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# SCIENTIFIC MEMOIRS

BY

## OFFICERS OF THE MEDICAL AND SANITARY DEPARTMENTS

OF THE

## GOVERNMENT OF INDIA

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# Studies on the Mouth Parts and Sucking Apparatus of the Blood-Sucking Diptera

No. 3.

*Lyperosia minuta, Bezzi*

BY

CAPTAIN F. W. CRAGG, M.B., I.M.S.,

*Assistant to Director, King Institute of Preventive Medicine, Madras*

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ISSUED UNDER THE AUTHORITY OF THE GOVERNMENT OF INDIA BY THE DIRECTOR-GENERAL, INDIAN MEDICAL SERVICE

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BOOK NO.
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# Studies on the Mouth Parts and Sucking Apparatus of the Blood-Sucking Diptera.

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## No. 3.

## Lyperosia minuta, Bezzi.

ALTHOUGH the mouth parts of *Musca* and its non-biting allies have been a favourite subject of research, especially among the older entomologists, the blood-sucking members of the group do not appear to have attracted much attention until the advent of the modern era of parasitology. Since the recognition of the rôle played by the blood-sucking arthropods in the transmission of disease the subject has come to have, in addition to the academic interest attaching to it, a certain practical importance, for it is through the proboscis that the infective stage of the blood parasite must pass when it is transmitted from one host to the other. A knowledge of the anatomy of this region, and of the mechanism of the complicated structures concerned in the act of feeding, is therefore essential to those engaged in the study of insect-borne disease.

The only recent accounts of the proboscides of the blood sucking Muscids are those of Hansen, who gave brief descriptions of *Stomoxys* and *Glossina* and of Stephens and Newstead, who described and figured the external mouth parts of the same flies in much greater detail, and the present writer's account of *Philæmatomyia insignis*. The descriptions of both on *Stomoxys* and *Glossina*, though they are accurate as regards the anatomical details, are incomplete, these authors having unfortunately had access only to dried and preserved material. This is a most serious handicap, for it is only by the examination of fresh material that one is able to study satisfactorily the complex mechanism of the proboscis, and this is one of the most important points. The suggestions regarding the nature of the biting action offered by the above authors are a good deal wide of the mark.

According to Austen the genus *Lyperosia* is intermediate between *Stomoxys* and *Glossina*. As regards the structure and general appearance of the proboscis it closely resembles *Stomoxys*, such differences as there are being only in matters of detail. The two are at once distinguished by the length of the palpi, which in *Stomoxys* are short, and in *Lyperosia* project almost to the tip of the proboscis. The internal structures show a rather greater degree of

specialisation than seen in *Stomoxys*, thus corresponding with the external characters. Notwithstanding the similarity of the two forms, however, I propose to give a detailed description of *Lyperosia*, for my observations differ in many points from those of the authors cited, and my view of the mechanism is so essentially different that a complete account will be necessary to ensure lucidity. The homology of certain of the parts with those of *Musca* will be pointed out in passing, leaving the details of this interesting branch of the subject to be dealt with in a further paper, which I hope to publish shortly.

## Methods.

The parts were studied first by the examination of cleared preparations, in order to become familiar with the chitinous skeleton of the proboscis. It was found convenient to place a large number of specimens in potash solution at the same time, and to remove them at intervals, so that preparations showing different degrees of transparency could be obtained. Dissection is most conveniently done after the preparations are cleared in clove oil, for many of the parts, for instance the labella, are so small that one runs great risk of losing them if they have to be subjected to any manipulation after removal from the rest of the organ. It is so difficult to mount such small objects in the desired position that it is best to mount a large number at the same time and preferably on the same slide, so as to increase the chances of getting the desired point of view. Dissection was performed under a Zeiss binocular microscope, with a magnification of from twenty to forty diameters. Carefully ground needles with various shaped points are essential. The dissection of fresh specimens is of the greatest importance in the study of the mechanism, for one often can decide what is the function of a muscle by pulling on it when one cannot be absolutely certain of the exact point of its attachment. The examination of flies recovering from a dose of ether is also very instructive, as one can actually see the same movements of the proboscis as are performed during the act of feeding, though they are, of course, convulsive and irregular.

For serial sections the combined paraffin and celloidin method was used. It is best not to attempt to cut a whole series from one preparation, but to cut away boldly one end of the specimen, so as to allow the fluids to penetrate freely. The chitinous walls themselves are practically impervious to the ordinary reagents, and it is advisable to perforate them with a needle at some unimportant point, in addition to making a free opening at one end. Bles's fluid was used as the fixative, followed by rapid dehydration in several changes of absolute alcohol; the shorter the time chitinous objects are left in absolute alcohol the more likely one is to get unbroken sections.

## General Account.

The proboscis (Fig. 1, Plate 1) consists of three parts, corresponding to those found in *Musca*, and more or less freely moveable on one another. The rostrum is hidden from view on the under surface of the head in the position of rest, and is much smaller than that of *Musca*. The haustellum, or proboscis proper, on the other hand, is elongated and narrowed, and projects horizontally forward in front of the head. It is not fixed in this position, but is capable of forward and backward movement, and elevation and depression, in exactly the same manner as that of *Musca*, though to a smaller extent. It consists of the usual parts, *viz.*, the labrum-epipharynx, hypopharynx, and labium, the latter forming the main bulk of the haustellum and concealing the other two in a groove on its upper surface. The labium is typically spindle shaped; its greatest breadth, about one-third of the total length, is situated at its proximal end, this portion being termed by Stephens and Newstead the "bulb." At the distal end the labium is divided into a pair of labella, which are completely separated from one another in the middle line in front and distally, but united in the proximal part of their posterior surface. They project beyond the labrum-epipharynx and hypopharynx. The wall of the rostrum is entirely membraneous and flexible, that of the haustellum chitinous and rigid, except at the place where the labium divides into the two labella, the chitin being here partly replaced by a soft membrane. That portion of the labellar wall which is external in the position of rest is chitinous.

The palps arise from the anterior surface of the rostrum about its middle. They are clavate, slightly flattened from side to side, and have a few short stout bristles scattered over the surface, and a coat of very fine recumbent hairs. Their length is about equal to that of the haustellum. At the base of each palp there is a small area extending downwards in which the membrane is chitinised. In the resting position the palps lie in front of and in contact with the proboscis, but when it is in use they move forwards and upwards so as to become almost perpendicular to it.

It will be well to refer here to the relation of the several parts of the proboscis to one another in the position of rest, and to the range of movement as seen in the living fly, comparing *Lyperosia* with *Musca* as regards these points. The most obvious difference between the two is that while in *Musca* the proboscis is completely retractile, in *Lyperosia* the haustellum in the position of rest remains completely visible and in a horizontal plane. The labella are not folded backwards on the lower (or posterior) surface of the haustellum, but remain fixed in the same line with it. The joints between the head and the rostrum and between the rostrum and the haustellum may be compared to the human shoulder and elbow, if one imagines the shoulder joint to be

capable of movement only in the same plane as the elbow joint. In *Musca* the position of rest is equivalent to that in which the upper arm is bent backwards horizontally behind the body, and the forearm flexed so that the two are in contact; in *Lyperosia* the amount of flexion of the upper joint is not quite so great, and the haustellum, which remains in a horizontal plane, makes an angle of about sixty degrees with the rostrum. The difference in appearance is simply due to the increased length of the haustellum in *Lyperosia*, and to the incompleteness of the retraction.

From this position movements can be performed which are in every respect similar to those of *Musca*, except that they are more limited in extent. The proboscis is extended by the straightening out of the two joints in the same way that the arm can be extended from the position indicated above until it is thrust out in front of the body. The two joints act together, but not always to the same degree, so that the tip of the proboscis may come to lie in any position within a quadrant of a circle the centre of which is the joint between the rostrum and the head, and the radius the line between this and the tip of the proboscis when fully extended; the upper limit of the quadrant is the horizontal line in which the proboscis lies in the position of rest, and the lower limit in the vertical line, that is, in the position of full extension in *Musca*. The range of movement from the periphery of the circle is of course limited to a distance less than twice the length of the rostrum. In the act of feeding the position occupied is about midway between the upper and posterior sides of the quadrant, and a short distance from the periphery, or, in other words, one of incomplete extension of both joints, whereas in *Musca* and in *Philæmatomyia* there is complete extension, a position only occasionally seen as an agonal phenomenon in *Lyperosia*. By means of these two joints the fly is enabled to move its proboscis about on the skin of the host, while selecting a suitable place to insert the biting parts, and in doing so it is assisted by the lateral and rotatory movements of the head and neck. It will be obvious at once that the whole arrangement of joints is adapted to ensure mobility, and that the proboscis is by no means the fixed organ it is sometimes assumed to be. It follows also that there can be no question of *vis a tergo* in the method of making the wound. The mechanism of these movements will be discussed when the anatomy of the parts has been described.

## The Rostrum.

The rostrum has the shape of an inverted and truncated cone, the length of which is slightly greater than the breadth. The relative lengths of the rostrum and haustellum are approximately as one to two, while in *Musca* the two

parts are about equal. In the position of rest the rostrum is retracted and can only be seen when in profile. Its wall is entirely composed of a tough but flexible membrane, attached above to the margins of the aperture in the head capsule, and below to the upper end of the labium and to the broadened upper end of the labrum. When the proboscis is fully extended the wall of the rostrum is smooth and taut, and presents four surfaces, anterior, posterior, and two lateral, but when retraction takes place the organ collapses and the wall is thrown into numerous folds, mainly on the posterior surface.

The rostrum is, strictly speaking, a part of the head which can be protruded, and is not composed of the true mouth parts. The internal structures consist of the pharynx, the salivary duct, certain important tracheal sacs, and the muscles which act upon the joint between it and the head and on the haustellum in the movements of extension and retraction. All these correspond with similar structures in *Musca*, but show certain modifications which must be noted.

The pharynx is contained within a chitinous fulcrum which is proportionately smaller than that of the non-biting forms, and narrower in proportion to its length. The lateral plates arise from the middle third of the lateral borders of the posterior plate, and their upper borders, which are much thicker than the rest of the lateral area, pass almost directly forwards to the anterior arch, which therefore lies more nearly opposite to the middle of the posterior plate than in *Musca*. The upper cornua are rather long, and turn slightly forwards at their terminations. The anterior plate of the pharynx, which with the posterior plate encloses the potential cavity of the pharynx, presents an interesting peculiarity in the arrangement of the sensory hairs. There are two sets, a lateral one corresponding to those described by Kraepelin in *Musca*, and a median set situated on the sides of the ridge in the middle line. The lateral set consists of eleven hairs, the position of which is easily seen under a low power on account of the circular clear areas on which they are set; they are arranged in pairs, but only irregularly so, for those of the left side are slightly distal to those on the right and the right hand member of the third pair is absent. The first (distal) pair is much larger than the others, and the second pair smaller, and placed nearer to the first than to those of the third; the median set are small and are just visible as clear spaces at the sides of the ridge, though of course on the opposite surface. There are two nearly opposite one another between the first and second pairs of the lateral set, and three others at irregular intervals proximal to this. This irregularity in structures which one would expect to be symmetrically arranged is rather remarkable.

The lower end of the fulcrum (Figures 11 and 12, Plate II), at the inlet of the pharyngeal cavity, is very different to that of *Musca* or *Calliphora*, being specially adapted to receive the duct which connects the pharynx with the

food canal in the haustellum. The lateral diameter of the fulcrum contracts until a four sided channel is formed, bounded in front and behind by the anterior and postérior plates of the pharynx, and at the narrowest point the anterior and posterior walls of the channel cease, while the lateral walls expand downwards and diverge from one another so as to form a sort of funnel, incomplete in front and behind, the concavity of the plates increasing as they diverge.

As described above, the length of the fulcrum is proportionately less than it is in *Musca*, and there is a considerable interval between the lower end of the pharynx and the end of the labrum-epipharynx. This interval is bridged over by a flexible duct, which is continuous with the food canal at the distal end of the haustellum, and terminates above between the lateral funnel-like expansions at the end of the pharynx, which I have just described. This duct corresponds in position and in function to the hyoid sclerite of *Calliphora*, and to the " chitin kapsel " of Kraepelin. Something of the kind appears to occur in all the flies of the Muscid group, and it will be of advantage to adopt for it a term which will be applicable to all. In the above flies, which are certainly more primitive than *Lyperosia*, it resembles a miniature pharynx, having the form of a cavity, communicating in front with the food channel between the labrum-epipharynx and the hypopharynx, just behind the point correctly regarded by Kraepelin as the mouth of the fly. It corresponds exactly with the first of the two cavities of the sucking apparatus of the Nematocerous Diptera, except that it has no dilator muscle and can take no active part in the mechanism of feeding. As it is always sound to name a structure common to many different forms from its appearance in the simpler rather than the more highly specialised forms, I suggest the name " buccal cavity " for this structure, a term which has the double advantage of referring precisely to its position and emphasizing its homology with the corresponding part in the more primitive Diptera.

The buccal cavity in *Lyperosia* (Figure 1, Plate 1, and Figure 30, Plate VI), then, has the form of a tube, which extends from the distal end of the haustellum to the inlet of the pharynx, and has length equal to about one-third that of the fulcrum. In the resting position it is bent forwards at a sharp angle, the upper half being nearly vertical and in line with the pharynx, the lower half horizontal and in line with the haustellum ; in the extended position of the proboscis the tube becomes straight. The structure of its wall illustrates an arrangement commonly met with in insect anatomy in situations where strength and flexibility are required in the same structure. It consists of two laminæ, and internal and an external one. The internal lamina is soft and membraneous for most of its length, and is attached to the chitinous duct

which is formed by the coalescense of the labrum-epipharynx and the hypopharynx at the distal end of the haustellum. At the upper end, where the duct is enclosed by the funnel-shaped expansion of the lower end of the pharynx, the membrane is replaced by thin but rigid chitin ; in this situation, of course, no flexion takes place. The outer lamina resembles, when seen from the side, a coarse tracheal wall. It consists of about thirty incomplete rings, very much thicker behind than at the sides, and open in front ; the open space between the rings in front diminishes towards the pharynx, and the terminal rings appear to be quite closed. The thickness of the posterior portion of the rings is so great that they come into contact with one another, and so have, when seen from behind, the appearance of a continuous band with a series of transverse ridges. The lateral portions of the rings in the lower half of duct terminate in minute forks, though those of the one side do not interlock with those of the other as do the more regularly arranged rings in the pseudotracheal channels of the house fly. The arrangement is admirably adapted to maintain the lumen of the soft inner duct, and at the same time to allow of flexion without occlusion.

The salivary duct (Figs. 30 and 31, Plate VI) lies in the middle line behind the pharynx and the buccal cavity. The distal portion is a simple chitinous tube with no cellular lining or differentiation of the wall, but after a short course this is replaced by a series of chitinous rings similar to that of the salivary duct of *Musca*. A short distance above the junction with the hypopharynx there is a small valve, acted on by a delicate muscle, precisely corresponding to that *Musca*.

The tracheæ of the rostrum play an important part in the mechanism of extension of the proboscis. There are two large lateral ones, rather of the nature of air sacs than true tracheæ, on either side of the fulcrum. In dissections of fresh flies one can often separate out these as white sausage-shaped bodies, filled with air ; in transverse sections they appear as irregularly crenulated circles much reduced below their natural size on account of the extraction of the air ; at the lower end of the rostrum they are reduced to the ordinary size and structure of tracheæ, and pass into the cavity of the labium.

The musculature of the rostrum is very difficult to study in so small a fly, and I have not succeeded in dissecting out all the separate bundles of fibres ; sections give one little help. The main bundles are however distinct enough, and do not differ from those described by Kraepelin in *Musca*. It is indeed remarkable how closely the arrangements correspond in the two forms. It will be convenient to discuss the separate movements and their musculature together. Starting with the proboscis in the position of rest, we have to consider first the nature of the mechanism by which the rostrum is extended on the head. The

method by which this is accomplished in the house fly has been dealt with with such conclusiveness by Kraepelin that it would be unnecessary to go inte the matter further than to say that there is nothing to indicate that the action is different in this fly, if it were not that the most important muscle of the rostrum has had assigned to it by Hansen the function of extension, in his description of *Stomoxys*. According to Kraepelin, extension of the rostrum on the head is accomplished by the distention of the air sacs of the rostrum, and this is easily demonstrated, as I have pointed out in the case of *Philæmatomyia*, by pressing on the head with a needle. The rostrum is in fact blown out in the same manner that the top of the puparium is forced off at the time of emergence of the imago. Now there is a pair of large muscle arising from the internal surface of the head cavity just in front of the aperture to the margins of which the wall of the rostrum is attached, and inserted into the posterior cornua of the fulcrum, and therefore tending to pull the fulcrum forwards. According to Hansen, the course of this muscle is a backward and upward one, so that its contraction causes the fulcrum to rotate on the fixed point formed by the anterior margin of the aperture, and thus extends the rostrum on the head, an exactly opposite view to that taken by Kraepelin, who regards it as rotating the fulcrum in such a way that its ower end passes backwards, that is, as a retractor of the rostrum, acting in association with another pair which will be referred to below. The direction of rotation really depends on the relation of the fixed point on which the rotation takes place to the line of action of the muscle ; if the fixed point at any period of the contraction of the muscle is below the line of the muscle, then the rotation must take place in a backward and upward direction, and retraction will result. If, on the other hand, the fixed point is above the muscle, then the lower end of the fulcrum must pass forwards and the result will be extension. The action of this muscle might be compared to that of a piston rod acting on a wheel : the direction in which the wheel will revolve is determined by the initial position of the wheel, and if the rod were to be exactly across the middle of the wheel there would, theoretically, be no rotation at all, but the whole wheel would be pulled bodily backwards. In this case, however, the "fixed point" is not really a permanent one, but can be altered by the action of other muscles tending to raise the lower end of the fulcrum, so that the line of action of the muscle is by no means a constant factor. Kraepelin recognised this, and regarded the two movements of rotation and upward displacement as taking place together, the point on which the rotation occurred being constantly displaced upwards and backwards by the action of another muscle. It is quite possible that the divergent views held by Kraepelin and Hansen may each represent a part of the truth, and that this muscle may function as both an extensor and a retractor of the rostrum, the

direction of rotation being determined by the action of other muscles ; but this is somewhat unlikely. The point depends really on the exact relation of the upper end of the fulcrum to the aperture in the head cavity in the position of rest, an anatomical detail on which it would be rash to speak with certainty.

The retraction of the rostrum takes place, like the extension, by means of rotation of the fulcrum on a fixed point formed by the apposition of the anterior arch of the fulcrum to the anterior boundary of the head capsule, and this is brought about by the contraction of the muscle discussed above. The pair of muscles which act in conjunction with it arise in the interior of the head, above the occipital foramen, and pass downwards through the whole length of the rostrum to be inserted into the upper end of the labium posteriorly. In addition to these comparatively large and definitely separated muscles, there are several other shorter bands of fibres, apparently corresponding to some at least of those described by Kraepelin and Hansen, but so small that it is impossible even in sections to make out their precise points of attachments. Some of these doubtless aid in the retraction of the rostrum, while others, inserted more anteriorly, appear to flex the haustellum on the rostrum.

The extension of the haustellum on the rostrum is accomplished mainly by a well-defined pair of muscles corresponding exactly to those described by Kraepelin as the "strecker der russel." They arise from the lower end of the fulcrum and pass upwards and outwards to the expanded upper ends of the labral apodemes, and will therefore thrust the labrum-epipharynx, and with it the labium, downwards and into line with the rostrum. The reverse action is brought about by a pair of muscles passing between the upper end of the fulcrum and the distal end of the apodemes, and lying in the front of the rostrum ; flexion is also probably assisted by some of the ill-defined groups of fibres situated, as indicated above, on the sides of the rostrum, some of which are inserted into the membraneous wall.

## The Haustellum.

The haustellum of this fly is a much more solid and compact organ than that of *Musca*, a much greater degree of rigidity being necessary for the efficient working of piercing mouth parts. The wall is almost entirely chitinous, and, as in *Stomoxys*, the labrum-epipharynx and hypopharynx lie concealed in a deep and thick "labial gutter." The external appearance has already been described.

The labrum-epipharynx is an elongate slip of yellow chitin of equal diameter throughout the most part of its length, thereby differing from that of *Musca*, which tapers from base to apex. Its upper surface is evenly rounded, and its lower surface deeply grooved to form, with the hypopharynx, the food

channel. On cross section it is seen to consist of two laminæ, the outer one, which represents the labral element, having a heart-shaped outline, while the inner lamina, which is the epipharynx, is oval. The two unite at the borders of the groove, and enclose between them a U-shaped space in which there is a small amount of loose cellular material, but no fan-shaped muscle similar to that found in *Musca* and *Philæmatomyia*. At the upper end of the channel the walls become much thicker and the space between them at first increases, so that the whole organ is a little broader than elsewhere and the food channel of a slightly greater capacity. Immediately beyond this point the channel undergoes transition into a closed duct, in the following manner. The outer and inner laminæ approach one another until they come in contact, and fuse to form one thick layer of chitin, the space between them being entirely obliterated; at the same time the edges of the groove formed by the epipharynx approach one another and unite, so that closed canal is produced. This point is therefore the true mouth of the fly, and lies anterior to the position of the mouth in *Musca*. The canal is at first oval in outline, being broader in its transverse diameter than in its vertical one, but in a short distance it becomes circular. The duct is produced upwards a short distance beyond the end of the labrum, and projects into the rostrum. Here it joins the duct already described as the buccal cavity.

The labral apodemes are so similar to those of *Stomoxys* that they call for no remark. They are attached to small pits on the lateral aspect of the labrum at its thickened upper end, the method of attachment being such as to permit of movement inwards when the apodemes are brought into line with the haustellum in the movement of extension. In the resting position the angle between the two apodemes is about fifty degrees; in the position of extension they are almost parallel.

The distal end of the labrum-epipharynx (Fig. 3, Plate 1, and Fig. 23, Plate 4) is modified in a very curious manner, which all the more calls for a detailed description in that no explanation of its function can be offered, though the structure is obviously a purposeful one. When seen from above, the lateral edges approach one another in a gentle curve, to form a point like that of a two-edged sword. The area between the converging margins and that portion of the blade immediately proximal to it has a totally different appearance to the rest of the blade. The upper surface remains as before described, an evenly rounded one, but on the under surface there is developed a conspicuous elongated elevation, about four times as long as it is broad, a little narrower in the middle than at the two ends, and equal in width at its narrowest point to one half the width of the whole organ. When seen in section the organ has at this point a complete rounded outline, with no trace of a

groove. The upper half of the section is more pointed than the lower, and the two are separated by a prominent groove, due to the fact that the raised portion of the under surface is constricted at its base. At the proximal end of this elevation the groove on the under surface of the rest of the labrum-epipharynx ceases abruptly in what is apparently a cul de sac, the margin of the raised portion being slightly concave backwards. This margin is situated at the junction of the middle third of the elevation with the upper third, and the elevation proximal to it consists of raised flanges on either side of the termination of the groove, which end abruptly as a pair of blunt tubercles projecting into the food channel. Proximal to these tubercles the margins of the groove show a slight concavity, and thereafter run parallel to one another in the ordinary manner.

The distal end of the elevation extends to within a very short distance from the extreme tip of the organ; at its broadest point it reaches almost to the limit of the converging margins. Beyond it, and reaching to the distal margin, there is a hollowed out tongue-shaped depression on the under surface. The lateral margins of this are raised and overlap the central portion in the middle third, and converge towards one another so as to form a narrowed portion which might be compared to the handle of a racket. The narrowed portion projects into the elevation of the under surface for nearly one-third of its extent, and has at a point just distal to its termination a pair of short curved tubercles set on either side of a slight expansion of the lateral diameter.

It will be seen that the groove of the epipharynx falls considerably short of the end of the organ, being separated from it in fact by the whole length of the elevation. At first sight one is apt to think that the purpose of the tongue-shaped depression at the extreme end must be to direct the food into the channel, and that the elevation is due to the union of the two lateral margins of the epipharynx in the same way that they are united at the upper end of the organ, and that the elevation is a hollow one through which the food passes. Examination of preparations under a very high power tends to confirm this view, for distinct clear space can be seen by focussing down through the elevation. Sections, however, do not confirm this, for they show only one continuous outline, with a little shrunken cellular tissue inside it, and no trace of even a membraneous inner tube, and it is clear that the food channel does actually end at the concave transverse ridge in the upper third of the elevation.

The only suggestion that occurs to one as regards the function of this remarkable structure is that it, in connection with the hypopharynx, acts in some manner as a valve to regulate the flow of blood into the food channel. It

can have nothing to do with the making of the wound, for the tip of the organ is far too thin and flexible to have any perforating power, and moreover—and this is an important point which will be referred to later—the labrum-epipharynx does not reach to the tip of the proboscis.

The sensory hairs of the labrum-epipharynx resemble those of *Musca* and *Stomoxys*. There are two opposite to one another at the level of the tubercles which project into the lumen at the distal end of the canal, and several others at irregular intervals along the course of the canal. Each consists of a short, stout cylindrical base, projecting into the lumen of the channel and a very fine hair arising from the apex of this. The hairs are all bent downwards in the direction of the canal.

The hypopharynx (Fig. 23, Plate 4, *et seq.*), like the labrum-epipharynx, is a much finer and more delicate organ than that of *Musca*. It is a thin flat slip of yellow chitin, containing in its middle line the salivary duct, and also serving by its apposition with the labrum-epipharynx to close in the food channel. Its distal end, which falls a little short of that of the labrum-epipharynx, is quite simple; it is not produced to a point, but terminates in a very much attenuated margin, in the middle of which the salivary duct opens. At the upper end of the haustellum the hypopharynx fuses with the labial gutter and disappears as a separate organ, only the salivery duct being left. Where the lateral portions of the organ cease the walls of the duct become much thicker and also become adherent to the closed canal formed by the union of the lateral margins of the epipharynx (Fig. 29, Plate 6). The salivary duct thus projects at the upper end of the haustellum below the commencement of the buccal cavity.

## The Labium.

The labium consists of two separate parts, the mentum and the labial gutter, which together form a cylindrical chamber enclosing the muscles and other structures. The shape of the labium in *Lyperosia* is intermediate between that of *Stomoxys* and that of *Glossina*, that is to say, the "bulb" is more pronounced than that of the former, and the whole not quite so pointed as that of *Glossina*. Distally it is divided into two labella, which differ so much from the rest of the labium that they constitute a distinct organ.

The mentum (Fig. 1, Plate 1) composes by far the largest part of the labium. It has the form of a spindle, composed of a plate bent to the shape, and evenly rounded except on the anterior surface, where there is an interval in which lies the labial gutter. The truncated upper end is continuous with the membraneous wall of the rostrum, and the lower end with the external

wall of the labella. The groove on the anterior surface is a deep one, the edges of the mentum turning backwards as well as inwards, and leaving an interval between them, in which the labrum epipharynx and the hypopharynx lie. There is no thickened lateral border such as is found in *Philœmatomyia*. On the external surface there are a few scattered short bristles, irregularly distributed. The whole length of the organ shows a series of transverse ridges and furrows, deeper and more numerous at the narrower part of the spindle, similar to the "striations" in *Stomoxys*; as will be seen later, these are of great importance in the mechanism of the proboscis. The lower end of the mentum is obliquely truncated from in front backwards and upwards, in such a way that the distal portion of the posterior border is in advance of the anterior border to an extent equal to the diameter of the labium at this point.

On the posterior surface of the distal end of the mentum there is a pair of small but stout chitinous sclerites, termed by Stephens and Newstead the *ventral sclerites* (Fig. 2, Plate 1). They are homologous with the forked rods at the end of the mentum in *Musca*. Each is wedge-shaped, with the broad end of the wedge directed distinctly, and forming a support for the U-shaped rod which separates the labium from the labella. This rod, termed by Stephens and Newstead the "fork," is the homologue of the rod commonly known as the furca in *Musca*. It has the shape of a wide U, and embraces the posterior half of the labium at its junction with the labella. In the resting position of the parts it is directed obliquely downwards and forwards across the external surface of the labella, reaching a little more than half-way across the surface. The middle portion of the furca is moulded to articulate with the ventral sclerites, on to which it is pressed by the action of the muscles inserted into it. A short distance external to the ventral sclerites, there is on each side, proximal to the furca, a small rod of chitin, attached to the edge of the receding margin of the mentum, and closely approximated to the posterior border of the furca, though not fused with it. This represents the second or distal division of the fork of the mentum as seen in *Musca*, where it is as long as and similar to the first division, and only separated from it by a slight thinning of the chitin. The furca and its "lateral sclerites" are not internal structures, as stated by Stephens and Newstead, but are thickenings of the external wall of the labella, the articulation lying between it and the ventral sclerites.

The distal end of the mentum has been described as being obliquely truncated, the posterior portion, which articulates through the ventral sclerites with the furca, being produced beyond the anterior. In this way a space is left between the border of the mentum and the furca, where there is no chitinous wall to the labium. This interval is filled in by a membrane which is attached

to the border of the mentum, and anteriorly becomes continuous with the external wall of the labellum; it has developed in it two thin chitinous plates, roughly oval in shape, and placed one behind the other on the anterior border of the organ. The plates are mere thickenings in the membrane, and have no chitinous attachments, and are much thinner than the chitin of the wall of the labium.

The labial gutter forms the bottom of the groove in the anterior surface of the labium, and supports the labrum-epipharynx and the hypopharynx. In its general features it resembles that of *Stomoxys*; it is, of course, the homologue of the shallow chitinous groove on the anterior surface of the labium of *Musca*, but on account of the great development of the muscles of the bulb it has come to have additional functions. It is a stout chitinous groove, U-shaped in the distal portion, but becoming more V-shaped towards the upper end. It extends the whole length of the labium, from the termination of the labrum and the formation of the closed portion food canal to the level of the lateral portion of the furca in the position of rest. As for the most part of its course it lies between the overlapping edges of the mentum it cannot be seen even in cleared preparations, but at the distal end it projects beyond the anterior border of the mentum and forms the anterior boundary of the membraneous space between the furca and the truncated end of the mentum, and can easily be distinguished through the thin wall in this situation. Throughout its length its lateral borders are attached to the adjacent borders of the mentum by a stout membrane, which, however, is of very limited extent, its width being just sufficient to fill in the sides of the space occupied by the labrum-epipharynx—a marked contrast to the corresponding membrane in *Musca*, which is very loosely arranged. At the distal end of the proboscis it is attached to the furca by means of a continuation of the same membrane, in the triangular space already referred to.

The sheet of chitin projecting into the cavity of the labium from the posterior surface of the labial gutter, and aptly termed by Stephens and Newstead the "keel," is present also in this fly, in a slightly modified form. It commences a little distance behind the end of the gutter, as a ridge equal in height to the depth of the groove, and of about the same thickness as the rest of the gutter. This extends for about one-fourth of the length of the gutter, and then becomes thinner, and approaches the base of the gutter again. The keel does not, however, cease at this point, but broadens out again and passes still deeper into the cavity of the labium as the latter becomes of greater diameter towards the bulb, until it almost reaches the posterior surface of the mentum. This upper part of the gutter is only a very thin sheet of chitin, easily bent in dissection, and difficult to see in cleared preparations.

At the upper end of the haustellum the labial gutter becomes much reduced in thickness, and becomes attached to the hypoharynx at the point where the latter is itself becoming narrower. Finally the two fuse together, and a few sections further up only the thickened salivary duct remains, and this, as previously described, becomes adherent to the food canal. This is precisely what happens in the case of *Musca*, except that in the latter fly the hypopharynx does not become adherent to the food canal. The two laminæ of the hypopharynx cannot be distinguished from one another, but this method of termination makes it probable that here, as in the Nematocerous flies, the salivary duct lies between one lamina which is a true outgrowth from the stomodæum and another which is derived from the anterior surface of the labium, that is, from the labial gutter. The chief difference between *Lyperosia* and *Musca* in this respect is that in the former the separation of the labial element from the labium has gone much further than in *Musca*. Separation of the hypopharynx from the labium appears to occur with the adaptation to blood-sucking habit, as one finds a similar state of affairs in the mosquito, where the hypopharynx, though not capable of taking part in the making of the wound, is completely separated from the labium in the female, and remains united with it in the male.

The distal end of the labial gutter (Figs. 4 and 5, Plate I, and Fig. 10, Plate II) is a somewhat complex structure, having become moulded in an intricate manner in order to take part in the articulation between the labium and the labella, and to assist in supporting them during the act of feeding. In the first place, the distal third of the gutter is much thicker than the remaining portion, and is curved a little downwards, that is, towards the furca. It forms a prominent chitinous bar bounding the upper side of the membraneous triangle in the region of the furca. Towards its termination it becomes separated into two distinct portions, with a narrow interval between them. The lower portion, coming from the bottom of the groove, retains the shape of a shallow gutter when seen in cross section, while the upper portion appears as a stout rod, flattened from side to side so that its vertical diameter is about twice its width. In other words, the gutter becomes deeper and at the same time its bottom portion becomes separated from its lateral walls. At the extreme end the lateral roads are slightly swollen, and terminate in blunt points. The lower portion is much more highly specialised. The most ventral portion is continued onwards to the level of the termination of the lateral rods, with a slight upward curve, but the lateral portions cease abruptly at the level of the swollen portion of the upper rods, so that when seen in profile the end appears as if it were sharply cut away from above, leaving a wide interval between the upper and lower portions of the gutter. Further details of the articulation

between this pointed end and the discal sclerite will be reserved until the chitinous framework of the labella has been discussed.

The muscles of the labium are very well developed, as they have to actuate the biting apparatus. The most important one is the retractor of the furca. This large and powerful muscle occupies the whole of the cavity of the bulb, arising from the internal surface of the mentum and from the "keel" of the labial gutter, which separates the muscles of the two sides. As it passes forward a tendon is developed in its middle, and as the diameter of the cavity decreases the muscle fibres give place as to a large round bundle of fibrous tissue, very conspicuous in all sections of the narrower part of the proboscis. This tendon is inserted mainly into the inner and posterior surfaces of the tip of each lateral arm of the furca, but it also sends out numerous branching fibres to the internal surface of the external plate of the labellum in the neighbourhood of the furca. Intermingled with the most internal fibres of this muscle in the middle and distal portions of the labium there are other fibres having an oblique direction, and passing from the internal surface of the mentum inwards and forwards; this band of muscle corresponds to that described by Stephens and Newstead, but in *Lyperosia* it does not appear to be inserted into the labial gutter. It has no tendon at any part of its extent, so that it is difficult to trace it to its insertion, and in any case it is a very small band. In addition to this there is in the distal part of the labium, in the region of the thick part of the "keel," a definite band of fibres passing from the posterior surface of the mentum in the region of the ventral sclerites and also proximal to them, directly across the cavity of the labium, to the base of the labial gutter, so that the bands of fibres are cut in their long axis in transverse sections of the proboscis.

It will be well to note here the relations of these muscles to those of *Musca*, in order to be able to understand their function in connection with the mechanism of feeding when we come to discuss the complex structures on which they act. The large retractor muscles in the bulb are quite evidently similar in their origin and insertion to the retractor muscles of the furca in *Musca*, those termed by Kraepelin *retraktor der unteren Chitingabel*; they are, however, enormously enlarged. The second set of fibres appears to correspond to the retractors of the discal sclerites (*oberen Chitingabel* of Kraepelin), while the third is evidently the same as the transverse set in *Musca*. The three sets of muscles are therefore retained, but one of them has increased to a very great degree, while the other two sets are much less conspicuous than in *Musca*, or even in *Philæmatomyia*. In addition there are a few fibres in the middle and posterior portions of the labium, which pass from the lateral extremities of the gutter across the front of the cavity to

the mentum; these do not correspond to anything found in *Musca*, and it is impossible to say what their origin may have been.

The only other structures to note in the labium are the nerves and tracheæ. As might be expected in so small a fly, one cannot trace them to their ultimate terminations, but there is one important point to note with regard to the tracheæ. From the end of the tracheal sac in the rostrum to the end of the proboscis the only tracheal structures to be found are a small pair of simple tracheæ, smaller indeed than one would expect to find, situated on either side of the keel of the labial gutter. These become very small in the distal part of the proboscis, and can only be distinguished in the labella by following them up in serial sections. There are no traces of anything resembling an air sac. The nerves pass down the cavity of the labium together with the tracheæ, and are remarkably large. They lie external to the tracheæ, one on each side, and at the upper end of the proboscis the two are of about equal size, but as they pass down the proboscis the tracheæ diminish in size much more than the nerves, so that at the junction of the labium and the labella the trachea appears in sections as a small clear area on the posterior surface of the nerve. It is evident that though the labella require a large supply of nerves, most of the tracheæ are destined for the supply of the muscles in the labium, and it will be a legitimate inference from this that the labella are very highly sensitive structures, and that the reflexes on which the control of the biting parts must depend are highly efficient.

## The Labella.

The structure of the labella is so extraordinarily complex that it would be almost impossible to describe it intelligibly were it not that one can trace, in some at least of the parts, a homology between this fly and the simpler, or at any rate the better known, non-biting flies. It will appear in the course of the description that according to my interpretation of the anatomy and physiology of the proboscis, that of *Lyperosia* is not essentially different to that of *Musca*, but is a modification of it, all the parts found in *Musca* being present here and fulfilling for the most part the same functions.

Regarded from this point of view the first thing that strikes one is the great reduction in the size of the labella. The transverse diameter of the two labella is the same as that of the narrowest part of the labium, and the vertical diameter only a little greater. Secondly, the labella, in the position of rest, are not folded backwards on the labium, but are extended in the same line with it, and are, as a matter of fact, incapable of being moved into the position of rest of *Musca*. Further, the fringes of macro-chaetæ which are so conspicuous in the non-biting flies are not present in *Lyperosia*.

The labella are oval in shape, slightly longer than broad, and deeper in the vertical diameter than in the transverse. They are completely separated from one another on the anterior surface by a narrow fissure, which is continuous with the groove on the anterior surface of the labium. The fissure extends round the blunt apex to the posterior surface, but about midway between the tip of the proboscis and the furca it terminates, and from this point the two are continuous with one another. Each labellum consists of an external and an internal wall, united at the side of the fissure, except where the two posterior surfaces are continuous with one another. The external wall on each side consists of thin plates of chitin separated from one another by narrow fissures, which are filled in by membrane, the arrangement being adapted to ensure rigidity and at the same time to permit of movement. The internal wall is composed of the biting teeth, the discal sclerite, and the membrane uniting it to the external wall.

When seen in cross section (Fig. 14, Plate III) the external wall of the labella appears as a oval ring of chitin, the long axis being directed vertically; the ring is incomplete on the anterior surface throughout the length, and in the distal half of the posterior surface. When examined in cleared preparations the plates of the two sides, convex externally, show certain well-defined fissures. The largest of these is on the posterior surface, and commences on each side a short distance external to the middle line and just distal to the furca; from this point the two run parallel to one another up to and a little beyond the point where the two posterior walls diverge at the fissure. Proximal to the commencement of these fissures and anterior to the furca the chitin of the external wall is very thin and semi-membraneous. At the side of each plate there is a similar membranecus interval posterior and distal to the end of the furca. On the anterior border of each labellum the continuous plate ceases gradually and is replaced by a thin membrane loosely arranged, and of course continuous with the membrane bounding the triangular space behind the furca. The membrane is of the same nature as the one in the same situation in *Stomoxys*, that is to say, it is composed of a clear and transparent (in cleared preparation) ground set with small squamæ arranged so that the clear spaces between them form a fine network. The squamæ or thickened areas in *Lyperosia* are however much smaller and less conspicuous than in *Stomoxy*.

The distal limit of this external plate is not well defined, but merges imperceptibly into the membrane of the inner wall. It presents a gently rounded contour, on which there is a row of ten short bristles arising from small raised bases, and forming a terminal fringe to the proboscis. Except for a few much finer and shorter hairs, two pairs of which are situated just

in front of the lateral end of the furca, and two more pairs, one internal and external to the membraneous interval on the posterior surface, near the termination of the median fissure, the external surface is naked.

The internal surface of each labellum consists of two distinct portions, one of which is freely moveable, the other being united with its fellow of the opposite side. The distal moveable portion corresponds to the inner surface of the labellum of *Musca*, while the fixed part is composed of the discal sclerite. It will be necessary therefore to describe these two parts separately.

The free portion of the internal surface of the labellum extends obliquely from the proximal limit of the median fissure on the posterior surface, forwards and upwards to the anterior surface, so that it occupies rather less than half the area of the labellum as seen from the side. It is entirely occupied by the biting teeth and their accessory structures, and is connected with the external surface by the thin and transparent membrane which forms the actual internal wall of the labellum in this situation.

The teeth (Fig. 6, Plate II) are very formidable weapons for so small a fly. There are in all eight on each side, three of the set being small and inconspicuous. All are roughly oblong in shape, slightly bent in an upward and forward direction, and with one exception, are bifid at the free end. Counting from the anterior or upper end of the set, the third tooth is the largest, the second and fourth equal in size and little smaller than the third, the fifth and sixth are of the same size and are smaller than the fourth, while the first is smaller still. The seventh and eighth teeth are rudimentary. The seventh resembles the others and is about the half the length of the sixth; the eighth, which is concealed in the angle formed by the two sets of teeth, is very small and its shape is difficult to be certain of. It is not bifid, but pointed, and has on each side of it two deep notches. All the teeth are united to one another at their bases by means of a stout but narrow ridge of chitin, into which the bases merge, so that the arrangement is not unlike that of the teeth of a comb. The ridge of chitin is gently curved along its proximal margin, in such a way that the cutting edges of the teeth are brought into the same straight line, the longest arising from the deepest part of the curve, the short ones from its two ends. The eighth and seventh teeth do not come into line with the others. When *in situ* the cutting edges of the teeth form an oblique line running from the front backwards and downwards, in the same direction as the end of the discal sclerite.

The accessory structures of the teeth may for convenience be termed collectively the *interdental armature*. That of *Stomoxys* has been elaborately described by Stephens and Newstead and the appearances seen in *Lyperosia*

are very much the same, although I have not been able to find some of the smaller structures. The armature consists of two sets of petiolated blades and one set of rod-like sense hairs. The proximal set of petiolated blades are delicate leaf-like processes arising in pairs between the teeth, one pair between each to adjacent teeth, and one pair external to the first tooth. Their length is about the same as that of the teeth next to which they lie, and they project distally so far that the tip of the tooth is opposite the middle of the blade. Each blade arises from the ridge of chitin to which the teeth are attached, at the point where the bases of the teeth join with one another. The pairs arising between the sixth and seventh and the seventh and eighth teeth are very much smaller than the rest. The surface of the blades is finely granulated, but they do not appear to have any coating of hairs. The distal set of blades are much larger and at the same time much more delicate than the proximal ones, and arise from longer stalks, so that their distal ends extend almost to the extreme limit of the internal surface of the labellum. On account of their extreme delicacy it is very difficult to make out their exact number and arrangement, for if one examines them in uncleared preparations the opacity of the other structures renders it impossible to trace them to their terminations, and in cleared preparations they become almost transparent. There appear to be seven pairs, of which the second to the sixth are equal in size, the first rather smaller, and the seventh less than half the size of the others. In shape they are similar to the blades of the proximal set, their length being rather greater than that of the teeth, their breadth about equal to that of the fifth and sixth teeth. The blade ceases at a little distance beyond the apices of the teeth, and they are presumably connected with the ridge of chitin at the bases of the teeth by a stalk, but this is either hidden from view by the blades of the first set or else is so exceedingly delicate that it becomes invisible in cleared preparations.

The rod-like hairs resemble those of *Stomoxys* and *Philæmatomyia*, but are relatively larger, being in fact the most conspicuous objects on the inner surface, next to the teeth. Each arises from a short but broad cylindrical base, and runs forwards and inwards so that it is raised a little from the surface of the membrane, above the level of the teeth. One side of the hair is deeply grooved, and the tip is bluntly rounded. I have not succeeded in finding the nerve ganglion at the base of the hair, but doubtless it exists.

The membrane which forms the internal wall of the labellum, and on which all these structures lie, is an extremely delicate and transparent one, and is apparently structureless. It corresponds to the pseudo-tracheal membrane in *Musca*, but since distension of the labella with blood no longer pays an important part in the mechanism of feeding, and since the size of the

labella has been so very much diminished with the adaptation to a blood-sucking habit, its extent has been reduced to the minimum, so that it now exists merely as a narrow sheet connecting the external wall with the ridge of chitin formed by the fusion of the bases of the teeth. There is of course no trace of the pseudo-tracheal channels, but, as I hope to show in a future memoir, there is reason to believe that the petiolated blades are derived from the rings of the pseudo-tracheæ, and moreover continue to fulfil the function of the channels so far as their filtering action is concerned.

We have next to consider the fixed portion of the internal wall. This is evidently derived from the discal sclerite, but the alteration has proceeded to such a degree that it will not be advisable at the present juncture to attempt to separate it into its component parts, since its homology only becomes evident when we trace it through the intermediate forms. The term discal sclerite may then be accepted provisionally, in place of the nomenclature used by the authors cited above.

The discal sclerite is composed of two plates of chitin, lying in the antero-posterior plane, united to one another below, and with their inner surfaces concave towards one another in their middle thirds. The distal margins of these plates are articulated to the teeth, and the proximal ends to the labial gutter. Its structure is so complex and at the same time so important in connection with the mechanism of the proboscis that it must be described in detail.

When a well-cleared preparation mounted on its side is examined, the teeth, discal sclerite, and the end of the labial gutter can be readily seen through the thin external wall of the labellum (Fig. 4, Plate I). One obtains a still better view if by a fortunate dissection one contrives to remove the external plate of one side and to leave the rest of the structures *in situ*. From this aspect one sees that the apices of the teeth form a line parallel to the distal margin of the labella, and that the ridge of chitin formed by their united bases lies about the junction of the distal and middle thirds of the labella, measured from the furca. The remaining two-thirds are occupied by the discal sclerite, which is closely apposed to the bases of the teeth in front and extends to the end of the labial gutter behind. It does not occupy the whole of the vertical depth of the labella, but only about one-third, and is situated much nearer the upper than the lower border. Its shape when seen from the side is as follows. It is roughly oblong, its long axis being in the long axis of the labella ; the distal end is wider than the proximal, and is parallel to the distal margin of the labella, that is to say, it is directed obliquely downwards and backwards. It is also slightly concave downwards to correspond with the convexity of the distal margin of the united bases of the teeth, which are so closely

pressed against it that the two appear united; there is however no chitinous union between them, and they are readily separated by dissection in potash preparations. The upper or anterior border of the sclerite is straight for its distal two-thirds, and in its proximal third dips suddenly downwards so as to leave a shallow notch, in which the lateral portion of the end of the labial gutter rests. The lower border of the sclerite is concave downwards, but its two ends lie equidistant from the border of the labellum. The proximal end is most irregularly shaped, on account of the complexity of the joint between the sclerite and the end of the labial gutter; its ventral third projects upward beyond the dorsal portion, and is bounded by a thickened ridge of chitin continuous with the concave lower border of the sclerite. This thickened portion, equal to about one-third the total width of the sclerite, terminates abruptly by bending again forwards, and from the slight projection thus formed a few strands of fibres can be seen to pass towards the lower angle of the sclerite in front, thus separating the lower portion of the sclerite, bounded by its concave margin, from the remaining portion. The part of the posterior border above this projection is ill-defined, as the chitin is here thinner than elsewhere. It has already been stated that the upper border dips suddenly downwards in its posterior third, where it is overlapped by the lateral part of the labial gutter; at its proximal limit it dips again downwards to join the projecting portion just described, and so forming a sharp angle. This angle is situated exactly in line with the sharply cut away distal end of the lower part of the labial gutter, and by careful focussing one can see that the sharp end of the gutter, which projects forward beyond the angle, in the manner already described, lies between the two sides of the discal sclerite, in fact, it projects into the interior of the sclerite for at least one fourth of its length; the ends of the lateral and lower divisions of the labial gutter are at the same level, but the former is outside, the latter inside, the sclerite.

One more point is well brought out by examination from the side. The wall of the sclerite is not of equal thickness throughout, but is thickened along the upper and lower borders, and at the articulation with the labial gutter. There is also an apparent thickening along the distal margin, but it is difficult to make out whether this is a part of the discal sclerite or if it is the ridge at the bases of the teeth. The thickening along the lower border, and the upturned end of the posterior border continuous with it, form a conspicuous hook-like piece, the significance of which will be seen later.

The discal sclerite when seen from the side appears to be a flat structure, and this is confirmed when we examine it from the front. It is not, however, a simple flat plate, as has already been hinted, but is composed of two plates with a narrow interval between them. This will be better understood if we

describe the appearance as seen in a cleared preparation mounted anterior side uppermost.

In the first place one must note that the two labella are not in contact with one another, but that they diverge from behind forwards, leaving a comparatively wide fissure between them. This is, I think, to be regarded as an artifact, due to the shrinkage in the making of the preparation; the two labella are in all probability closely apposed to one another in the natural condition of rest. Allowing for this in the interpretation of the appearance seen, the two sides of the discal sclerite appear from this point of view as parallel or slightly diverging ridges, the edges of the plates. By careful focussing one can make out that the two plates are concave on their opposing surfaces, bounding a cavity open only on the anterior surface, and probably closed in the natural condition of the parts by the apposition of the anterior edges of the plates (Fig. 7, Plate II). The joint between the sclerite and the labial gutter is seen by careful focussing in a well-cleared preparation. At the most anterior (dorsal) point one can distinguish the two lateral rods derived from the end of the labial gutter, overlapping the most proximal portions of the upper borders of the sclerite, and lying a little to their outer side. At a lower level the projecting pointed end of the lower part of the labial gutter comes into view (Fig. 8, Plate II), and it is seen that the poin corresponds to the middle third of the floor of the gutter; when seen from above it is not unlike a J pen in shape. At either side of the base of this point the edges of the gutter are transverse. It is clear from this that the middle portion of the gutter does actually project into the cavity between the two walls of the sclerite. At this level there comes into view a stouter piece of chitin, at the distal end of the sclerite, which marks the point where the two labella are united on the posterior surface, and by focussing a little lower than this (Fig. 9, Plate II) one sees that it forms the point of a long and narrow triangle, the base of which is situated proximal to the joint between the labial gutter and the sclerite. The base, which is a well marked transverse band, lies at a lower level than the apex, and, as one may infer from the fact that the lateral portions come into focus before the middle portion, is itself so bent as to be convex downwards. The significance of this apparent triangle will be evident by comparing it with the lateral aspect. It is, in fact, the lower triangular portion of the discal sclerite. The pointed apex is the most distal limit of the lower border of the sclerite, a point where the two lateral walls are attached to one another, and the base is the upturned edge of the lower border, which when seen from the side appears as a hook-like projection.

To confirm the above observations it is necessary to examine the labella in serial section.

Figure 14, plate III, represents a section through the distal portion of the labella, at a point where the two are still separate. The external chitinous plates of the two sides form an oval outline, with the long axis in the vertical plane. Inside this there are seen the two sets of teeth parallel to one another in the long axis of the labella, and separated from one another by a narrow interval, which, by the way, is probably an artifact due to shrinking. At the upper end the teeth are united to the external plate by a strong membrane, which is thrown into numerous folds; at the lower end the junction is less definite, being formed by loose strands of fibres. At the lower end of the section one sees some of the rod-like hairs cut into irregular but recognisable fragments, and some of strands of yellow chitin which are probably the stalks of the petiolated blades. The free portions of the teeth are shaded lightly, and show an irregular outline due partly to fractures and partly to the teeth of the two sides not being cut in exactly the same plane; in the sections they are of a bright canary yellow colour, like that of the piercing stylets of the Nematocerous Diptera. The more deeply shaded portion into which the teeth merge is stained a deep purple by Delafield's hæmatoxylin, and is of a fibrous nature. It forms a continuous band which unites the bases of the teeth to the edge of the discal sclerite, and it is by virtue of the flexibility and strength of this band that, as will appear later, the teeth are retained in position and yet can be turned completely backwards on the edge of the sclerite.

Sections distal to this have much the same appearance, except that they show the fringe of hairs on the distal border of the labella, and in these one can note the central canal which perforates them, and the enlarged base, which bears the same relation to the hair as the basal joint of the antenna does to the rest of the appendage. The rod-like hairs do not show a central canal, nor can one recognise in them the groove which they appear to have when examined in cleared preparations.

As the teeth are traced upwards the darkly stained band of fibres at their bases becomes more regular in outline until it forms a continuous band on either side of the labella, and after a few sections the bands of the two sides unite on the lower side. The membrane on the external aspect of the labella then becomes continuous from side to side and the labella are open only on the anterior aspect.

A few section above this we have the appearance represented in figure 15, Plate III. The teeth have disappeared, and in place of them we find only the discal sclerite, composed here of two lateral plates in the vertical plane, united at the lower end only. In the upper and lower thirds the two plates are almost parallel to one another, but in the middle they diverge so as to present opposing concave faces, limiting a circular space. In the interval between the two at

the lower end there appears a separate piece, oval in outline, pointed at its ends, and almost filling up the interval between the two lateral walls in this situation. In the next few sections this piece enlarges, becomes more rounded, and is more and more closely approximated to the lateral plates, until it fuses with them. The distal end of this free piece is situated at the point where the two labella fuse with one another on the posterior surface, and it can be seen in this situation in cleared preparations. As it broadens out distally the two lateral halves become a little separate from one another, and a small amount of loose cellular tissue appears in the space.

In the sections proximal to this point there is a rapid change in the appearances, once we pass to the upper end of the discal sclerite. Figure 16, Plate III, represents a section just behind the point where the free median plate has fused with the lateral plates. We see here that the external plate has undergone a considerable change and now presents an irregular outline, marked by two furrows on either side of the middle line; the median portion of the sclerite is now fused to the lateral portions, and shows some loose cells in its interior. The two plates of the sclerite are now divided into an upper and a lower portion. A few sections distal to this the division commences at the upper limit, and passes down as we progress from the labella to the labium. In the middle of the lower portion of the section there appears another free piece anterior to the one already noted, as shown in the figure. We have therefore two lateral and anterior portions, a U-shaped lower or posterior plate, and a middle piece fused in the angle between them, and now another piece of solid yellow chitin anterior to this. The two lateral pieces are the ends of the upper portions of the labial gutter, the anterior piece in the middle is the end of the middle portion of the gutter, and the rest belongs to the discal sclerite. As we pass upwards from this point the discal sclerite becomes steadily reduced in size while the labial gutter comes to occupy more and more of the section. In the next figure (Fig. 17, Plate III) we see that the anterior middle piece has increased in breadth and in depth, and the vertical extent of the lower U-shaped piece has become much less, and at the same time it is wider. The gutter rests on two notches on the inner sides of the sclerite, which is here rather V-shaped. In the next figure, which represents the next proximal section, the middle portion had definitely assumed the shape of the gutter, and has become connected with the ends of the lateral portions, while it is embraced by the now rather wider part of the sclerite. Still higher up the sclerite becomes much thinner and recedes behind the gutter, where it appears as a wide arch. A few sections higher up it appears only as a narrow arched hand behind the gutter, the two portions of which remain quite separate from one another. Above this it ceases, and at the level of the furca (Fig. 21, Plate IV), the two

halves of the gutter unite with one another by bands of fibres. Proximal to this the keel of the gutter begins to appear and the section passes through the ventral sclerites.

In the distal portion of the labella, then the food canal commences between the teeth. As we shall see later, the vertical portion of the interval between the two sides at this part of the proboscis does not exist in the state of action, but the true permanent canal begins at the distal sclerite, about the point depicted in figure 23, Plate IV. Its commencement is bounded by the two sides of the discal sclerite, and above this by the labial gutter. The labrum-epipharynx and hypopharynx do not appear in the section till we reach a point just proximal to the thick ends of the ventral sclerites.

## The Hæmatocœle of the Labella.

So far only the inner and the outer walls of the labella have been described. Distal to the point of fusion on the inferior surface each labellum has a complete inner and outer wall, as shown in figure 14, Plate 3, and throughout the labella are separated on the anterior surface of the labium. The space seen in the sections between the inner walls of the two labella in the position of rest is probably an artifact due to the different degrees of shrinkage between the chitinous and membraneous portions; the two inner walls, normally in contact with one another in the resting state, correspond to the pseudo-tracheal membrane of the house fly. The potential space between them represents, as will be seen presently, an invagination of the distal end of the proboscis, which can be done away with by the retraction of the outer wall. Between this inner wall and the chitinous outer wall there is a space, which is continuous with the hæmatocœle of the labium and through it with that of the rest of the body; this space, as shown in the sections, which are accurate drawings traced with the aid of a camera lucida, contains a number of large and irregularly shaped cells, which are the corpuscles of the blood of the fly. In the drawing they are depicted as actually seen in the preparations, and show obvious shrinkage and deformity, due of course to the drastic treatment which is necessary to get even tolerably good sections of such a resistant and impermeable region. Most of the cells are free in the space, while others, which are probably of different origin, appear to be attached to the inner and outer walls. The number and distribution of these cells differs a good deal in different preparations, but they are generally most numerous in the distal part of the labella. From the point of view of the parasitologist, the existence of this blood space in the labella is of some importance, on account of the opportunity it offers for the passage of any parasite which once becomes free in the body cavity to pass into the wound made by the fly. The only obstacle to be encountered is the thin inner wall of

the labellum. The connection of this blood space with the mechanism of the proboscis will be discussed later, but it should be noted here that this very small and definitely bounded space represents the wide interval between the inner and outer wall which is found in the labella of the non-biting flies, when the labella are distended.

## The Mechanism of Feeding.

Having now described the anatomical structure of the proboscis, we are in a position to consider the mechanism by which it acts in the making of the wound and in the absorption of the blood. It will be evident that such extraordinarily complex structures as are found in the labella must have an equally complex method of action, and it will be well at the outset to state that since the difficulties in the way of observing the actual working of the organ, or producing the actions by artificial means, have proved insurmountable, the explanations offered hereafter are in the nature of working hypothysis, and do not pretend to be a complete account of all the factors which may come into play when the insect feeds. So many remarkable features have appeared in the course of the investigation that one hesitates to assume that the subject is exhausted, and although what has been found agrees in the main principles with what occurs in other flies, one must be prepared to find that further study will reveal yet more complications.

So far the whole description of the anatomy has referred to the parts in the position of rest, and all the sections are drawn from specimens fixed in that position. Sometimes, however, one can succeed in fixing a proboscis in another position, which, there is reason to believe, is that into which it passes during the process of feeding and, as I hope to show, it is the change from the one position to the other that it is the essential act by which the wound is made. It will be necessary to describe the appearance of the labella in this position (Fig. 13, Plate II); the attitude taken up by the haustellum and the rostrum has already been dealt with.

The specimens which I have obtained fixed in this position were got by pressing forcibly on the head while the fly was immersed in the fixative, and mounting without clearing. I have found that the action of the potash in dissolving the soft structures always results in bringing the proboscis back to a position of rest, and that unfortunately precludes any detailed examination of the chitinous parts. It enables one to assume, however, that the position is attained, and retained by the action of the muscles, and that when the muscles relax, as happens when they are dissolved by the potash, the position of rest is again assumed.

In the position of action, as we may provisionally term it, the appearance of the labella is totally changed. The internal surface becomes external,

and the length of the organ is reduced. In other words, the distal end of the proboscis is evaginated. The two labella now present a rounded appearance, with no trace of the fissures on the anterior and posterior surface, and all the structures which in the position of rest lie on the internal surface and point distally now lie on the external surface and are directed backwards. The distal margin of the organ is formed by the bases of the teeth, which, it should be noted, form a concave border directed downwards and backwards, not in the direct transverse axis of the proboscis. At each end of the tooth plate there is a short forward projection, and if one focusses carefully one sees that these are the two ends of the anterior border of the discal sclerite, which lies immediately behind the united bases of the teeth. The teeth themselves arch upward and backward from their bases, so as to point in the direction of the long axis of the proboscis, and the petiolated blades and rod-like hairs lie in line with them. Behind these there lies the fringe of hairs, which in the resting state form the distal fringe. They are now, however, directed backwards well out of the way of the teeth. The external plate of chitin is displaced backwards so as to reach the furca, and it, and the smaller plates of chitin which lie in the triangular space between the end of the labial gutter and the furca, are very loosely arranged, and ruckled up. The position of the furca is important. Instead of being arranged as a transverse arch, it is rotated backwards so that it makes an angle of half a right angle with the long axis of the labium, pointing upwards and towards the head. The lateral arms of the furca are thus displaced backwards for a distance equal to the length of the external plate. With regard to the labium, the transverse ridges and furrows are much more conspicuous than they are in the resting condition. As I have been unable to obtain cleared preparations fixed in this position the position of the labrum-epipharynx and hypopharynx cannot be defined, but it is evident that their distal ends must now be much nearer the distal end of the proboscis than they are in the resting position.

We have now to discuss the possibilities of the proboscis as a biting and piercing organ, and in doing so it will be convenient to clear the ground by noting certain limitations under which the organ is placed by reason of its anatomical structure. In the first place, the labrum and the hypopharynx are placed at once out of court; they do not reach to the end of the proboscis, and even supposing that they could reach it in the evaginated condition, they could not project sufficiently far to be effective unless the discal sclerite were already inserted into the wound. Moreover, they are not provided with cutting ends, but are more or less flaccid.

The arrangement of the joints of the proboscis is such that it is not adapted for the propagation of force from the body of the fly, as any pressure from

behind would tend to fold up the organ. This point has already been dealt with.

The cutting weapons must therefore be the teeth, and the teeth only, and the question to decide is as to the particular motion by which they act. Stephens and Newstead, in their account of *Stomoxys*, have suggested that they cut by a semirotatory motion, after the manner of a carpenter's auger, the muscles involved being those which pass between the gutter and the wall of the labium. This hypothesis cannot stand, for it would necessitate the presence of a joint adapted for a rotatory motion between the teeth and the rest of the proboscis, and such a joint does not exist and is not described by them; indeed, the only joint which would be of use for such a method of action would be one between the base of the labial gutter and the mentum, assuming the teeth to be firmly fixed on the end of the discal sclerite and that the sclerite was firmly fixed on to the end of the labial gutter. Rotatory motion of any sort would be a very extraordinary deviation from the type of motion possible in *Musca*, and in the case of *Lyperosia*, as in *Stomoxys*, it is put entirely out of the question on account of the nature of the articulations.

The one motion about which there is no doubt is that of the eversion of the labella and the upward displacement of their outer walls. One can see this take place under ether, and can produce it by pulling on the muscles of the bulb in dissections. These muscles are by far the largest in the proboscis, and one would naturally expect them to play an important part in the mechanism of the making of the wound. By their contraction they cause the furca to be rotated in an upward direction, on the fixed point provided by its articulation with the ventral sclerites, in such a way that its lateral arms are displaced from their transverse position to one in which they make with the long axis of the labium an angle of about half a right angle, the ends of the furca pointing towards the head, and as the rotation takes place the chitinous external wall of the labellum is also displaced, both on account of its intimate connections with the furca and because it receives directly some of the fibres of insertion of the tendon of the muscle of the bulb. Now the internal walls of the labella are firmly attached to the distal end of the discal sclerite, and the sclerite itself is practically a fixture on the end of the labial gutter, so that what happens when the full amount of traction is exercised on the outer walls is that the invagination is undone, and the end of the discal sclerite becomes the most distal point of the proboscis, as is shown in figure 13. As this unfolding takes place the teeth, which are firmly attached to the end of the discal sclerite, are rotated through about half a circle, so that their serrated points come to point upwards instead of downwards.

This movement of the teeth constitutes, I believe, the essential act in the mechanism of the proboscis, and it is by a repitition of this movement that the

wound is made. I have referred in a previous paper to the rapidity of action of which insect muscle is capable, and the action of the muscles of the bulb in undoing the invagination at the end of the labella, and so causing the teeth to press upwards, appears to me to be another instance of it. The muscles which are inserted into the furca are not only much larger in this fly than they are in *Musca*, but they are proportionately very much larger than those of the anterior set, and are undoubtedly the dominant motive force in the proboscis.

Retraction of the furca is not the only result of the action of these muscles. It has already been pointed out that the labrum-epipharynx and the hypopharynx do not reach to the distal end of the proboscis in the resting position. In fact, they are so much shorter than the combined labium and labella that their distal ends only appear in sections about the level of the furca, and distal to them there is the whole length of the discal sclerite. Now the discrepancy in length is partly compensated for by the retraction of the labellar walls, by means of which the distal end of the discal sclerite becomes the terminal point of the proboscis, but even this is not sufficient, as is clearly shown by actual measurements of cleared proboscides, to bring their distal ends into such a position that they can perform their functions, and further shortening is required before they can reach the wound. This is accomplished by the shortening of the whole of the mentum. In the early part of this paper it was stated that the whole of the chitinous wall of the mentum is traversed by a closely set series of ridges and furrows. Now these do not present the same appearance in all preparations, and a careful comparison of those in proboscides which are in the position of rest and those in the position of action shows that the more the lateral arms of the furca are displaced backwards the more marked the ridges and furrows become, and it follows that in each individual specimen the more marked the furrows are the shorter the mentum will be, for the crinkling of the wall must reduce its length. I have been unable to obtain a cleared preparation in which complete evagination has occurred, but I have no doubt that if one could obtain one it would show that the evagination of the labella and the crinkling of the mentum taken together had reduced the total length of the labium just sufficiently to bring the labrum-epipharynx and the hypopharynx to the distal end of the proboscis. The muscles of the bulb, the retractors of the furca, bring this about by pressing the furca on the ventral sclerites, so that the movement of the furca is an actual displacement as well as a rotation on its fixed point.

The labrum-epipharynx and the hypopharynx are of course quite incapable of being moved on the labium, owing to the close attachments at their proximal ends. The labial gutter cannot move on the mentum, for, although there is no firm chitinous union, they are closely held together by means of the membrane which unites their lateral borders throughout their length, and at the proximal

end the attachment is still more close. When the mentum is shortened the labial gutter must therefore remain of the same length, and it is a little difficult at first to see how this difficulty is to be overcome, for if the two remain in the same plane retraction of the mentum alone will not affect the relations of the discal sclerite and the terminations of the labrum-epipharynx and the hypopharynx. Two points which have already been mentioned help to solve this difficulty. In the first place, the proboscis when in use is not held perpendicularly, but points a little forward, and the distal margins of the discal sclerite form a line parallel to the surface of the skin of the host when the proboscis is held at this angle, as will be seen from figures 1 and 5, Plate 21. If the angle at which the labella make with the labium in the position of rest be compared with that in the position of action, it will be seen that in the latter case the angle is considerably greater, that is to say, the retraction of the mentum is accompanied by a flexion of the joint between the labial gutter and the discal sclerite. The amount of flexion is small, but it is enough to materially shorten the distance between the base of the labium and the opening at the distal end of the discal sclerite. This flexion is produced by the action of the retractors of the furca, acting through traction on the inner walls of the labella.

By means, therefore, of the contraction of the retractor muscles of the furca, the most powerful muscles in the proboscis, the furca is rotated so that its arms pass in the direction of the head, and so carries with it the external wall of the labella, which are turned inside out, the teeth being drawn through the wound and exercising their obvious cutting function as they go ; it is also displaced bodily upwards, room for it being made by the actual shortening of the mentum. The discal sclerite is at the same time flexed on the end of the labial gutter, and in this way the distance between the proximal and distal ends of the labium is so shortened that the labrum-epipharynx and the hypopharynx come to be at the same level as the end of the discal sclerite. They are thus in a position to form the tube up which the blood can be sucked, and the hypopharynx can transmit its saliva directly into the wound. We have next to consider how the parts pass from the position of action thus attained to the position of rest, in order to be able to repeat the movement. There is obviously no muscle which can directly invaginate the end of the labella, and undo the furrowing of the mentum, and we must look for some indirect method by which this can be accomplished. Here a comparison with *Musca* helps considerably. In *Lyperosia*, as in *Musca*, there is a well developed transverse muscle, situated, as already described, in the distal portion of the labium, and the simple acceptance of the similarity of function between this and the corresponding one in the non-biting flies provides a rational explanation of

the method by which the labella are returned to the position of rest. In *Musca*, according to Kraepelin, the contraction of this muscle drives the blood into the space between the inner and outer walls of the labella, and thus assists in distending them so as to bring the pseudotracheal membrane into action. In *Lyperosia* the relations of the labellar walls to the labium are considerably altered on account of the fixation of the organ in a definite position, the backward and forward rotation of the discal sclerite being very limited, but the distension of the intralabellar space can still occur, and is brought about by the same mechanism as in *Musca*, that is to say, respiratory movement, aided by the transverse muscle. The result in this case is that when the blood is forced down into the labella the invagination at their distal end is reproduced, and the two internal walls come again in contact with one another, and at the same time the contraction of these fibres, by reducing the transverse diameter of the labium, must increase the longitudinal diameter, and thus undo the furrowing of the wall. The eversion of the teeth, which is the essential feature of the action of the proboscis, is thus accompanied by evagination of the labella, and the passage back again to the position of rest by a corresponding invagination; evagination being a reduction, and invagination an increase, in the length of the labium. The fixed point from which the labellar walls can be forced out, and back to which they can be drawn, is the distal end of the discal sclerite, to which they are attached.

There remains only to consider the mechanism by which the discal sclerite is returned to the position of rest. Again a comparison with *Musca* affords valuable assistance. We have seen that the discal sclerite is articulated, in a most complex manner, with the end of the lanial gutter, and that there is in *Lyperosia* a small bundle of muscle fibres which correspond with the anterior and mesial set in *Musca*, the retractors of the discal sclerite. The exact point of insertion of these fibres, which have no terminal tendon, is difficult to make out, but they can be traced to the proximal end of the sclerite. Whether they are actually inserted into the sclerite or to the membrane in its vicinity will not affect the action, for the fibres are definitely anterior to the larger muscle of the bulb, and must act on the joint in an opposite direction. The joint between the discal sclerite and the end of the labial gutter having then been flexed by the indirect action of the retractor muscle of the furca, it can be straightened again by the anterior muscle fibres, and these two actions follow one another each time the teeth are drawn through the wound at the eversion and closing of the labella. Eversion of the teeth is of course carried out against the resistance offered by the skin of the animal on which the fly is feeding, and consequently the muscles which bring it about are

very highly developed, while the closing of the teeth is carried out without any special resistance, and the muscles are not more developed than in *Musca*. We may suppose that after each contraction the labella are thrust a little deeper as the wound is made, until blood is reached. When this occurs the proboscis is probably held in the fully retracted position, so that the labrum-epipharynx and the hypopharynx are in the most advantageous position for collecting the blood.

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## EXPLANATION OF REFERENCE LETTERING.

a. a., axial apophysis, or ventral portion of the discal sclerite.
a. f., the fissure between the two labella on the anterior or dorsal surface.
ap., apodeme of the labrum.
b., the bulb.
b. c., the buccal cavity.
c., blood cell, in the hæmatocœle of the labellum.
c. p., the distal chitinous plate in the membraneous area of the labella.
c. p., the proximal ditto.
c. s., the cul de sac at the end of the labrum-epipharynx.
d. ph., the dilator muscle of the pharynx.
d. s., the discal sclerite.
e. f., the external fringe of hairs on the labella.
ex. h., extensor of the haustellum.
ex. p., external plate of chitin in the labellar wall.
ev., elevated area on the ventral aspect of the labrum-epipharynx.
f., the fulcrum.
f.', the anterior arch of the fulcrum.
f.'', the funnel-shaped lower end of the fulcrum.
f. b., strong fibres uniting the upper end of the labial gutter and the lateral borders of the mentum.
f. c., the food canal.
f. t., fibrous tissue uniting the teeth to the discal sclerite.
fu., the furca.
fu. f., fibrous band connecting the two lateral arms of the furca internally.
hy., hypopharynx.
k., keel of the labial gutter.
lb., labella.
l. ep., labrum-epipharynx.
l. g., labial gutter.
l. g.', the dorsal portion of the labial gutter, forming the sides of the groove.
l. h., labral hairs.
l. r., lateral rods, corresponding to the distal portion of the fork of the mentum in *Musca*.
m., membrane forming the wall of the rostrum.
m. a., membraneous area between the chitinous walls of the labella and the mentum.
m.', the transverse muscle of the labium.
m.'', the anterior and mesial set of muscles, which act on the joint between the discal sclerite and the labial gutter.
m'''., the retractor muscle of the furca, with its tendon.
m. a., membraneous area between the labium and the labella.
mt., the mentum.
n., nerve.
p., the palp.
p., the distal petiolated blades.
p.', the small proximal set of petiolated blades.

ph., the pharynx.
r., the ridge of chitin which connects the furca with the external chitinous plate of the labella.
r. r., retractor of the rostrum.
r. h., rod-like hairs.
s. d., salivary duct.
t., teeth.
tl., t. 6., the first and sixth teeth, counted from the dorsal side.
tb., tubercles at the distal end of the labrum-epipharynx.
tr., trachea.
v. sc., ventral sclerites.

## PLATE I.

Figure 1.—The proboscis in profile, drawn from a potach preparation. The position is one of slight extension, and only the structures of one side are drawn. Note the extent and position of the membraneous area near the furca, and the transverse ridges and furrows on the mentum.

Figure 2.—A view of the posterior surface of the labella, to show the furca and its attachment to the external wall of the labella on each side, and its articulation with the ventral sclerites.

Figure 3.—The ventral aspect of the labrum-epipharynx at its distal end, to show the curious nature of the termination of the food canal, which ends in the cul-de-sac. c. s.

Figure 4.—The end of the labium and the labella in side view. The middle portion of the external wall is shown as cut away to disclose the discal sclerite *in situ*, with its attached teeth.

Figure 5.—Outline of the labial gutter at its distal end, where the lateral dorsal and the middle ventral portions are separated.

PLATE I.

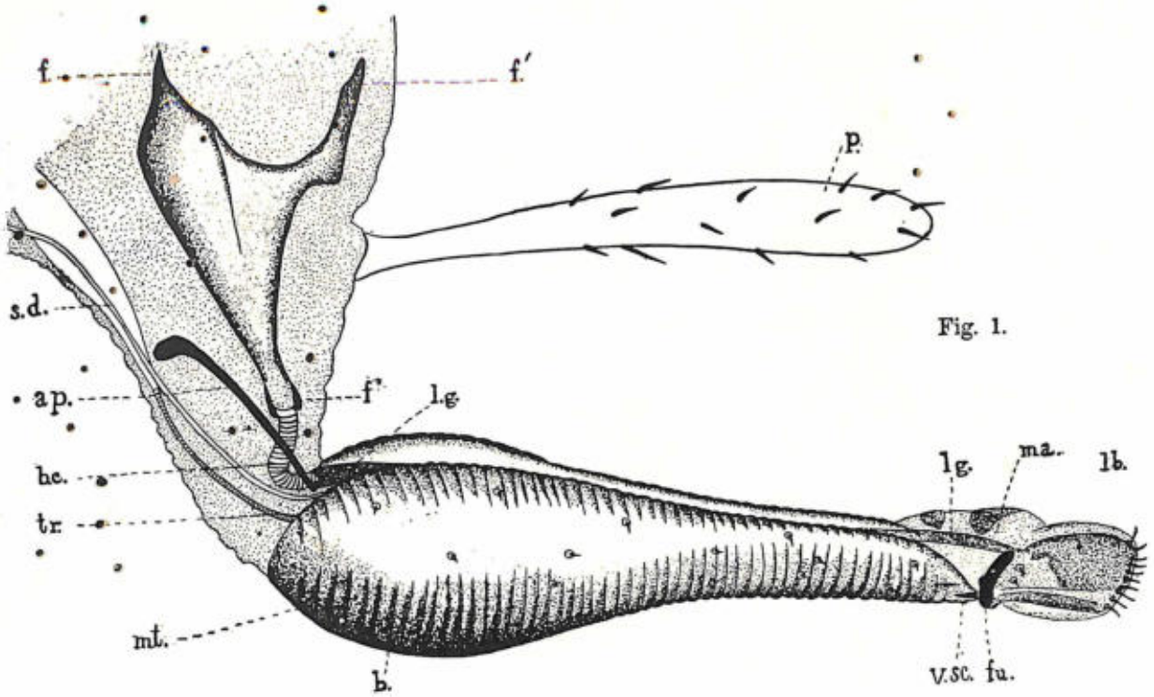



Fig. 1.

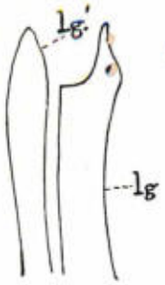



Fig. 5.

Fig. 2.

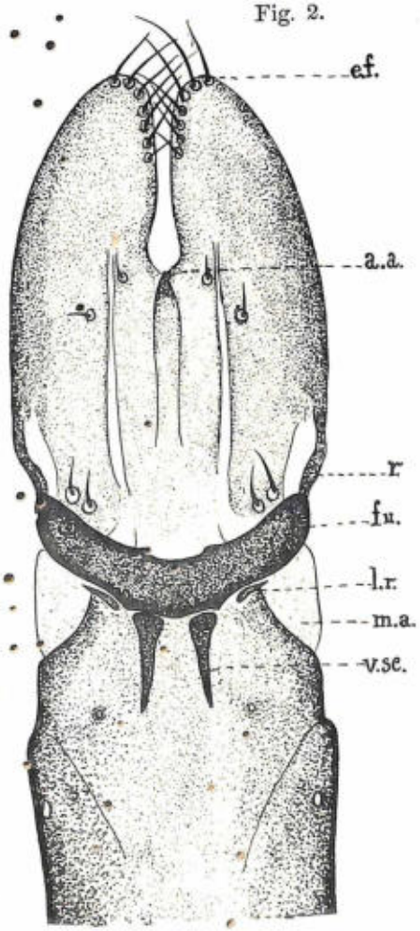



Fig. 3.

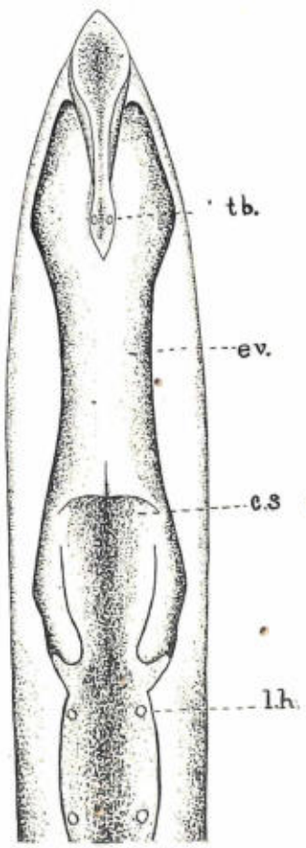
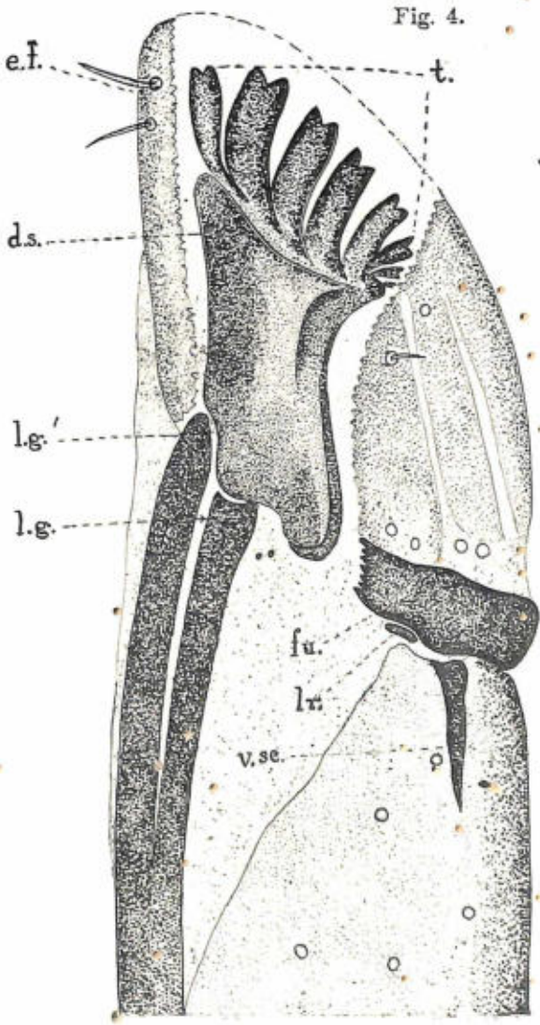



Fig. 4.

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## PLATE II.

Figure 6.—The teeth and their accessory structures, dissected off the discal sclerite. Note that, although the teeth differ in size, their cutting ends are brought into line by the curvature of the attached ends.

Figure 7.—The labella as seen in a well cleared preparation, mounted dorsal side uppermost. In this drawing the portions nearest the microscope were in focus.

Figure 8.—The same preparation, at a slightly lower focus. Here the ventral portion of the labial gutter is shown, and the lateral arms of the furca, which arch forwards from the posterior surface so as to come into focus.

Figure 9.—The same preparation, at a lower focus. Here the furca is seen from the front, and the whole length of the triangular axial apophysis is in view.

Figure 10.—The distal end of the labial gutter, as seen in a dissection. Note the separation of the dorsal and ventral portions.

Figure 11.—The distal end of the fulcrum, showing the funnel-like expansion and the buccal cavity.

Figure 12.—The proximal end of the food canal in the haustellum, showing the tube formed by the fusion of the epipharynx and the stomadeal portion of the hypopharynx as it projects from the haustellum into the rostrum.

Figure 13.—The labella in the position of action.

Fig. 6.

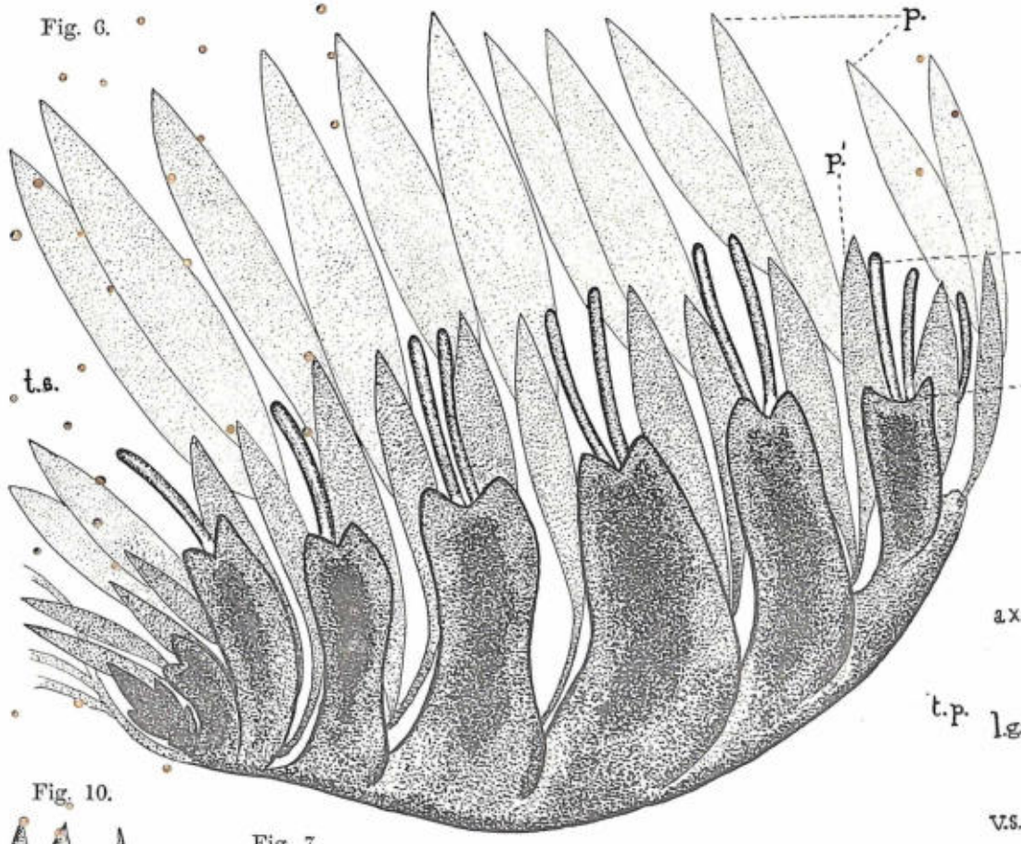



Fig. 9.

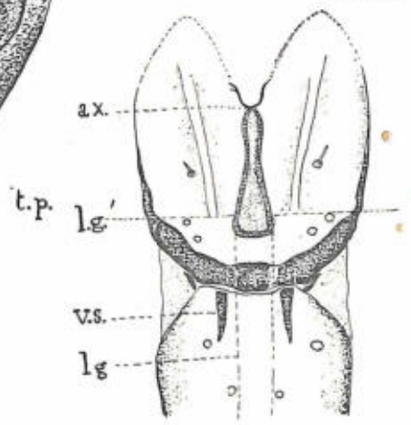
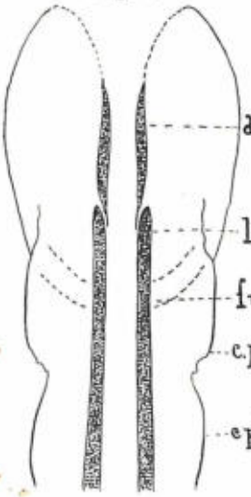



Fig. 10.

Fig. 7.

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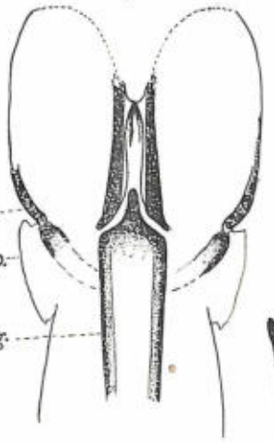

Fig. 13.

Fig. 11.

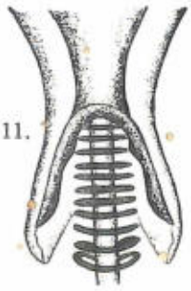

Fig. 12.

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## PLATE III.

Figure 14.—Transverse section through the labella in the position of rest, at the level of the teeth. The space in the middle between the labella is an artifact due to shrinkage. The irregularity in the outline of the teeth is due to the slight obliquity of the section.

Figure 15.—A transverse section a little higher up than the last figure, passing through the discal sclerite and the tip of its axial apophysis. Note the fusion of the two posterior walls of the labella at this point.

Figure 16.—A transverse section above the level of the teeth. The ends of the labial gutter are seen in the upper part of the section, projecting in front of the discal sclerite as seen in figure 4, Plate I. The axial apophysis is here united to the rest of the discal sclerite, occupying the ventral angle. Note the strong bands of fibrous tissue which unite the two external walls in this situation. Also compare the size of the tracheæ and nerves with those in figure 24, Plate V.

Figure 17.—The next proximal section. Only the joint arrangements are shown in this and the next three figures. Note the disappearance of the axial apophysis and the appearance of the ventral portion of the labial gutter, which is however separated from the dorsal portion by the intervention of the dorsal and lateral part of the discal sclerite.

Figure 18.—The next section, showing the widening of the labial gutter, and the approach of the ventral and lateral portions. The ventral portion of the gutter rests on two lateral projection of the discal sclerite.

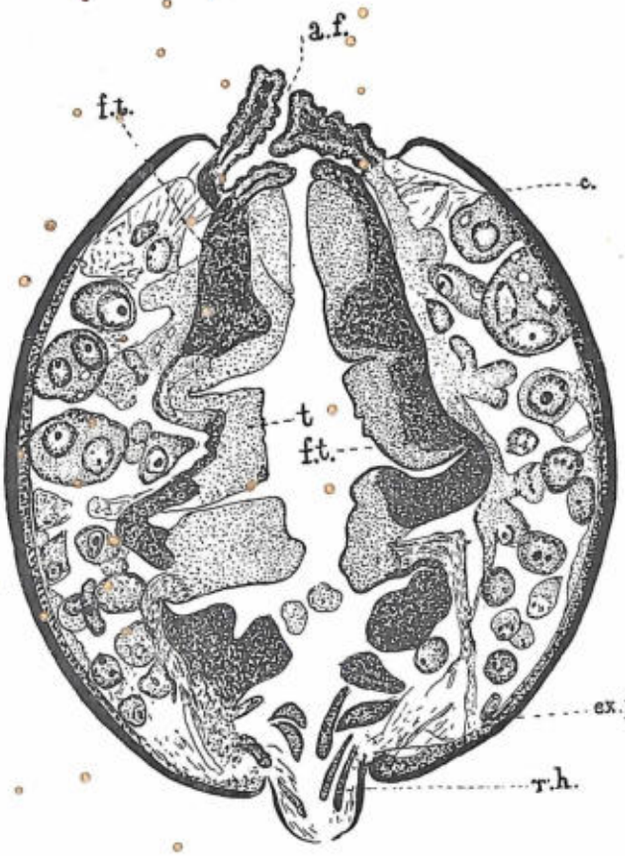



Fig. 14.

Fig. 15.

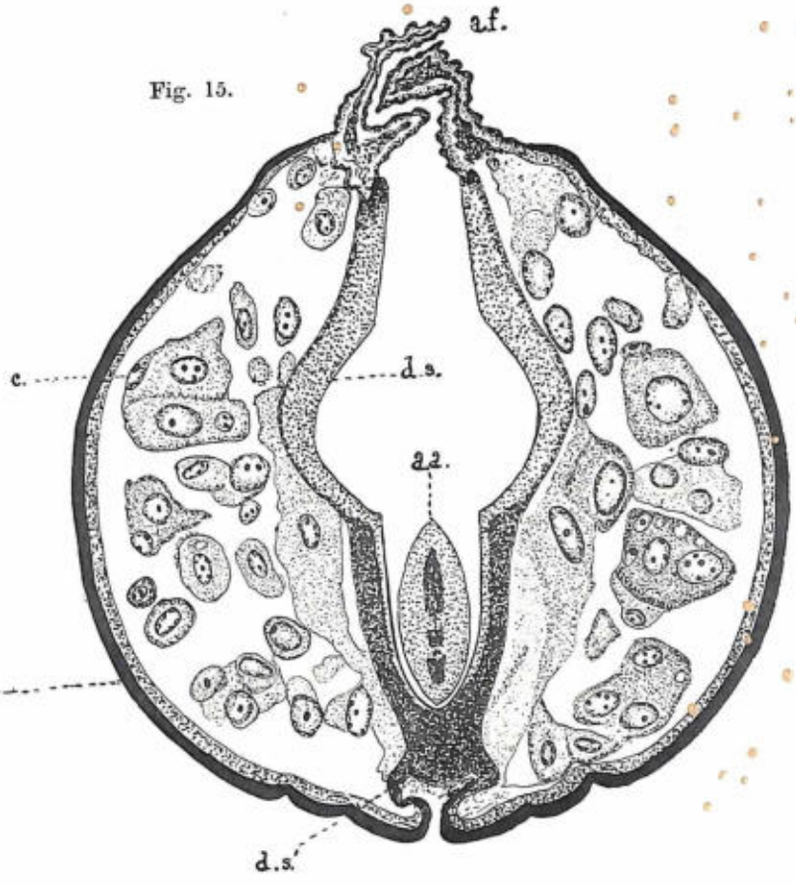
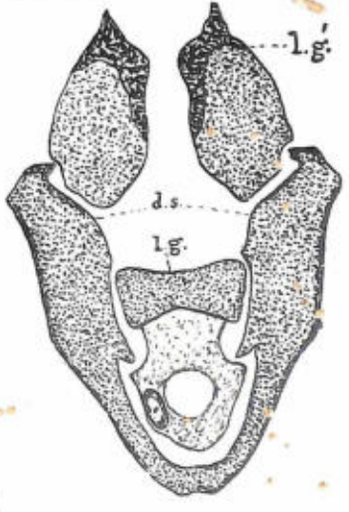



Fig. 17.



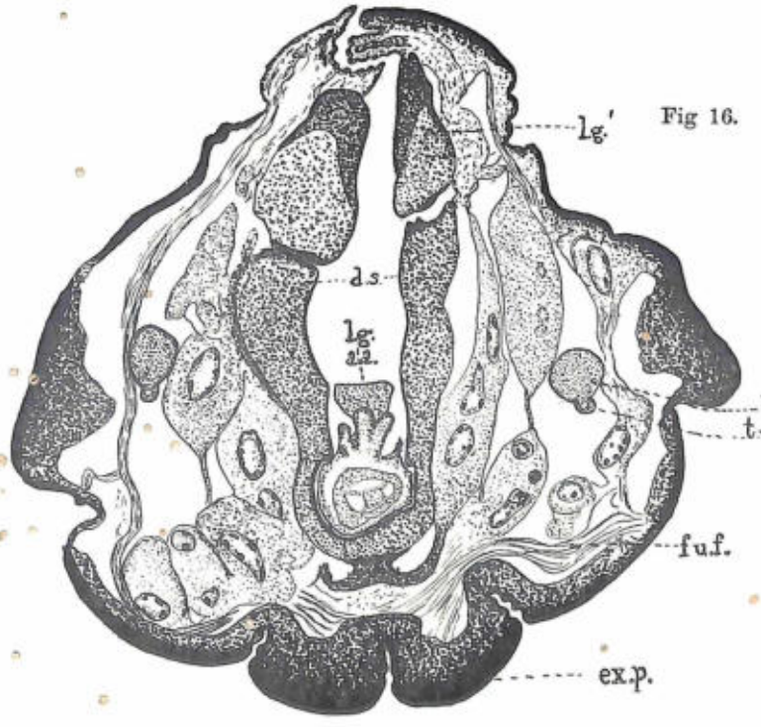




Fig 16.

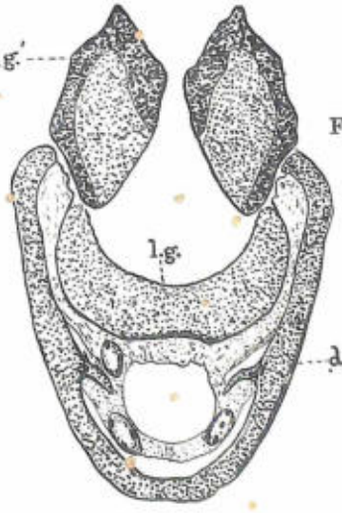



Fig. 18.



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## PLATE IV.

Figure 19.—A transverse section a little higher up. Here the discal sclerite is very much reduced in size, and has passed altogether behind the labial gutter.

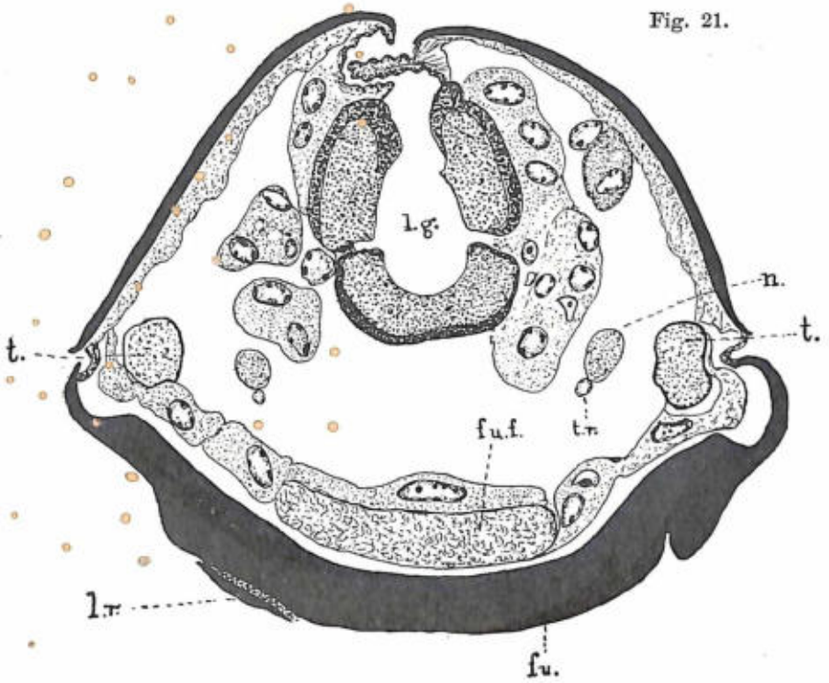
Figure 20.—The next section. This has passed through the upturned end of the discal sclerite, as seen from the front in figure 8, and from the side in figure 4.

Figure 21.—Section through the region of the furca. Note that the discal sclerite has completely disappeared, that the two portions of the labial gutter are united by fibrous tissue, and that the keel of the labial gutter is not present at this point. There is a well-marked band of fibrous tissue passing across the labella at the level of the furca.

Figure 22.—Section a little higher up than the last, showing the first appearance of the keel. The dorsal half of the labium at this point is bounded by membrane only. Compare other drawings of this area, figures 1, 4, 7, 8, 9. The ventral sclerites make their appearance at this level.

Figure 23.—Section at the level of the first appearance of the labrum-epipharynx and the hypopharynx. This section passes through the 'elevation' on the tip of the labrum-epipharynx.

Fig. 21.



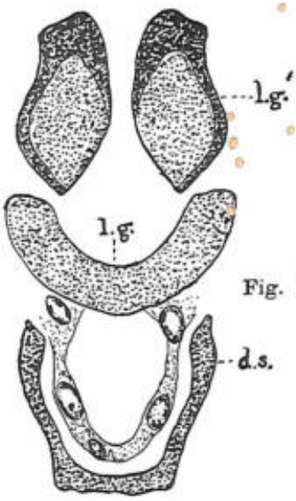
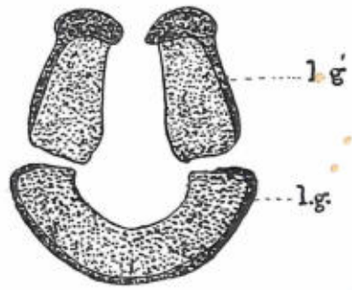




Fig. 19.

Fig. 20.



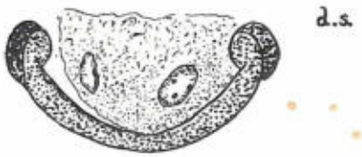




Fig. 22

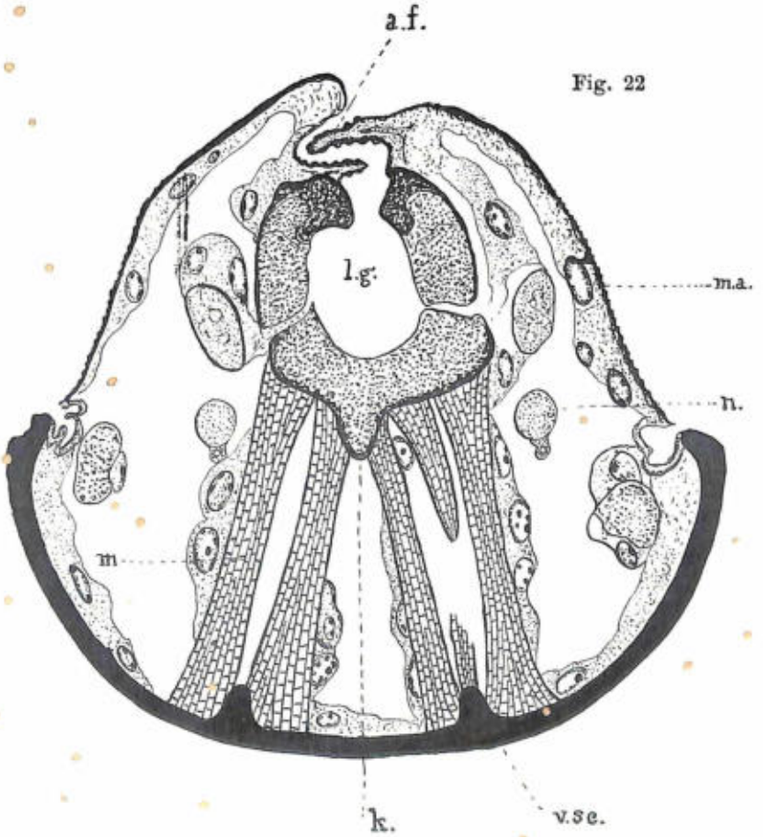



Fig. 23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## PLATE V.

Figure 24.—The next section above the last, showing the commencement of the food canal, between the labrum-epipharynx and the hypopharynx. The two divisions of the labial gutter are completely united. The appearance of a central space in the labrum-epipharynx and the hypopharynx is an artifact due to shrinkage. Probably the division of the concavity in the under surface of the former organ has been produced in the same way, as no trace of it can be found in fresh preparations.

Figure 25.—The food canal in the labial gutter, as seen in the greater part of the length of the labium. Note the firm fibrous membrane which unites the borders of the labial gutter with the mentum.

Figure 26.—A transverse section of the haustellum about the middle of its length. As in the other sections, allowance must be made for the shrinkage in the interpretation of the appearances seen. The spaces between the muscle fibres are artificial, and are due to the unequal shrinkage of the chitinous wall and the softer contents. Only a very small portion of it represents true hæmatocœle.

Figure 27.—The food canal in the upper end of the haustellum. The outline of the labrum-epipharynx is altered, and the salivary duct has thicker walls. The membrane connecting the labial gutter with the mentum is here replaced by a thin sheet of chitin.

Figure 28.—A section a little above that of the previous figure, and at the extreme upper end of the haustellum. The labrum and the epipharynx are here separating, the labrum to fuse with the membraneous wall of the rostrum, which is above continuous with the clypeus, and the epipharynx to unite with the upper lamina of the hypopharynx to form a closed canal.

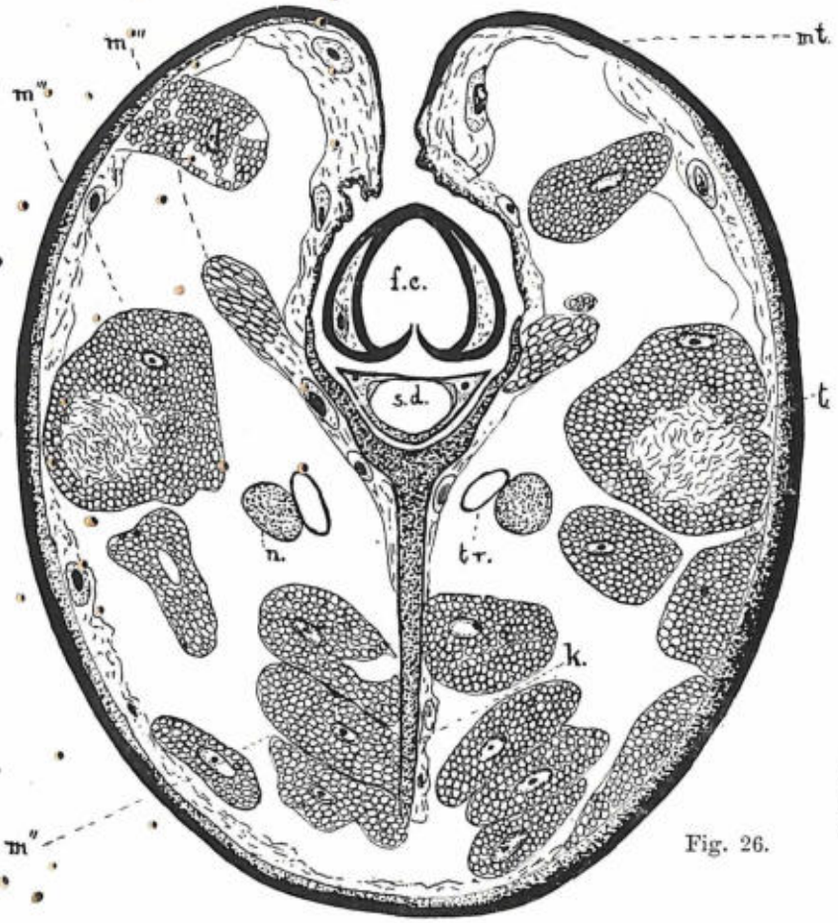



Fig. 26.

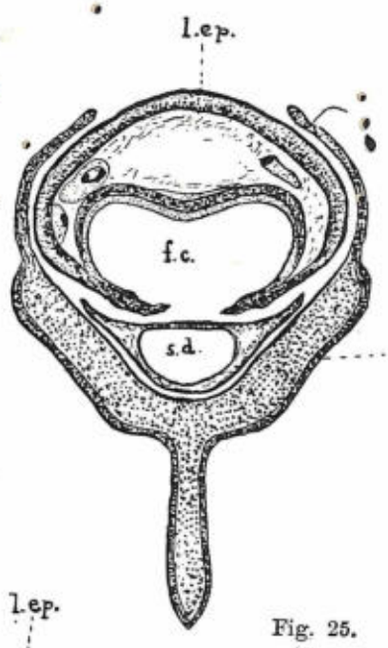



Fig. 25.

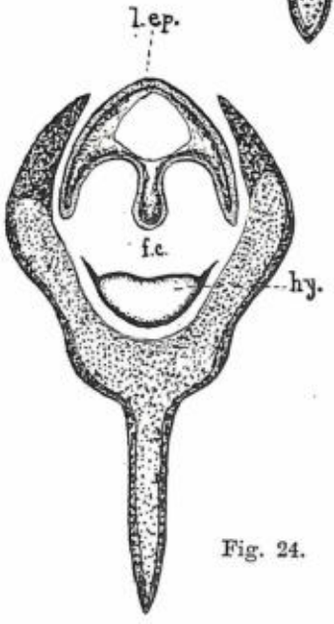



Fig. 24.

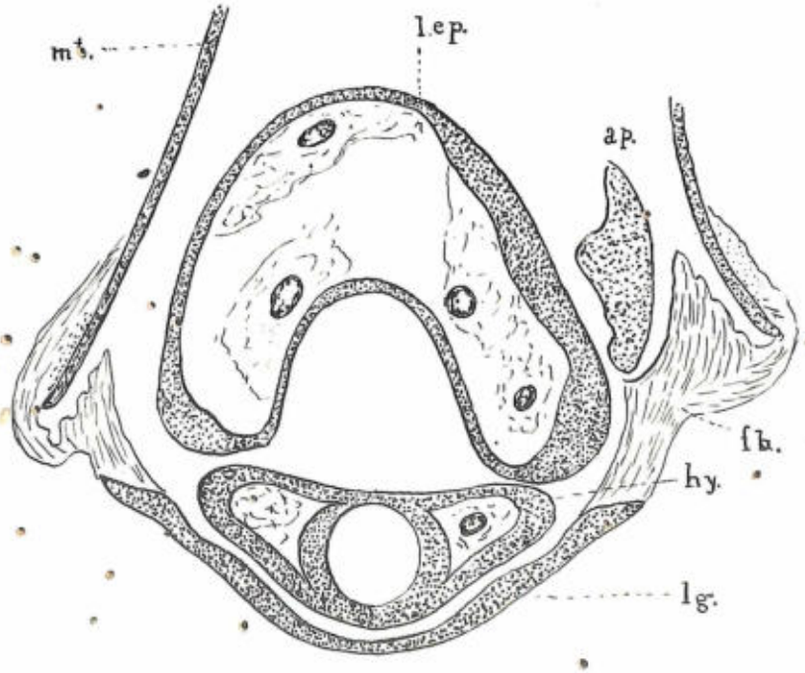



Fig. 28.

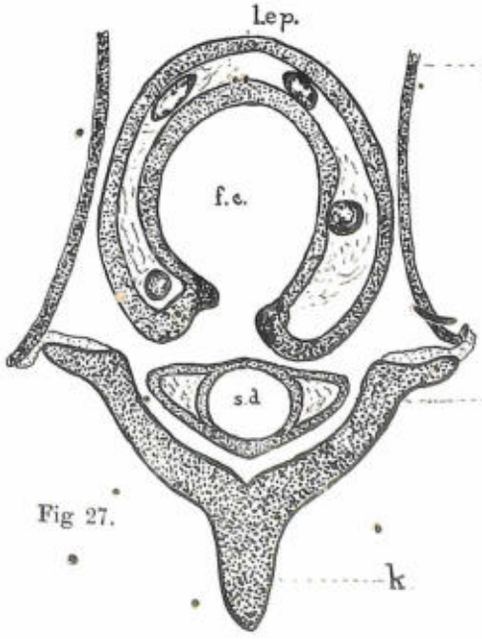



Fig 27.

## PLATE VI.

Figure 29.—This shows the closed canal formed by the union of the epipharynx and the hypopharynx. The lower lamina of the latter has fused with the labial gutter above this point.

Figure 30.—A section through the lower end of the rostrum, showing the separation of the food canal and the salivary duct, and the apodemes of the labrum. The rostrum was distended when the specimen was fixed, but the subsequent treatment has dissolved out the air from the air sacs, and left an empty space of considerable extent, in this section and the next.

Figure 31.— A section through the middle of the rostrum, showing the pharynx. The salivary duct has receded to the posterior part of the rostrum.

Fig 29.

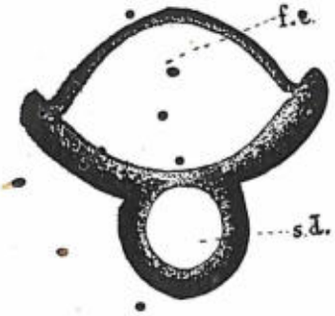



Fig. 30.

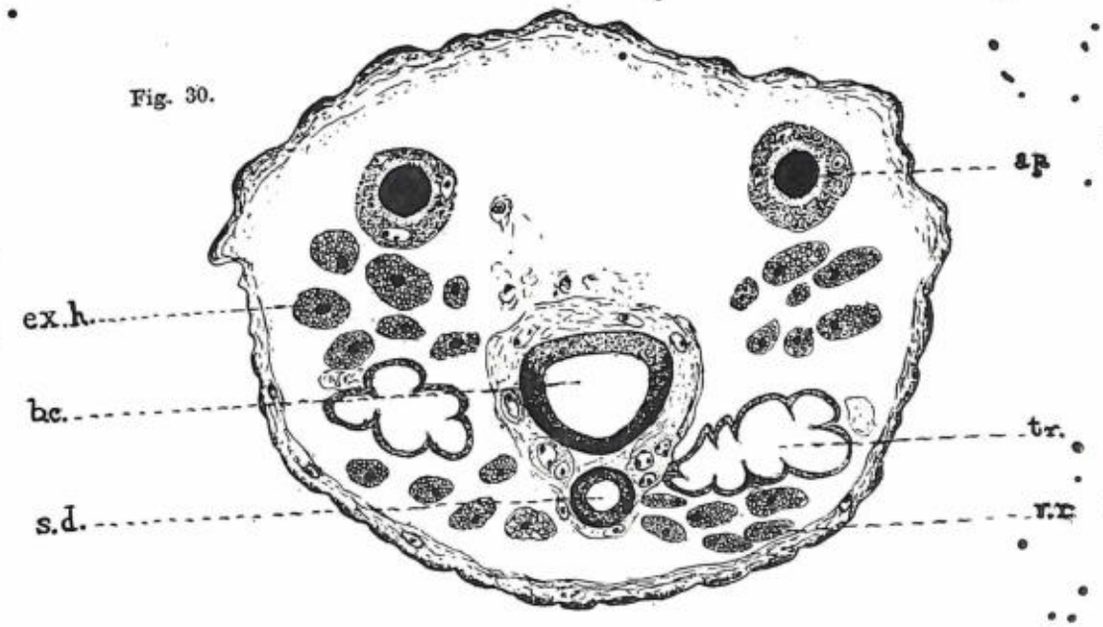
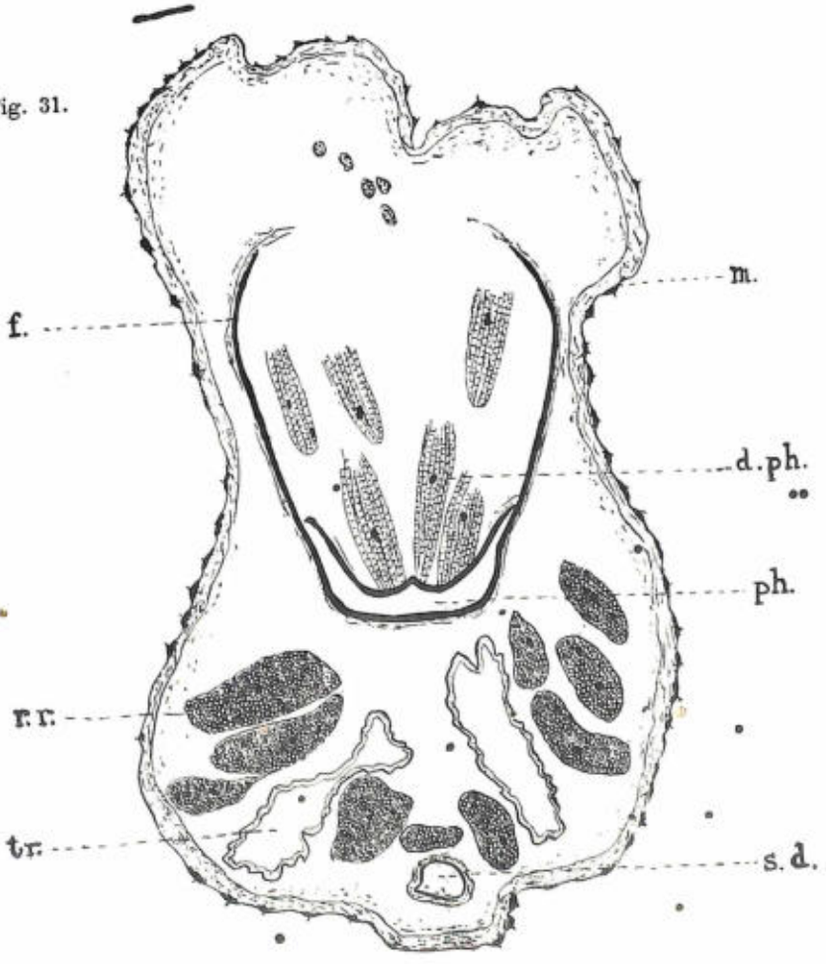



Fig. 31.

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F. W. C. DELET

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