Menotyphla.

In the Lipotyphla the sublingua has disappeared, but the lytta persists in *Erinaceus* and *Talpa*. Lateral organs have appeared in *Erinaceus* alone. In the Talpidæ and Soricidæ the apical vallate triangle has disappeared, but the primitive triangle persists in other families. Fungiform papillæ are scanty, and there is no large cluster of conical and fungiform papillæ on the apex of the tongue. All these characters, when traced backwards, meet in a tongue which resembles the primitive Mammalian tongue minus the sublingua. The change which led to the Lipotyphlous tongue was similar to that which led to the Creodont tongue (text-fig. 38).

In the Menotyphla, as in the Primates alone of all other Mammals, all the characters of the primitive Mammalian tongue persist, but two distinct types of change in the tongue can be observed. In the Macroscelididæ, as exemplified by *Rhynchocyon*, the sublingua has become reduced as in *Tarsius*. But in *Tupaia* the sublingua has become specialized as in the Lemuroidea. The dorsum is primitive and lateral organs are absent, but the lytta is present. Thus the tongues of the Menotyphla are more primitive than those in the Lipotyphla.

The Lipotyphla and Menotyphla diverged from a common stock, whose members possessed all the characters of the primitive Mammalian tongue.

The Importance of Tupaia.

It is now well known that *Tupaia* agrees with the Prosimiæ in many anatomical details, and I now desire to add the characters of the tongue to the long array of structures examined by other authors. But I limit the term here to the Lorisidæ, Galagidæ and Chiromyidæ and *Tarsius*. There are, it is true, some resemblance between the tongue of *Tupaia* and those of the Lemuridæ, but the latter have undergone much specialization in various directions. The tongue of *Tupaia* agrees with those of the Prosimiæ except the Lemuridæ as follows:—

1. There are three circumvallate papillæ in a triangle.
2. Lateral organs are absent.
3. Fungiform papillæ are not numerous, and there are few or none on the apex of the tongue.
4. There is no marked concentration of tactile conical papillæ on the apex of the tongue.
5. The sublingua and lytta are present.

With the exception of the specializations of the sublingua, which take the form of denticles on its anterior border in *Tupaia* and the Lorisidæ and Galagidæ, all these features are characters of the primitive Mammalian tongue. *Tarsius* has no denticles on its anterior sublingual margin, so its features resemble those of the primitive Mammalian tongue.

Tupaia differs from all Primates except *Homo* and *Simia* in

that the orifices of Wharton's ducts do not open on the extremity of a process of mucous membrane called the frenal lamella.

Tupaia differs from the Lorisidæ and Galagidæ and agrees with *Tarsius* in the following particulars:—

1. The sublingua is closely fixed to the under surface of the tongue, and is reduced in size. It has a very thick median ventral keel ending anteriorly in an expansion.

2. The lytta is double, and there is no lytta of the sublingua. In these features *Tupaia* and *Tarsius* differ from all other Mammals.

Tupaia agrees with the Lorisidæ and Galagidæ and differs from *Tarsius* in having sublingual denticles, which are associated with procumbency of the lower incisor teeth. Procumbency of these teeth is a specialization, for it is absent in the Notharctid and Adapid ancestors of Lemuroidea. Hence it is evident that *Tupaia* has Prosimian characters, with a preponderance in favour of *Tarsius*.

The only placental Mammals possessing a sublingua and lytta are the Prosimiæ and Menotyphla, and it was shown above that the dorsum of the tongue is primitive in all except the Lemuridæ. Now the lytta and sublingua are heritages from the Reptilian tongue, so they cannot be new developments acquired independently in the Prosimiæ and Menotyphla. Hence we must assume that these groups of animals had a common origin from Mesozoic Menotyphla, the animals which Gregory terms the insectivorous pre-Primates. The sublingua would be unspecialized.

Evolution of the Tongue in the Primates (text-figs. 43–45).

The Prosimiæ fall into two groups—Lemuroidea and Tarsioidea—which represent different lines of evolution from common ancestors, and we can deduce the characters of the tongues of the Prosimiæ Primitivæ. The Lorisidæ, Galagidæ and *Tarsius* all agree in the possession of the primitive type of dorsum. The sublingua is specialized in the Lemuroidea, but reduced and unspecialized in *Tarsius*. Hence we have two widely dissimilar types of change in the sublingua; and when we trace them back they meet in a tongue with a primitive dorsum and an unspecialized, unreduced sublingua as in the Mesozoic Menotyphla. So the tongues of the Prosimiæ Primitivæ showed little advance, if any, beyond these. The changes in *Tarsius* have continued on in the Anthropoidea, and the specialization of the sublingua and other features put the Lemuroidea out of the direct ancestry of Man.

The true Lemurs have become highly specialized as follows:—

1. The tongue has enlarged.
2. The sublingua is specialized.
3. The lytta has vanished.

4. Lateral organs are well-developed.
5. The vallate papillæ form a Y.
6. Conical and fungiform papillæ are very numerous.
7. There is a great concentration of papillæ on the apex of the tongue.

The tongues of the Lemuridæ are as specialized as those of the Simiidæ.

In *Tarsius* the primitive dorsum is retained, but the sublingua and lytta are undergoing reduction. And when we trace these characters, and those in the Primitive Monkeys, to be next described, they meet in Tarsioids, whose tongue shows a small advance on the condition present in the Prosimiæ Primitivæ.

In Primitive Monkeys the tongue shows an advance over that of their Tarsioid ancestors in two ways—the reducing changes in the sublingua and lytta proceeded farther, and the tactile and gustatory organs began to increase. The characters would be:—

1. Lytta absent.
2. Sublingua small.
3. Vallate papillæ still have the primitive triangle.
4. There were small lateral organs.
5. The papillæ concentrate at the apex of the tongue.

With the exception of the characters of the sublingua all these features are present in the Hapalidæ, which are more primitive than all other Anthropoidea in the characters of the tongue. And it is shown below that the Cebidæ are more primitive than the Catarrhini, and more specialized than the Hapalidæ in the characters of the tongue; so the primitive monkey tongue belonged to a Platyrrhine monkey.

All the Monkeys and Gibbons have completely lost the sublingua, whereas the Great Apes and Man have retained it wholly or in part. Hence the Monkeys and Gibbons have evolved farther than the great Apes and Man in the elimination of the last heritage of the Reptilian tongue.

The progressive increase in the tactile and gustatory papillæ, which began in the Primitive Monkeys, is probably associated with the greater use of the hands, jaws and tongue in the manipulation of food.

The Cebidæ have become more specialized than the Hapalidæ in the characters of the tongue in the following ways:—

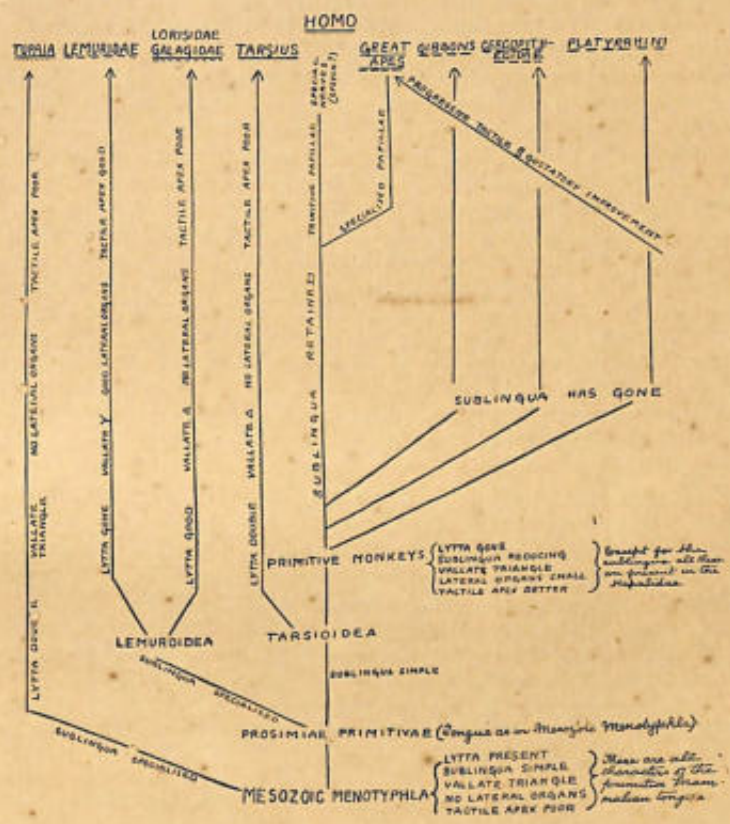
1. The tongue has enlarged.
2. The lateral organs are better developed.
3. The number of vallate papillary types has increased.
4. Papillæ are more numerous on the apex of the tongue.

The Catarrhini have advanced farther than the Platyrrhini in the specialization of the tongue. The lateral organs are better developed and there is a thick cluster of papillæ—both tactile and gustatory—on the apex of the tongue. The Gibbons have advanced beyond the Cercopithecidæ in the following directions:—

1. The lateral organs have so increased that they are as well developed as those in the Chimpanzee.
2. The vallate papillæ have increased to form a Y.
3. The conical papillæ on the base of the tongue have become very large except in the Siamang.

Thus it can be seen how the tactile and gustatory papillæ

Text-figure 43.



Evolution of the tongue in the Primates. The underlinings in the top line are as follows: ——— primitive tongues; — — — specialized tongues; ..... primitive features predominate; ═══ specializations predominate.

exhibit a progressive increase from those in the Primitive Monkeys up to those in the Gibbons.

In the stock of the great Apes and Man the sublingua is retained, but it is larger in the young than that in the adult. It is frequently absent in the Orang, and this would be in favour

of the view that that animal separated from the stock of the African Simiidæ and Man.

The Gorilla and Chimpanzee show an advance over Man in the characters of the tongue. Their tongues have much larger lateral organs, and the conical papillæ on the bases are enormously developed. In Man, on the contrary, the lateral organs are poor, and there are no larger conical papillæ on the base at all. Differences are also seen in the vallate papillæ. In Man the sides of the primitive triangle have been filled in to produce a V, but they form a Y in the Gorilla and Chimpanzee.

Sir Frederick Mott has recently detected peculiar nerve-endings in the apex of the human tongue, and he thinks they may be associated with speech. They are absent in the Chimpanzee.

The results which I have thus stated agree with those obtained by workers in other subjects, notably Professor Elliot Smith and Dr. Gregory of the American Museum of Natural History. But it is noteworthy that my results have been obtained by a totally different method. Professor Elliot Smith has made use of the progressive losses of the olfactory sense, and the progressive increase in the neopallium which has resulted from improved vision, touch and hearing. In my method the features running through the whole Order are the progressive loss of the heritages from the Reptilian tongue, and the progressive increase in touch and taste functions of the tongue. There may possibly be a relation between the diminution in olfaction and the increase in taste.

It is not mere coincidence that the progressive specialization in the tactile and gustatory functions of the tongue begins in the Primitive Monkeys in which the complete visual apparatus—maculæ luteæ, incomplete optic decussation, and prefrontal ocular co-ordinating centre—has been established.

In a proper phylogenetic tree there should be a persistence of primitive features from the roots right up to the top of the trunk; and the branches represent animals which fell out. And if text-figures 38 and 43 are compared, one can see a direct line extending from the primitive Mammalian tongue right up to the tongue of Man.

Inter-relation of the Tongue and other Sense-organs.

There is an intimate relation between the type of vision, the tactile and muscular functions of the hands, the loss of vibrissæ and the specialization of the apex of the tongue. And the evolution of these functions has run on parallel lines.

The different types of visual apparatus are well known, but it will be necessary to refer to the main points here, in order to demonstrate how changes therein run parallel to changes in the tongue. There are really three types of vision—panoramic, binocular and stereoscopic, but we are only concerned here with the last two. In *binocular vision* the images from the two eyes

are fused by the brain to form one, and the animal does not perceive clearly the details, depth and texture of objects. Moreover, it moves its head as a whole in order to bring objects to a point equidistant from the two eyes. In *stereoscopic vision* the animal sees clearly depth, details and texture of objects, and its eyes move independently of the head. Moreover, each eye can adjust its position independently of the other, so that clear images of an object looked at are focussed on corresponding points on the two retinæ. The latter point is important, because the object may not be equidistant from the two eyes as the result of obliquity or directness with reference to them. The apparatus necessary for the two types can be seen in a comparison between *Tarsius*, which has binocular vision, and Man, who has the most perfect stereoscopic vision. Between these extremes the other Primates can be ranged in an ascending series.

In *Tarsius* (text-fig. 44) the eyes are devoid of maculæ luteæ on which, as corresponding points, images can be focussed. And each eye is controlled by the opposite side of the brain, because the optic nerves cross completely in the optic chiasma (B). The oculomotor nucleus (C) consists of two lateral parts united together, and between them is a small central nucleus. The Edinger-Westphal nucleus is unsplit. In higher Primates the centre for convergence of the eyes develops in the central nucleus, and the Edinger-Westphal nucleus becomes the nucleus of accommodation. In Man (text-fig. 45), as in Monkeys and Apes, there are sensitive maculæ luteæ in the eyes, which are corresponding points on which objects are focussed. Each eye is controlled by both sides of the brain, because the fibres of the optic tracts are so arranged that some pass to each hemisphere from each eye. The oculo-motor nucleus undergoes progressive changes. The nucleus of accommodation is split up in all animals from Marmosets to Man, but the nucleus of convergence enlarges progressively to reach its highest development in Man.

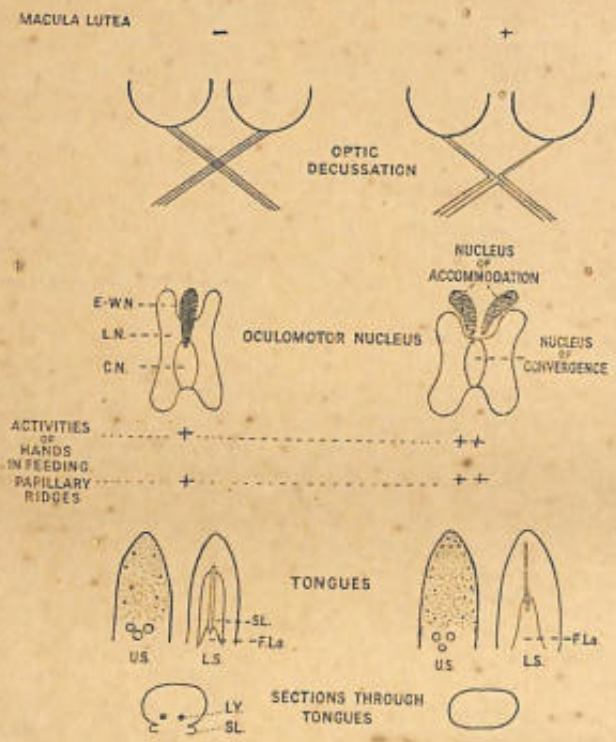
In text-figs. 44 and 45 it is shown how the papillary ridges on the fingers and the papillæ on the apex of the tongue become more and more highly developed from *Tarsius* up to Man. And the muscular activities of the hand improve and are more and more guided by the eyes. It is the action of the hand, resulting from the improved vision, which has led to the specialization of the tongue, as can be seen by a study of the Carnivora. These animals have stereoscopic vision with sensitive spots on the retinæ but no maculæ, to enable them to judge distance in pouncing on their prey, but they do not convey food to their mouths with their paws, and the apical papillæ on their tongues are not specialized*.

Stereoscopic vision with maculæ enables animals to see the details, colour and textures of foods, and a wider range of substances will appear to them as good to eat. Under the guidance

* Thus Carnivora like other animals which use their jaws to seize food have no specialization of the apex of the tongue.

of the eyes they will pluck fruits or grub for insects, or they will catch insects on the wing. The hands convey these numerous foods to the mouth, and the point of the tongue comes forwards (see p. 742). The greater number of foods applies a greater number of chemical substances to the point of the tongue and the tongue

Text-figure 44.



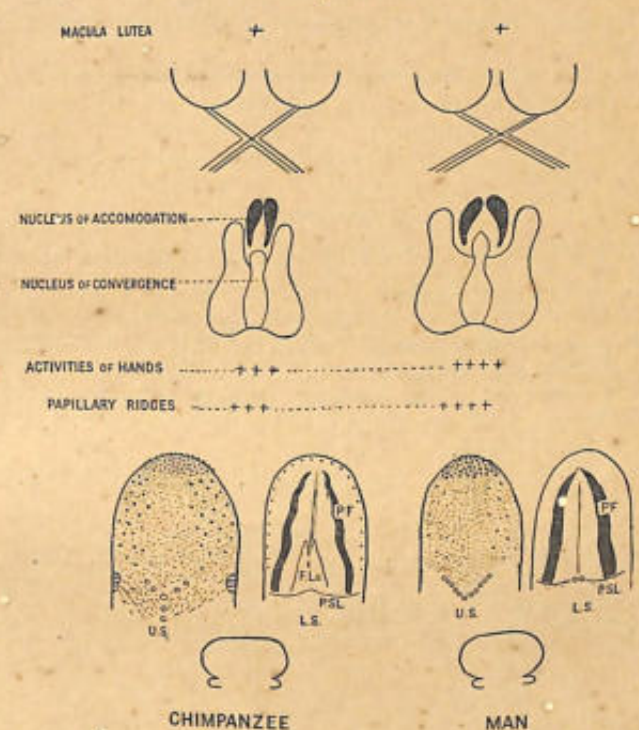
Evolution of the inter-relation of eye, hand and tongue. C.N., central nucleus of Perlia; E-W.N., Edinger-Westphal nucleus; F.La., frenal lamella; L.N., lateral nuclei; LY., lytta; SL., sublingua; LS., US., lower and upper surfaces of tongue. The oculo-motor nucleus of *Tarsius* is by the late Professor John Hunter, that of the Marmoset is after Brewer.

perceives the texture of foods by touch. And the result of the interaction of all these factors is specialization of the apex of the tongue. Moreover, it must not be forgotten that the human infant gains information of its environment by touching objects with the point of its tongue.

It is known that the maculæ luteæ have developed as the result of prolonged arboreal life and the use of the hands in feeding, and another result is the specialization of the apex of the tongue.

The question may be asked why *Lemur* has a specialized apex, but *Nycticebus* has not, although both have procumbent lower incisors, and both use their hands in feeding. But a study of

Text-figure 45.



Evolution of the inter-relation of eye, hand and tongue. The oculo-motor nuclei are after Brouwer. P.F., plica fimbriata; P.SL., plica sublingualis. Other letters as in text-fig. 44.

diet and habits will explain. *Lemur* is a diurnal animal with some binocular vision. It selects food by smell and by ocular perception, particularly the latter. It conveys food to the mouth on many occasions by hand, and sometimes it seizes it in its jaws. But the tongue explores the food in every instance before it is ingested, this action being favoured by the procumbent incisor teeth. *Nycticebus* is a nocturnal, mainly insectivorous animal

with better binocular vision than *Lemur*. Its colour sense is probably absent. When inspecting food it moves its head about whereas *Lemur* usually keeps it steady. What it does in the dark we do not know, but the apex of the tongue does not get so much work to do as in *Lemur*. *Tarsius* is similar to *Nycticebus* in its lingual characters.

Lemur can use its tongue as an explorer and detector of taste impressions because of its procumbent lower incisors. The human infant can do so because of its toothless jaws, and its fungiform papillæ are more numerous than those in the adult. When teeth develop the hand places the food past the teeth and the tongue touches it.

The observations recorded in this paper demonstrate the close inter-relation of eye, tongue and hand: and the progressive increase in these structures is intimately related to the loss of olfaction and the steady increase in the neopallium.

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The following are my former papers on the Mammalian tongue.

1. General Introduction. P. Z. S. 1920, pp. 115–129.
2. Family Simiidæ. P. Z. S. 1921, pp. 1–29.
3. ,, Cercopithecidæ. P. Z. S. 1921, pp. 277–322.
4. Cebidæ and Hapalidæ. P. Z. S. 1921, pp. 497–524.
5. Lemuroidea and Tarsioidea. P. Z. S. 1921, pp. 741–755.
6. Summary of the Tongues of the Primates. P. Z. S. 1921, pp. 757–767.
7. Cetacea, Sirenia and Ungulata. P. Z. S. 1922, pp. 639–657.
8. Carnivora. P. Z. S. 1923, pp. 129–153.
9. Edentata, Dermoptera and Insectivora. P. Z. S. 1923, pp. 515–529.
10. Rodentia. P. Z. S. 1924, pp. 725–741.
11. Marsupialia and Monotremata. P. Z. S. 1924, pp. 743–755.

31. Notes on East African Batrachians, collected 1920–1923, with the Description of four new Species. By Arthur Loveridge, C.M.Z.S., F.E.S.

(Submitted for publication by permission of the Director of the Museum of Comparative Zoology, Cambridge, Mass., U.S.A.)

[Received March 7, 1925: Read April 21, 1925.]

(Plates I., II.*)

The following notes are based on a collection of Cæcilians, Toads, and Frogs made by the writer during two and a half years in Tanganyika Territory (late German East Africa). There have also been included some few specimens from the 1915–1919 collection which were not available for Miss Procter's paper †; the jar which held them having been mislaid was not recovered till after her paper was in the press.

Representatives of all the East African families were collected, nineteen of the twenty-six genera, and very nearly half the species. The numbers are distributed as follows:—

Family.	*Genera.*	*Species.*	*No. of Specimens.*
Cæciliidæ	3	3	3
Pipidæ	1	2	134
Bufonidæ	2	6	40
Ranidæ	9	26	302
Brevicipitidæ	4	5	132
Total...	19	42	611

Nearly half the collection is now in the Museum of Comparative Zoology, and for convenience of future reference the Museum's registration numbers for such specimens are given. Other numbers given refer to specimens now in the collection of the University of Michigan Museum.

It was originally intended that Miss Joan Procter, F.L.S., should work over and write up this collection, which was brought home in June 1923; but, owing to pressure of other work and engagements, she found herself unable to do so, and forwarded the collection to me here in January 1925. I take this opportunity of thanking Miss Procter for having provisionally sorted out many of the specimens and kindly correcting the proofs of this

* For explanation of the Plates see p. 791.

† Procter, 1920, Proc. Zool. Soc. pp. 411–420.

paper during my absence. To my chief, Dr. Barbour, I am also very grateful for much advice and help given in various difficulties.

The principal item of interest, if the identification be correct, is the discovery of *Scolecomorphus* in the Uluguru Mtns. This Cæcilian genus was described in 1883, with the "probable vicinity of Lake Tanganyika" given as its type-locality. Günther in 1892 recorded it from Nyasaland. It was also remarkable that as only three Cæcilians were taken, and all on or near the Uluguru Mtns., that they should represent the only three species known from the Territory.

The finding of *Bufo anotis* Blgr. a thousand miles north of its type-locality in Mashonaland and the occurrence of a new and related species in central Tanganyika Territory are also worth noting. The affinity between the fauna of the Usambara and the Uluguru Mtns. is again emphasized by the finding of many interesting species in the latter range which were described from the Usambara Mtns. and only known from their type-localities. These two widely-separated ranges are forest outliers of the West African rain-forests, with whose faunas they show relationship.

From East to West and South to North the localities mentioned in this paper are:—

TANGANYIKA TERRITORY.

Morogoro District—Mkuyuni, Bagilo, Uluguru Mtns., Tindiga, Kisanga, Madazini, Uliya, Kipera, Kilosa, Mbwenyi.
Dodoma District.—Ikikuyu, Itende, Pwaga, Mahaka, Saranda, Ndogwe, Gwao's.
Kondoa Irangi District.—Ulugu, Mkalama, Semo River, Mariyoshi River.
Mwanza District.—Sagayo, Nyambita.
Bukoba District.—Kabare.

KENYA COLONY.

Frere Town, Nairobi, Parklands, Kisumu.

Should difficulty be found in locating any of these places, some of which are only native villages, they are marked upon a map of Tanganyika Territory that appeared in the 'Proceedings of the Zoological Society' for 1923, facing page 685.

CÆCILIIDÆ.

BDELLOPHIS VITTATUS Boulenger.

Boulenger, 1895, Proc. Zool. Soc. p. 412, pl. xxiv.
Nieden, 1915, Mitt. Zool. Mus. Berlin, vii. p. 389.

1 (M. C. Z. 10301). Bagilo, Uluguru Mtns., 1922.

This specimen has been compared with the type by Miss Procter, who identified it. It is more than twice the size of the

type, and is the largest example recorded, as it measures 345 mm. in total length. It is 9 mm. in greatest diameter. It has 140 circular folds as against 125 in the type, but Nieden has recorded a specimen from the Nguru Mtns. (which lie half-way between the Usambara and Uluguru ranges) that measures 208 mm. and has 148 body-rings. My specimen also differs in coloration from Boulenger's plate and description in that the whole of the back is black, not merely a narrow band along the vertebral line. The present record extends the known southward range considerably, as the Uluguru Mtns. are approximately 120 miles south of the Usambara.

It is difficult to see how *B. unicolor* Boettger can stand as a distinct species, though probably a good colour race. The only difference between it and *B. vittatus* appears to lie in the fact that the relatively narrow black vertebral band of Boulenger's figure (said to be a broad band in the text), and which covers the whole upper surface in my Uluguru specimen, has so spread in *B. unicolor* as to cover the ventral surface to the exclusion of any yellow. Peccetoni in Witu, K.C., the type-locality of *B. unicolor*, lies about sixty miles farther north of the Usambara than Bagilo does to the south. The diameter into the body-length is 24·61 times (Peccetoni), 26·66 times (Usambara), 36·33 times (Uluguru). All the other characters mentioned by Boettger are now recognized as being well within the range of *B. vittatus*.

(?) Scolecomorphus kirkii Boulenger.

Boulenger, 1883, Ann. Mag. Nat. Hist. (5) xi. p. 48.
Günther, 1892, Proc. Zool. Soc. p. 555.
Nieden, 1913, 'Das Tierreich: Gymnophiona,' p. 28, fig. 20.

1 (M.C.Z. 10302). Bagilo, Uluguru Mtns., 22.vii.21.

Found dead upon a path by one of my native collectors. It is obviously a young one, its total length being only 82 mm. The colouring is uniform blackish olive above and below, but the tail and underside of the head are yellow in spirit. Dr. Thomas Barbour, who kindly examined and identified it for me, says that while it is undoubtedly a *Scolecomorphus* as far as one can judge by its dried skin agreeing with the figure and description, its identification with *kirkii* must be regarded as provisional until fully-adult specimens can be obtained from the Uluguru. Too much reliance should not be placed on the record until confirmed by further material.

Boulengerula boulengeri Tornier.

Tornier, 1897, 'Kriechthiere Deutsch-Ost-Afrikas,' p. 164.

1 (M.C.Z. 9502). Mkuyuni, S.E. of Uluguru Mtns., 30.viii.16.

This rare Cæcilian was obtained under rather unusual circumstances during the East African campaign. We were busily

engaged in "digging-in" under an unpleasant shell-fire, when it was unearthed by one of my fellow troopers in the Mounted Rifles. He humourously called out that one of my snakes had escaped, and that, if I did not come over and take charge of it at once, he would run his bayonet through it. Needless to say, when I saw what it was I very gladly "took charge of it."

It was identified by Dr. G. A. Boulenger. It measures 165 mm. in length and is yellowish-grey in colour both above and below, tinged with black on the tip of the tail and snout. Hitherto the species has only been known from its type-locality in the Usambara Mtns. The present record tends to further demonstrate the homogeneity of the vertebrate fauna of these two widely-separated mountain ranges.

PIPIDÆ.

XENOPUS LÆVIS (Daudin).

Bufo lævis Daudin, 1803, Hist. Nat. des Rainettes, p. 85, pl. xxx. fig. 1.

Xenopus lævis Boulenger, 1905, Proc. Zool. Soc. ii. pp. 248-250.

Xenopus victorianus Ahl, 1924, Zool. Anz. Leipzig, lx. pp. 270–271.

3 (M.C.Z. 10302*a*). Bagilo, Uluguru Mtns., 18.v.22, 13.vi.22.

Ahl has recently described a clawed frog from Bussisi, Victoria Nyanza, under the name of *Xenopus victorianus*. The description is apparently based on a single individual collected by Emin Pasha. The characters cited by Ahl, as distinguishing it from *X. lævis*, seem to me hardly of specific importance when one takes into consideration the great variation exhibited by all species of this genus, many of which, like *lævis* and *müellerí*, have very extensive ranges. The points of distinction emphasized by Ahl are:— (i.) Larger eye. Noble *, after studying a series of over 260 *X. tropicalis*, showed that in specimens of the same size and from the same locality there was over a millimetre difference in the diameter of the eyes. *X. fraseri* Blgr., which was in part described on the basis of this character, had subsequently to be referred to the synonymy of *tropicalis*. (ii.) The fact that the two inner fingers are of equal length and longer than the two outer ones. This is the typical condition in my long series of *X. muelleri*, but there are many departures from the rule. Even my three *X. lævis* are every one different in their respective finger-lengths, and not always the same on both hands! Thus (*a*) has the inner two of equal length and longer than the two outer ones, like Dr. Ahl's *victorianus*; (*b*) has the first and third of equal length, with the second slightly longer and the fourth slightly shorter; (*c*) has the right hand like "*b*," but on the left hand,

* Noble, 1924, Bull. Am. Mus. Nat. Hist. xlix. art. ii. p. 161.

while the fourth finger still remains the shortest, the first, second, and third increase in length in the same order. (iii.) The shorter tibia, which in *victorianus* is contained three times in the length from snout to vent, and in *lævis* from two to two and a half times, as stated by Ahl. In my three specimens it varies from one and three-quarters to two and a quarter times. This last character seems to be the only one of any value, and might well be included within the range of variation of the species.

The characters in which *victorianus* differs from *muelleri* are all established characters of *lævis*, though the presence or absence of vomerine teeth in *Xenopus* has been shown by Boulenger * to be without even specific importance.

I have also recently examined a basketful of half-grown, dried, clawed frogs from Kissalo Market, S.W. Uganda, which were brought back for the Museum of Comparative Zoology by Dr. J. C. Phillips from his 1923–24 expedition to the Kivu region. These frogs are exposed for sale as an article of diet by the Bahutu natives. After soaking some of these frogs for examination, I have little doubt that they belong to this species, which Boulenger has recorded from Uganda, and Tornier from Bukoba and Kafuro.

XENOPUS MUELLERI (Peters).

Dactylethra muelleri Peters, 1844, Monatsber. Akad. Wiss. Berlin, p. 37.

Xenopus muelleri Boulenger, 1905, Proc. Zool. Soc. ii. pp. 248–250; Noble, 1924, Bull. Am. Mus. Nat. Hist. xlix. art. ii. pp. 157–160.

29 (M.C.Z. 10303–8). Parklands Forest Reserve, Nairobi, 22.iii.15.
84 (M.C.Z. 10309–14). Kilosa, 30.iii.21, 15–30.iii.22.
1 (M.C.Z. 10315). Ndogwe, 30.ix.22.
8 (M.C.Z. 10316). Sagayo, 8.xi.22.
9 (M.C.Z. 10317). Zanzibar, 7.viii.23.

Called *Hamuru* in Kinyaturu, *Kisisulu* in Kinyiramba.

Mueller's Clawed Frogs were so abundant in a stream at Kabete that I took as many as six with one sweep of a net on February 20th, 1915. One individual found its way into our semi-flooded trenches at Arusha on April 17th, 1916, whilst the wells from which we drew our water-supply at Handeni in June 1916 literally teemed with them; and as these wells were very deep, there was no way, so far as I could see, in which they could escape from them. Others were seen in freshwater pools among the rocks near the shore at East London, South Africa, where I caught one which was sharing its retreat with some crabs.

The series of twenty-nine from the Forest Reserve were all taken from one pool, one of several left in the bed of the stream which flows through the forest. The stream dries up at the end

* Boulenger, 1919, Revue Zool. Africaine, vii. fasc. 1, p. 3.

of the rainy season, but the larger pools persist until the advent of another rainy season, except in years of unusual drought. The same conditions obtain in the Nairobi River out in the open sun-baked plains, where clawed frogs are just as numerous as in the gloomy pools of the Forest Reserve.

Individuals ranged in size from 40 to 90 mm. (snout to vent measurements). The three largest specimens were all females (77 to 90 mm.), the largest male only measuring 72 mm. When taken they were uniformly dirty drab, but on being washed free of mud and slime showed considerable variation in colouring, which was noted at the time as follows:—"Dorsal surface mud-coloured, with mottlings and usually some half-dozen irregularly-scattered black spots. One individual had only two spots, but these were exceptionally large and noticeable. The 'tuber-like lateral lines' of Boulenger remind one strongly of the cicatrices which many of the African races raise on their chests and faces as tribal marks. Ventral surface whitish grey, with reddish blood-like mottlings about the throat. Posteriorly, and on the whole lower surface of the hind-limbs, orange with grey spots. In one specimen (10306) the orange extended anteriorly to the fore-limbs; this individual was very light-coloured dorsally. The smallest specimen (10307) had no orange whatever, but was mottled with grey and white over the whole of the lower surfaces. One adult has only two black claws on its hind-feet instead of the usual three."

Coloration of a live Kilosa frog taken on 30.iii.21. was: "Above dark olive. sides lighter. Below dirty white, under surfaces of limbs bright orange, spotted with pearly grey. In the young the fine grey spots on the belly are so numerous as to cover the whole of the under surface of the belly and the bright orange limbs." Many of the Kilosa specimens taken on this date were very young, and only measured 20 mm.; the largest adults were slightly smaller than the Nairobi ones. After heavy rain I found one of these creatures floundering about in a muddy road.

At Sagayo, specimens were obtained by my collector in pools left in the bed of the Simiyu River. These examples, from 40 mm. upwards in length, were bright orange over the *entire* under surface, but retained the usual mottlings. Only two individuals were under 40 mm. long, and these were but faintly tinged with orange.

At Ndogwe—a dry and arid region when I was there—I was surprised to find this species present in great numbers in a small muddy pool, which had been dug out by the natives, between two big boulders. The region seemed so unsuitable for aquatic frogs—the soil was sandy and the vegetation chiefly consisted of dense, and frequently impenetrable, thorn-bush.

One Nairobi frog (10303) had the heads of two soldier-ants (*Dorylus nigricans*) attached to it as evidence of a past attack from which it had escaped victorious—amphibian war medals.

BUFONIDÆ.

BUFO BRAUNI Nieden.

Nieden, 1910, Sitz. Ges. Naturf. Berlin, p. 450.

6 (M. C. Z. 10324–6). Bagilo, Uluguru Mtns., 5. v. 22, 3. vi. 22.

These range in size from 26 to 90 mm., and show great variation in dorsal markings. The largest has a well-marked chevron uniting the occipital region with the supraoculars; on the others this is only represented by black blotches. The comparative smoothness of the præfrontal region is not noticeable in the young. This is a very distinct species, previously only known from the type-locality—Amani in the Usambara Mtns.

BUFO CARENS A. Smith.

A. Smith, 1849, Illus. S. Africa, iii. pl. lxviii. fig. 1.

2 (M. C. Z. 10327–8). Kilosa, 14. iii. 21.
4 (M. C. Z. 10329). Ikikuyu, Dodoma, 12. ii. 23.

The two Kilosa toads were taken in embrace; the male measures 71 mm. and the female 60 mm.; both are in exceptionally fine condition. In two of the Ikikuyu toads the lateral fold, generally noticeable in males and sometimes used as a key character, is only indicated by a dark band, light-edged above.

The Ikikuyu toads were found in a big pool, below and to one side of a small waterfall in a rushing rock-bound torrent coursing down the mountain side and hedged in on either hand by almost impenetrable scrub. They were all engaged in inflating their vocal sacs, the resultant noise being of little assistance in locating them. They were resting among an accumulation of debris, consisting of branches and vegetation swirled into this backwater, and were not very difficult to catch. My collector secured all four by wading in behind them, approaching his hand cautiously beneath the water, and seizing their hind-legs while their attention was diverted to me. Some of them dived at his approach, but soon reappeared.

BUFO REGULARIS Reuss.

Reuss, 1834, Mus. Senckenberg. i. p. 60.
Noble, 1924, Bull. Am. Mus. Nat. Hist. xlix. art. ii. pp. 168–174.

7 (M. C. Z. 10318). Nairobi, 29. iii. 15.
7 (M. C. Z. 10319). Kilosa, 7. iii. 21, 16–19. iii. 22.
2 (M. C. Z. 10320). Saranda, 10. iii. 22.
1 (M. C. Z. 10321). Kipera, 5. viii. 22.
1 (M. C. Z. 10322). Mariyoshi River, 15. x. 22.
1 (M. C. Z. 10323). Frere Town, 31. xii. 22.

Called *Tandu* in Kinyiramba and Kinyatùru.

Square-marked Toads were met with in almost every locality where a toad could live, and on this account were not collected.

They were common in Pooma, and two brought me whilst there were a bright brick-red colour, harmonizing well with the soil. Even while held in my hand the dorsal markings came out distinct in dark green, and the red began to fade away.

The toad from Mariyoshi River was taken at a point where the river cuts across the Mwanza-Mkalma path. When I was there it was the height of the dry season, and the only sign of a river was its broad and sandy bed. I instructed my men to dig for water in the sand, and when they had dug down two feet I espied this young toad, very plump and swollen with moisture. On being picked up it discharged a considerable jet of water. Water was reached at four feet below the surface.

The advent of the heavy rains in March over a good deal of the Territory would appear to cause these toads to leave their æstivating quarters and move about in search of breeding-pools. The actual breeding-season, however, varies as widely as the climatic conditions in different parts of Tanganyika Territory.

The Square-marked Toad forms the staple food of such snakes as the Black-necked Cobra (*Naia nigricollis*), Night Adder (*Causus rhombeatus*), and the Puff Adder (*Bitis arietans*), in whose stomachs they were frequently found; as well as in those of the Spotted Wood-Snake (*Philothamnus semivariegatus*) and the Nilotic Monitor (*Varanus niloticus*). A young one was snapped up by a captive Giant Chameleon (*Chamæleon melleri*).

BUFO ANOTIS Boulenger.

Boulenger, 1907, Ann. Mag. Nat. Hist. (7) xx. p. 48, pl. iii.

1 (M. C. Z. 10330). Ulugu, Usshora, 7. xi. 21.
1 (Univ. Mich. 61393). Nyambita, Mwanza, 10. xi. 22.
2 (M. C. Z. 10331–2). Kabare, Bukoba, 15. i. 23.

These conform exactly with the description of Swynnerton's Earless Toad, of which three males were found in the Chirinda Forest, Mashonaland, in 1907. Apparently none of my specimens are full grown, as they only measure 20 to 24 mm. as against 40 mm. in the types which were adult.

BUFO MICRANOTIS, sp. n. (Pl. I. fig. 1.)

Female (M. C. Z. 10333). Kilosa, 24. i. 21.
Male (M. C. Z. 10334). ,, ,,
Male (Univ. Mich. 61367). Uluguru Mtns., 1. iii. 21.

Type. No. 10333, Museum of Comparative Zoology. An adult female from Kilosa, Morogoro District, Tanganyika Territory. Collected by A. Loveridge, January 24th, 1921.

Affinity. Near *Bufo anotis* Boulenger.

Diagnosis. Smaller size of breeding male, which is 22 mm. in length from snout to vent as against 40 mm., which is the length

of the type of *Bufo anotis*, which is also a breeding male. Absence of webbing on hind-feet and shorter toes; tubercles on belly and hinder part of back not so pronounced as in *anotis*. Difference in colour of males and presumably in females, the female of *anotis* being unknown; entire absence of gamboge-yellow on throat and belly in *micranotis*, thus:—

Throat of male gamboge-yellow, unspotted. Length 40 mm..... *anotis.*
Throat of male and female white, heavily marbled with black. Length 22 mm..... *micranotis.*

Description. Crown without bony ridges; head as long as broad; snout pointed, truncated, projecting beyond the mouth, with strong canthus; loreal region nearly vertical, slightly concave; interorbital space flat, much broader than the upper eyelid, no tympanum. Fingers short, blunt, with strong double subarticular tubercles, first shorter than the second; toes without web, very short, first and fifth scarcely larger than the metatarsal tubercle; two round, subconical, metatarsal tubercles; subarticular tubercles under the fourth toe paired, distinct; no tarsal fold. The longest toe of the adpressed hind-limb reaches the posterior border of the eye in the female type (in the paratype Kilosa male it reaches the anterior border of the eye; in the paratype Uluguru male it reaches the tip of the snout). Upper and lower parts covered with small smooth warts, most numerous and strongly developed on the head, widely scattered on the posterior part of the back. Parotid glands present, but not very noticeable, extending backwards to the shoulder.

Coloration. In life, above chocolate-brown, darkest on head, a very few black specks on back; limbs chocolate-brown, very indistinctly blotched. Below white, so heavily marbled with black anteriorly as to only show a few white specks and blotches; posteriorly a large patch free from black pigmentation.

The colour of the Kilosa male as noted in life was: "Snout to back of eyes dark sepia, remainder of head and back blotchy grey-brown, with small patches of sepia; sides sepia-coloured; limbs coloured above and below grey-brown. Below white, heavily marbled with black so as to almost obliterate white except for a small patch in the pre-anal region."

In spirit the female remains the same; the two males are slightly different from the colour noted in life. They are pale brown above, black on head and sides of face; in the centre of the back is a pair of noticeable and distinct pale blotches; the back shows black specks similar to those found on the female.

Measurements:—

Female,	length from snout to vent	23	mm.
Kilosa male,	„ „	22	„
Uluguru male,	„ „	20	„

Remarks. The pair from Kilosa were taken *in coitu* by my native collector, Salimu bin Asmani; they were taken near the boma, probably in the Government shamba, or along the river.

In the reduction of the first and fourth finger and first and fifth toe, as well as in general appearance, this little toad shows a striking similarity to the figure of *Atelophryne minuta* Boulenger* from Basile, Fernando Po, which Noble† regards as synonymous with the Brevicipitid described by Andersson‡ as *Didynamips sjostedti*. That the Kilosa specimens are not Brevicipitids I am assured by Dr. Barbour, who has kindly examined their structure, which is arciferal. They furnish, then, a case of parallelism in development, probably due to a similarity in habits.

PSEUDOPHRYNE VIVIPARA Tornier.

Tornier, 1905, Sitzber. Akad. Wiss. Berlin, ii. p. 855.

3 (M. C. Z. 10335–6). Bagilo, Uluguru Mtns., v. 21, 28. iv. 22, 16. v. 22.

These three examples of Tornier's Viviparous Toad measure 57 mm., 54 mm., and 27 mm. respectively. The smallest is pale brown above, slightly purplish below; the three-quarter grown individual is chocolate-brown above, purplish black below; the adult is almost uniformly coloured, being black above and purplish black below; none of them exhibit any trace of markings. Both the larger individuals are females with a few big eggs in their ovaries.

RANIDÆ.

RANA MWANZÆ, sp. n. (Pl. II.)

Two females (M. C. Z. 10337–8). Sagayo, Mwanza, 8. vi. 22.

Type. No. 10337, Museum of Comparative Zoology. An adult female from a pool in the otherwise dry bed of the Simiyu River at Sagayo, Mwanza, Tanganyika Territory. Collected by A. Loveridge, November 8th, 1922.

Affinities. Related to *Rana beccarii* Boulenger of Eritrea and *Rana ehrenbergii* Peters of Arabia.

Diagnosis. It differs from *beccarii* in having a conspicuous tympanum; first finger longer than the second; shorter hind-limb, the tibio-tarsal articulation only reaching the shoulder instead of angle of mouth; small metatarsal tubercle. It differs from *ehrenbergii* in the tympanum being equal to the diameter of the orbit instead of half the diameter; and the fingers, which are blunt and not pointed.

Description. Habit stout. Vomerine teeth in two oblique groups, commencing on anterior inner border of choanæ; nine teeth in each group; length of each group much greater than diameter of choanæ; the distance between the groups where they approach each other is less than the transverse diameter of the choanæ. Three tooth-like prominences on front of lower jaw.

* Boulenger, 1906 (for 1905), Ann. Mus. Stor. Nat. Genova, xlii. p. 159, pl. i. fig. 3.
† Noble, 1924, Bull. Am. Mus. Nat. Hist. xlix. art. ii. p. 278.
‡ Andersson, 1903, Verh. zool.-bot. Ges. Wien, liii. p. 143.

Head depressed, considerably broader than long; snout broadly rounded, slightly truncate at tip; canthus rostralis indistinct; loreal region concave, grooved; nostrils tubular, directed upwards, the distance between them about equal to the width of the upper eyelid; nostrils about equidistant from tip of snout and anterior border of eye, or slightly nearer the former; eyes supero-lateral; the interorbital space very slightly narrower than the upper eyelid: tympanum very large, equal in size to the diameter of the orbit. Fingers moderately short; first longer than second, about equal to fourth; third longest, not webbed, but with distinct narrow dermal margins, except on the outer surfaces of first and fourth; tips of fingers very slightly swollen, subarticular tubercles well developed; the elbow when pressed forward reaches the angle of the mouth. The tibio-tarsal articulation of the adpressed hind-limb falls far short of the tympanum; the metatarsal tubercle reaches the eye; tibia two and a quarter times in length from snout to vent; toes long, well developed, fully webbed to their very tips, which are rounded and dilated; an elongate, blunt metatarsal tubercle, measuring slightly more than one-half the length of the inner toe; a narrow tarsal fold. Skin on snout smooth, pitted on head, rugose on sides of head, very rugose on back, which is covered with smooth warts; a more or less conspicuous transverse fold unites the posterior ends of the orbits, and is continued as a strong fold from the orbit over the tympanum.

Coloration. Uniformly plumbeous above, posterior surface of hind-limbs faintly spotted with pinkish white: below pinkish white, the whole of the lower surfaces marbled with brown.

Measurements:—

	♀ *Type.*	♀ *Paratype.*
Snout to vent	130 mm.	123 mm.
Length of head	42 ,,	42 ,,
Breadth of head	48 ,,	46 ,,
Diameter of orbit	10 ,,	10 ,,
Diameter of tympanum ...	10 ,,	10 ,,
Length of tibia	58 ,,	56 ,,
Length of foot	85 ,,	85 ,,

Remarks. I was spending the night in a tree over a water-hole in the sandy bed of the Simiyu River, where a lion had been drinking the night before, when I heard grunting noises that I imagined were being made by wild pigs coming down to drink. The noise, however, increased in volume, until I realized that it was being made by batrachians larger than any I had previously met with. When Salimu arrived shortly after dawn, I set him to drag the pool with my mosquito-net, but it only resulted in the capture of these two females. Both were full of eggs which measured 2 mm. in diameter. The larger frog weighed 8 ozs. and was over five inches in length. The nostrils and strongly-webbed

hind-feet lead one to suppose that the species is largely aquatic in its habits and, as a result, has escaped being taken by collectors before.

RANA OCCIPITALIS Günther.

Günther, 1858, Cat. Batr. Sal. Brit. Mus. p. 130, pl. xi.

No specimens of this ranid were met with, but as records of its occurrence in East Africa are rare, I take this opportunity of remarking that there are three examples in the Museum of Comparative Zoology (M. C. Z. 2514, 5970, 9474) from Uganda and Kenya Colony; one of the latter was collected at Laikipia by Dr. Glover M. Allen. They appear to be correctly identified, but the toes do not terminate in the small knobs of the original description, being rather pointed.

RANA MERUMONTANA Lönnberg.

Lönnberg, 1907, in Sjöstedt, Kilimandjaro-Meru Exp. i. part 4, p. 21, pl. i. figs. 4 *a* & 4 *b*.

1 (M. C. Z. 10339). Kabare, Bukoba, 15. i. 23.

A male, length 43 mm. The vomerine teeth extend backwards to the level of the posterior border of the choanæ. Diameter of tympanum about three-quarters, not half, diameter of the eye. Tibio-tarsal articulation of the adpressed hind-limb reaches beyond the eye, but not beyond the tip of the snout. Lips white, not dark brown. It has two very noticeable pale dorso-lateral lines from the posterior border of the eyes to the hind-limbs. With these exceptions my specimens agree well with Lönnberg's description of his single specimen from Mt. Meru.

RANA NUTTI Boulenger.

Boulenger, 1896, Ann. Mag. Nat. Hist. (6) xviii. p. 467; 1909, Trans. Zool. Soc. xix. p. 240, pl. viii. figs. 1 & 2.

9 (Univ. Mich. 61380, 61388–9). Nairobi, 24 & 29. iii. 15.

Not fully grown, the series measuring from 40 to 58 mm. Nutt's Frogs were found spawning at Morogoro on 7. ii. 1917. Frogs either of this species or *Rana oxyrhynchus* were recovered from the stomachs of Banded Mongoose (*Mungos mungo colonus*) at Morogoro, a Swahili Genet (*Genetta suahelica*) at Kilosa, a Short-billed White Heron (*Mesophoyx intermedius brachyrhynchus*) at Kilosa, and a Hammer-headed Stork (*Scopus umbretta bannermani*) at Makata River. An East African Green Snake (*Chlorophis neglectus*) was taken at Nairobi in the act of swallowing one, and an Olive Water-Snake (*Natrix olivaceus*) at Dar es Salaam fed on them. It is remarkable how very few frogs were found, considering the hundreds of stomachs of various creatures which were examined.

RANA OXYRHYNCHUS A. Smith.

A. Smith, 1849, Illus. Zool. S. Africa, iii. pl. lxxvii. figs. 2 & 2 *a–c*.

6 (M. C. Z. 10340). Nairobi, 24 & 29. iii. 15.
29 (M. C. Z. 10341–6). Kilosa, 17. i. 21, 17. iii. 21, 16–18. iii. 22, 1. viii. 22.
1 (M. C. Z. 10347). Itende, 15. ii. 23.
14 (M. C. Z. 10348–53). Kisanga, 26. ii. 23.

The three largest of these fifty specimens are naturally females, and all measure 55 mm. in length; they are from Kilosa and Kisanga. In the Kisanga frogs the dorsal folds are not nearly so pronounced as in the Nairobi examples.

RANA MASCARENIENSIS Duméril & Bibron.

Duméril & Bibron, 1841, Erpét. Gén. viii. p. 350.

8 (Univ. Mich. 61387). Nairobi, 22–24. iii. 15.
3 (M. C. Z. 10354). Mahaka, 2. ii. 22.
1 (M. C. Z. 10355). Saranda, 10. iii. 22.
2 (M. C. Z. 10356). Gwao's, 3. x. 22.
1 (M. C. Z. 10357). Nymbita, 10. xi. 22.
2 (M. C. Z. 10358). Kisumu, 18. xi. 22.
1 (M. C. Z. 10359). Frere Town, 31. xii. 22.

The largest, a Nairobi female, measures 62 mm.; the two examples from Gwao's are the smallest, being only 20 mm. in length. Two examples from Mahaka, one from Saranda, and one from Nyambita lack the broad, yellowish vertebral band which is present in all the others.

RANA DELALANDII (Duméril & Bibron).

Pyxicephalus delalandii Duméril & Bibron, 1841, Erpét. Gén. viii. p. 445, pl. lxxxvii. figs. 1, 1 *a*, 1 *b*.
Rana delalandii Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 31.

1 (M. C. Z. 10360). Semo River, 15. x. 22.
1 (M. C. Z. 10361). Sagayo, 9. xi. 22.
6 (M. C. Z. 10362–3). Nyambita, 10. xi. 22.
1 (M. C. Z. 10364). Itende, 15. ii. 23.

These beautifully marbled rather toad-like frogs were taken at night; most of them were found hopping about on the path along which we were marching. The vertebral stripe is lacking in all except three of the Nyambita frogs.

The Itende specimen is far larger than any of the others. It measures 85 mm. as against a range for the rest of the series of 35 to 40 mm. It also lacks their characteristic mottlings, being reddish brown on the back with a good deal of black along the

sides; the markings on the hind-limbs are identical with those of the other specimens. The first finger is shorter than the second, while it is very slightly longer in the other frogs of the series. The toes are a little more webbed, and the large metatarsal tubercle of the adpressed hind-limb reaches the level of the eye. The back is rougher and much more warty than in the others, but not more so than in a Kagiado specimen taken in 1915. It is a female, and presumably a very old one if I am correct in referring it to *delalandii*, from which it does not appear to differ in any essential details.

RANA ORNATA (Peters).

Pyxicephalus ornatus Peters, 1878, Monatsber. Akad. Wiss. Berlin, p. 207, pl. ii. fig. 7.
Rana ornata Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 33.

1 (M. C. Z. 10365). Kilosa, 25. iv. 22.

This single specimen is only 40 mm. in length. The Ornate Frog appears to be scarce in East Africa, as this is the second individual taken by me during eight years. The type-locality is Taita, K.C.

RANA BARBOURI, sp. n. (Pl. I. fig. 2.)

1 (M. C. Z. 10366). Nyambita, 10. xi. 22.

Type. No. 10366, Museum of Comparative Zoology. An adult female taken on swampy ground on path to Sagayo, half-a-mile outside Nyambita, Mwanza, Tanganyika Territory. Collected by A. Loveridge, November 10th, 1922.

Affinity. Nearly related to *Rana miotympanum* Boulenger of Angola, which is n. n. for *Hildebrandtia angolensis* Nieden, 1908, a preoccupied name in the genus *Rana*.

Diagnosis. It has hair-like clavicles and undoubtedly belongs to the African subgenus *Hildebrandtia* of Nieden, as cited by Boulenger * in his synopsis of the species. It agrees with *Rana miotympanum* in the remarkably truncate snout, and in the interorbital space being narrower than the upper eyelid. It differs in the tympanum being equal to, instead of half, the diameter of the eye, and the toes being three-quarters, instead of one-third, webbed.

Description. Vomerine teeth in two series close to the inner borders of the choanæ. Head feebly depressed, broader than long; snout rounded, abruptly truncate in front of the nostrils, shorter than the orbit; canthus rostralis obtuse, loreal region concave; nostril much nearer the end of the snout than the eye; interorbital space nearly as broad as upper eyelid; tympanum distinct, as large as eye. Fingers short, blunt, first very slightly longer than the second, about equal to the fourth, third

* Boulenger, 1919, Trans. Roy. Soc. S. Africa, viii. part 1, p. 36.

longest; toes moderate, blunt, three-quarters webbed, the web extending as a narrow margin to the first joint from end on longest toe, which is the fourth; third and fifth about equal length; subarticular tubercles small, inner metatarsal tubercle small, rounded, no outer metatarsal tubercle; a slight tarsal fold. The tarso-metatarsal articulation of the adpressed hind-limb reaches the eye; tibia equals half the length from snout to vent. Skin smooth above and below, a distinct dorso-lateral fold.

Coloration. Greyish brown above, dorso-lateral fold white, numerous inconspicuous white spots on sides anterior to hind-limbs, also on the thighs. Four indistinct cross-bars on the tibia. Below uniformly white.

Measurements:—

Snout to vent	35·5	mm.
Length of head	12	,,
Breadth of head	13·5	,,
Diameter of orbit	2·5	,,
Diameter of tympanum	2·5	,,
Length of tibia	18	,,
Length of foot	27	,,

RANA ADSPERSA (Duméril & Bibron).

Pyxicephalus adspersus Duméril & Bibron, 1841, Erpét Gén. viii. p. 444.

Rana adspera Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 33, fig.

10 (M.C.Z. 10367). Kilosa, 17. iii. 22.
1 (M.C.Z. 10368). Nyambita, 10. xi. 22.
3 (M.C.Z. 10369). Frere Town, 31. xi. 22.

All of these specimens are immature; the largest (Nyambita) is 119 mm. in length, and the largest of the Kilosa series is only 89 mm. as against 152 mm. (6 inches), which is the measurement of an adult South African example in the Museum of Comparative Zoology. The Kilosa specimens with their smooth, frog-like skins are very different in appearance to the extraordinary rugose, warty, and toad-like adult; the Nyambita Bull-Frog is intermediate.

The coloration of a Kilosa specimen as noted in life was "plumbeous above, a pale green dorsal stripe from upper lip to vent, three vertical light stripes from upper lip to eye, the last two connected, or almost connected by a horizontal bar. Sides, and to a lesser extent back, vermiculated with whitish and greenish markings. Semicircular orange patches around the bases of all four limbs; posterior border of mouth to fore-limb pale green. Whole of lower surface pure white, the throat with very striking brown vermiculations and yellow spots. The mottling of the throat is most noticeable in young individuals, and disappears with age."

These African Bull-Frogs were taken in a swamped mealie-field, the water being more than a foot deep. My native collector, returning from his first visit to the place, reported that he had heard something "grunting" among the mealie-stalks, and mistaking it for a leopard, turned and ran. Later he had seen the snout of a bull-frog appear above the water to the accompaniment of the same deep noise. He described it as the biggest frog he had ever seen. In the evening I accompanied him to the spot, but though we heard several frogs, they were so wary that I was unable to catch sight of one. Neumann collected two in the Usambara and at Tanga. Lönnberg records six from Tanga collected by the Swedish Expedition, but the species rarely figures in collections of East African Batrachians.

CHIROMANTIS XERAMPELINA Peters.

Peters, 1855, Arch. Naturg. xxi. part 1, p. 56.

9 (M. C. Z. 10370–3).	Kilosa, 14–31, iii. 21.
2 "	Mbwenyi, 17. iv. 23.
1	Mkalama District, xi. 21.

The largest of this series measures 65 mm. In life these tree-frogs are whitish grey or dirty white and become much darker in spirit.

Many of the interesting meringue-like froth "nests" of this species were collected, one of which I have before me as I write, the only one that was successfully preserved. It measures 130 × 120 × 110 mm. (approximately $5\frac{1}{4} \times 4\frac{3}{4} \times 4\frac{1}{4}$ inches), is roughly spherical in form, and attached to three leaves, which form a cap for the upper end as it hangs from the branch of a tree. A colourless, jelly-like substance exuded from the anus of the frog forms the basis of the meringue, being worked up into a froth by the hind-limbs of the female. The process has been described in the case of an allied species *C. rufescens* (Günther) by Lang and quoted by Noble *. I imagine that the "nest" is made during the night, and, as far as my experience goes, is always made over water, though this was not the case with *C. rufescens*, whose "nests" were found "often at a distance from the water."

These "nests" were found during the heavy rains, all my dates being between February 7th and April 22nd. The first "nest" found at Mbwenyi on 7. ii. 21 was carried home and hung over a wash-basin. The following day the tadpoles hatched, from the eggs in the centre of the "nest," and shortly afterwards, due apparently to their energetic wriggling, were precipitated into the basin of water beneath. At Kilosa, on 16. iii. 21, two nests were found on a single branch only nine inches apart. On the 22nd of April in the same year I found a "nest" attached to a stalk of matama which was growing in a swamp. There was only one tree in the swamp, and that was on the far side, the

* Noble, 1924, Bull. Am. Mus. Nat. Hist. xlix. art. ii. p. 231.

swamp being a large one. As I touched the "nest" it fell in half, a lot of liquid and wriggling tadpoles falling into the water. The upper half of the "nest," which remained attached to the stalk, was deeply concave, and had some half-dozen tadpoles stranded on its smooth surface. About a month previously Mr. C. F. M. Swynnerton found a "nest" attached to a rock which was jutting out of a pool. At Kibakwe, on 9. ii. 23, several "nests," or remains of the same, were found hanging from thorn-bush sprays over what had recently been a puddle, but was then damp mud. At Kisanga, on 24. ii. 23, a "nest" was found dependent from a thorn-bush only two feet from the surface of a small pool in the centre of some acres of swampy ground. I attempted to dry this "nest" by exposure to the sun, but following a heavy dew on the night of the 26th, many scores of tadpoles hatched out the following day.

CHIROMANTIS PETERSII Boulenger.

Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 93, pl. x. fig. 1.

1 (M. C. Z. 10375). Gwao's, 10. x. 21.
(M. C. Z. 10376). Nyambita, 11. xi. 22.

The length of the frogs in this series ranges from 38 to 45 mm. It is a frog of dry thorn-bush country, unlike *C. xerampelina*, which seems to show a preference for moist and leafy ravines or swamps.

At Dodoma specimens of Peters's Tree-Frog were found clinging to thorn-bushes in an arid sandy waste during the hottest hours of a December day, and yet retaining their moisture. From time to time one would emit a bird-like note; indeed, when hearing this cry for the first time, I started searching for a young bird, but came upon the frog. This was no easy matter, for although the bush was destitute of foliage, the frog was so cryptically coloured that it was difficult to distinguish it from the branch to which it was clinging.

PHRYNOBATRACHUS NATALENSIS (A. Smith).

Stenorhynchus natalensis A. Smith, 1849, Illus. Zool. S. Africa, iii. Appendix, p. 24.
Phrynobatrachus natalensis Günther, 1862, Proc. Zool. Soc. p. 192. Procter, 1920, Proc. Zool. Soc. p. 413.
Phrynobatrachus ranoides Boulenger, 1894, Proc. Zool. Soc. p. 644, pl. xxxix. fig. 2. Procter, 1920, Proc. Zool. Soc. p. 413.
Phrynobatrachus boulengeri de Witte, 1919, Rev. Zool. Africaine, vi. fasc. 2, p. 6. Procter, 1920, Proc. Zool. Soc. p. 413.

6 (M.C.Z. 10377). Nairobi, 26. iii. 15, 3. iv. 15.
24 (M.C.Z. 10378–82). Kilosa, 15–31, iii. 21, 13. iii. 22, 1. viii. 22.
2 Ulugu, 7. xi. 21.
1 (M.C.Z. 10384). Sagayo, 9. xi. 22.
1 (M.C.Z. 10385). Nyambita, 10. xi. 22.
1 (M.C.Z. 10386). Frere Town, 31. xi. 22.
4 (M.C.Z. 10387). Mbwenyi, 6. i. 23.
18 (M.C.Z. 10388–93). Ikikuyu, 12. ii. 23.
4 (M.C.Z. 10394). Itende, 15. ii. 23.
Tadpole (M.C.Z. 10383). Kilosa, 4. ii. 23.

This large series exhibits all the variations referred to by Miss Procter, and two of the Itende specimens are strikingly different from the others in coloration, as they are pale grey chequered with black.

Noble* appears to be right in relegating *P. boulengeri* and *P. ranoides* to the synonymy of *P. natalensis*. Though I have no examples of *boulengeri* from its type-locality in Portuguese East Africa, I have re-examined the specimens identified with that species by Miss Procter, and find that they can be matched with individuals in the present series which show every gradation between the forms. Frogs taken from the same pool at Kilosa on the same day vary greatly in the extent of dilation of the tips of fingers and toes.

Among the Kilosa series was one individual (No. 10382) which I at once singled out on account of its superficially different appearance. It is uniformly nut-brown above, white beneath, the latter largely obscured by brown mottlings. It very closely matches the smaller† of the two Morogoro specimens referred by Miss Procter to *P. ranoides*, and which were doubtless compared with the type. Moreover, it also falls naturally to *P. ranoides*, as characterized in de Witte's key ‡, yet on comparing it with the more typical *P. natalensis*, excepting for its colour and its more sharply-pointed fingers and toes (in which respect it does not agree with the Morogoro frog), I can find no character by which it may be separated from all the other individuals taken at Kilosa. At a glance it appears to differ in its sharper and more depressed snout, but, as already indicated, others may be found almost matching it in this respect. It does not compare well with the figure of *ranoides*, and differs from the description of that species in its snout being shorter than the diameter of the orbit, an indistinct or absent tympanum, and perfectly smooth skin. Its length is 26 mm.

The following note made in the field serves to confirm Chapin and Lang's observations (Noble, p. 191). "The small frogs were found in embrace in small rock-pools left by the subsidence of

* Noble, 1924, Bull. Am. Mus. Nat. Hist. xlix. art. ii. p. 189.
† The larger specimen not being available for comparison.
‡ De Witte, 1921, Rev. Zool. Africaine, ix. fasc. 1, p. 9.

the river, which, however, was still running strong. The females were spawning; the eggs were a pale straw-colour" (Ikikuyu, 12.ii.23). A pair were taken in embrace at Nairobi on 3.iv.1915.

The tadpole found in my wash-basin at Kilosa on 4.ii.23 is referred to this species with due reserve. It measures 14 mm. from snout to anus, tail 21 mm., hind-leg 11 mm.

ARTHROLEPTIS WAHLBERGI A. Smith.

A. Smith, 1849, Illus. Zool. S. Africa, iii. Appendix, p. 24.

14 (M. C. Z. 10395–7). Uliya-Madazini Road, 2.iii.23.

These frogs were found hopping about among leaves in a water-logged forest through which the road passes. They range in size from 11 mm. to 28 mm. There is considerable diversity in coloration: some are ashy-grey with distinct blackish markings, others uniformly dark on the back so that the markings are obscured; the throats in all the specimens are more or less speckled or mottled.

ARTHROLEPTIS STENODACTYLUS Pfeffer.

Pfeffer, 1893 (1892), Jahrb. Hamb. Wiss. Anst. x. pt. 1, p. 93.

Arthroleptis whytii Boulenger, 1897, Proc. Zool. Soc. p. 802, pl. xlvi. fig. 3.

4 (M. C. Z. 10400). Kilosa, 18 & 24.iii.21, 21.v.22.
4 (M. C. Z. 10401). Bagilo, 2–9.v.22.
2 (M. C. Z. 10398–9). Uliya-Madazini Road, 2.iii.23.

The series range in size from 23 to 42 mm. (Uliya), and in coloration to the same extent as *A. wahlbergi*, noted above. The largest individual is a female from Uliya-Madazini Road, and is the only one with a broad pale brown line from snout to anus; some of the others have a thread-like white vertebral stripe or a raised line.

A. whytii Blgr. being now regarded as a synonym of the present species, the frog referred by Miss Procter to *A. whytii* (P. Z. S. 1920, p. 414) belongs to the present species. Its locality was Uluguru Mtns., which was accidentally omitted in printing.

One Kilosa example, collected in a log of decayed wood, has two siafu (*Dorylus nigricans*) attached to it; another was recovered from the stomach of a young Puff Adder (*Bitis arietans*).

ARTHROLEPTIS ? ADOLFI-FRIEDERICI Nieden.

Nieden, 1910, Sitzber. Ges. Naturf. Freunde Berlin, p. 440; 1912, Wiss. Ergeb. Deutsch. Zentr.-Afrika-Exp. iv. p. 175, pl. v. figs. 4 *a–c*.

22 (M. C. Z. 10402–7). Kilosa, 1. viii. 22.

Dr. Barbour agrees with me in provisionally referring these small frogs to *adolfi-friederici* in the absence of specimens for comparison. They agree substantially with the somewhat meagre description. Nieden's figures accompanying a later reference are also not available. The type-locality for *adolfi-friederici* is the Rugege Forest, Central Lake Region, but its range extends as far west as the Cameroons. Noble has suggested that *adolfi-friederici* is a synonym for *A. pœcilonotus* Peters or *A. variabilis* Matschie, with examples of both of which I have compared my specimens. They are certainly very close to *A. pœcilonotus* but not to *A. variabilis*, but as my specimens are very young, I hesitate to draw too definite conclusions.

Arthroleptis minutus Boulenger.

Boulenger, 1895, Proc. Zool. Soc. p. 539, pl. xxx. fig. 4.

1 (M. C. Z. 10408). Kilosa, 1. viii. 22.
1 (M. C. Z. 10409). Kisumu, 18. xi. 22.
1 (M. C. Z. 10410). Frere Town, 30. xi. 22.

The Kisumu specimen is the largest, measuring 16 mm., and differs from any I have taken before in its very pale colour, which thows up in sharp relief the bars and squarish markings on limbs and back.

Arthroleptis bottegi Boulenger.

Boulenger, 1895, Ann. Mus. Stor. Nat. Genova, (2) xxxv. p. 16, pl. iv. fig. 3.

23 (M. C. Z. 10411–6). Gwao's, Singida, 3. x. 22.

Originally described from Auata River, Somaliland, this species has already been recorded from Uganda and Kilimanjaro; the present record extends its known southward range some 200 miles. They were taken in a pool at the base of a rocky kopje, situated in typical sandy thorn-bush country.

A. bottegi was described from a single individual. The present series agree well with the description, while exhibiting a wide range of variation at the same time. In length they measure 20 to 27 mm.; the type was 34 mm. The tibio-tarsal articulation of the adpressed hind-limb, which reached the eye in the type, does so in most of the present series, though some fall just short and others nearly reach the end of the snout. Some individuals are perfectly smooth, others almost toad-like in their wartiness. Three have very narrow vertebral lines, pale brown in spirit, one individual only has a broad brown band, black-edged, extending from snout to vent, the bordering lines passing over the eyelids and converging to the anus.

ARTHROLEPTIS OGOENSIS Boulenger.

Boulenger, 1906 (for 1905), Ann. Mus. Stor. Nat. Genova, (3) ii. p. 162, pl. i. figs. 7 & 8.
Arthroleptis rouxi Nieden, 1912, Wiss. Ergeb. Deutsch. Zentr.-Afrika-Exp. iv. p. 178, pl. v. figs. 5 *a*–*b*.

2 (M. C. Z. 10417–8). Bagilo, 16. v. 22.

A male measuring 19 mm. and a female of 23 mm., almost certainly breeding and probably taken in embrace. Neither has the fine vertebral line mentioned as sometimes present in *A. ogoensis* and present on the 16 mm. solotype of *A. rouxi*. Boulenger's species was described from Lambaréné, Ogowe, and it is quite in conformity with other findings to meet with a West African species in the forest outlier of the Uluguru Mtns. The sole differences between *ogoensis* and *rouxi*, which came from the Buddu Forest, near Lake Victoria, appear to be as follows:

First and second fingers equal. Distance between the two metatarsal tubercles considerably less than the distance between the inner metatarsal and the tarsal tubercle	*ogoensis*.
First fingers distinctly shorter than second. Distance between the inner metatarsal and the tarsal tubercle is somewhat less than the distance between the two metatarsal tubercles	*rouxi*.

Though Boulenger states in the text that the first and second fingers are of equal length, the two figures on pl. i. show them as shorter. In the specimens before me the first is shorter than the second on all four hands, but the metatarsal tubercles are as far from each other as the inner tubercle is from the tarsal tubercle. Under these circumstances it is hardly warrantable to regard *A. rouxi* as a distinct species.

ARTHROLEPTIDES MARTIENSSENI Nieden.

Nieden, 1910, Sitzber. Ges. Naturf. Freunde Berlin, p. 445.

6 (M. C. Z. 10419–21). Lutheran Mission, Uluguru Mtns., 15. xii. 21.

Ranging in size from 26 to 57 mm. The type was 59 mm. My adult is a female full of black eggs 1·6 mm. in diameter. Hitherto the species has only been known from the type-locality, Amani, Usambara Mtns.

Below the abandoned Lutheran Mission, in the hills behind Morogoro, a stream comes tumbling down the steep declivity with considerable force. At one spot there is a waterfall which empties itself into a rock-bound pothole, which is so water-worn as to be very slippery.

It was here that my wife and I found these frogs sitting in niches or on ledges almost beneath the waterfall. Catching them was a difficult undertaking, not merely on account of the slipperiness of the rock and the swiftness of the stream, but

also because of the agility of the frogs. When approached they would leap from their niches to some boulder, and thence from rock to rock across the stream, adhering to their slimy surfaces by means of the extraordinary dilations on fingers and toes. Nieden has very aptly likened these to similar structures of *Polypedates*. At times frogs would be struck by the spray and carried into the stream, but being strong swimmers, they would strike out for the rocky side of the channel and clamber out. The name of *Arthroleptides* selected by Nieden, while describing their similarity to *Arthroleptis* in the absence of vomerine teeth, is apt to convey a wrong impression of size, as the species of *Arthroleptis* are generally diminutive, while *Arthroleptides martiensseni* is as large as an average European Common Frog.

KASSINA SENEGALENSIS (Duméril & Bibron).

Cystignathus senegalensis Duméril & Bibron, 1841, Erpét. Gén. viii. p. 418.
Cassina senegalensis Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 131.

2 (M. C. Z. 10422). Kilosa, 31. iii. 21, 18. iii. 22.

The first a male 39 mm. long, the second a young one of 23 mm. The following note was made at Nairobi on 7. iv. 15:—"The last three nights the 'wait' note of the Ranas has been less noticeable, and a croak, like that of a bubble of air breaking on the surface of a pond, has taken its place. To my surprise the cry did not come from the water, but from the damp grass, and by listening carefully it could be heard in the depths of the termite hillocks. I captured some of the handsome little frogs responsible for the noise, and found they were all males of *Kassina senegalensis*, which differ from the females in having an adhesive disc on the throat. They were being answered from the ponds—probably by the females."

HYPEROLIUS CONCOLOR (Hallowell).

Ixalus concolor Hallowell, 1844, Proc. Acad. Nat. Sci. Phil. ii. p. 60.
Rappia concolor Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 124.

1 (M. C. Z. 10423). Kabare, Bukoba, 6. ii. 23.

Roux has already reported this species from Bukoba in 1910. My frog agrees well with specimens from the Congo identified by Noble, and is structurally identical with the brief description. Its length is 32 mm. Flesh-coloured, so heavily covered with minute black specks as to appear grey, these specks are fewer on thighs and feet, and there is no dorso-lateral stripe; under surfaces white.

HYPEROLIUS GRANULATA (Boulenger).

Rappia granulata Boulenger, 1901, Ann. Mus. Congo, (1) ii. fasc. 1, p. 4, pl. ii. fig. 3.

2 (M. C. Z. 10424–5). Kipera, 7. viii. 22, 5. viii. 23.

Lengths 19 and 20 mm. The one greyish, with a few large black specks in the tympanic region; the other greyish, minutely speckled with black over the whole dorsal surface. During a bush fire one of these frogs was observed hastily ascending the trunk of a tree. It would assuredly have been shrivelled by the fierce up-draft which was seen to centre around each tree.

HYPEROLIUS PUNCTICULATA (Pfeffer).

Rappia puncticulata Pfeffer, 1893, Jahrb. Hamburg Wiss. Anst. x. p. 99. Procter, 1920, Proc. Zool. Soc. p. 415, fig. 2.

3 (M. C. Z. 10426–7). Kilosa, 15. iii. 21, 1. viii. 22.

Boulenger* has stated that he regards *puncticulata* as a var. of *H. nasuta* (Günther). Noble has placed the former in the synonymy of the latter, which was described from Duque de Bragance, Angola; but on comparing my specimens with the figure and description of *nasutus* I found very little similarity. Their snouts are not acutely pointed, canthus rostralis is hardly angular, loreal region is concave, not flat; one individual has the belly smooth, in the others it is granular. Boulenger has added to Günther's description that the tibio-tarsal articulation nearly reaches the tip of the snout. In my youngest specimen, which is undoubtedly the same species as the largest, it only reaches the shoulder, in the other two the eye. Noble remarks that it may only reach the eye in what he calls *nasutus*; but as my specimens do not have the combination of characters which he mentions, it seems advisable for me to use Pfeffer's name, particularly as I have no *nasutus* material with which to compare them.

They measure from 27 to 37 mm. in length. One individual has dorsal markings exactly like the one figured by Miss Procter; the other two are greyish or flesh-coloured, minutely speckled with black on the upper surfaces; the largest frog has a curious light spot ringed with brown on the occiput.

HYPEROLIUS PLATYRHINUS (Procter).

Rappia platyrhinus Procter, 1920, Proc. Zool. Soc. p. 416.

1 (M. C. Z. 10428). Nairobi, 3. iv. 15.
25 (M. C. Z. 10429–34). Nyambita, 11. xi. 22.

The measurements of the Nairobi frog are almost identical with those of the type, the only difference being ·5 mm. in the length

* Boulenger, 1911, Ann. Mus. Civ. Stor. Nat. Genova, v. (xlv.) p. 169.

of the tibia, which is that much longer in the present specimen. An obvious slip has crept into the original description, where it says that the length of the tibia is $1\frac{1}{6}$ times in length from snout to vent, whereas the table of measurements shows that it is twice in length from snout to vent. The present example is greyish white above, finely speckled with black pigment cells, but lacks markings. Beneath it is yellowish in spirit.

The Nyambita series, measuring 18 to 29 mm., are very variable in their markings, or lack of them. Some specimens have a handsome black zigzag line along the sides, black blotches and vermiculations on lips and throat, front limbs, tibia, and hind-feet; in all of them the femur is bright pink, and in life is only exposed as the frog leaps away. There is generally minute spotting on the dorsal surface. All these frogs were found upon the stems of twenty yards of manyara hedge, which they shared with half-a-dozen species of strange mantids and a snake (*Psammophis subtæniatus*) which was coiled and sunning itself at a height of five feet from the ground.

HYPEROLIUS MARMORATUS Rapp.

Rapp, 1842, Arch. Naturg. viii. pt. 1, p. 289, pl. vi. figs. 1 & 2.

1 (M. C. Z. 10287). Lake Edward Nyanza, v. 24 (Dr. J. C. Phillips).

This widely-distributed and very variable tree-frog was not taken by the writer during 1920–23, but a male has recently been presented to the Museum of Comparative Zoology by Dr. Phillips, who obtained it during his recent ornithological trip to Central East Africa. It measures 27 mm., is slate-grey above and on fore-limbs and tibia, marbled with black; the femur (probably red in life) is almost colourless, and the foot is less pigmented than other exposed surfaces.

HYPEROLIUS ARGUS Peters.

Peters, 1855, Arch. Naturg. xxi. part 1, p. 57.

1 (M. C. Z. 10435). Tindiga, 23. vii. 21.
2 (M. C. Z. 10436–7). Bagilo, 15. xi. 22.
1 (M. C. Z. 10438). Kipera, 5. v. 23.

The first was taken clinging to a grass-stem in a swamp, the last was on a leaf of maize in a plantation. The series measure 30, 31, 32, 34 mm. The Bagilo frogs are similar to the light brown ones described by Miss Procter. The other two have the canthal band plus many ocellar spots on back and limbs. In life the Tindiga frog was olive on the back, fore-limbs, and tibia; the canthal band and dorsal ocelli silvery white, bordered or ringed with black, thighs ochraceous, hands and feet reddish.

MEGALIXALUS LOVERIDGII Procter.

Procter, 1920, Proc. Zool. Soc. pp. 418–419, fig. 4.

1 (M. C. Z. 10439). Uliya, near Kilosa, 3. iii. 23.

Agrees well with the description and figure of the type except in colouring, for it lacks the faintly-marked dorsal band, also it is flesh-coloured above and white beneath. The tympanum is not discernible.

LEPTOPELIS BOCAGII (Günther).

Cystignathus bocagii Günther, 1864, Proc. Zool. Soc. p. 481, pl. xxxiii. fig. 2.

Hylambates bocagii Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 133, figs.

1 (M. C. Z. 10440). Sagayo, 1. xi. 22.

I am indebted to Dr. G. K. Noble for the identification of this specimen, which he now places in the genus *Leptopelis*. I take this opportunity of remarking how greatly his report on the Congo collections of the American Museum has facilitated my work on the present collection

This frog, which was taken at 3.30 A.M., differs in colouring from Günther's type, though undoubtedly the same species. The Sagayo specimen is pale brown; a very broad, black-edged, chocolate-brown band extends from snout to vent, widest in the middle, where it occupies almost the entire back. A dark transverse band uniting, and across both upper eyelids. Below uniformly pinkish white, with very faint brown vermiculations on the throat. Its tympanum nearly equals the diameter of the eye: not "much smaller" (Günther) or "somewhat more than half" (Boulenger). The upper parts are covered with minute, smooth, rounded warts, not "smooth." The fingers and toes are not dilated at their tips to any appreciable extent, certainly not like those shown in Günther's figure, or the "small disks" mentioned by Boulenger. Length 43 mm.

LEPTOPELIS RUFUS Reichenow.

Reichenow, 1874, Arch. Naturg. xl. pt. 1, p. 291, pl. ix. figs. 1*a*, 1*b*.

1 (M. C. Z. 10441). Uluguru Mtns., 1. iii. 21.

A female measuring 61 mm. This is a West African species described from Victoria at the foot of the Cameroon Mtns.: the present record, though first for the Uluguru Mtns., is not first for the Territory, as it has been reported from the Usambara Range. My specimen does not match very well with a fine series of *L. rufus* from the Cameroons in the Museum of Comparative Zoology. Perhaps with more material it may be found that the isolated forests of the Usambara and Uluguru hold a distinct local race.

BREVICIPITIDÆ.

PHRYNOMANTIS BIFASCIATA Smith.

Brachymerus bifasciatus Smith, 1849, Illus. Zool. S. Africa, iii. plate lxiii.

Phrynomantis bifasciata Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 172.

4 juveniles (M. C. Z. 10443).	Frere Town, viii. 20.
60 tadpoles (M. C. Z. 10444).	Kilosa, 23. iii. 21.
20 adults (M. C. Z. 10445–8).	Kilosa, 30. iii. 21, 18. iii. 22.

One of the Frere Town toads was found about three feet from the ground in the decayed trunk of an acacia-tree, the others were beneath flower-pots and discarded drums in a garden. The Lumbo specimens recorded by Miss Procter were taken in a hole beneath a stone, and were the only batrachians, with the exception of a *Breviceps*, met with during the six months spent at that place. Their colouring, as noted at the time, was :—" Above black with pinkish-red stripe from eye to thigh, an arrow-head or V-shaped red mark over the region of the urostyle, the apex of the mark being posterior, fore- and hind-limbs spotted with red. Beneath paler, mottled with grey and dirty-white. Length 38 mm."

Of the Kilosa series, I noted " Colour very variable. Black above (though on closer inspection it will be seen that the dorsal area is really brown with vermiculations, and a fine deep black vertebral line), with two broad vermilion bands extending from the nostrils along the supra-ocular region almost to the hind-limbs; limbs black, spotted with vermilion; a constant vermilion patch of very irregular shape in the region of the urostyle; one or more vermilion spots on back in the area enclosed by the lateral vermilion bands. Under surface of throat black, breast and belly pale grey, with white spots giving a marbled effect. One female very pale, almost white beneath. A very strong seaweedy smell. Copious excretions from the skin when handled. They move with alacrity when pursued, and climb well up the wall of a room in which they are confined; taking advantage of every inequality of its surface, some have climbed a foot from the floor."

The following note was made at Kilosa on 30. iii. 1921 :—

"At 10 P.M. last night two terrific claps of thunder were, shortly afterwards followed by the greatest downpour of the last three months—the rains commenced a month ago. About 4 A.M. I arose and heard a tremendous toad chorus, apparently quite close to the house. At 8 A.M. I sent my collector off to locate them. At 5 P.M. I accompanied him to the place where they were. The water had drained off the Otto Plantation hill on to a large area of low-lying ground covered with mealies (Indian corn), whose stalks were from twelve to fourteen feet high. It was about a mile, as the crow flies, from the house, and yet the

horus could be plainly heard there. When within half-a-mile of the swamped area the noise resembled that of an 'ngoma' or native dance, with outbursts of cheering at regular intervals.

"We waded in among the stalks, but the songsters were very much on the alert, and the sounds appeared to recede a hundred feet away on every side. The water was a foot deep, and numbers of drowning insects tried to clamber up our legs; the majority were weevils and staphylinids; the stems of the plants harboured many, and comfortably installed on one maize-stalk was a Spotted Wood-Snake (*Philothamnus semivariegatus*), which I bagged. At last I caught sight of one of the vocalists, and recognized it as *Phrynomantis*. It was standing on a broken maize-stem with its fore-legs on a leaf above, so that its body was almost vertical. It inflated a large gular sac, paused, then released the air in unison with hundreds of others all over the swamp. This, then, was the cause of the simultaneous and timed outbursts of cheering, for nothing describes the noise better."

On 22. iv. 1921 thousands of young were found on the road as they left the swamp. They lacked the gaudy red markings of the adults, and this is just when one would assume that they most stood in need of their "warning colours"; they were brownish, with the pattern showing more distinctly than in the adults.

On 13. iii. 1922 I noted that the heaviest downpour of the past two and a half months occurred the preceding night. It rained throughout the night and nearly all the following day without cessation. At 5 P.M. I went down to the flooded mealie-fields, where this year the stalks are only between six and nine feet high. Many of the *Phrynomantis* had already spawned. On the 18th my collector brought me the first young of the year.

I examined the stomachs of half-a-dozen of the adults. One was empty, five contained termites, including "soldiers," the hind-leg of a very small grasshopper, a weevil, wing-cases of several small beetles, with a number of ants to complete the menu.

BREVICEPS ULUGURUENSIS, sp. n. (Pl. I. fig. 3.)

1 (M. C. Z. 10442). Bagilo, 29. v. 22.

Type. No. 10442, Museum of Comparative Zoology. Sex indeterminate, probably juvenile, from Bagilo, Uluguru Mtns., Tanganyika Territory. Collected by A. Loveridge, May 29th, 1922.

Affinity. Near *Breviceps verrucosus* Rapp, of South Africa and Uganda.

Diagnosis. Much greater length of hind-limb; absence of a shovel-shaped inner metatarsal tubercle; a very long and slender fourth toe, which is more than twice the length of the third; the outer toe somewhat longer than the inner. Coloration,

which is uniform purplish brown above and below, with a very indistinct reddish lateral streak. From *B. mossambicus* Peters, which is the only other member of the genus found in Tanganyika Territory, it is distinguished by its very warty back and granular belly, *B. mossambicus* being smooth-skinned.

Description. Habit extremely stout; snout indistinct, more pointed than in *B. verrucosus*; mouth small; eyes rather small, directed forwards; tympanum absent. Limbs moderately short; the tarso-metatarsal articulation of the adpressed hind-limb reaches the tympanic region. Second finger slightly longer than first, slightly shorter than fourth, third much the longest. Toes blunt; outer toe somewhat longer than inner, subarticular tubercles not as distinct as in *B. verrucosus*; no shovel-shaped inner metatarsal tubercle. Upper surfaces with small warts; belly granular.

Coloration. Uniform purplish brown above and below, with a very indistinct reddish lateral streak.

Measurements:—

Snout to vent	27 mm.
Length of head	9 ,,
Breadth of head	11 ,,
Diameter of orbit	2·5 ,,
Length of tibia	12 ,,
,, ,, foot	18 ,,
,, ,, fourth toe	6 ,,

Remarks. The "heels" of this specimen are very swollen as a result of heavy infestation by larval ticks. It is just possible that this state may be responsible for the absence of a shovel-shaped tubercle. Two of the larvæ have evacuated from the abdominal skin, leaving two small pits.

I have compared the new toad with examples of *B. verrucosus*, *B. adspersus*, and *B. mossambicus* in the collection of the Museum of Comparative Zoology.

BREVICEPS MOSSAMBICUS Peters.

Peters, 1855, Arch. Naturg. xxi. part 1, p. 58.

1 (M. C. Z. 10449). Ikikuyu, 10. ii. 23.
1 (M. C. Z. 10450). Itende, 15. ii. 23.
2 (Univ. Mich. 61392). Pwaga, 15. ii. 23.

These were all taken on paths in the very early morning following nights of heavy rain. As far as my limited experience of this species goes, it is always associated with reddish soil, a soil that is particularly favoured by a certain species of termite. Termites, of course, are to be found almost everywhere in East Africa whatever the soil. Is the restricted distribution of this narrow-mouthed toad to be explained by its preference for a particular species of termite that is only found in the red soil? The four specimens measure from 13 to 46 mm.

HEMISUS MARMORATUM (Peters).

Engystoma marmoratum Peters, 1855, Arch. Naturg. xxi. part 1, p. 58.

Hemisus marmoratum Boulenger, 1910, Ann. S. Afr. Mus. v. p. 535.

30 (M. C. Z. 10451–3). Kilosa, 15-18. iii. 22, 21. v. 22.
1 (M. C. Z. 10454). Sagayo, 9. xi. 22.
2 (M. C. Z. 10455). Uliya-Madazini Road, 3. iii. 23.

One of the Kilosa specimens was found in the rotting trunk of a coconut palm, and has the heads of three soldier-ants (*Dorylus nigricans*) attached to it. This is the largest of the series and measures 32 mm. Twenty-seven of the Kilosa toads are young ones which have just lost their tails. One whose tail is not quite absorbed measures 15 mm., but others which have lost theirs are a couple of millimetres shorter. The 31 mm. female from Sagayo is full of large eggs.

CACOSTERNUM BOETTGERI (Boulenger).

Arthroleptis boettgeri Boulenger, 1882, Cat. Batr. Sal. Brit. Mus. p. 118, pl. xi. fig. 6.

A series in the Nairobi Museum which I collected on swampy ground at Parklands, Nairobi, in 1915 were omitted from the report on the 1915–1919 collection, and are not available for discussion in the present paper.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. *Bufo micranotis*, sp. n.
" 2. *Rana barbouri*, sp. n.
" 3. *Breviceps uluguruensis*, sp. n.

PLATE II.

Rana mucosa, sp. n.

EXHIBITIONS AND NOTICES.

March 17th, 1925.

Prof. E. W. MacBride, F.R.S., Vice-President, in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of February, 1925:—

The registered additions to the Society's Menagerie during the month of February were 80 in number. Of these 53 were acquired by presentation, 14 were deposited, 9 were purchased, 3 were received in exchange, and 1 was born in the Menagerie.

The following may be specially mentioned:—

1 Indian Swamp-Deer (*Cervus duvaucelli*), ♂, presented by H.G. The Duke of Bedford, K.G., President Z.S., on February 11th.

2 African Leopards (*Felis pardus*) from the Cameroons, presented by Messrs. John Holt & Co., Ltd., on February 25th.

6 Viscachas (*Lagostomus trichodactylus*), from Buenos Aires, purchased on February 11th.

1 Lesson's Parrot (*Amazona lilacina*), from Ecuador, new to the Collection, received in exchange on February 28th.

The Secretary exhibited, and made remarks upon, a photograph of a young Reindeer (*Rangifer tarandus*) born in the Menagerie, showing a series of dark stripes extending from the shoulder to the hips.

Fossil mammalian remains.

Mr. Warren R. Dawson, F.Z.S., exhibited some fossil mammalian remains recently discovered in the City of London, and made the following remarks:—

"By the courtesy of the Chairman of Lloyd's I am able to exhibit three specimens of fossil mammalian remains recently brought to light in the course of the excavations for the new Lloyd's Building in Leadenhall Street in the City. The site was originally occupied by East India House, but the excavations for the new building reach to a much lower level than did the foundations of the former building. The first specimen (text-fig. 1) is the head of the femur of a Mammoth, and was found in the River Gravel at a depth of twenty feet below the present street level. The second specimen (text-fig. 2) is a series of fragments of two molar teeth of the same species, and consists of a number

Text-figure 1.—Head of the femur of a Mammoth.

Text-figure 2.—Fragments of two molar teeth.

Text-figure 3.—Right ulna of a Woolly Rhinoceros (*R. antiquitatis*).

of parallel plates which were formerly united by dentine. These were found, also in the Gravel, at a depth of thirty-seven feet. The third specimen (text-fig. 3) is the most interesting, and was found in the bluish-grey argillaceous soil which underlies the Gravel, and which is redeposited London Clay, at a depth of forty-two feet below road level. It is the right ulna of the Woolly Rhinoceros (*R. antiquitatis*). This specimen has been presented by the Committee of Lloyd's to the British Museum (Natural History), in which at present the British species are represented only by skulls and teeth, so that a complete limb-bone is an accession of considerable scientific interest."

Mr. M. A. C. Hinton, F.Z.S., added the following observations :—

"While remains of Rhinoceros occur commonly in many British Pleistocene deposits, complete limb-bones are rare. The ulna from Lloyd's is the first perfect example of that bone to come to the Museum from a British source, and it is an important accession. The deposit in which the bone was discovered forms part of the Third (or lowest) Terrace of the Thames. At this horizon we find at many places, *e. g.*, Ponders End in the tributary valley of the Lea, a characteristic late Pleistocene fauna comprising an Arctic Lemming (*Dicrostonyx henseli* Hinton) and a Vole (*Microtus anglicus* Hinton) resembling some of the Asiatic species of "*Stenocranius*." The Rhinoceros of this horizon is, so far as skulls and teeth from several localities indicate, *Rh. antiquitatis* Fischer, and therefore the present ulna may be provisionally referred to that species.

"An elaborate account of the ulna of *Rh. antiquitatis* has been given by Tcherski (Mém. Acad. Imp. Sci. St. Pétersbourg, xl. 1892, pp. 421–426), who had four perfect and five imperfect examples before him from the Pleistocene of Jana Land and the New Siberian Islands. Our specimen is rather larger than any of those recorded by Tcherski, but I have not been able to spare sufficient time to master all the points raised by this writer in his description of the bone. The following measurements may be compared with those given in Tcherski's table :—

1. Greatest length, from the anterior part of the distal articular surface to the olecranon, 515 mm. (466–485 Tcherski).
2. From the same point to the nearest end of the outer lobe of the articular surface for the humerus, 345 (283–322).
3. From the same point to the tip of the *processus coronoideus*, 426 (356–397).
4. Long diameter of distal articular surface (in middle line), 53 (47–53).
5. Transverse diameter of distal articular surface, 42 (38–41).
6. Greatest breadth of distal end (antero-posterior), 73 (72–89).
7. Do. transverse, 56 (46–69).

8. Width of shaft (transverse) at the *spatium interosseum*, 56·5 (47–58).
9. Antero-posterior diameter of shaft at this point, 54 (43–51).
10. Least length of olecranon, from tip of *processus coronoideus* along the anterior margin, 157 (155–167).
11. Greatest antero-posterior diameter of olecranon from the tip of *processus coronoideus*, 128 (120–126).
12. Least antero-posterior diameter of olecranon, 93·5 (88–105·5).
13. Greatest antero-posterior diameter of the end of the olecranon, 117 (109–115).
14. Greatest transverse width of end of olecranon, 79 (87–93).
15. Least width of anterior margin of olecranon, 32 (26–31).
16. Longitudinal diameter of *cavitas semilunaris* from the tip of *processus coronoideus*, on the outer side (without radial portion), 80 (78–84).
17. Ditto on the inner side, 96 (89–97).
18. Ditto in the middle line (not including radial surface), 59 (52–61).
19. Ditto on outer side, but including radial surface, 102·5 (91–102).
20. Greatest width of the lower end of *cavitas semilunaris*, 96 (94–106)."

April 7th, 1925.

Prof. E. W. MacBride, F.R.S., F.Z.S., Vice-President, in the Chair.

The Secretary exhibited, and made remarks upon, a photograph showing the new Monkey-hill enclosure, now in course of construction in the Society's Gardens.

Dr. F. B. Stowell exhibited, and made remarks upon, a series of spectrographs taken through Vita-glass.

Dr. H. H. Scott, M.D., M.R.C.P., F.Z.S., exhibited lantern-slides showing the lower jaw and part of the intestine of a Tiger which had died in February of acute intestinal obstruction. The dried skull and the intestine at the site of obstruction were also exhibited. The jaw showed two sinuses leading to an abscess at the root of the right lower canine tooth. By destruction of the root and absorption this canine was fully half an inch shorter than the left. There were signs of periodontitis and pyorrhœa alveolaris.

Dr. Scott interpreted the probable sequence of events as follows:—The dental condition would result in considerable pain on mastication and consequent bolting of food. A large piece of bone had thus been swallowed whole and, some 16 feet below the pylorus, had completely occluded the bowel. Violent peristalsis had then led to twisting of the gut for 6–7 feet above the blockage with strangulation. The mesentery thereby became congested and unduly fragile and had torn; through the rent another 8 feet of the gut lower down had passed and this in turn became strangulated. Death was due to general peritonitis, the result of the double obstruction.

Mr. R. H. Burne, M.A., F.Z.S., exhibited, and made remarks upon, a series of hair-balls taken from the stomachs of an Ox and of a Peccary, and also balls of fish-bones probably from the alimentary canal of some Cetacean.

Mr. E. G. Boulenger, F.Z.S., exhibited, and made remarks upon, some specimens of exuviæ of Crustacea from the Society's Aquarium.

April 21st, 1925.

Prof. J. P. Hill, F.R.S., Vice-President, in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of March, 1925:—

The registered additions to the Society's Menagerie during the month of March were 122 in number. Of these 81 were acquired by presentation, 11 were deposited, 29 were purchased, and 1 was born in the Menagerie.

The following may be specially mentioned:—

1 Chimpanzee (*Anthropopithecus troglodytes*), ♀, from the Cameroons, presented by J. A. Ogilvie, Esq., on March 29th.

1 Black-fronted Duiker (*Cephalophus nigrifrons*), ♂, from the Belgian Congo, presented by G. S. Young, Esq., on March 12th.

1 Tamandua Anteater (*Tamandua tetradactyla*), from S. America, purchased on March 25th.

1 Royal Starling (*Cosmopsarus regius*), from Abyssinia, new to the Collection, deposited on March 26th.

1 Solitary Cuckoo (*Cuculus solitarius*), from Uganda, new to the Collection, presented by Mrs. L. M. Seth-Smith on March 21st.

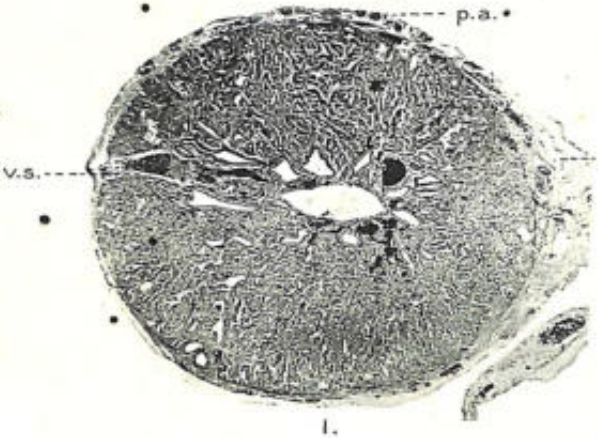
1 Lammergeier (*Gypaëtus barbatus*), from the Pyrenees, presented by Capt. E. J. P. Pelley, O.B.E., on March 12th.

Dr. G. M. Vevers, F.Z.S., read a letter from Mr. R. C. Samuels, F.A.I., giving an account of pieces of Reed stated to have been removed from the head of an African Elephant.

Mr. H. C. Brooke, F.Z.S., exhibited, and made remarks upon, living specimens of hairless Mice.

Mr. G. C. Robson, M.A., F.Z.S., exhibited, and made remarks upon, a remarkable modification of the Tentacle in an Œgopsid Cephalopod.

Mr. F. Martin Duncan, F.R.M.S., F.Z.S., exhibited, and made remarks upon, an improved method of illumination which he had devised for use in zoological research.



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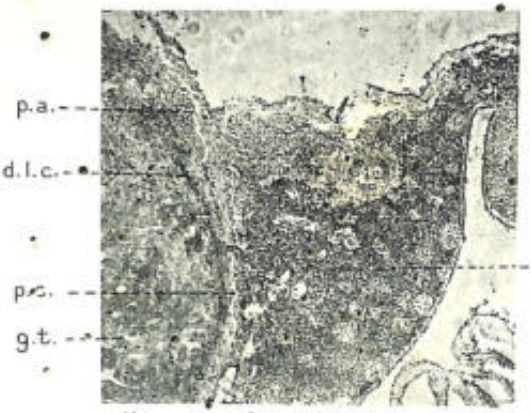

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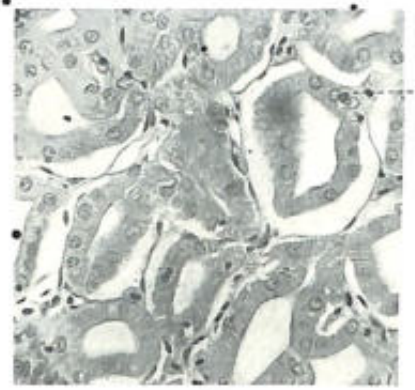
COMPARATIVE MORPHOLOGY OF CÆCAL GLAND OF SELACHIAN FISHES.



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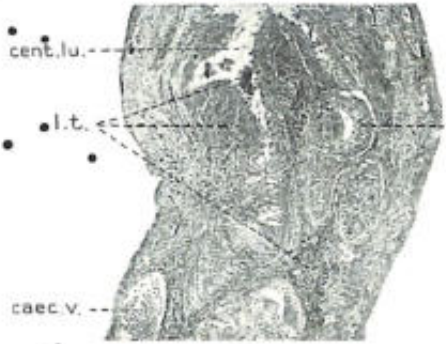

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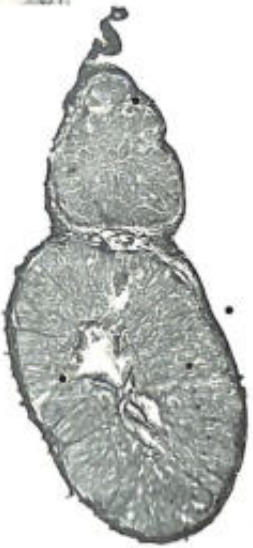

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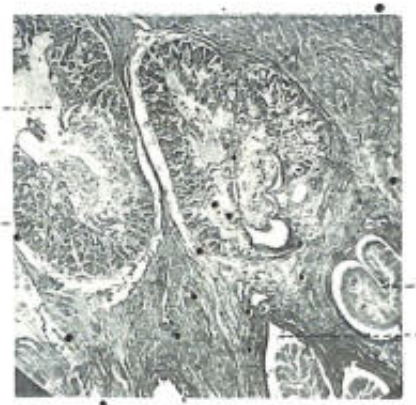

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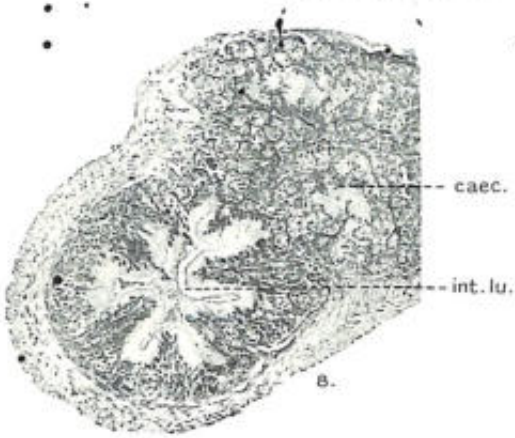
COMPARATIVE MORPHOLOGY OF CÆCAL GLAND OF SELACHIAN FISHES.



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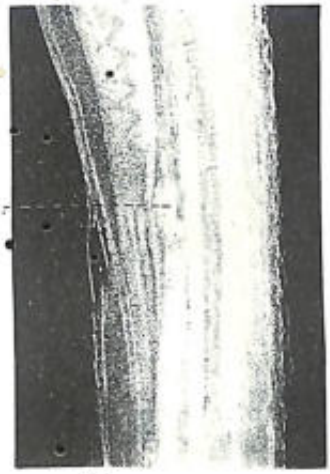

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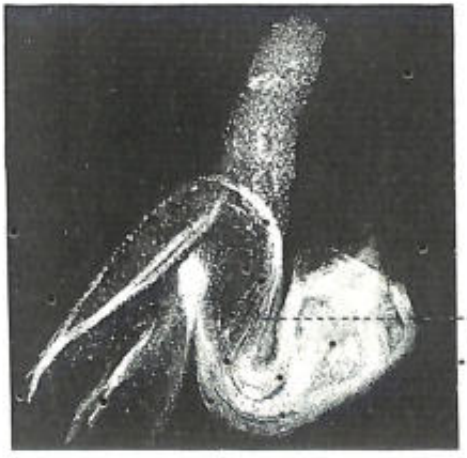

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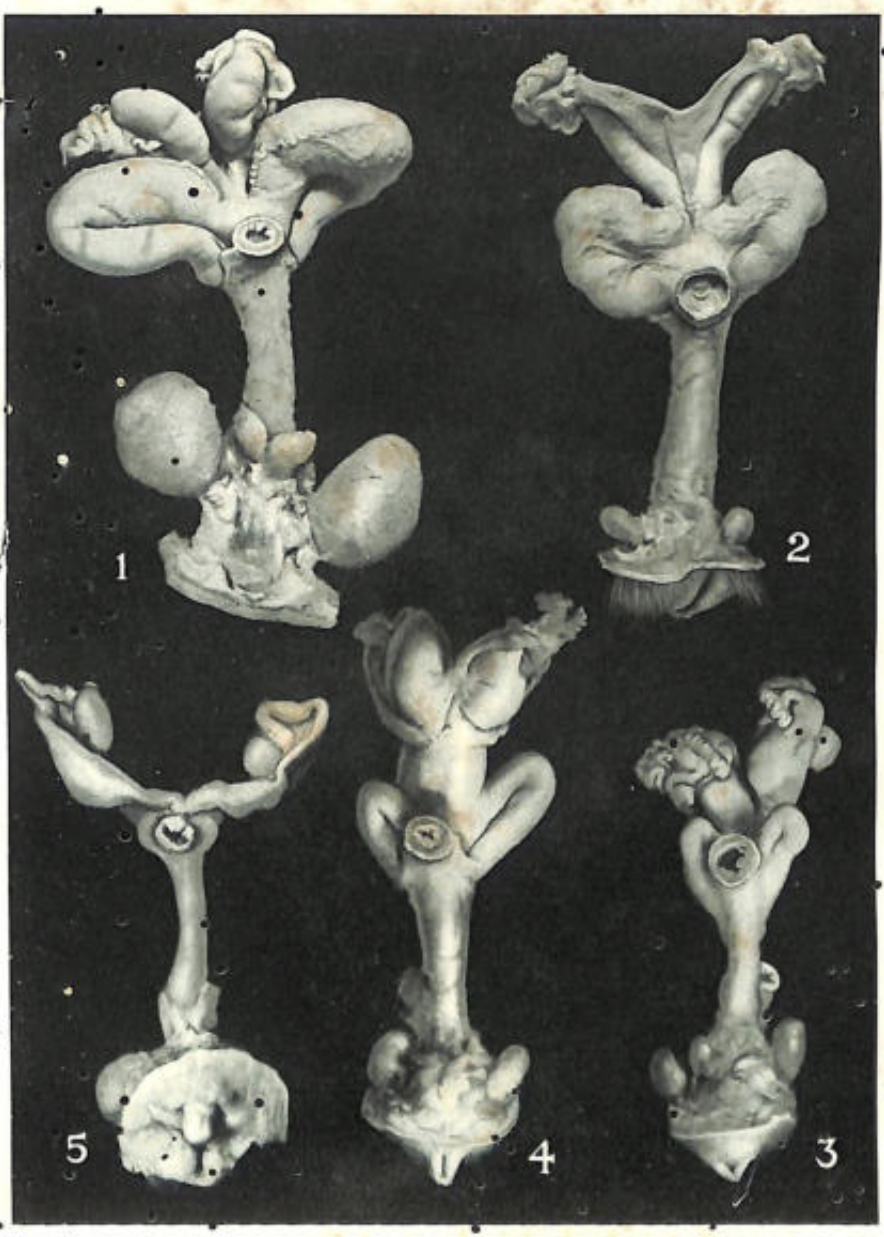
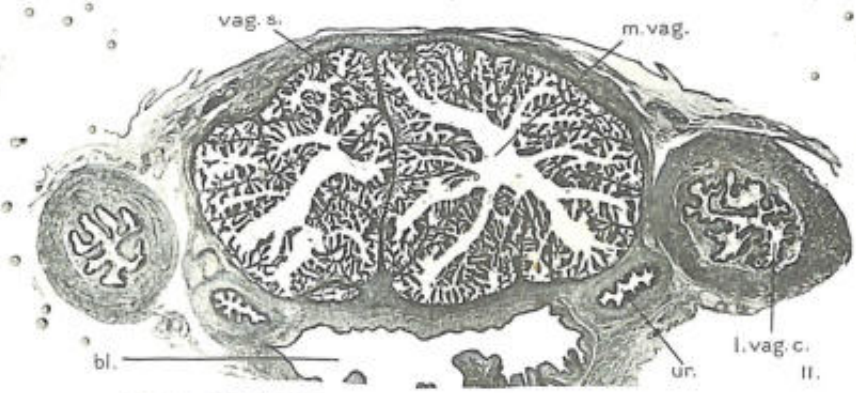
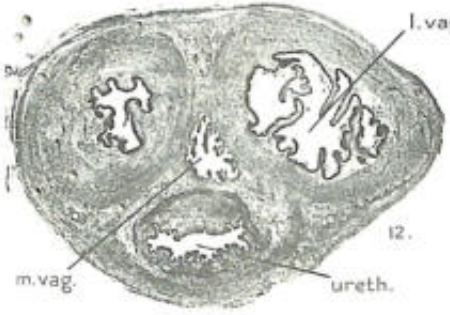
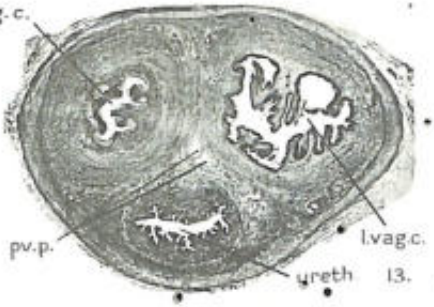


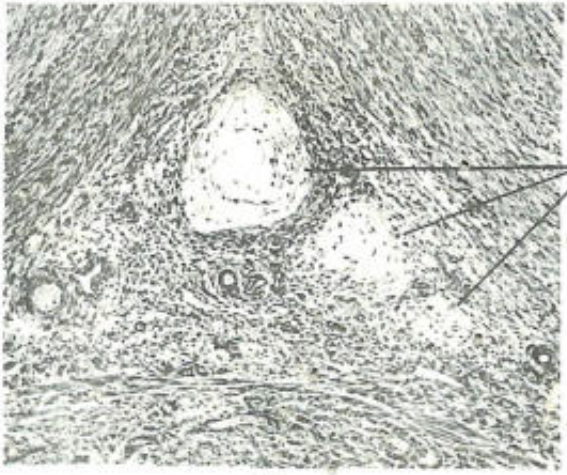
1. *D. aurita.* 2. *M. nudicaudatus.* 3. *M. opossum.* 4. *Caluromys philander.* 5. *Chironectes minimus.*

6. *Marmosa cinerea.* 7. *M. murina.* 8. *Monodelphis americana.*
9. *M. domestica.* 10. *M. theresa.*









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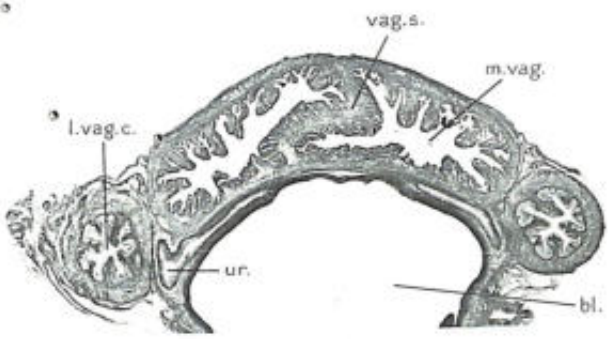
DIDELPHYS AURITA.



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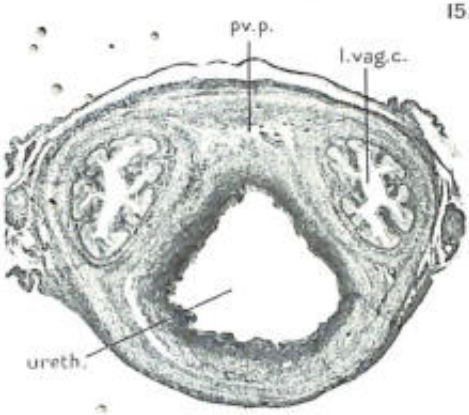

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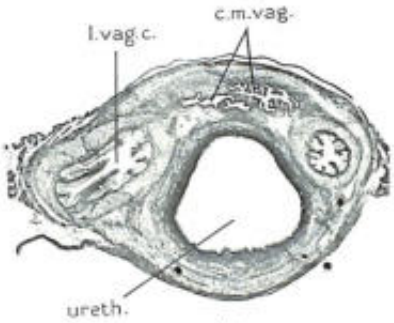

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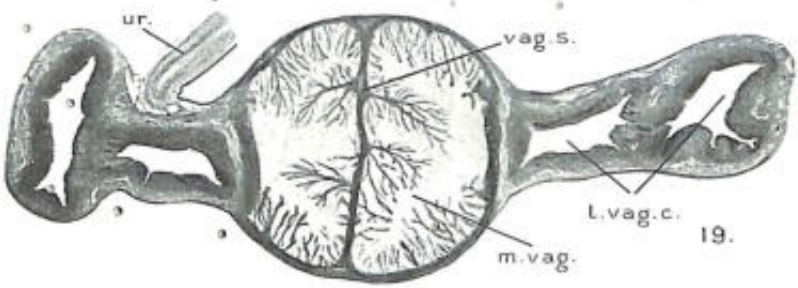
METACHIRUS OPOSSUM (15 - 17), M. NUDICAUDATUS (18).



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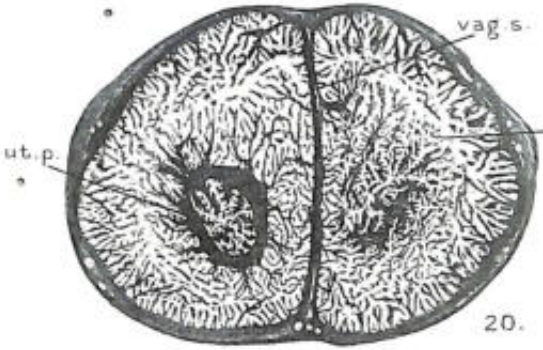

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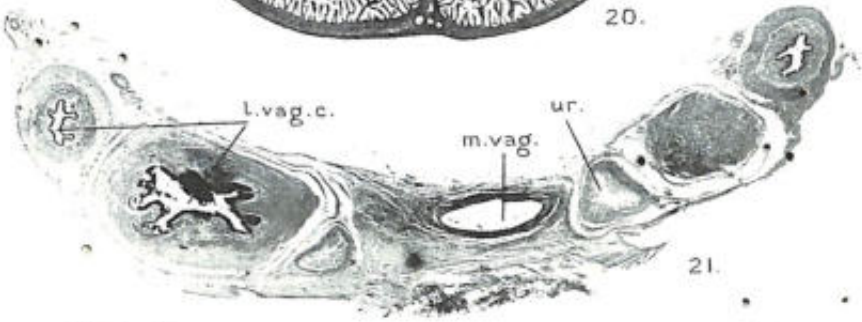

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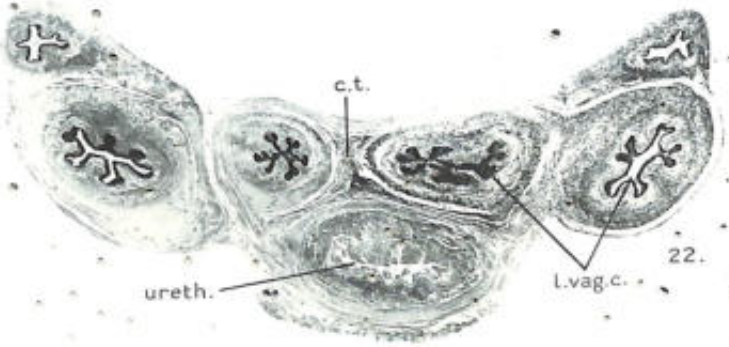

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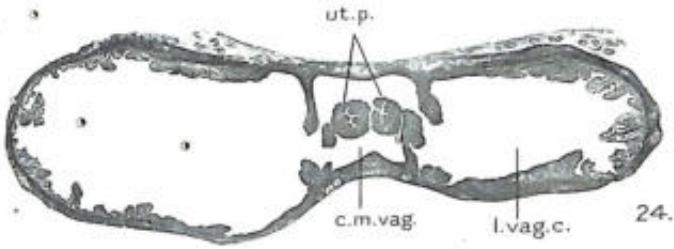
CALUROMYS PHILANDER (19, 20), M. MURINA (21, 22).



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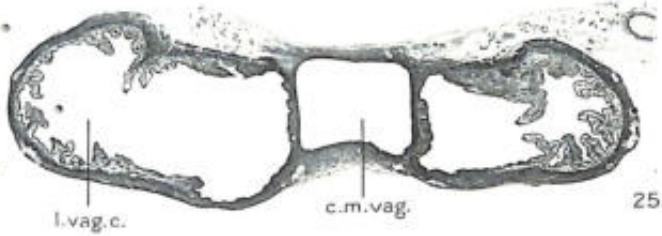

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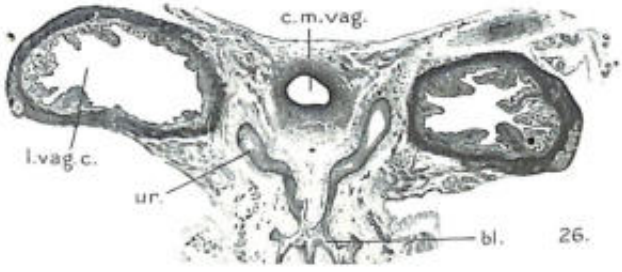

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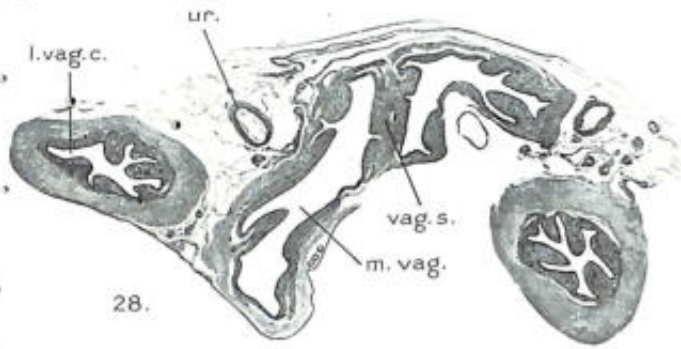
MARMOSA CINEREA.



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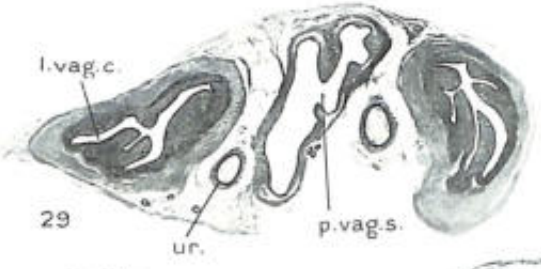

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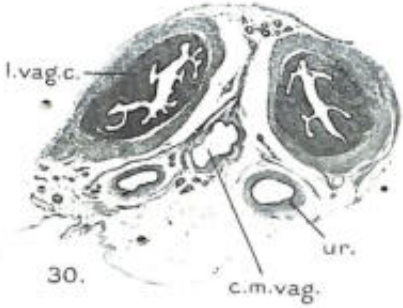

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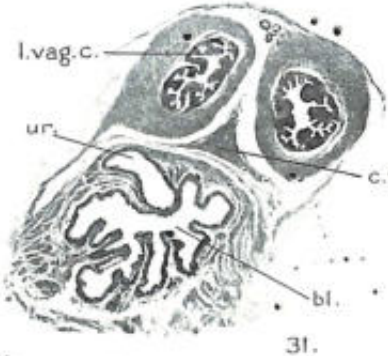

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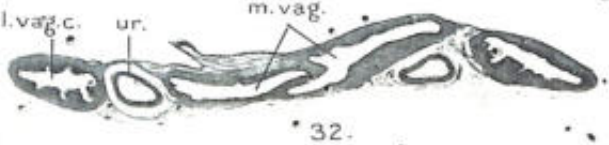
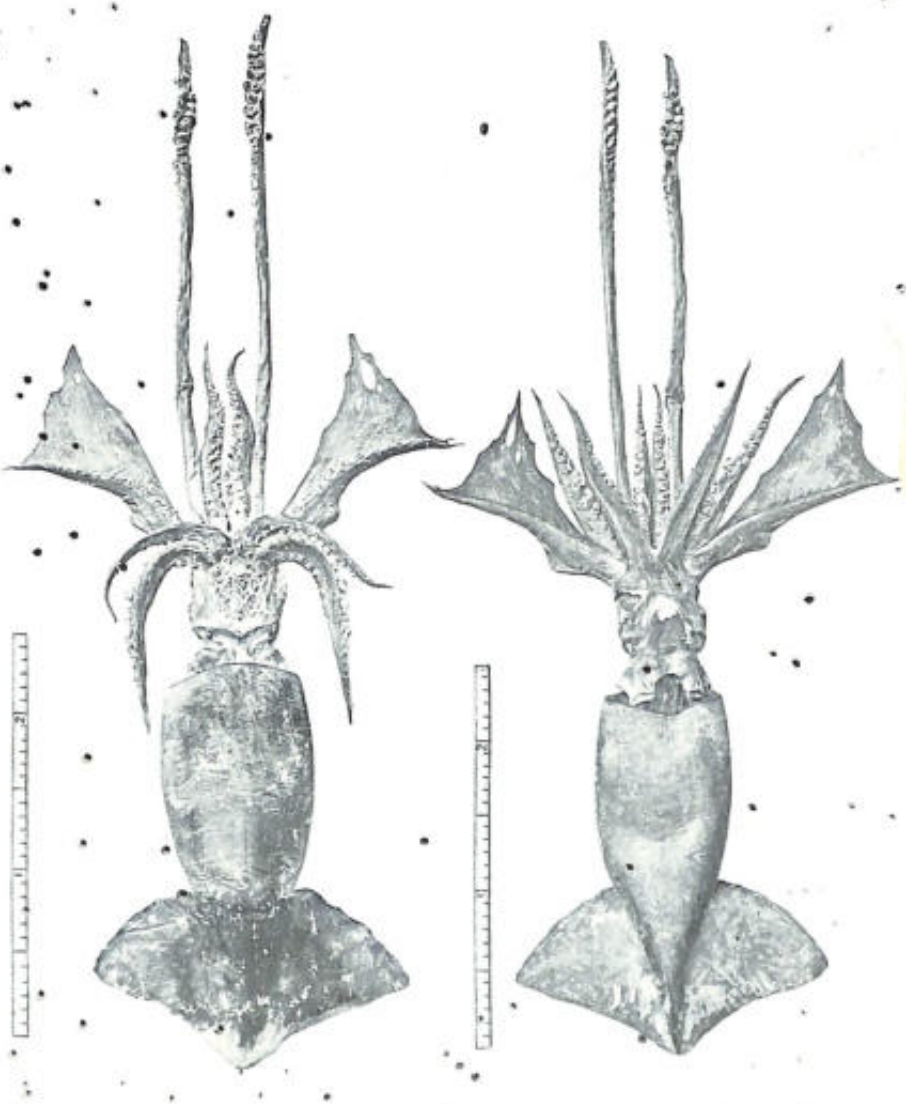
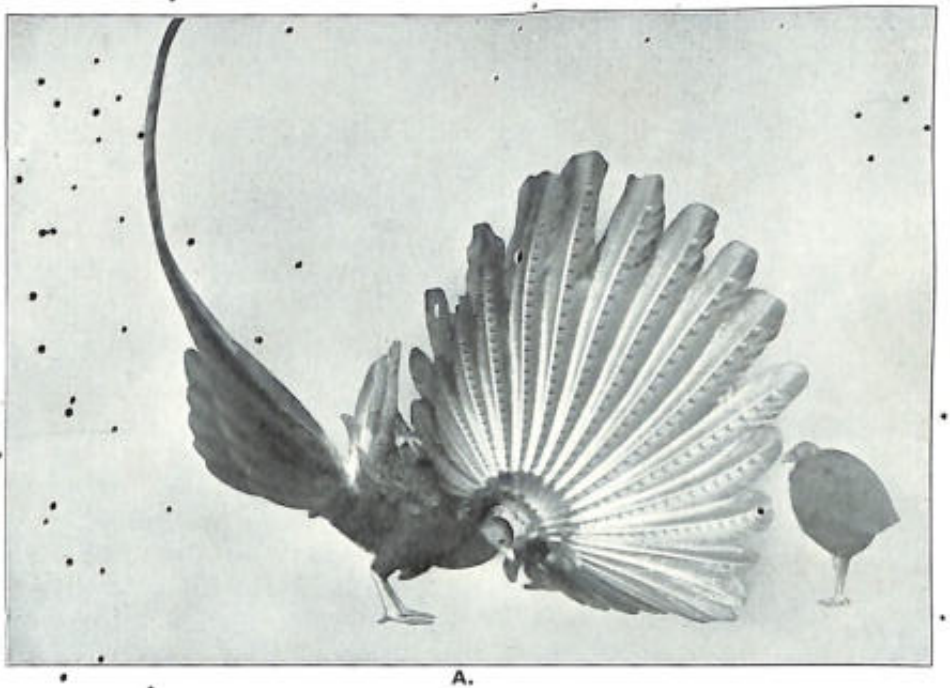


32.

M. AMERICANA (28 - 31), M. DOMESTICA (32).



STENOTEUTHIS CAROLI. x $\frac{1}{15}$



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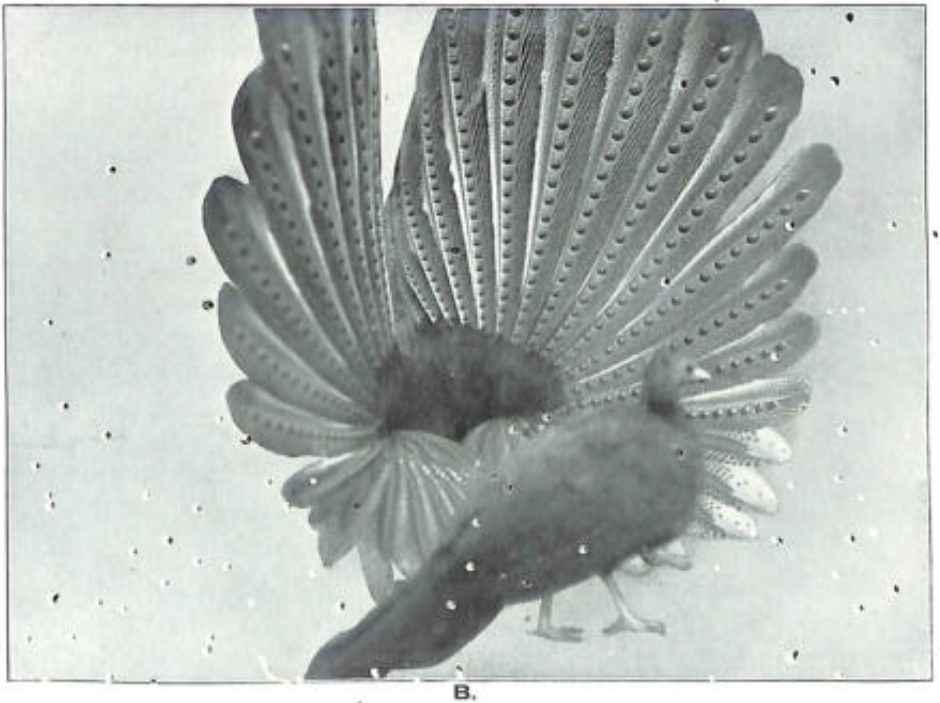
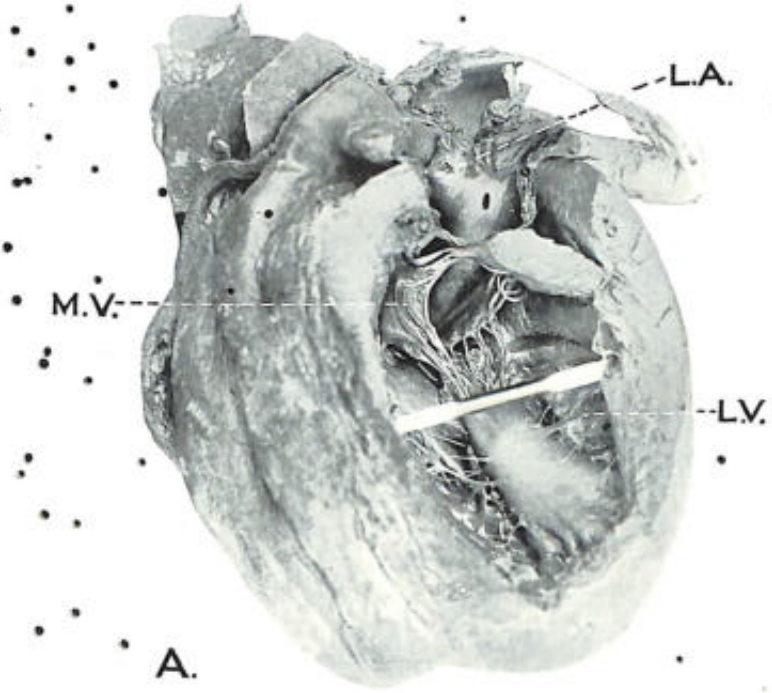


B.

ARGUS PHEASANT (*ARGUSIANUS ARGUS*) IN DISPLAY.

A. Side view. B Front view.



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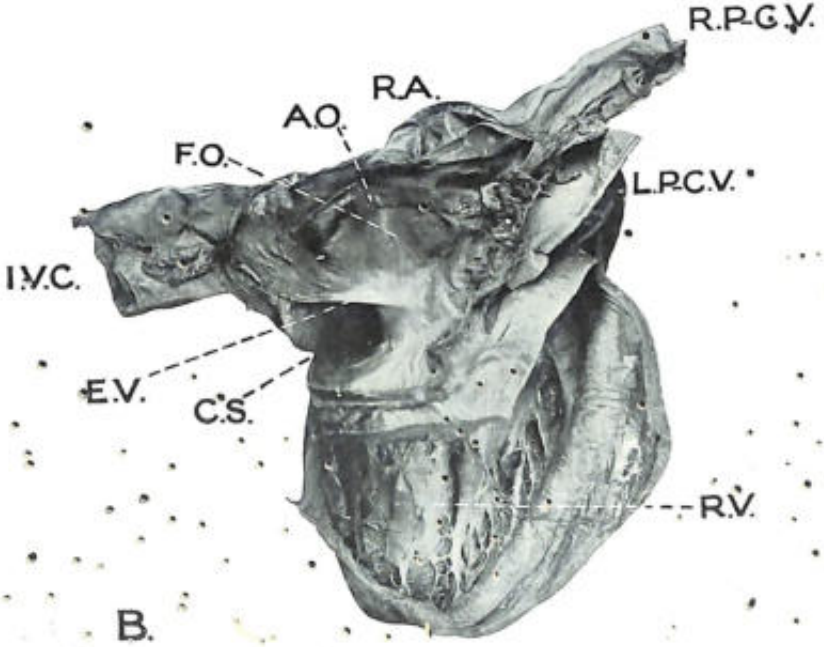
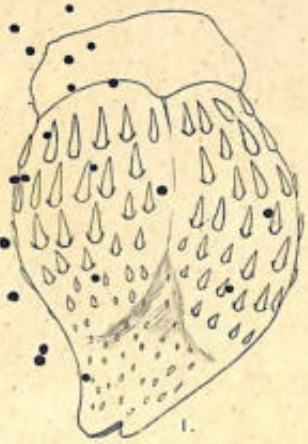


B.

ORYCTEROPUS AFER.

FŒTAL AFRICAN ELEPHANT.



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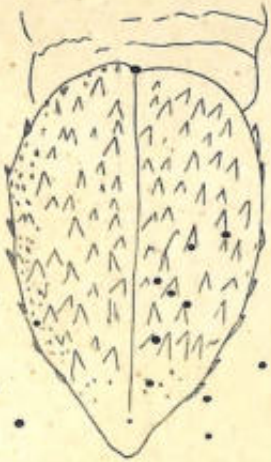

9.

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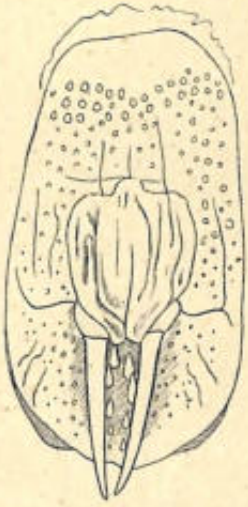
3.



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5b.

6a.

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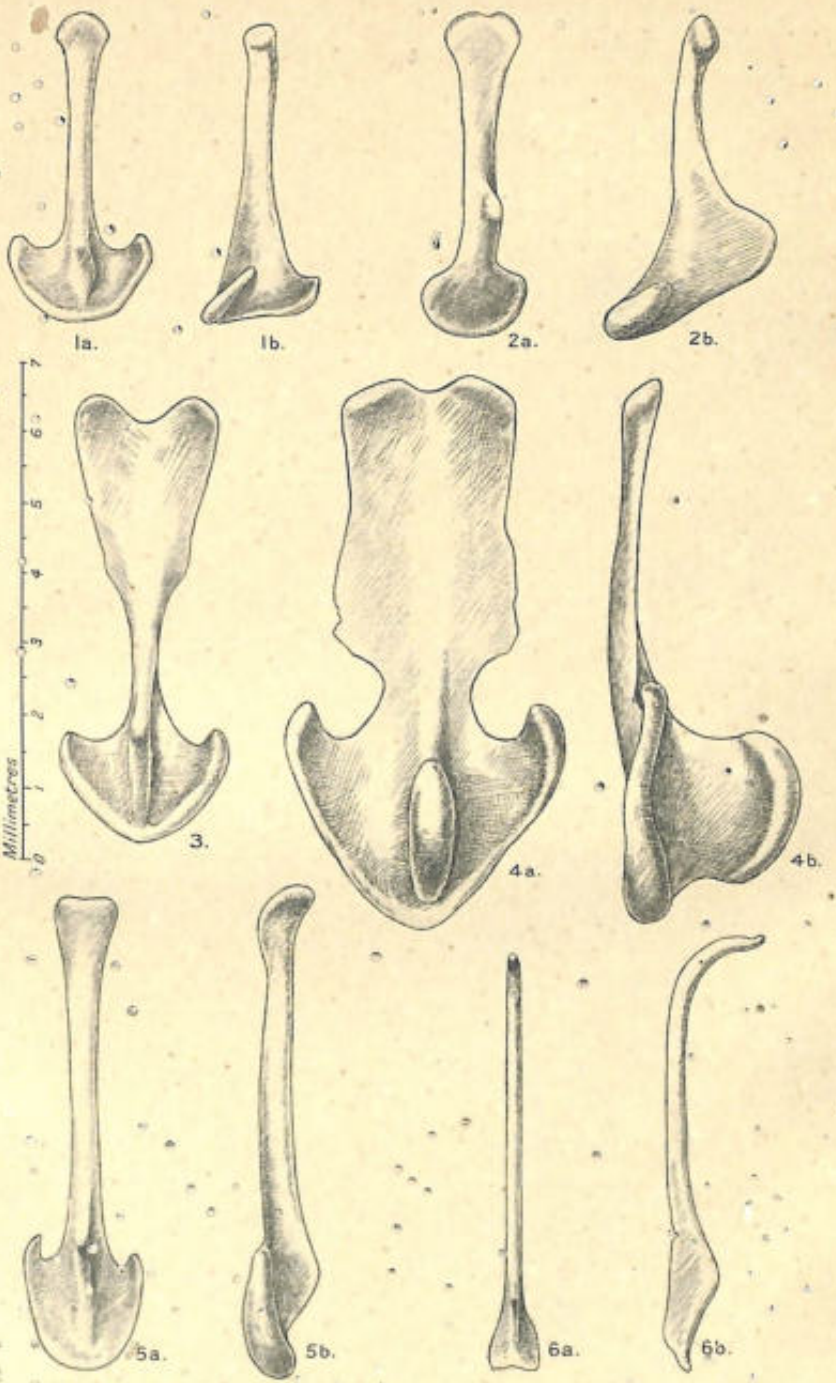

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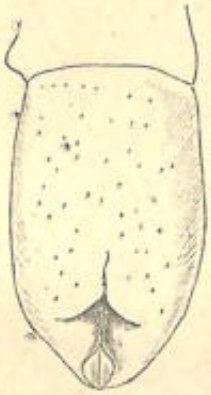

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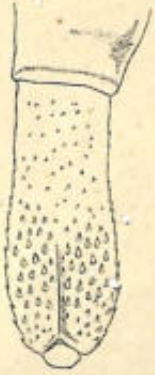

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EXTERNAL GENITALIA IN DIPODIDÆ AND ZAPODIDÆ.

1a.

1b.

2a.

2b.

3a.

3b.

4a.

4b.

5a.

5b.

6a.

6b.

B. Vinogradov, del.

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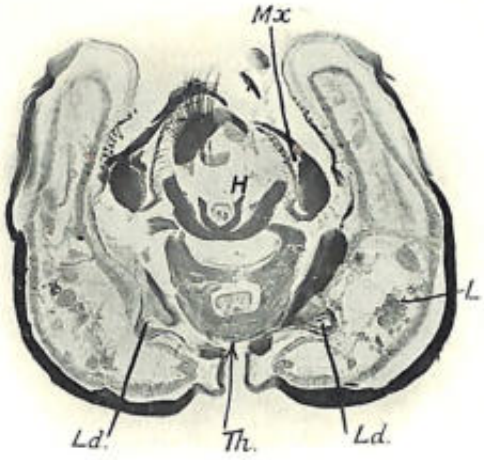
1.



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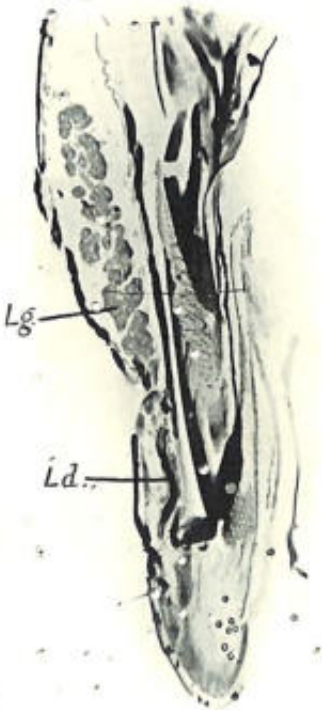


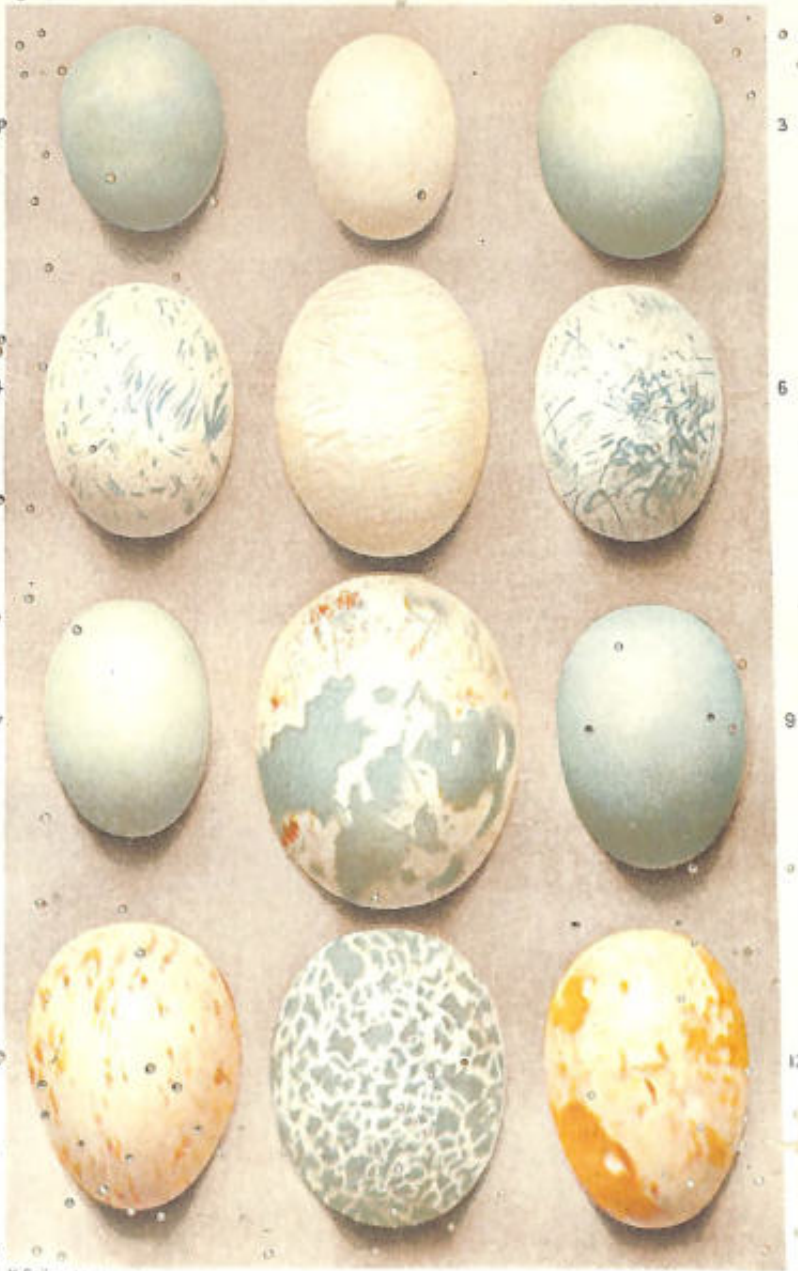
2.

STRUCTURE OF MOUTH-PARTS IN ASILIDAE

2.

1.

STRUCTURE OF MOUTH-PARTS IN ASILIDAE.



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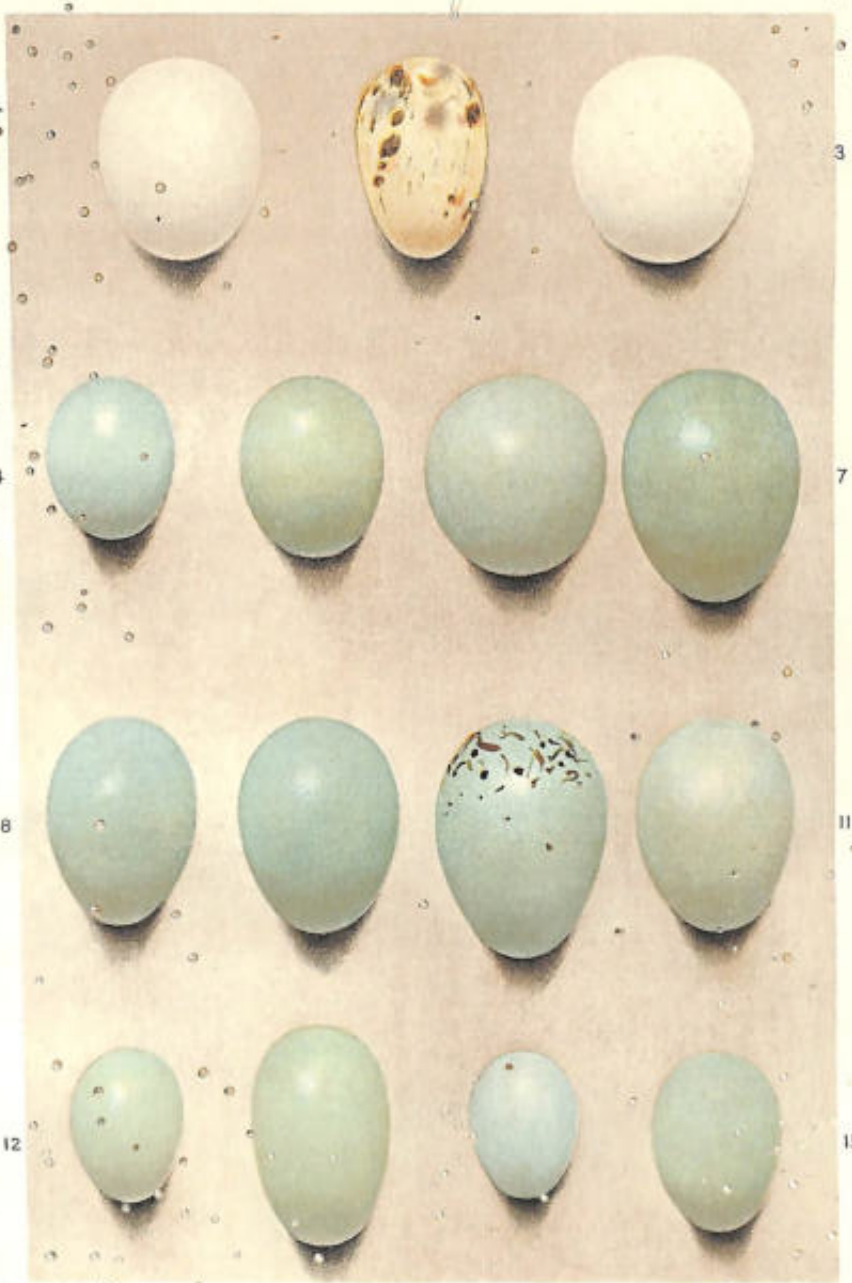

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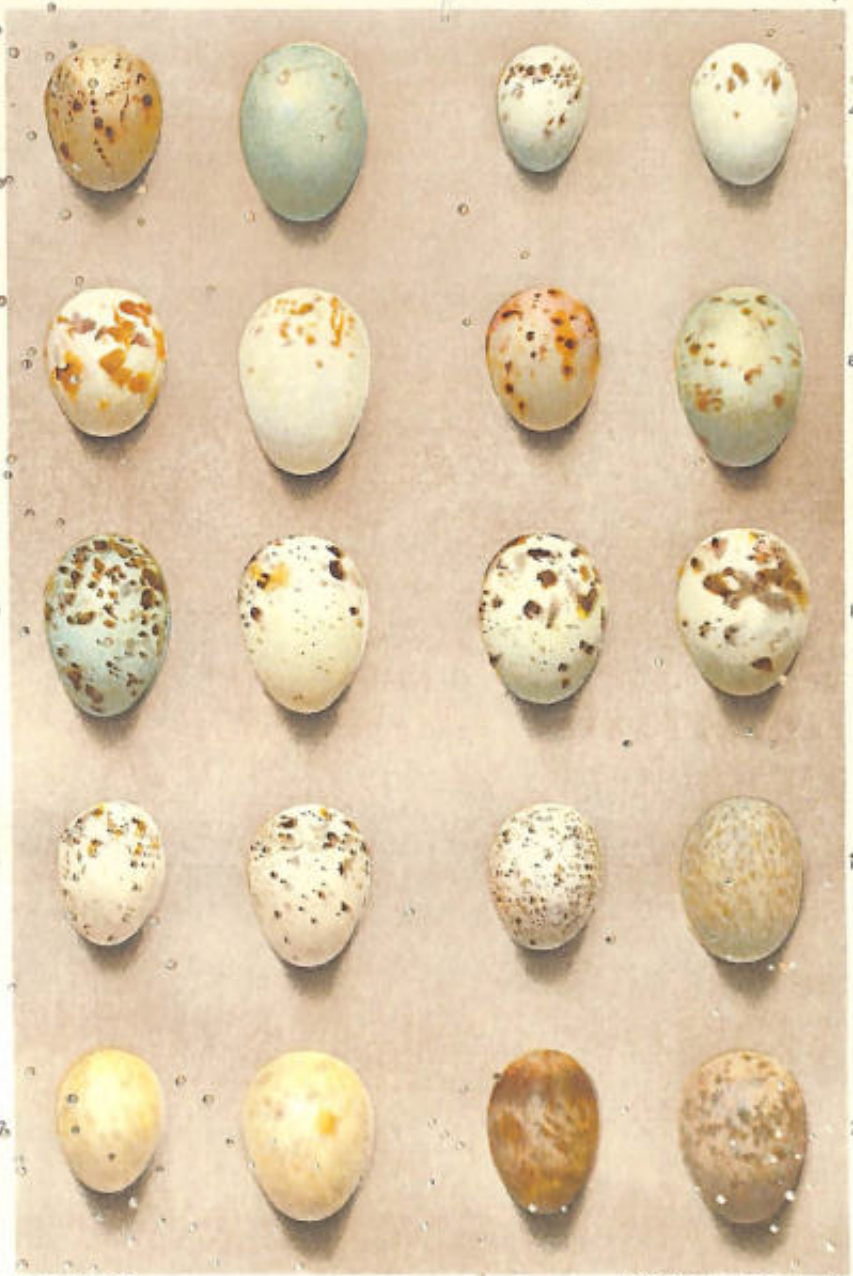

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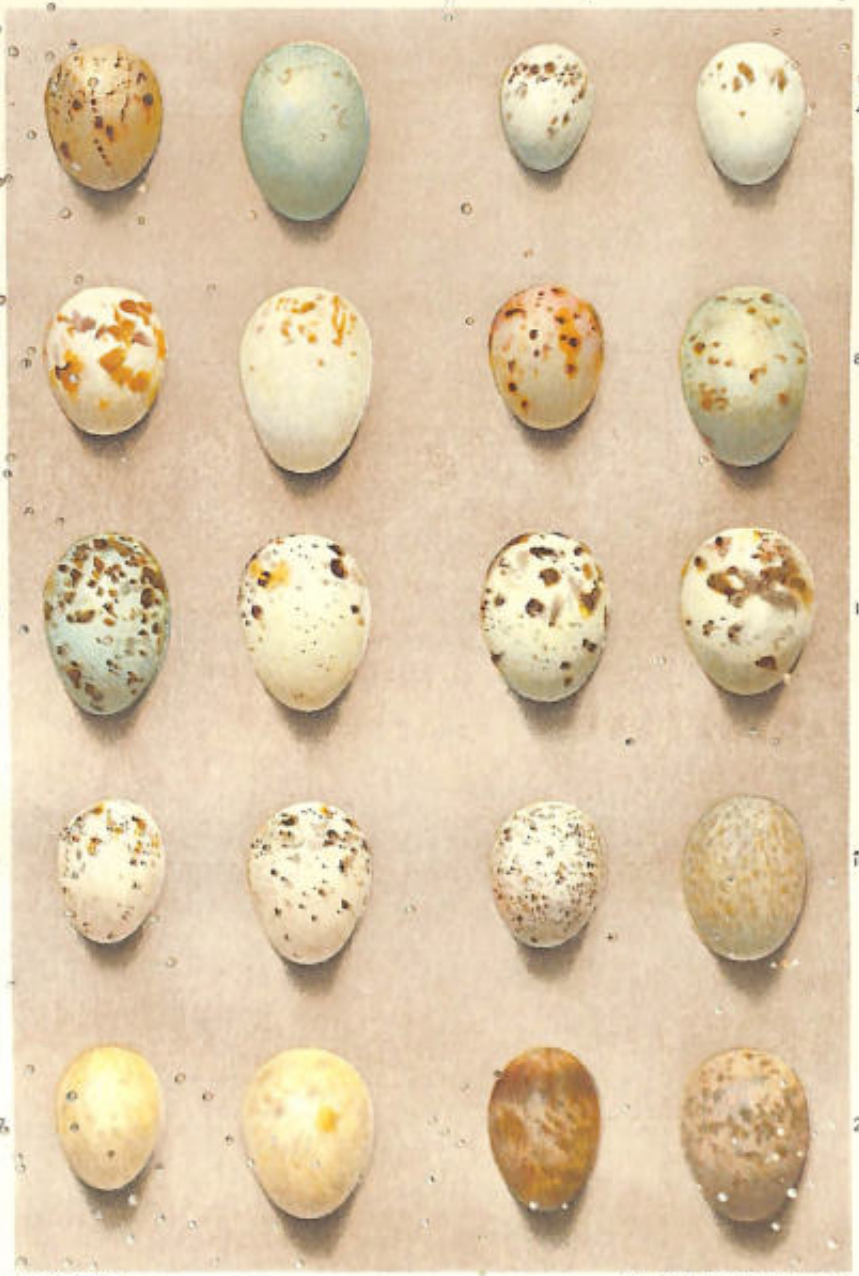
EGGS OF PARASITIC CUCKOOS AND HOSTS.



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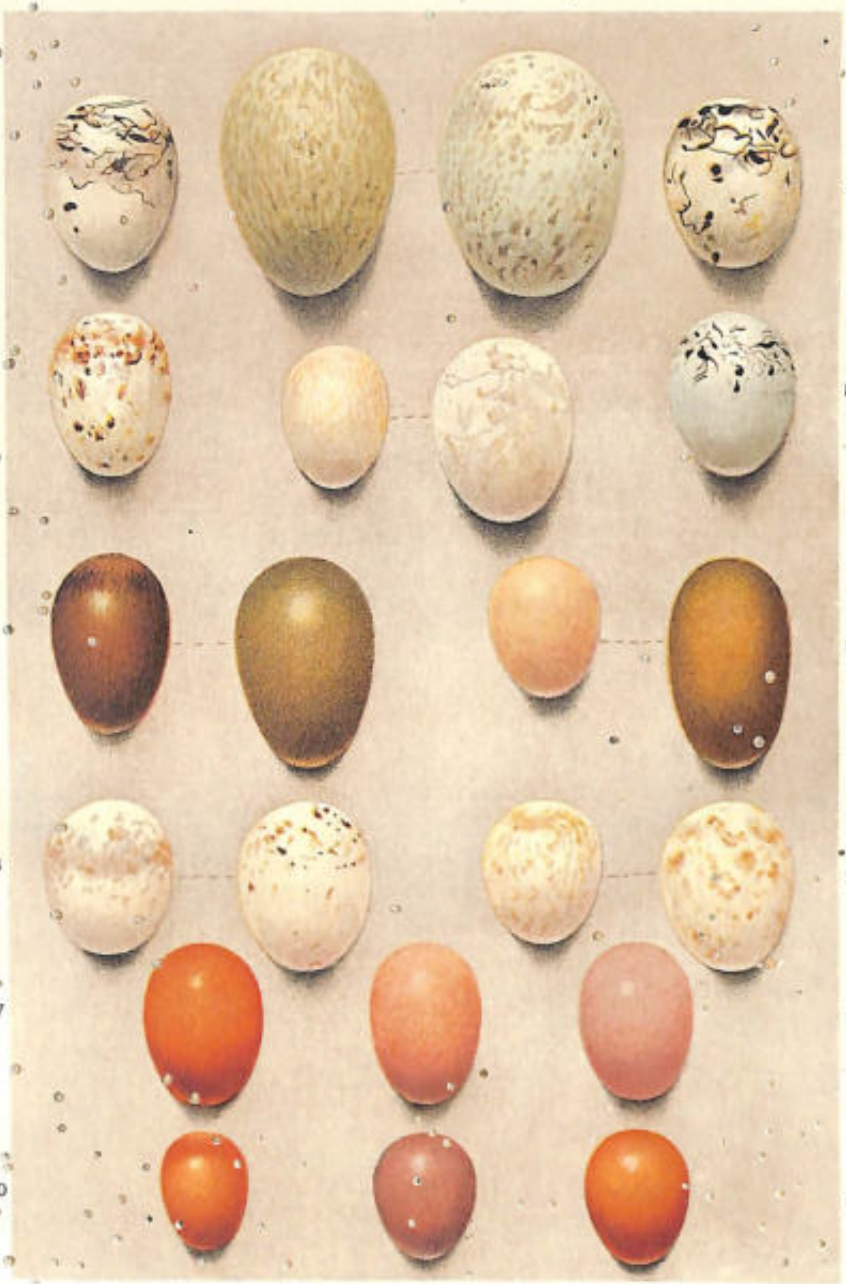

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EGGS OF PARASITIC CUCKOOS AND HOSTS.

NESTLING CUCKOOS AND HOSTS.

1. *BUFO MICRANOTIS*, SP.N. 2. *RANA BARBOURI*, SP.N.
3. *BREVICEPS ULUGURUENSIS*, SP.N.

RANA MWANZÆ, SP.N.

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