THE WORLD OF
AMPHIBIANS AND REPTILES

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AND
REPTILES

by
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PREFACE

A combined account of the numerous vital activities of two or more related groups of animals makes a very pleasing task. It presents an opportunity for comparing the various phenomena exhibited by different zoological groups and so, by consideration of the simplest examples, gaining an understanding of those which are more complex. Such an undertaking is all the more interesting because it has not been achieved, at least not in recent decades.

This is more particularly the case in a combined survey of the life of amphibians and reptiles, two classes of vertebrate animals which are of especial importance from a phylogenetic standpoint. It is true that at the present time there is an extensive and fundamental literature dealing with them, but there is no recent treatise devoted to their ecology and ethology, divorced from their taxonomy. The only works of this kind were written by the world-famous Viennese herpetologist Franz Werner, who died in 1939. These are two small works on amphibians and reptiles, of which one carries the sub-title "Körperbau und Lebensweise" (Structure of the body and habits) and the other "Anpassung der Organe an die Lebensweise" (Adaptation of the organs to the mode of life). But both these books appeared in 1910 and so are half a century out of date! It is true that Thomas Barbour's book "Reptiles and Amphibians. Their habits and adaptations" (1926) has a similar theme, but it does not cover general problems and, moreover, its arrangement is strictly taxonomic. G. Kingsley Noble's "The Biology of the Amphibia" (1931) is excellent and complete for its time, but deals with only part of the subject; and the same reservation also applies to the works of Fernand Angel (1947, 1950). James Oliver has recently shown how extremely interesting an effective synthesis of the ecology and ethology of amphibians and reptiles can be. In his book he does, in fact, consider the species of the United States and Canada and the scope is broad.

When, some time ago, my esteemed colleague Professor Bourlière asked me whether I would undertake the preparation of a volume dealing jointly with amphibians and reptiles for the illustrated "Living Nature" series, I accepted readily. Such a project had long been part of my programme of work, but until now I have been unable to approach the subject except on the occasion of two symposia held during the final terms of students at the Johann-Wolfgang Goethe University at

Frankfurt-am-Main. In preparing the manuscript of the present book I have endeavoured to show that the subject is exceedingly wide and varied. So, I have been compelled to confine myself to essentials, merely indicating some problems and omitting others entirely, since the text could not be expanded on account of the wealth of the illustrations. The most important part of the account has been devoted to the exotic amphibians and reptiles so that our native species are, unfortunately, inadequately discussed and figured. Nevertheless I hope that my work will serve as a synopsis for a future, more detailed study of this very enthralling subject.

My thanks are due to the editor, and to Professor Bourlière, already mentioned, who has assisted me in the matter of illustrations for this work and in many other ways. For their assistance in the reading of the proofs I am indebted to Miss Margot Pearl and Miss Erika Schirner. Equally I wish to thank the following who have courteously lent their photographic records: Messrs. Eibl-Eibesfeldt, Haupt, Petter, Rosenberg, Schmidt, G. Senfft, Warham, de Witte for the colour photographs; Messrs. Barruel, Bertolf, Breder, Cagle, Cansdale, Cott, Davis, Dragesco, Dunton, Eibl-Eibesfeldt, E. Fischer, H. Fischer-Wahrenholz, Fisher, Géry, Hajek-Halke, Haupt, Hoogerwerf, Hoppe, Lippens, Maplestone, Marcuse, Oeser, Orth, van Riper, Roedle, Rosenberg, de la Rüe, Schmidt, G. Senfft, W. Senfft, Snyder, Stubenvoll, Tweedie, Uekerus, Warham, Wermuth, and de Witte for the black-and-white photographs. The choice of illustrations, their arrangement and their enlargement have been ensured by the editor.

The author holds himself responsible only for the original German text.

Pl. I. The best-known representative of the Californian newts, *Taricha torosa*, called the Californian Newt in the United States. × 1. *Photograph* by Senckenberg Museum (Haupt).

One of the rarest salamanders of Asia Minor known only from a few specimens: *Mertensiella luschani*. × 1 approx. *Photograph by* Rosenberg.

CHAPTER ONE

CLASSIFICATION AND ANCESTRAL HISTORY

Amphibians and reptiles are two classes of chordate animals (Chordata) which are the most highly developed animal group characterised by an internal axial skeleton. This consists of a firm dorsal rod, the notochord, which forms the basis of the spinal column both in the evolutionary history of the group and in the development of the individual organism. Tunicates (Tunicata) and lancelets (Acrania), lampreys (Cyclostomata) and fishes (Pisces), birds (Aves) and mammals (Mammalia) are other classes of chordates. Of these, fishes, birds and mammals are grouped together with the amphibians and reptiles as the Vertebrates because they have a notochord only in the early stages of development; this is later replaced by a vertebral column. The other existing classes of chordates, i.e. tunicates, lancelets and lampreys, have no vertebral column.

Two of the present-day orders of amphibians are so well known that a detailed description of their bodily appearance is superfluous; they are the newts and salamanders which form the Tailed Amphibia or urodeles (Caudata), and the frogs and toads which contrast with them as Tailless Amphibia or Anura (Salientia). The urodeles, with about 400 species and subspecies, are few in number compared with the anurans, whose species may be estimated at 2,500. The third order of recent amphibians are the worm-like, limbless caecilians (Gymnophiona), some of which have small calcareous scales under the skin; they live in the tropics and to-day there are only about 70 different species.

Earlier naturalists applied the name Amphibia (i.e. living both in water and on land) to reptiles as well, though nowadays they are recognised as fundamentally different creatures easily distinguishable by their external horny scales or shell-like covering. The most familiar examples are the lizards (Sauria) and the snakes (Serpentes) which are often united in a single order under the name of " scaly-reptiles " (Squamata). Apart from the consideration that the absence of limbs is in no way a differential character, the two groups are, in truth, not easily distinguishable. Lizards and snakes are to-day the reptilian orders with by far the largest number of species, containing some 6,000 known species, divided more or less equally between the two.

Whilst horny scales, which may be large or small or sometimes appear in the form of ossified platelets, are characteristic of both these groups of reptiles, the alligators and crocodiles (Crocodylia) have a stout armour composed of ossified horny plates. At the present day they form only a small group containing not more than 21 species. The tortoises and turtles (order Testudines), whose external appearance is familiar to everyone, also belong to the reptiles; according to the latest authoritative list, they total some 321 recognisable forms belonging to 210 species. Finally the "bridge-lizards" (Rhynchocephalia) form the fifth order of living reptiles; they are typically lizard-like in appearance but are primitive creatures and are represented at the present day by a single species only, with 3 subspecies (col. pl. IX, pl. 36).

Even the largest of the extant amphibians and reptiles are only dwarfs compared with those of prehistoric times. Thus the largest frog *(Rana goliath)* is scarcely more than 30 cms. (11.8 inches) long and the Giant Salamander *(Megalobatrachus japonicus)* only 160 cm. (63 inches), whereas the skull alone of the largest prehistoric amphibian *(Mastodonsaurus)* was 100 cm. (39 inches) long! The giants amongst the reptiles are to be found amongst the crocodiles and snakes; the Sharp-snouted and Orinoco Crocodiles *(Crocodylus acutus* and *intermedius)*, 7 metres (22.9 feet) long, are probably only slightly smaller than the Estuarine Crocodile *(Crocodylus porosus)* and the Gharial *(Gavialis gangeticus)*. The record, however, is held by the Reticulate Python *(Python reticulatus)* and the Anaconda *(Eunectes murinus)*, some 10 metres (32.8 feet) long or perhaps, in the case of the latter, somewhat more. The longest, and also heaviest, lizard is the Komodo Monitor *(Varanus komodoensis)*, 3 metres (9. 8 feet) long, whilst among the tortoises and turtles the marine Luth *(Dermochelys coriacea)* may have a shell-length of nearly 2 metres (6.6 feet) and a weight of three-quarters of a ton. These are, certainly, very imposing creatures but are nevertheless dwarfed by the monsters of the remote past such as the *Brachiosaurus* which was 23 metres (75 feet) long and 13 metres (42.6 feet) high.

At the present time both amphibians and reptiles are only poorly represented. In the remote past, in the palaeozoic and mesozoic eras of the earth's history, the rich variety of forms was markedly greater. Indeed, these two classes of animals once played a most significant part in the evolutionary development of the vertebrates. Amongst the amphibians, some 300 million years ago, the vertebrates completed the vital evolutionary transition from life in water to life on land; the vast evolutionary tree of all the land-dwelling vertebrates, including the mammals and man, with its multitudinous ramifications, therefore has its roots in the amphibians. No less important in vertebrate evolution are the reptiles, since they are the immediate ancestors of the two highest classes, birds and mammals. Thus, the amphibians and reptiles occupy a half-way position in the pattern of vertebrate evolution, a fact which is reflected in their anatomy and physiology.

With few exceptions fishes breathe by means of gills. In amphibians, however, gill-breathing, which occurs very frequently in the immature stages (larvae), is generally replaced by lung-breathing, which is the only method of respiration in reptiles. In fishes there is a simple heart consisting of a single auricle and ventricle which contain only venous blood. Amphibians, however, have two auricles; when lungs develop the circulation of the blood is transformed from a single to a double circuit; to the main, systemic body circulation a smaller lung circulation is added. The separation between the two is, however, incomplete since only a single ventricle is present and this receives both venous blood from the general circulation and arterial blood from the lungs. It is much the same with the reptiles, although in their case the first stage of division of the ventricle into a right, venous and a left, arterial half is apparent; the division may develop to the point of leaving only a small hole in the dividing wall. In birds and mammals only are there two completely separate ventricles and also two separate circulations, an arrangement that makes a fundamental improvement in the organisation and functioning of the organs.

As regards body temperature, reptiles (together with amphibians and fishes) belong to the lower vertebrates; their temperature is mainly determined by that of their surroundings and it immediately falls when external sources of heat fail. They are, therefore, animals of variable temperature (poikilothermal or exothermal) in contrast to birds and mammals with constant temperatures (homoiothermal or endothermal), where the body warmth is produced inside the animal, and is independent of the environment. Their plumage or hair-covering provides a special heat-insulating mechanism; an envelope of air is retained round the body and this prevents loss of heat to the outside. Thus in contrast to the amphibians and reptiles, the warm-blooded animals are able to live continuously in regions of extreme cold, as for instance in the arctic regions or the glaciated zones of high mountain ranges.

There are, however, characters which place the reptiles, as opposed to the amphibians, amongst the higher vertebrates. In this category, for instance, is the structure of the excretory system. Fishes and amphibians have, in their larval and embryonic stages, a functional pronephros which is replaced by a mesonephros that discharges through a mesonephric duct into the

Pl. 3. The West African clawed-toad, *Xenopus fraseri*, is entirely aquatic. ×1.2. *Photograph by* W. Senfft.

The Surinam Toad of South America, *Pipa pipa*, is as completely aquatic as its relatives the clawed-toads. ×0.7. *Photograph by* Senckenberg Museum (Haupt).

Pl. 4. In the Midwife Toad, *Alytes obstetricans*, the male (left) carries the egg strings on his hind limbs. ×1. *Photograph by* Rosenberg.

The " Crapaud Sonneur ", *Bombina variegata*, has glistening yellow spots on its ventral surface. ×1. *Photograph by* G. Senfft.

Pl. 5. The South American Escuerzo, *Ceratophrys dorsata*, is a powerful predator. ×0.5. *Photograph by* Cott.

Pl. 6. The Chilean Water Frog, *Calyptocephalella gayi*, is one of the largest South American frogs; its larva, too, is of giant size. ×0.5. *Photograph by* Rosenberg.

Eleutherodactylus flavescens from the island of Haiti. A frog that lays its eggs on land and has no larva. ×1. *Photograph by* W. Senfft.

Ceratophrys ornata, a near relative of the Escuerzo figured on Plate 5. ×0.8. *Photograph by* W. Senfft.

cloaca. The reptiles resemble the higher vertebrates in having pro- and mesonephros only temporarily. In their case a metanephros develops as the final organ of excretion and this has its own duct, namely the ureter. It is the same type of kidney that birds and mammals have. Whereas in amphibians and many fishes the male reproductive cells are carried to the mesonephros so that this functions simultaneously as the seminal duct, in reptiles, birds and mammals it subserves this function (as epididymis) only; the mesonephric duct of the amphibians which, from its function, can be described as a urinogenital duct, has in the reptiles become exclusively a genital duct.

Likewise in their method of fertilisation, egg-structure and development, reptiles stand closer to the birds and mammals than to amphibians and fishes. Amphibians and fishes are water-dwellers and fertilisation is usually external, whereas in reptiles the sperm is introduced by the male into the female's genital tract. The eggs of amphibians have a gelatinous capsule, but those of reptiles have a firm parchment-like or calcareous shell. Larval stages, present in amphibians and fishes, never occur in reptiles. Whilst the developing embryos of amphibians and fishes have, as a rule, no special covering membranes, the embryos of reptiles, birds and mammals develop an inner and an outer membrane (amnion and chorion) as well as an embryonic urinary bladder (allantois) which arises as a bladder-like evagination of the hinder part of the intestine. On account of the presence of the inner membrane, the amnion, reptiles, birds and mammals have been grouped together since the time of Ernst Haeckel (1866) as the Amniota in contrast with the amphibians and fishes as the Anamnia. On the other hand, up to about the middle of last century zoologists did not, on the whole, regard amphibians and reptiles as two separate classes of vertebrates. Linnaeus (1758), for instance, called them all Amphibia, but Laurenti (1768) called them Reptilia.

It is no less instructive to investigate how the five classes of vertebrates behave in relation to certain fundamental requirements of animal life, namely water and sunlight. In this respect, too, amphibians and reptiles occupy an intermediate position.

For fishes, as everybody knows, water is the proper environment. Just as air is our medium, so water is that of fishes. With very few exceptions all their organs, those of locomotion, nutrition, respiration and reproduction are so constituted that they can function only in water. In air they fail to function and death of the organism follows. Furthermore, though most species of fishes can only live either in sea water or in fresh water, there are a large number that can flourish in both, as, for instance, the many migratory fishes. Just as animal life may once have originated in the ocean, so we have every reason to believe that the chordate line of evolution also began in the sea. Although at present it is generally held that fish originated in inland waters, there is no doubt that the ocean has become their true home. Only a very few forms (lung-fishes and mud-skippers) have become adapted to a temporary sojourn in air.

Although the transition from water to land, so vitally important in vertebrate evolution, took place in the class Amphibia, these animals are really aquatic. Though a very few have become terrestrial, even these need either a very high humidity or at least occasional accumulations of water in order to thrive. Most amphibians show their dependence on water by the fact that their skin is very porous and rapidly dries out. In most of them fertilisation is external and the reproductive process, therefore, is often accomplished in water; the young, too, are mostly aquatic and, like fish, breathe by gills. Some continue to live entirely in water even as mature animals: instances are : — some salamanders, e.g. the Giant Salamander, the Mud Puppy and the Olm; many frogs, e.g. the clawed-toads *(Xenopus)* and Surinam-toads *(Pipa*, pl. 3), certain large Andean frogs of the family Leptodactylidae, *Pseudis* among the Hylidae, *Pseudobufo* among the true-toads and a whole series of true-frogs. Characteristic of all amphibians — in contrast to fishes — is their intolerance of sea water; there are no marine forms among them and only very few, like the Variable Toad *(Bufo viridis)* and a few species of *Rana*, do not shun brackish water.

Perhaps the oldest reptiles may also have been dwellers in inland waters where they may have led an amphibious existence. Those forms living to-day are predominantly terrestrial and, unlike the amphibians, have become largely independent of water and are even to be found in extremely dry environments. In contrast to the amphibians, their skin is protected against water-loss by horny scales or scutes, fertilisation is internal and even their eggs, enclosed in a firm shell, are far more resistant to desiccation, though not so much so as those of birds. Probably, except turtles and crocodiles, all recent reptiles that live by, or in, water have become secondarily adapted to aquatic life. This applies not only to the amphibious lizards (e.g. Sea Iguanas, a few monitors) and snakes (e. g. Anaconda) but also to the exclusively marine forms like the remarkable sea-snakes. As for the few species of marine turtles living to-day, they are to be regarded as secondarily adapted to marine life like the many sea reptiles of the remote past. The same applies also to sea birds and marine mammals, among which the seals and whales have become secondarily adapted to an oceanic existence in an astonishingly perfect way.

Why did the ancestors of the amphibians — we have every reason to suppose that they were certain kinds of fish (Crossopterygia) — leave the water and make the transition to life in air, initially, of course, very damp air? Why, later, did the reptiles return again to the sea, the cradle of the chordate line? We shall probably never succeed in giving the correct answers to these questions; but some speculations on the problems may be permissible.

In both cases it was probably the limited extent, if not the instability, of the environment which favoured the transition from life in water to life on land or vice versa. Oceans are notable for their permanence but not the inland waters; these are formed and soon cease to exist. Moreover, many are present only transiently and dry up for long periods. The extant lung-fishes — relatives of the previously mentioned Crossopterygia — show certain characteristics which enable them to survive times of drought. It is therefore understandable that life in changeable waters such as lagoons, stagnant pools and brooks sets a particularly high survival value on all characters favouring life in air, for example, protection from desiccation, and the development of special organs of locomotion, breathing and mode of reproduction. Under such conditions, animals endowed with this type of attribute have certainly a better prospect of surviving than aquatic animals lacking such adaptations. A similarly stringent selection doubtless existed amongst land animals on small islands which, perhaps as a result of processes connected with the earth's development, were threatened with increasing inundation: here, on the other hand, any characteristics that favoured life in water — and particularly in the ocean — had survival value. Thus one can perhaps visualise the conditions of life under which, for example, the first fishes or amphibians came on shore or certain snakes (Hydrophidae) became marine animals.

Just as the need for water differs in different groups of vertebrates, so does the need for sunlight. The sun gives light and warmth. Most amphibians are, like fishes, very undemanding in this respect. The large majority are nocturnal and shun the light, and their heat requirements are not high. Reptiles are different. Here nocturnal forms (e.g. most geckos) are in the minority; the majority have become diurnal the better to enjoy the warmth-giving sunlight. In fact, most species actively seek the sunshine and only then develop their full activity. It is noteworthy that most birds, too, are attracted by bright light — in contrast to most mammals; but as warm-blooded creatures the sun has lost its importance for them as a source of warmth.

On the basis of this sketch the essential differences — not concerning the skeleton — between the present-day amphibians and reptiles are as follows. The amphibians have a highly glandular, porous skin, which lacks horny scales or scutes (only some caecilians have tiny calcareous scales), and which is also an important respiratory organ. In addition, breathing is by gills, especially in the young stages, but is later replaced by breathing through lungs. The pronephros serves the embryonic stage as an excretory organ and is followed by a mesonephros which simultaneously serves as a duct for the germ cells of the male. These cells are not normally introduced by the male into the female genital tract. The eggs have no firm shell, having at most a gelatinous envelope except in viviparous forms. Embryonic membranes and allantois are lacking. Larval forms are of common occurrence and are very different from the parents (e.g. tadpoles); they undergo a metamorphosis.

In contrast to this, in reptiles the skin is always covered by horny, sometimes ossified, scales and scutes which are arranged in a definite, regular pattern. The skin is not especially glandular, is almost impervious to water, and is of scant importance for respiration. Gill-breathing never occurs, lungs serving exclusively for respiration. The metanephros is the excretory organ; the mesonephros is excretory in function only in the embryo but serves as a genital duct in the adult male. Fertilisation is always internal, the sperm being introduced into the female genital apparatus by the males' intromittent organs; these are absent only in *Sphenodon*. Except in viviparous forms, the eggs have a stout shell and, as in birds and mammals, there are embryonic membranes in the form of amnion and chorion, and an allantois. Larval forms do not occur.

How far, then, can palaeontology provide clear evidence supporting the view advocated here of the intermediary position of the amphibians and reptiles within the phyletic sequence of the vertebrates? Which of the connecting links between fishes and amphibians, amphibians and reptiles, reptiles and birds and reptiles and mammals are known from the remote past?

At one time it was naturally supposed that the connecting link between fishes and amphibians was amongst the still extant lung-fishes (Dipnoi). Three genera of these strange creatures exist: *Protopterus* in Africa, *Lepidosiren* in South America and *Epiceratodus* in Australia. They are apparently quite primitive fishes that, in addition to gills — the larvae furnished with external gills are very reminiscent of those of newts — also breathe by means of lungs; these were at one time considered to be functionally modified swim-bladders. They are paired in *Protopterus* and *Lepidosiren*, but unpaired, and on the right-hand side, in *Epiceratodus*. By means of these organs the lung-fishes are able to thrive in water deficient in oxygen, and it is known that the African lung-fishes can even survive for several months enveloped in a mucous capsule in mud where the waters have dried up. Another essential feature of the lung-fishes is the presence of choanae, or internal nares that open on the roof of the mouth, and which are characteristic of air-breathing vertebrates; they permit respiration without the mouth being opened. The choanae represent a marked advance, especially for animals that breathe air but live in water.

In other characters, however, the lung-fishes are in part very primitive but in part so specialised that they cannot be interpreted as the certain forebears of the Amphibia and consequently of the terrestrial vertebrates. Thus, for instance, they still have a notochord; in the skull certain essential components are wanting, like the maxilla, premaxilla and the dentary portion of the lower jaw; teeth, which have degenerated completely around the edge of the mouth, are replaced by characteristic dental plates. Whilst closer examination of the structure of the dipnoans, especially of the skull, reveals no resemblances to that of the amphibians, some other fishes, namely the crossopterygians, show quite astonishing relationships to certain primitive amphibians.

Crossopterygians, so called from the structure of their paired fins which are characterised by a scaly peduncle, are ancient fishes known since the Devonian (e.g. *Osteolepis)*. Until a few years ago it was generally believed that they became extinct in the Cretaceous. Consequently there was a scientific sensation when, at the end of 1938, a living representative of the Crossopterygia was discovered off the east coast of South Africa; this famous greenish-blue fish, about 1.5 metres (4.9 feet) long, was named *Latimeria chalumnae* — a living fossil in the truest sense. Recently eleven further specimens have been caught, especially in the vicinity of the Comoro Islands (between East Africa and Madagascar) and these have now been studied anatomically.

The recent discovery that the ancient bony-fishes had lungs in addition to gills is very noteworthy: like the lung-fishes previously mentioned they, also, were able to breathe in two ways; the swim-bladder of the higher fishes is, therefore, derived from lungs and not vice versa, as was formerly assumed. The ancient crossopterygians, also, were capable of lung-breathing, an ability which *Latimeria*, that lives on the ocean floor at a depth of about 300 metres (164 fathoms), subsequently lost; this fish has once more become a gill-breather exclusively.

No less essential for the understanding of phyletic relationships was the discovery that choanae, or internal nares, were characteristic of the crossopterygians (except the specialised *Latimeria)*. Chiefly on the basis of this character, which occurs in no other representative of the very varied fish stock except the lung-fishes, it is customary to group the crossopterygians and dipnoans together in a group of common kinship (subclass), the Choanichthyes, in contrast to all the remaining bony-fishes, the Actinopterygia or "ray-fins". The structure of the scales also confirms this grouping. Within the Choanichthyes, the dipnoans have only the importance of a side-branch; the true stem of the amphibians goes back to the crossopterygians.

Their close relationship with the amphibians is indicated especially by the astonishing similarity of their skulls; not, of course, the skulls of the extant salamanders and frogs, but rather the very bony skulls of certain amphibians of the remote past which are known as the Labyrinthodontia. These were the salamander-like amphibians, sometimes very impressive and several metres long, of which a great number of forms lived during the late Palaeozoic (Carboniferous, Permian) and early Mesozoic (Triassic); many of them bore, especially on the belly, a covering of bony scales corresponding with that of the crossopterygians and the young stages had external gills like the larvae of newts ("Branchiosaurus").

How close is the similarity in cranial structure between a crossopterygian and a labyrinthodont is shown by a skull, about 15 cm. (5.9 inches) long, found in the Upper Devonian of Canada (i.e. about 300 million years ago); this was given the generic name *Elpistostege* and no one can say with certainty whether it is a representative of the crossopterygians or of the labyrinthodonts — i.e. a fish or an amphibian. In the arrangement of the bones of the roof of the skull — here it is particularly a question of the position of the parietal bone which is pushed further back in the labyrinthodonts than in the crossopterygians — *Elpistostege* is a " missing link " between the two vertebrate classes. The discovery of the paired limbs of *Elpistostege* would probably clarify the position; the fundamental difference between the crossopterygians and the amphibians consists, as is well known, in the fact that the latter, as terrestrial animals, have a limb constructed of three segments (upper arm or femur, fore arm or tibia, hand or foot) which terminates in several processes. In the paired fins of the crossopterygians, however, only the first two sections corresponding with those of land vertebrates can be identified whilst the last section, basically pentadactyl (tetradactyl only, of course, in recent amphibians), is completely wanting and appears for the first time in the terrestrial vertebrates.

A further surprising resemblance between the crossopterygians and the labyrinthodonts must be mentioned: the fine structure of the teeth. The name labyrinthodont derives from the numerous folds of dental enamel which, in cross section, give a picture resembling a labyrinth. It is remarkable that the teeth of the crossopterygians also show the same fine labyrinthine folding as the labyrinthodonts, an order of Amphibia that, as will be discussed later, has shown itself to be of the utmost significance in the phylogeny of the reptiles.

At the base of the reptiles' phylogenetic tree there is a very noteworthy genus: *Seymouria*. These salamander- or lizard-like creatures, about 60 cm. (23.6 inches) long, are referred by some investigators to the labyrinthodonts but by others to the most ancient reptilian group, the cotylosaurs. *Seymouria* is, therefore, another "missing link", this time, however, between the amphibians and reptiles. The strongly ossified skull, with paired openings for the nostrils and eyes, with a large unpaired opening for the parietal organ and with the temporal region roofed over, agrees completely with the cranial structure of the labyrinthodonts. Teeth were present on the vomerine bones, just as they also occur in many amphibians; and in other respects, too, the skull shows connections with the amphibians. It had, to be sure, only a single occipital condyle which is also the case amongst the primitive amphibians, whereas the modern amphibians — like the mammals — have two. On the other hand, the shoulder-girdle, and also the pelvis and the limbs, show certain features characteristic of the reptiles. In vertebral structure *Seymouria* combines reptilian characters with those of amphibians. Consequently, this noteworthy genus stands exactly on the dividing line between the amphibians and reptiles. On the basis of skeletal characters there appears therefore to be no sharp boundary between the two vertebrate classes. Such a fixed line of demarcation was, however, at least indicated in the formation of the internal organs, the egg- and embryonic membranes. According to the latest investigations *Seymouria*, since it appears to have a gill-bearing juvenile stage, would seem to stand nearer to the amphibians.

There can be hardly a doubt that the reptile stem has its roots in the labyrinthodonts. The earliest reptiles were the cotylosaurs, that lived during the late Palaeozoic and early Mesozoic and which included some small and some quite large forms about 2 metres (6.5 feet) long. Their skull was strongly ossified, very like that of the labyrinthodonts, but generally speaking built on a narrower and higher pattern. The temporal notch, for the auditory organ, generally well marked in the labyrinthodont skull (and in *Seymouria)* has disappeared and there are no open-

Pl. 7. *Engystomops pustulosus* from Salvador. Left, the frog twice natural size. *Photograph by* G. Senfft. Right, its mud nest half natural size. *Photograph by* Mertens.

Foam nest of the tropical American Giant Frog *(Leptodactylus pentadactylus).* ×0.5 approximately. *Photograph by* Breder.

Pl. 8. South American Giant Toad, *Bufo marinus*, swallowing a young rat. ×0.6. *Photograph by* Rosenberg.

The Colombian *Bufo blombergi*, first discovered in 1951, also reaches a size comparable with that of *Bufo marinus*. ×0.6. *Photograph by* Senckenberg Museum (Haupt).

ings in the temporal region. The cotylosaurs were phylogenetically the most important group of reptiles from which at least a large part of the remaining orders of reptiles are descended; in addition to the four or five recent orders there were no fewer than thirteen in former times. They blossomed to the full during the Mesozoic, the middle period of the earth's age, a time span of 125,000,000 years that ended 60,000,000 years ago.

At that time the reptile world showed an immense multiplicity of forms, whilst birds and mammals had scarcely come into existence. In the oceans the ichthyosaurs (Ichthyosauria) and the nothosaurs and plesiosaurs (Sauropterygia) bestirred themselves; the continents were populated by the giant dinosaurs (Saurischia, Ornithischia); and the flying-reptiles (Pterosauria) soared in the air — to mention only a few of the most conspicuous groups of primeval reptiles. Even the crocodiles, which are to-day represented by only a few species, showed a wide range of development, and the same applies also to the "bridge-lizards", of which only a single species *(Sphenodon punctatus)* survives to-day — and on only a few small islands near New Zealand at that. The ancestors of the birds — strangely enough they were probably the same thecodonts from which the dinosaurs, crocodiles and flying-reptiles are descended — belong to the oldest period of the Mesozoic era (Trias), as do the therapsids, which may be considered to be the undisputed ancestors of the mammals.

CHAPTER TWO

GEOGRAPHICAL DISTRIBUTION

Amphibians and reptiles are found on all the continents except the Antarctic; the oceans also are inhabited by a few turtles and snakes. The urodeles (salamanders and relatives) are characteristic of cool, temperate regions and especially of the northern hemisphere; all other amphibians and all the reptiles, on the other hand, find their optimum environments in warm countries. Their species are particularly numerous in the damp tropics, whilst the warm dry areas, too, are generally very rich in lizards. Even small islands are not without amphibians and reptiles; often, indeed, very tiny islands are colonised by lizards as the only representatives of the terrestrial vertebrates.

Except in the case of the salamanders, the closer one approaches the temperate zone the more marked is the decrease in the number of families, genera and species of amphibians and reptiles. Only a few reach or cross the Arctic Circle: amongst the salamanders *Hynobius keyserlingii* and, amongst the frogs, the Common Frog *(Rana temporaria*, pl. 19) and the Moor Frog *(Rana arvalis)* in the Old World and the Wood Frog *(Rana sylvatica)* in the New. The northern limits of distribution of the Siberian Frog *(Rana chensinensis)* and the European Common Toad *(Bufo bufo)* also coincide approximately with the Arctic Circle in places. Amongst the reptiles, on the other hand, the Arctic Circle in Europe is crossed only by the Common Lizard *(Lacerta vivipara)* and the Adder *(Vipera berus*, pl. 71) and almost reached by the Slow Worm *(Anguis fragilis*, pl. 51). In North America, and more specifically in north-west Canada, the range of the Ribbon Snake *(Thamnophis sirtalis)* extends farther north than that of any other reptile but without apparently crossing the Arctic Circle. In the southern hemisphere the distributional range of a small iguana *(Liolaemus magellanicus)* reaches farthest south; it lives in Tierra del Fuego, at the southern tip of South America. Thus the extreme southern boundary of our animals occurs far from the Antarctic Circle.

A diminution in the multiplicity of forms can, however, also be observed in the high mountain ranges. Nevertheless the 3,000 metres (9,850 feet) line in the Alps is reached, if not passed, by, for example, the Common Frog *(Rana temporaria)*, the Alpine Salamander *(Salamandra atra)*, the Common Lizard *(Lacerta vivipara)* and the Adder *(Vipera berus)*. *Lacerta galloti* has been observed at somewhat over 3,000 metres on the Pico de Teyde on Teneriffe in the Canary Islands, and a snake *(Thamnophis scalaris)* and a rattlesnake *(Crotalus triserialus)* at over 4,000 metres (13,120 feet) in Mexico. In the Peruvian Andes various frogs live at a similar altitude, amongst them the gigantic *Batrachophrynus microphthalmus*, whilst an iguana *(Liolaemus multiformis)* reaches an altitude of approximately 5,000 metres (16,400 feet). The presence of amphibians and reptiles has been established at equally remarkable heights in the Himalayas; thus, for a salamander *(Batrachuperus pinchoni)* 4,000 metres, for a small skink

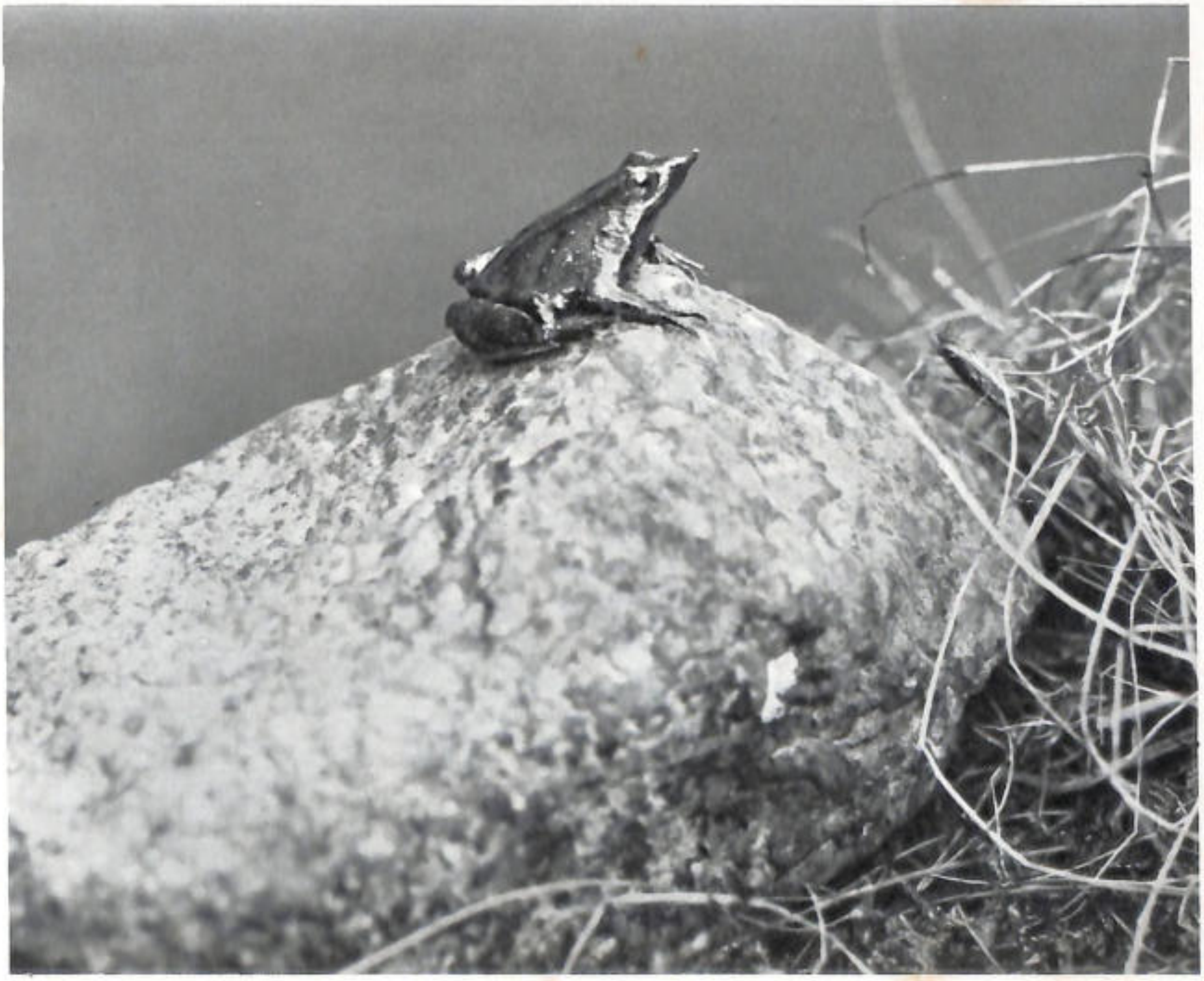
Pl. 9. The Japanese race, *Bufo bufo japonicus*, of the European Common Toad is more brightly coloured and larger than the Central European form. ×0.8. *Photograph by* Senckenberg Museum (Haupt).

Pl. 10. The South American *Bufo typhonius* (in the centre of the picture) scarcely stands out from its surroundings. Cryptic coloration. ×0.3. *Photograph by* Cott.

Amongst the toads there are also some leaf-dwellers such as the small West African *Nectophryne afra.* ×2. *Photograph by* W. Senfft.

Pl. 11. A male of the Central American *Dendrobates auratus* nursing its brood; two tadpoles have firmly attached themselves to its back. ×2. *Photograph by* W. Senfft.

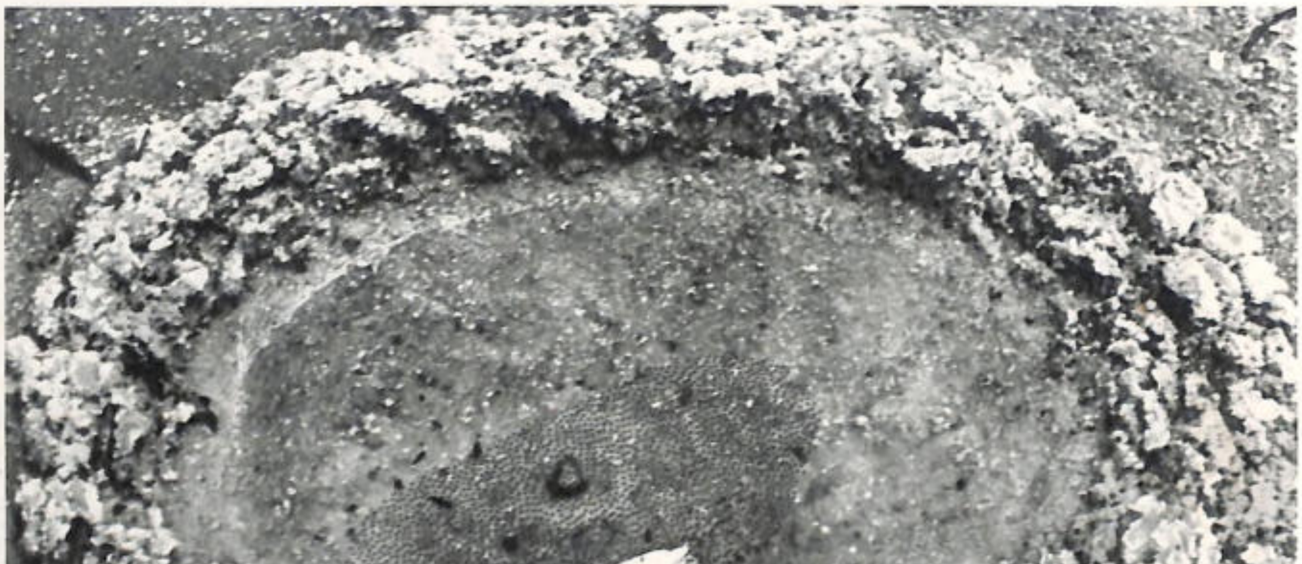
Darwin's Frog from Chile *(Rhinoderma darwinii)*. The male's unique method of nursing the brood is described on page 168. ×1.2. *Photograph by* Rosenberg.



Pl. 12. Brazilian tree-frog, *Hyla albomarginata*, in sleeping posture. ×1. *Photograph by* Senckenberg Museum (Haupt).

(Right) *Hyla leucophyllata*, one of the most charming representatives of the Brazilian tree-frogs. Its colour in life is chocolate-brown and silvery white. ×1.5. *Photograph by* W. Senfft.

Mud nest, with eggs, of a large tree-frog akin to *Hyla faber*, in French Guiana. ×0.5. *Photograph by* Géry.



(Leiolopisma ladacensis) 4,270 metres (14,000 feet), for the European Variable Toad *(Bufo viridis)* 4,285 and 4,560 metres, for a pit-viper *(Agkistrodon himalayanus)* 4,800 metres, and for a sand-agama of the family Agamidae *(Phrynocephalus theobaldi)* 5,185 metres. Even at heights of 5,300-5,400 metres (17,384-17,712 feet) lizards of the same genus are said to occur. On the other hand, it is found that on many isolated mountains in the tropical zone, amphibian and reptilian life ceases at a very low altitude: thus, on the 4,170 metres-high Mount Kinabalu, in North Borneo, no reptiles live above 2,440 metres; on Rindjani, nearly 3,800 metres high on the island of Lombok, I failed to find amphibians above 2,500 metres and reptiles above 2,000 metres. My observations on the slopes of Cameroon Mountain were not very different.

Since amphibians and terrestrial reptiles find it hard to surmount natural barriers, such as high mountains and arms of the sea, and can be transported, except by human agency, only with difficulty, the zoogeographical regions have their distinctive types in both classes. For about a century it has been customary in zoogeography to distinguish the following six regions: the Palaearctic for the faunas of Europe, North Africa (north of the Sahara), and North and Central Asia; the Ethiopian for the fauna of Africa (except the north) and Madagascar; the Oriental for the fauna of southern Asia and the western part of the Indo-Australian archipelago; the Notogaean for the fauna of Australia together with that of the eastern Indo-Australian archipelago, New Guinea and the adjacent islands further east; the Nearctic for the fauna of North America and the Neotropical for that of South and Central America. Obviously, these faunal areas are not sharply defined where they are not separated by oceans; where their boundaries occur on the mainland or cut through an archipelago, transitional zones are interpolated and the study of these is particularly attractive for zoogeographers.

In spite of the vast extent of the Palaearctic region, its fauna of amphibians and reptiles (herpetofauna) is relatively poor in genera and species. This contrasts with the geological past when, in the Tertiary, a rich herpetofauna used to live in the Palaearctic; its species belonged in part to genera which are nowadays restricted to the tropical zone and, in particular, to the Oriental region. At the present time, however, families such as the true-toads (Bufonidae), tree-frogs (Hylidae), true-frogs (Ranidae), geckos (Gekkonidae) and skinks (Scincidae), which in other regions are so rich in variety, are represented here by only a few forms. The chamaeleons (Chamaeleonidae), monitors (Varanidae), amphisbaenians (Amphisbaenidae), blind-snakes (Typhlopidae), boas (Boidae) and cobras (Elapidae) only just reach the Palaearctic on its southern edge. Terrestrial and fresh-water tortoises, with only five genera, are also scanty and crocodiles (with the exception of the Chinese Alligator *(Alligator sinensis)*, whose habitat can perhaps be still reckoned as Palaearctic) are completely absent. These are, however, all negative distinguishing features; amongst the positive characters of the Palaearctic Region, the urodele families Salamandridae and Hynobiidae may be mentioned as showing a rich variety of forms in the west and east respectively, as well as the few species of the giant-salamander group (Cryptobranchidae) and the olms (Proteidae); strangely enough, the lungless salamanders of the family Plethodontidae, which are so abundantly developed in the New World, are only represented by a single species in the Palaearctic. Of the Palaearctic Anura the Discoglossidae must be mentioned; amongst them are the Firebellied Toad and the Midwife Toad, and also the spadefoot-toad family (Pelobatidae); among reptiles there are the true-lizards (Lacertidae, with the almost exclusively palaearctic genera *Lacerta, Psammodromus, Ophisops, Acanthodactylus, Scapteira)*, a number of agamas (Agamidae), harmless-snakes (Colubridae) and, above all, vipers (Viperidae); the pit-vipers (Crotalidae) occur only in the east, more especially the south-east, of the region.

It is remarkable that in the temperate zone of the Palaearctic certain species exist which have spread over the whole vast area, i.e. they occur from the Atlantic coasts of Europe to the coasts of the Pacific and sometimes as far as Japan also. The European Common Toad *(Bufo bufo)*, the Common Frog *(Rana temporaria)*, the Agile Frog *(Rana dalmatina)*, the Edible Frog *(Rana esculenta)*, the Tree Frog *(Hyla arborea)*, the Common Lizard *(Lacerta vivipara)* and the Adder *(Vipera berus)* are examples of this. Other species, too, like the Sand Lizard *(Lacerta agilis)* and the Grass Snake *(Natrix natrix)* are widely distributed as far as Siberia. Yet their range is not always continuous, but is interrupted at many points. Various factors can be responsible for such discontinuity: in the aquatic Amphibia, for instance, drought can break up their original homogeneous environment into isolated areas; in the warmth-loving reptiles a cooling of the climate — probably caused by the Ice Ages — may likewise produce a similar discontinuity. The inhabited areas may be separated by very wide interspaces: thus, for example, the genus *Bombina* is distributed in Europe and Asia Minor on the one side and in eastern Asia on the other, but is completely absent from the vast area in between.

Similar habitat discontinuities also appear within the herpetofauna of Europe-western Asia; the Parsley Frog *(Pelodytes)*, belonging to the spadefoot-toads, occurs only in south-western Europe and the Caucasus; the Painted Toad *(Discoglossus)* exists only in south-western Europe and north-western Africa on the one side and in Israel on the other. The strange, limbless amphisbaenids of the genus *Blanus* live only in the Iberian Peninsula and north-west Africa in addition to western Asia, and are completely absent from the region in between. Yet the distribution of all these animals cannot have been discontinuous formerly. One has the impression that this phenomenon can be partly traced back to the cooling of the climate as a result of the Ice Age glaciation of Central Europe, but partly also to the associated climatic changes in North Africa: the wet Pluvial period with rich vegetation has now been succeeded by a far drier period less propitious for moisture-loving species. In consequence, many animals died out and many had to re-adapt themselves. A bush- or tree-dweller, like the chamaeleon, becomes a ground-dweller in the Sahara.

In contrast to that of the Palaearctic, the Nearctic or North American herpetofauna (which extends in the south to include the middle of Mexico, approximately) appears to be rich in variety of forms. This is shown especially by the urodeles and tortoises: although the family Salamandridae is only represented by two genera, North America is nevertheless the land of such highly diversified families as the Ambystomatidae (pl. 1) and Plethodontidae (pl. 2), the amphiumas (Amphiumidae), the sirens (Sirenidae), and the snappers and mud-turtles (Chelydridae, Kinosternidae). The freshwater-turtles (Emydidae) and the softshell-turtles (Trionychidae), too — but not the land-tortoises (Testudinidae) — are represented there by incomparably more forms than in the Palaearctic. In addition to *Alligator mississipiensis*, the genus *Crocodylus*, also, is present in the Nearctic though only at its extreme southerly edge. Toads (Bufonidae), tree-frogs (Hylidae) and true-frogs (Ranidae) show a greater variety of forms than in the Palaearctic; to these must be added the Ascaphidae and Pelobatidae and, in the south, the Leptodactylidae and Microhylidae. Amongst lizards, the exclusively Old World chamaeleons and monitors are absent, as well as the lacertids and agamids; the geckos and skinks, too, are not rich in species, the first-mentioned being even poorer than in the Palaearctic. By contrast, however, the anguids, the iguanas and teyou-lizards, the two latter apparently immigrants from South America, have developed a great variety of forms. Exclusively nearctic are the smaller families Anniellidae, Xantusiidae and Helodermatidae. The true-snakes (Colubridae) show a very large number of genera and species. Of the cobra-group, only the coral-snakes *(Micrurus, Micruroides)* are present. Whilst the true-vipers (Viperidae) are absent, the pit-vipers (Crotalidae), and especially the rattlesnakes, show a multiplicity of species. These herpetofaunal differences are so important that it does not appear justifiable to unite the Nearctic region with the Palaearctic as a single unit, the Holarctic, as sometimes happens, mainly on the evidence of the mammals.

In the Nearctic, as in the Palaearctic, some amphibians and reptiles have discontinuous distributions. Here, too, the influence of the Ice Age was of immense importance to the North American herpetofauna, since the glaciers reached as far south as 38°N. in a few places. The present northern limit of distribution of certain salamanders, lizards and snakes coincides with the limit of the ice sheet in former times. Following the retreat of the ice, steppe formation occurred, as it did in Europe, and this extended further eastwards than to-day. The eastern habitats of a few turtles *(Emys blandingii, Terrapene ornata)* have persisted until the present time as relics of the post-glacial steppes. On the continent of Europe, the alpine mountain chain stretching from east to west acted as a barrier to the northerly post-glacial extension of many warmth-loving animals; by contrast, in North America these creatures were able to spread northwards with much greater ease from their retreats during the glaciation. No doubt this accounts for the fact that the herpetofauna of North America is much richer in warmth-loving

Pl. II. Amongst the most impressive representatives of the frogs of North Queensland is the Giant Tree Frog *(Hyla infrafrenata)*, a huge creature attaining a length of nearly six inches. This gorgeous leaf-green animal can change its colour to deep olive-brown whilst the silvery white stripes along the lower lip and tibia may become copper-coloured. Its lymph is peculiar on account of its intense arsenic-green coloration. × 1. *Photograph by* Senckenberg Museum (Haupt).

forms, coming from the south, than is the Old World. Thus, species of warmth-loving lizards and turtles now occur surprisingly far to the north, both in the east and west.

The Ethiopian region, which adjoins the south-west of the Palaearctic, has no urodeles or tree-frogs (Hylidae) at all; instead, there are a number of caecilians (Gymnophiona) and narrow-mouth-toads (Microhylidae) which have an otherwise circum-tropical distribution. Especially noteworthy is the occurrence in Africa of the ancient clawed-toads, which belong to the family Pipidae that is otherwise distributed only in South America. In Africa there is an abundance of species of toads (Bufonidae) and true-frogs (Ranidae); in addition, the Rhacophoridae, which replace the tree-frogs ecologically, exhibit a rich variety of forms. The pond-tortoises (Emydidae) are absent, their counterparts being certain sideneck-turtles (Pelomedusidae). Land- and softshell-turtles, as well as crocodiles, likewise have their characteristic forms in Africa, especially the former. A lizard family endemic in the Ethiopian region is the Cordylidae (including the Gerrhosauridae). The geckos (Gekkonidae), chamaeleons, skinks and amphisbaenians (Amphisbaenidae) have numerous species; but, on the other hand, the agamas and monitors, which are undoubtedly immigrants from the east, are poor in genera or subgenera. Strangely enough, a few genera of true-lizards *(Lacerta, Algyroides, Eremias)*, which are typical of the Palaearctic, occur in the Ethiopian region. Amongst the snakes mention must be made of the blind-snakes (Typhlopidae) and thread-snakes (Leptotyphlopidae), as well as the boas (Boidae), the cobra-group (Elapidae) and the vipers (Viperidae); the colubrids are amazingly abundant, whilst the pit-vipers (Crotalidae) are absent.

Probably in no zoogeographical region does the contrast between forest- and steppe-fauna stand out so sharply as in the Ethiopian. A vast forest belt stretches from the equatorial west coast to the coastal regions of the east, and is bordered on the north, east and south by savannas and steppes; these project like peninsulas into the forested regions, especially in the south. The forest islands in East Africa, mainly restricted to the volcanic peaks, must at one time have formed part of the great equatorial forest belt, since their fauna agrees to a considerable extent with that of the West African forests. At the same time, relationships with the Oriental fauna can be discerned amongst the forest animals, relationships which are naturally also to be seen in the Ethiopian steppe-fauna. Thus there are forest-dwelling genera (e.g. the gecko *Cnemaspis* and snakes of the genus *Boiga)* which also live in the forests of southern Asia although their Ethiopian and Oriental environmental niches are widely separated from each other at the present day.

The large island of Madagascar is acknowledged to occupy a special zoogeographical position, and especially as regards its herpetofauna. This island is separated from the mainland by the Mozambique Channel which, though only 300 km. (186 miles) wide, is up to 3,000 metres 1,640 fathoms) deep. It is remarkable that several of the families previously mentioned as belonging to the African mainland are not found on the neighbouring Madagascar; there are no caecilans, no clawed-toads, and no true-toads, and, in addition, the true-frogs (especially the genus *Rana)* are scanty; among reptiles one seeks in vain for Malagasy representatives of the agamas (Agamidae), true-lizards (Lacertidae), monitors (Varanidae), amphisbaenians (Amphisbaenidae), and thread-snakes (Leptotyphlopidae); moreover, Madagascar is free from markedly venomous snakes, certainly from both the cobra-family (Elapidae) and the vipers (Viperidae, Crotalidae). On the other hand, Madagascar is the home of many bush-frogs (Rhacophoridae) and narrowmouth-toads (Microhylidae), geckos (Gekkonidae, col. pl. VI), chamaeleons (Chamaeleonidae), girdle-lizards (Cordylidae: Gerrhosaurinae), skinks (Scincidae) and snakes (Colubridae), that have many genera and species endemic there. One species only of crocodile *(Crocodylus niloticus*, pl. 34*)* is present and, amongst the tortoises, only a few land-tortoises and sideneck-turtles live there. But what gives the Madagascan herpetofauna its individuality are those well-known groups of animals whose centres of distribution to-day lie in South America.

Thus, among lizards, the iguanas (Iguanidae) are very characteristic of South America and the southern part of North America. Several species of this family, belonging to two genera, are, however, also native to Madagascar. They are so like their neotropical relatives that, not knowing whence they came, one would unhesitatingly declare them to be of South American origin! The Boa Constrictor of the tropical New World *(Boa constrictor)* has a near relative in Madagascar, and likewise the genus *Corallus*. Not a few amongst the colubrid snakes of Madagascar are so reminiscent of South American genera that their kinship can scarcely be doubted. There is, in Madagascar, a sideneck-turtle of the same genus *(Podocnemis)* which is widely distributed in the eastern parts of tropical South America. Amongst the amphibians of Madagascar connections with tropical America are not discernible, though they are clear in other groups of animals and even among plants: the Madagascan "Traveller's Tree" *(Ravenala madagascariensis)* has a counterpart *(Ravenala guayanensis)* in north-eastern South America, too! To explain this phenomenon, there is no escaping the hypothesis of an ancient connection of Madagascar with the Afro-Asian mainland which was also, in former times, colonised by organisms that are now neotropical.

If one visits the west of the Oriental region, say Pakistan, one is first of all most surprised at the faunal similarity with the north-east of the Ethiopian region; one sees the same genera of lizards (e.g. *Agama, Uromastyx, Acanthodactylus, Eremias)* and snakes (e.g. *Coluber, Psammophis, Naja)*. But one soon makes acquaintance also with characteristic elements of the Oriental fauna, the further one advances eastwards into southern Asia. Except for the absence of the pipids there are the same families of Anura as in Africa, to which are added the spadefoot-toads (Pelobatidae), which are otherwise distributed over the Holarctic. But the tortoise fauna of the Oriental region is totally different from that of tropical Africa. There, the true pond-tortoises (Emydidae) are completely absent; but they are represented in south and south-east Asia by no less than 18 genera — that is, twice as many as in North America, which is so rich in these creatures. The Oriental softshell-turtles (Trionychidae) abound in species, but the land-tortoises (Testudinidae) have fewer forms and the sideneck-turtles are completely absent at the present day. Among crocodiles the Gharial family (with a single species) is at present restricted to the Oriental region; of the true crocodiles the Mugger *(Crocodylus palustris)* shows close relationships with the Ethiopian Nile Crocodile; the rest, amongst them one genus *(Tomistoma)*, are endemic. Among lizards, very many geckos, agamas (including the well known flying-lizards of the genus *Draco)* and skinks are very characteristic of the Oriental region, as well as several monitors and, finally, the small but phylogenetically remarkable family, the Lanthanotidae. The small New World family Xenosauridae is represented by a genus in south-east Asia. On the other hand, the Ethiopian Cordylidae are absent and the chamaeleons, too, occur very sparsely only in the south-west of the region. The snakes of the Oriental region are worthy of note on account of the shield-tails (Uropeltidae), confined to the Indian subcontinent, and also on account of the ancient but species-poor families of rainbow-snakes (Xenopeltidae) and cylinder-snakes (Aniliidae), which are both otherwise peculiar to the Neotropical region (pl. 63). The thread-snakes (Leptotyphlopidae) live only in the north-west, whilst the blind-snakes (Typhlopidae) and the boas (Boidae) are widely distributed. The true-snakes (Colubridae) are also very abundant in species. Finally, the Oriental region is the only faunal kingdom in which are found all four of the groups of venomous snakes most dangerous to man; as well as the vipers (Viperidae) and pit-vipers (Crotalidae) there is also the cobra-group (Elapidae) and the sea-snakes (Hydrophidae) derived from it.

The Oriental region, where the steppe fauna predominates in the west and the forest fauna in the south and east, has no sharp line of demarcation from the Palaearctic. On the evidence of the herpetofauna, the western boundary would run from the Persian Gulf through Baluchistan and the Suleiman range; the northern boundary, however, would follow the southern edge of the Himalayas and then along the course of the Yangtse-kiang. But where is the eastern boundary of the Oriental region to be found, and where does the western boundary of the Notogaean or Australian region occur? There can be no doubt that the Greater Sunda islands, Sumatra, Java and Borneo, as well as the Philippines, have been colonised by an Oriental fauna that has spread over ancient land connections between the islands. But how is the fauna of Celebes and the Lesser Sunda islands to be assessed? It is well known that Wallace thought he had found a sharp line of demarcation between the Great Sunda islands Borneo and Celebes as well as between the Lesser Sunda islands Bali and Lombok: Borneo and Bali, with Java as the nearest island to the west, should on this basis be Oriental, but Celebes and Lombok, on the contrary,

Pl. 13. Brazilian " Smith " *(Hyla faber).* ×1. *Photograph by* Rosenberg.

Mud nest of a giant tree-frog, probably akin to *Hyla faber. Photograph by* de la Rüe.

Pl. 14. The giant tree-frog, *Hyla vasta*, of Haiti produces a dermal secretion which causes a burning sensation on the human skin. ×1. *Photograph by* W. Senfft.

Pl. 15. The Brazilian leaf-frog, *Phyllomedusa rohdei*, is a climber. It has gaily coloured orange flanks in life. ×1. *Photograph by* G. Senfft.

Central American leaf-frog *(Agalychnis moreletii)* active by night. ×1.2. *Photograph by* Senckenberg Museum (Haupt).

Sleeping during the day the Central American leaf-frog retracts its eyes inwards to their full extent. ×1. *Photograph by* Senckenberg Museum (Haupt).

Pl. 16. *Phyllomedusa burmeisteri*, like all leaf-frogs, has a vertical pupil which expands in the half-light. ×1.2. *Photograph by* W. Senfft.

Corythomantis brunoi belongs to the tree-frogs (Hylidae) and lives in the bromeliads of the shores near Rio de Janeiro. ×1. *Photograph by* W. Senfft.

Notogaean. On the whole this may prove correct for the avifauna; but one would draw the boundary differently for mammals since the marsupials, the typical animals of the Australian fauna, are certainly present on Celebes but not on Lombok. Amongst the reptiles and amphibians, markedly Notogaean forms are little in evidence in the area of the Lesser Sunda islands. None the less, various frogs here, the sideneck-turtles, several lizards, like the well-known monitor of Komodo (an island between Sumbawa and Flores) (pl. 54, 55), and snakes can be characterised as Notogaean. Even if a strict criterion favouring the Notogaean elements is applied, it is evident that the fundamental basis of the herpetofauna of Celebes is Oriental. And it is not very different on the islands of Lombok, Sumbawa, Flores and some others lying further to the east. The proportion of Oriental forms is always greater here than that of Notogaean. Of course, the more one goes eastwards the more it diminishes whilst the Australian ever more strongly claims recognition.

For amphibians and reptiles the Notogaean region first begins on the Moluccas and Timorlaut. Its most important evolutionary centre is situated on the Australian continent. New Guinea, with the island world of Melanesia and Micronesia, as well as New Caledonia, New Zealand and the extensive Polynesian archipelago belong to the Notogaean region in their herpetofaunas. Of course, it should be noted that the majority of the islands of Micronesia and Polynesia have no native reptile fauna but one that has travelled there passively; the amphibians reach their eastern limit on the Fiji Islands and so are absent from most of the islands of Oceania. The Australian fauna lives predominantly in open country, definite forest types being found mainly in the north-east of the continent, on New Guinea and a few islands.

The marsupials are well known as the most characteristic mammals of the Australian faunal region. Amongst the reptiles one would point to the snakeneck-turtles (Chelidae) and the cobra-group (Elapidae, pl. 70, col. pl. XIV) as the dominant forms of the Notogaean region. The first-mentioned, a special family of the sideneck-turtles, now lives elsewhere only in South America; the latter are distributed over all parts of the world, except Europe, but nowhere do they attain such a great multiplicity of forms as in Australia. About two-thirds of all the Australian snakes are numbered amongst the cobra-group; on the other hand, the vipers and pit-vipers are completely absent from Australia, reaching their eastern limit in the Indo-Australian transitional areas mentioned previously. The few remaining Australian snakes are assigned to the blind-snakes (Typhlopidae), boas (Boidae) and harmless-snakes (Colubridae). Sea-snakes (Hydrophidae) are common on the warmer coasts. In Australia the geckos (Gekkonidae), agamas (Agamidae), monitors (Varanidae) and, above all, the skinks (Scincidae) have developed a very great variety of forms; endemic in Australia are the small family of finfoot-lizards (Pygopodidae) and a crocodile *(Crocodylus johnsoni)*. In Australia the only prominent frogs are the tree-frogs (Hylidae) and the Leptodactylidae which are elsewhere so richly represented in tropical America. True-toads (Bufonidae) and the Afro-Asian Rhacophoridae are completely absent; the narrowmouth-toads (Microhylidae) and the true-frogs extend only as far as New Guinea or north-east Australia.

The Notogaean islands contain some very remarkable peculiarities in the field of herpetology: New Guinea, for example, has a phylogenetically important turtle *(Carettochelys insculpta)*, the most primitive form of the softshell-turtles; the Fiji and Tonga Islands have an iguana *(Brachylophus fasciatus)* which, like the iguanas of Madagascar, points to zoogeographical connections with the New World; New Zealand has the famous Tuatara *(Sphenodon punctatus*, pl. 36, col. pl. IX) which, as previously mentioned, is the sole surviving representative of an entire order of reptiles (Rhynchocephalia) and, in addition to this, a very primitive genus of frogs *(Leiopelma)* which is perhaps related to the North American tailed-frog *(Ascaphus)*.

This survey shows that in Australia there are animal groups that occur not only in the Oriental and Ethiopian regions — as, for example, the agamas and monitors — but in the neotropical or South American regions as well. Amongst these are numbered the Leptodactylidae among frogs and the snakeneck-turtles (Chelidae). The true tree-frogs (Hylidae), on account of the rich variety of their species, recall the New World. To explain these mutual interconnections, which have their counterpart in the marsupials, there was at one time a tendency to postulate an earlier distribution over an Antarctic, or at least south Pacific continent. But, following the finding of fossils in recent years, it has been proved that in the Cretaceous and lower Tertiary the marsupials were spread over the northern hemisphere (southern Asia, northern Africa, Europe), so that such an hypothesis is no longer essential. In our opinion the north Pacific Bering's bridge is capable of explaining the faunal interchange between the Old and New Worlds, and the southern hemisphere as well. The tree-frog family, which even to-day still occurs in the northern hemisphere, probably shows how in former times the distributional area of the snakeneck-turtles (Chelidae) and other animal groups was defined. Were the tree-frogs now to become extinct in the Palaearctic and Nearctic, the result would be the discontinuous distributional territory of the Leptodactylidae, which (like the marsupials) are so characteristic not only of the Notogaean but also of the Neotropical region. Whether the present distribution of the snakeneck-turtles (Chelidae) can be explained in the same way seems, however, to be doubtful, since fossil remains of these animals have not been found anywhere outside the areas in which they occur to-day.

South America, the Neotropical region, is also, like Australia, a kingdom in itself for the herpetological zoogeographer. The number of families of amphibians and reptiles that occur here is, however, far larger. Amongst the amphibians, caecilians (Gymnophiona) live here, as in the Ethiopian and Oriental regions. Salamanders (Plethodontidae), too, are not completely wanting, for they have reached South America along the cordilleras. The Surinam-toad family (Pipidae) is native here as in Africa, and the peculiar Brachycephalidae (col. pl. IV) are endemic in South America. As already mentioned, the true tree-frogs (Hylidae) and the Leptodactylidae are very richly developed, as are the true-toads (Bufonidae) and the narrowmouth-toads (Microhylidae); the true-frogs, however, only occur in the north of the region. As for the neotropical reptiles, the pond-tortoise family (Emydidae with only two genera) and the land-tortoises (Testudinidae, with only one genus) have receded; the mud-turtles (Kinosternidae), too, though so widely distributed in North America, play only a minor part in the neotropical kingdom, and softshell-turtles are absent altogether. South America is, therefore, the realm of the sideneck-turtles since here, and here only, their two families, the Pelomedusidae and Chelidae, occur side by side; the former is otherwise found only in the Ethiopian, and the latter in the Notogaean region. The Alligatoridae are richly developed but the true crocodiles (Crocodylidae) are only present in the north of the region. South America may be the true home of the iguanas (Iguanidae) and the teyou-lizards (Teiidae, pl. 56, col. pl. X) which have spread from here into North America, and the former as far as the Old World (Madagascar, Fiji and the Tonga Islands). Usually the lizards in South America are not developed to great diversity, as the neotropical geckos (Gekkonidae), skinks (Scincidae), slow-worms (Anguidae) and amphisbaenians (Amphisbaenidae) show. Amongst the snakes, the pit-vipers (Crotalidae) are especially noticeable on account of the wealth of their species though the rattlesnakes, so typical of the Nearctic, are extremely poor in number of forms. The representatives of the cobra-group are the coral-snakes (col. pl. XIII) — numerous species, but only two genera — whose singular coloration is copied by many harmless-snakes (Colubridae); these latter, moreover, are extremely rich in variety. Of the other groups of snakes in the Neotropical region, the blind-snakes (Typhlopidae), the thread-snakes (Leptotyphlopidae), the boas (Boidae) and the cylinder-snakes (Aniliidae) should be mentioned. The Andes form a very important faunal barrier in South America. West of the Andes, which are an insuperable obstacle for most species, the herpetofauna is incomparably poorer in species and many groups characteristic of the Neotropical region are completely absent.

Amongst the neotropical islands the Galapagos Archipelago must be given prominence since it exhibits a typical South American fauna, though this is partly modified in some respects; amphibians are completely lacking there. Most noteworthy of all are the giant Elephant Tortoise *(Testudo elephantopus*, pl. 28) and iguanas such as the Land Iguana *(Conolophus subcristatus)* and the celebrated Sea Iguana *(Amblyrhynchus cristatus*, pl. 49); all these creatures are absent from the mainland. The remaining reptiles (small iguanas, geckos and snakes) belong to genera that are widespread in South America. Whilst at one time the Galapagos archipelago was regarded as the remnant of a mainland mass formerly connected with South America, the tendency now is to consider it to be of oceanic origin; according to this theory, the terrestrial fauna would have found its way there accidentally by transportation over the sea. The fauna

Pl. III. A representative of the polymorphic and multi-coloured frog genus *Hyperolius* from tropical Africa. × 1.3. *Photograph by* Senckenberg Museum (Haupt).

A distinctive cloud-forest frog from Rancho Grande, Venezuela, *Atelopus cruciger*. × 1.3. *Photograph by* Senckenberg Museum (Haupt).

of the West Indies presents a similar problem; there can probably be no room for doubt that the Greater Antilles have been joined together, at least partially, and the same can be assumed regarding the Lesser Antilles. It is, however, questionable when a union with the mainland really existed. The herpetofauna of the Antilles is in the main Neotropical, even though there is also a whole series of endemic genera there, especially amongst the lizards and snakes.

In the north a Central American transition zone is interposed between the Neotropical and the Nearctic regions. Here, in addition to purely neotropical forms (such as, for instance, Giant Toads, Green Iguanas, Boa Constrictors) which live principally in the lowlands and along the hot coast, there are also some Central American endemics (e.g. Black Iguanas and basilisks). Nearctic genera and species, especially of amphibians and snakes, are associated with the others predominantly in the mountains. This motley assemblage of the Central American transition zone is understandable if one bears in mind the geological history of Central America. This indicates that, during the Tertiary, South America was cut off from the rest of America for a long time; there were straits connecting the Pacific and the Atlantic across Central America; to be precise, across the isthmus of Tehuantepec (southern Mexico), across the Nicaragua depression and across Panama. The present Central American land-bridge was therefore, for a time, broken up into single islands so that not only the South American, but also the Central American fauna was able to evolve completely independently.

If, in the course of the earth's history, parts of continents are submerged beneath the sea, the reptiles may be compelled to adopt first an amphibious and then a completely marine mode of life. In the distant past many reptilian stocks have changed over to life in the sea, and even at the present time there are marine reptiles. It seems that, in contrast to the amphibians, the transition from land to life in sea water is not very difficult for reptiles.

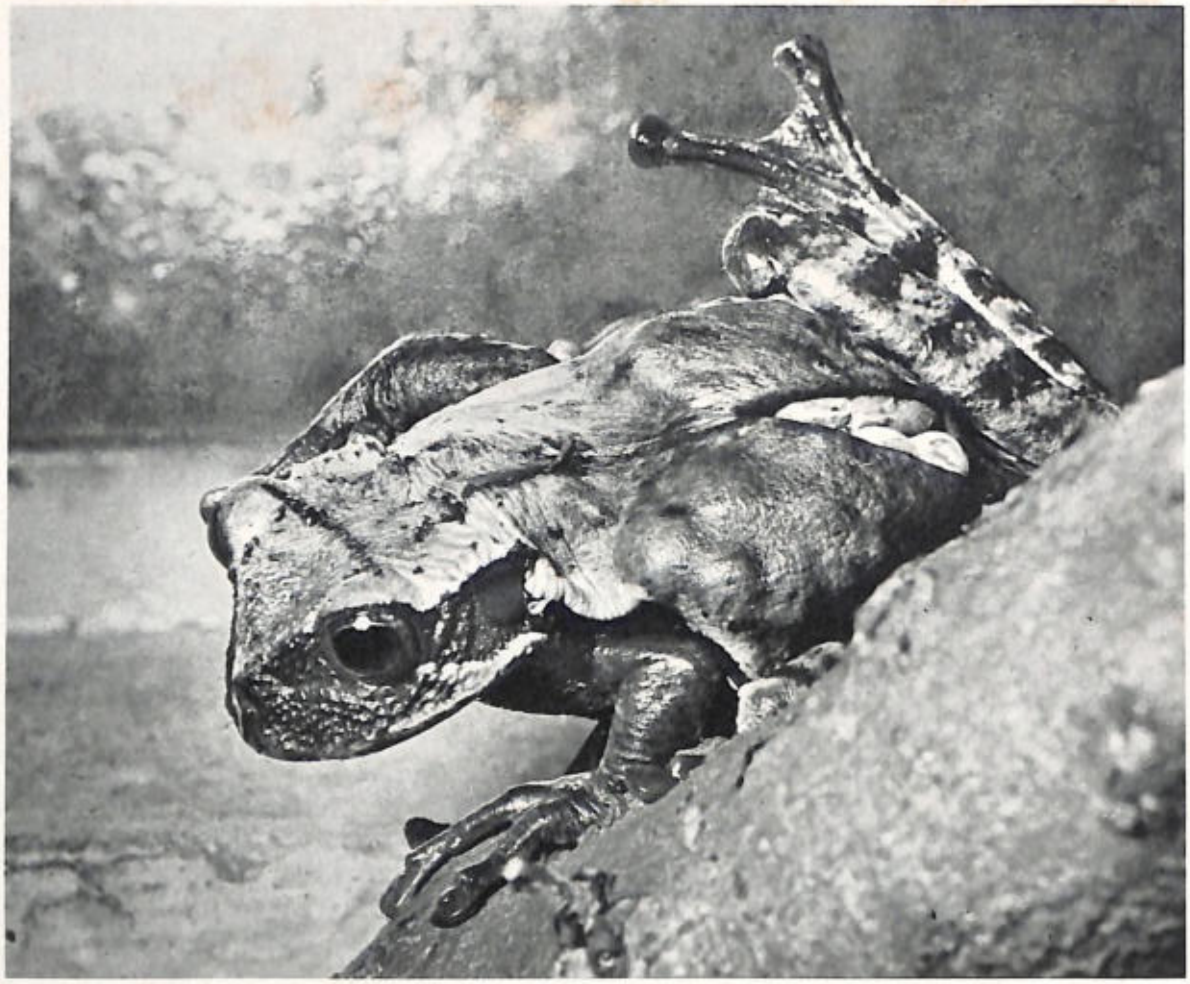
In a few instances it is clear that fresh water has formed an intermediate stage in the transition to a marine habitat. This applies to those reptiles that still live to-day in the brackish water of river mouths or in tidal lagoons, like certain opisthoglyphous and aglyphous snakes. Amongst the latter (the Acrochordidae) *Chersydrus granulatus*, the sole marine representative of the aglyphous snakes, very probably found its way into the sea from fresh water where its larger relative, *Acrochordus javanicus*, still lives to-day. Perhaps the same can be assumed in relation to the present-day marine turtles, of which there are only five species in so many genera *(Caretta, Lepidochelys, Chelonia, Eretmochelys, Dermochelys)*; these have been unable to achieve complete independence from the land since pregnant females must always return to it. There are, also, at the present time numbers of terrapins that have a preference for the brackish water of the tidal zone; examples are *Clemmys caspica* in south-east Europe, *Kinosternon bauri* and *Malaclemys terrapin* in North America, *Pelusios subniger* in West Africa, *Callagur borneoensis* in Sumatra, and *Carettochelys insculpta* in New Guinea. Finally, certain crocodilians are also more or less regular inhabitants of waters within the tidal zone. From this habitat many make incursions into the sea; in the Sunda Archipelago, as I was able to observe for myself, the Estuarine Crocodile *(Crocodylus porosus)* has become entirely marine in many places.

Nevertheless, migration into the marine environment need not always take place via fresh water; reptiles can make their way into the sea direct from the land. How the conquest of this environment, originally foreign to these creatures, is slowly accomplished can be clearly seen amongst the many originally purely terrestrial lizards that live on islands. On Malpelo Island, off the west coast of South America, there is a species of slow-worm *(Diploglossus hancocki)* which stays on the high-tide mark; its food consists of marine crustacea. In the Sunda Islands and in Queensland a few forms of skinks are known which have a similar mode of life; for example *Ablepharus boutonii burdeni* which, along with fishes of the genus *Periophthalmus* and crabs, lives on the rocky coast of the island of Padar. Another example is the Mangrove Lizard *(Emoia atrocostata)*, which can swim and dive in salt water; its food consists of crustaceans and it has been seen in pursuit of fishes in the limpid pools of the intertidal zone. Above all, however, the Sea Iguanas *(Amblyrhynchus cristatus*, pl. 49, col. pl. IX) of the Galapagos must be mentioned; for them marine plants have provided an entirely new source of food. A factor which produces an extension of habitat of this nature is apparently the restricted living space on islands, to which can be added, no doubt, an occasional food-shortage which must often make itself felt particularly with animals, like snakes. that prey on vertebrates.

It is not improbable, therefore, that the true sea-snakes (Hydrophidae, pl. 70), whose centre of distribution is the Sunda Archipelago, the greatest island region in the world, were formerly insular animals that made their way from the land to the sea direct, without a detour through inland waters. In contrast to the estuarine-snakes (Acrochordidae) previously mentioned, there are no genuine freshwater inhabitants amongst the hydrophids; virtually all avoid fresh water and they never penetrate far upstream in the rivers. Only the Indian *Hydrophis obscurus* is more commonly found in brackish water, and on the island of Luzon in the Philippines, *Hydrophis semperi* lives in the non-saline crater lake Taal, which is connected with the sea; there, however, this snake must be considered either as a marine relict or as a secondary immigrant from the sea. Of all the sea-snakes — there are some 50 species in 16 genera — only a single one, *Pelamydrus platurus*, has become truly oceanic; all the others are inhabitants of shallow water, preferring the close proximity of the coast.

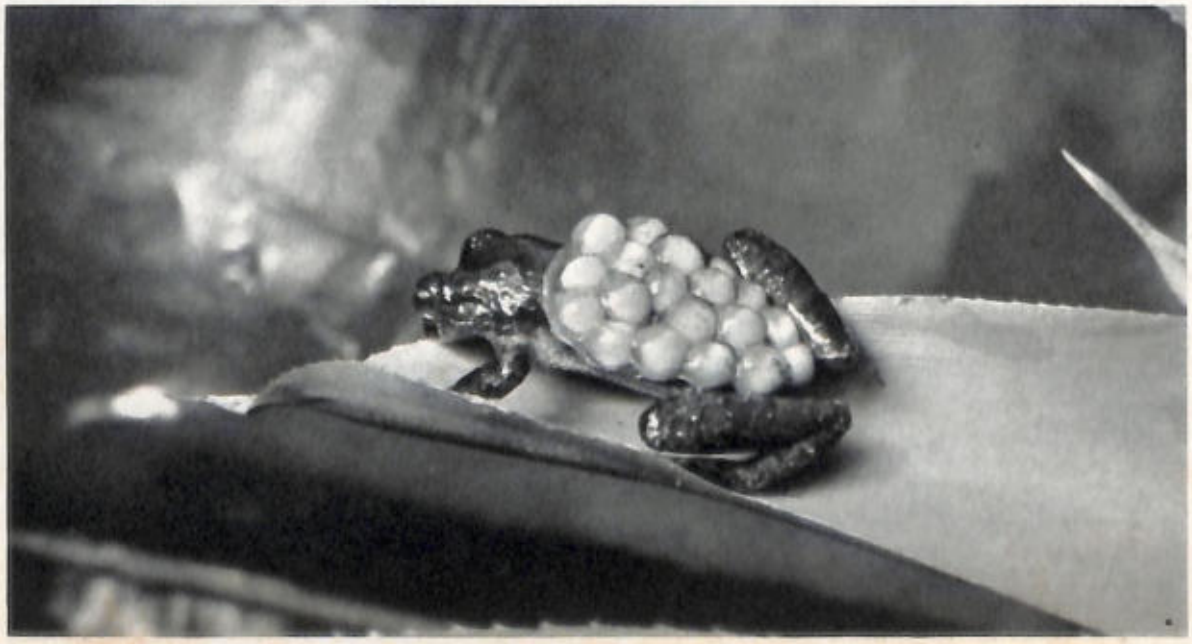
The distribution of marine reptiles is restricted to warm water. In the colder seas they appear only as chance visitors. Thus, indeed, various species of marine turtle enter the North Sea, but only very infrequently. A marine turtle that lives in the Gulf of Mexico *(Lepidochelys olivacea kempii)* arrives on the British coasts with the Gulf Stream now and then, and the curious Leathery Turtle *(Dermochelys coriacea)* is occasionally driven off course as far as Norway. Two distributional regions for marine reptiles can be differentiated, an Indo-Pacific and an Atlantic. Marine turtles, to be sure, are indigenous in both regions, but they occur, apparently, as different subspecies in each. But what distinguishes the two regions above all are the Squamata, for all the purely marine snakes, poisonous as well as non-poisonous, occur only in the Indo-Pacific region; the same applies also to the marine lizards (in the wider sense) that have been mentioned previously.

Pl. 17. Female marsupial-frog *(Gastrotheca ovifera)* from the cloud-forest of Rancho Grande, Venezuela. The folds of skin on the rump mark the opening of the brood pouch. ×1. *Photograph by* Senckenberg Museum (Haupt).



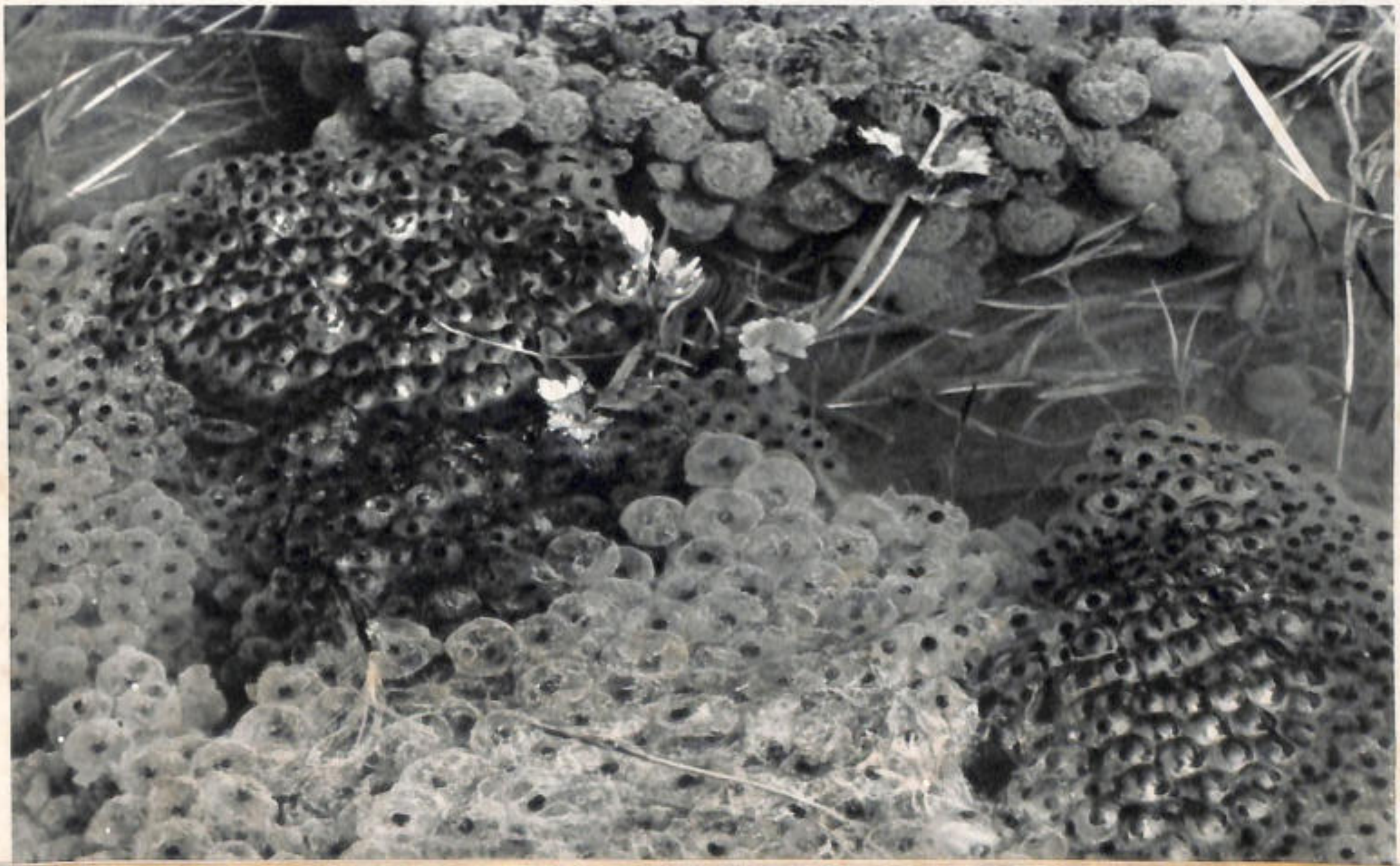
Pl. 18. The same marsupial-frog as in Plate 17, but with eggs in the brood pouch. ×1. *Photograph by* Senckenberg Museum (Haupt).

In this tree-frog, *Flectonotus goeldii*, the female carries her eggs exposed on her back. ×1.3. *Photograph by* Oeser.



Pl. 19. *Rana temporaria* is the most abundant frog of central and northern Europe. ×1. *Photograph by* Orth.

Spawn of *Rana temporaria*. ×1. *Photograph by* Roedle.



Pl. 20. European Edible Frog, *Rana esculenta*. In contrast with *Rana temporaria* this animal always lives, during the warmer parts of the year, in and about water. ×1. *Photograph by* G. Senfft.

CHAPTER THREE

BODILY FORM AND LOCOMOTION IN RELATION TO ENVIRONMENT

Amphibians and reptiles are as varied in their external appearance as in their differing potentialities for locomotion; form and movement indicate, in the clearest manner, relationships to the substratum or medium on, or in, which the animals live. Firm ground makes different demands from loose sand, a rocky wall from a tree-top, a stream from the open ocean. The variety of appearance is further increased by the fact that reptiles with or without well-developed limbs appear in every kind of environment; and even amphibians with vestigial limbs not infrequently occur side by side with those that are active runners and jumpers. It is instructive to compare the different bodily forms and methods of locomotion in the four different environmental regions: on firm ground, in loose soil, above the earth's surface and, finally, in water.

On the ground the four-legged, more or less long-tailed "salamander-type" is widespread, not only amongst urodeles but also amongst many reptiles; it is characteristic of the majority of lizards, of all crocodiles and of the Tuataras. The customary slow gait of these animals on land — and also of the differently constructed tortoises — is commonly known as walking, and the rapid progression as running or racing. In this process the body is often slightly raised so that it is supported on the limbs and often on the tail as well. The movement of the limbs proceeds in a definite sequence. After forward movement of a fore limb, the hind limb of the opposite side is moved forward, or vice versa. In slow walking the body is supported for a short time on three limbs (and the tail), but in running, when a fore and a hind limb are moved forward at the same time, only on two. The length of the tail in very swift-moving lizards is generally two to two and a half times as long as the head and body combined; if the tail is shorter than the rest of the body, as in many salamanders, some geckos and the gila-monsters *(Heloderma*, pl. 52), then in most instances the animals are fairly slow-moving. Excessive tail length, as in many south-eastern Asiatic lizards of the genera *Takydromus* and *Calotes*, where the tail can be four or five times as long as the head and body, tends towards a reduction in speed. In many lizards the speed is quite remarkable and may reach 24-28 km. (14.9-17.4 miles) per hour, as in *Cnemidophorus* (col. pl. X). This, however, can only be maintained for relatively short distances — in contrast to the mammals.

Many lizards, when running rapidly, are able to rise on to their hind limbs and to travel on these alone for a distance, the tail stretched out backwards acting as a counterpoise. This mode of locomotion is best known in many agamas, like the Australian Frilled Lizard *(Chlamydosaurus kingii*, pl. 44) and the Water Lizard *(Physignathus lesueuri)* as well as in some iguanas like the tropical American basilisk *(Basiliscus*, pl. 48) and others. Many of these lizards appear to be capable of this type of locomotion only if they have previously had an opportunity to attain a high speed on all four legs during which the quadrupedal running changes over to bipedal as a necessary concomitant of their much shortened fore limbs. Nevertheless, I have observed that, at least in *Basiliscus*, running on the hind limbs alone can follow immediately from a position of rest.

Many lizards are capable of leaping. In this case the body is thrust upward and forward by both hind limbs simultaneously so that the animal is air-borne for a short time. Sometimes this upward thrust is helped by the tail; in salamanders adept at jumping it plays the principal part in springing off the substratum. Admittedly, however, the leaping mode of progression, which is accomplished by the hind limbs whilst the fore limbs are only used in landing, is most widespread amongst the Anura, the frogs and toads. The most agile of these usually have a markedly acuminate head and, in spite of the long and enormously powerful hind limbs, a decidedly streamlined form. In addition to the Agile Frog *(Rana dalmatina)*, which can achieve jumps nearly 2 metres (6.6 feet) long and 1 metre (3.3 feet) high, the same genus contains many equally good, or even better, jumpers in other parts of the world. All good jumpers are universally small to medium-sized; very large frogs are relatively poor jumpers, as, for instance the Bull Frog *(Rana catesbeiana)* or Goliath Frog *(Rana goliath)*. In North America the tiny Cricket Frog *(Acris gryllus)*, a representative of the tree-frogs, is known as an outstanding jumper; its leaps amount to 36 times its own body-length (in the Bull Frog only 9 times). In contrast to these there are some frogs and toads that cannot jump; they can only crawl or walk.

Many salamanders and lizards whose locomotion is crawling or walking have, additionally, a serpentine movement of the whole body. This happens in animals of sturdy build with well-developed limbs as well as in slim, elongate ones where the limbs are small or completely absent, as in some lizards (pl. 59), snakes, salamanders and caecilians. In these cases the flexibility of the vertebral column is increased and makes possible, especially in the elongate snakes, the maximum degree of serpentine movement, i.e. horizontal undulations, which, by pressure against firm resistance to right and left of the snake, produce a forward creep. Even the smallest resistances that prevent the "slip" of the undulations are exploited by the snake so that the animal can glide forward extremely rapidly. It is obvious that, in general, short snakes must be slower than elongate species and, especially, long-tailed ones. *Coluber flagellum* is one of the swiftest snakes of the United States and attains a speed of 1.6 metres a second; normally it does not travel so fast and only covers 0.13 metres in a second. Some limbless lizards, too, like certain Australian finfoot-lizards (Pygopodidae) can be very swift, but the majority, like the European Slow Worm (pl. 51), are definitely inferior to snakes.

There are, however, snakes which do not progress by this method, or not entirely, but by a completely rectilinear creeping. This is the "caterpillar principle", in which single segments of the ventral scales slide forward, become anchored and draw the rest of the body after them in a straight line. This kind of locomotion can be observed in many boas and vipers but the elongated colubrine snakes are not adapted for it. Many caecilians appear to creep forward after the manner of earthworms but are able to change over to "snaking". A further method of locomotion in snakes is based on the concertina principle; the anterior part of the body is pushed forward by means of a horizontal loop until it has found a support and then the rest is drawn after it. Finally, mention must be made of "sidewinding", that is peculiar to some few vipers living exclusively on fine desert sand, like the Horned Viper *(Aspis*, pl. 74) and the Carpet Viper *(Echis)* in North Africa and western Asia, some dwarf puff-adders (e. g. *Bitis peringueyi*, pl. 75) in South Africa and the Horned Rattlesnake *(Crotalus cerastes*, pl. 79, 80) in California, known to the Americans as the Sidewinder. This locomotion is based on the principle of the laterally rolling spiral where the snake's body does not rest on the substratum over its whole length, but is in contact with it at only two points that shift from front to rear. In consequence the snake does not move straight ahead, i.e. not in the extension of its longitudinal axis, but sideways. Since sidewinding has for a prerequisite the absence of lateral resistance points, which is the case on fine desert sand, it can also be observed, exceptionally, in other kinds of snakes on a completely smooth substratum.

Pl. IV. *Brachycephalus ephippium*, a little frog characteristic of the rain-forest of central and southern Brazil. ↑× 2. *Photograph by* G. Senfft.
In spite of their scientific generic name, *Dendrobates*, these highly coloured little frogs are not tree-dwellers but live in herbaceous vegetation. The species, *Dendrobates pumilio*, figured here is called the Strawberry Frog on account of its colour. × 2. *Photograph by* G. Senfft.

Locomotion **under the earth's surface** is important not only to many amphibians but to many lizards and snakes. Amongst amphibians, most caecilians and some salamanders and frogs live underground. The latter usually have the practice of digging in by means of metatarsal tubercles which have evolved into sharp-edged shovels; with these they slowly shovel themselves in backwards and thus construct a longer or shorter burrow in the earth. This naturally collapses after a time. The best-known example of such a digging frog is the European Spadefoot Toad *(Pelobates fuscus)* of the family Pelobatidae. Other good burrowers are found amongst the families Bufonidae, Leptodactylidae, Microhylidae (pl. 22) and even the Ranidae. Characteristic of many of these subterranean animals is a strongly ossified skull which serves as a protection against the caving-in of masses of earth or sand. The Australian *Myobatrachus* may be contrasted with all these digging frogs, for it burrows forwards by means of its enormously strongly developed fore limbs rather than with its hind limbs.

Amongst lizards that burrow in earth or sand, or live there permanently, numerous adaptive modifications associated with this mode of life are developed. Thus, the head is often wedge-shaped with a very robust rostral shield which sometimes forms a horizontal (infrequently vertical) cutting edge. The eyes may degenerate or be provided with a transparent lower lid that may be completely fused with the upper. As a protection against sand grains, small projecting scales may appear on the edges of the eyelids comparable with the eyelashes of mammals. The external opening of the ear, too, may be protected by reduction in size or by the development of scales that overlap it, and the same applies to the nostrils. If the limbs are used for burrowing, the sides of the fingers and toes often have little scales developed as a kind of fringe to increase their digging capacity, a character that has arisen as a complete convergence in several sand-dwelling geckos, agamas, iguanas, lacertids and skinks. Completely unique, however, are the "sand-swimming webs" of *Palmatogecko rangei* (col. pl. VII), a delicate nocturnal lizard from the South-west African desert, in which the fingers and toes are connected by webbing; these serve simply as shovels and are of the highest importance to the animals burrowing in the fine desert sand.

In gliding forward through sand the limbs seldom function by their shovelling movements only. Even in short and stockily built sand-dwellers, like the well known Medicinal Skink *(Scincus scincus)* of the Sahara, aptly termed "poisson de sable" by the French, a snake-like movement of the whole body provides a very powerful additional thrust. This skink, with its streamlined form, is so completely adapted to swimming through sand that its capture with a naked hand is as difficult as that of a fast-swimming fish. The animal can dive into the sand as quick as lightning, as can many iguanas *(Uma)* and lacertids *(Aporosaura)* too, though their progress beneath the surface is surpassed by that of the skinks. Relatives of the Medicinal Skink in the deserts of Africa, Asia and Australia very commonly show a strong tendency towards degeneration of the limbs, whilst the whole body becomes more attenuated. In extreme instances the limbs disappear completely without any consequent impairment of the agility of the lizards which are entirely dependent upon serpentine motion; whoever has tried to capture such creatures by hand will confirm this. In no less than nine families of lizards does this degeneration of limbs occur; from the evolutionary standpoint genera such as *Chamaesaura*, *Tetradactylus*, *Chalcides*, *Sceloles* and *Rhodona* that show every transition from the pentadactyle to the di- or monodactyl condition, or even to the complete absence of limbs, are especially instructive. Usually degeneration affects the fore and hind limbs equally. If they do not keep pace it is the fore limbs in which degeneration is more marked. (Exceptions: *Chirotes* among the amphisbaenians and *Ophiognomon vermiformis* among the teyous.)

In lizards the degeneration of limbs does not invariably go hand in hand with subterranean life; it may appear in species living on the surface, as is shown, for instance, by the southern European Eyed Skink *(Chalcides chalcides)* and the Slow Worm *(Anguis fragilis)*. The legs degenerate particularly amongst those that live on surfaces clothed with dense vegetation where progress by serpentine movement of the body is easier than walking or running. Limbs are even more superfluous for locomotion in firm soil where, as a result, completely limbless lizards with eyes that are very degenerate or even absent, predominate, e.g. especially, amphisbaenians (Amphisbaenidae), blind- and thread-snakes (Typhlopidae, Leptotyphlopidae) and, among amphibians, the caecilians. In contrast to locomotion in sand or loose soil, serpentine movement is not possible in firm ground: here locomotion follows the principle of caterpillar- or earthworm-creeping with which, as in the case of the amphisbaenians, movement is possible either forward or backward. In addition, there is also "thrust creeping"; as a consequence of the animal — an amphisbaenian or snake — thrusting its hinder end against the ground the body is pushed forward. For this reason, in subterranean lizards, and especially snakes, one finds that tails are short and muscular, with their tips enlarged and studded with small tubercular or thorny scales; in many blind-snakes the tail terminating in a spine may have the same function. It is noteworthy that the inhabitants of narrow crevices, particularly in and under rocks and in tree-trunks as well, have an unusually heavily depressed, that is to say quite flattened, shape. This is manifest in nearly all crevice dwellers among the geckos, agamas, iguanas, night-lizards (Xantusiidae), lacertids and skinks. There is even an East African "Crevice Tortoise" *(Malacochersus tornieri)* that has a completely flattened, incompletely ossified carapace and which lives in shallow cavities under rocks.

The appearance of the inhabitants of environments **high above the earth's surface** is quite different; essentially different, too, is their method of locomotion. Amongst the tree-dwelling snakes, it is true, we again find the undulatory principle; the exceptionally long and slender, and sometimes laterally compressed tree-snakes, especially, are perfect masters of the art, for they can crawl forward among the branches with very great speed and dexterity. Generally their tail is not, or is but little, adapted for true prehension — i.e. for a firm grip on the branches; that is generally the case, however, in heavy, slow-moving forms such as certain tree-boas and tree-vipers. Arboreal lizards with a prehensile tail are also known; there are certain skinks (e. g. the giant *Corucia zebrata)*, a tree-monitor *(Varanus prasinus)*, a few slow-worms, agamas and iguanas as well as the majority of chamaeleons (col. pl. VIII).

In these remarkable, strongly laterally compressed creatures one can speak of definite "prehensile climbing". For not only is the tail an efficient prehensile organ but their feet also form completely prehensile pincers, which are formed in this way: two toes on each foot are enveloped in a common skin and are set in opposition to the other three which are also connected together externally. On the fore-foot the two outer oppose the three inner toes, on the hind-foot the three outer oppose the two inner. That chamaeleons can therefore climb only fairly slowly is understandable. This "prehensile climbing" is also indicated in a few other lizards, as, for instance, the South American iguanid genus *Polychrus* (pl. 47), where the 2-3 inner toes on the fore-foot can be opposed to the rest, whilst on the hind-foot the fifth toe is opposable. The best-known "prehensile climber" amongst the tree-frogs is the tropical American genus *Phyllomedusa* (pl. 15, 16), in which the inner finger and inner toe can be opposed to the other digits. These pretty tree-frogs climb easily and surely in the branches of bushes and trees during the darkness of the night.

On large vertical surfaces, such as rock cliffs or tree-trunks, claws are specially important to many lizards. Under these conditions they may have considerable curvature and needle-sharp points that can be driven into the bark. With their aid certain arboreal agamas *(Gonocephalus)* can cling so tightly that in catching these lizards it is easier to tear off their claws than to loose them from their hold. For the rest, many lizards can achieve exactly the same agility on vertical surfaces many metres above the surface as on level ground. Snakes, too, are able to display astonishing speed under these conditions, since they have the knack of exploiting the least projection, the slightest unevenness, as a point of support. In many climbing snakes (e.g. *Chrysopelea)* a well-marked angularity is developed along each side of the belly and tail and this helps in securing a grip.

Yet another adaptation for locomotion on tree-trunks is produced by the occurrence of thorny structures on the lower surface or on the sides of the tail. This part of the body then acts as an organ of support or resistance, and its anti-skid properties make it difficult for the animal to slip off. Thus, for example, the whole under-surface of the tail of the Saw-tailed Lizard *(Holaspis guentheri)* of equatorial Africa is covered with strongly keeled scales; the inner surfaces of the hind limbs as well, including the toes, and especially the sides of the tail, are nota-

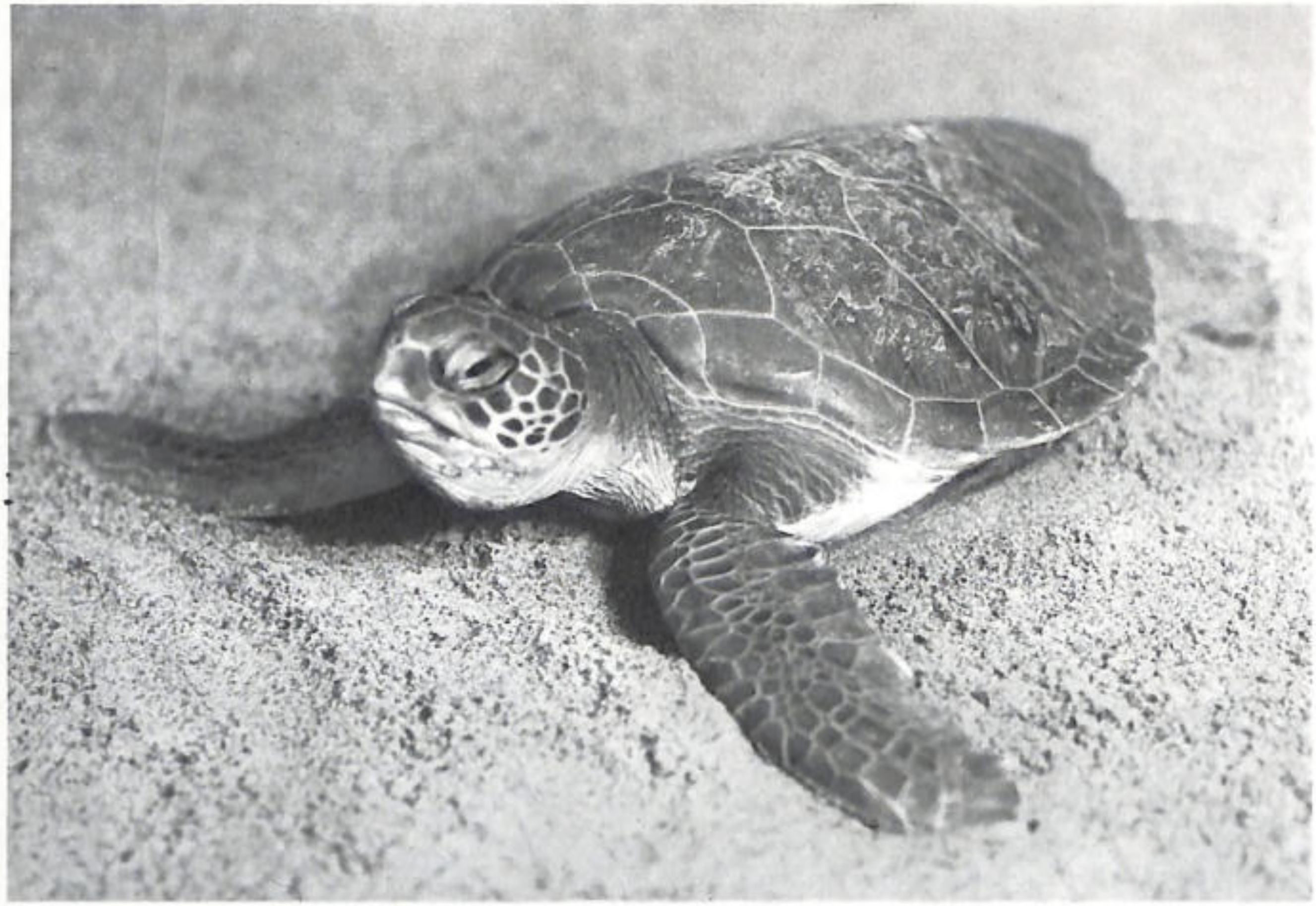
Pl. 21. When croaking, male Edible Frogs inflate two vocal sacs. × 0.5. *Photograph by* Roedle.

Pl. 22. The Javan Flying Frog, *Rhacophorus reinwardtii*, has extensive webbing between the fingers and toes. ×1. *Photograph by* W. Senfft.

The African bush-frog, *Leptopelis karissimbensis*, lays its eggs on land. ×1. *Photograph by* de Witte.

Pl. 23. *Hemisus marmoratus guineensis* is an inhabitant of tropical Africa which, when in danger, inflates itself enormously. ×1.5. *Photograph by* de Witte.

Glyphoglossus molossus is one of the most extraordinary representatives of the Microhylidae on account of the shape of its head. It lives in Siam where it is very abundant in places and is used for human consumption. ×1. *Photograph by* Senckenberg Museum (Haupt).



Pl. 24. Green Turtle *(Chelonia mydas)*. The marine turtle most sought after on account of its flesh. The shell of adults reaches more than 3 feet in length. *Photograph by* Rosenberg.

In young Leathery Turtles *(Dermochelys coriacea)* the length of the fin-like fore limbs is especially striking. Adults reach a length of nearly 7 feet. The juvenile is figured natural size. *Photograph by* Rosenberg.

bly denticulate. In the leaf-green Spiny-tailed Lizard *(Lacerta echinata)*, coming from the same habitat and environment, the scales on the anterior part of the tail are spiny, whilst in the Oriental flying-lizards *(Draco)*, thorny or strongly keeled scales are present on the under-surface of the root of the tail.

But if, on the other hand, adhesive discs occur beneath the fingers and toes, then the above-mentioned structures, even the claws, may be superfluous. In both lizards and frogs adhesive organs of this kind are to be found. They are very common in the latter and are not confined to the true tree-frogs (Hylidae); they are present in the externally very similar Rhacophorids, as well as in many species of true-frogs (Ranidae), the leptodactylids and brachycephalids; they are even found in some narrowmouth-toads (Microhylidae) in which group they may at times (e.g. *Platyhyla)* reach a very considerable size. In some toads *(Nectophryne*, pl. 10) that live in bushes, broad adhesive plates are developed on the under-sides of the hands and feet instead of adhesive discs. All these adhesive devices of the Anura function not only through the reduction of atmospheric pressure which may develop in the spaces between them and the substratum, but also through the extrusion of a glandular secretion which strengthens the adhesion. The whole of the under-surfaces of the limbs and belly also supplement the adhesive action of the suction discs, and small froglets, and even salamanders, that have no other adhesive devices, can readily stick to smooth leaves, bark or glass plates by this means.

The adhesive ability of a number of lizards distinguished by genuine suction lamellae is based on a quite different principle. These are most fully developed in the majority of geckos (pl. 38-40) where the claws may be degenerate. Homologous structures are present also in many iguanas *(Anolis* and relatives), skinks *(Aulacoplax)* and — apparently in the first incipient stages — in a few true-lizards (Lacertidae). Very fine, brush-like, little bristles are the real instruments of adhesion; they are seated on the adhesive lamellae on the under-surfaces of the fingers and toes in thick cushions and can be pressed against the minutest unevennesses of the substratum. The adhesive lamellae of many geckos are especially large and with them the animals are able to run about even on the under-side of completely smooth surfaces. A single toe of a gecko, with suction lamellae, can support a weight many times greater than that of the whole gecko. In some African geckos *(Lygodactylus, Diplodactylus)* similar adhesive lamellae have even been developed on the tip of the tail and, in the usual head-downward resting position, they undoubtedly make it possible for the feet to relax. The iguanid genus *Anolis*, which, in general, has feebler adhesive lamellae than the geckos, also, curiously enough, takes up a resting posture head downward for preference. An upside-down position on the substratum is usually avoided by all amphibians and reptiles, a sign that their sense of balance is exceptionally well developed; nevertheless, a position back downward on the under-side of leaves, branches, stones and the like is possible for a few lizards and tree-frogs.

As in mammals so amongst the amphibians and reptiles, there are a few species capable of parachute flight or even gliding flight. Thus, in some large New World tree-frogs of the genus *Hyla*, very well-developed natatory membranes between the fingers and toes can reduce the speed of descent after the animal has jumped off. This is the case to an even greater extent in some Indo-Malayan Flyng Frogs of the genus *Rhacophorus* (pl. 22), that are provided with enormous webs between the fingers and toes and occasionally with fringes of skin on the fore-arm, foot and the outer side of the fifth toe. Parachute jumpers of this kind amongst the reptiles are the Indo-Malayan Parachute Gecko *(Ptychozoon*, pl. 41) and the Malagasy Leaf-tailed Gecko *(Uroplatus*, col. pl. VI); they are much depressed, bark-coloured, nocturnal lizards with fringes of skin on the flanks, broad tails and webbing between the fingers and toes. In these arboreal animals the velocity of descent may be reduced to some extent by the cutaneous appendages.

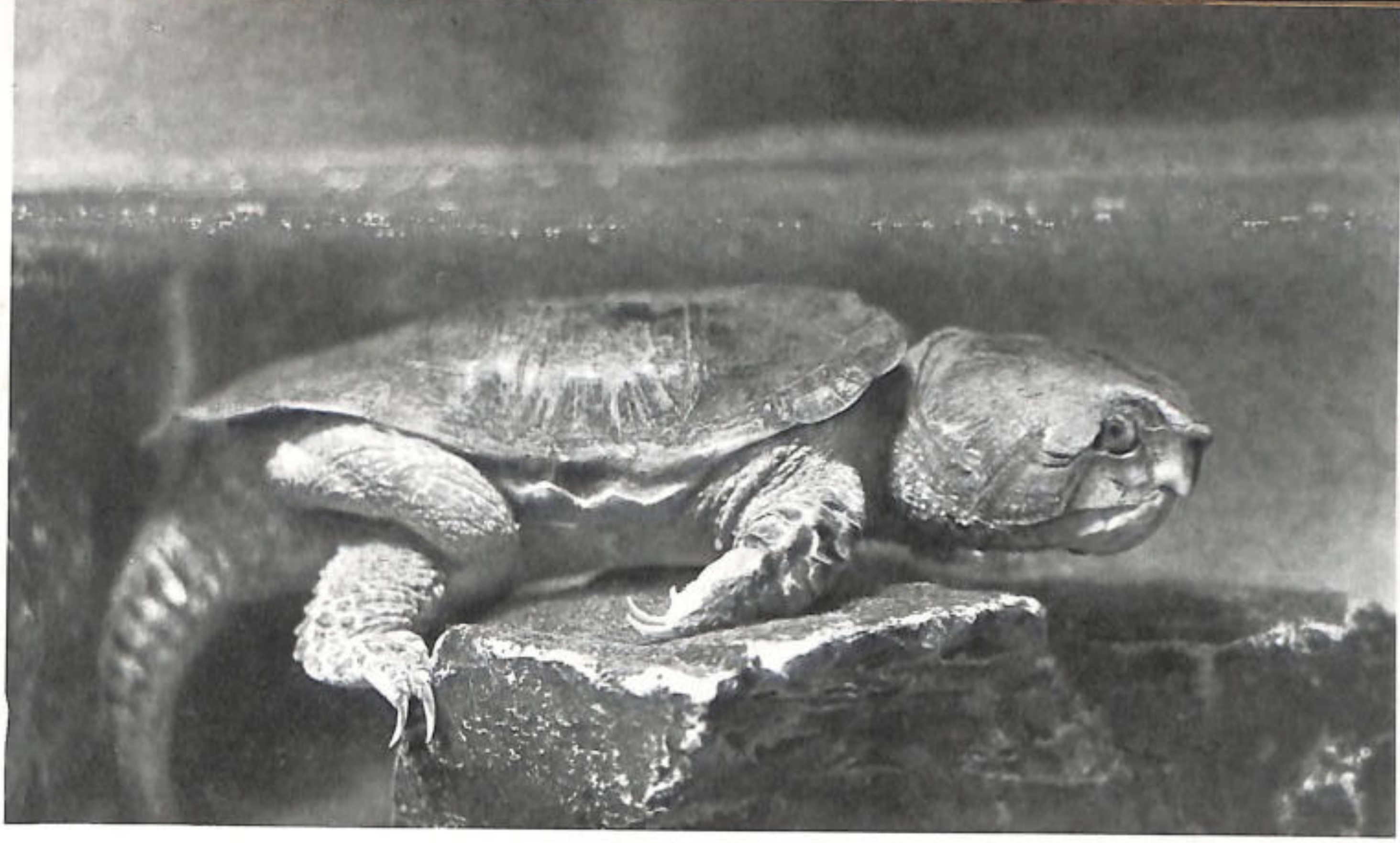
In contrast to these parachutists stand the gliders, of which, indeed, there is only a single agamid genus, the flying-lizards *(Draco);* about 15 species are distributed through the Indo-Oriental region. In these medium-sized animals (20 to barely 40 cm., 8-16 inches, long) true flying membranes are developed on each side of the body; these can be spread outwards and are supported by elongated ribs. Let us examine a flying-lizard at rest on a tree-trunk, though, indeed, like the Parachute Gecko and the Leaf-tailed Gecko, it is not easily found on account of its bark coloration. The flying-lizard usually becomes noticeable for the first time as the result of a slight nodding of the head and a spreading of the yellow gular sac. Suddenly it runs forward a short distance, leaps into the void and, spreading out its very strikingly coloured wing-membranes, floats away! The little creature lands again, with the greatest surefootedness, head upward on a nearby tree-trunk at a distance of 10-15 metres (33-49 feet), though the flight-path travelled has dropped to a slightly lower level. Certain tree-snakes *(Chrysopelea, Dendrelaphis)* stretch out the body, spread their ribs and draw in the belly as they jump from a high tree, but whether they should be considered as gliders, or better as parachutists, must be cleared up by further observations.

Now, what structural peculiarities do the water-dwelling amphibians and reptiles show and how is their locomotion **in water** brought about? Since all reptiles and the majority of amphibians are dependent on air-breathing, even when they live permanently in water, their lungs must be capacious, since they have a hydrostatic function to perform in addition to respiration. Furthermore, the nostrils must be so situated that on rising to the surface for breathing, they come into contact with the air with the greatest possible ease. They lie, therefore, at the extreme tip of the snout, or at least on its upper surface; this is best illustrated in the crocodiles in which the closely approximated nostrils open on a small prominence, or some water-tortoises (Matamata, softshell-turtles, pl. 31, 32) and even frogs (*Pipa*, pl. 3), which have a small proboscis-like projection for the two nostrils. Again, in markedly aquatic forms, the eyes lose their original position on the sides of the head and shift upwards, just as in many snakes that live in the domain of very fine desert sand. And like the sand reptiles, the water-dwellers have developed the most varied arrangements to protect the nose, ear, mouth cavity, and even the oesophagus, against the intrusion of water.

Now, as far as progression and the organs of locomotion in water are concerned, the forms not, or but little, adapted to life in water show the same locomotion as on land; many salamanders and tortoises progress along the bottom under water by walking or running just as they do in air; the creeping type of salamander, aquatic caecilians and many water-snakes creep on the mud or sand under water by undulations of the body exactly as in air. But in the animals which are free-swimming in the water and more markedly adapted for aquatic life, rowing appears as the most important kind of locomotion; and movement by rowing can be accomplished pre-eminently with the tail, with the fore limbs, with both fore and hind limbs or with the latter alone.

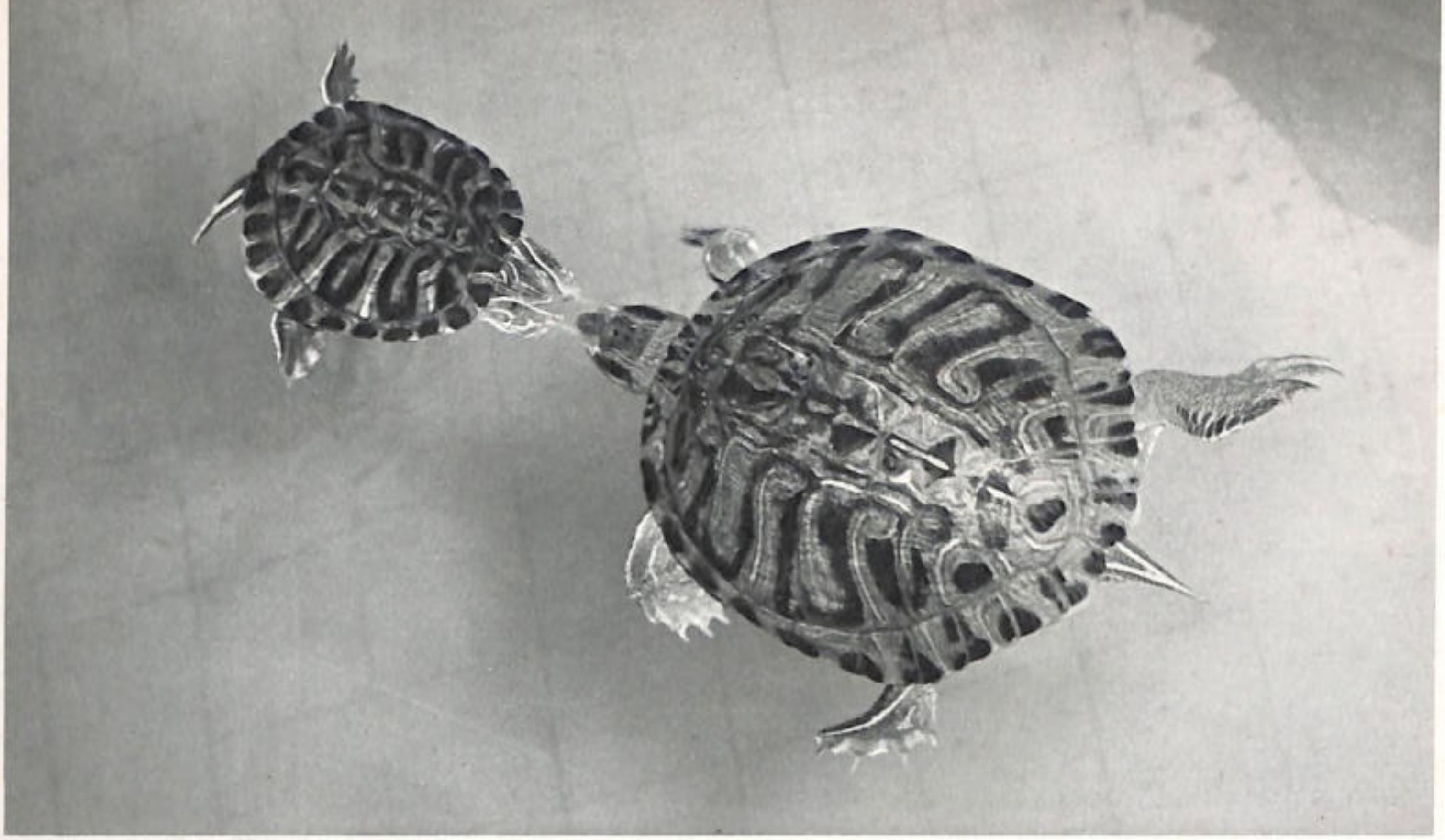
Rowing movement with the tail is essentially no more than a modification of the sinuous undulation so widespread on land. In fact, one can see that many elongate salamanders *(Amphiuma, Proteus, Siren)*, aquatic caecilians *(Typhlonectes)* and especially snakes, which are good swimmers, progress in water by undulations of the whole body. In the true sea-snakes (Hydrophidae) the end of the tail is strongly flattened from side to side and fin-like and thus substantially improved in efficiency for its function as an oar. In these sea-snakes as in other true water-snakes (e.g. Acrochordidae) the eyes and the nostrils are displaced right onto the top of the head; the nostrils, and also the narrow oral slot for the protrusion of the tongue, have arrangements for their closure. In swimming the hinder end of the body of these animals is generally bent downwards to make it easier for them to swim upward and reach the surface of the water in order to breathe. Some sea-snakes, at least, can swim as well backward as forward. The most important locomotory organ in aquatic lizards like the Galapagos Sea Iguana *(Amblyrhynchus cristatus)*, and some monitors *(Varanus)*, as well as in all crocodilians is, again, the tail paddle; when these reptiles are swimming the limbs are held against the body even though the hinder ones of crocodiles are equipped with swimming webs. In the European water-newts *(Triturus)* and in frog larvae the laterally compressed tail, usually provided with broad fringes of skin, forms a paddle and movement through the water is achieved by its action alone. To prevent their being swept away in the strong currents, many frog larvae that undergo their development in streams have large suckers on the under-side of the trunk or in the region of the mouth; these crop up convergently in different groups.

Limbs may serve as very effective paddles in lieu of the tail. This is especially the case



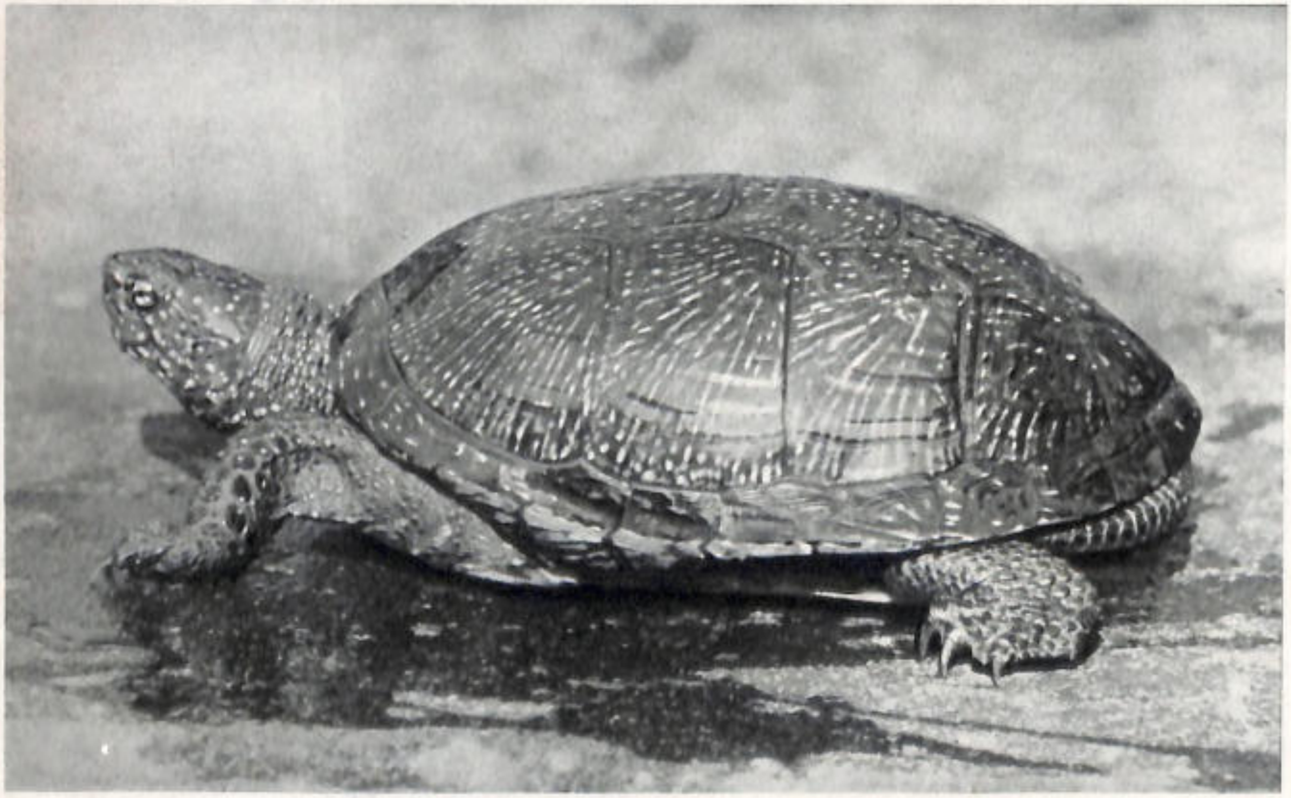
Pl. 25. The Large-headed Terrapin, *Platysternon megacephalum*, is a predatory inhabitant of the cool streams of south-east Asia ×0.5. *Photograph by* Uekerus.

The North American mud-turtles, like *Kinosternon subrubrum steindachneri* figured here, have knife-sharp jaws. ×2. *Photograph by* G. Senfft.



Pl. 26. North American Red-ear Turtles, *Pseudemys scripta elegans*, during courtship; male on the left. ×0.3. *Photograph by* Cagle.

The European Pond Tortoise, *Emys orbicularis*, has unfortunately become rare in Central Europe nowadays. ×0.6. *Photograph by* Senckenberg Museum (Haupt).



with the aquatic tortoises amongst which, as is well known, there are excellent swimmers. The fore limbs here play the most important part in progression. In the marine turtles in particular *(Chelonia* and related genera, *Dermochelys*, pl. 24), and in the New Guinea softshell-turtle (*Carettochelys insculpta)* they have become fin-like; the claws, rendered superfluous, are degenerate and are absent on the powerful flippers of the Leathery Turtle *(Dermochelys coriacea)* which is without doubt quite the fastest swimmer amongst the marine turtles. All the marine turtles are notable for the grace of their swimming; they glide along in the water like birds of prey in the air. The much shorter hind limbs, though generally equipped with well-developed webs, play a subordinate part as paddles; their participation cannot, however, be dispensed with, particularly for steering. The good swimmers amongst the water-tortoises have strongly depressed, disc-shaped shells; in the marine species — but also in a number of freshwater forms — certain parts of the bony armour have degenerated, apparently to reduce the specific gravity. The primitive bony armour of the Leathery Turtle, mentioned above, is almost completely degenerate and is replaced by small and lighter platelets of bone arranged like a mosaic. In contrast to these swimming virtuosos stand the heavy, more tectiform shells of the terrestrial types *(Sternotherus, Kachuga)*. The duration of submergence is very considerable and may amount to an hour and a half in crocodiles and about one hour in marine turtles.

As is well known, the Anura (i.e. frogs and toads) swim by means of their hind legs, which are longer and stronger than the fore limbs; as in jumping when on land, both hind limbs are thrust backward simultaneously and so drive the frog forward for a short distance. To increase the thrust for swimming, extensive webs occur between the toes in all the truly aquatic anurans of the most widely different families. The small, exclusively aquatic frogs of the genus *Hymenochirus* are exceptional in having short webs between the fingers as well; they are, indeed, moved like paddles when swimming, as they are in the related clawed-toads *(Xenopus)*. The Indian water-frogs, *Rana cyanophlyctis*, are so unbelievably agile that they are able, by a rapid succession of short leaps, to move for several yards on the surface-film of the water before they dive down.

Oddly enough, there are lizards which are equally able to run over the surface of water. Whoever has been in Central America knows the basilisk (pl. 48), especially *Basiliscus vittatus*, which has been mentioned on account of its bipedal running gait. If there is a stretch of water near a startled basilisk, it tends as a rule to make for it first of all. As soon as it has reached it, however, the lizard does not dive but runs for several yards further over the surface using only its hind limbs, and only then submerges beneath the water! This strange mode of locomotion is, apparently, possible for the basilisk, especially when the animal is small and light, because it has attained a high speed; the widely spread toes, provided with well-developed fringes of skin, prevent it from sinking for a few yards. Anolis-like iguanas *(Deiroptyx)* live in Cuba and these are similarly able to run over the surface of water without sinking.

CHAPTER FOUR

RELATIONS WITH THE INANIMATE WORLD

The amphibians and reptiles, like most animals, stand in a completely harmonious relationship with the world around them. This may be inanimate, and chiefly concerned with the medium and climatic factors, or animate, in so far as it represents supplies of food, enemies or social and sexual partners. Amongst the factors of the inanimate environment we have already discussed the substratum and water-habitat in relation to bodily form and the different types of locomotion. We now have to consider yet other relationships of the amphibians and reptiles to their inanimate world and especially to air, to water, to temperature and to light.

Air provides, for all reptiles and for most amphibians, the oxygen which is almost always essential for animal life and which is usually taken up by means of lungs. In amphibians, cutaneous and pharyngeal respiration play such an essential role that a number of terrestrial salamanders have been able to dispense completely with pulmonary, in favour of cutaneous, respiration. A few aquatic amphibians, in which gill-breathing may persist throughout life, are also dependent upon breathing through the skin. It is worth noticing that in a few tortoises that live permanently in water some villi in the pharyngeal region are profusely supplied with blood-vessels and can act as a supplementary respiratory organ; while in the sea-snakes (Hydrophidae) the mucous membranes of the mouth are so richly provided with blood-vessels that gaseous exchange could take place there. In these animals, generally, the whole skin is very rich in blood capillaries so that one could conceive of cutaneous respiration here as well. It is uncertain whether the capacious anal sacs of water-tortoises have a respiratory function.

Without **water** amphibians, even the toads which, with their thick, tough skin are best adapted to arid conditions, cannot long remain alive. Very few reptiles, likewise, can survive for a period of weeks without an intake of water which is obtained from their vegetable or animal food or directly by drinking. Although amphibians are so very dependent on water, they are, strange to say — with the probable exception of a few salamanders — unable to drink. To compensate for this their skin, and that of the lumbar region especially, is capable of absorbing water from the environment and also of releasing it again in times of drought. That is impossible for reptiles, or only possible to a limited extent, on account of their covering of horny scales; yet experiments on snakes have revealed that the water-loss of moisture-loving animals in dry surroundings is greater and more rapid than in species of an arid environment. Furthermore, it is surprising that in some lizards from extremely dry regions, such as the spiny Moloch *(Moloch horridus*, col. pl. VII, pl. 45) in Central Australia and the equally spiny girdle-lizards *(Cordylus giganteus)* in South Africa, the skin is hygroscopic.

To some extent reptiles pass through an "amphibian stage" during their development in the

Pl. V. The Speckled Terrapin, *Clemmys guttata*, is one of the most charming representatives of the rich tortoise fauna of North America. × 1. *Photograph by* Senckenberg Museum (Haupt).
The richly coloured Dura Terrapin, *Kachuga tecta*, lives in the region of the Indus. × 0.6. *Photograph by* Senckenberg Museum (Haupt).
In the event of danger the Box Turtle, *Terrapene carolina*, can close its carapace completely by means of the movable parts of its plastron. The male of the form most commonly found in the eastern United States is generally recognisable by its ruby-red iris. × 0.5. *Photograph by* Schmidt.

egg. The eggs of most reptiles with their parchment-like shell absorb, in contrast to birds'eggs, an appreciable volume of water from their surroundings and as a result their volume and weight are considerably increased; but on the other hand, they can also lose water easily and shrivel up. A Grass Snake's egg *(Natrix natrix)* through direct contact with water can increase its weight by about 22 % in the first three days. The increase in weight of *Lacerta* eggs during their development, by water uptake from their surroundings (and also from the air), is significant. The initial weight of the egg in relation to its weight during the last third of its development may be in the ration of 1: 2.9. The freshly hatched young is also markedly heavier than the egg when laid: in *Lacerta sicula* the ratio of the initial egg-weight to that of the freshly hatched animal is 1: 1.07—1: 1.32. Likewise in many tortoises and crocodiles, an uptake of water by the eggs during incubation has been established; in marine turtles it may be as much as 42 %. The hard-shelled eggs of geckos and land-tortoises are likely to be the most resistant to loss of moisture.

The effect of a warm spring- or summer-rain upon the emergence of some European amphibians from their hiding places, e.g. the Spotted Salamander *(Salamandra salamandra*, pl. 1), is well known. In the arid regions of the tropics the activity and breeding period of amphibians coincides with the onset of a rainy period even more than in our countries. There are arid savannahs, for instance in South Africa and in western and central Australia, where amphibian life needs to make itself inconspicuous the year round. When, however, sudden rainfall sets in the frogs appear out of the ground in swarms that are often unimaginable. Every collection of water, even the smallest pools, are then full of them and their voices sound from all around. The animals immediately proceed to pair, the tadpoles develop into young frogs with astounding speed and immediately the drought returns the whole world of frogs disappears for several months into holes in the ground and other hiding places. Water-tortoises and other reptiles in arid tropical regions show an equally high dependence on rainfall for their active life. But, in general, one is very surprised that a reptile fauna of very great variety can flourish in the kind of extremely arid region like, for example, the Namib with an annual rainfall of only 3 cm. (1.2 inches). Relative humidity is not so essential for the thermal regulation of reptiles as it is for amphibians, which can tolerate high air temperatures only in suitable humidity.

A few species living in arid regions store up water in fairly large amounts. The "water-reservoir" frogs *(Cyclorana)* that live in the driest areas of Australia are well known; the quantity of water they hold in their bladder, and especially in their tissues, is so large that the natives use them to quench their thirst. Many land-tortoises, for example the Californian *Gopherus polyphemus agassizii*, store up a great deal of water in the bladder; this may be derived from the vast amount of vegetable food they consume. Perhaps the fatty tissue in the tails of some lizards of the arid zones (e.g. *Heloderma*, geckos, skinks) also serves for water storage, since the cell membranes of fatty tissue can absorb and release water, and when fat is oxydised water is liberated.

Reptiles are far less sensitive to the salinity of water than amphibians, although the larvae of a few species are able to develop in brackish water. Some marine reptiles have "salt glands" in the orbital or nasal region to assist the kidneys in excreting excess salt. In addition to the distinctly marine reptiles, already mentioned several times, there is also a considerable number of lizards, snakes, tortoises and crocodiles that live in the tidal zone or in strongly brackish water. A peculiar phenomenon is that many lizards and snakes on soil with a high salt-content tend to be black in colour; examples are *Eryx miliaris* in the region north of the Caspian Sea, *Mabuya* in the coastal zone of South-west Africa and *Tropidurus* in Peru. The same phenomenon is often encountered also in reptiles on very small islands and on high mountains; but here it may well be associated with the conditions of temperature and light peculiar to this environment.

Of all the factors of the inanimate environment, **temperature** is the most decisive and significant in the life of amphibians and reptiles since, as exothermal organisms, they derive the heat vitally necessary to their existence from their surroundings. Consequently, their distribution over the globe is dependent upon the minimum seasonal temperature to a far greater extent than that of the warm-blooded (endothermal) birds and mammals. The activity of amphibians and reptiles is largely determined by the temperature of their surroundings, although their daily rhythm is not so strongly influenced by it as one would have expected. Nevertheless, as soon as the temperature falls below a certain level, motion ceases, they take no food and are incapable of reproduction. Reptiles or amphibians are completely incapable of any significant production of body heat. Incubating females of a few species of python furnish an exception, perhaps, since it has been established that they have a temperature a few degrees above that of their surroundings (see p. 162).

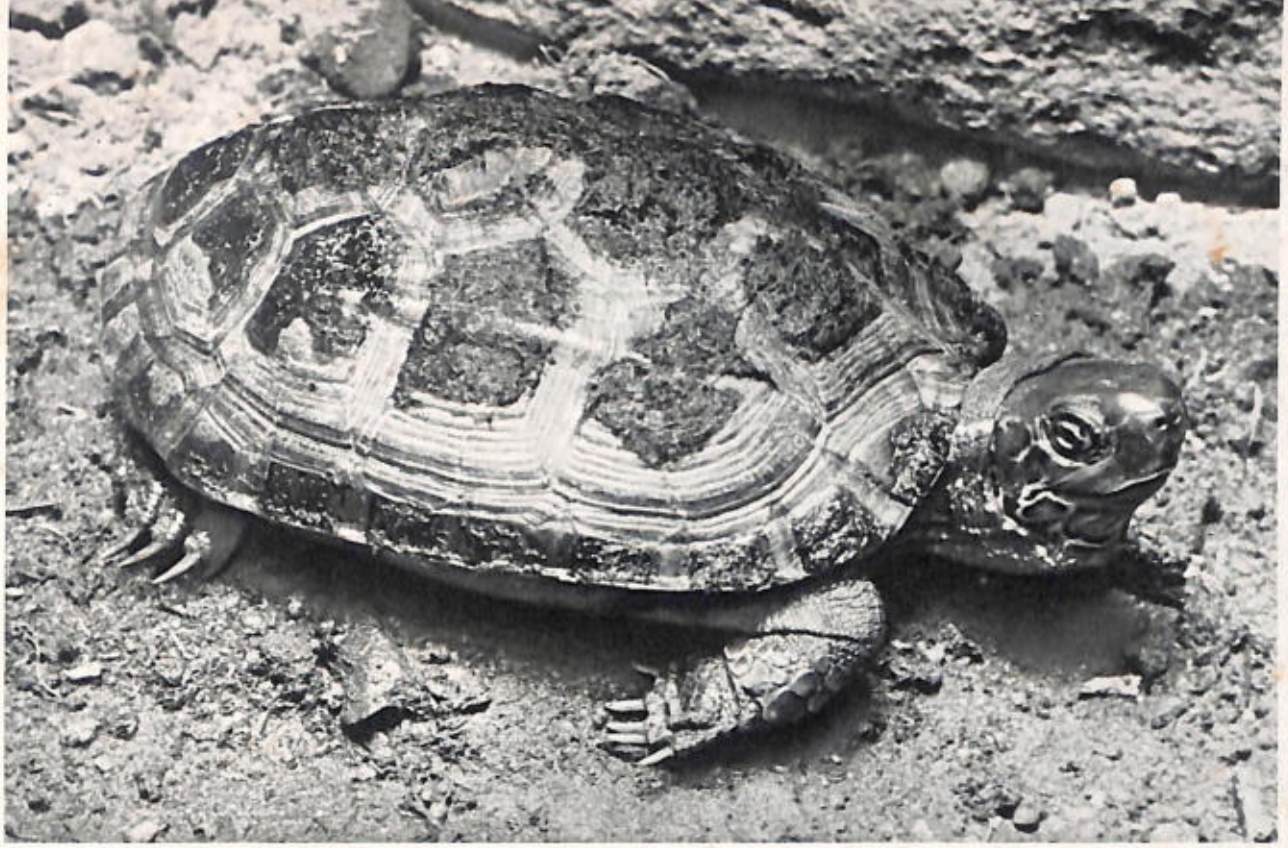
It was formerly assumed that amphibians and reptiles have a body temperature equal to that of the ambient air (or water). By and large, however, that is applicable only to the majority of amphibians and to nocturnal reptiles or those that live entirely in water. The temperature of the substratum is far more important than that of the air in relation to the body temperature of diurnal reptiles. A lizard resting on a flagstone warmed by the sun may have a body temperature of 35°-37° C. (95°-98.6° F.) even when the air temperature is only 12°-15° C. (53.6°-59° F.). Indeed, body temperatures of lizards have been precisely determined which were between 29°-31° C. (84°-87.8° F.) higher than that of the air. Accordingly, a reptile is capable of developing its full activity at an air temperature that would normally constrain it to complete immobility. In most diurnal reptiles the thermal sense, which directs them to a source of heat (thermotaxis), is very well developed. This exploitation of sources of heat consists either of exposing the body to the sun's rays or in seeking out a warm substratum in order to absorb heat by direct contact. In both cases many lizards have the habit of greatly flattening their body dorso-ventrally. The amphibians make far fewer demands on heat than the reptiles; nevertheless, species of frogs exist, such as the edible-frogs *(Rana esculenta, ridibunda;* pl. 20, 21), which seek out the sun's rays to bask and, in the damp tropics, there are great numbers of frogs which may be described as thoroughly thermophile. Frog larvae have been found in thermal springs of + 40° C. (104° F.).

In central European amphibians the preferred temperatures, i.e. the degree of warmth which the animals seek in their surroundings as the optimum for a certain period, lie around 21° C. (69.8° F.) according to the latest measurements. The preferred temperature of the Slow Worm *(Anguis fragilis*, pl. 51) has been ascertained to be about 28° C. (82.4° F.); for the remaining lizards the values lie around 33° C. (91.4° F.). These preferred temperatures need not be identical with the animals' normal activity temperatures.

In the Californian reptiles, activity temperatures vary between 15° (59° F.) and 42° C. (107.6° F.), the latter lying quite close to the lethal maximum for many species. The activity temperatures in nocturnal lizards and in snakes are lower than in diurnal lizards. For the latter the average value has been ascertained as 37.3° C. (99.1° F.), for snakes only 31.1° C. (88° F.) and for a nocturnal lizard occurring in the same region only 24.4° C. (76° F.). A skink *(Eumeces fasciatus)* living in the eastern United States has an optimum body temperature of 34° C. (93.2° F.), but its activity is scarcely affected by temperatures several degrees lower, since pairing can still take place at 21° C. (69.8° F.) and feeding at 16° C. (60.8° F.); at 10° C. (50° F.), however, normal movement is no longer possible. The study of a Californian iguana, *Sceloporus magister*, shows, furthermore, how very far apart the temperature limits for the different vital activities can lie; this little animal normally takes food at a body temperature of about 30° C. (86° F.), but excretion was most frequently observed at 37°-38° C. (98.6°-100.4° F.).

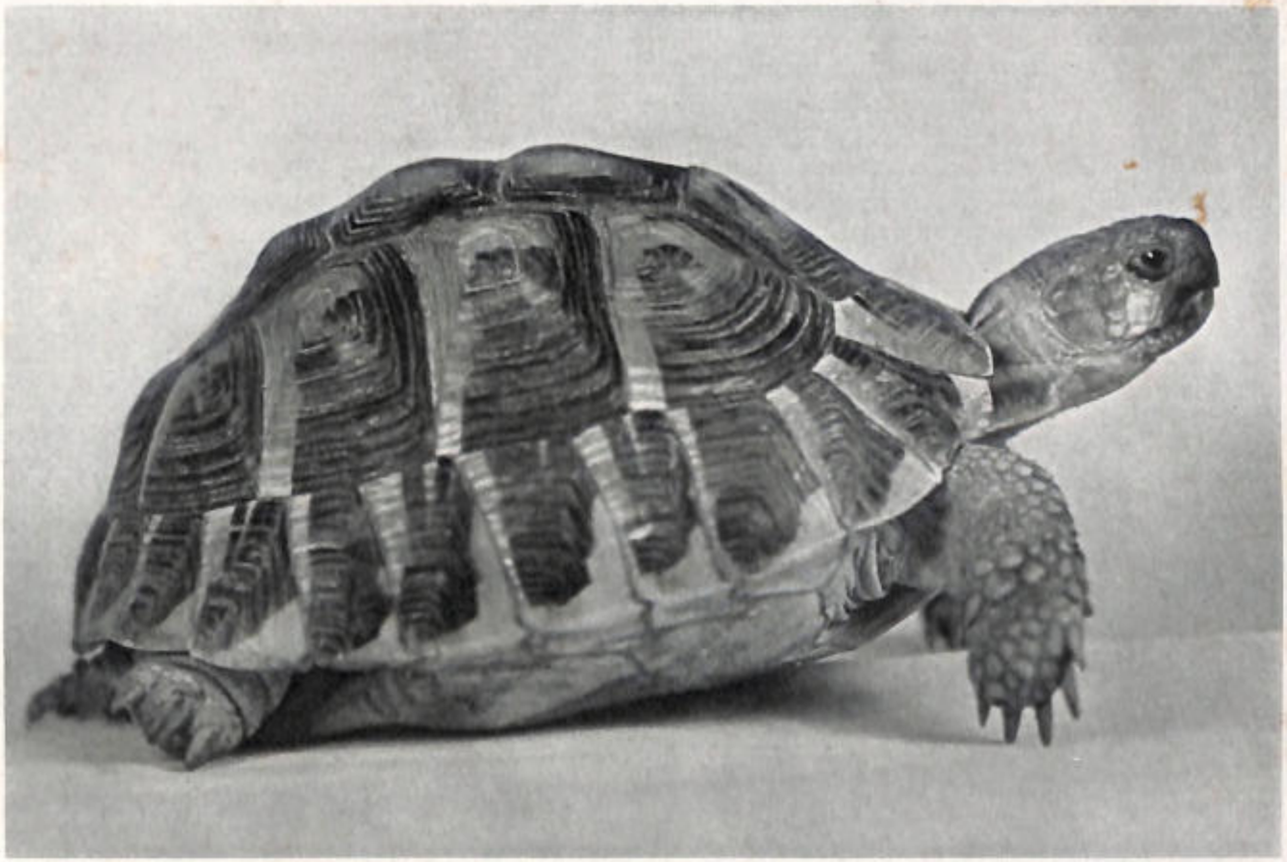
An unusually high preferred temperature, somewhat over 45°C. (113° F.), has been ascertained for the Starred Lizard *(Agama stellio)*. That is most astonishing since it is very near the upper limit that reptiles can directly withstand, namely 47.7° C. (117.9° F.). None the less, it must be emphasised that in Californian iguanas *(Sauromalus obesus)* body temperatures of 42.2° C. (109-8° F.) and even, for *Dipsosaurus dorsalis* — probably only exceptionally — 47.2° C. (117° F.) have been measured. Prolonged exposure to very high temperatures can induce sterility; this has been ascertained in certain lizards *(Xantusia)*.

In contrast to these lizards, the activity temperatures of other reptiles are lower. Thus the normal body temperature of the Greek Tortoise *(Testudo hermanni*, pl. 27) during activity varies between 16° and 32° C. (60.8° and 89.6° F.); at 34° (93.2° F.) the tortoise seeks refuge in the shade and when the cloacal temperature is 35°-36° C. (95°-96.8° F.) in the sun the critical maximum is reached. Crocodiles, too, seem to be sensitive to great heat; if they are placed in the mid-



Pl. 27. In the Chinese Terrapin, *Chinemys reevesii*, algae have settled on the dorsal shell, but curiously enough they do not encroach on the " annual rings ". ×1. *Photograph by* Senckenberg Museum (Haupt).

The western Mediterranean subspecies of the Greek Tortoise, *Testudo hermanni robertmertensi*, has a light spot beneath the eye and a higher carapace than the eastern race. ×1. *Photograph by* Wermuth.



Pl. 28. Elephant Tortoise, *Testudo elephantopus*, in its natural habitat on the Galapagos Islands. ×0.1. *Photograph by* Eibl-Eibesfeldt.

day sun without water they die within an astonishingly short time. Of all reptiles, however, the celebrated Tuatara *(Sphenodon punctatus*, col. pl. IX, pl. 36) is least in need of warmth; its optimum temperature, about 12°-18° C. (53.6°-64.4° F.), is lower than that of any other reptile! On Stephen Island, near New Zealand, the following values were obtained on the basis of numerous measurements: in April, at an air temperature of 9.4°-14.0° C. (48.9°-57.2° F.) (average 12.2° C., 54° F.), the body temperature was from 6.2°-12.2° C. (43°-54° F.) (average 11° C., 51.8° F.); and in November, when the Tuatara displayed full activity in an air temperature of 8.8°-13.7° C. (47.9°-50.7° F.) (average 11.4° C., 52.5° F.), the body temperature was only 7.6°-13.3° C. (45.7°-55.9° F.) (average 10.6° C., 51.1° F.)! Within the two classes of vertebrates such low temperatures are otherwise found in frogs *(Batrachophrynus, Telmatobius)* which live permanently in cold water (about + 10° C., + 50° F.) in the high Andes, or in the Tailed Frog *(Ascaphus truei)* living in the high mountains of north-west America, or in cave-salamanders, such as the Olm *(Proteus anguinus)*. Amongst the amphibians, very many salamanders are, in general, noted for the fact that they prosper best in cold air, i.e. below 20° C. (68° F.).

How, then, is thermal regulation effected in the amphibians and reptiles? It scarcely exists amongst the former, especially the salamanders, although the evaporation of water through the skin is a means for reducing too high a body temperature. The reptiles, on account of their horny body-covering, are incapable of doing this, or can only do it to a very slight degree. Yet crocodiles can be observed in times of great heat lying on the bank always with open mouth; in this case the mouth cavity is the place where evaporation takes place and this produces a cooling effect. Many lizards, too, behave in the same way when it is hot, as may be readily observed in the terrarium. Similar behaviour was proved to occur in tuataras kept at too high a temperature.

In addition, mention must be made of colour change aiding thermal regulation. It has been observed that many lizards capable of physiological colour change (geckos, agamas, chamaeleons, anoles) assume a quite dark colour — in many species almost black — in the sun in the morning when it is still cool, to turn to account the invisible radiation. Since dark colours have a stronger receptivity for radiant heat than light ones, the animal's coat colour raises the body temperature much more quickly. But if the temperature rises so that it becomes too hot for the animal — for the Mastigure *(Uromastyx)* an air temperature of 41° C. (105.8° F.) is critical — the dark colour suddenly changes to a quite light one, in many lizards pale yellow; in this way heating beyond the optimum is avoided. It is of interest that similar thermo-regulation by colour change has been observed in snakes also. Observations on the European Tree Frog and on a few tropical bush-frogs that can be almost white in colour in the scorching sun, show that many frogs also behave in the same way.

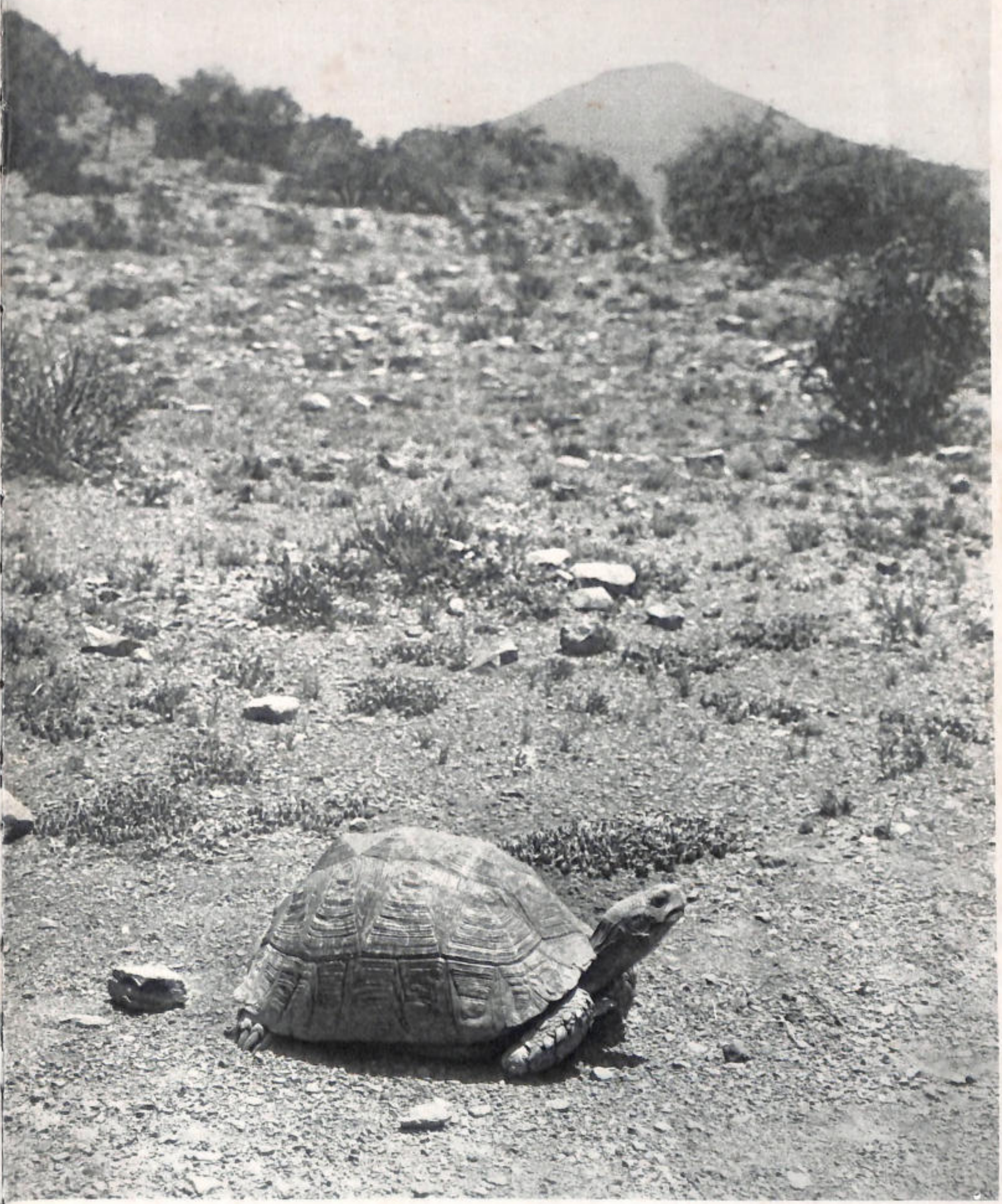
This heat-regulation by colour change is especially important for those creatures that are unable to escape the heat by making quickly for deep hiding places. The periodic searching-out of warm, sunny spots and shady haunts is a very important expedient for heat control amongst diurnal reptiles. In this simple way the species of *Lacerta* in Europe normally guard against wide fluctuations of body temperature during their periods of activity. By alternating between exposure to the sun's rays or concealment of parts of its body in a cavity, the Californian Sidewinder *(Crotalus cerastes*, pl. 80) can maintain its body temperature at a fairly constant optimum level, that is to say from 31° to 32° C. (87.8°-89.6° F.). Observations on another small sand-snake *(Chionactis)* have shown that it constantly discriminates between the different layers beneath the sun-warmed upper surface of the sand in favour of the temperature near its own optimum; it is indeed substantially cooler at a depth of 25 cm. (9.8 inches) than at about 5 cm. (2 inches). Essentially similar behaviour is also shown by sand-dwelling lizards in the most diverse regions. If captive reptiles in an overheated terrarium have no cooler hiding place, even large species that prefer arid conditions, such as the Gila Monster *(Heloderma suspectum*, pl. 52) or the Desert Monitor *(Varanus griseus)* betake themselves into the water basin. That is clearly the reason why the earlier curators, who mistakenly kept the Tuatara much too warm, so often found it in the water. According to the latest research on lizards, the pineal eye plays an important part in temperature control: it prevents the lizard from exposing its body to the sun's rays too much.

It is easy to understand that young animals, and small individuals of the same species in general, not only get warm more easily than large ones, but also lose their heat much more quickly when cooling down. That explains why young lizards often emerge from hibernation in early spring sooner than old animals; in the spring sunshine they reach their activity level much more quickly than the old ones, which become sufficiently active to capture their prey only late in the day. This is, perhaps, one of the reasons why gigantism in reptiles does not occur in temperate regions; after cool nights large animals warm up much too slowly for them to put all their vital functions to work. Added to this is the recurrent annual break of several months' duration which the winter brings with it, and which forces all cold-blooded animals into a resting stage. Very large reptiles, like crocodiles, pythons and giant lizards, can thus only prosper in regions with a uniformly warm climate, i.e. in the range of the tropical belt. Bergman's rule, which is generally applicable to homoiothermic vertebrates, can therefore have scarcely any validity for amphibians and none for reptiles. On the contrary, one observes that with an increasingly cooler climate (and this depends on both latitude and altitude) there is, in many species, not only a reduction in total size but also a slight shortening of the limbs and tail; according to Allen's rule, loss of heat is thereby made more difficult. Perhaps these correlations are due to the direct influence of temperature since, for example, an increase in the number of vertebrae and rows of scales in some lizards *(Aprasia)* and snakes *(Thamnophis)* may be occasioned by the heat of summer during their embryonic development. Likewise, it has been established that temperature has a decisive influence upon the form of the regenerated tail of lizards; the Moorish Gecko *(Tarentola mauritanica*, pl. 37), as is well known, can regenerate a tail that has been broken off; at a lower temperature (+ 28°C., + 82° F.) the tail grows to a shorter stump than at a higher temperature (+ 35°C., + 95° F.) and is covered with large, overlapping, keeled scales; at the higher temperature not only is the regenerated part longer, but it is also covered with small, juxtaposed, smooth scales.

In these circumstances it is to be expected that temperature must influence the development of amphibians and reptiles in yet other ways. And so it is indeed: the reproduction of these animals is, in most cases, by the laying of eggs, but there are also species in which the young are born alive, or leave the egg-shells during, or shortly after, laying (ovoviviparity). Such ovoviviparous species are, more particularly, common inhabitants of the cool regions of the north or south temperate zones or of high mountains. Almost half the central European reptiles are ovoviviparous *(Anguis fragilis, Lacerta vivipara, Coronella austriaca*, the species of *Vipera)*. Further examples of this phenomenon are the two European species of *Salamandra*, several chamaeleons in East and South Africa, a sand-agama *(Phrynocephalus)* in central Asia, the New Zealand geckos, and, in the high mountains of the New World, some iguanas and salamanders. Nevertheless, ovoviviparity is not limited to cool regions exclusively, but can also appear as a family character; for instance, most Boidae, Crotalidae, Cordylidae, Xantusiidae and a major portion of the Scincidae bear living young. The only examples of ovoviviparous frogs are small African toads of the genus *Nectophrynoides*. Ovoviviparous caecilians *(Typhlonectes)* are also known.

For species that live in cool regions and bear living young the advantage of ovoviviparity is clear. Since the pregnant female actively seeks out sources of warmth, the eggs will, under climatically unfavourable conditions, be "brooded out" with greater speed and safety than if they were laid in holes in the ground, or similar hiding places, and left to their fate. Furthermore, ovoviviparity is by no means always determined by heredity, but is directly dependent upon temperature or climate: the Common Lizard *(Lacerta vivipara)*, a species that bears living young, as its scientific name indicates, is an egg-layer in the Iberian Peninsula, i.e. in the south. In the farthest north, however, the summer is evidently too short for the development and birth of the young; the females of the ovoviviparous lizard, like the Adder too, therefore proceed to hibernate in the pregnant condition and deposit their young in the spring. Hibernation of the young animals inside eggs laid in the autumn also occurs, e.g. in the European Pond Tortoise *(Emys orbicularis*, pl. 26) and the Tuatara *(Sphenodon punctatus)*.

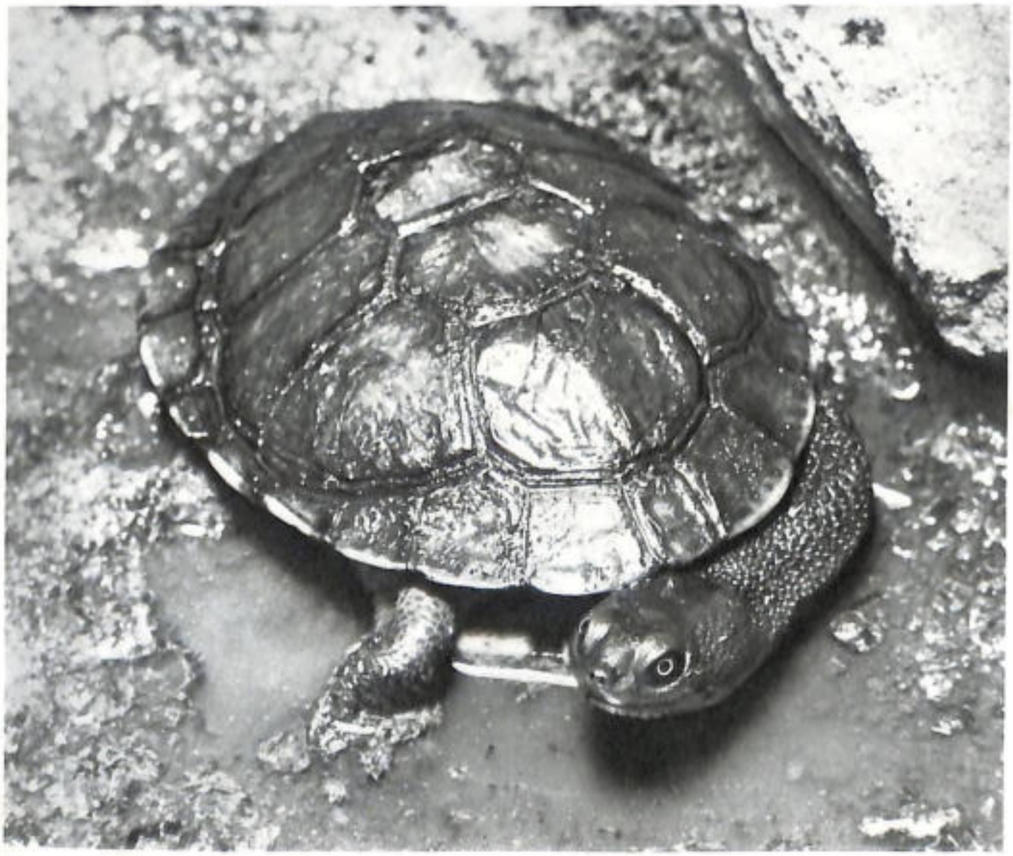
In central Europe and northern America amphibians and reptiles usually have a "winter sleep" lasting about 5-7 months, in the far north and in high mountains even some 8-9 months.

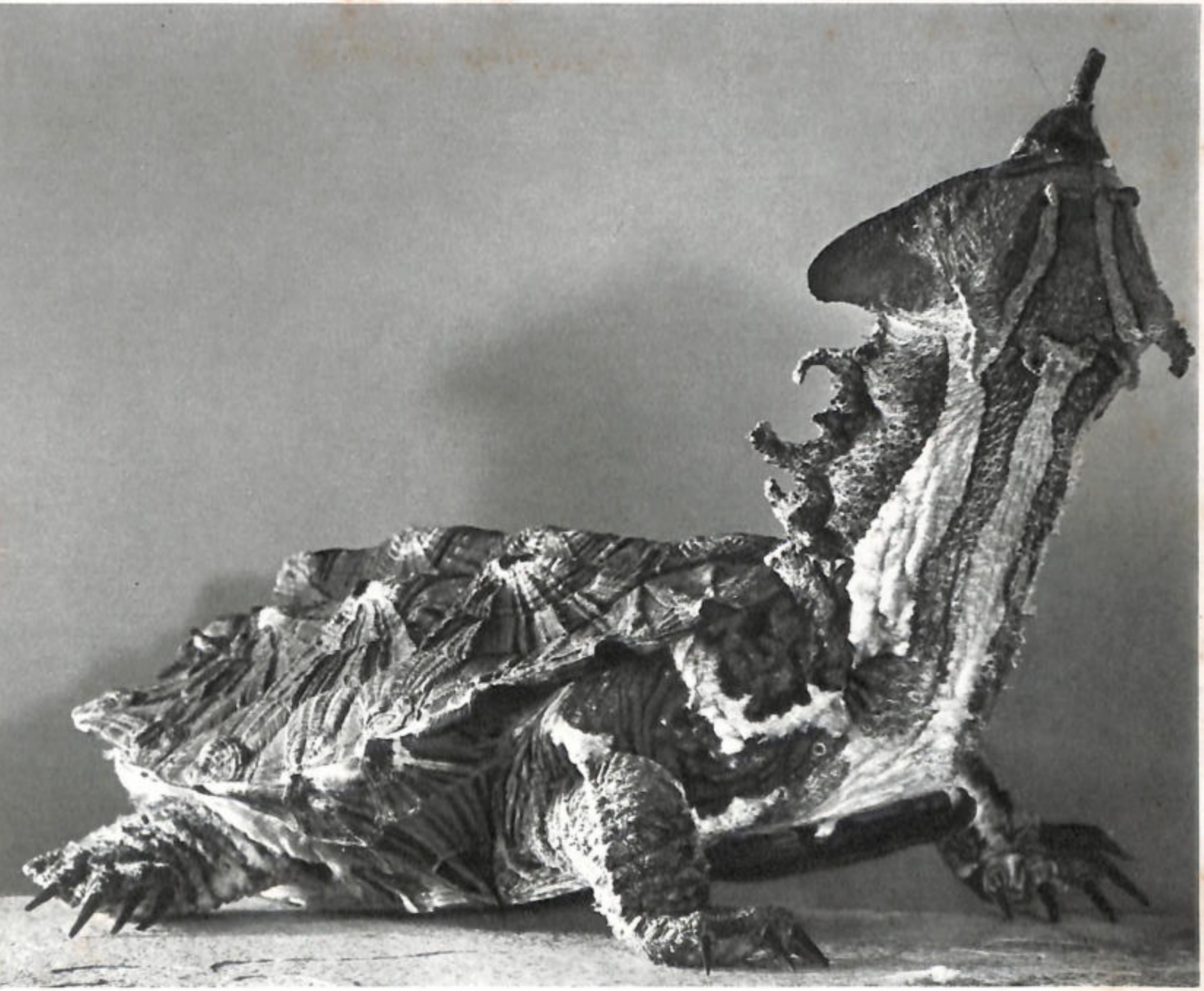


Pl. 29. Leopard Tortoise, *Testudo pardalis*, in its natural habitat in East Africa. ×0.1. *Photograph by* Cott.

Pl. 30. The West Australian snakeneck-turtle, *Chelodina oblonga*, has an unusually long neck which is bent sideways when danger threatens. ×0.5. *Photograph by* Warham.

The South Australian Mullentypery, *Chelodina longicollis*, in the act of flexing its neck. ×0.5. *Photograph by* Senckenberg Museum (Haupt).





Pl. 31. The Matamata *(Chelus fimbriatus)* is unique amongst the turtles because of its cryptic coloration. This turtle is endemic to the waters of tropical South America. ×0.5. *Photograph by* Schmidt.

Pl. 32. African softshell-turtle, *Trionyx triunguis*, during egg-laying. ×0.1. *Photograph by* Cott.

It is astounding that a vertebrate can survive when the total period of its active life does not extend for more than 3-4 months! In the Mediterranean countries many kinds which need warmth, like land-tortoises, hibernate for 5-6 months, whereas a minority less sensitive to cold, like the wall-lizards, for example, come out to bask on warm days even in January. On the whole it appears as if the so-called hibernation of amphibians and reptiles is, perhaps, not a homogeneous phenomenon: in many species it is certainly only a "winter numbness", clearly caused by temperature, whereas in others it is an inherited seasonal cycle. Thus it has not been possible, for example, to change frogs kept at a low temperature in midsummer to a condition similar to that of the winter quiescence. There are lizards which, in autumn, cease feeding independently of the temperature conditions and hide in their places of concealment, whereas in spring the influence of increasing warmth on the termination of the resting period is easily seen. The loss of weight of all animals during their hibernation is amazingly small.

Clefts in the earth, places of concealment under stones, tree-trunks, between roots or in ant-hills, holes dug by the animal itself, and the like, serve as sleeping places during the winter, provided they are frost-free. The North American Alligator *(Alligator mississipiensis)* over-winters in mud holes, 3-5 metres (10-16 feet) deep, which it has dug itself. Water, too, is sought by many species for the winter; the Common Frog *(Rana temporaria*, pl. 19), usually terrestrial in habits, is an absolutely aquatic animal from about the middle of October until spring; it remains beneath the covering of ice for several months and is consequently dependent upon its cutaneous respiration. In the U. S. A. the Leopard Frog *(Rana pipiens)* spends the winter in water, as do many aquatic tortoises, such as the European *Emys orbicularis*. Running water is preferred on account of its higher oxygen content. Occasionally one comes across large aggregations of hibernating animals on land, or in water; the most suitable resting places bring them together, and during this process thigmotactic stimuli certainly play a part as well. These mass assemblages in winter are known more especially in snakes, salamanders and frogs.

During an abnormally cold winter the mortality rate of hibernators can be high, since animals exposed to the action of frost for a lengthy period perish. All the snakes placed experimentally to hibernate in the ground at depths of 15-30 cm. (6-12 inches) failed to survive the winter, whilst animals placed at a depth of 45-90 cm. (1.5-3 feet), and so beneath the limits of frost, remained alive. Amphibians and reptiles lack any "warning device" such as characterises the true hibernators among the mammals; that is the installation of a heat regulator by which the animal can be awakened from its winter sleep when the minimal temperature is reached. Many amphibians and reptiles, it is true, allow themselves to be supercooled, i.e. the body temperature can fall below 0° C. (32° F.). Thus, for example, the Wall Lizard *(Lacerta muralis)* withstands temperatures of —4.58° C. (23.8 F.), the Sand Lizard (*Lacerta agilis)* of —4.75°C. (23.4° F.) and Horsfield's Tortoise *(Testudo horsfieldi)* even — 5.4° C. (22.3° F.); but, of course, it depends on the duration of the action; frogs, with their moist skin, are more susceptible. In an experiment lasting one hour the two lizards mentioned above in each case readily withstood minimum temperatures as low as —1.1° C. to —1.3° C. (30°-29.7° F.), and Common Frogs even —1.4° (29.5° F.). In comparison *Alligator mississipiensis* dies at +4° C. (39.2° F.), and so cannot be supercooled. It is remarkable that after the supercooling limit has been reached, a jump in temperature to about —0.5° C. (31° F.) ensues and not until then do the body fluids freeze. This rise in temperature, therefore, is insufficient to operate a "warning device" as in the true hibernators.

Common Frogs which have been frozen solid in ice must perish, since their body fluids freeze at —0.54° C. (31.03° F.). On the other hand, it has been recorded that newts frozen for a short time survived after thawing out. A Siberian land-salamander *(Hynobius keyserlingii)* was recently found still alive at a depth of 14 metres (46 feet) in clay soil in the permafrost zone. It is known that in certain terrestrial salamanders a loss of water takes place before hibernation and as a result of this the possibility of being frozen up is reduced. Pond Tortoises *(Emys orbicularis)* that have been ice-bound need not necessarily pay for it with their lives. It is reported of a North American Musk Turtle *(Sternotherus odoratus)* that when its winter quarters dried up it struggled over the snow to the neighbouring stream. Swarms of Common Frogs *(Rana temporaria)* were once found in Asturias wandering over a snow-field. As a curiosity it may be mentioned that a gecko was once caught on the snow in winter on the highest part of

Pl. 32. African softshell-turtle, *Trionyx triunguis*, during egg-laying. ×0.1. *Photograph by* Cott.

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The opposite of hibernation is "aestivation" which, for many animals, could perhaps be more correctly described as "drought stagnation", about which something has already been said. After all, it is striking that the Sand Lizard *(Lacerta agilis)* is much more rarely encountered around its haunts in midsummer, roughly from July to the middle of August, than in spring or late summer. Similar observations can be made on other reptiles in the Mediterranean countries.

Whilst a definite amount of heat is necessary to amphibians and reptiles, **light** is not absolutely vital to all; not a few species thrive even when light is permanently excluded, e.g. various cave-salamanders, and lizards and snakes living permanently underground. For many species, however, light is equally as important as warmth and sources of food: hence the majority of reptiles do not avoid the light, but rather do they seek it and are, therefore, positively phototactic. The alternation of day and night, light and darkness, is most distinctly reflected in the manner of life of most amphibians and reptiles; the diurnal animals stand in contrast to the nocturnal; the crepuscular are intermediate between the two. Most lizards and tortoises are diurnal, most amphibians nocturnal. Amongst the lizards the majority of geckos and xantusians are active by night; a few skinks are crepuscular. The Tuataras and crocodiles also only become fully active in the dark, whereas amongst the snakes diurnal and nocturnal forms are about evenly balanced.

Some species behave differently according to age, place, or time of year, in regard to their periods of activity within each twenty-four hours. For instance, many frog larvae differ in their phototaxis according to the stage of development and correspondingly avoid the light at one time and darkness at another. Toads *(Bufo)* in their youth often seek the light, but, in contrast, darkness when old. In the far north and in high latitudes the Adder *Vipera berus* (pl. 71, 72), because of its need for warmth, is much more of a diurnal animal than a nocturnal one, as it is in lower latitudes. This venomous snake, exactly like many North American rattlesnakes, is active in the twilight or at night in summer, but by day in early spring and autumn. Many newts that live in darkness for the greater part of the year carry on their courtship in waters illuminated by the springtime sun.

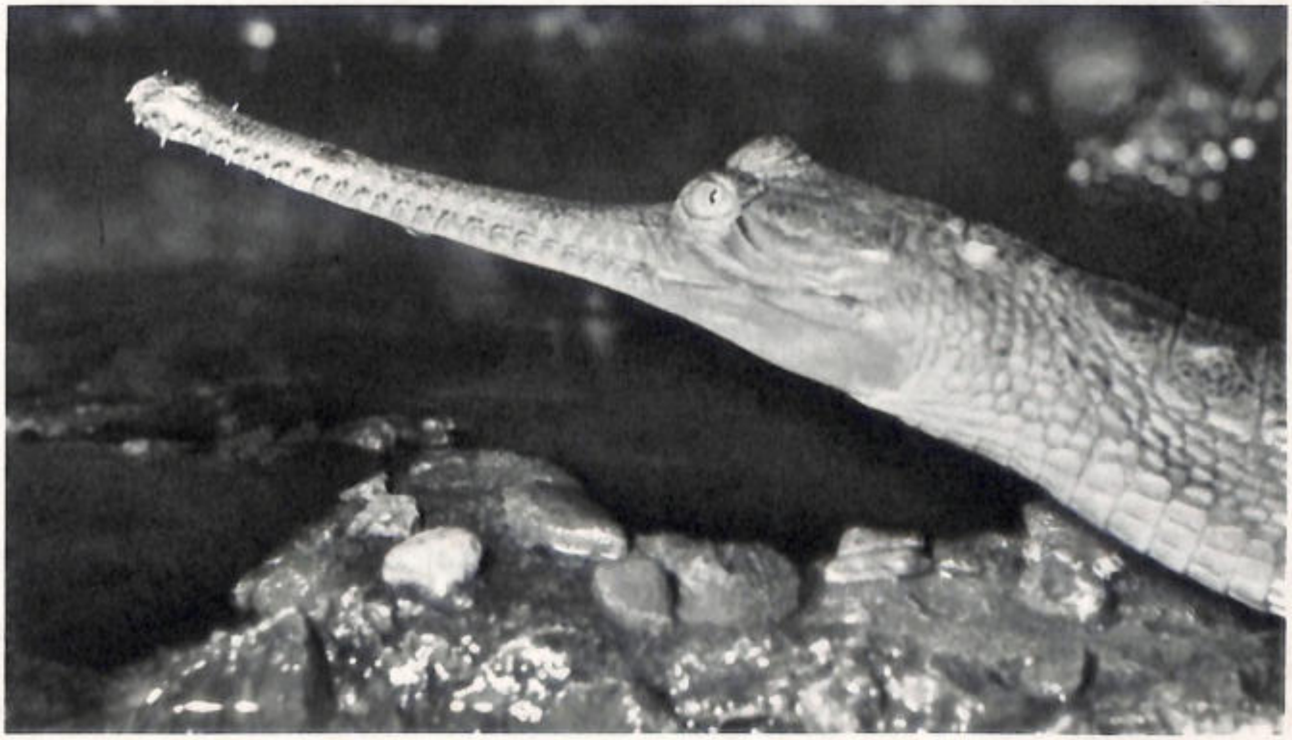
The sun's position appears to be of very great importance for the orientation of some reptiles. That is shown by observations on the Greek Tortoise *(Testudo hermanni)* that were published as early as 1934, but ignored hitherto, as well as by experiments on the North American Box Turtle *(Terrapene carolina*, col. pl. V) carried out quite recently. According to these, the tortoises are capable, even in strange territory, of following a definite direction or selecting the correct path according to the sun's position. Thus the direction-finding of the tortoises would call to mind that of birds. Obviously it is much more precise in the latter since, for example, orientation by the tortoises appears to be inhibited when the sky is overcast.

The relationships of light to the pigment of amphibians and reptiles are very distinct. In those that live permanently in the dark there is very often a reduction of pigment. Thus, for instance, not only are the cave-salamanders (such as *Proteus*, *Typhlotriton* (pl. 2) ,*Typhlomolge* and others) nearly or quite devoid of pigment but there are similar "bleached" species among lizards and snakes that are purely nocturnal or live permanently underground. It is curious that a cavernicolous species has been discovered in each of these two latter orders of reptiles: a small iguana, *Anolis lucius* from the bat caves of Cuba and a two metres (6.6 feet) long snake, *Elaphe taeniura ridleyi* from the large caves near Kuala Lumpur, where it feeds on bats. Both are remarkably light in colour: the *Anolis* is pale and translucent with brick-red transverse bars and the snake, called the "White Snake", is distinctly lighter than the parent form living outside the caves.

Although the physiological colour change of amphibians and reptiles is fundamentally controlled partly by hormones and partly by the nervous system, its connections with the conditions of exposure to light are often very evident. Like the cavernicolous animals already mentioned, most of the lizards that change colour are quite pale at night. It is indeed at night that one can find chamaeleons more easily, on account of their pale colour, than by day when they are protected by their usual green or grey coat-colour. Conversely, many amphi-

Pl. 33. Central American caiman, *Caiman crocodilus fuscus*, from Salvador. ×0.1. *Photograph by* Fischer.

Head of a young Gangetic Gharial, *Gavialis gangeticus*. ×0.3. *Photograph by* Marcuse.



Pl. 34. Nile Crocodile, *Crocodylus niloticus*, basking in the sunshine on the beach. It reaches a length of 20 feet. *Photograph by* Cott.

bians take on darker tones at night; reddish spots may, in the absence of light, be intensified or diminished, and so on. Colour change according to the intensity of illumination of the background is also widespread and can be seen in many amphibians and, especially, their larvae. Recently it was demonstrated even amongst water-tortoises *(Chelodina)*.

Surprisingly, the skin of the abdominal cavity (peritoneum) in many lizards is black; perhaps this is concerned with screening off injurious light-rays. Newly-hatched wall-lizards do not have the peritoneal pigment, as yet, and are thus unable to withstand full sunlight; only after 3-4 days does this photophobic condition disappear. Reptiles with a predilection for darkness are sometimes so photophobic that in broad daylight a condition of tonic immobility sets in. The very poisonous snakes of the genus *Bungarus*, in particular, roll themselves up into a tight ball in the daytime, with their head hidden in it, and nothing will induce them to bite.

The connections with light are most clearly shown by the differing developments of the photoreceptor organs. In some amphibians (e.g. *Xenopus)* a cutaneous light-sense may be developed in addition to eyes. In the animals of permanent darkness, eyes are vestigial or completely atrophied, as, for instance, in many cave-dwelling salamanders and in the subterranean caecilians, lizards and snakes. Amongst these animals there are numerous blind species in which there is no trace whatsoever of eyes externally, since their vestiges lie not only under the skin but even beneath the bones of the skull. Crepuscular and nocturnal animals, however, often have considerably enlarged eyes, as, for example, many bush-frogs, geckos and snakes. Nevertheless, it is remarkable that in a few cave-salamanders the degree of atrophy of the eyes — and that of the pigment — may vary from one individual to another.

A roundish to elongately oval form of pupil is the most widespread amongst the amphibians and reptiles. A vertically elliptic pupil is, however, also known and is almost exclusive to the crepuscular and nocturnal forms. This pupil shape is characteristic of a number of frogs, as well as the Tuatara, all crocodiles and several lizards and snakes. Some frogs, however, have an approximately rhomboidal or triangular pupil. A few tree-snakes *(Ahaetulla*, col. pl. XII, *Dryophiops*, *Thelotornis*, pl. 68) are characterised by a remarkably long, horizontal pupil shaped like a key-hole and have a very long, pointed snout. Since the pupil is extended considerably more towards the anterior than towards the posterior margin of the eye, the significance of this pupil shape, no doubt, lies in making binocular vision possible, i.e. the unimpeded view through two eyes of a single field of vision. As far as we know, diurnal amphibians and reptiles are capable of colour vision, although their ability to distinguish colour, by means of a colour filter, may be different from our own.

Screening off the light-rays is achieved principally by contraction of the pupil. As a result of this, the round pupil of a few nocturnal snakes (*Chilolepis diadema*, *Elaphe flavirufa)* can contract to a small point in glaring light. Vertical pupils contract to a narrow slit or to vertical figures with denticulate edges. Eyelids, also, may take part in the screening-off process as, for example, in agamas and *Anolis*. In a few lizards that are active in very bright light *(Eremias)* black pigment may appear inside their eyelids — often provided with transparent windows — apparently in order to reduce the intensity of the light and so permit acuter vision; this suggests comparison with our ultra-modern dark sun-glasses used in southern countries.

The shining of the eyes in darkness found in crocodiles, lizards and many frogs has nothing to do with the production of light, but depends on a light-reflecting device (tapetum lucidum) that acts like a concave mirror; this is present in the eyes of many crepuscular animals to intensify the light stimulus. It remains to be ascertained whether the glowing of a small lizard *(Procloporus shrevei)* of the family Teiidae is to be referred to this principle or to another. This little creature lives in caves in Trinidad and the male sex is distinguished by a row of light spots on each side of the back; these light up distinctly in the dark. Nothing of a like nature occurs in the amphibians, although a tree-frog is apparently able to produce a luminous secretion.

CHAPTER FIVE

FOOD AND FEEDING

As with all the larger groups of animals, the amphibians and reptiles can be divided into herbivores and carnivores; between the two are the indiscriminate feeders or omnivores. The carnivores strongly predominate and include all the amphibians in the metamorphosed state, as well as all snakes, crocodiles and the Tuatara. Most lizards and tortoises, also, are carnivorous. True herbivores occur in only a few genera of lizards and tortoises, whilst those with a tendency towards omnivorous habits are more numerous; their diet consists mainly of carrion. For instance, a few large agamas, iguanas and other lizards, as well as water-tortoises, are accounted omnivorous since the animal and vegetable fractions of their diet are approximately equal, though generally there is some variation according to age, environment and time of year.

Change of diet conditioned by age is particularly noticeable amongst frogs and toads; as aquatic larvae the large majority are plant and mud feeders, though animal food is not abjured entirely. The larvae of the African Clawed Toad *(Xenopus*, pl. 3) are plankton feeders, and only a few frog larvae, e.g. the tadpoles of the large South American Escuerzo *(Ceratophrys*, pl. 5, 6), lead a truly predatory life. After metamorphosis, however, all frogs and toads are purely carnivorous, although the "meat" is supplied mainly by insects and other invertebrates such as spiders, millepedes, molluscs and worms. It is different with the salamanders; even as larvae they have vital need of an animal diet in addition to detritus, and this persists after metamorphosis. Whenever plants are found in the stomach contents of adult salamanders, e.g. algae in aquatic species, it is always a case of material ingested by accident. Amongst lizards there may be a reversal of what happens amongst frogs: young Mastigures *(Uromastyx)* and Green Iguanas *(Iguana)* incline more to an animal diet than adults, which often feed almost exclusively on plants. The Green Turtle *(Chelonia mydas*, pl. 24) perhaps behaves in the same way, at least in some parts of the ocean. Young crocodiles feed to a considerable extent on invertebrates, in addition to fish and frogs, but the former are no longer appreciated when they become adult. The age-conditioned change of diet of many snakes is similar. The seasonal cycle of appearance of food-animals also plays a part; grasshoppers, which provide an abundant food supply for lizards in midsummer and autumn, are absent in spring.

Even if cannibalism is interpreted to mean that the victim is devoured only by members of the same species, then this "perverted taste" is very widespread amongst amphibians and reptiles: for most carnivorous species do not hesitate to eat the young of their own kind. Lizards, frogs, newts and salamanders can devour their own offspring with the greatest relish! The same kind of thing happens in snakes, too, but only when the adults are snake-eaters, e.g. the New World King Snakes *(Lampropeltis)* or the African species of *Mehelya*. On the other hand, it would never occur to the frog-eating Grass Snake *(Natrix natrix*, pl. 67) to pounce on its young.

There are forms that are narrowly specialised in relation to their food, though these are

Pl. VI. The Green Gecko of Madagascar, *Phelsuma madagascariensis*, is one of the most richly coloured of all lizards. × 0.6. *Photograph by* Senckenberg Museum (Haupt).

In the Leaf-tailed Gecko, *Uroplatus fimbriatus*, the resemblance to bark is unusually close. × 0.6. *Photograph by* Petter.

exceptions. Amongst them, for instance, is the Australian Thorny Devil *(Moloch horridus*, col. pl. VII, pl. 45) which feeds almost exclusively on terrestrial ants of a specific size; the North American horned-lizards *(Phrynosoma*, pl. 49) and many anurans have a similar main diet. Tree ants form the staple diet of the flying-lizards *(Draco)*. True termite-eaters occur among the thread-snakes *(Leptotyphlops)*. The thirst-snakes (Dipsadinae) of the neotropical and Oriental regions live exclusively on snails. Certain water-snakes eat only crustacea and a few terrestrial snakes prey on other snakes, even venomous ones. A small, harmless North American Scarlet Snake *(Cemophora coccinea)* lives mainly on reptiles' eggs, whilst the African Egg-eating Snakes *(Dasypeltis*, pl. 68) are interested solely in birds' eggs; their Indian counterparts *(Elachistodon)* perhaps behave in the same way. Claims that Egg-eating Snakes also eat fruit need substantiating. The best-known specialist herbivore is the Sea Iguana *(Amblyrhynchus cristatus*, col. pl. IX, pl. 49) of the Galapagos; it feeds exclusively on algae and wrack from the intertidal zone.

Small species of amphibians and reptiles must have food more frequently than large ones. In all parts of the world there are small froglets and little lizards, of many different families, that take food every day. Most tortoises also probably feed every day, especially when young and when they are in their periodic phase of annual activity. Many have two sharply defined feeding times within the diurnal cycle; the land-tortoises, for instance, eat their fill of vegetable material in the forenoon hours, then pause for a period of 3-5 hours and go in search of food once more in the afternoon. Many lizards also go in search of insects twice a day. Despite this frequent consumption of food, amphibians and reptiles need to eat much less frequently than birds and mammals and, provided they are not deprived of water, can easily subsist with much longer intervals between their meals. Thus, for example, tortoises and crocodiles, and also large lizards, fast for months without being harmed. However, those best known for lengthy abstentions from feeding are amongst the snakes; of these, even small species, like the deserticolous Australian bandy-bandys *(Rhynchoelaps, Vermicella*, col. pl. XIV), are able to do without food for 6-12 months without any consequent great loss of weight; usually, of course, small snakes are more sensitive to deprivation of food than large, and particularly stout, ones like the African puff-adder *(Bitis*, pl. 76). Amongst these and the boas, some are noted for record fasting and have managed to subsist for more than a year without food. The decisive factor, of course, is the state of the animal's health and the available reserves in its tissues.

The next question, then, is how amphibians and reptiles find their food and how they recognise it. In the simplest cases many species lie quietly in or near their hiding places and simply wait until some quarry or other ventures near. A few large aquatic salamanders, for example, behave like this; they remain motionless on the bottom for a long time and frequently snap at any object that suddenly appears in sight and that is of the same size as their usual prey. There are frogs, too, which do not go forth in search of food but remain half concealed and snap at suitable objects that appear in their vicinity; the large South American Escuerzos *(Ceratophrys*, pl. 5, 6) are an example of this simple method of capturing prey. Many snakes, likewise, and especially the stout and sluggish members of the venomous cobra-group, seldom go hunting for their prey but prefer to lie in wait. Whether the vividly coloured tip of the tail of some young vipers *(Agkistrodon)* serves as bait is at present uncertain. The giant Alligator Snapper *(Macrochelys temmincki)* certainly has a bait in the form of a worm-like process on the middle of its tongue. When this animal rests on the muddy bottom, inconspicuous in spite of its size, and feels hungry it opens its jaws and waves the flesh-coloured, vermiform process to and fro; fishes are deceived by this, come swimming to the bait and are captured as the turtle closes its jaws with a snap. On the other hand, other forms such as land-tortoises, large iguanas, monitors or snakes, methodically set out to look for food when hungry.

Of all the sense organs, that of sight is the most important for the recognition of food in amphibians and reptiles. This is true for the herbivores and for most of the carnivores. The vision of terrestrial frogs, most lizards and a few snakes is adjusted to the perception of movement rather than to perception of form, and so they cannot recognise their prey unless it is in motion. All frogs, with the exception of the aquatic and a few ground-dwelling species, prefer to starve rather than snap at completely immobile quarry such as dead insects. Many lizards, too, become aware of, and snap at, their prey only when it moves. In doing this they are in the habit of making fairly long jumps, just as many frogs pounce when snatching their food. Amongst snakes the large-eyed diurnal forms, which are primarily dependent on sight for the recognition of prey, such as *Ahaetulla* (col. pl. XII) and *Thelotornis* (pl. 68), begin to hunt their food as soon as it moves.

In addition, the chemical senses, and especially the sense of smell, are important in food recognition. Amongst amphibians it is well developed in the urodeles, in both aquatic and terrestrial animals. In the frogs it plays a less important part, although it is known to exist in a few species, especially in the aquatic clawed-toads *(Xenopus)*. The ability to smell is excellently developed in tortoises; terrapins of the genus *Geoemyda* recognise the smell of bananas at a distance of 2-3 metres (6.5-10 feet) on land. The true land-tortoises *(Testudo*, pl. 27-29) can select suitable plants from amongst those available to them with great accuracy, apparently by using their sense of smell.

Most lizards have good olfactory powers. In addition, the tongue of lizards and almost all snakes plays a role as original as it is important, without, however, being a sense organ in itself: many lizards and all snakes are known to be in the habit of "licking", i.e. continually putting out and retracting their tongues so that odorous substances are picked up and transported to Jacobson's organ. The tongues of monitors (pl. 53-55) and snakes are particularly delicate in operation since the two tips fit exactly into the two small cavities in the roof of the mouth which are the openings of Jacobson's organ. The tongue is not, apparently, brought into any contact with an object that is being investigated; since the odorous materials in the air suffice for recognition, one can speak of smelling and not of tasting. The true sense of taste is, however, very delicate in most amphibians and reptiles; lizard-eating snakes that have inadvertently seized a frog release it immediately; lizards which have captured insects with an unpleasant smell drop them and rub their jaws on plants and stones. In tortoises strictly individual tastes can be observed in which habit plays a large part.

The mechanical senses are less important in food recognition than the chemical, whilst the sense of hearing probably has no significance. In the subterranean caecilians or Gymnophiona the sense of touch is probably well developed; they have small tentacles which are rapidly protracted and withdrawn. Moreover, the sense of touch is important to the aquatic clawed-frogs *(Xenopus*, pl. 3); their eyes are small and, in addition to the sense of smell, their senses of touch and vibration are all the better developed; these are situated in the lateral-line organs distributed all over the body. The tips of the fingers, also, are extremely sensitive to touch as one can discover by feeding a clawed-toad. In the related Surinam-toad *(Pipa*, pl. 3) the tactile organs are situated on the finger-tips which terminate in star-shaped prominences. But many salamanders are also able to locate their prey with the aid of lateral-line organs which react to disturbances of the water. Even simple contact stimuli are sometimes effective for recognition of prey; this is the case in salamanders and probably also in a few snakes. Many frogs, especially tree-frogs, can be trained to react by fierce snapping when any particular object merely touches the tip of the snout. The mouth aperture of some tropical frog larvae is surrounded by a remarkable funnel; to what extent tactile stimuli participate in making it possible for this funnel to pick up minute particles floating on the surface-film of the water remains to be investigated.

The so-called pit-vipers (pl. 77) have a very remarkable organ that serves for the accurate location of their prey, in their facial pit, which is a cavity between the eye and the nostril. Whilst it was formerly interpreted as an organ for the perception of atmospheric vibrations emanating from the prey, the most recent investigations have shown that it serves as an infra-red receptor; the sensitivity of this facial pit is so great that fractions of a degree Centigrade are perceived by it. Thus a rattlesnake can apparently detect the presence of its warm-blooded quarry with the utmost certainty. The labial pits of some boas (e.g. *Python)*, and perhaps also the supranasal sacs of the puff-adders and their relatives *(Bitis, Pseudocerastes)*, may have a similar function; we know nothing, however, about the function of the peculiar axillary pits in many chamaeleons.

For seizing the quarry, teeth are used primarily, as in the amphibians, crocodiles, Tuataras, lizards and snakes. Some crocodiles (e.g. *Gavialis*, pl. 33, *Tomistoma*, *Crocodylus cataphractus*,

Pl. 35. West African Long-snouted Crocodile, *Crocodylus cataphractus*, in its natural habitat. In life it is about 10 feet long. *Photograph by* Dragesco.

Pl. 36. The Tuatara *(Sphenodon punctatus)* is the sole living representative of an ancient reptilian stock which, 130 million years ago, was also found in Europe. Now it occurs only on a few small islands near New Zealand. The specimen figured is being kept alive by the author. ×0.6. *Photograph by* Senckenberg Museum (Haupt).

pl. 35) have very long snouts and their jaws, furnished with numerous teeth, are admirably suited to seizing frogs and other quarry. The teeth are often very pointed and slightly recurved; to make holding the prey easier, many snakes throw one or more coils around it. The function of the teeth in the jaws is often assisted by additional tooth-rows or groups of teeth situated on the roof of the mouth. The caecilians have two rows of teeth in the upper jaw and one or two rows in the lower; in the Tuatara there is also a double tooth-row in the upper jaw posteriorly. In most cases frogs only have teeth in the upper jaw, but these suffice to grip their prey almost as firmly as does a beast of prey. The true-toads (Bufonidae, pl. 8-10) lack teeth in the upper jaw, as well, and are completely toothless. There are urodeles *(Siren, Pseudobranchus)* which are toothless except for the vomerine teeth; their jaw-teeth are replaced by horny plates. These latter are present in all tortoises amongst which no toothed forms whatever exist at the present day. Their powerful horny jaws are, however, admirably suited to seizing food both in terrestrial and aquatic forms.

But the amphibians and reptiles have yet other methods of catching their prey. The method of "gape and suck" is very widespread amongst aquatic forms; water is sucked in by suddenly opening the jaws. The prey is swept by the current of water into the mouth where it is held fast by a swift closure of the jaws. In this process the jaws do not serve directly for holding, but have a function similar to that of the hoop of a net. To increase the suction some aquatic newts develop rather broad fringes on their lips which degenerate again at the transition to life on land. Capture by suction is also practised by water-tortoises and is most striking in the Matamata *(Chelus fimbriatus*, pl. 31) which has an unusually wide mouth. Frogs that feed under water, such as the giant Andean frogs *Batrachophrynus* and *Telmatobius*, a few Ranidae and members of the genus *Pseudis* also make use of a basically similar method of capturing food. The clawed-toads *(Xenopus)* and their relatives, strange to say, use the hands to grasp the food and push it into the mouth, a practice that is elsewhere foreshadowed by some terrestrial anurans such as toads and tree-frogs.

Finally the tongue can also be of the greatest importance in the capture of prey, especially amongst the terrestrial amphibians. They snap with their viscous, eversible tongue at tiny food-animals which adhere to it. The tongue can be either mushroom-shaped, with a muscular stalk, as in a few salamanders, or attached in front with the hinder part capable of being flapped outwards; some other salamanders have this arrangement and many anurans in which the hinder margin often has two lobes. The mushroom-shaped tongue rests on a very long stalk in the terrestrial salamanders of the genus *Hydromantes* which is represented in Europe as well as in western North America; in this case it can be shot out to an extraordinary distance. The well-known catapult-tongue of the chamaeleons functions in an analogous fashion, though on a different anatomical basis; it may also, perhaps, act as a grasping organ. In these slow-moving lizards the tongue can be shot out to distances almost equal to the length of their own bodies! Large chamaeleons with their adhesive tongues can, moreover, capture not only insects of all kinds but even small lizards and new-born mice. The "effective range" of chamaeleons is as amazing as their accuracy. Furthermore, other lizards, particularly in the related families Agamidae and Iguanidae, use their tongues to lick up their prey, provided that it does not exceed a certain size. The Tuatara also uses its tongue, which is somewhat swollen, to lick up small prey, especially insects, whilst large quarry is seized with the jaws.

The question that now arises is: how is the prey overpowered and rendered defenceless or killed? Amongst those which have adhesive tongues this question does not arise; the prey is definitely handicapped by the mucus of the tongue, though it often arrives in the oesophagus and stomach whilst still alive. It is, of course, not very different with all those victims that are sucked into the mouth. Many snakes, too, swallow their struggling victims alive, as, for instance, the Grass Snake *(Natrix natrix*, pl. 67); if such a snake is disturbed shortly after a meal it occasionally regurgitates the frog it has swallowed; and the frog is often still sufficiently lively to hop away quickly and save its life.

In many other cases, however, the jaws and their musculature are used in overpowering the prey; the victim is crushed between the jaws (that are either armed with teeth or have horny sheaths) or at least so damaged that it is rendered helpless and can be swallowed. Most lizards, crocodiles and tortoises (pl. 25) do this; large lizards usually stun or kill a quarry capable of defending itself by shaking it violently or by rolling on it, a method frequently employed by the crocodiles. The strength of snakes' jaws is not in itself enough, as a rule, to render the quarry helpless or to kill it. The behaviour of the thirst-snakes (Dipsadinae) forms a unique exception; they insert the lower jaw into the opening of a snail's shell, drive their enlarged, somewhat recurved teeth into the snail's body by a lateral rotation of the jaw, draw it out with great skill and immediately devour it. A quite exceptional method amongst reptiles is employed by the thread-snakes *(Leptotyphlops phenops)*; it has recently been observed that they methodically suck out the abdomen of termites.

To make their prey defenceless, snakes most commonly employ their trunk muscles or poison fangs. Many snakes are able to strangle their prey in a very short space of time; whilst a mouse is still firmly gripped in the jaws it is enveloped with lightning speed by two, three or more coils which contract and after a few seconds, or at most minutes, the victim is dead. Then the coils relax and the snake releases its prey. Next it is examined from all directions by the snake's tongue until the head is found; it is gripped once again in this region and swallowing can begin. Many terrestrial snakes (pl. 66) that feed on small mammals and birds usually behave in this way and some also adopt this method to overpower lizards, other snakes and even frogs; but, generally, cold-blooded prey is not released after constriction, ingestion beginning even before the victim is dead. A few North American snakes are in the habit of constricting not one, but two mice at the same time before swallowing them; that is an adaptation to certain mice *(Peromyscus)* which live in couples. Constriction of the prey is very characteristic of all boas (pl. 60-62), where even the end of the tail may participate in forming coils round the victim, which is often as big as a deer. Otherwise the hindmost parts of the body play a part in overpowering prey only in the crocodiles, which stun their victims by blows of their powerful, muscular tail.

Nevertheless, by far the most remarkable phenomenon is the snakes' poisoning of their prey. Venomous snakes, it is well known, are widely distributed; they live in all parts of the world, although there are large islands where venomous snakes, at least those dangerous to man, are wanting; examples are Madagascar, the Greater Antilles, Sardinia, Corsica, Crete, the Balearics and so on. The venom glands lie on either side of the head behind the eye and are derived from salivary glands (parotids). Thus the venom of snakes is simply modified saliva. It is injected into the victim by means of specially enlarged and modified teeth in the upper jaw; they may have a longitudinal groove on their anterior or lateral aspect or be tubular, i.e. perforated internally by a canal. The venom glands are connected to the fangs by a venom duct.

By and large we can distinguish three major groups of venomous snakes according to the structure of the poison apparatus. First the Opisthoglypha, in which the two or three hindmost teeth of the upper jaw are enlarged and grooved. To this group belong the usually only slightly poisonous snakes which are not always closely related to one another but, together with the non-venomous Aglypha, form the family Colubridae. They have a wide distribution in the warmer countries, but are only sparingly represented in Europe and Australia. Only two species, the African Boomslang *(Dispholidus typus*, pl. 69) and *Thelotornis kirtlandii* (pl. 68) can be dangerous to human beings; only recently the well-known herpetologist Karl Patterson Schmidt fell a victim to the bite of *Dispholidus* in Chicago.

The second group is the Proteroglypha. These are the real venomous snakes (Elapidae) and the sea-snakes (Hydrophidae, pl. 70). In them a greatly enlarged venom fang stands on the upper jaw of each side and this is usually followed by a few smaller teeth; its groove is sometimes converted into a canal. This poison fang, together with the upper jaw-bone (maxilla) on which it is inserted, is only very slightly moveable and is directed vertically downwards. This group includes the notorious cobras *(Naja*. col. pl. XII, pl. 69) of Africa and Asia, as well as the spitting-cobras *(Hemachatus)* and mambas *(Dendroaspis)* in the first-mentioned continent and the kraits *(Bungarus)* in the other. They are absent from Europe; in the New World they are represented by the true coral-snakes *(Micrurus* and two related genera). Australia is especially rich in these poisonous snakes; there the death-adder *(Acantophis*, pl. 70), tiger-snake *(Notechis)* and Taipan *(Oxyuranus)* are among the snakes most dangerous to man.

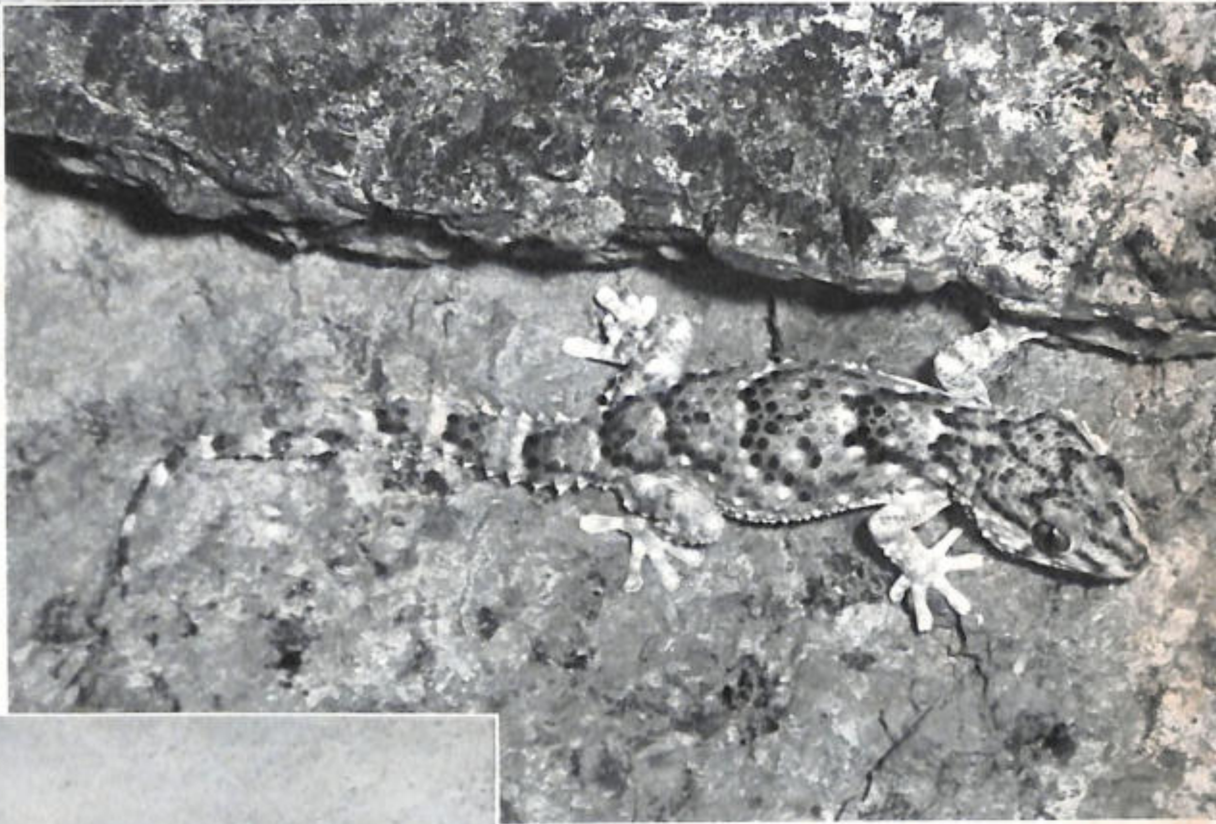
In the third group, the Solenoglypha, the venom fang is very long and always tube-like;

Pl. 37. *Gymnodactylus milii* is characterised by a fatty, turnip-shaped tail. A native of Australia. ×1. *Photograph by* Rosenberg.

In this gecko, *Eublepharis macularius*, also, the tail is very rich in fat. It lives in the arid zones of south-western Asia. ×0.8. *Photograph by* Senckenberg Museum (Haupt).

Moorish Gecko, *Tarentola mauritanica.* The commonest representative of the gecko family in the western Mediterranean countries. ×0.9. *Photograph by* Barruel.

Pl. 38. The young of the South-west African gecko *Pachydactylus bicolor* looks quite different from the adult (see below). ×1. *Photograph by* Senckenberg Museum (Haupt).



Amongst the most abundant geckos in eastern and southern Africa is *Pachydactylus* **bibronii.** ×0.8. *Photograph by* Cott.

Adult *Pachydactylus bicolor*, whose juvenile stage is figured above. ×1. *Photograph by* Senckenberg Museum (Haupt).

Pl. 39. The North African Fan-footed Gecko, *Ptyodactylus hasselquistii*, is noteworthy on account of its singularly strongly developed adhesive discs. ×1. *Photograph by* Rosenberg.

In the Australian Spiny-tailed Gecko, *Diplodactylus strophurus spinigerus*, the spines of the tail are soft and serve for the expulsion of a bitter liquid in moments of danger. ×1.5. *Photograph by* Senckenberg Museum (Haupt).

Pl. 40. Head of the East Indian Tokay, *Gekko gecko*, the most impressive in appearance of the Asiatic geckos. It is noticeable for the vertical pupil, characteristic of most geckos, which contracts to a narrow slit in sunlight. ×1.5. *Photograph by* W. Senfft.

because of the mobility of the much shortened upper jaw-bone it is usually folded down to point backward when the jaws are closed, and erected when the jaws are opened. Behind these venom fangs stand one or two replacement fangs, and this is also the case in the preceding group. The Solenoglypha comprise two families, the vipers (Viperidae) and the pit-vipers (Crotalidae), both of which contain species genuinely dangerous to man. Both families are wanting in Australia and the Viperidae in the New World, whilst the Crotalidae are absent from Africa and virtually so from Europe. The best-known genera are *Vipera* (pl. 71-73), *Bitis* (col. pl. XV, pl. 75, 76), *Aspis* (pl. 74) and *Echis* among the Viperidae; and *Agkistrodon* (pl. 76), *Trimeresurus*, *Bothrops* (col. pl. XVI, pl. 77), *Lachesis* (pl. 78) and *Crotalus* (pl. 78-80) among the Crotalidae.

The venom is a mixture of very varied components: in addition to the poisonous elements such as neurotoxins (nerve poisons) and haemotoxins (poisons of the blood), there are, more especially, digestive enzymes which start digestive processes immediately after the bite. The composition of the venom varies from species to species and even within the same species the proportions may be different. On this account a poisonous snake may not be immune to the bites of other species or even to the bites of certain of its own species; on the other hand, non-venomous snakes are known which are immune to the bites of venomous ones. There are snakes like the opisthoglyphous water-snake *Fordonia leucobalia*, whose venom is very toxic to the crabs on which it feeds, but not to fish or amphibians. Even apart from the Opisthoglypha there are many aglyphous species of snakes, which are not supplied with special poison fangs but which have a salivary secretion that is slightly toxic to their prey. A small, "non-venomous" snake, *Rhadinaea flavilata*, for instance, is in the habit of holding a captured frog in its jaws long enough for it to be paralysed by the action of the saliva; this may take, on occasions, 1-3 hours. Apart from the opisthoglyphous *Dispholidus* and *Thelotornis*, many proteroglyphs and solenoglyphs — both adults and juveniles — are a serious danger to human beings unless serum treatment is taken at the earliest possible moment.

Because of their venom all poisonous snakes doubtless have an advantage over the non-venomous when it comes to acquiring food. The venom, for instance, enables them to kill, without risk to themselves, a quarry that could be dangerous to them. The strike preceding the bite, and the bite itself are performed so rapidly that the human eye is unable to follow them; measurements of this have been made which show that the cobras are slower than the rattlesnakes and their allies, which open their mouths much more widely when biting — up to 180° — than the cobras. Most poisonous snakes, except the opisthoglyphs, make a practice of releasing their victim after the bite and only begin to devour it when death has occurred; that may be the case after a few seconds, although it may sometimes be several minutes, or even hours before the victim is dead. The prey is found with certainty, even at great distances, the snake orientating itself with the aid of Jacobson's organ and the constant use of its tongue. A snake is therefore able to swallow, without risk, quarry that can defend itself. As in the case of strangled prey, swallowing usually commences at the head (col. pl. XVI). If the prey is small and inoffensive it is often not released after the bite, but swallowing begins immediately or after a short interval. This latter behaviour is characteristic of opisthoglyphous snakes whose poison fangs are situated far back in the upper jaw. Finally, poisoning of the quarry brings the advantage of a certain acceleration of the digestive process; this may even begin before the victim has been swallowed! It has been proved that rats naturally envenomed by the snake are digested more rapidly than dead, unpoisoned ones.

Amongst lizards, in contrast to the snakes, there is a single venomous genus, which contains only two species, *Heloderma horridum* in western Mexico and *Heloderma suspectum* (pl. 52) in the south-western United States and the adjacent parts of Mexico; the two form a single family, the Helodermatidae. In these rather sluggish lizards the venom is produced by a gland which is likewise a modified salivary gland; it is secreted at the base of some of the teeth of the lower jaw which are furrowed in front and behind. The venom of *Heloderma* also contains digestive enzymes. But since the food of these venomous lizards consists mainly of eggs, nestling birds and new-born mammals it is probable that the original function of the venom apparatus — to facilitate the capture of food — has been lost and it has now become more effective as a weapon of defence.

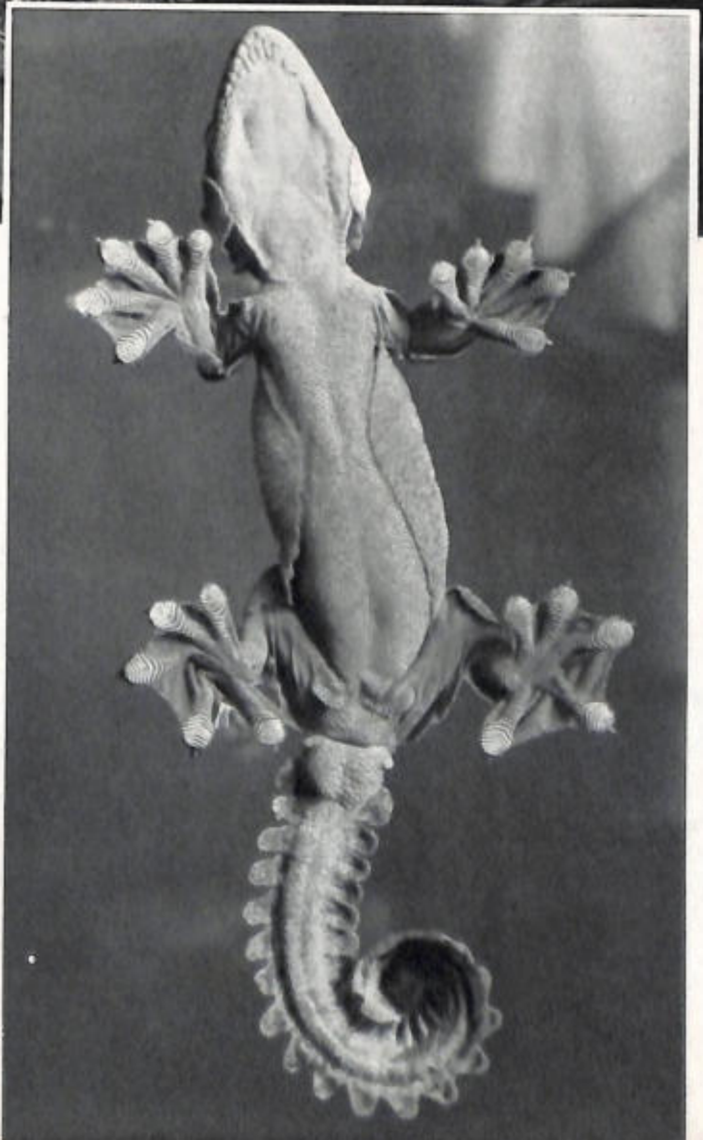
The prey of all metamorphosed amphibians and of most reptiles is swallowed whole; the feeble, pointed teeth that these animals often have are scarcely fitted for chewing. All snakes behave in this way even when their prey is several times wider than their head. Snakes, however, are easily able to swallow such large prey because not only are certain of the cranial bones moveable but they are also connected together with elastic ligaments, especially the two rami of the lower jaw. These can, therefore, be pulled widely apart from one another so as to be able to admit large-sized prey. The skin on the head, neck and trunk is, likewise, very elastic. When a snake tries to swallow its food, one has the impression that the jaws are being drawn over the prize; in connection therewith the small, slightly recurved teeth function like barbed hooks.

Lizards, as a rule, also swallow their prey whole, after making a few chewing movements of the jaws. Many victims are thus crushed; an earthworm, for example, may have a piece bitten off. There are a few species with blunt conical teeth *(Tupinambis, Dracaena,* pl. 56) which are admirably fitted for crushing hard-shelled food, especially crustacea and snails; some skinks, too (for example, *Tiliqua gerrardi)*, have a dentition suitable for crushing snail shells. In the Nile Monitor *(Varanus niloticus*, pl. 54), the teeth of young animals are thin and pointed whereas those of old ones are stout, blunt and conical; this change is fully in keeping with the nature of the food-animals, since young monitors eat much softer prey than old individuals. Among the tortoises, which have no teeth, the masticatory surface is especially broad in some species of *Graptemys* which use them to crush their hard-shelled prey. Otherwise tortoises are in the habit of chewing their food with their horny jaws and tearing off pieces from larger prey; the clawed fore limbs help in this procedure. If two or more tortoises seize a victim simultaneously they can each tear pieces off it. In a similar situation crocodiles also behave in the same way. In addition they make use of their own very peculiar method, which has already been mentioned; they begin to rotate, each on its own axis, and in this way tear the booty apart. Having done this, the crocodiles have the habit of shaking the fragment to bring it into a position in which it can be swallowed.

In some tortoises the edges of the jaws are so sharp that they can cut off a piece of their prize. Amongst the monitors the same thing is possible in the case of the powerful Komodo Monitor *(Varanus komodoensis*, pl. 54, 55) whose hind teeth are as finely serrated as a knife in a canteen of modern cutlery. In old specimens of the Tuatara *(Sphenodon punctatus)* serrated crests are formed on the jaws because of the deposition of numerous masses of dentine between the teeth. In consequence the jaws are especially effective for chewing the prey with a sawing action. In addition, the tortoises that are preponderantly vegetarian — and this applies to both terrestrial and aquatic forms — have quite pronounced sawing instruments. The horny edges of the jaws and the double or triple ridges on the masticatory surfaces are often distinctly serrated; the underlying jaw-bones, also, often correspond with this structure, and this is particularly well shown by the Indian river-turtle *Batagur baska*, for instance. Thanks to this modification the tortoises are able systematically to cut off pieces of vegetable matter. The small horny teeth and horny jaws of frog larvae, resulting from cornification of the superficial layers of the skin, act as rasps for gnawing plants and dead animals.

The adaptation of the African Egg-eating Snakes of the genus *Dasypeltis* (pl. 68) to a completely monotonous and apparently not always readily obtainable diet is very remarkable. As already mentioned, this consists of birds' eggs exclusively. Eggs even as large as a hen's egg are consumed without difficulty by snakes which are scarcely bigger than the European Smooth Snake *(Coronella austriaca)*. This is made possible by the unusual elasticity of the lower jaw, which, like the upper jaw and the palatine bone too, carries only a very few small teeth posteriorly. When the egg is swallowed it slips into the oesophagus past the cervical vertebrae; the ventral processes (hyp-apophyses) of some of these are elongated and directed forward and pierce the oesophagus. They work like a saw and bore through the egg-shell, which is finally crushed with the co-operative action of the powerfully developed neck muscles; as a result, the contents of the egg are discharged into the oesophagus. Just as the digestive system of the snail-eating Dipsadinae is little burdened by the snail's shell, so that of *Dasypeltis* is unaffected by egg-shells, for they are regurgitated. Apophyses for this purpose are also found in a few egg-eating species of the genus *Elaphe*.

Pl. 41. The South-east Asian Parachute Gecko, *Ptychozoon kuhli*, is characterised not only by extensive webbing between the fingers and töes but also by numerous flaps of skin on the sides of the body and tail. ×1. *Photograph by* W. Senfft.



The same Parachute Gecko seen from below. The flaps of skin are very easily seen and serve not only to increase the similarity to bark but also, probably, to reduce the speed of descent when falling. ×1. *Photograph by* W. Senfft.

Pl. 42. A sand-agama, *Phrynocephalus mystaceus*, in resting posture. ×2. *Photograph by* Senckenberg Museum (Haupt).

The same lizard on the defensive with the flaps of skin spread apart and thus simulating a gigantic mouth. ×2. *Photograph by* Senckenberg Museum (Haupt).

CHAPTER SIX

PROTECTION AGAINST ENEMIES

Amphibians and reptiles have very many enemies: all classes of vertebrates from fishes to mammals, and even invertebrates such as spiders, scorpions and scolopendrid centipedes, contain species that prey on them. Not only frogs and the smaller lizards, but all the remaining groups of amphibians and reptiles face a world of enemies. It must not be forgotten that even the largest and most powerful species, such as certain iguanas and monitors, boas, crocodiles and tortoises, are delicate creatures when young and are equally liable to fall victims to a host of enemies. Very young tortoises and turtles, in particular, whether living in the oceans, in fresh water or on land, are a much coveted prize for many other vertebrates and especially for birds and mammals. In addition, the amphibians and reptiles have enemies of their own kinds; these need not necessarily always be cannibals but — especially amongst the lizards — they occur as rivals in a narrowly circumscribed region and are part of the social order. It is not surprising, therefore, that both classes of vertebrates have an abundance of characters whose function is to protect the animal from its enemies.

Protection against enemies can be achieved in the most diverse ways: by flight or concealment, or alternatively by very striking behaviour such as warnings or threats, or again by deception or bluff, and finally by defensive and offensive weapons. In a few particularly impressive defence reactions these different categories may be combined.

Amphibians and reptiles most frequently escape from their enemies, which are usually recognised visually, by flight, though this may also be caused — as in salamanders — by sounds and vibrations and even, as in certain toad larvae, by olfactory irritants (repellants). Anyone who has ever tried to capture these animals knows that some lizards and snakes, and also other groups including the allegedly sluggish salamanders and tortoises, show remarkable agility when they take to flight. As a rule, the fugitives make for a hiding place that is not easily accessible. Frogs, water-tortoises and water-snakes which bask in the sun at the water's edge or on branches of trees overhanging water let themselves fall into the water, dive down and try to escape their pursuers by burying themselves in the mud. On land it is a hole, a cavity under a stone, a cleft in a rock or tree in which the hunted animal feels safe. If the animal does not normally use a definite hiding place it simply grubs into the earth, especially into loose sand (pl. 75), with the same end in view.

Not infrequently the victim escapes its pursuers during flight only because it has a protective coloration. Species that live on dark soil or mud are often exactly as dusky in colour as their background; on sandy soil lizards and snakes are sand-coloured, their hue being identical with that of the sand on which they live, whether it is white, yellowish or red (col. pl. VII). Frogs, lizards and snakes that live on tree-trunks are bark-coloured, whilst their relatives which are constantly surrounded by green foliage have a distinctly green livery (col. pl. II, XII). The

Caucasian Agama *(Agama caucasica)* is grey like the rocks of its environment, but if it lives on reddish boulders it is flecked with orange to brick-red spots. In the same way the Australian Blue-tongued Skink *(Tiliqua occipitalis*, col. pl. XI) has a much more intense deep red in its coat colour on the brick-red sands of Central Australia than in West Australia, where it lives on paler sand. The south-west African rock-geckos *(Rhoptropus)* are represented by a very light-coloured species on light marble, but by a dark, almost black, one on crags of black dolerite. Nevertheless, they can live side by side but without straying onto the background inappropriate to them! In some lizards physiological colour change helps towards the acquisition of this kind of protective coloration although it need not always serve the purpose of concealment.

Sometimes protective coloration is accompanied by protective shape; the animal imitates inanimate objects or parts of plants in its surroundings, not only in its colour but in its shape as well (pl. 10). In such cases one usually speaks of procryptic resemblance. Many a chamaeleon and tree-frog, for instance, can be so like a leaf, either green or withered, that it is only noticeable when it moves. Some much-flattened broad-tailed geckos (e.g. *Phyllurus* in Australia, *Ptychozoon* on the Sunda Islands, *Uroplatus* in Madagascar, col. pl. VI, pl. 41) are deceptively like the bark of a tree, whilst a few unusually slender snakes *(Ahaetulla*, col. pl. XII, *Oxybelis*) are no less similar to green or grey-brown twigs or lianas. The strange, elongate processes on the head of the Madagascar snakes of the genus *Langaha* also increase the resemblance to parts of plants. The broad, flat head of the Matamata *(Chelus fimbriatus*, pl. 31), which is provided with curious little cutaneous flaps on its sides, likewise probably has a cryptic function, although in this case, of course, it may be less significant as a protection from enemies than as camouflage to aid in the capture of its prey. In other water-tortoises a procryptic condition arises through a more or less luxuriant algal growth that settles on their carapace.

It is very remarkable that behaviour changes go hand in hand with the development of procrypsis. Thus, not a few of those species that have protection exhibit a distinctly limited development of the instinct to flee. For instance, a Parachute Gecko *(Ptychozoon)* remains motionless on the bark of a tree as an enemy approaches, as if it were "conscious" of its protective dress, whereas another less well-protected gecko hastily scurries off. A tree-snake which resembles a liana, e.g. the neotropical *Oxybelis aeneus*, behaves in much the same way and is, consequently, relatively easy to catch. The Malagasy snake *Mimophis mahfalensis*, that resembles a dry twig, stays completely motionless for a long time with its head stretched out at an angle and so is overlooked by its enemies.

"Shamming dead" is also a very effective method of defence against enemies. There are some small tree-snakes of the group Dipsadinae which simply allow themselves to fall to the ground when danger threatens and remain lying there motionless like a slender branch. In this connection, other snakes take up a position on their backs when motionless. Other examples of feigning death are known amongst procryptic lizards *(Brookesia*, col. pl. VIII, *Echinosaura)*. A Girdle Lizard *(Cordylus cataphractus*, pl. 50) rolls itself into a ball when pestered and bites its own tail; North American relatives of the European Slow Worm have the same habit, which is also recorded in monitors. Though this has nothing to do with procrypsis, it is difficult, if not impossible, for snakes to swallow animals in these postures. Many snakes in case of danger roll themselves up into a motionless, compact ball in the middle of which the head is usually concealed; this is a widespread form of akinesis, especially amongst the smaller boas. Feigning death is also known amongst the frogs and toads; its best-known form is the "Unkenreflex" — a lordotic arching of the back and a simultaenous raising of the limbs so that their lower surfaces are turned upwards. This singular defensive posture, with eyes closed and breathing suspended, is not confined to the firebelly-toads or "Unken" *(Bombina*, pl. 4) but may also be seen in a similar form in other groups of anurans.

Finally, in this connection, let us refer to the familiar yet curious phenomenon of autotomy. Many lizards, when seized by the tail, very readily break off this part of their body. The piece of the tail which has broken off usually twitches convulsively and whilst the pursuer is dealing with it the pursued escapes by flight. The tail breaks off at specific places along the vertebral column in the tail, and these are situated, not between the vertebrae, but within a vertebra, and, what is more, at a narrow, unossified zone. In one agama *(Gonocephalus subcristatus)*, however,

Pl. VII. *Palmatogecko rangei.* This gecko lacks adhesive discs but has extensive webbing between its fingers and toes. It is a characteristic animal of the vast sand dunes of the Namib desert in south-west Africa. × 1. *Photograph by* Senckenberg Museum (Haupt).
The spinose Thorny Devil, *Moloch horridus*, is among the strangest lizards, not only of Australia but of the whole world. × 1. *Photograph by* Warham.

the planes of fracture lie between two caudal vertebrae. This is the case with certain salamanders (e.g. *Batrachoseps)* which also practise caudal autotomy. In all cases the stump of the sloughed tail grows again, though it never quite reaches its original length: many urodeles can even regenerate lost limbs. In snakes the tip of the tail may sometimes break off easily, as in the genera *Sibynophis* and *Dromicus;* but regeneration does not take place here. In the Tuatara *(Sphenodon)* the tail can be broken off and regenerated, and partial regeneration of a damaged tail tip has been observed even in crocodiles.

It is remarkable that in certain geckos and skinks the external skin can be easily stripped off. If one holds a small gecko (e.g. an Indo-Australian *Peropus* or a *Geckolepis* from Madagascar) between the fingers it tries to escape by sloughing off large pieces of its skin — even including the innermost layer — so that it looks naked. In an astonishingly short space of time a new skin is formed over the damaged areas: a very remarkable protective device indeed, which may be of considerable value to its owner.

In general, all these protective devices are directed primarily towards concealment from the enemy, except some of the last-mentioned cases of akinesis. Now, defence against an enemy can also be achieved, not by concealing behaviour but, on the contrary, by deceiving or bluffing the enemy by behaviour that attracts attention; this may develop to the point of becoming a warning (to enemies of a different species) or a threat (towards rivals belonging to the same species). There is a whole range of defence reactions of this type amongst the amphibians and reptiles and they generally operate, like the concealing reactions, through the visual sense, though they may also be directed at the chemical and mechanical senses.

Thus, an animal that is habitually cryptozoic can intimidate by very striking colours, especially when it displays this attire unexpectedly. In this category, for instance, are the coral-snakes, which live only in the warmer areas of the New World, and whose body is ringed or cross-banded with red, yellow (or white) and black (col. pl. XIII). Amongst them there are highly venomous species *(Micrurus)* and a number that are venomous to a limited extent or are completely harmless. Since the latter enjoy the protection of the poisonous species which are usually avoided by enemies, the "coral livery" of the snakes has been regarded as a case of mimicry, i.e. an imitation by an unprotected species of one that is protected by the effects of selection.

Striking colours like these are widespread among salamanders (col. pl. I) frogs (col. pl. III, IV) and lizards. In the latter, rapid colour change often serves as a defensive colour: thus, chamaeleons often assume an almost black colour studded with bright yellow spots as a manifestation of excitement. Some lizards, however, are not content with that; they can, in addition, display, as a warning or a threat, certain vividly coloured parts of the body that are completely hidden when at rest. The gular sacs of the iguanid genus *Anolis* (pl. 47), which are generally very brilliantly coloured, are in this category. These are folds of skin which can be suddenly expanded to display the usually dazzling pattern on the skin between the scales; white, yellow, red, green and even black may appear, sometimes in divers combinations.

A few anurans and a number of lizards and snakes (pl. 65) have the habit of opening their jaws wide in the presence of an enemy and in doing so the intimidating action is often emphasised by the vivid colouring of the cavity of the mouth. In the Australian Shingleback *(Trachydosaurus rugosus*, col. pl. XI, pl. 58), for example, when the jaws are opened in threat the carmine-red mucous membrane forms an effective contrast to the cobalt-blue tongue, whilst in the Water Mocassin *(Agkistrodon piscivorus)* the buccal cavity is white, so that this snake has been dubbed "Cotton-mouth". In other snakes, moreover, when the interstitial skin on the anterior part of the body is displayed it is often distinctly more brightly coloured than the actual scales. When adopting a threatening attitude the agama *Leiolepis belliana*, of south-eastern Asia, flattens its body to display the unusually bright purple and yellow transverse bars on its flanks.

But the shape of the body may be even more drastically changed as a warning or a threat, so that the enemy is shown the greatest possible surface area. The simplest method is to lift up the whole body, or parts of it. A posture of this kind is most impressive when the body is raised up to such an extent that it is supported only on the hind limbs with the fore limbs clear of the ground. Many chamaeleons adopt this attitude by anchoring themselves to branches by their prehensile tails. An Australian monitor *(Varanus gouldii*, pl. 53) has also been observed in the same posture. Raising themselves up on all four limbs occurs in many lizards. Even the absence of limbs does not prevent reptiles from reacting in a similar way, as is evidenced by some snakes. As a defence reaction a small Australian venomous snake *(Vermicella annulata)* has the habit of raising one or more coils of its body quite vertically, thus creating a most strange effect. The tail may also be raised vertically in defence by lizards as well as snakes.

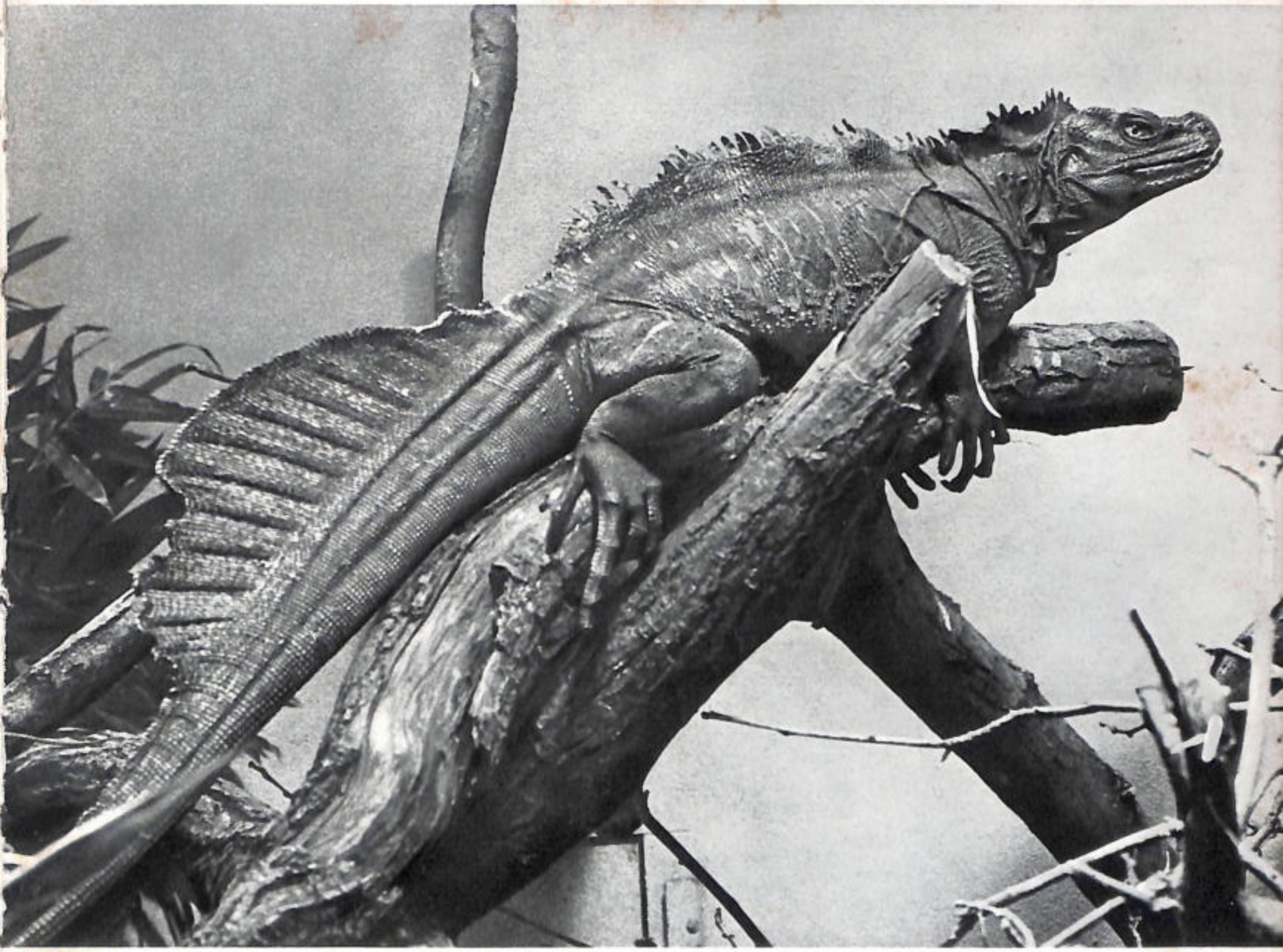
Inflation of the body is also very commonly practised and dilatation achieved in this way also serves to secure the animal more firmly in a hole or crevice. Inflation is practised by many toads and frogs, snakes and lizards. In chamaeleons the lungs extend into many tubular, blind-ending sacs that penetrate between the viscera; in consequence these animals can inflate their bodies enormously when irritated and create an impression of imposing size. By inflating themselves a few snakes may appear twice their normal size (col. pl. XII). There are snakes which are able to inflate their cervical regions in a most grotesque fashion, as, for example, the Chicken Snake *(Spilotes pullatus)* or a related species *(Phrynonax sulphureus)* which then gives the impression that it has swallowed a large egg. The mechanism for this dilatation consists of air sacs near the trachea or great distensibility of the lungs.

Just as inflation is used as a defence against enemies, flattening of the body is of common occurrence amongst lizards and snakes. The flattening may be from above downward (dorso-ventral) or from side so side (lateral). The former is characteristic of many snakes, as in the Grass Snake *(Natrix natrix)* and its relatives. This reaction is, however, best developed in the cobras *(Naja*, col. pl. XII), where the anterior cervical ribs are not only very moveable but are also considerably elongated. They operate the hood, a shield-shaped expansion of the neck which, in one African species *(Naja melanoleuca)*, displays a striking black and white cross-banding on its lower surface; the Spectacled Cobra *(Naja naja*, pl. 69) of south-east Asia, on the other hand, has a spectacle marking on its upper surface. In addition to these very venomous snakes a large number of completely harmless snakes adopt a very similar defensive posture.

To give an impression of more imposing size some lizards flatten the body from side to side; the deceptive effect is enhanced by the erection of dorsal crests or ridges of skin. The appearance of a lizard produces a distinctly more intimidating effect when unfamiliar structures appear in the head region. In this category, for instance, is the spreading of the gular sac in *Anolis* and other lizards, which has already been mentioned. The gular appendage of the Australian Bearded Lizard *(Amphibolurus barbatus)* occupies a special position. In this case not only the skin of the throat, which is covered with spiny scales, but also the very spiny skin at the corners of the mouth is supported by the cornua of the hyoid bone in such a way as to produce a very spinous dewlap drooping transversely to the longitudinal axis. The display of this almost black "beard" is accompanied by a threatening opening of the jaws and the exhibition of the yellowish-green lining of the mouth.

Almost stranger still is the effect created by a western Asiatic sand-agama *(Phrynocephalus mystaceus*, pl. 42) which spreads out large folds of skin edged with spiny scales at the corners of its mouth. When the animal is at rest these folds of skin form only a narrow fringe, but when it is annoyed they are spread apart; then, as a result of an influx of blood, they take on the deep rosy-red colour of the lining of the mouth and give the illusion of an enormously enlarged mouth. This gives the harmless lizard a particularly ferocious appearance. The huge ruff of the Australian Frilled Lizard *(Chlamydosaurus kingii*, pl. 44) is, however, undeniably the most imposing. In this creature the cutaneous folds are situated, not at the corners of the mouth but further back, on the sides of the neck. When danger threatens they are spread apart to form a gigantic umbrella-like structure standing vertical to the longitudinal axis of the body and coloured yellow, scarlet and steel-blue. The mouth is opened simultaneously with the opening of the collar. Finally, the occipital lobes of many chamaeleons, which can be spread out vertically from the neck, are head appendages with an intimidatory function.

All these reactions are associated with specific movements. But movement alone can also act as a menace. Many lizards, for instance, reveal their agitation by a rapid rhythmical raising and lowering of the body on all four legs; others show it by gently rocking to and fro on all four legs. The curious nodding of many lizards as well as the warning protrusion of the tongue in



Pl. 43. The Sail Lizard, *Hydrosaurus amboinensis*, gets its name on account of the high crest of skin on the anterior part of the male's tail. It is the largest member of the agama family and reaches a length of more than 3 feet. The native country of this lizard is the eastern part of the Indo-Australian archipelago. *Photograph by* Rosenberg.

Pl. 44. Australian Frilled Lizard, *Chlamydosaurus kingii*, unfolding its immense collar to intimidate enemies. × 0.3. *Photograph by* Maplestone.

many snakes (the tongue remains stretched out for some time) belong in this category. Stabbing movements of the head can also be executed and these simulate biting but without ever touching the enemy. The salamander *Ensatina eschscholtzii* lashes its tail. A few lizards also do this, whereas others curl and uncurl their tails; snakes, however, vibrate their hind quarters.

Certain snakes protect the head, the most vital part of the body, by using their tail to simulate a head. A small North American relative of the boas *(Charina bottae)* rolls itself up into a ball when it is disturbed; at the same time it lifts its tail up conspicuously and waves it to and fro, whilst its head remains unobtrusively on the ground. The impression of resemblance to a head may be even more convincing when the tail carries a distinctive marking, such as a red spot, whilst the remainder of the body resembles the background. When such a snake *(Cylindrophis rufus*, pl. 63) shows its tail, the enemy is deceived, taking this part of the body, which looks like a head poised for attack, for the head itself. This is particularly the case among snakes which have the end of the tail with markings simulating the head and where, to complete the illusion of similarity to the head, the tail end executes more lively movements than the head end. This kind of "head mimicry" (i.e. imitation of a part of the body capable of defending itself by one that is defenceless) is shown by the tails of a few harmless tropical snakes (pl. 64); it is significant that they are called "two-headed" snakes by the natives of very different countries.

There can, however, be defensive reactions which do not stimulate the visual but, rather, the chemical senses. Thus, for example, the secretion of nauseous substances is very common among snakes, but rarer among lizards. Most snakes have special glands at the base of the tail; by means of these the Grass Snake *(Natrix natrix)* can produce a stinking substance. Completely harmless dwarf-snakes are known whose odorous secretions are so sharp and pungent that, though defenceless, they are avoided by habitual enemies of snakes. Many tortoises (e.g. *Sternotherus*, *Clemmys*, *Pelomedusa*, *Chelodina*, etc.) and amphibians are also able to produce repulsive smells, quite apart from those engendered by the widespread discharge of excrement.

South-eastern Asia is the home of a non-venomous snake *(Macropisthodon rhodomelas)* which is able to flatten its neck like a cobra; when it does this it liberates a viscous, bitter-tasting secretion from the glands of the cervical region and thus wards off its enemies. The Australian Spiny-tailed Geckos *(Diplodactylus strophurus spinigerus*, pl. 39) make a counterpart to this; they are able to eject lymphatic fluid, which seems to have a disagreeable taste, to a distance of one or two feet through the soft spines of their tails. Perhaps it is permissible to refer in this connection to the curious squirting of blood from the eye in the North American horned-lizard (*Phrynosoma*, pl. 49), to the spitting of blood by the West Indian dwarf-boas *(Tropidophis)* and the emptying of the urinary bladder in many species. Although the effect of these defence reactions upon the enemy still remains to be investigated, it is an established fact that the widespread cutaneous secretions of amphibians are poisonous. In the firebelly-toads (pl. 4), the hylids (col. pl. II, pl. 12-14), true-toads (pl. 8-9) and some brachycephalids (col. pl. IV) and in many salamanders as well, e.g. the Spotted Salamander *(Salamandra salamandra*, pl. 1), the secretions are capable of irritating the sense of taste or the mucous membranes of the assailant to such an extent that it desists from further attacks on its victim. The Californian salamander *Ensatina eschscholtzii*, already mentioned, has so many poison glands on the upper surface of its tail that it is not molested by its enemies — small snakes of the genus *Diadophis* — though they unfailingly attack tailless salamanders of the same species!

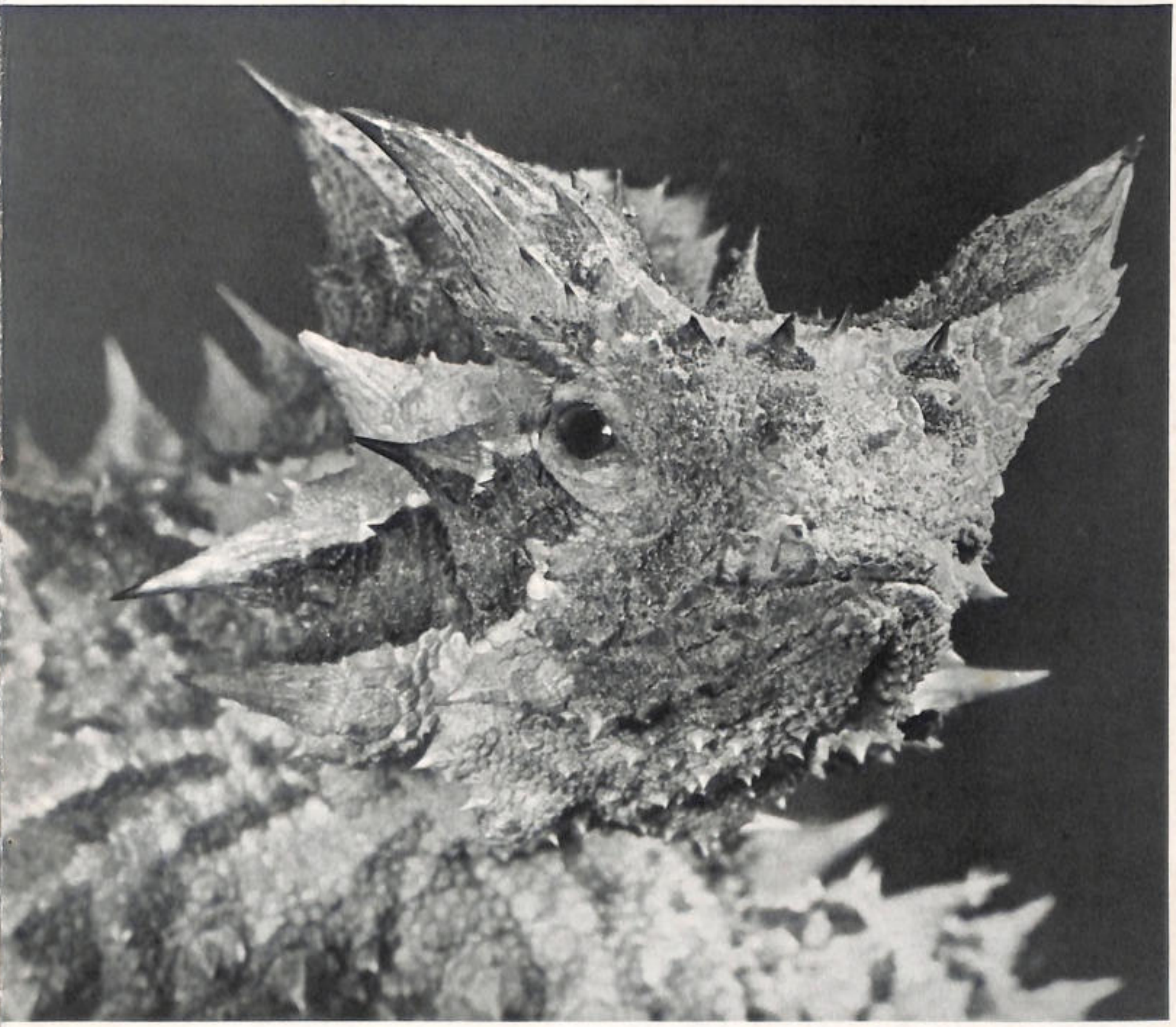
There are further reactions which exert an irritant and deterrent action on the hearing of the enemy, though they only play a minor role among amphibians and reptiles. As soon as they are caught, many frogs give a shrill cry; this is probably most penetrating in the Hispaniolan *Eleutherodactylus inoptatus*, though it is also heard from the Common Frog *(Rana temporaria)*. Some lizards do the same thing even when they are fighting one another; examples are the lacertas of the Canary Islands, the Australian finfoot-lizards *(Lialis burtoni)* and many geckos. The latter, as well as the crocodiles and the Tuatara, have a true voice. The shrill defensive cry of the Tokay *(Gekko gecko*, pl. 40) is very distinct, whereas the Tuatara and young crocodiles produce rather croaking sounds. Hissing or puffing sounds, produced by means of the respiratory tract, are of common occurrence in crocodiles as well as in the larger lizards and snakes. A very few reptiles are able to produce sounds by means of epidermal structures, i.e. by means of scales. In this connection, mention might be made of some desert-dwelling vipers of northern Africa and western Asia *(Aspis, Echis*, pl. 74); when disturbed they produce a noise deceptively like a hiss by rubbing together coils of the body which is equipped with peculiarly serrated scales. Strangely enough, the Egg-eating Snakes *(Dasypellis*, pl. 68) produce a similar warning noise in the same way.

As previously mentioned, many snakes are in the habit of vibrating the tip of the tail as a manifestation of excitement. If, in these circumstances, the tail pulsates against a substratum such as sand, wood, or dry leaves, a distinct noise, sometimes a rattle, results. An example of this is the well-known Bushmaster *(Lachesis muta*, pl. 78), which, with a length of four metres (13 feet), is amongst the largest solenoglyphs. The scales on the under-side of the tip of its tail are spiny and with these it produces, on a suitable substratum, a noise that recalls the rattle of the rattlesnakes.

It is not a very great step from snakes such as these to the rattlesnakes *(Sistrurus, Crotalus*, pl. 78-80) which have a special organ, the tail rattle, for generating sound. This is formed as follows; the terminal caudal scale of newly-born specimens is shed in the usual way with the rest of the skin during their first moult, but is not sloughed at the second and subsequent moults; it remains socketed on to the annular constriction of the one in front of it. In this way a long chain is produced, consisting of terminal scales shackled on to one another anteriorly; these form the individual segments of the rattle. Since the hindmost segments of the rattle, which are the oldest and, at the same time, the smallest, are lost in the course of time, one cannot always compute the number of successive ecdyses from the number of segments composing a rattle. From two to five segments are added to the rattle annually; nevertheless, the rattles of the majority of adult rattlesnakes contain only 5 to 9 and more than 14 are present only very exceptionally.

Like other species without a rattle, rattlesnakes indicate irritation by rapid lateral vibrations of the tail, thus creating a very characteristic noise. The speed of the vibrations depends upon body temperature: at +8° C. (46.4° F.) it is 17 cycles per second, but at 36° C. (96.8° F.) it is 88. The rattling of the larger species can be heard at a distance of more than 30 yards, but of smaller species at only a few yards. Now, what is the importance of the rattling for these remarkable creatures? It cannot serve as a means of mutual communication between the sexes since, in regions where rattlesnakes are abundant, the noise is never heard with undue frequency during the breeding season, nor has it been noticed to be any more frequent amongst animals that have been successfully mated in captivity. Nor can it be explained as a call for enticing prey since, if they are not disturbed, the snakes remain silent even when extremely hungry. On the other hand, the rattling is a characteristic warning signal: it serves to protect the snakes, which live principally in open country, by warning potentially dangerous enemies before they get bitten. Observations have shown that even small carnivores are deterred from attacking rattlesnakes. Consequently, the rattling not only preserves the fangs but also conserves the store of venom which is so important for acquiring food. It is, therefore, a purposeful protective device, analogous to the clashing of the scales in *Aspis* or the display of the "hood" in *Naja*.

There are, of course, defence reactions which produce a contact stimulus, only, and this frightens off or intimidates the enemy or adversary. A protective device becomes the more effective the more it simulates the characteristic actions of a genuine fight. Thus we see that, amongst amphibians, some toads *(Bufo)* butt their adversary with inflated body and head held low. This reaction is much more common amongst reptiles; many snakes execute striking movements at their adversary using the fore-part of the body but without actually biting. The Grass Snake *(Natrix natrix)* sometimes strikes repeatedly at an aggressor but scarcely ever attempts to bite. The efficacy of this type of butting is increased the more the head is provided with sharp edges, spines or horns. There are species, especially among chamaeleons, and in the male sex particularly, that have horns which are used in the sham fights between rivals; in spite of their pointed weapons, they seldom inflict serious wounds on each other. Jabs



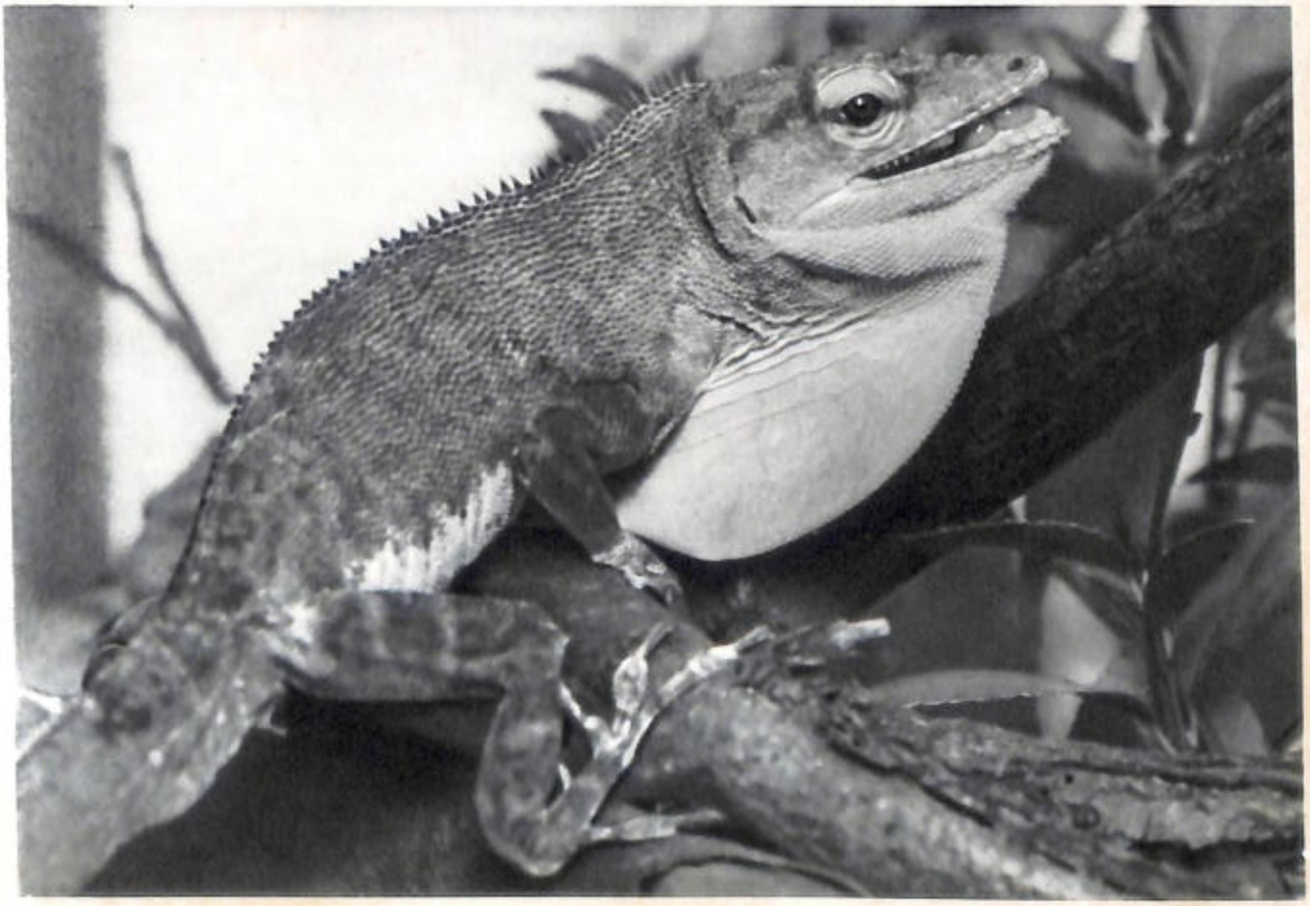
Pl. 45. Head of the Thorny Devil or Moloch *(Moloch horridus)*. Compare with the coloured plate VII. ×5. *Photograph by* Warham.

Pl. 46. African Flap-necked Chamaeleon, *Chamaeleo dilepis*, sloughing its skin. ×1. *Photograph by* G. Senfft.

This Central American iguana, *Corythophanes cristatus*, recalls a chamaeleon in the shape of its head. ×1. *Photograph by* Rosenberg.

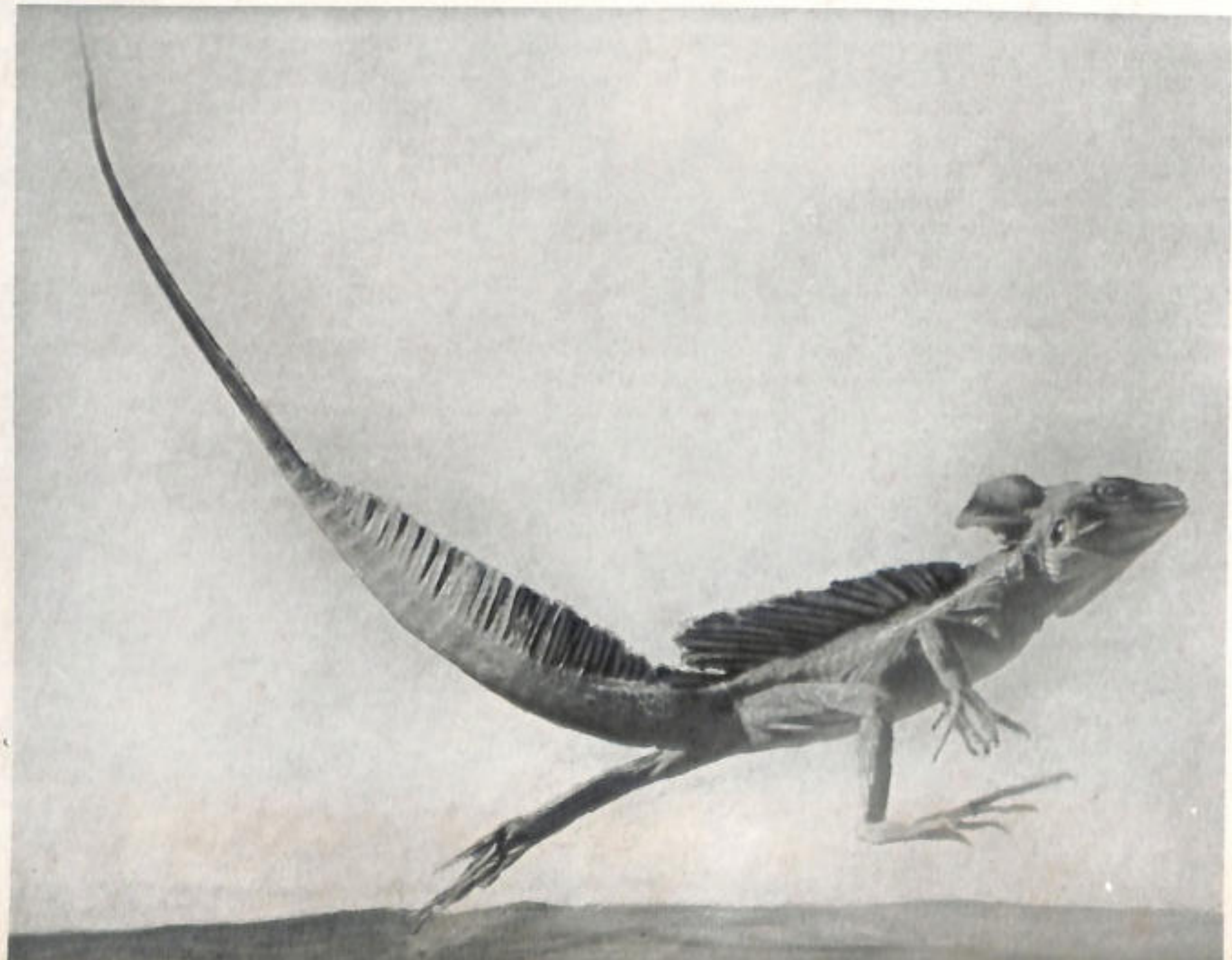
Pl. 47. This South American iguana, *Polychrus acutirostris*, is also reminiscent of a chamaeleon in its grasping feet, prehensile tail and eye-structure. ×0.6. *Photograph by* Rosenberg.

Giant Anole of Haiti, *Anolis ricordii*, displaying its immense gular pouch. ×1. *Photograph by* Rosenberg.



Pl. 48. Head of the Green Basilisk, *Basiliscus plumifrons*, from Costa Rica. ×1. *Photograph by* Rosenberg.

Common Basilisk, *Basiliscus basiliscus*, running on two legs. ×0.2. *Photograph by* Snyder.



or blows can, however, be imparted by other parts of the body, too, especially by the tail. A few snakes possess a very peculiar defence mechanism in their tail, which ends in a spiny scale; if one holds a snake with a spiny tail *(Typhlops, Oligodon)* tightly one very quickly feels the effects of this weapon as the tip of the tail is pressed really hard against the skin of the aggressor.

From such defensive reactions it is but a short step to the functions of the actual weapons of defence or protection whose importance bears little relationship to the warnings, threats and deceptions previously discussed. Thus some lizards can mete out blows with their tails that are scarcely less effective than those of crocodiles of equal size. In the larger monitors, especially, the muscular power of the tail is quite astonishing. Its effectiveness may be increased by the modification of the caudal scales into spines as, for instance, in the spinytail-iguanas *(Ctenosaura)* and the mastigures *(Uromastyx)*. The rest of the body may likewise be covered with spiny scales as, for instance, in many girdle-lizards *(Cordylus*, pl. 50), skinks *(Tribolonotus*, *Egernia*, pl. 59), horned-lizards *(Phrynosoma*, pl. 49) and, above all, *Moloch horridus* (col. pl. VII, pl. 45). Ossification may endow the spines, and especially the scales, with great strength, as is shown by some lizards (pl. 51) and, pre-eminently, the crocodiles. Some frogs are known which have a bony dorsal shield under the skin. The skull, too, may be very heavily ossified and in some anurans it is used for blocking up the entrance to their hiding places (e.g. a hole in the ground or the leaf-cup of a bromeliad). Strange to say, some lizards with spinose tails *(Uromastyx)* use the hinder end of the body for the same purpose.

It is clear that the strongly ossified shell of the tortoises constitutes a very fundamental protection against enemies. In general it is stouter amongst the terrestrial tortoises than in the aquatic forms. When danger threatens the head and limbs are withdrawn inside the protective armour. If the neck is very long, as in the snakeneck-turtles of Australia (pl. 30) and South America, it is bent round sideways between the carapace and plastron. In a few genera of tortoises (e.g. *Kinosternon*, *Terrapene*, col. pl. V) discrete sections of the plastron are moveable so that the shell can be closed completely. The Hinged Tortoise *(Kinixys)* can achieve the same result with the moveable hinder part of its carapace. In tortoises with a small, or incompletely ossified, shell other protective characters are developed in compensation: thus, both the Snapping Turtle *(Chelydra)* and many softshell-turtles *(Trionyx*, pl. 32), which have only a small bony shell, show a very great readiness to bite: the remarkable Crevice Tortoise *(Malacochersus tornieri)*, with its soft, flat shell, shows a readiness to take to flight, a characteristic which is also very marked in the softshell-turtles.

The claws are another important weapon of defence, especially in all the tortoises, the larger lizards and the crocodiles. Frogs, too, are known that have sharp claws, but these are, of course, not homologous with reptilian claws. Amongst them must be mentioned not only the singular clawed-toads *(Xenopus, Hymenochirus)* but more especially the Hairy Frog *(Trichobatrachus robustus)*, in which the terminal phalanges of the second, third and fourth toes are recurved and claw-like and have points as sharp as needles; these pierce the skin on the under-side of the tips of the toes and can be retracted after use. For this reason one can scarcely hold a Hairy Frog in one's hand, since it scratches at once and draws blood. The claws are not only an efficient weapon for the frog but also an instrument by means of which it can anchor itself between the stones in the swift-running water of its habitat. The claws of the Clawed Salamander *(Onychodactylus)* probably also serve the same purpose.

From what has been said before, it is clear that the jaws, whether with or without teeth, can also be a very effective weapon in real combat. It is not generally known that there are salamanders that defend themselves by biting. Thus the Amphiuma *(Amphiuma means)* is as capable of biting as the Escuerzos *(Ceratophrys*, pl. 5, 6) and their relatives *(Telmatobius)* among frogs; some other species of frogs in other groups also bite. The bites of the larger lizards, crocodiles, tortoises and snakes may be not only extremely painful but also dangerous; this, of course, applies particularly to the venomous snakes whose venom equipment originally served the purpose of acquiring food and not of protection against enemies. No venomous snake would attack human beings unless it had been unduly provoked.

Nevertheless, a few venomous snakes use their venom in a very remarkable way, not for capturing their prey but for defence against an enemy: these animals are, in fact, able to spit venom. Amongst the best-known spitting snakes, apart from the Ringhals *(Hemachatus hemachatus)*, there are the Black-necked Cobra *(Naja nigricollis)* in Africa and the Spectacled Cobra *(Naja naja*, pl. 69) in Asia; the latter, to be sure, has adopted the strange habit of spitting venom only in a few areas of its immense habitat. The poison fangs of these animals show certain peculiarities; in particular, the orifice of the channel at the tip of the fang is not directed downward and backward, as is usually the case, but more upward and forward. Thus the poison can be discharged at an enemy to a distance of six to eight feet; at the same time the snake aims at the attacker's eyes. The venom of these snakes — in contrast, for instance, to the poison of *Bitis* that is not ejected — has the property of penetrating into the eye of the enemy, where, on occasions, it causes serious lesions.

Pl. VIII. The male of the East African *Chamaeleo jacksoni* is characterised by three stout horns on its head. × 0.8. *Photograph by* Senckenberg Museum (Haupt).

The Leaf Chamaeleon *(Brookesia spectrum boulengeri)* resembles a dried leaf. × 1. *Photograph by* de Witte.

CHAPTER SEVEN

ASSOCIATIONS AND COMMUNITY LIFE

An animal's biological environment need not be merely of importance as a source of food or of enemies; it may also be shared with the animal's social or sexual partners, i.e. it may contribute in some manner towards the building of a community. In this way an association of animals of the same or of different species may be formed, comprising many individuals or only a few, sometimes only two. Finally, an association may be constituted on a sexual or predominantly genetic basis, or be totally unconnected with reproduction. The problem, therefore, concerns a variety of factors which recur in widely differing ways in the life of amphibians and reptiles.

Whoever has observed these creatures in the wild state knows that many amphibians and reptiles do not lead solitary lives, but are found in large numbers in certain places. Edible Frogs *(Rana esculenta*, pl. 20, 21) bask, sometimes in dozens, on the banks of ponds; frog larvae form shoals numbering many hundreds or even thousands in the sun-warmed waters of pools and between these shoals groups of newts swim around. The visitor to the southern Alps, Italy or Sicily will certainly remember the extraordinary number of lizards encountered there; from even a single vantage-point one can sometimes see half a dozen or more of these graceful creatures in the sunshine! A further well-known example of associations of this kind among reptiles is found in the swarms of tortoises basking on large stones or branches of trees overhanging the surface of water, spectacles that one encounters again and again especially in south-eastern Europe and the United States.

In all these cases can one speak of communities in the social sense? The most important characteristic of an animal community — in contrast to a plant community — is not merely gregarious occurrence, as such, but the aggregation of the single individuals in such a manner that they have some kind of mutual inter-relationship. When, therefore, some frogs or lizards are congregated together merely on account of favourable living conditions — perhaps a particularly sunny spot or a plentiful food supply — that is, of course, an assemblage of animals but not a true community or society. This applies, for instance, to the groups of toads or geckos that collect at night in the tropics to hunt the thousands of insects attracted by the light of a lamp.

In the same way, the great assemblages of tree-frogs *(Hyla)* which congregate, for example, in the immediate neighbourhood of small river-pools during the summer in the arid areas of central Australia are not communities. They form a society for the first time when the drought increases and the waters dry up completely; then, masses of tightly packed frogs are to be found under the still damp mud, in crevices or similar retreats, and in this way they survive the unfavourable season. Each individual can profit from an aggregation of this kind since there is less danger of loss of moisture when the frogs are tightly packed together. The same thing is venom. Amongst the best-known spitting snakes, apart from the Ringhals *(Hemachalus hemachalus)*, there are the Black-necked Cobra *(Naja nigricollis)* in Africa and the Spectacled Cobra *(Naja naja*, pl. 69) in Asia; the latter, to be sure, has adopted the strange habit of spitting venom only in a few areas of its immense habitat. The poison fangs of these animals show certain peculiarities; in particular, the orifice of the channel at the tip of the fang is not directed downward and backward, as is usually the case, but more upward and forward. Thus the poison can be discharged at an enemy to a distance of six to eight feet; at the same time the snake aims at the attacker's eyes. The venom of these snakes — in contrast, for instance, to the poison of *Bitis* that is not ejected — has the property of penetrating into the eye of the enemy, where, on occasions, it causes serious lesions.

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The large masses that appear in the winter-quarters of amphibians and reptiles are on the border-line between assemblages and communities. They are brought together there by particularly favourable conditions. But one certainly cannot speak of a community in the case of the Common Frog *(Rana temporaria*, pl. 19) which forms a very loose association in icy water. It may be different in the case of tightly packed animals outside the water, because, in a medium that is a poor conductor of heat, a massing of individuals may bring an advantage to each single one by conserving the heat. Large migratory associations have also been observed in reptiles and amphibians; in these, orientation, i.e. the maintenance of a definite direction, is made easier for the individual animals by migration as a community. This applies, for example, to salamanders which all follow the same direction towards their winter-quarters, to toads struggling towards their spawning pools and to marine turtles pressing onward to their nesting sites.

As mentioned earlier, communities of this kind may consist not only of individuals of one and the same species but of very different species. This obtains, for instance, in regard to hibernating communities in which salamanders may be associated with frogs and tortoises with snakes, and this is the case, also, in communities formed for survival in times of drought. Naturally, positive advantages accrue to the benefit of the different species forming the community. Of these communities of mixed species, the following play a definite part amongst amphibians and reptiles.

Most frequently it is simply that two species of animal live together, a phenomenon called habitat-synoecy. In this, the one species benefits from the living accommodation provided for it by the other, whereas the association is a matter of indifference to the latter. Thus, in the south-eastern United States the Gopher Tortoise *(Gopherus polyphemus)* lives in burrows 3-7 metres (10-23 feet) long which it constructs itself and into which it retires in times of great heat, during rain, and in winter. Usually the tortoise shares its burrows with the Gopher Frog *(Rana capito)* which finds there, in addition to shelter, a supply of food consisting of insects that have also withdrawn into the burrows. Another case of synoecy which some birds and marine turtles share, is only very short-lived; Boobies were once observed in the north-east Pacific using the carapaces of a large shoal of swimming-turtles *(Lepidochelys olivacea)* as a resting platform. Although this is an isolated phenomenon, some invertebrates nevertheless frequently attach themselves to marine turtles and sea-snakes and thus are passively transported over vast distances. The Cirrepedes, a group of crustaceans, contain genera of this kind, such as the universally known barnacles *(Balanus)* and goose-barnacles. Among the latter there are some large forms *(Conchoderma)* which have been shown to be synoecious partners of the Leathery Turtle *(Dermochelys coriacea)*. The herpetological collection of the Senckenberg Museum has a preparation of a sea-snake *(Laticauda semifasciata)* showing several small barnacles on its paddle-like tail and underneath the head.

Even fishes have been observed as associates of marine reptiles. It was found that the Sucker Fish *(Echeneis)* and the Pilot Fish *(Naucrates)* never left a Leathery Turtle. Whilst the Sucker Fish can attach itself firmly to the back of the turtle by means of its large sucker and be passively transported, the Pilot Fish swims actively and follows indefatigably behind large fishes in order, probably, to devour the scraps that fall when they eat. That is certainly the advantage they derive from following marine turtles; possibly the excreta also contain particles that can be utilised by *Naucrates*. An association in which the species benefiting from the partnership share the same food is described as a special kind of synoecy and called commensalism. It is possible that the fishes of the genus *Caranx*, which have been known, on occasions, to be companions of the sea-snakes, are also commensals, but this has not yet been proved. True commensals are seldom found amongst amphibians and reptiles; there are, however, predacious synoecists, i.e. associates or companions to whose predatory feeding habits their hosts fall victims.

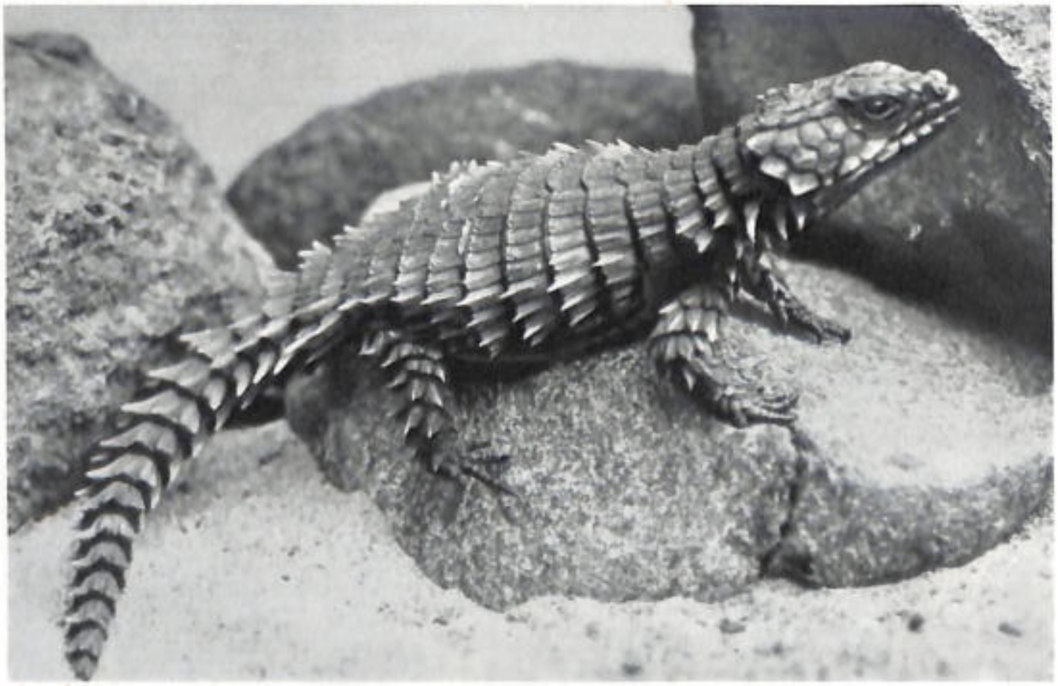
Thus, in all countries there are numbers of anurans, lizards and snakes which are known

Pl. 49. Two male Galapagos Island Sea Iguanas, *Amblyrhynchus cristatus*, fighting. Compare with the coloured plate IX. *Photograph by* Eibl-Eibesfeldt.

Horned Lizard, *Phrynosoma cornutum*, from the southern United States. ×1. *Photograph by* Rosenberg.

Pl. 50. *Gerrhosaurus nigrolineatus*, a large lizard of the African steppes. ×0.6. *Photograph by* Rosenberg.

In the South African *Cordylus cataphractus* most of the scales are converted to plates armed with spines. ×1. *Photograph by* Rosenberg.



Pl. 51. The Glass Snake, *Ophisaurus apodus*, of south-eastern Europe and western Asia is a relative of the European Slow Worm, *Anguis fragilis* (see below). × 0.5. *Photograph by* Rosenberg.

In the European Slow Worm, *Anguis fragilis*, limbs are completely degenerate externally, whereas in *Ophisaurus* vestiges of the hind limbs are still recognisable externally. ×1. *Photograph by* Rosenberg.

Pl. 52. *Heloderma suspectum* and a second species belong to the one and only poisonous lizard genus. It is endemic in the south-western United States and northern Mexico. Their nearest relatives are the Old World monitors. ×0.6. *Photograph by* Rosenberg.

to prefer to live in ant or termite colonies. The Slow Worm (pl. 51) is sometimes found in ant-heaps. In tropical regions the amphisbaenians (Amphisbaenidae) frequently live with termites in their mounds. Some skinks, teyous, gerrhosaurids and other groups of lizards also live in the same way, as well as some of the blind-snakes, thread-snakes and various different groups of colubrine snakes. Many lay their eggs in these places and in this way obtain not only protection against enemies but also reap the benefit of a constant temperature. Furthermore, as a result, the newly-hatched young ones have food at their disposal, since not only termites, but also ants and their pupae (the so-called "ants' eggs") form an important foodstuff for many lizards and anurans, and indeed for some snakes (especially for *Leptotyphlops)*. Naturally, actions of this kind result in the destruction of single animals, only, but the whole insect kingdom is never in any danger.

Just as the burrows of the Gopher Tortoise, mentioned above, have their characteristic synoecist in the Gopher Frogs, the holes of the Prairie Dog *(Cynomys socialis)* of North America, a rodent related to the Ground Squirrel, are likewise inhabited at times by synoecists; not only by the Burrowing Owl *(Speotyto cunicularia)* but also by the Prairie Rattlesnake *(Crotalus viridis)*. The latter is, of course, not a wholly innocuous guest, but a usufructuary enjoying threefold advantages, after the pattern of the guests of ants and termites mentioned above. The snake uses not only a good hiding place but one which is also warmed by its warm-blooded host; it has, moreover, been proved to attack the young of its hosts. A similar life is led by the Tuatara *(Sphenodon punctatus*, col. pl. IX, pl. 36) which, on some islands, lives in the three-feet-deep underground burrows of certain sea birds *(Puffinus, Majaqueus, Oestrelata);* on Stephen Island, for instance, the soil is partly undermined by nesting holes of this kind. The fact that in this area so many nestling chicks are victims of the rapacity of the famous reptile is in no way injurious to the continued existence of the birds.

If two species live together and both partners benefit from doing so, we speak of symbiosis. This kind of cohabitation is very uncommon in our two classes of vertebrates. The often quoted symbiosis between the Egyptian Plover *(Pluvianus aegyptius)* and the Nile Crocodile has received no corroboration in recent times; the little bird was supposed to free the crocodiles, as they lay basking in the sun, from their ectoparasites and even to cleanse their mouths; in return it was supposed to enjoy the protection afforded by the close proximity of these reptiles. The hypothetical symbiosis between the Nile Crocodile and the Spur-winged Plover *(Hoplopterus spinosus)* is equally unfounded; the latter is supposed to benefit from the protection afforded by the proximity of the crocodiles which, on their part, are alerted by its "warning" cry. But one can definitely talk of symbiosis between a few insular lizards and certain sea birds which nest in colonies. On certain Adriatic islands, for example, lizards *(Lacerta melisellensis)* related to the Wall Lizard are very numerous where sea-gulls breed. It has been observed that the lizards rid the birds of their ectoparasites, such as bird-lice (Mallophaga) and mites, by eating the parasites. In an environment such as a small rocky islet whose food resources are not over-abundant, this habit is certainly an advantage for the lizards which should not be underestimated. It is worth noting that precisely similar relationships between birds and lizards exist on the famous guano islands off the Peruvian coast where millions of cormorants and other guano-producing sea birds breed; there the numerous lizards *(Tropidurus peruvianus)* behave in the same way, so that they are symbionts useful to mankind also, and enjoy legal protection in consequence.

The presence of algae on the inner surface of the external egg-covering of some species of amphibians is an instance of symbiosis with plants. It has been found that in *Ambystoma maculatum*, a North American salamander, eggs with an algal overgrowth produce larger embryos, hatch earlier and have a lower mortality than eggs without algae. On the other hand, the algae also benefit since they grow more rapidly on eggs containing embryos than in egg-shells from which the embryos have been removed.

Neither amphibians nor reptiles are known to be parasites, that is to say animals which obtain their nourishment from other animals and are, consequently, more or less harmful to them. Both these two classes of vertebrates, however, serve as hosts to countless external and internal invertebrate parasites, e.g. some flies and their larvae, ticks, mites, linguatulids, leeches, round-worms and flat-worms, as well as protozoa. Sometimes these parasites cause the death of their host and this is always the case with toads which are attacked by a fly *(Lucilia)* whose larvae develop in their nostrils.

To return to the associations of amphibians and reptiles of the same species, which were discussed at the beginning of the chapter, e.g. frogs sitting at the edge of a pond, or lizards sunning themselves on a wall: although mass assemblies of this kind, brought about primarily by external factors, do not have the character of a true community, it can nevertheless very well happen that a definite order reigns in the dispersion of the single individuals (e.g. the two sexes and their young); this indicates that even in a simple congregation of individuals there may be a form of social conduct.

Amongst the amphibians and reptiles there are clearly only relatively few species whose members move around far and wide and at random. This certainly occurs amongst the marine turtles and sea-snakes. On land, wandering species of this type, e.g. the Horned Viper *(Aspis cerastes*, pl. 74) of the Sahara, are similarly associated with a very uniform environment, i.e. the sandy desert. Snakes seem to be inclined to a really nomadic existence, but by far the greater number of reptiles and amphibians have a very restricted habitat. Even when a species is distributed over a very wide range, the individual animal is often content with only a very small area. The Sand Lizard, for instance, is distributed from western Europe over the whole of central and eastern Europe as far as central Asia; but in spite of this the individual lizards live, year in year out, in an area of only a few square yards and always return to the hiding place in it. Every lizard-hunter takes advantage of this behaviour; if he has failed to catch a lizard the first time at a certain spot he can try his hunter's luck again at exactly the same spot some time later.

Land and freshwater tortoises, also, often have only narrowly circumscribed living areas, which in the case of the water-tortoises may, however, extend over several pools. In the east of the United States, for example, the widely distributed Red-ear Turtle *(Pseudemys scripta elegans*, pl. 26), which is a popular aquarium animal, resorts constantly to well-defined positions on the bank which are, on the average, 30 yards long, and they always return to them. In waters where there are many turtles, it can be seen that a particular stone, or inclined tree-trunk, is always sought out by the same individual for basking in the sun. The living spaces of the North American Box Turtles *(Terrapene c. carolina*, col. pl. V) have a diameter of at most a hundred yards. If they are transported elsewhere, even to places unfamiliar to them, they show their homing instinct by returning to their old familiar quarters; they obviously cannot rely on precise topographical knowledge and recent investigations show that they orientate themselves by the sun.

The regular haunts of some salamanders and frogs are even smaller. Amongst the latter there are some species (e.g. the North American *Rana clamitans)* whose haunts on the banks are separated from each other by very small inter-spaces of only 6-10 feet. In an experiment of five years' duration it was found that half the specimens of a North American frog *(Scaphiopus holbrooki)* that were studied covered a distance of less than about 33 feet. A single frog of this species lived in one and the same hole for more than four years! Some toads *(Bufo)* show a similar love of home, although some migrate considerable distances in spring to certain fixed bodies of water to mate and to spawn.

In contrast to the environment (biotope), an ecological concept applicable to the species, we term the area in which one, or perhaps a few, individuals live as the home range (German: Wohnbezirk). The home range can, as we have just said, be very small, but it may also — as in the case of *Bufo* — be divided into two distinct and widely separated areas which are each inhabited according to the season of the year. Now, there are occupied areas whose owners defend them in a surprising fashion against unwanted intruders much in the same way as a bird defends its nest; in such cases one does not speak of home ranges, but of territories. A territory embraces either the entire home range in which an individual passes its active life or only a small part of it, separated from a neighbouring territory by a no-man's-land. In this case the individual has both a home range and a territory which may be very small and consist only, for instance, of a stone, tree-trunk, fence-post or the like.

A home range may be occupied by one or more individuals of the same sex, or different sexes.

Pl. IX. The head of the well-known *Sphenodon punctatus* calls to mind one of the iguanas (Iguanidae). × 1. *Photograph by* Senckenberg Museum (Haupt)
The Sea Iguana *(Amblyrhynchus cristatus venustissimus)* of Hood Island, Galapagos Islands, in its natural habitat. This subspecies has a remarkable coloration and attains only 30 inches instead of the 54 inches of the typical race. *Photograph by* Eibl-Eibesfeldt.

In a territory conditions are normally more stringent; generally it is inhabited by a single male with which one or more females and also young animals may be associated. It is the male which is very aggressive towards other males and defends his territory, although females, when they occupy separate territories of their own, may ward off unwelcome intruders. Territories of this kind may be either retained during the whole active period or taken up only during the breeding season. Apart from crocodiles *(Alligator mississipiensis)*, a territorial sense has only been definitely proved to exist among reptiles in a few groups of lizards: certain geckos, agamas, iguanas, true-lizards and skinks. Chamaeleons, too, probably have territories and the Tuataras *(Sphenodon punctatus)* as well, since they are characterised by marked pugnacity. Snakes and tortoises, on the other hand, probably have home ranges but not territories, and the same applies to amphibians, although the first steps towards territorialism are thought to have been observed in frogs (*Phyllobates trinitatis*, *Rana clamitans)*.

The methods employed to defend a territory against intruders — which are mostly individuals of the same species and the same sex — are often harmless; for instance, visual signals such as sudden colour change, display of a vividly coloured gular sac, increasing the size of the body by inflation or flattening, erection of dermal folds, opening the mouth, nodding movement of the head and other reactions intended to "impress" which have been discussed in a previous chapter. The territorial sense is very widespread in the iguanid genus *Anolis*: as soon as a male of the common Green Anole *(Anolis carolinensis)* becomes aware of another male approaching its territory it spreads out its gular sac, sometimes erects a dermal fold on its neck, and alternately raises and lowers the anterior part of its body. The opponent behaves in the same way unless it prefers to withdraw. If it does not withdraw, the attempts at mutual intimidation continue until a fight develops and one of the two adversaries is put to flight.

In most cases the fights are harmless — they are sham fights or attempts to intimidate. Even the very pugnacious male chamaeleons armed with horns only rarely do serious damage to each other. Fights are also very frequent among the Sea Iguanas *(Amblyrhynchus cristatus*, pl. 49) which often lie in great hordes on their native lava-flows and where a territory is occupied by a single male and several females. These conflicts between the males are, however, usually a kind of ritual, preceded by characteristic behaviour designed to impress. In *Amblyrhynchus* fights ending in injury are much rarer and actually only occur when a fleeing male suddenly finds itself in a foreign territory by mistake. The equally frequent combats (often after a brief phase of intimidation) characteristic of the males of the true-lizards, such as *Lacerta viridis* (pl. 57), *agilis*, *muralis* and many others, may indeed end disastrously for the combatants within the confined space of a terrarium; in the open, however, it is probable that they very rarely end in serious injury.

It is interesting to note that some other reptiles that do not occupy territories, but only home ranges, also fight during the breeding season. The actions of some tortoises are most peculiar when they do this; the land-tortoises *(Testudo)*, for example, chase each other and try to drive their adversaries into a corner by repeatedly bumping them with their shell, biting at the same time. The attacker is always a male, though the one attacked may be a female. Fighting is also known to occur in other genera such as *Gopherus* and *Terrapene*. Even more curious are the battles between some snakes at the breeding season, as for instance, the Adder, the Asp, the rattlesnakes and certain colubrine snakes. Only the males participate, the females remaining passive. Combat follows an attempt at intimidation which consists of raising the anterior part of the body which is bent into an S-shape. Then two or more animals begin chasing each other and coiling round each other, the body being generally held erect whilst this is going on. During this strange behaviour there is never any attempt to use the teeth and the participants remain completely unharmed, so that, here again, the "fight" must be put in the category of intimidatory behaviour or "ritual challenge". Its true significance is not clear; whether it is the last vestige of a former territorial sense (or the first rudiment) appears debatable (pl. 72).

Whenever a lizard with a territorial sense moves to new ground it is in the habit of giving a signal; if a male *Anolis*, for example, jumps on to a new branch it advertises its new property by spreading its gular sac; under similar circumstances agamas give a signal by nodding their heads. A number of nocturnal lizards emit sounds; the house-geckos, which are so extraordinarily abundant in the Indo-Australian archipelago, make chirping sounds which appear to have the same significance as the gular sacs and vivid colours of the lizards previously mentioned, i.e. to advertise a territory. When the body of a male Californian gecko, *Coleonyx variegatus*, is touched it emits a high-pitched note which serves to defend its small territory. It is not yet certain whether the well-known far-sounding "Tokay" call of the male *Gekko gecko* (pl. 40) in Java has a similar function or whether it serves to lure the females. The voice of male Green Frogs *(Rana clamitans)* appears to have both these functions, to keep other males away from their territories and to attract females. Finally, it has recently been established that there is a relationship between the bellowing of alligators and territorialism. Although the real significance of these strange noises is not yet clear, they are nevertheless associated with life in a community. It is obvious that all these noise-producing animals — in contrast to the snakes — must have auditory faculties. Whether some lizards (e.g. geckos) mark their territories by repeatedly depositing their excrement in the same place is a problem that calls for investigation.

The pugnacity of many male lizards, which manifests itself in intimidatory behaviour and in fighting, leads on, in many instances, to an important community-forming principle — the hierarchy. In a group of individuals occupying a territory each animal has its own fixed social position. The strongest male rules over all the others, the second strongest is subject only to the strongest and dominates all the others, and so on.

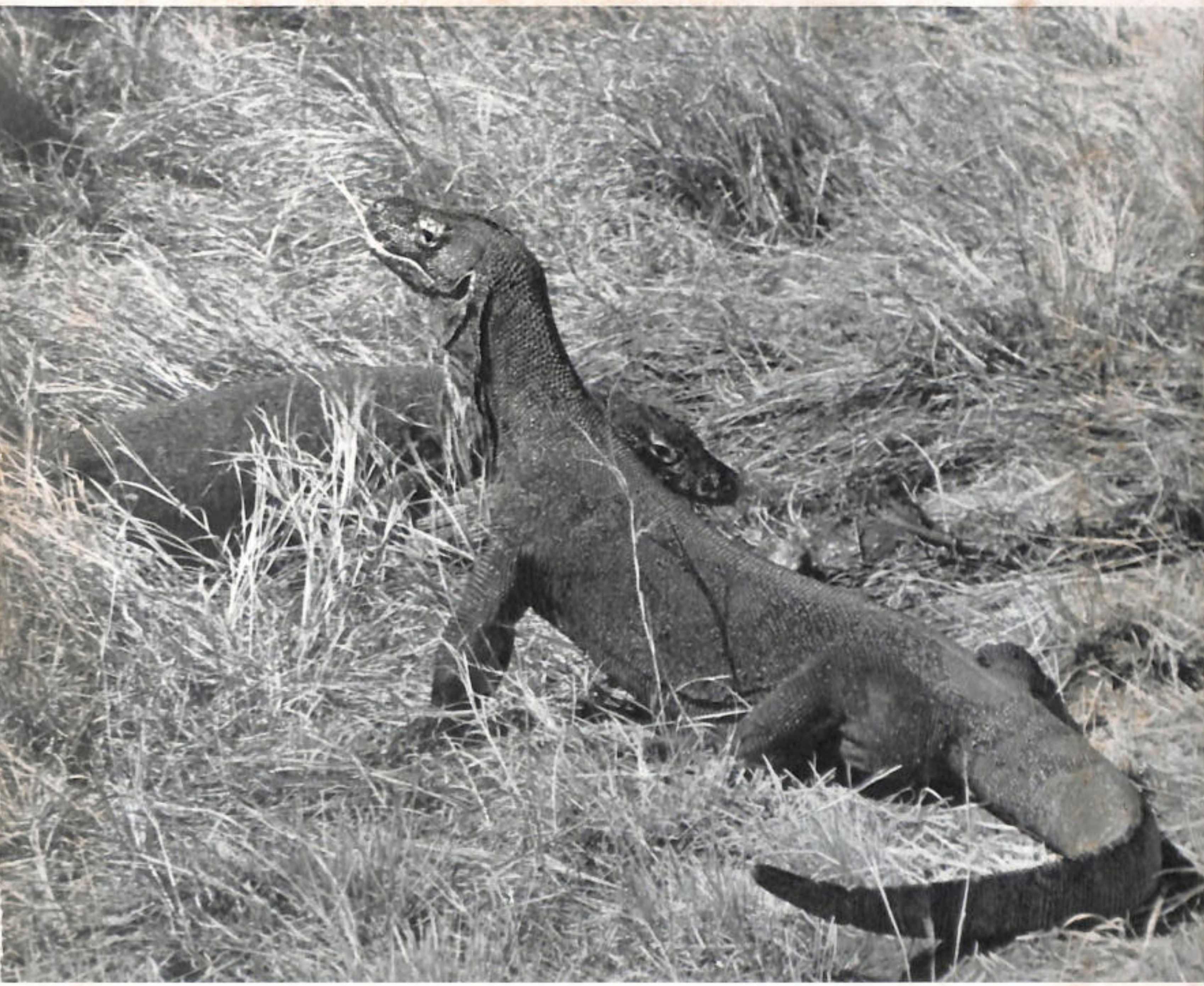
This type of hierarchy can be observed in a terrarium containing a number of Wall Lizards, and is doubtless of frequent occurrence in lizards characterised by a territorial sense and a high population-density; a social hierarchy has been recognised especially in iguanas, such as *Anolis* and *Sceloporus* and some large species of the genus *Ctenosaura*. The density of population is often very high, especially on the smaller islands, so that some territories are probably inhabited by two or more males. This explains why not a few island-dwelling lizards are known to be extremely pugnacious.

In conclusion, there remains the important question — what advantages do animals derive from the social behaviour described here, especially from territorial possession and the territorial struggles and reproductive clashes? Even though the individual may be endangered by the latter, and so debarred from reproduction, the struggle has a real significance for the posterity of the species. This is achieved because, in general, it is the strongest and healthiest male that is allowed to mate. It is precisely because of the struggles between combatants of the same sex and species that vigorous individuals are successful in mating and so propagate their own stock to the benefit of the species. Finally, the whole territorial system brings advantages with it; not only does it ensure an equal distribution of the sexes in a particular region but it also prevents deleterious overcrowding.

Pl. 53. Gould's Monitor, *Varanus gouldii*, is the most widely distributed of all the Australian monitors. Its hiding places are holes in the earth which it digs for itself or which are derived from other animals. ×0.8. *Photograph by* Warham.

Pl. 54. Two Komodo Monitors, *Varanus komodoensis*, meet. *Photograph by* Hoogerwerf.

The Nile Monitor, *Varanus niloticus*, leads an amphibious life. Its length exceeds 6 feet. *Photograph by* Lippens.



Pl. 55. Komodo Monitors, *Varanus komodoensis*, in their natural habitat on the island of Komodo in the Sunda archipelago. It is the largest lizard of the present day, reaching a length of nearly 10 feet. *Photograph by* Hoogerwerf.

Pl. 56. The Armoured Teyou, *Dracaena guyanensis*, comes from tropical South America and lives mostly on hard-shelled invertebrates which it crushes with its broad, flat teeth. ×0.3. *Photograph by* G. Senfft.

CHAPTER EIGHT

SEX AND REPRODUCTION

In all amphibians and reptiles the sexes are separate and hermaphrodites (intersexes) occur only as exceptions. These seem to be of more frequent occurrence amongst the Anura, where intersexes, and even sex reversal, has been observed under certain conditions. Bidder's organ, found in all males of the true-toad family (Bufonidae), is in fact a functionless, vestigial ovary attached to the male sex-gland, and under experimental conditions this vestige can be transformed into a functional ovary. Amongst the reptiles intersexes apparently are commonest in the Island Jararaca *(Bothrops insularis)* of the very small Brazilian island Queimada Grande. Pure males or pure females are rare; most specimens are hermaphrodite and, in addition to possessing well-developed male intromittent organs, also bear embryos.

Reproduction in both classes is, with one certain exception, bisexual. It is often possible to recognise males and females from their external appearance without an anatomical investigation. Sex-differentiating characters of this kind are known as secondary sex characters in contrast to the primary differences in the structure of the sex organs themselves. As a rule they develop for the first time in sexually mature animals and may be either permanent, i.e. for life, or only temporary, i.e. only appear during the breeding season.

Differences in body size, for instance, belong to the first category. Since the female accommodates the eggs, which are often produced in large masses, she is generally larger than the male. This applies to some urodeles, and to most anurans, tortoises and snakes. Male lizards, however, which frequently have a predilection for fighting, are considerably stronger and bigger than females; this can be seen in many iguanas (e.g. *Anolis)*, agamas, monitors, lacertids and others. Males are larger than females in, for example, the Tiger Salamander *(Ambystoma tigrinum*, pl. 1) among urodeles and the Hairy Frog *(Trichobatrachus robustus)* amongst the anurans; in many other species the sexes are of the same size.

Correlated with the differences in body-size, the body-shape may also show secondary sex characters. Male lizards may be more thick-set and have a deeper head and longer tail than females. This latter characteristic is also found in males of snakes and tortoises in spite of their smaller size. It is understandable that constant sex differences should be manifest in the scaly covering, and especially the number of scales, in lizards and snakes. In some species of chamaeleons, agamas (pl. 43) and iguanas the males carry high, sail-like crests on their backs or on the base of the tail, or are provided with horn-like adornments on their heads; there are, however, some species of lizards where the females are also horned. In males the dorsal crests of scales are usually higher and more strongly developed than in females.

In addition, the male often has a more striking and more handsome colour pattern or is capable of more vivid change of colour. Thus, for instance, the velvety black, red-headed males of the small Central American geckos, *Gonatodes fuscus*, contrast sharply with the plain grey-brown females; and the same obtains for many agamas, iguanas and others. The iris of the male Box Turtle *(Terrapene c. carolina*, col. pl. V) is ruby-red whereas that of the female is brown. It is rare that the female is the more beautiful, though this is the case, for example, in a few species of anurans of the genera *Bufo*, *Phyllobates*, and *Hyperolius*, in a few chamaeleons, and in the Speckled Terrapin, *Clemmys guttata* (col. pl. V), where the female has large, bright yellow spots on the head. The males of the redear-turtles *(Pseudemys scripta* and its relations) become melanic with age and lose their pretty pattern, whereas the females keep it throughout life. Sex colour-differences are, in general, uncommon among tortoises and equally so in snakes. In the European Smooth Snake *(Coronella austriaca)* males tend to have a reddish hue, but in the Adder *(Vipera berus)*, on the other hand, the females show this tendency; a few tropical forms are known where similar tendencies occur. In anurans colour differences between the sexes are equally rare; the commonly occurring dark throat colour of male frogs is generally associated with the distensibility of the vocal sacs.

As will be shown later, a number of other secondary sex characters are, like the vocal sacs of anurans, closely associated with sexual life (pl. 21). This applies, for instance, to the many diverse forms of clasping organs which enable the male to grasp the female securely; structures of this nature, which are most frequently found on the limbs but which also occur at the base of the tail, are known in many amphibians and reptiles and will be discussed in another connection. The marked development of various cutaneous glands in some male amphibians and the peculiar, long claws on the fore-feet of male water-tortoises of the genera *Chrysemys* and *Pseudemys* (pl. 26) are of importance in the mating of the sexes, just as the brood sac on the back of female marsupial-frogs *(Gastrotheca*, pl. 17) is important in the care of the brood. In a number of other instances, however, the significance of some almost equally well-defined sex differences is still not clear.

A very slender tree-snake, *Langaha nasuta*, lives in Madagascar and the long rostral processes of this genus have been mentioned previously (procrypsis). But the rostral process of the female, with its denticulate edge, seems so different, and it is also so variable in shape, that at one time the two sexes of *nasuta* were taken for three distinct species. The female of *Langaha alluaudi* appears even more strange; it not only has a rostral process shaped like a leaf whose edges are curled up until it almost forms a tube, but also a small horn above each eye; these are absent in males, which have only a long simple process on the snout. Furthermore, the sex-difference in eye-size of the Indo-Malayan tree-snake *Dendrelaphis picta* is peculiar but, equally, of unknown significance; the male has a distinctly larger eye than the female. In the North American bull-frog, *Rana catesbeiana*, and its relatives, the male is distinguished by a much larger tympanum than the female. Sexually mature males of other frogs from tropical West Africa are characterised by the presence of a bony process in the tympanum or by tooth-like prominences on the lower jaw, structures whose function is not yet clear.

In contrast to these permanent sex characters are those which occur periodically at the breeding season and then disappear again. They, too, show a similar diversity and there are a number of obvious examples in the European fauna. Everyone familiar with lizards is aware of the vivid grass-green colour of the head and flanks of the Sand Lizard *(Lacerta agilis)* in spring and that it turns into a dull brown in midsummer. The male Green Lizard *(Lacerta viridis)*, on the other hand, displays a superb cobalt-blue throat at about the same time. This colour change of males at the breeding season is also encountered in many exotic lizards; the head of the North American Broad-headed Skink, *Eumeces laticeps*, is coloured bright brick-red, and so on. And in a few water tortoises, too, "nuptial dresses" of this kind are known in the male sex, as, for instance, in the Indian *Batagur baska* and in the Sumatran *Callagur borneoensis*. The female, too, may put on a nuptial dress, though this is seldom more brightly coloured than that of the male: this is the case in a small deserticolous iguana of California, *Crotaphytus wislizenii*, where the belly and the sides of the body and tail are coloured salmon-pink, whilst this adornment is absent in the males.

Bodily form, also, may occasionally undergo a periodic change differing according to the sex. The male of the large, West African, Hairy Frog *(Trichobatrachus robustus)* shows hair-

Pl. X. *Diploglossus lessonae* of northern South America is a relative of the Slow Worm, *Anguis fragilis*. As in many lizards, the juveniles, in the foreground, have a livery completely different from that of the adults (cf. *Pachydactylus bicolor*, pl. 38). × 1. *Photograph by* Senckenberg Museum (Haupt).
One of the swiftest of all lizards is the extremely richly coloured *Cnemidophorus lemniscatus* from the north of South America. × 1. *Photograph by* Rosenberg.

Pl. 57. The Green Lizard, *Lacerta viridis*, inhabits the warm countries of southern Europe, but also occurs in a few climatically favoured places north of the Alps. The specimen figured came from Lieberose, Brandenburg. ×1. *Photograph by* W. Senfft.

Pl. 58. In defence the Shingleback, *Trachydosaurus rugosus* (compare coloured plate), opens its jaws menacingly; the cobalt-blue tongue contrasts with the carmine mucous membrane of the mouth. ×1.5. *Photograph by* Warham.

Head of the Eyed Lizard, *Lacerta lepida*, with threateningly opened jaws. ×1.2. *Photograph by* Barruel.

like proliferations of the skin 10-15 mm. (0.4-0.6 of an inch) long, at the breeding season; they are completely absent in the female. The well-known nuptial dress of the newts *(Triturus)* is at least equally striking. This consists not only in an intensification of the often sumptuous colours, but also in the development of cutaneous folds on the back and tail, whose height and shape differ according to the species; in addition, there may also be broad dermal fringes on the toes, swimming webs, folds of skin along the tibia, ridges on the back and thread-like structures on the tip of the tail. Striking characters of this kind almost always distinguish the male sex, the females being usually content with a very modest garb. Once the breeding season is over, the nuptial dress loses its significance at once and quickly degenerates, the male newts becoming similar to the females.

Such transitory sex characters may be of quite a different kind. There are salamanders in which the teeth of the lower jaw increase in length at the mating season. In the same way organs for grasping or holding may be either permanent or only developed from time to time. Finally, the temporary secondary sex differences may also extend to the organs concerned with care of the brood; though the brood pouches of female marsupial-frogs are permanent, the "cells" of female Surinam-toads *(Pipa)* only develop at the breeding season and degenerate again afterwards.

Many other secondary sex characters have special functions to fulfil and this has already been pointed out on several occasions. But, however different these functions may be, they are mostly related in some way to reproduction itself or at least to behaviour that is ultimately connected with it. Thus, secondary sex characters may serve in bringing the sexes together or in sex recognition, and in preventing cross-mating of different species; they may also make possible, or at least facilitate, courtship, pairing and the fecundation which is frequently dependent on it; and finally, they may be used in depositing the eggs and in incubation. In discussing these phenomena various secondary sex characters of amphibians and reptiles will be mentioned again.

Males and females are generally about equal in number amongst reptiles and amphibians. Sometimes the males predominate, as in several species of toads *(Bufo)* and perhaps also in the Tuatara *(Sphenodon)*; the converse is true of some crocodiles and geckos, such as the Indo-Pacific *Hemidactylus garnotii*, where males appear to be extremely rare, and they are completely absent in a few races of the Armenian Rock Lizard (e.g. *Lacerta saxicola armeniaca)*. In comparison with their relatives, where males are not at all uncommon, no one has ever found a male of this subspecies either in the wild state or amongst the numerous young lizards raised from eggs in captivity! These lizards seem to propagate, like many invertebrates, parthenogenetically and it is, therefore, quite possible that similar unisexual reproduction will be discovered in other lizards such as geckos.

Sometimes parthenogenesis may be simulated; that is, female tortoises and snakes have been observed to lay fertile eggs without any known previous mating. A female tropical African Night Adder *(Causus rhombeatus)* that was kept in captivity without a male laid eggs again and again at monthly intervals, and they hatched. The explanation of this phenomenon is that, under certain circumstances, the spermatozoa in the female's genital duct (uterus) may remain alive for a long time and retain their viability. Female Diamondback Terrapins *(Malaclemys centrata)*, kept apart from males, may lay eggs which are fertile even after four years, and a snake *(Leptodeira annulata)* was able to lay fertilised eggs at least five years after the last pairing. This delayed fertilisation (amphigonia retardata) does not seem to be exceptional and may, perhaps, also be found in some lizards. It is also known that female salamanders are able to store up spermatozoa for a fairly lengthy period. The importance of this phenomenon is quite clear; in places where the population density is low, as in some snakes, it is not necessary for the two sexes to come together on every occasion and so the female lays fertile eggs or gives birth to previously developed young.

Monogamy is known amongst reptiles that have no pronounced territorial sense but only occupy home ranges; thus, for instance, in some colubrid snakes *(Coluber)*, in the cobras *(Naja)* and in the South African Girdle Lizard *(Cordylus cataphractus*, pl. 50). In these animals one can definitely speak of temporary monogamy. In such cases the meeting of the two sexes naturally presents no difficulty, and that is also the case among lizards where the male is polygamous and territorial and among snakes which engage in mass hibernation and proceed to mate immediately afterwards.

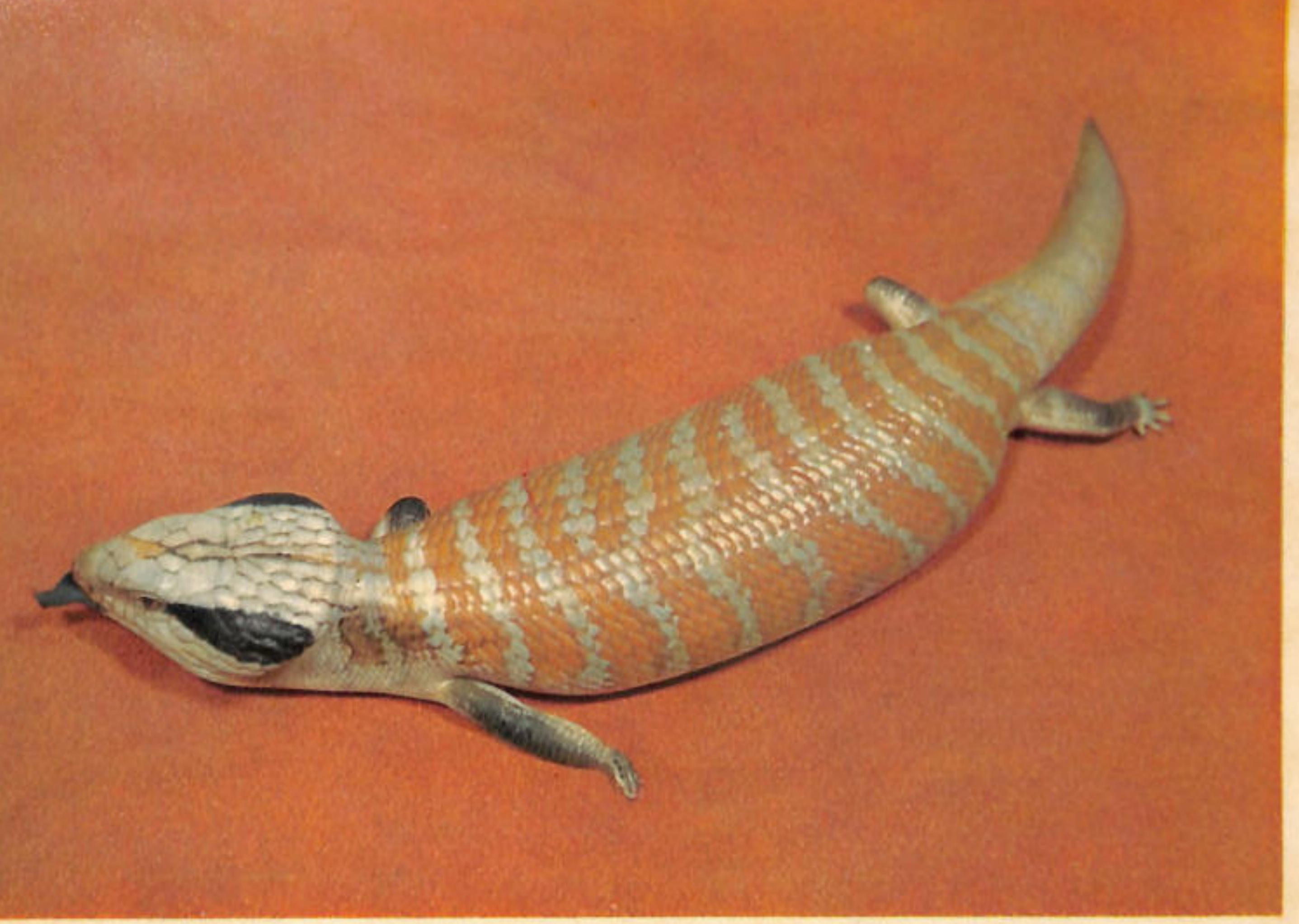
In comparison, other animals are obliged to make fairly long journeys to meet their sexual partners. The stimuli that initiate these migrations are extremely varied in their nature. They may, for example, be visual, as in the marine turtles where the males find the females when they return to the sea after depositing their eggs on the shore. Acoustic stimuli may also be instrumental, as in certain anurans where the rutting males attract females by croaking (pl. 21), and the same is assumed in regard to the voices of alligators and caimans. In certain snakes and salamanders olfactory stimuli play an important part in bringing the sexes together, just as, apparently, the smell of pond-weeds probably attracts Common Frogs *(Rana temporaria)* and causes them to congregate in a certain pool in spring. An increase in the oxygen content of the water caused, for instance, by its rate of flow, may also be a decisive factor in mating. Maximum atmospheric humidity brought about by sudden rainfall can also trigger off breeding migrations; afterwards, the animals either move persistently downhill under the influence of gravity or rely upon their topographical memory. The latter method would seem to be the most likely in the case of the spawning migrations of toads.

Further, for successful pairing the selection of the right partners is of the utmost importance. Two factors are essential; first, the partner must be of the same species and secondly, of the right sex. The first requisite is essential to prevent hybridisation and so to procreate fertile offspring. Experiments have, in fact, shown that hybridisation is not very difficult amongst amphibians. The best-known naturally occurring amphibian hybrid is *Triturus "blasii"*, a hybrid resulting from the crossing of Crested and Marbled newts. And among reptiles, too, hybrids are known, not only between subspecies, but between species: thus, for example, between the Diced Water-snake and the Grass Snake (pl. 67), between different species of vipers and rattlesnakes, and so forth.

The creation of such hybrids, which are prejudicial to the continued existence of the species, is clearly rendered more difficult by the following consideration: the preliminaries to pairing, the so-called mating- or courtship-play practised by the males of many salamanders, tortoises, lizards and snakes, acts not only as a sexual stimulant upon the female, but is an important character for species-recognition because it is peculiar to each species. At the same time, the secondary sex characters themselves, in so far as they relate to size, for instance, or may otherwise be visible as ornamentations or weapons, are efficacious in species-recognition; and, furthermore, in nocturnal animals, such as the salamanders, there are specific olfactory and auditory stimuli. Amidst the babel of voices in a nocturnal concert of frogs in the tropics, sounds probably play a vital part in isolating the different species. It is, indeed, the diversity of the voices which makes it possible for sexual partners of the same species to find each other among so many species all active at the same time and place. The same result can, of course, be achieved when allied species have different reproductive periods.

And now, how does mutual recognition of the sexes take place to prevent futile pairing by individuals of the same sex? In diurnal animals the visible sex differences certainly play an essential part, in so far as they are revealed by body size, for instance, or by shape, or the development of cephalic appendages, dorsal crests and so on. Many male lizards approach females with the same intimidatory posturing which they display to other males and if the partner does not react with "counter intimidation" it is recognised as a female. The striking colour characters of the males play a leading part in this; for example, the blue throat of male Green Lizards or the green flanks of the Sand Lizard. The male of the North American Fence Lizard *(Sceloporus undulatus)* is the colour of dull bark, but has a longitudinal stripe of cobalt-blue on either side of the belly which only becomes visible when it raises itself slightly on its limbs and flattens its body from side to side. If these blue markings on the male are painted over with grey, it is taken for a female by other males. In other lizards, behaviour, often in combination with colour characters, is most important for the recognition of a sexual partner. It must be admitted that some of the apparently inexplicable secondary sex characters may possibly serve

Pl. XI. Two large Australian skinks. Above, the central Australian Blue-tongued Skink *(Tiliqua occipitalis)* on its natural substratum of red sand; below, the Shingleback, *Trachydosaurus rugosus*, of Australia, also called the Pine-cone Lizard. × 0.5. *Upper photograph by* Senckenberg Museum (Haupt); *lower by* Rosenberg.



for sex-recognition; for example, the red iris of male Box Turtles *(Terrapene carolina*, col. pl. V) or even the rostral appendages, so radically different in the two sexes, of the Madagascar tree-snakes *(Langaha)* that are equipped with eyes for twilight vision.

Visible characters of this kind are, of course, of no consequence to purely nocturnal animals and this is confirmed by the fact that in amphibians the sexes are rarely coloured differently. The aquatic newts of the genus *Triturus* are an exception, but their reproductive activity takes place in the daytime and they are, accordingly, provided with sex characters that act on the visual as well as on the olfactory sense. In the Field Frog *(Rana arvalis)*, which also mates by day, the males are characterised by a sky-blue colour which probably serves as a character for sex-recognition. In a very few frogs (*Tomodactylus)* females call as well as males, but the two have notes of a different pitch. More frequently warning cries serve as sex-recognition characters; if, for instance, a male Common Toad *(Bufo bufo)* tries to grasp another male, the latter warns off the unwanted partner by short whimpering "kung-kung" noises; these sounds induce the amorous male to relax its embrace. In this reaction tactile stimuli also, of course, play an essential part. The assaulted male toad jerks its head upward and backward, and at the same time sets up a vibratory movement of its flanks. In other frogs the essential feature for recognition of the right sex by a copulating male is the difference between males and females in the tension of the flanks, caused by the egg-masses. Other tactile stimuli may arise from the nature of the skin of the partner's back; in several species of frogs of quite different families the males, in contrast to the females, have, for example, spiny, very warty or smooth backs. A different tactile stimulus of this kind suffices to restrain a male from a long embrace of another. It would not be far wrong, perhaps, if the unique "hairiness" of the male Hairy Frog was interpreted as a sex-recognition character of this kind.

The chemical senses, naturally, can also help towards separating the sexes in similar circumstances, and the sense of smell may be the most effective. Several salamanders have "hedonic" glands on the chin, the lower eyelid, the cheeks and the base of the tail. A specific odour has been detected in the skin of snakes; several species have a nuchal gland, others *(Malpolon)* a nasal gland which produces a secretion that is distributed by the snout on to the sides of the anterior part of the body. Its function is still unknown, like that of the numerous dorsal glands of certain agamas *(Phrynocephalus)*, but it can be assumed that it serves for sex-recognition. The musk glands in the lower jaw of crocodiles probably have a similar function. In sex-recognition olfactory and visual stimuli may, of course, be combined.

The actual mating is often preceded by special "nuptial play", and its importance as a specific character has already been mentioned. It is most remarkable in many aquatic tortoises, where each species behaves in its own peculiar way. The male of the Red-ear Turtle *(Pseudemys scripta elegans*, pl. 26), characterised by long claws on the fore limbs, swims in front of the female in such a way that their snouts almost touch; then the male stretches its fore limbs straight out in front, with their outer surfaces turned inwards, and executes rapid vibratory movements with the long claws. Other water-tortoises rapidly extend and withdraw their fore limbs in front of the female and others, again, make curious movements with their heads in similar circumstances.

In many lizards the nuptial play begins with intimidatory posturing; only when the rival is recognised as a sexual partner does the menacing attitude change over into courtship; this may be shown by change of posture, of gait or of head movements. A female that is ready to mate may respond to this courting by creeping closer, by nodding, by arching the back or other, similar movements. Among snakes, too, the courtship between the sexes at first resembles the breeding fights of males. In the Aesculapian Snake *(Elaphe longissima*, pl. 66) the two partners chase each other with uncanny speed, overcoming all obstacles in their path, until the male succeeds in coming alongside the female. Then the male coils around the female, but the chase continues. Eventually both animals raise the anterior parts of their bodies vertically so that they form a lyre-shaped figure, whilst their posterior parts remain coiled together. These "dances" may last for more than an hour before actual copulation takes place. The males of other snakes indulge in rubbing, pushing or weaving movements in such a way that their chins press against the nape of the female's neck.

Courtship play is widely practised amongst the salamanders and precedes the deposition of the spermatophore by the male. Among anurans courtship is unusual, though mention must be made of the Central American poison-frogs *Dendrobates auratus*, pl. 11. Before the eggs are laid these beautiful metallic-green, black-spotted creatures jump at, and on, each other pell-mell; this "play" may last two or three hours, and has been compared by an observer with the combat reaction.

The next point to be considered is pairing or copulation, which is often associated with fertilisation, but is by no means synonymous with it, since the latter is possible without any copulation. This happens in many salamanders; for instance, in primitive forms such as the Giant Salamander *(Megalobatrachus japonicus)* and its North American relative, the Hellbender *(Cryptobranchus alleganiensis)*. The females of these species lay their strings of eggs and the males, which scarcely come into contact with the females, then fertilise them. Fertilisation in this manner is spoken of as external and, amongst amphibians, is characteristic of both the salamander families Hynobiidae and Sirenidae as well as of the anurans, with few exceptions. On the other hand, fertilisation is internal in all other salamanders, in two genera of frogs, in caecilians and in all reptiles; in these animals the sperm cells are introduced into the female's genital tract where fertilisation takes place.

In anurans the process of pairing and fertilisation is perfectly simple. The rutting male places himself on the gravid female and grasps her from above with his fore limbs, usually in the region of the armpits (amplexus axillaris) or, more rarely, in the lumbar region (amplexus lumbaris). When the eggs are expelled, which is often a result of the pressure of the embrace, they are immediately inseminated by the male. The green and black poison-frog *Dendrobates auratus*, previously mentioned, forms an exception, since no amplexus at all has been observed in this species; in fact, the spawn is deposited on the ground and fertilised immediately afterwards by the male which is nearby. It is possible that amplexus and copulation do not occur in any members of the genus *Dendrobates*.

In order to make certain of a firm embrace, most male frogs develop special adhesive organs which belong in the category of secondary sex characters. Thus the so-called "nuptial pads" may appear as rough, warty, cutaneous excrescences on the upper surface of the first finger, and perhaps others; similar warty or spiny structures may also occur under the arms, on the hind limbs, on the belly or on the breast where they may resemble two well-developed nipples. Instead of warts on the first finger a spinous process (prepollex) may be developed, and this may be bifurcate. Associated with these developments the fore limbs of many male frogs are much stouter and more muscular than those of females. Some species of the neotropical genus *Leptodactylus* have reached the maximum in this respect; the males may have arms many times larger than those of the females.

The only frog in which internal fertilisation has been definitely proved to occur is the Tailed Frog *(Ascaphus truei)*, which lives in the extreme north-west of the United States; the male has a tail-like appendage 5-6 mm. (0.19-0.23 of an inch) long. This remarkable distensible organ is, however, simply a tubular extension of the cloaca and is inserted into the female's cloaca during coition and impregnation ensues. Perhaps it is an adaptation to the swift-flowing water which is the environment of *Ascaphus* and which is, obviously, unsuitable for external fertilisation. Internal fertilisation is also assumed to occur in the viviparous African toad *(Nectophrynoides)*. Finally, amongst amphibians, internal fertilisation has been found in the caecilians (Gymnophiona) where the males have their own peculiar "intromittent organ" which here, also, is merely an extension of the cloaca but which, in contrast to that of *Ascaphus*, is withdrawn again after use.

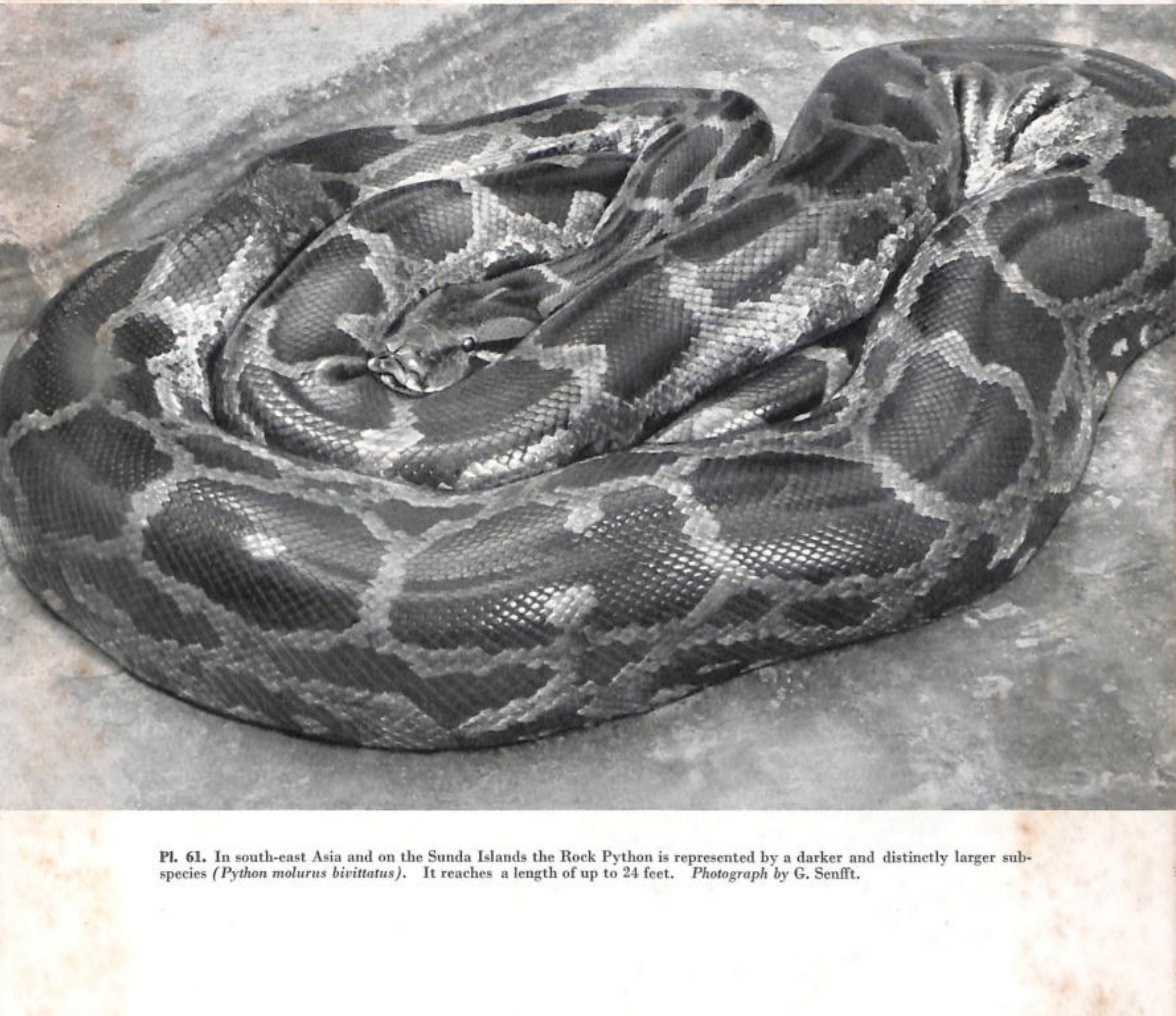
The method of fertilisation in the urodeles is quite different and, in comparison with the frogs, most complicated except in the case of the few forms previously mentioned which are characterised by external fertilisation. When fertilisation is internal in this group of amphibians, the males deposit a spermatophore, that is to say, a gelatinous, and often delicate, capsule resembling a disc, or a bell or a beaker, in shape and which contains the mass of sperm. These spermatophores are taken up by the cloaca of the females and the mass of sperm subsequently dissolves out of the capsule, the sperm cells escaping and fertilising the eggs. Sometimes, as in

Pl. 59. *Mabuya multifasciata* from south-east Asia, a typical representative of the world-wide skink family. ×1. *Photograph by* Rosenberg.

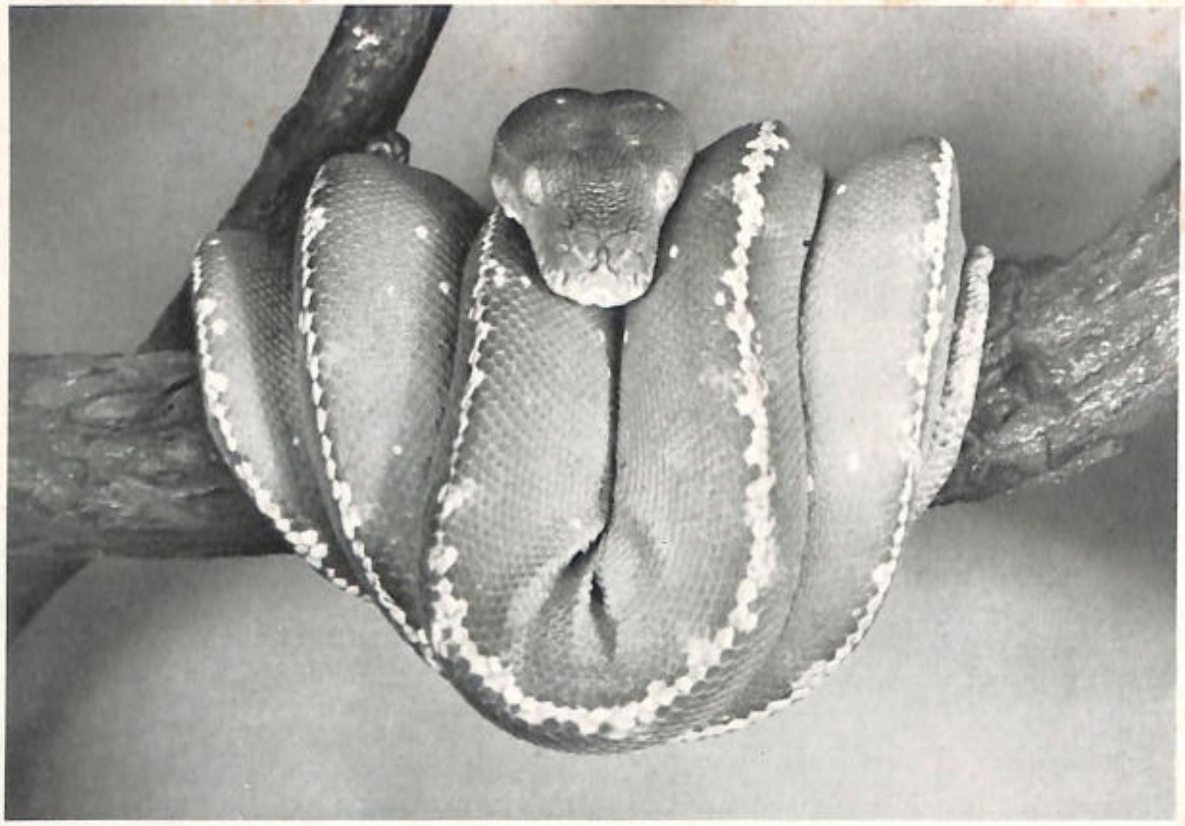
Not all skinks have smooth scales as this spiny *Egernia stokesii* of Western Australia shows. ×0.5. *Photograph by* Rosenberg.

The family Amphisbaenidae contains highly modified, externally worm-like lizards. It is represented by *Diplometopon zarudnyi* from south-west Asia. ×1. *Photograph by* Senckenberg Museum (Haupt).

Pl. 60. An Indian Rock Python *(Python m. molurus)* strangling its prey. ×0.3. *Photograph by* Fisher.



Pl. 61. In south-east Asia and on the Sunda Islands the Rock Python is represented by a darker and distinctly larger subspecies *(Python molurus bivittatus)*. It reaches a length of up to 24 feet. *Photograph by* G. Senfft.



Pl. 62. A remarkable instance of convergence in reptiles concerns two boas, each belonging to a different subfamily. In life both are leaf-green and have a dorsal pattern of white. The upper is *Chondropython viridis* (Pythoninae) from New Guinea, and the lower *Corallus caninus* (Boinae) from tropical South America. ×0.5. *Photographs by* Hoppe (upper) and Stubenvoll (lower).

the Spotted Salamander, the spermatozoa may be stored up for a long time in the female's spermatheca.

In the Spotted Salamander (pl. 1) the taking up of the spermatophore is preceded by true copulation. The male slips from behind underneath the female so that its back is in contact with her belly; then, for a short time, it clasps the female firmly by passing its fore limbs over hers and then the spermatophore is deposited. Other salamanders embrace their partner from above, or from one side, so that the hind limbs are brought into play too; and again, in others, jaws and tails may act as grasping organs. To prevent slipping on the smooth, slimy skin some male salamanders have callosities or spurs as secondary sex characters on the fore limbs, hind limbs or the base of the tail *(Pleurodeles, Euproctus, Mertensiella)*. In the Plethodontidae the male's hedonic head glands, previously mentioned, have a stimulatory significance; the male rubs its head against the female and then deposits a spermatophore which is taken up by the female.

In the European newts *(Triturus)* the courtship which precedes the picking-up of the spermatophore is even more complicated although copulation does not take place. The male, in its finest nuptial array and distinguished by greatly swollen cloacal lips, follows the female which is recognised by both sight and by scent. Then he posts himself in front of the female and makes wagging tail-movements which carry scent to her from his prominent, hair-like cloacal glands. If the female perceives it and is ready to spawn she advances towards the male and repeatedly pushes her snout against his tail; this stimulates the release of the spermatophore from the male's widely open cloaca. The female follows directly behind the male and, using the lips of her cloaca, lifts the mass of sperm off the jelly-like base, the actual spermatophore. The sperm-mass gets into the cloacal opening where the sperm cells escape.

True intromittent organs apart from the cloaca are lacking in the amphibians. They are, however, present in all the recent reptiles, with the single exception of the primitive Tuatara: they are single in tortoises and crocodiles, but paired in the lizards and snakes, though only one organ is used in copulation. When at rest the presence of an intromittent organ in reptiles is scarcely noticeable except for some thickening of the base of the tail; when it is functional it is everted from the cloacal cleft. This occurs during mating which, by and large, shows less diversity than amongst the amphibians.

Male tortoises preparatory to copulation approach the female from behind, climb on to its shell, grip it firmly with the fore limbs and sometimes bite it in the neck. This position is made easier by the plastron of various male tortoises being concave. Mating is accomplished by the male pushing its cloacal opening under the female's tail. In crocodiles the female is firmly held at the nape of the neck by the male's fore limbs, so far as any conclusion regarding other crocodilians can be drawn from the behaviour of the male Mississippi Alligator. Then the male bends the hinder part of his body to one side and under the female until his cloaca comes into close proximity to hers.

The male's bite, to hold the female securely, is important in the mating posture of lizards. In the agamas the canine teeth, which are used for this purpose, are larger in males than in females. The male uses its jaws to secure a firm grip either on the fore part of the body, on the flanks or even further back, in the lumbar region, according to its species. Then it twists its body along the female's side so that its cloacal opening touches that of the female; at the same time the hind limb nearest the female straddles her back, or the base of her tail, to ensure a firm hold. The male's femoral glands, which are present along the lower surface of the thighs and in the pre-anal region and which secrete a waxy substance during the breeding season, may, perhaps, have an adhesive function; it is not known whether they are designed for tactile stimulation of the female. The thorny scales, which are present in the anal region of the males of some lizards, also appear to function as adhesive organs. In this connection, also, attention should be drawn to the apparently similar function of the considerably larger vestigial limbs in males of certain serpentiform lizards *(Pygopus, Dibamus)*. Only the penis nearest to the female's cloaca is functional on each occasion.

In snakes pairing may be similarly accompanied by a bite on the nape of the neck, though this action is less common than amongst lizards and apparently does not occur at all in venomous species. The male is prevented from sliding off during the embrace by sometimes having more strongly keeled scales or by the keels having knob-like structures on them, or by claw-like vestiges of the hind limbs in certain boas and pythons, or by spiny structures on the ventral scales in some sea-snakes. Nothing is known about the function of the knobbed tubercles of some male snakes, though they may, perhaps, be tactile. Since the intromittent organs are furnished with horny spines, the union of the sexes is very intimate as a rule; it lasts for several minutes or even for hours.

Only a few amphibians and reptiles have no definite mating times; they are generally dependent upon climatic rhythm. In the tropics it is often the beginning of the rainy season, and in the temperate zone the beginning of the warm season of the year, which determines the onset of breeding in amphibians and reptiles. Some species propagate during the whole of the time of the year that is propitious, others complete their reproductive business within a few weeks,if not days, and others, again, pair anew towards the end of the season. Egg-laying may coincide with pairing, as in the anura; in reptiles it may take place some weeks or months later. The duration of pregnancy is longer in viviparous species than in their oviparous relatives. The intervals between egg-laying, or parturition, vary greatly; in the temperate zones most amphibians and reptiles have only one clutch or litter a year, but in the far north the interval between two litters may amount to two years. It has been discovered that the Green Turtle *(Chelonia mydas)* in some places only produces a clutch every three years, but in others, however, it lays eggs 7-12 times in one year. The Wall Lizard often lays two or three times in summer, with from two to eight eggs on each occasion.

The number of eggs in a clutch also varies considerably. Amongst the anurans, for instance, there is a diminutive Cuban species, *Sminthillus limbatus*, which, so far as is known, only lays a single egg; in contrast to this, there is the Common Toad *(Bufo bufo)*, for example, which at a single laying deposited 6,840 eggs; the number is even greater, up to 12,000, in *Bufo viridis*, and in the case of a female of the North American *Bufo woodhousei* as many as 25,644 eggs have been counted! Among reptiles, geckos and *Anolis* are characterised by very small clutches, consisting, as a rule, of two, but sometimes of only a single egg; they are, however, laid several times in a season. In contrast to these, the marine turtles lay very large clutches of 150-200 eggs. The same applies to viviparous lizards and snakes: some bring only one or two young into the world, as, for example, some venomous sea-snakes, but others produce large numbers. The number of young in a litter of the Karung *(Acrochordus javanicus)* and some venomous terrestrial snakes *(Notechis, Bitis, Bothrops)* may be as many as 70-72, and in harmless colubrids *(Thamnophis, Natrix)* even 85-101. The number of eggs and young is usually greater, the larger the mother is.

The eggs of amphibians have gelatinous envelopes of variable thickness which enclose a yolk-mass surrounded by a membrane; this yolk may or may not be pigmented. Reptiles' eggs have a shell that is either flexible and parchment-like, or hard and calcareous. The latter is characteristic of all crocodiles, some tortoises and some lizards. In the vast majority of cases, the egg-shell is white and pigment is very rarely present *(Phenacosaurus)*. In addition to the well-known ovoid shape, eggs which are spindle-shaped and spherical are known, the latter in a few lizards and tortoises only. The smallest reptilian eggs have a maximum longitudinal diameter of 2-3 mm. (0.08-0.12 of an inch), the largest 90-120 mm. (3.5-4.7 inches) *(Crocodylus, Varanus komodoensis, Python)*.

Reptiles generally lay their eggs in the ground, where the female digs holes or cavities expressly for this purpose. The eggs of a few lizards are deposited in the open, in a sheltered place, against rocks or tree-trunks to which they adhere because the shells are sticky immediately after being laid; by reason of this peculiarity, the eggs of a lizard's or a snake's clutch may form a solid clump. Suitable places may attract several pregnant females, e.g. geckos or snakes, and, in consequence, enormous masses of eggs are formed which look like a single clutch. The females of purely aquatic reptiles, if they are oviparous, always look for a place on land where they can bury their eggs and, to this end, some marine turtles undertake long migrations.

In contrast to the reptiles, the vast majority of amphibians lay their eggs in water. Their spawn forms cushions, balls, clusters, clumps or strings varying in length, thickness and arrange-

Pl. XII. A Javanese tree-snake, *Ahaetulla prasina*, characterised by a horizontal pupil, in typical threatening posture: the animal inflates the anterior part of the body so that the black and white skin between the scales becomes visible. × 1. *Photograph by* Senckenberg Museum (Haupt).
South African cobra, *Naja nivea*, in the defensive attitude typical of the species. Length of the animal about 5 feet. *Photograph by* Senckenberg Museum (Haupt).

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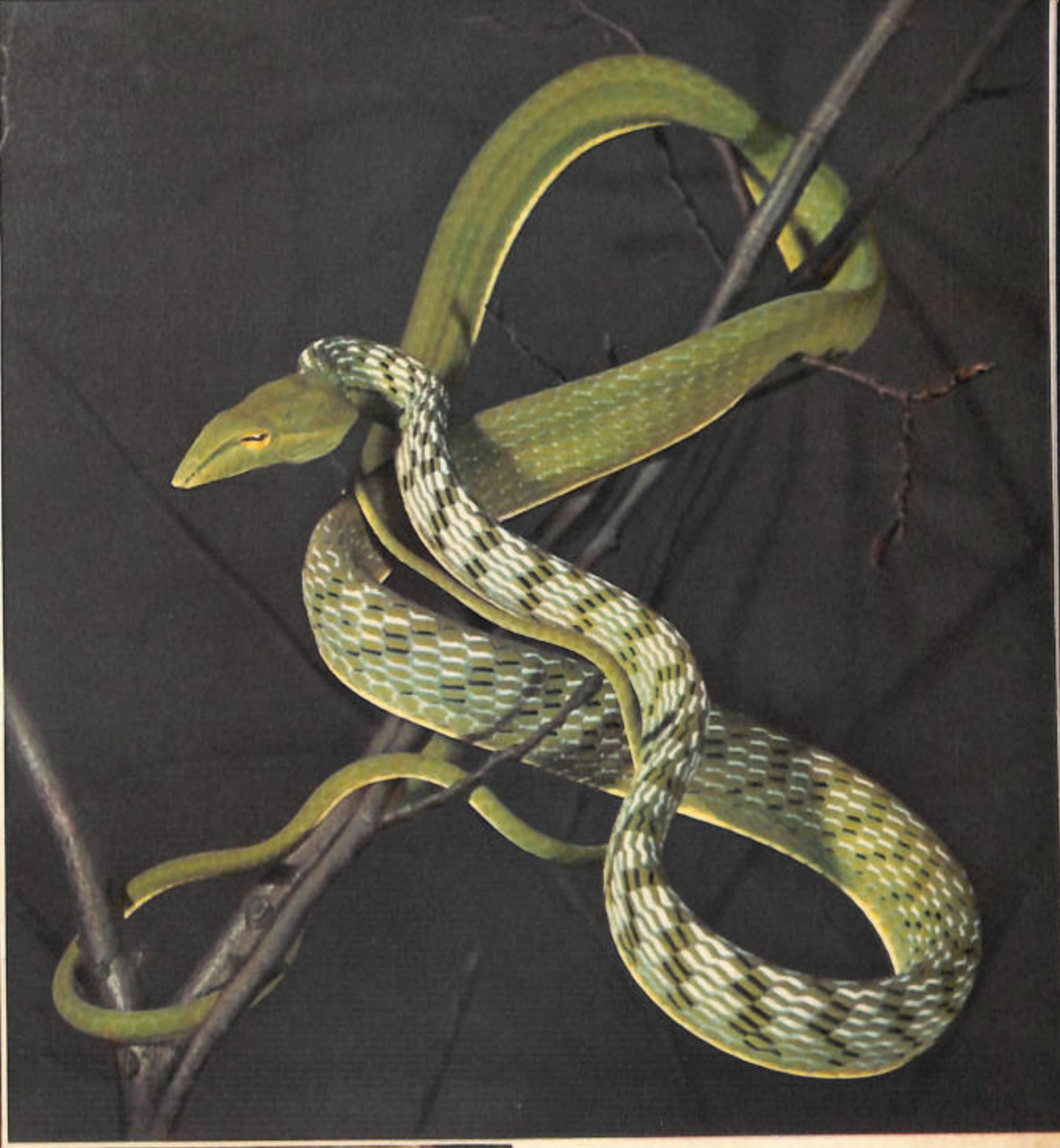
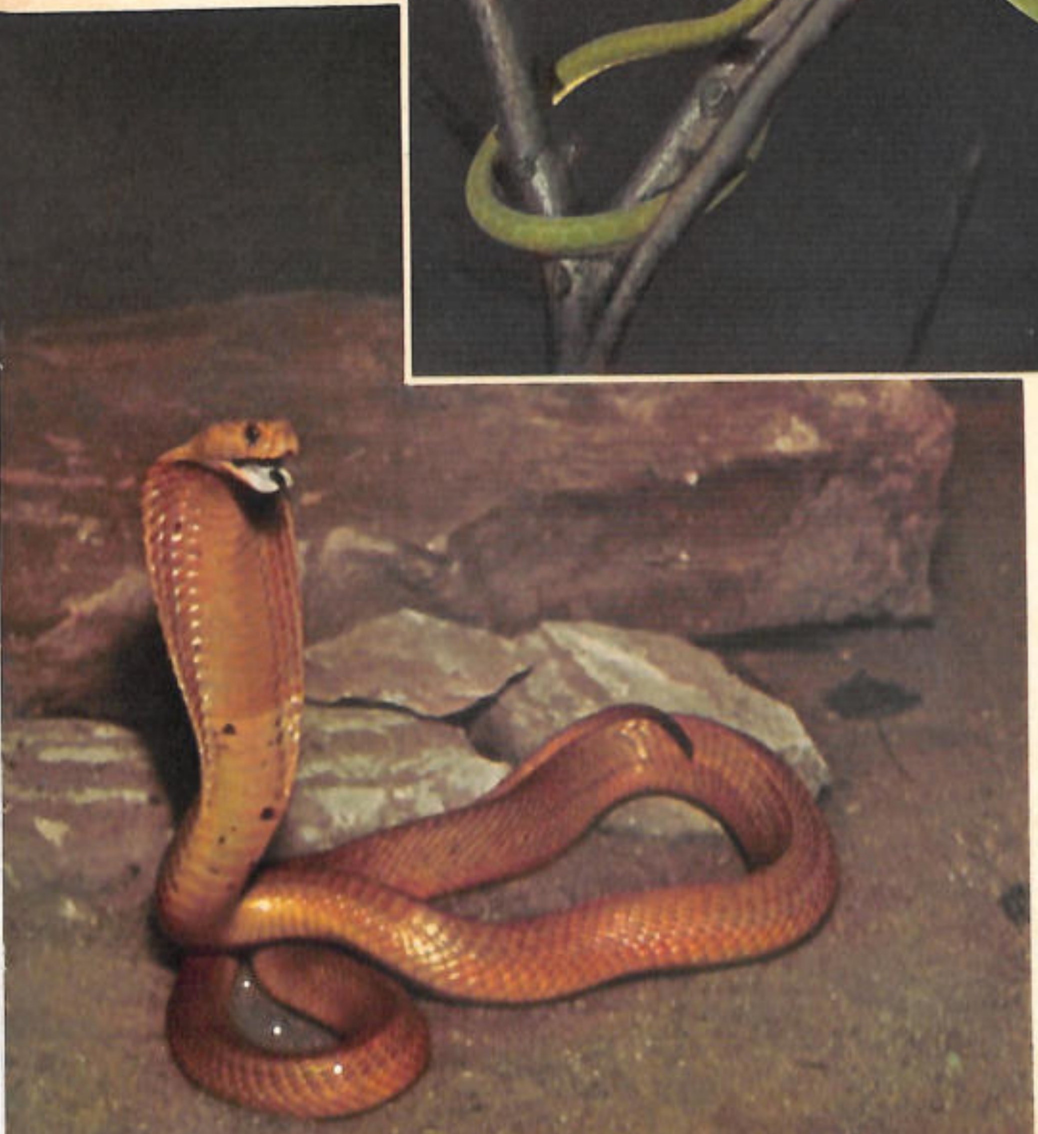
South African cobra, *Naja nivea*, in the defensive attitude typical of the species. Length of the animal about 5 feet. *Photograph by* Senckenberg Museum (Haupt).





ment. Nevertheless, many species lay their eggs singly, often attached to the substratum, such as stones or parts of plants, by means of special attachments formed by the females. Finally, many amphibians of all three orders have made a change and use the land, or even their own bodies, on which to deposit their eggs; this is clearly bound up with the subject of parental care and will be discussed in the next chapter.

CHAPTER NINE

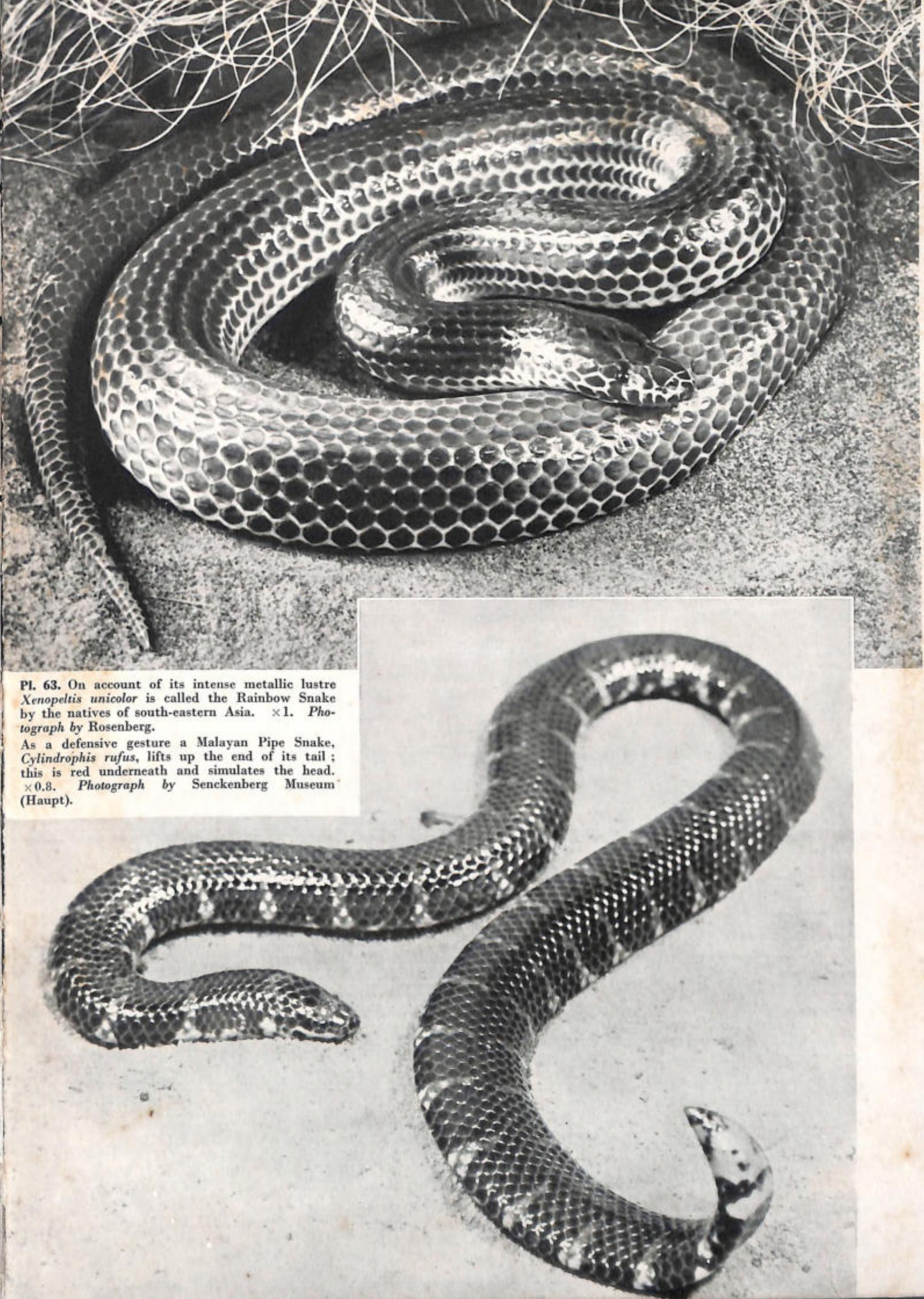
DEVELOPMENT, GROWTH AND DURATION OF LIFE

The eggs of amphibians and reptiles develop under the influence of the external temperature, and the length of the incubation period depends upon this factor. It may last only a few days (2-5), or even less in some anurans, or some weeks, and even months, in many reptiles, though in this case retention of the eggs in the oviduct may considerably shorten the time taken to reach maturity. Under certain circumstances eggs may hibernate in the process of development, as in pond-tortoises *(Emys)* and Tuataras *(Sphenodon)*, so that the total incubation period may be more than a year. Possibly the dark yolk pigmentation of the Common Frog *(Rana temporaria*, pl. 19), which spawns in very early spring, assists the development of the embryo because of its capacity to absorb heat from the sun's rays. And it is equally probable that the heat of fermentation of vegetable matter rotting in compost heaps and nest-mounds, accelerates the development of snakes' and crocodiles' eggs which are laid in such places.

Before they emerge from the egg many amphibians develop unicellular glands on the snout and their secretion to some extent digests the egg-membrane near the head and releases the embryo. In young frogs of the genus *Eleutherodactylus* (pl. 6), which emerge from the eggs fully developed, a tiny, spine-like egg-tooth appears on the tip of the upper jaw and this slits open the egg-shell before hatching. These egg-teeth, which disappear soon after hatching, are very widespread amongst lizards and snakes. In geckos, strange to say, they are double and in crocodiles and tortoises their place is taken by a pointed, horny callosity on the snout. The mechanical splitting open of the egg-shell is facilitated by the chemical action of an enzyme secreted by the embryo which dissolves the shell from inside.

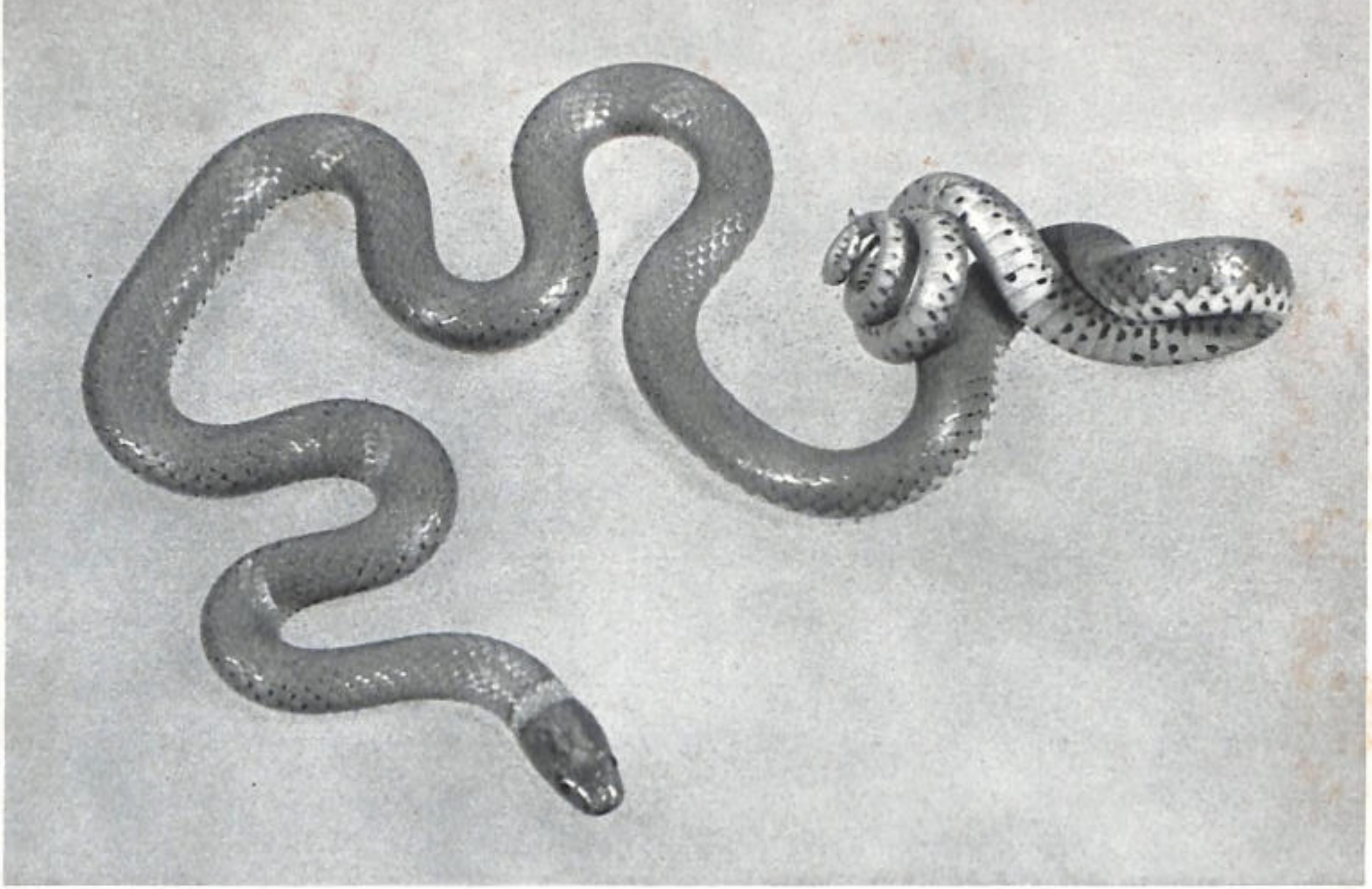
The young of all reptiles at birth resemble their parents, though their bodily proportions, colour and pattern may be different. In many cases the head is relatively larger and the tail shorter than in the parents. Their colour may also be more vivid, and the markings more striking; where, in old animals, the pattern consists of spots, or is lost, the juvenile stages may have sharply defined longitudinal stripes, or vice versa. In amphibians the young, newly-hatched salamanders and caecilians are frequently not unlike their parents, apart from their external gills, which are generally absent in adults. The anurans, however, usually appear very different when first hatched from the egg: they are the well-known frog larvae or tadpoles which have external gills and a tail; but not, as yet, any limbs.

This latter character applies also to certain newly-hatched salamanders where the limbs (first the anterior and then the posterior, be it noted) appear in the course of development outside the egg-membrane. In frog larvae the external appearance changes greatly during growth:

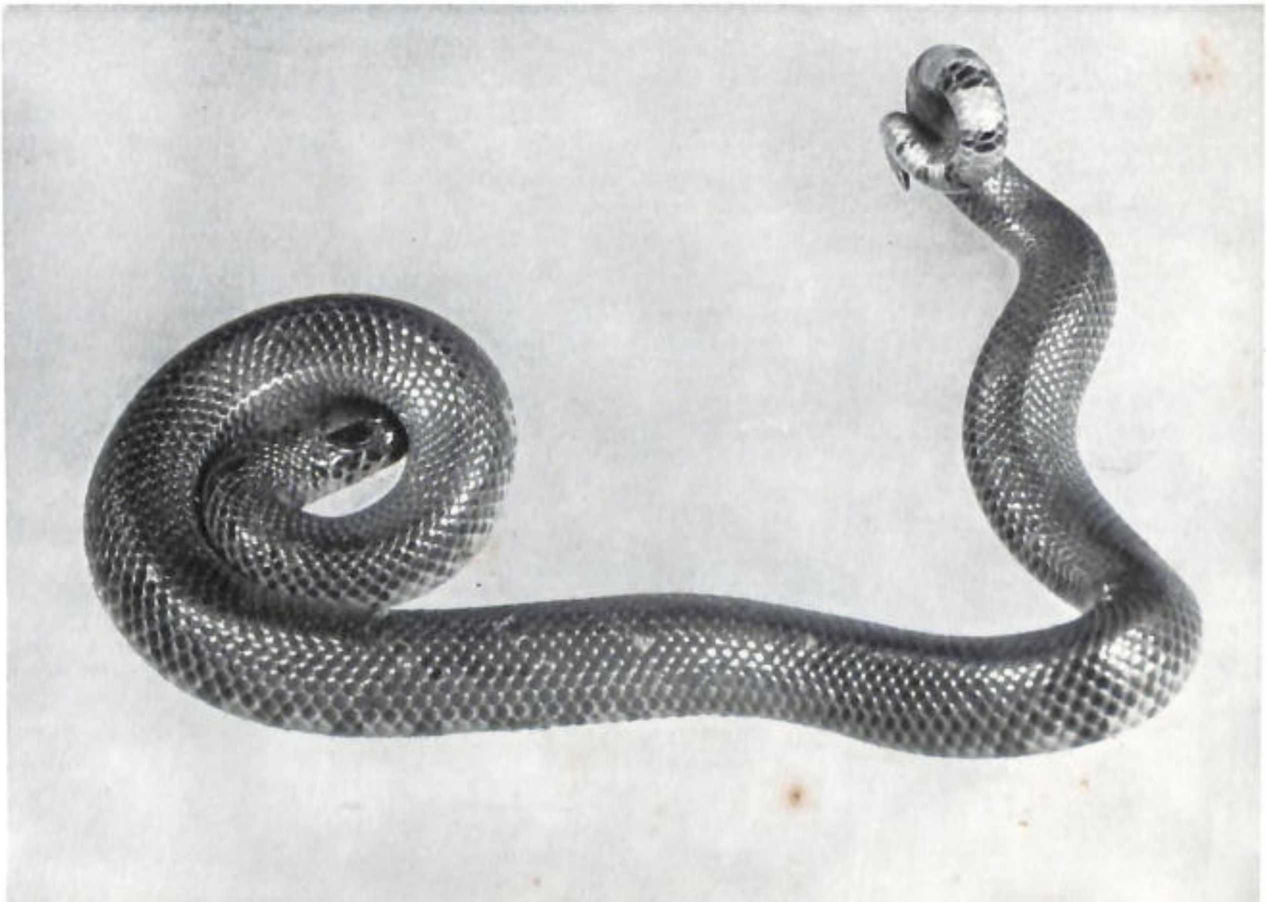


Pl. 63. On account of its intense metallic lustre *Xenopeltis unicolor* is called the Rainbow Snake by the natives of south-eastern Asia. ×1. *Photograph by* Rosenberg.

As a defensive gesture a Malayan Pipe Snake, *Cylindrophis rufus*, lifts up the end of its tail; this is red underneath and simulates the head. ×0.8. *Photograph by* Senckenberg Museum (Haupt).



Pl. 64. The same habit as that of the Pipe Snake (Plate 63) is met with in yet two other snakes, both from North America : *Diadophis amabilis* (above) from the western United States, and *Farancia abacura* (below) from the south-eastern United States. The head is often held concealed under the body. ×1.5 (above) and 0.5 (below). *Photographs by* Davis.



the external gills are replaced by internal ones and the hind limbs appear, at first as little buds just in front of the base of the tail. When the tadpole has grown considerably the fore limbs break through the skin, whilst the tail, gills, and the unique horny jaws degenerate soon afterwards and finally disappear; at this stage the larva comes to look like a frog for the first time. Tadpoles vary greatly in their form according to their environment and mode of life. In contrast to the free-swimming type, with high dermal crests on the tail which lives in still waters, there is a streamlined type with a dorso-ventrally flattened body and low tail; the tail is even lower and longer in larvae which do not live in water but in damp air. The structure of the larval mouth-armature also shows distinct correlations with the environment.

By no means all amphibians undergo a metamorphosis. There are many salamanders, apart from viviparous forms such as the black Alpine Salamander *(Salamandra atra)*, in which metamorphosis does not occur. In this connection especial mention must be made of the species of the North American genus *Plethodon* which lay their eggs on land and from which fully developed young salamanders are hatched. Many anurans, too, have a similar direct development which must be particularly advantageous in places where there are no permanent pools or streams. This kind of development is characteristic of, for instance, the primitive New Zealand frog *Leiopelma*, as well as of the numerous species of the tropical American genus *Eleutherodactylus* (pl. 6) and of various representatives of the true-frogs (Ranidae), bush-frogs (Rhacophoridae) and narrowmouth-toads (Microhylidae). The eggs of all these frogs are invariably laid on land; they are large and have much yolk, so that they are much less numerous than where the eggs are entrusted to water.

Amphibians and reptiles which lay their eggs on land have often developed a peculiar, and at times astonishing, form of parental care; this occurs less frequently amongst those which deposit their eggs in water. It is, however, always exceptional, since the vast majority of amphibians and reptiles take no interest in their offspring. Parental care is first indicated by the building of a nest for the reception of the spawn and this occurs in many frogs. The most important nest-building materials are mud, foam, and leaves. The Brazilian tree-frog *Hyla faber* (pl. 13), so named on account of its call which sounds like "smith", constructs very remarkable nests of mud. The male of this large species constructs annular dykes of mud in shallow water close to the bank and these enclose circular pools about 25 cm. (10 inches) in diameter; the inner surface of the dykes is carefully smoothed down with the fore limbs. Pairing and egg-laying take place in these crater-like nests and the tadpoles, protected from fish and other enemies, complete their development and metamorphosis in them.

Foam nests of varying size are constructed on the surface of the water, or on the bank, by a whole series of American and Australian frogs of the family Leptodactylidae (pl. 7), and these afford similar protection to the spawn and developing embryos. They consist of an albuminous mass which the female extrudes from her cloaca along with the spawn. This mass is frothy, or is beaten up into a foam by means of the hind feet, and, being interspersed with air bubbles, floats in water. In some species, such as the Australian *Limnodynastes tasmaniensis*, the female's fore-feet are employed; these have spatulate fingers and are used to force air bubbles from the surface of the water backward under the belly to the cloaca where they mix with the spawn. In this foamy mass the spawn is well protected and can develop without hindrance into tadpoles, which leave the nest either before or after it disintegrates. When these foam nests are constructed on land, or sometimes in a hole in the ground, the foam acts as an effective safeguard against the danger of desiccation.

In Africa and Asia some bush-frogs of the family Rhacophoridae, such as the well-known Javan Flying Frog *(Rhacophorus reinwardtii*, pl. 22), construct foam nests on or between the leaves of a bush or tree. In this case both sexes take part in its construction; the male, on the back of the female during amplexus, moves his hind limbs in unison with hers to beat up the foam. These nests contain the spawn and for a certain length of time provide well-adapted accommodation for the larvae when they hatch; the foam inside the nest becomes progressively more fluid, whilst the outside dries to form a firm integument; then the larvae are washed by rain into pools where their development is completed. Finally, similar nests may be made from leaves alone, without foam. The adhesive substance for the purpose is provided by the gelatinous envelopes of the eggs, which are so sticky that they hold the rolled-up leaves together. The beautiful leaf-frogs *(Phyllomedusa)* of South America and their relatives of the genus *Agalychnis* (pl. 15, 16) in Central America build leaf nests of this kind which are filled with spawn and which are usually suspended from branches overhanging water.

In contrast to these anuran nest-constructors, one finds only a scattering of very primitive builders among the reptiles. In the vast majority of cases they are content with making a hole in the ground and filling it in again after laying their eggs. The colubrine snake *Farancia abacura* (pl. 64) of the south-eastern United States shows unusual care for its offspring and constructs a rather ingenious nest; it excavates a bottle-shaped chamber in damp, sandy soil and this communicates with the outside world by a vertical passage. In contrast to this, the notorious King Cobra *(Naja hannah)* builds a nest, not in the ground but on the surface; the anterior part of the body is bent into a loop and, with this, dead leaves and other decaying vegetable detritus is scooped together. The eggs are laid at the bottom of this pile whilst the mother coils herself round on top of it.

Such a method of constructing nests is unknown amongst lizards but it is practised by crocodiles. Amongst the latter, the female of the Mississippi Alligator has the habit of scraping together all kinds of vegetable detritus mixed with mud into a mound in some sunny spot near its aquatic haunts; the mound may be up to three feet high and six feet in diameter. After the hillock has been compressed by repeatedly crawling over it, the female opens the top of the nest and deposits a clutch of 20-70 eggs in it; the small opening is then filled in again with nest material and levelled off. The Caimans in South America and the Estuarine Crocodile *(Crocodylus porosus)* in the Indo-Australian region build similar nests. The Nile Crocodile, on the other hand, buries its clutch in dry sand without constructing any special nest. In the nests of vegetable matter described, a constant, humid warmth prevails and measurements indicate that the temperature is almost always somewhat higher than the external temperature.

The construction of nests of this kind may also be associated with true parental care. It has been definitely reported that female crocodiles, after laying, remain in the vicinity of the nest to guard the clutch of eggs. It has been proved that, in the case of the Estuarine Crocodile, the female withdraws about a yard from the nest and excavates a small depression in marshy soil; in this it remains for the whole of the incubation period, splashing water on to the nest from time to time with its tail. The Nile Crocodile also is said to remain in the neighbourhood of its nesting site and to visit it every night; if the place is fenced in the mother may destroy the enclosure. According to some reports, the Mississippi Alligator guards its nest in the same way but more recent observers deny any parental instinct on the part of the Alligator and explain the presence of the female on or around the nest as incidental to looking for a sunny resting place.

According to various reports, a few snakes also usually keep watch over their eggs or even "brood them out". Such behaviour is known, for instance, in the harmless colubrine snakes *Farancia abacura* mentioned above, in the viper *Agkistrodon rhodostoma*, in the various species of *Naja* and *Bungarus*, which are likewise venomous, and especially in the giant snakes of the genus *Python*. What the "brooding out" consists of in these cases is not at all clear, since snakes are exothermal creatures and the source of their body heat is mainly the external temperature. Nevertheless, a snake lying in the sun, even when the weather is cool, may become perceptibly warmer than the air and so some benefit might accrue to the clutch of eggs. It seems doubtful whether a female python "brooding" its clutch can raise its own body temperature 7° or even 10°-12° above that of the air, as earlier observers claimed. Since these observations were made on captive animals kept in heated cages, the perceptibly higher body temperature of the python in relation to the air temperature might well be attributable to the effect of heating by conduction from the floor. It is our opinion, in any case, that the problem of egg-incubation in pythons needs critical re-examination!

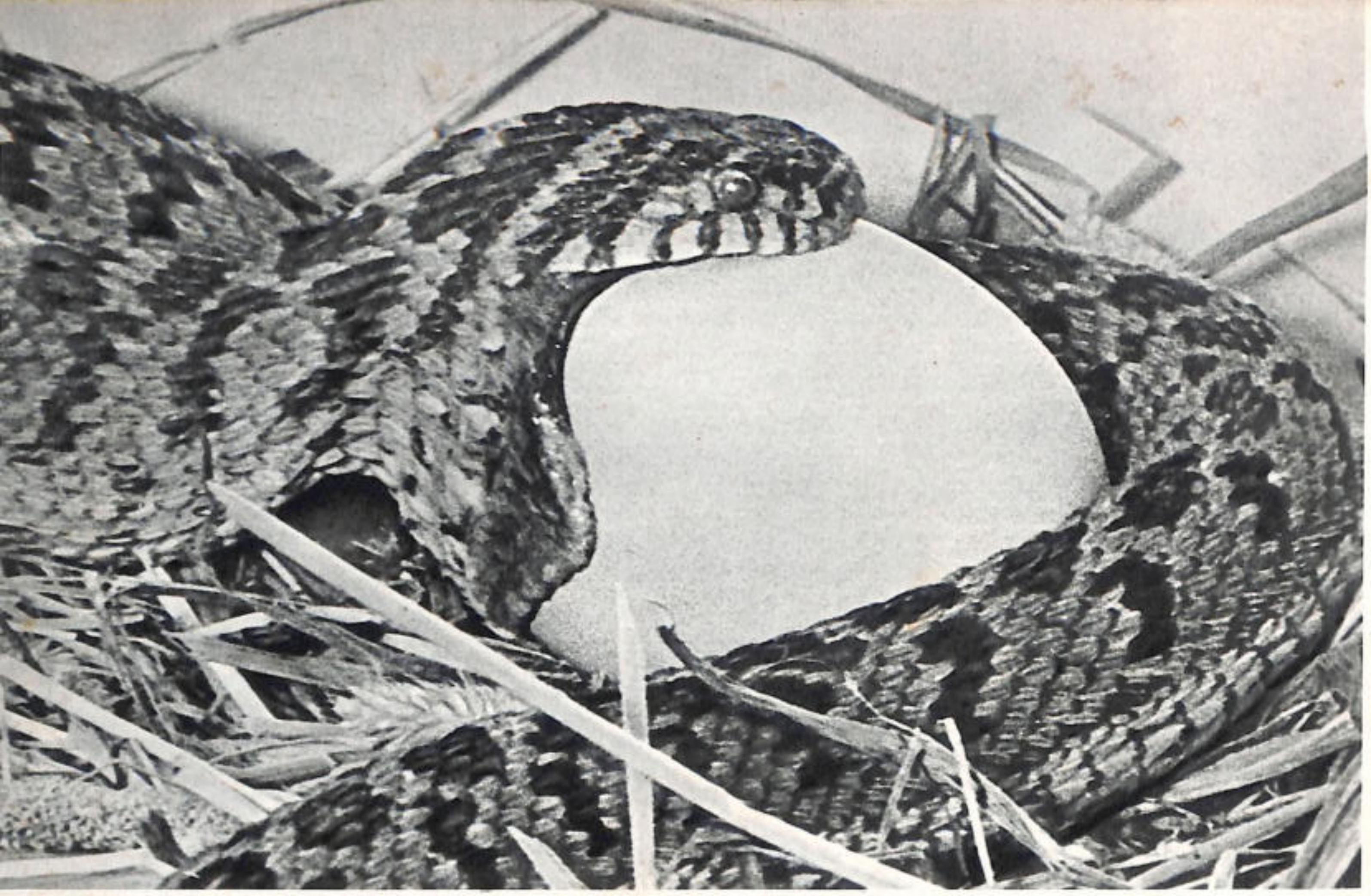
Lizards are also known which coil themselves round their eggs in the same way, e.g. the Glass Snake *(Ophisaurus ventralis)* and some related species. It has been reported from various quarters that the female Green Lizard *(Lacerta viridis*, pl. 57) not only remains near its eggs but comes back again even after being driven off. Similar reports have been made about some

Pl. 65. The beautiful, green tree-snake, *Leptophis ahaetulla*, from tropical South America opens its jaws threateningly when in danger, but seldom decides to bite. ×1. *Photograph by* van Riper.

Pl. 66. One of the most charming land snakes from southern Europe and western Asia, the Aesculapian Snake (*Elaphe longissima*). Undoubtedly it was formerly more widely distributed than to-day; in central Europe it has survived only in a few favourably warm spots. ×0.7. *Photograph by* G. Senfft.

Pl. 67. The Diced Water-snake, *Natrix tessellata*, is an amphibious snake of south-eastern Europe and western Asia. Its food consists predominantly of fish. ×1. *Photograph by* Fischer-Wahrenholz.

Head of the commonest European snake, the Grass Snake (*Natrix natrix*). ×1. *Photograph by* G. Senfft.



Pl. 68. The African Egg-eating Snake, *Dasypeltis scabra*, swallowing a hen's egg. ×2. *Photograph by* Dunton.

The African tree-snake, *Thelotornis kirtlandii*, has a defensive posture similar to that of *Ahaetulla prasina*, shown on coloured plate XII. A horizontal pupil is characteristic of both snakes. ×0.8. *Photograph by* Cansdale.

North African lizards and they should certainly be verified; whether the Common Iguana *(Iguana iguana)* is characterised by such a strong parental instinct as is claimed for it appears to be equally uncertain. On the other hand, it has long been known with certainty that the North American skink *Eumeces fasciatus* shows parental care; the female remains in the nesting hole from the time the eggs are laid until they hatch and acts as their nurse. She turns the eggs and pushes them together into a heap; in addition, she not only wards off small foes but promotes the incubation by the warmth of her body which is derived from basking in the sun from time to time. The parental care of the brood is even more complete in a related species *(Eumeces obsoletus);* the mother turns the eggs regularly during their incubation, assists the young to hatch, ensures undisturbed feeding conditions for them, and finally licks their cloacal regions to keep them clean, just as a nursemaid washes her charges.

Guardianship of the eggs by amphibians has been conclusively proved on many occasions. Thus, the females of caecilians belonging to different genera in Ceylon, on the Seychelles and in Brazil hold their clutch of eggs in their coils. One can hardly speak of true guardianship in these cases, but rather of protection against desiccation. The female of the elongate Amphiuma *(Amphiuma means)* of North America also coils itself round its eggs, and, generally speaking, there is in this part of the world a whole series of small salamanders whose females never leave their eggs. Males, too, may exhibit parental care; thus in the Giant Salamander *(Megalobatrachus japonicus)*, its North American relatives and the Olm *(Proteus anguinus)*, it is the father which stays beside the string of eggs and guards it. In view of the large size of these animals, the guardianship, for instance against the attacks of predatory fish, is really effective; in addition, the father by oscillatory movements keeps the eggs supplied with oxygenated water. It can be assumed that the European *Andrias scheuchzeri*, a very near relation of the Giant Salamander, exercised similar parental care 10 million years ago! In contrast to the urodeles there are only isolated anurans (e.g. *Rhacophorus microtympanum* in Ceylon) where the females remain near the spawn.

Quite a number of species of frogs of different groups have solved the problem of "guardianship" of the eggs in another way — the frog does not stay with the spawn, the spawn stays with the frog; for it is deposited on the parent's body and is carried around until such time as the tadpoles or young frogs hatch out. For this type of parental care the parents may develop certain organs as secondary sex characters designed for the reception of the eggs and to serve as brood carriers.

In one group of South American tree-frogs, belonging to the widespread family Hylidae, there is a distinct trend towards this type of parental care, which takes the form of the female carrying its spawn around on its back until such time as the tadpoles, or fully developed froglets, emerge from the egg-capsules. These curious frogs are not only small species of 2-3 cm. (0.8-1.2 inches) but may be giants of 10 cm. (4 inches) and referable to several genera; if they are compared with one another one can clearly trace progressive improvement in the provisions for parental care. In the simplest case the female has a narrow cutaneous fold on each side of the back, and this prevents the spawn from slipping off sideways *(Cryptobatrachus evansi)*. These folds may broaden out to form a cutaneous border along the margins of the back and thus form a bowl adapted for carrying the eggs *(Flectonotus goeldii*, pl. 18). Finally, the folds of skin may fuse together over the back and form a brood sac completely closed except for a slit; these are the true marsupial-frogs *(Gastrotheca)*. The slit may be fairly large, as in *Gastrotheca ovifera* (pl. 17, 18) or its edges may be further fused to leave a rather small opening, as in *Gastrotheca marsupiata*.

The spawn carried by these frogs consists of few eggs, but they are rich in yolk; in *Gastrotheca pygmaea*, for instance, there are only 4-7 eggs but in the large *G. ovifera* up to 50. In these species the eggs develop in the brood sac completely, so that fully formed froglets, and not tadpoles, emerge to the light of day. There are, however, marsupial-frogs such as *Gastrotheca marsupiata* which "give birth" to frog larvae; in these instances the number of eggs is greater, and may be as many as two hundred. The process by which the eggs are introduced into the brood sac was not known until recently; in *Gastrotheca ovifera* it has been observed that the spawning female, in amplexus with the much smaller male astride her back, raises her body on her hind limbs so that the eggs, as they are extruded and fertilised by the male, slide down one by one, as if on an inclined place, into the orifice of the brood sac. On the other hand it seems that the spawn of *Gastrotheca marsupiata*, whose eggs are smaller, is introduced into the orifice, which is also much smaller, with the assistance of the male's hind limbs.

Yet another and totally different group of frogs which, curiously enough, also lives in South America, has adopted the same form of parental care; they are the Surinam-toads (Pipidae), which are aquatic, in contrast to the arboreal marsupial-frogs. Unlike the latter they do not have an undivided brood pouch but honeycomb-like pits in the skin, each of which encloses a single egg. They are formed after the female has extruded the eggs from her cloaca, which is evaginated like a huge sack underneath the male whilst he is in amplexus. The male apparently helps the female in doing this, for he not only squeezes the eggs out of the cloaca but, by the pressure of his body, distributes them evenly over her back. An operculum is formed over each cell of the "honeycomb" and the eggs undergo their development beneath it, either to the larval stage *(Pipa parva, P. carvalhoi)* or to tiny frogs *(P. aspera, P. snethlageae, P. pipa*, pl. 3). After the offspring have left them, the cells degenerate.

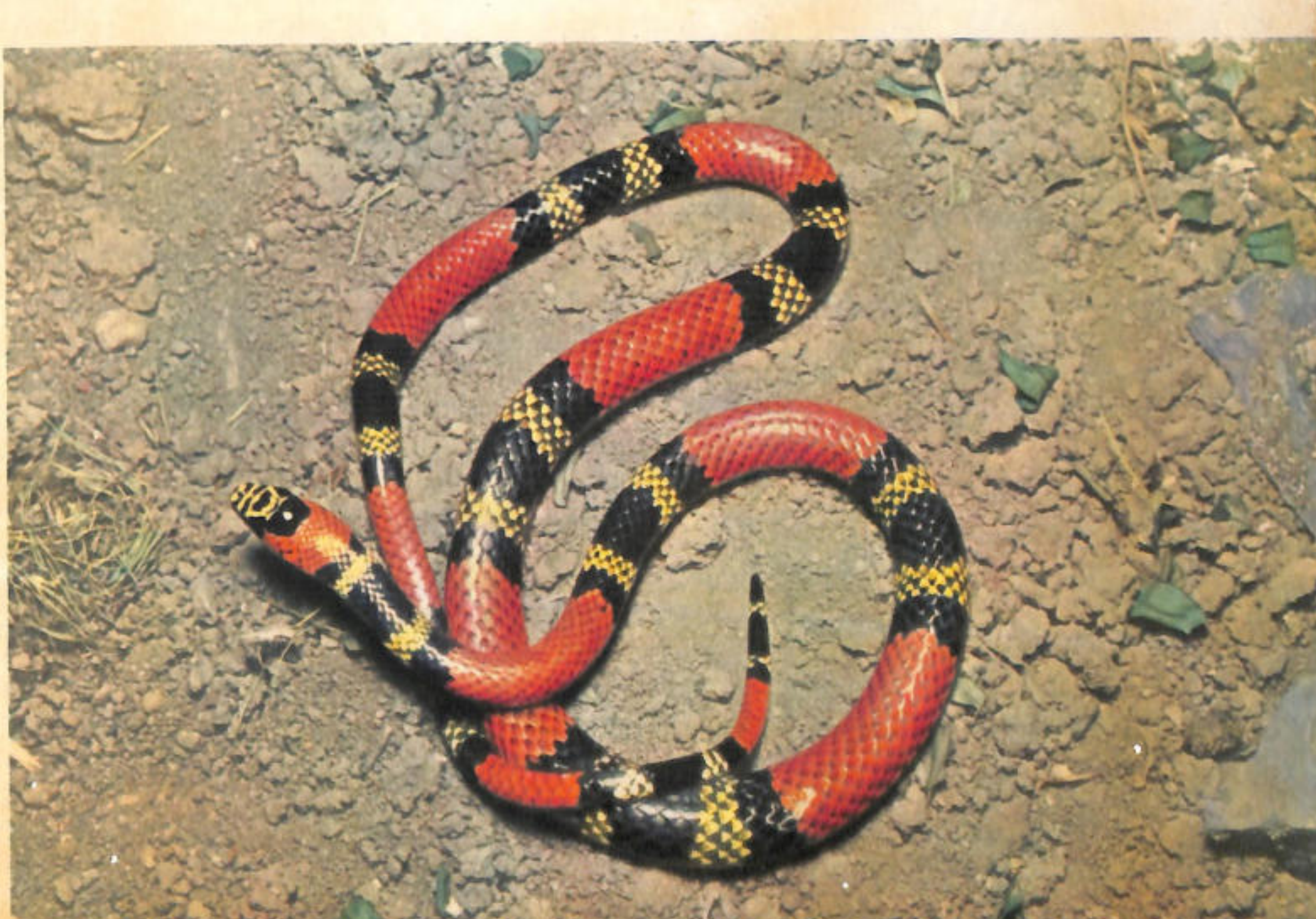
In all the instances mentioned hitherto it was the mother which was concerned with the care of the brood. The father may, however, sometimes take over this function whilst the mother does not trouble further about her progeny after spawning. There are, however, only a few instances of this phenomenon, the best known being the European Midwife Toad *(Alytes obstetricans*, pl. 4), which is related to the firebelly-toads. In contrast to the other anurans of this part of the globe, the sexes pair on land and not in the water. The male entwines the egg-string round his hind limbs, as they are expelled from the female's cloaca, and carries them around for two or three weeks, that is to say, until the eggs are ready to hatch. Then the male repairs to a pool where the spawn is shed and the larvae hatch and develop, like those of other anurans. The second example is Darwin's Frog *(Rhinoderma darwinii*, pl. 11) in Chile. Here the male's vocal sac serves, uniquely, as a brood pouch. The female lays her eggs, singly, on land where they are fertilised and undergo the first part of their development outside the parent's body. However, as soon as the embryos begin to stir inside the eggs, the "snapping-reflex" is released in the male which is still near the spawn. As a result, the embryos are taken into the male's mouth and thence into his vocal sac, where they undergo their further development. Subsequently they are released into the world, by the father, as completely, or nearly completely formed froglets.

No less strange is the parental care shown by some male frogs which carry newly-hatched tadpoles around on their backs unenclosed; the original purpose of this was, no doubt, to carry them to a sheet of water. This form of parental care is known in a frog from the Seychelles *(Sooglossus)* as well as in certain tree-climbing frogs endemic in tropical America *(Dendrobates*, pl. 11 and *Phyllobates)*, which are, however, not at all closely related to the species from the Seychelles. The eggs of these frogs are deposited on land and the emergent tadpoles attach themselves firmly to their father's back by suction; they are carried around by the male until they fall off in a pool where they continue their development. In *Sooglossus*, however, the larvae probably metamorphose into young frogs on the father's back.

Apart from these examples there are only a few instances among amphibians and reptiles where parental care is concerned, not with the egg, but with young which have already been hatched, or are in the process of hatching. Guardianship of newly-hatched young salamanders may occur to a limited extent in certain species and mention might also perhaps be made, in this context, of the temporary association of young pythons in the immediate neighbourhood of their mother. It is commonly reported that in the Nile Crocodile, and similarly in the South American Caimans, the female opens up the nesting site on hearing the croaking which the young ones make inside the eggs shortly before they hatch; without this help the juveniles would often be unable to dig their way out and would inevitably be smothered. In addition, it is said that the female crocodile leads her offspring to the water; but this may be doubted, since young aquatic tortoises find the water of their own accord and without difficulty, being attracted by the intensity of the glare reflected from the surface-film of the water. Effective obstetric assistance is given by the mother herself in the case of the viviparous Desert Night Lizard *(Xantusia vigilis)*, whose young are surrounded by an integument when they are born; the mother grasps them with her mouth and ruptures the envelope. Sometimes she even seizes those young

Pl. XIII. The venomous coral-snake *Micrurus frontalis* of Brazil has the habit of raising its tail when in danger. × 0.5. *Photograph* by Mertens.

The completely harmless snake *Simophis rhinostoma* is deceptively like the poisonous coral-snakes of the genus *Micrurus*. × 1. *Photograph* by Senckenberg Museum (Haupt).



which appear with the tail and hind limbs in advance and draws them out. As in the case of some other viviparous lizards (e.g. *Trachydosaurus*, col. pl. XI), the after-birth is eaten by the mother.

Retention inside the parent's body is advantageous to the developing young not only on account of the protection afforded against the action of the climate or of enemies but also because nutritive materials are often supplied by the mother. This is the case not only in those lizards which have a placenta, like certain skinks, but also in caecilians which are supplied in the uterus with nutritive material from the mother. The nutrition of viviparous salamanders *(Salamandra atra* and occasionally *S. salamandra)* is also well known; the embryos eat a yolky pulp which arises from the breaking-down of eggs that are not developing. In the Alpine Salamander 40-60 eggs reach the oviduct but only one or two form embryos, and this is at the expense of the remaining eggs. Young Surinam-toads, which are enclosed in cells on the mother's back, or juveniles of Darwin's Frog, for whom their father's vocal sac serves as a brood chamber, may possibly be provided with nutriment by the parental organism.

Most amphibians and reptiles grow more rapidly than is generally supposed. Many species of frogs and lizards, for instance the dwarf species of the genera *Eleutherodactylus*, *Hyla* and *Phrynobatrachus*, as well as geckos, anoles and others, reach sexual maturity before they are even a year old. The Bull Frog *(Rana catesbeiana)* on the other hand, is sexually mature when 4-5 years old, and *Alligator mississipiensis* at 6 years, whilst several tortoises, females especially, may only be able to reproduce after 11-12 years. Nevertheless, there are some chelonians which attain sexual maturity in a much shorter time (2-5 years). The determining factor is more particularly the size that has been reached rather than the age. Thus, the larvae of some salamanders, especially in the genus *Ambystoma*, mature so rapidly under the influence of endocrine secretions that metamorphosis does not take place and the animals, in spite of their gills and other larval characters, become sexually mature (neoteny). Among anurans giant larvae are occasionally developed though they are not capable of reproduction.

The speed of growth is very variable and may be subject to some fluctuation within the species; for example, the sex which achieves the greater size grows the faster. Increase in size is greatest in earliest youth: in agamas *(Phrynocephalus)* it may be more than half a millimetre (0.02 of an inch) a day during the first four weeks and in an iguana *(Crotaphytus collaris)* a daily increase of about 1 mm. (0.039 of an inch) in the length of the head and body has been measured in the first week; these animals double their original length in the first eight weeks. Then the rate of growth diminishes and ceases entirely during the period of winter rest. Red-ear Turtles *(Pseudemys scripta elegans)* at hatching have a carapace 25-28 mm. (1-1.1 inches) long and grow to a length of 75 mm. (3 inches) in two or three years, as one can check by the growth rings on their horny plates; after that, growth continues at the rate of about 15 mm. (0.6 of an inch) a year. A Mississippi Alligator is about 20 cms. (7.9 inches) long when it leaves the egg; after one year it has a length of 67 cms. (26.3 inches) and, after two years, 120 cms. (47.2 inches). At six years the male is 180-250 cm. (71-94 inches), and the female 160-180 cms. (63-71 inches) long, and a nine-year-old male may be close on 3 metres (9.8 feet) long. An Elephant Tortoise *(Testudo elephantopus*, pl. 28) from the Galapagos during seven years in captivity increased in weight from 29 to 350 lbs. The increase in size is slower in some large amphibians such as the Bull Frog *(Rana catesbeiana)*, which metamorphoses during the second or third summer after hatching and at the age of 4 or 5 reaches a size of 100-126 mm. (3.9-5.1 inches). The Tuatara appears to grow very slowly, a characteristic that is probably associated with the cool climate in which it lives.

There are some species of amphibians and reptiles which show no signs of further growth after reaching sexual maturity and others which continue to grow. Many dwarf forms belong in the first category and most crocodiles, apparently, in the latter, though the yearly increase of sexually mature individuals is very slight. But the continued growth explains why, among crocodiles, giants are often found which greatly exceed the average size. In various species growth may cease for some time after sexual maturity is reached and then begin anew.

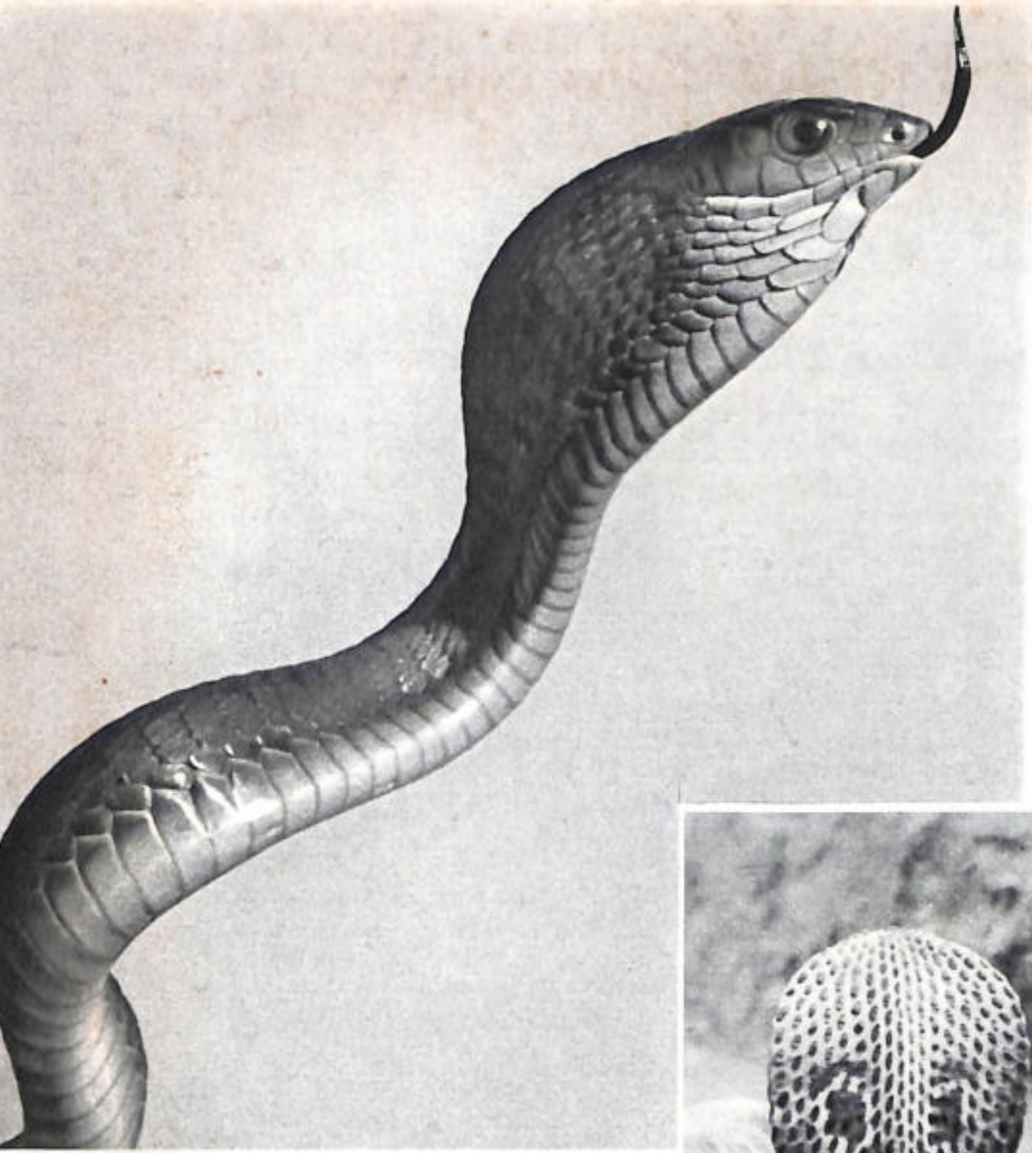
The normal occurrence of sloughing in amphibians and reptiles is often associated with their growth. This phenomenon is, however, dependent upon a number of other factors, such as nutritive conditions, humidity, the endocrine organs and, especially, the temperature. During their active period all lizards shed the old skin (i.e. the horny layer, stratum corneum, of the epidermis) every 4-6 weeks, and it generally peels off in separate shreds, often with assistance from the jaws; some species eat the cast skin, probably as a purely reflex action. All snakes, as well as some serpentiform lizards, slough their skin in one piece, on the average every 1-3 months. In a few water-tortoises the old skin is regularly sloughed not only on the neck and limbs, but the horny shields of the shell are also renewed. No such renewal of the horny plates has been observed in land-tortoises and crocodiles, but all amphibians slough. It is worth recording that there are tree-frogs (e.g. *Hyla cinerea*, *H. crepitans)* which slough every evening during their active cycle, whereas others, such as the toads, do it every other day. The amphibians, like some lizards, swallow their old skin and this may be seen not only in frogs but also in newts.

Reptiles reach a great age. Records of snakes which have been kept in captivity under suitable conditions for more than two decades are not uncommon. In this category there are, for instance, the Anaconda *(Eunectes murinus)* and the Black-necked Cobra *(Naja melanoleuca)* each with 29 years, the Indigo Snake *(Drymarchon corais couperi)* with 24 years, the Leopard Snake *(Elaphe situla)* and the *Boa constrictor* each with 23 years, and so on. Lizards are, for the most part, not so long-lived as snakes, although some remarkable examples are known, such as a Slow Worm *(Anguis fragilis)* which in one instance lived to the age of 54; in another a 46-year-old male mated with a female at least 20 years old. The venomous *Heloderma suspectum* has been kept 25 years in captivity and even very small lizards, such as the Mediterranean *Phyllodactylus europaeus* have been kept alive, with careful attention, for more than 20 years in a terrarium. Amongst anurans, the larger toads *(Bufo)* are the longest-lived and, amongst urodeles, large salamanders *(Megalobatrachus*, *Cryptobranchus*, *Amphiuma*, *Ambystoma);* but here, too, there are small species such as the Japanese *Triturus pyrrhogaster*, which survive in perfect health for over 25 years. Another Japanese salamander *(Hynobius naevius)* lived in the author's care for 21 years — a very considerable age for so small a creature when one bears in mind that the little creature was already adult when its captive life began. The record among amphibians is held by the Japanese Giant Salamander with 55 years; among toads the Common Toad *(Bufo bufo)* has been shown to have a life-span of 36 years in captivity.

About the same life-span (50-56 years) is known in captive alligators of both species, but it is the tortoises which live longest. Here there is a whole series of examples showing that various species enjoyed good health in captivity not merely for half, but for a whole, century. According to some records a Box Turtle *(Terrapene c. carolina)* reached an age of 123 years in the wild state, and another 138 years; a Black Seychelles Tortoise, *Testudo sumeirei*, now extinct, is said to have been 152, and perhaps 200 years old and thus to be amongst the oldest of all known animals. The Tuatara is also very long-lived; those in Uppsala and Dublin have become famous, the latter surviving for 33 years in captivity. In New Zealand one animal survived in captivity for as long as 77 years.

The longevity of the Tuatara, is, perhaps, like its slow growth-rate, associated with the cool temperature of its habitat, since its whole metabolism, in fact, is much more sluggish than that of any other reptile. An additional, important contributory factor to its longevity is the annual winter rest of several months. Certain lizards in northern regions do, in fact, achieve a longer life-span than in southern regions; in the latter an animal is active for the whole 365 days in a year, whereas in the north these 365 days of active life correspond to a period of two years approximately, if one assumes a six-month period of no activity. Thus the Fence Lizard *(Sceloporus undulatus)*, for example, never reaches an age of more than two in Florida, where it is active throughout the year, and less than 94 % survive for one year; in the north of the U. S. A. (Maryland), on the other hand, where these lizards rest for the five winter months, their life-span is more than 4 years and the maximum age is probably reached at 8 years.

It is understandable that under the natural conditions of life in the wild state the average life-span must be quite different, and indeed very much shorter, than in captive animals. A population of any kind of small frogs is generally replaced in the course of a single year by other individuals, whereas the same species may be kept in captivity for several years. Experiments



Pl. 69. Although this tropical African tree-snake, *Dispholidus typus*, belongs to a group of snakes that is only slightly venomous, it can be dangerous to man. It stretches its tongue out as a threatening gesture. ×0.5. *Photograph by* Fisher.

The spectacle-like marking is easily discernible on the neck of the Spectacled Cobra, *Naja naja*, which, when threatened, expands its neck to the shape of a shield. ×0.2. *Photograph by* Rosenberg.

Pl. 70. Sea-snake *(Laticauda colubrina)*. This animal is a representative of the venomous Hydrophidae which live mainly along the coasts of the tropical Indo-Pacific region. ×0.5. *Photograph by* Tweedie.

Although the Australian Death Adder, *Acanthophis antarcticus*, belongs to the venomous cobra-group (Elapidae), its outward appearance gives the impression of a viper. In defensive posture it blows itself up and looks nearly twice as thick as it really is. ×0.5. *Photograph by* Senckenberg Museum (Haupt).

Pl. 71. The most widely distributed and commonest poisonous snake of Europe is the Adder *(Vipera berus)*. The animal inhabits a vast area stretching from south-west Europe to eastern Asia. ×1. *Photograph by* G. Senfft.

The colour of the Adder is very variable; even completely black specimens occur. ×1. *Photograph by* Rosenberg.

Pl. 72. During the mating season male Adders, *Vipera berus*, engage in mutual pursuit but without biting one another. Similar "nuptial combats" occur in other snakes, too. ×0.5. *Photograph by* Hajek-Halke.

with *Anolis carolinensis* revealed that no less than 98% of two hundred marked individuals failed to survive for a year in the wild state and not a single *Anolis* remained alive longer than 16 months. Yet this pretty lizard can, with careful attention, easily be kept alive in a terrarium for 2-4 years! Thus, in unfettered nature, there are not only factors which operate favourably but others which continually threaten the existence of animal species. It is the continual overproduction of progeny which ensures that the posterity of the species is not endangered.

CHAPTER TEN

RELATIONSHIP TO MAN

In discussing the relationships of amphibians and reptiles to the world around them we have not hitherto considered an essential factor — namely Man. But a work devoted to the lives of these animals should not be concluded without considering man's importance to them. For man is, indeed, the worst enemy of many amphibians and reptiles; he restricts or completely destroys their natural habitat and kills millions of them every year either wantonly through ignorance or because they provide valuable raw materials or other commercial goods. It is self-evident that at least an equally large number of amphibians and reptiles succumbs in Nature's "struggle for existence", but only very rarely does one find an animal lying dead in the open which has not perished at the hands of man!

Man has exercised a deep and lasting influence on the distribution of amphibians and reptiles as he has on that of other groups of animals. The clearing of their original habitats for cultivation, the destruction of virgin forests in all parts of the world and the ruthless draining or poisoning of their native waters have greatly restricted the natural distributional areas of many species and reduced their stocks. Nevertheless, it must be admitted that man's actions in these respects do not always operate negatively but may, on occasions, have a positive value; in the landscape transformed by man, the so-called "developed" areas, not a few amphibians and reptiles may find more suitable living conditions than under natural conditions and, as a consequence, their distributional range is increased. Thus, in southern Europe, for instance, Wall Lizards can be seen to prefer living on fences and walls or ruins or other heaps of rubble created by man; in these spots they sun themselves in their dozens. The lizards perceptibly decrease in abundance the more remote they are from such places. In north temperate latitudes lizards choose as their habitat vineyards, cemeteries, railway embankments and rubbish dumps. Not only the Wall Lizards *(Lacerta muralis)*, but the Sand Lizards *(Lacerta agilis)*, too, are characteristically associated with man's activities and their popular German name "Zauneidechsen" (Hedge Lizards) is most aptly chosen. The Common Lizard *(Lacerta vivipara)*, on the other hand, tends to avoid human activities and its distribution is hardly encouraged by land development.

Animals associated with land development are found in even larger numbers in the tropics; cocoa, coffee, banana and sugar-cane plantations and rice fields have an undeniable attraction for some amphibians and reptiles. Rice fields, in particular, with their warm, shallow water, muddy bottom and profuse insect life, provide the most favourable conceivable living conditions for many frogs. To capture certain kinds of frogs in Java one has to go into the paddy fields! And some water-snakes, mostly relatives of the Grass Snake, have followed the frogs into the rice fields. Tortoises also, and certain lizards which disport themselves on the bunds of the

Pl. XIV. The West Australian Bandy-bandy, *Rhynchoelaps bertholdi*, is a typical sand-dweller Although belonging to the cobra-group (Elapidae) it is harmless to man. × 1. *Photograph by* Mertens.

Amongst the most beautiful snakes of western Australia is *Vermicella calonota*, a cobra also harmless to man. × 1. *Photograph by* Senckenberg Museum (Haupt).

rice fields and delight in the damp substratum, often find equally suitable homes there. The irrigation channels also present many strictly aquatic species with a ready means of extending their original distributional range; and artificial ponds or other devices for collecting water, such as cisterns, serve in the same way, especially if they are constructed in places with a low rainfall.

Even the very close proximity of human settlements may be a decisive factor in attracting some lizards, snakes and anurans. This passes almost unobserved in our latitudes, although it is well known that the Grass Snake looks for village manure-heaps to lay its eggs and that, in the evening twilight, the alleys of small villages in the east of central and southern Europe may swarm with Green Toads *(Bufo viridis)* which are on the look-out for insects. In the tropics, however, it is not only toads, but even tree-frogs and other arboreal frogs which flourish in man's company; in Queensland and Brazil there are species of *Hyla*, for example, which readily take up residence in the rooms of houses, and are called house-frogs in consequence. Similar behaviour has been observed in some snakes — and not only in small snakes, such as the genera *Lycodon* in southern Asia, *Boaedon* in Africa or *Leptodeira* in America, but also in very large species such as the Indian Rat Snake *(Ptyas mucosus)* or even boas of various genera. Moreover, venomous snakes, such as various species of *Bungarus* and *Naja* in southern Asia, quite frequently wander into native huts and even the houses of Europeans in search of their prey.

Lizards exhibit the greatest predilection of all reptiles for living in and around houses. In tropical Africa the superb Common Agama *(Agama agama)* is a constant companion of man and lives not only in the shady village trees but is also found in large numbers in the thatched roofs of the negroes' huts; many smooth-lizards *(Mabuya)* also live in similar places. In the warmer areas of America and in the Antilles a number of species of *Anolis* are associated with man's activities, and in Brazil the keeltail-iguanas of the genus *Tropidurus* follow in the wake of development in the same way. In south-eastern Asia the large Kabara Goya *(Varanus salvator)*, despite its timidity, prefers to be associated with man.

It is, however, the geckos which, in warmer countries, can be described as the animals most typically associated with human dwellings and habitations. They can be considered as synoecists, or even as symbionts of man, to whom they owe an enormous extension of their original distributional boundaries. It is noticeable that in the Mediterranean countries the small *Hemidactylus turcicus* is much more common in houses than in the open country. But in the tropics the number of related house-lizards is astounding, especially in southern Asia and in the islands of the Indo-Australian archipelago. As soon as the lamps are lit in the evening they emerge from all corners and crevices, from holes and crannies, and commence their very profitable occupation of capturing insects. The huge, red-spotted Tokay *(Gekko gecko*, pl. 40) also joins the crowd of small house-geckos. Although these creatures occur so abundantly in houses, scarcely a specimen is ever to be seen far from human habitations.

If one looks for the reasons for this remarkable dependence of so many amphibians and reptiles on mankind, the answer is not far to seek. For many species the cultivated areas offer better prospects than virgin soil; a wall of loose stones provides more and better hiding places than a smooth, natural, cliff face; manure heaps and refuse tips, garden beds and plantations, farm buildings and houses, often provide better feeding conditions for insectivorous anurans and lizards as well as for those snakes which prey on mice and rats. There is no doubt that ecological factors associated with feeding play a major part in the "anthropophily" of many, probably of all, amphibians and reptiles. As for the house-geckos, living in human habitations offers, in addition, a considerable measure of protection against their many natural enemies — large lizards and snakes, birds of prey and raptorial mammals. Since these geckos normally live either on cliffs or tree-trunks, a transition to life in houses was naturally easy, for the latter scarcely differ ecologically from their original homes. Their nocturnal mode of life also decisively favoured this transition.

Mankind has widely distributed these associates of his activities — and also a considerable number of those which shun them — partly by inadvertence but at times deliberately; sometimes he has spread them so far and wide that their original boundaries have become obliterated. For example, the occurrence at the present day of some lizards such as *Lacerta perspicillata* or *sicula* on the Balearic island of Minorca, or the appearance of certain anurans in the south-eastern

United States, on Bermuda, Hawaii or New Zealand, can only be explained by the activity of man, i.e. by the recent development of his means of transport. For reasons mentioned previously, geckos are especially easily transported. Amongst them, for example, the small Turkish Gecko *(Hemidactylus turcicus)* has been transported from its original habitat in the Mediterranean countries to Cuba and southern North America where it has become established. Its relative, the larger *Hemidactylus mabouia*, has been transferred from the warmer parts of Africa and Madagascar to similar parts of the New World. Other species of geckos, such as *Peropus mutilatus* which originated in south-east Asia and in the Indo-Australian islands, have also penetrated into America, whilst *Hemidactylus brookii* and *frenatus* have settled in three continents — Asia, Africa and America — through the agency of man. Dozens of additional examples of the transport of amphibians and reptiles by human agency could easily be mentioned. One of the strangest is that of a poisonous sea-snake *(Laticauda colubrina*, pl. 70) from the Indo-Pacific region which was run over by a cyclist in March, 1914 in a busy street in Magdeburg and was handed over to the museum in that city!

Only isolated species, however, are involved in voluntary or involuntary association with man's activities. It should not be erroneously concluded that man's influence has been really beneficial except to a very few lizards, snakes and anurans. Unfortunately his destructive influence on amphibian and reptile life is far greater and, apart from the progressive destruction of natural habitats already mentioned, is attributable to two factors: firstly to the fact that certain reptiles are a menace to human life, and secondly that some species are a source of desirable raw materials or have a certain commercial value.

Only large crocodiles, very large boas and pythons, a number of venomous snakes and the two species of poisonous lizards *(Heloderma*, pl. 52) are actually dangerous to man; and, amongst these groups, only the venomous snakes constitute a real menace, on account of their abundance and widespread occurrence in certain countries. Clearly the number of venomous species is not very large in comparison with the total number of snakes: if the latter number is estimated at 3,000 species, scarcely more than 300 are really dangerous to human life and, of these, about 50 are exclusively marine. Even in Australia, a continent in which 77 % of all the terrestrial snakes belong to the venomous family Elapidae, not more than 22 species, out of a total of 67 in this group, constitute a danger to man. According to the latest statistics, 30,000-40,000 deaths from snake-bite are reported annually in the whole world; the heaviest mortality appears to be in Burma and India with 15 cases per 100,000 of the population in the former and 5 in the latter. In the United States, the country with the most rattlesnakes, not more than 71 deaths definitely attributable to snake-bite were registered in the years 1950-54, i.e. about 14 annually. This figure indicates that, in about every 10,000,000 of the population, not more than a single annual fatality can be charged to the account of the venomous snakes. And how many fatal traffic accidents are there annually in the U. S. A. amongst the same number of people? In no other country, of course, is serum therapy against snake-bite so excellently organised as in North America. In all countries the danger from other reptiles, such as large crocodilians and boas or pythons, is considerably less than that from venomous snakes and, as a rule, is virtually insignificant. Even the two venomous lizards *(Heloderma)* are of no great importance as a source of danger to man and this is shown by the fact that one species, *Heloderma suspectum*, enjoys legal protection in the U. S. A.

Unfortunately the whole world of snakes has to pay a heavy penalty for the accidents caused by venomous species; and not only all snakes, whether very venomous, slightly so or completely harmless, but also the many limbless, and so more or less snake-like, lizards are often slaughtered. "I kill every snake wherever I come across one" was a remark once made to the author by a man who lived in an area where few venomous snakes were to be found. It is particularly deplorable that the many harmless coral-snakes in tropical America so often have to pay with their lives for their resemblance to their venomous, but numerically much less abundant, prototypes. Regions that are completely free from venomous snakes dangerous to man have been discussed previously.

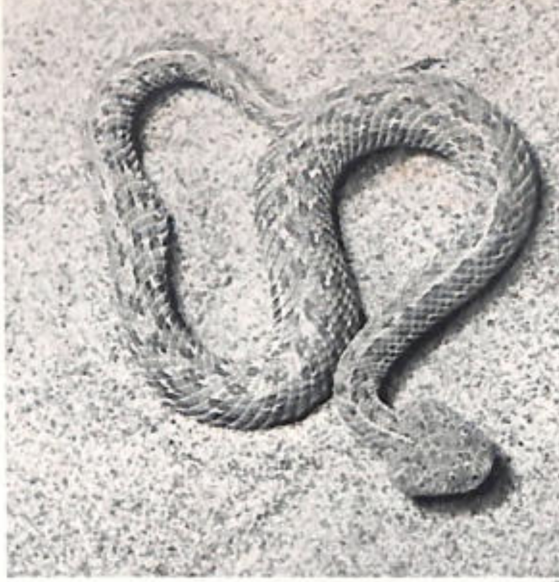
From the earliest times man has hunted many of the large species of reptiles and amphibians because he found their flesh palatable and because he also needed their fat. In this connection

Pl. 73. The Sand Viper, *Vipera ammodytes*, is a relative of the Adder and lives in south-east Europe; it is characterised by a scaly process on the tip of the snout. ×1. *Photograph by* Rosenberg.

The Kufi of south-west Asia, *Vipera lebetina*, also occurs on European soil, on the island of Milos in the Cyclades and some neighbouring islets where a special subspecies *(schweizeri)* lives. This form is remarkable in being oviparous and not viviparous, as is usual. ×0.5. *Photograph by* Bertolf.

Pl. 74. In its locomotion the North African Horned Viper, *Aspis cerastes*, is a "sidewinder". By rubbing together the specially modified scales of its flanks it produces a noise deceptively like a hiss. ×1. *Photograph by* W. Senfft.

A relative of the Horned Viper which it resembles, the hornless Asp, *Aspis vipera*, is also an inhabitant of the North African deserts. ×1. *Photograph by* Rosenberg.



Pl. 75. The South-west African Dwarf Viper, *Bitis peringueyi*, digs itself into the sand in the same way as the two species of *Aspis* figured on Plate 74. The picture shows the animal shortly before burrowing.

The same animal begins to dig in at the tail.

The viper is now almost completely hidden in the sand.

The snake has now disappeared in the sand as far as the upper surface of the head and the black tip of the tail. ×1. *Photographs by* Senckenberg Museum (Haupt).

Pl. 76. The Gaboon Viper, *Bitis gabonica*, is the largest of the African vipers and is distinguished by its extremely long poison fangs. ×0.3. *Photograph by* Rosenberg.

The Copperhead, *Agkistrodon contortrix*, is a venomous snake of the eastern United States which is as impressive as it is common. ×0.5. *Photograph by* Rosenberg.

snakes are of no great importance, although the flesh of the very large boas and pythons is prized by the natives of nearly all countries where they occur; and canned fillets of Florida rattlesnake are not disdained by well-to-do Americans, if only as a curiosity. On the other hand, sea-snakes form a popular delicacy in Japan and thousands are caught annually in the Philippines and shipped to Japan where they are served fried or smoked. In the tropics large lizards also provide much-appreciated meat and large iguanas — one species bears the significant scientific name of *Iguana delicatissima* — regularly appear on the market in South America. Crocodile flesh, especially the tail musculature, is as much prized as that of certain tortoises. The German name Suppenschildkröte ("Soup Turtle") for *Chelonia mydas* (pl. 24) indicates its culinary importance. In the United States Diamondback Terrapins *(Malaclemys terrapin)* and Snapping Turtles *(Chelydra serpentina)* are much in demand in the kitchen. In former times the giant land-tortoises of the Galapagos, Aldabra and a few other islands played a part in the dietary of seafarers; to-day, in the age of canned foods, there is no longer the same dependence on them, the more so since the stocks of each species have seriously declined. But turtles' eggs are in demand everywhere, especially amongst the natives; they are derived mainly from the previously mentioned Green Turtle *(Chelonia mydas)* and the annual production of eggs from a single island region may run into millions. It is good to know that nowadays the crop of turtles' eggs is controlled by law in many countries.

The demand for some tortoises *(Malaclemys)* and for certain frogs, whose legs are a delicacy, is so great that it cannot be met by the capture of wild specimens. In consequence a change-over has been made to rearing them in "farms". This applies especially to the North American Bull Frog (*Rana calesbeiana)*, for which the demand is so great that it has been exported to other countries for breeding purposes: thus, for example, no less than 766,262 pounds of bull-frogs' legs were exported in the year 1948 to the U. S. A. from Cuba alone, where this frog is not indigenous! In addition to this giant species, some other related but smaller species are used for the same purpose in North America; in central and southern Europe the legs of Edible Frogs, Marsh Frogs, Common Frogs and Agile Frogs are eaten. Related species serve the same purpose in eastern Asia, whilst in South America large species of the family Leptodactylidae are used instead; in the lakes of the high Andes the giant species of *Batrachophrynus* and *Telmatobius* occur and these are much in demand for the table and are roasted whole. In Japan the Giant Salamander is much esteemed for its very palatable flesh.

Many additional millions of snakes, lizards and crocodiles, and frogs too, must be slaughtered since they furnish a valuable leather. It is frightening to see the huge masses of reptile skins of various sorts which are sometimes piled up in the warehouses of the large leather firms. There one may see monitors and teyous, iguanas and mastigures, pythons and colubrid snakes of all kinds, karungs *(Acrochordus)* and vipers, crocodiles and alligators, and, on occasions, the skins of the larger species of *Bufo* and *Rana*. The Mississippi Alligator first came to the fore round about 1800 because it provided a hard and durable crocodile-leather. At the beginning of the present century nearly 200,000 skins of this crocodilian came on the market annually, most of them from Florida. The output for the year 1929 was quoted as 190,000 skins, but for 1939 only 80,000. In the year 1942 the number dropped still further, namely to 18,000, and in the year 1943 to as few as 6,800. In 1944 the alligator was granted legal protection and since that time large specimens may be killed only during a limited season. If that precaution had been neglected the Mississippi Alligator would probably be numbered amongst the exterminated animals to-day! All the true crocodiles are equally heavily trapped for their leather, but the South American Caimans are less hunted on this account; their ventral skin, which is the only part of a crocodile's hide that is of commercial value, has bony nodules similar to those of the dorsal skin and consequently can only be tanned with difficulty.

The Hawksbill Turtle *(Eretmochelys imbricata)*, which inhabits all the warmer seas, is the only tortoise that is caught for its tortoiseshell, which is both beautiful and valuable. Unfortunately its reddish-brown horny plates adorned with a yellow flame-like design are often made up into rather tasteless souvenirs for tourists. It is equally regrettable that millions of young crocodiles are used for the same purpose and provide a considerable source of gain in the tropics. In the United States, at one time, the Mississippi Alligator, stuffed, fitted with glass eyes and varnished, was offered to tourists and found a ready sale. When the alligator was protected by law the enterprising Americans imported quantities of young Spectacled Caimans *(Caiman crocodilus)* from the south of the continent every year, and now offer them for sale in Florida as alligators. Even the sharp-snouted ***Crocodylus johnsoni*** from northern Australia, so valuable in scientific collections, has not escaped the same sorry fate of being a souvenir article in Queensland!

There are also living souvenirs in the herpetological sphere; newly-hatched alligators and caimans, as well as land- and freshwater-tortoises, are examples. On the whole, the sale of living reptiles and amphibians for amateurs of aquaria and terraria, for exhibition in zoological gardens and similar institutions, or for scientific study in laboratories, has become an important branch of the trade in animals. In central Europe thousands upon thousands of land- and pond-tortoises, of Green and Wall Lizards, of Grass Snakes and tree-frogs are imported every spring for these purposes from Italy and the Balkan countries. In the United States the same thing happens with small cooters of the genus *Pseudemys* (especially the pretty green "red-eared" *Pseudemys scripta elegans)* and Map Turtles *(Graptemys)*, as well as with *Anolis carolinensis*, which, because of its highly developed powers of changing colour, is erroneously called "chamaeleon". Not only venomous snakes but native species of all other kinds are collected for the large "Snake Parks" such as exist in the majority of countries overseas; there they are "cared for" until their death, which, in most cases, is not long delayed. At this point it may be appropriate to recall that in countries with a predominantly Mohammedan population the exhibition of snakes, and especially of cobras *(Naja)* by "snake charmers", is a widespread practice.

Many venomous snakes, whose bites may have serious consequences for human beings, are kept in captivity for the production of antidotes, the so-called snake sera; the use of these at the right time can almost always save the life of a person bitten by the snake. In speaking of snake venom it must not be forgotten that the venom itself is used as a medicament. This applies also to some venoms extracted from the cutaneous glands of anurans which are used in medicine, especially in China; but South American natives use that from the poison-frogs *(Dendrobates)* for poisoning their arrows. Generally speaking, many amphibians and reptiles are of great therapeutic importance, especially amongst Asiatic peoples. The Medicinal Skink *(Scincus scincus)* was formerly used even in Europe as a remedy for the most diverse complaints; nowadays, however, it is probably in demand only amongst the Mohammedans.

Frogs, as is well known, play very important parts as laboratory animals in connection with a great many kinds of research in the fields of biology and medicine. The young biologist is indebted for his first acquintance with vertebrate anatomy to "the frog"; in Europe this is generally *Rana esculenta* or *ridibunda*, in the United States *Rana pipiens*, and in southern Asia *Rana tigerina*, whilst in the African, South American and Australian laboratories large frogs, often of quite different groups, are sacrificed for the same purpose. Even greater is the number of frogs which are sacrificed daily in the interests of science for countless physiological or medical research purposes, from the discovery of galvanic currents to pregnancy diagnosis. The experimental animals for this latter purpose, it is true, must remain alive if the demonstration is to succeed. It was originally believed that only female Clawed Toads *(Xenopus laevis)* from South Africa were suitable for this purpose and, in consequence, these animals were bred in great numbers for the laboratories of the whole world. To-day it is realised that the same demonstration can be carried out, almost more simply, with males of the ordinary laboratory frog.

From this brief survey it is clear that the amphibians and reptiles have not been without influence in the cultural development of mankind. Thanks to his exceptional brain, man has realised how to use to his own advantage many other animals as well as a number of species of amphibians and reptiles. It is gratifying that in most civilised countries there is to-day an appreciation of the fact that many of these creatures bring advantages to humanity in still other ways. As destroyers of pests of various kinds they play an important part in the biological balance of nature. Consider the many insectivorous lizards and frogs. The geckos and other lizards that live in and about houses, and frogs too, destroy directly countless mosquitoes, flies and other troublesome domestic pests which are often vectors of dangerous diseases. Consider also the innumerable insect pests which cause devastation in gardens and plantations and which

Pl. XV. *Bitis caudalis*, characterised by a small horn above each eye, is the commonest venomous snake of south-west Africa that is dangerous to man. × 1., *Photograph by* Senckenberg Museum (Haupt).

The African tree-viper *Atheris squamigera* is very variable in colour; besides yellow there are also green and brown specimens. × 1. *Photograph by* Rosenberg.

are most effectively checked by toads. One of the largest tropical toads, *Bufo marinus*, has been domesticated for precisely this reason and has been introduced into different countries, even into Hawaii, New Guinea and Australia. But here, as so often happens, man has gone decidedly too far: certainly the toads kill the vermin, but the harmless native fauna also falls victim to their insatiable appetites and its continued existence is threatened. There are large numbers of snakes, both venomous and non-venomous, which devour mice and rats; there are even snakes innocuous to man which attack the venomous species. The benefits which all these animals bring are, without doubt, far greater than the damage which some disease-carrying species cause or which others occasionally inflict, e.g. in fish farms, by their predatory habits.

It is very commendable that in many civilised countries a number of amphibians and reptiles threatened with extinction have been placed under legal protection. It is to be hoped that many other countries will follow the example of some European countries, the United States of America, South Africa and New Zealand (where that very famous reptile, the Tuatara, enjoys the most rigorous legal protection) and, in doing so, also take a protective interest in the crocodilians, which are so intensively hunted, and which, like the Tuatara, are the very last surviving remnant of a formerly extremely abundant order. Many Asiatic peoples have, of course, venerated gharials and softshell-turtles as sacred animals from time immemorial, and there are temples in those regions where tortoises and snakes are protected by superstitious beliefs. Those enjoying such a privileged position are, however, but a diminishing few. How vast, then, is the array of these creatures that must be sacrificed every day for the benefit of mankind?

The list of reptiles exterminated in our day and age, which already includes several iguanas and tortoises, must not be allowed to increase further. The conservation of nature is amongst the most pressing problems of the present century. It is our duty to preserve for posterity on our ever-diminishing globe the much maligned amphibians and reptiles which have played such an important part in the lives of almost all peoples, even in their mythology, and which to-day are still of immense consequence to mankind.

SYSTEMATIC CLASSIFICATION OF THE RECENT AMPHIBIANS AND REPTILES

AMPHIBIA

Caudata; Newts and Salamanders

1. Hynobiidae.
2. Cryptobranchidae.
3. Ambystomatidae.
4. Salamandridae.
5. Plethodontidae.
6. Amphiumidae.
7. Proteidae.
8. Sirenidae.

Salientia; Frogs and Toads

1. Ascaphidae.
2. Discoglossidae.
3. Pipidae.
4. Pelobatidae.
5. Leptodactylidae.
6. Bufonidae.
7. Rhinophrynidae.
8. Brachycephalidae.
9. Hylidae.
10. Ranidae.
11. Rhacophoridae.
12. Microhylidae.

Gymnophiona; Caecilians

1. Caeciliidae.

REPTILIA

Testudines; Turtles and Tortoises

1. Cheloniidae.
2. Dermochelyidae.
3. Chelydridae.
4. Kinosternidae.
5. Platysternidae.
6. Dermatemydidae.
7. Emydidae.
8. Testudinidae.
9. Carettochelyidae.
10. Trionychidae.
11. Pelomedusidae.
12. Chelidae.

Crocodylia; Alligators and Crocodiles

1. Alligatoridae.
2. Crocodylidae.
3. Gavialidae.

Rhynchocephalia; Tuataras

1. Sphenodontidae.

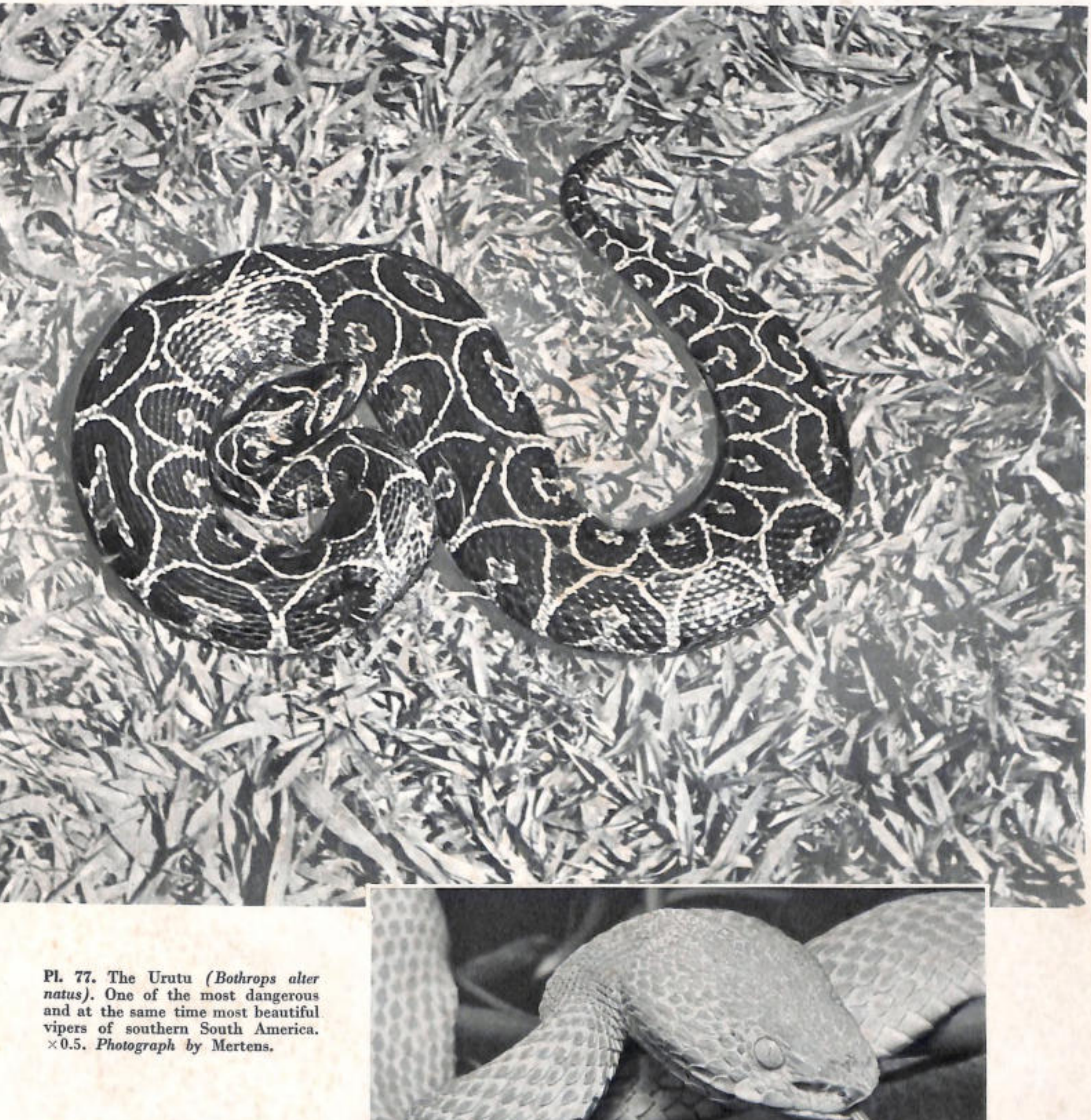
Sauria; Lizards

1. Gekkonidae.
2. Pygopodidae.
3. Agamidae.
4. Chamaeleonidae.
5. Iguanidae.
6. Xantusiidae.
7. Cordylidae.
8. Teiidae.
9. Lacertidae.
10. Scincidae.
11. Dibamidae.
12. Anguidae.
13. Anniellidae.
14. Xenosauridae.
15. Helodermatidae.
16. Varanidae.
17. Lanthanotidae.
18. Amphisbaenidae.

Serpentes; Snakes

1. Typhlopidae.
2. Leptotyphlopidae.
3. Aniliidae.
4. Uropeltidae.
5. Xenopeltidae.
6. Boidae.
7. Acrochordidae.
8. Colubridae.
9. Elapidae.
10. Hydrophiidae.
11. Viperidae.
12. Crotalidae.

Pl. XVI. A tree-viper of tropical America, ***Bothrops schlegeli***, one of the Crotalines, in the act of devouring a frog. × 1. ***Photograph by*** **Rosenberg.**

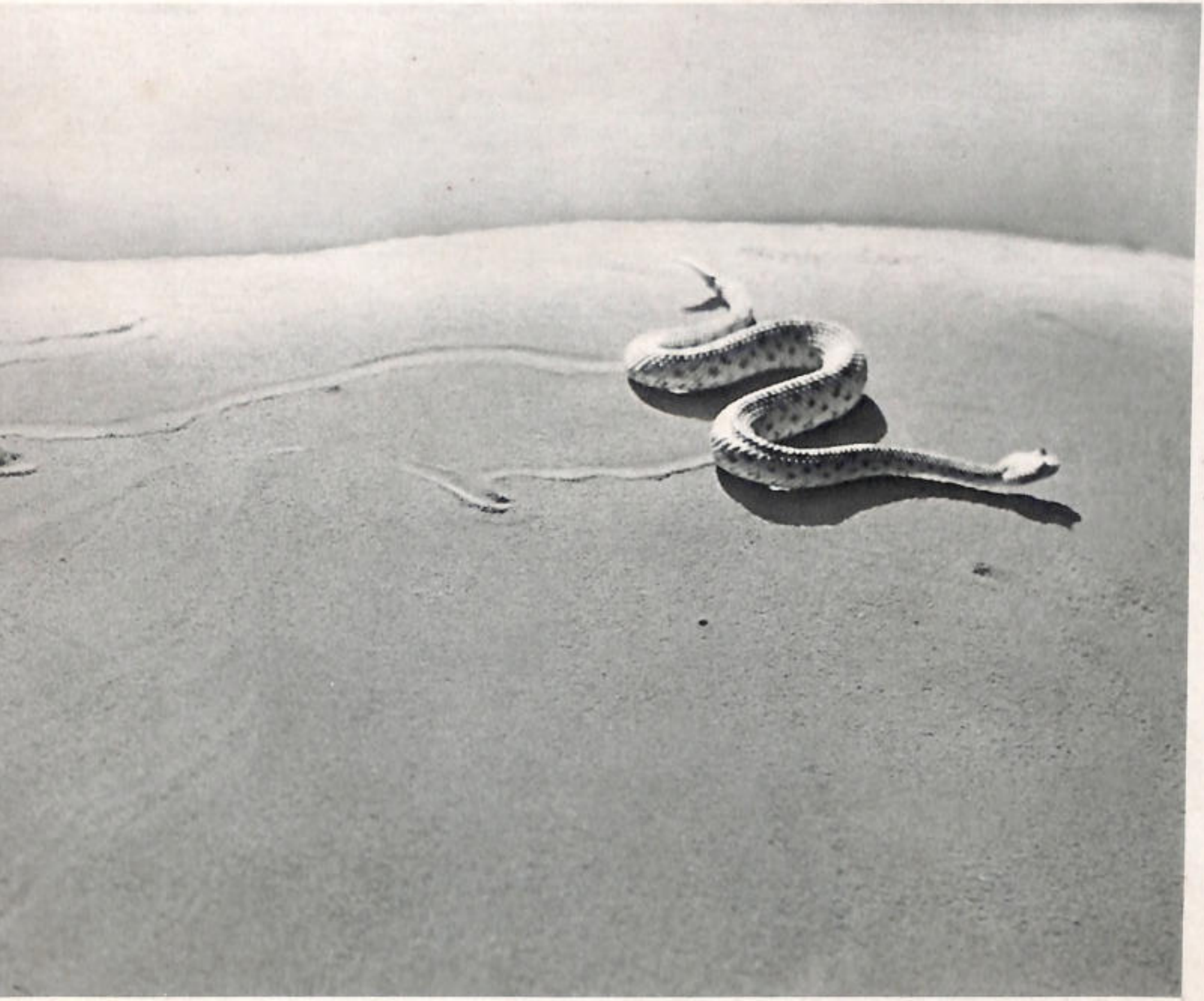


Pl. 77. The Urutu *(Bothrops alternatus)*. One of the most dangerous and at the same time most beautiful vipers of southern South America. ×0.5. *Photograph by* Mertens.

Head of a Central American tree-viper, *Bothrops bicolor*. Between the eye and the nostril a deep pit is clearly visible; this contains a thermoreceptor sense-organ which enables it to detect its warm-blooded prey. ×1. *Photograph by* Senckenberg Museum (Haupt).

Pl. 78. *Lachesis muta*, with a length of 13 feet, is not only the most imposing representative of the numerous venomous snakes of South America but, together with the Asiatic King Cobra, *Naja hannah*, is amongst the largest of all poisonous snakes. *Photograph by* Rosenberg.

Two South American rattlesnakes, *Crotalus durissus terrificus*, from the Butantan Institute, São Paulo. Whereas in North America many and various species of rattlesnake are to be found, South America is colonised, generally speaking, only by the *Crotalus durissus terrificus* figured. There it is considered to be one of the most fearsome venomous snakes. (In the left-hand specimen the rattle can be clearly seen.) ×0.2. *Photograph by* Mertens.



Pl. 79. The Horned Rattlesnake, *Crotalus cerastes*, from California. This small rattlesnake is called Sidewinder by the Americans because it moves forwards, not like most other snakes by sinuous movements, but by throwing single loops of the body forwards and to one side. ×0.3. *Photograph by* van Riper.

Pl. 80. Sidewinder, *Crotalus cerastes*, at rest. The rattle is plainly visible at the tip of the tail. ×1.2. *Photograph by* W. Senfft.

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In the following list we have only been able to mention a very limited number of herpetological publications (and only books are referred to) which deal with the lives of amphibians and reptiles in the most diverse parts of the earth. Much detailed information on this subject is often included in works that are mainly systematic in their approach, but we have been unable to mention them here through lack of space; this applies also to many articles published in scientific periodicals.

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COLOURED PLATES

Pl. I. The best-known representative of the Californian newts, *Taricha torosa*, called the Californian Newt in the United States. × 1. *Photograph by* Senckenberg Museum (Haupt). — One of the rarest salamanders of Asia Minor known only from a few specimens : *Mertensiella luschani*. × 1 approx. *Photograph by* Rosenberg.......... 13

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