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CONTENTS

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THE EXCRETORY SYSTEM OF YOUNG AMPHIBIAN LARVAE

By

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Most vertebrate animals below reptiles in the evolutionary scale possess a kidney system which includes a larval pronephros and an adult mesonephros.

For a number of reasons it is probable that embryologists have studied embryos and larvae of amphibia—which group includes frogs and newts—more widely than those of any other group, and among the many organs whose development and function have been investigated is the paired pronephric system; first discovered by Müller about 130 years ago.

With rare exceptions at least one functional pronephros (and its duct) is essential if a young amphibian larva is to survive, though later the mesonephros is the main, and ultimately the sole excretory organ. Because of the relative ease with which amphibian embryos survive micro-surgery, and in particular owing to the accessibility of the pronephros and of its duct, embryologists are provided with an admirable embryonic organ system—which incidentally can be fairly accurately measured—for the study of fundamental processes of growth and development.

The sites of origin of a variety of organs, in representatives of most of the vertebrate groups, have been recognized on the surface of the early developing egg by the method of vitally staining with dyes, or by excision or transplantation of specific regions of early embryos, and thence tracing their future development. These sites have been illustrated on so-called fate maps. Presumptive, or prospective pronephric tissue is no exception, and is first recognizable in the blastula, when development has reached a stage roughly represented by a yolky ball of cells. It is located underneath the boundary of the future muscle tissue, close to that of the future gut. Later on, after various formative movements, which proceed during embryonic development, the future pronephros (and its duct) is ultimately situated just behind the throat or gill slit region, between the upper body musculature (somites) and the lower musculature of the gut and body wall (lateral plate). The presumptive pronephros is now termed the intermediate cell mass and includes a number of pronephrotomes, or pronephric segments (fig. 1). From the latter a tubular system develops, which opens into the coelom, or body cavity, by a number of separate openings, or nephrostomes (fig. 2, fig. 6), and leads behind into an elongated duct, which discharges into the cloaca, or hinder external opening of the gut.

Pronephric function commences very early in development, probably just before the first spontaneous movements of the larva take place.

Leading from the main arterial blood vessel, or dorsal aorta, are a pair of oval-shaped capillary masses, or glomeri, each one juxta-posed against its associated pronephros and suspended in the coelom (fig. 6).

In life fluid diffuses from the blood across the glomerular membrane surface and into the body cavity—though no doubt coelomic fluid is derived from other sources also—and thence enters the pronephros via the nephrostomes.

Fig. 1

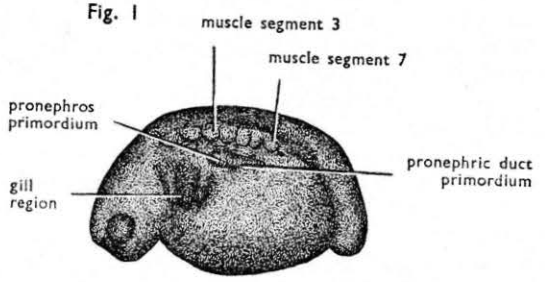


Fig. 2

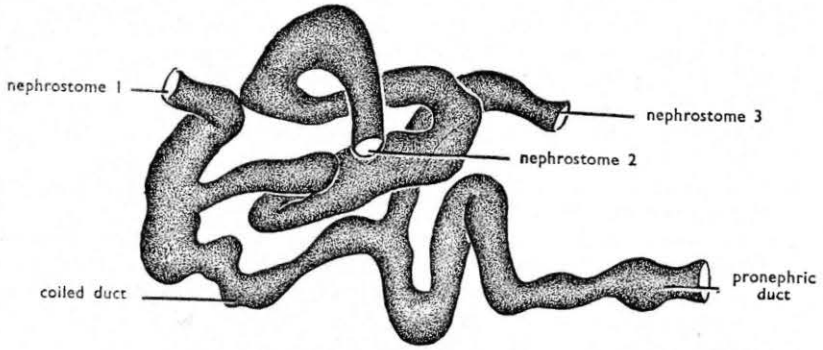


Fig. 3

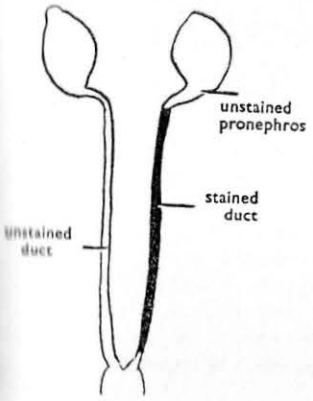


Fig. 4

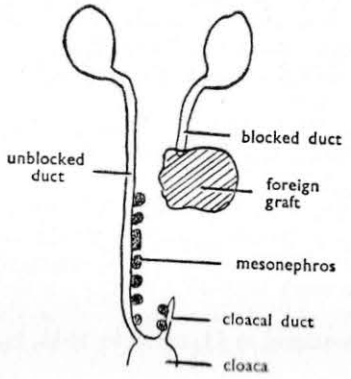
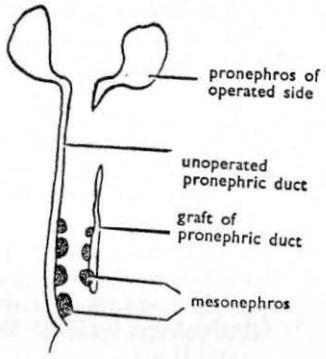


Fig. 5



Movement of fluid into the pronephros is probably assisted by cilia in the walls of its tubules opening into the coelom. It is believed that in specific regions of the complexly coiled mass of tubules essential metabolic substances are reabsorbed, to return to the circulation in the large venous sinuses which surround the pronephros. It is likely, however, that the primary function of the pronephros is one of osmotic regulation; baling out of the larva surplus fluid which has entered, and in this way preventing waterlogging. Nearly all larvae become swollen with fluid, or oedematous, and succumb after either bilateral extirpation of the pronephros (bilateral pronephrectomy), or blockage of their ducts. Oedema does not ensue after removal of one pronephros (unilateral pronephrectomy), for though there is no regeneration of the extirpated pronephros, the remaining partner, acting for two, undergoes the phenomenon of compensatory hypertrophy. In the process component cells of the pronephric tubules increase in number (hyperplasia), each cell also individually enlarging (hypertrophy), compared with the normal condition. In addition tubule lumina are greatly expanded, together with that of the duct (fig. 7).

About 60 years ago Brauer described the pronephros in the larva of a primitive legless amphibian called *Hypogeophis,* as originating from about a dozen repetitively arranged tubules, each one derived from a separate body segment and redolent of the hypothetical ancestral kidney, or archinephros, suggested by Goodrich. The latter structure of ancestral vertebrates probably consisted of a series of undifferentiated tubules extending along each side of the body, each one opening from the coelom and thence leading into a common collecting duct, which transmitted coelomic products, and perhaps also germ cells, to the exterior. In evolution, development led to the differentiation of three specific and recognizably different regions, the pro-, meso- and metanephros. The most posterior, the metanephros, or adult kidney, develops only in reptiles, birds and mammals (which possess a vestigial pronephros), but its structure is in many ways similar to that of the mesonephros, which provides strong evidence of their original common derivation; such organs are termed homologous.

The evolutionary development of the amphibian pronephros can only be deduced—with caution—from a study of the development of living specimens, for no fossil sequence has been, or is likely to be, discovered. Examination of paired pronephroi from various larvae of living genera reveals that the trend is for the number of functional tubules to be steadily reduced. The largest number of about a dozen is recognized in legless amphibia (Apoda), thence 5 or 6 in primitive tailed forms (Urodela), leading through a number of forms to merely two tubules in more specialized newts like *Triturus* and *Ambystoma.* Among tail-less forms (Anura), there are usually three functional tubules included in the pronephros, though occasionally four are recognized.

A good deal is now known (in both qualitative and numerical terms) about the segmental relationships of these tubules to the overall body segmentation. (Fox, 1962a.)

Knowledge of those factors which influence pronephric growth and development is meagre. After unilateral pronephrectomy in young larvae the remaining pronephric system presumably compensates functionally, for it copes with the added work normally performed by its extirpated partner. In the process it enlarges. This response, first discovered in larvae of *Ambystoma* by Ruth Howland at Harvard in 1916, has since been confirmed many times.

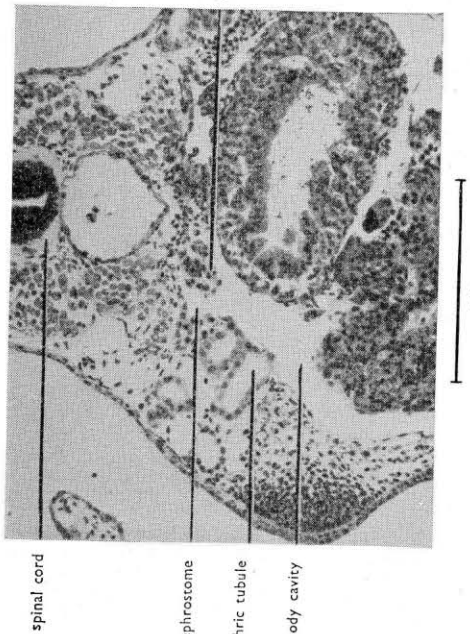


Fig. 6

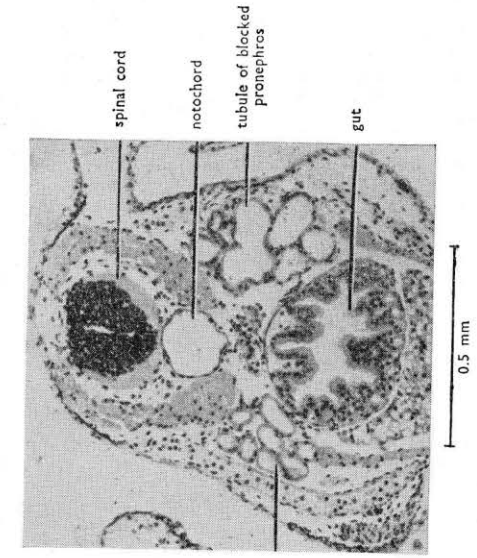


Fig. 8

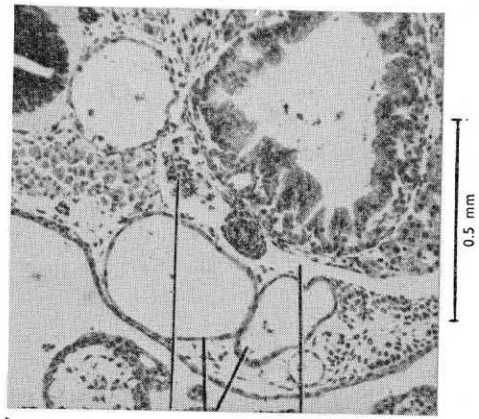


Fig. 7

Evidence from recent experiments suggests that in a single remaining pronephros, fluid tension within the tubules may be one factor which elicits hyperplasia and increase in cell volume; it likewise stretches tubule walls to expand their lumina (figs. 7, 11). There is no evidence to lend any support to the view that pronephric growth-stimulating substances —circulating within the blood vessels or in the body fluids—are active, though the existence of these cannot be ruled out (Fox, 1960). The fact that the primordium of a pronephros, transplanted from an axolotl larva into another of similar age, differentiates into pronephric tubules when not in communication with the ceolom, and thus presumably is subjected to a reduced or non-existent coelomic fluid pressure, suggests that tension is only part of the story (figs. 9, 10). Again Holtfreter (1944) has shown that disassociated cells of primordia of pronephric systems of amphibian larvae will reaggregate *in vitro* into tubules of normal pattern, and a host of complex mechanisms embracing mutual reactions of the cells have been invoked to explain such processes.

Furthermore, unilateral blockage of a pronephric duct results in compensatory enlargement of the other unblocked pronephros, and in a similar, though not quite identical, response by the blocked pronephros (fig. 8) (Fox, 1957). Thus the paired organs, by their very presence, do not directly inhibit each others' growth (see Fox, 1956, 1963).

Before metamorphosis of an amphibian larva, functional continuity of a pronephros is essential for the maintenance of its size and shape, for tubules unconnected with the coelom, or that portion of a duct behind a region where a lesion has been made, will collapse and ultimately degenerate. At the onset of metamorphosis normally the pronephros and the anterior portion of its duct commence to degenerate, the hinder portion of the duct remaining to serve as a mesonephric duct of the adult kidney. Details of the degeneration process have recently been described in *Rana temporaria,* the common frog, in terms of distinct larval stages, throughout the period of metamorphosis (Fox, 1962b).

The whole organ is invaded and digested by certain white blood cells called lymphocytes, and progressively becomes smaller, until by the end of metamorphosis it is hardly recognizable. Retrogression is not the result of cessation of function; rather the opposite is true, for the tubules at first are open into the coelom and continue backwards into a completely canalized duct. Hence the pronephros is probably functional for some time after degeneration has proceeded to some extent. Nor did the structural pattern and rate of degeneration alter after unilateral pronephrectomy, for a remaining pronephros, in a host so treated, generally degenerates in a similar manner to that of the paired organs. Increased function neither hastens nor inhibits its degeneration (Fox, 1962b, c).

Reduction of thyroid activity inhibits pronephric degeneration, but after thyroid recovery, or administration of its hormonal secretion thyroxine, degeneration recommences.

Nevertheless the fact that pronephric degeneration, with its intense lymphocytic activity, operates at metamorphosis simultaneously with the degeneration of other organ systems—in a milieu where there is a high level of thyroid hormone—suggests causal relationships of great complexity. It has been suggested, on good authority, that the mechanism might well be an auto-immune reaction—a term used to describe complex immunological processes whereby an animal becomes intolerant of certain of its own

tissues; this is a hypothesis of profound nature and worthy of serious investigation.

The origin, development and properties of the pronephric duct have received considerable attention from embryologists. Until about twenty-five years ago these problems were mainly investigated in the classical manner, by straightforward descriptive analysis from microscopic serial sections.

More recently, however, various problems have been dealt with experimentally. At the end of the nineteen-thirties O'Connor showed that the pronephric duct of urodele larvae mainly originated from an anterior primordium (often called blastema), situated close behind, and in appearance part of, the pronephros rudiment (fig. 1). If the former is vitally stained by a dye such as Nile-blue sulphate, then as development proceeds the stained cells can be traced to the cloaca; this suggested that the pronephric duct was formed from tissue which grew backwards by its own individual growth (fig. 3). This view conflicted most strongly with earlier prevailing ideas, that the duct originated *in situ* from presumptive tissue situated along the side of the body.

A host of other experiments on embryos of amphibians and the chick, including extirpation or cautery of the duct rudiment, or of its growing tip, or its blockage by foreign graft tissue, resulted in the absence of the duct behind the site of operation. Such work gave further strong support for O'Connor's conclusions (fig. 4).

Nowadays O'Connor's "grow-back" theory of duct development is the one most widely held. Nevertheless, duct development may be even more subtle than this. The evidence still does not preclude the possibility that duct primordial cells, instead of giving rise to the entire duct, may induce, or stimulate in some way, competent or receptive tissue along the side of the body to develop into duct cells; anterior duct blastema cells may or may not contribute to the finally developed structure. Obstruction of the future duct cells may well have prevented the induction from taking place, though the presence of stain in the hinder duct cells, and nowhere else, suggests that the anterior duct blastema cells do materially participate in duct formation.

An attempt to provide further information on this problem is at present being made by the author and Dr. Louie Hamilton, of Middlesex Hospital Medical School, utilizing haploids (specimens whose cells contain a single set of chromosomes, from one parent only), and diploids (normal specimens whose cells contain a double set of chromosomes, from two parents), of larval *Xenopus;* front and hind halves of these two types of embryos are surgically grafted together to produce chimaeras.

The second major problem, which has been strenuously investigated by embryologists interested in the properties of the pronephric duct, is the influence of the pronephric duct upon the development of the mesonephros.

It is now known that the presence of the duct is necessary to trigger off, or influence in some way, mesonephros differentiation (figs. 4, 5).

Over twenty years ago O'Connor concluded that the primordium of an amphibian mesonephros has the power of independent formation of clumps of cells, but in order to differentiate into tubules some inductive or stimulating influence from the pronephric duct is essential. Among different genera the relative importance on the one hand of the potential for independent differentiation, and on the other hand of reaching the necessary threshold, or level of induction required, varies. It is as though the organ has the inherent ability to proceed some way along the pathway of develop-

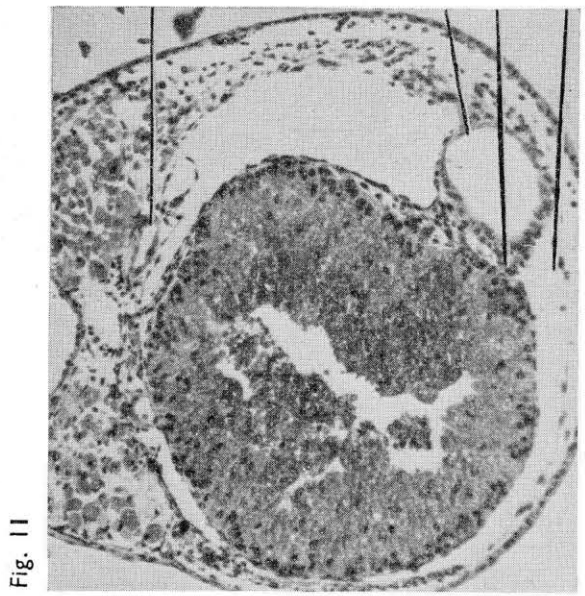


Fig. 11

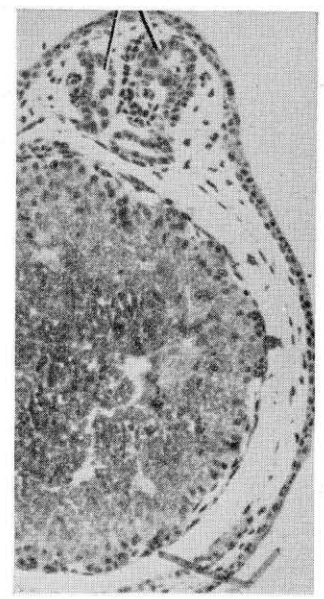


Fig. 10

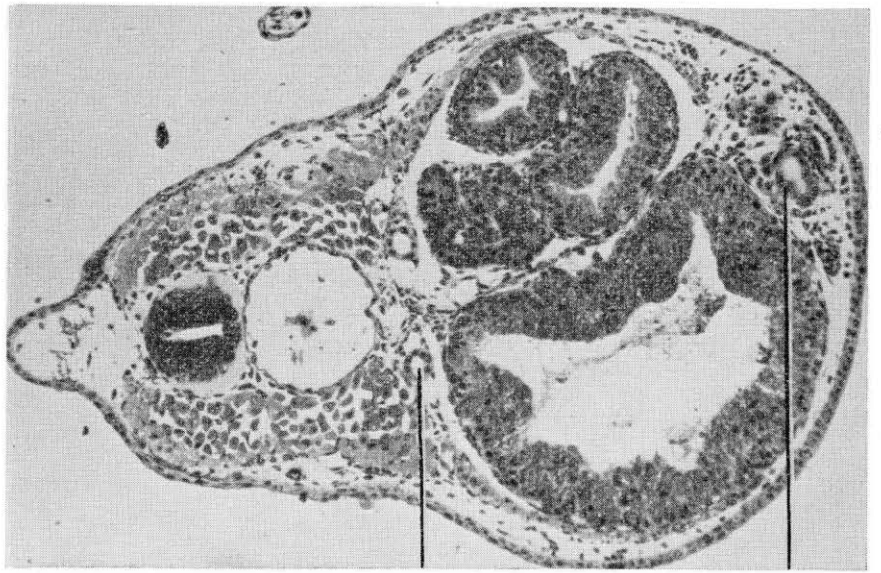


Fig. 9

0.5 mm

ment, but requires an extra nudge to continue its progress to its final destination.

Gruenwald (1952) has extensively studied this subject in chick embryos. The same process here also occurs in the development of the mesonephros and the metanephros. The latter requires an inductive influence from the ureteric bud–the actual primordium of the adult kidney duct—which grows forwards from the hind end of the mesonephric duct into the cells which ultimately will form the future adult kidney, to stimulate tubule differentiation. Of profound interest is the fact that the various effects on the urinogenital system, produced in the chick by obstruction of the development of the mesonephric duct, occur occasionally in spontaneous malformations in human embryos. It is thus inferred that similar developmental relationships in the urogenital system exist here also.

The ability of nervous tissue (among other tissues) to influence mesonephros development in amphibia, and of the metanephros also in the chick and mouse, has been exploited by Grobstein and his co-workers in Stanford University in America to investigate induction processes in the development of the kidney, using cellulose ester membrane filters. These studies seem of fundamental importance in embryological development.

Enough has been written to show that a study of the development of the pronephric system in amphibian larvae reveals many fundamental embryonic processes, whose mechanisms are only obscurely understood.

These include : its precocious determination in the blastula—the anteroposterior axis is already laid down by the middle of the two-layered or gastrula stage—and those factors that govern growth, differentiation and degeneration of the tubules. Other processes not wholly understood are direction of growth of the duct and its inductive influence on the differentiation of the mesonephros. Likewise much has to be learned of causality in phenomena such as compensatory hypertrophy and hyperplasia, and control of organ size, and it is hardly necessary to add of its physiological properties also.

The tiny pronephros (and its duct) of, for example, an approximately 19 mm. long larva of *Ambystoma* (Fox, 1961), is barely 0.5 mm. long, about 0.025 mm.^{3} in overall volume and includes about 2,000 cells, each of whose calculated individual volume is about 8,000 μ^3. The organ is indeed for the biologist a veritable miniature treasure house, waiting to be explored.

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Explanation of Figures

Photomicrographs by Mr. C. Atherton of the Department of Zoology, University College, London.

Fig. 1. Embryo of *Ambystoma* 2-3 mm. long, showing the pronephros and duct rudiments situated below segmental muscles 3 and 4 (pronephros) and 5, 6 and 7 (duct).

Fig. 2. Pronephros of the frog *Rana pipiens*. Specimen 4-6 mm. long. After an illustration by Field in a classical paper published at Harvard, in 1891.

Fig. 3. Diagrammatic representation of O'Connor's experiment where stain is found only in the cells of the pronephric duct, after its first formed anterior duct primordium only had been stained.

Fig. 4. Diagrammatic representation of an experiment on the embryo of the frog *Rana fusca* by Van Geertruyden (1946). There is no pronephric duct behind the graft of foreign tissue, which blocked the anterior duct rudiment, and no mesonephros develops on that side for there is no stimulation by the duct on the primordium of the mesonephros. The tiny cloacal duct normally develops independently of the rest of the duct and has induced mesonephros tissue.

Fig. 5. Diagrammatic representation of an experiment on the embryo of *Rana fusca* by the same worker in fig. 4. The pronephric duct rudiment was totally removed and thence grafted back into the operated specimen. Mesonephric cells develop only in the region of the grafted duct.

Fig. 6. Photomicrograph of a transverse 10μ section of an axolotl larva 10 mm. long, showing the pronephric tubules, nephrostomial opening into the coelom and the glomus.

Fig. 7. Section as in fig. 6 of an axolotl larva 9 mm. long, previously unilaterally pronephrectomized and containing a donated pronephric tissue graft in its hinder region (see fig. 10). The remaining functional pronephros is hypertrophied and hyperplasic, as in non-grafted but similarly operated specimens, and is not influenced in any apparent way by the presence of the graft.

Fig. 8. Section as in fig. 6 of a larva of *Triturus helveticus* 10 mm. long. The right pronephric duct is blocked further back and its blocked pronephric tubules are enlarged. Similarly its functional unblocked partner shows compensatory enlargement, when compared with pronephroi of controls. It may be inferred that reciprocal inhibition of growth by paired pronephroi *in situ* is unlikely.

Fig. 9. Section as in fig. 6 of a control axolotl larva (with paired pronephroi) 9 mm. long; containing a graft of poorly developed pronephric tubules, not in communication with the body cavity.

Fig. 10. Grafted pronephric tubules in same specimen of fig. 7. Notwithstanding its unilaterally pronephrectomized condition, and hence compensatory hypertrophy of its remaining pronephros, the graft tubules and in particular their individual cell volumes, are similar to those grafts of controls (see fig. 9). The results do not support the view that pronephric compensatory growth is the result of chemical stimulation, for if this were so, then grafts in either a "compensating or non-compensating" environment would be expected to differ in appearance.

Fig. 11. Section as in fig. 6 of the hinder region of a control (with paired pronephroi) of a 10 mm. axolotl larva. Graft tubules open into the body cavity via a nephrostome, and swelling is probably the result of pressure by intratubular coelomic fluid, driven into the tubules by cilia. Hydrostatic pressure is presumably one major factor stimulating pronephric growth.

INTRODUCED SPECIES OF AMPHIBIANS AND REPTILES IN MAINLAND BRITAIN

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The native fauna of mainland Britain is very small compared with that of continental Europe. In the last glaciation of the Ice Age, the great ice sheets stretched almost as far south as the Thames, and only with their recession could the fauna of warmer climates spread back from the southern part of Europe. At this time the area of the English Channel was occupied by dry land, so that movement across this was relatively easy. With the invasion of the sea and the opening of the Channel Gap some 5,000 years ago, those species which had already entered the country were separated from the ones which had not yet reached so far north. Since then, any changes in the British fauna can only be due to extinction of some and further passage across the sea by others, whether aided or unaided by man. In the case of the amphibians and reptiles, such passage (apart from the occasional turtles) has invariably been aided.

The present-day species of amphibians and reptiles which reached this country unaided make a meagre list. They comprise only two toads, one frog, three newts, three snakes and three lizards. Species used in attempts at naturalization far outnumber these, yet success has been very infrequent. The motives for the enlargements of alien species appear to have been varied, ranging between desire to see if these could establish themselves or to liberate captive specimens and the discarding of unwanted pets or even the escape of captive specimens. Casual escapes are unlikely to have taken place in such numbers as to form breeding populations, except in the case of common pets such as tortoises. A summary dealing with the various aliens known to have been introduced in one or other of these ways is given below.

SALAMANDRIDAE

Fire salamander (*Salamandra salamandra*). Frequently kept in captivity in this country, and escaped specimens may account for the odd records, including that of the possible colony near Heysham, Lancashire, recorded by Fitter (1959) as existing in the early part of this century.

Alpine newt (*Triturus alpestris*). Malcolm Smith (1951) recorded a colony of this species which had survived for many years in a garden in Surrey. This may be the same colony as that mentioned by Fitter (1959), which is in the environs of the establishment from which the stock originated.

PLETHODONTIDAE

Pyrenean newt (*Hydromantes genei*). Four or five of this inconspicuous species have been released in South Devon, but the result is not known (Chaplin, 1963).

DISCOGLOSSIDAE

Painted frog (*Discoglossus pictus*). Lantz (1950) has stated that he reared this species to adulthood by releasing the young froglets and collecting the adults in later years. There may possibly still be survivors of his stock in the Manchester area. Frogs of this species freed in North London during recent years are still found in the neighbourhood of their release site.

Midwife toad (*Alytes obstetricans*). Malcolm Smith (1949, 1950) has recorded the facts about the well-known colony of these toads in Bedford. About 1903 they were first heard calling and are believed to have been imported accidentally among plants from the South of France. When their main breeding pond was filled in (1922), about a dozen were used to found a new colony a quarter of a mile away. They are still breeding on both sites, and a third colony has also established itself at Bedford. A new colony was founded near Worksop in 1947. A South Devon colony started with two egg-carrying males about ten years ago still thrives (Chaplin, 1963).

Fire-bellied toad (*Bombina bombina*). Over the past fifty years, colonies started at Woburn have all died out, while one in Surrey does not show breeding activity (Fitter, 1959).

Yellow-bellied toad (*Bombina variegata*). A colony was started in South Devon a few years ago, and has since bred and still thrives (Chaplin, 1963).

PIPIDAE

Platanna (*Xenopus laevis*). This species is known to be capable of breeding outdoors in this country, and a number of metamorphosed tadpoles were released in Kent about 1955, but almost certainly perished rapidly, following a cloudburst and spate. Whether they would have survived a severe winter is very doubtful.

BUFONIDAE

Green toad (*Bufo viridis*). One pair was liberated into a garden pond in the Isle of Wight a few years ago, and spawned there (Boyce, 1963). There is no evidence that this introduction has been successful.

HYLIDAE

European treefrog (*Hyla arborea*). Colonies have been set up on numerous occasions, but have thriven in only a few cases, e.g. the Scilly Isles, Lundy, Cambridge, Suffolk (Fitter, 1959). Fifty liberated in South Devon in 1937 disappeared (Taylor, 1948) and a more recent attempt there also seems to have failed (Chaplin, 1963). There is a non-breeding colony in Surrey (Fitter, 1959), while a couple of dozen released a few years ago in Kent resulted in a solitary male calling on two occasions the following May.

In Hampshire and the Isle of Wight the record is of greater interest. About 120 years ago an introduction at St. Lawrence in the south of the Isle of Wight failed (Fitter, 1959), but about 55 years ago a breeding colony was set up there and survived for a number of years (Taylor, 1948). No real search for it has recently been made, and it is uncertain whether it still survives. A colony founded at Freshwater throve for years until the breeding pond was filled in, 25 or more years ago. Approximately 50 were liberated at Brighstone in 1952 and two batches of spawn were found the next year, but the treefrogs subsequently vanished (Frazer, 1963). Others have been introduced at Freshwater recently, but it is too early to assess the degree of success here. In the last two years a breeding colony has been discovered in Hampshire, and local inquiries have disclosed that it has flourished for about 50 years (Robinson, 1963). When I visited it one night in May, 1963, five or six males were calling. The pond is one to two feet deep, in an exposed situation, and the water was appreciably warm to the touch : the pond dries out later in the summer.

Mediterranean treefrog (*H. meridionalis*). Introduced into South Devon a few years ago, but seems to have died out (Chaplin, 1963).

Pacific treefrog (*H. regilla*). A dozen or so males and a female introduced into South Devon a few years ago failed to breed (Chaplin, 1963).

Ewing's frog (*H. ewingii*). A colony of this Australian treefrog was founded in Cornwall by the introduction of a dozen adults in 1951 (Larking, 1955). This colony throve and bred annually in a small artificial pond, even after very cold weather. However, the extreme weather of last winter finally proved fatal to them, as well as to a number of British frogs and newts in the same pond (Larking, 1963).

RANIDAE

Edible frog (*Rana esculenta*). Much of the history of this species in England has already been given by Fitter (1959). The evidence suffices to show that the original introduction into the Cambridgeshire fens must have been around 200 years ago (if they were not indigenous then). These frogs were of the Southern European form *lessonae*. Others of the northern race *esculenta* were introduced in 1837 into Norfolk from Paris, while five years later these were reinforced with others from Belgium. In these Broads they are said to have survived until 50 years ago. Frogs of this race seem to have been found to the north of Thetford by 1820 and to have survived there until 40 years ago. In Shropshire, a colony started about 1840 lasted some 60 years. Colonies which seemingly failed to survive for very long periods of time were founded in a number of southern counties, but the picture is very complex. Some Scottish introductions also failed. One or two localities south and north of London have been inhabited during post-war years, but several of the larger colonies have become extinct when the ponds were built over. In Woburn Park, Bedfordshire, there seems to have been an earlier failure (Fitter, 1959), but later introductions survived and bred, so that a large colony of all ages was seen there a few years ago (G. F. Boyce, 1963). Probably the most recent temporary success in introduction has been the half-dozen introduced into a Surrey garden a few years ago, which rapidly deserted this for a pond on the adjacent common, where they appear to be still surviving.

Marsh frog (*R. ridibunda*). The story of the introduction and successful colonization of Romney Marsh has been given recently by Menzies (1963). More recently a sub-colony has been founded in the Somerset levels, eight were released in Yorkshire, while others have been liberated north of London. It is too early to assess the success of these, but the Somerset colony appears to be building up its numbers. On the other hand, Fitter (1959) reports a nucleus of 70 released near Wicken Fen in 1939, which were never seen again.

Bullfrog (*R. catesbiana*). A colony was in existence in Surrey for a period 60 years ago (Fitter, 1959).

CHELYDRIDAE

Snapper (*Chelydra serpentina*). A Surrey colony started 60 years ago still contained a few large specimens 40 years later (Fitter, 1959).

TESTUDINIDAE

European pond tortoise (*Emys orbicularis*). Various introductions from time to time have been partially successful. Malcolm Smith (1951) has pointed out that this species was one which successfully colonized this country after the Ice Age, but which failed to maintain itself, probably because a succession of cold summers could prevent its eggs from hatching, so that there was a total reproductive failure in one generation. Deliberate releases have taken place in Surrey, Bedfordshire, Suffolk and the Isle of Wight, apart from accidental escapes like the animal I found at Bagley Wood in 1938, which could undoubtedly be connected with the numbers on sale in the Oxford Market at that time. A number were released in Suffolk in the mid-1890s and by 1929 several young were found (Fitter, 1959). The tortoises were still thriving nearby in 1934 (Taylor, 1948). The Isle of Wight colony was founded at St. Lawrence about 1906, and 40 years later I spoke to an old man who recalled seeing them for some years afterwards but not recently. One had reached Carisbrooke by 1907 (Fitter, 1959), and another was found wandering on Chale beach in 1952 (Frazer, 1963). Some nine specimens were taken on rod and line in a series of small ponds in North Surrey during 1948. As postwar importation of these species had not started by then, they are presumed to have survived in the area for some years (G. F. Boyce, 1963).

Painted terrapin (*Chrysemys picta*). Another species released in Surrey 60 years ago, where they survived for 40 years. A small number set free in Middlesex in 1945 (Fitter, 1959), probably belonged to this species.

Greek tortoise (*Testudo graeca*). A common pet which escapes easily. Fitter (1959) records the release of a dozen in County Dublin in 1906. Our climate is not favourable to the reproduction of this species.

Moorish Gecko (*Tarentola mauritanica*). A pair released in South Devon survived for three or four years, although not breeding.

LACERTIDAE

Green Lizard (*Lacerta viridis*). This species has been introduced on a number of occasions. In the Isle of Wight in 1899, where they still survived as late as 1934; in Surrey, 1905-10; and in North Wales (20, 1931, where they could still be found in 1935). A hundred were introduced into South Devon in 1937 and some could still be found nine years later (Taylor, 1948). A more recent Surrey colony survives but does not breed (Fitter, 1959).

Wall lizard (*Lacerta muralis*). In some cases the information on this species is not related to any particular subspecies, but details of certain colonies show the form liberated. For understanding of the survival pattern it may perhaps be best to consider each subspecies separately.

A. Subspecies unknown. Two thriving colonies have been discovered in the past two years in the Isle of Wight. Specimens have not been examined in the flesh, and no information is available on the origin of these colonies. Two hundred were liberated in Devon in 1937 (Taylor, 1948), but although occasional ones may still be found, this colony is obviously not successful (Chaplin, 1963). Another small colony is said to be established in Surrey (Fitter, 1959).

B. Ssp. *muralis*. In 1932 a dozen were released in a Surrey locality containing old walls, with two more the next year, and these have formed a very thriving breeding colony (Malcolm Smith, 1951).

C. Ssp. *campestris*. A dozen liberated in a South Devon area with suitable walls two or three years ago were never seen again. In another South Devon locality, some of this form were released in company with ssp. *nigriventris* and rapidly disappeared. It has been suggested (Chaplin, 1963) that in fact ssp. *campestris* lives in sandpits and embankments or similar places and cannot survive among walls and rocks.

D. Ssp. *nigriventris*. A nucleus of fifteen released in South Devon ten years ago have bred annually since then, and the colony now numbers several hundred, in marked contrast to the ssp. *campestris* liberated with them. It therefore seems likely that failure to survive in the wild when colonies of this species are released may be due to the wrong form being placed in a particular habitat (Chaplin, 1963).

Madeiran wall lizard (*Lacerta dugesi*). Some which were released during the last decade in South Devon soon disappeared (Chaplin, 1963).

Eyed lizard (*Lacerta lepida*). Some specimens were released in Surrey in 1932, but failed to survive (Fitter, 1959).

COLUBRIDAE

Viperine snake (*Natrix maura*). The source of two of this species found together in Kent in 1953 (Edwards, 1953) is not known.

Tessellated snake (*Natrix tesselatus*). One in South London in 1955 is also of unknown origin, but as with many other odd specimens found, these have probably escaped from captivity.

There are few records of deliberate release of foreign snakes in this country, though in one case a dealer may have freed a number of Dark Green Snakes (*Coluber jugularis*) when he found these were unsaleable.

It is apparent that a great number of different species have been liberated in this country at one time or another, yet relatively few of these have succeeded in colonizing the land. As might be expected, a number of species have survived for years but have not bred successfully, and here our climate must have played its part. The majority of species considered have overwintered successfully for a while, though the extreme conditions in 1962-1963 proved fatal to one of these.

The introduced species can be classified, therefore, as :

1. Species which cannot survive our normal conditions of weather, terrain and soil. These must be presumed to include the madeiran wall lizard, eyed lizard, ssp. *campestris* of the european wall lizard (at least under the conditions where it has been liberated hitherto) and the platanna.
2. Species which can survive under normal conditions, but which are killed in exceptionally severe winters, e.g. Ewing's treefrog.
3. Species of which the adults can survive even under severe conditions, but where breeding never takes place, or only in exceptional summers. These include the snapper and other american terrapins, as well as the greek tortoise, the geckos, green lizard and the bullfrog. The fire-bellied toad is also included here.
4. Species where the eggs can normally hatch or the young be born, but there they cannot reach adulthood. These may possibly include the green treefrog in some parts of the country.
5. Species which have not been introduced originally in sufficient numbers to produce success. The painted frog and fire salamander come into this group, which also probably includes a number of introductions of green treefrogs, where not enough have been liberated in one place to allow sufficient females to survive until the next breeding season. There is the further complication that this species is imported in large

numbers when taken at the breeding ponds, so that there will be far fewer females than males, while at worst a whole consignment of 500 may only contain one or two females. At best, an unsorted batch of 100 liberated would only be expected to contain about ten females.

6. Species which apparently succeed in establishing themselves, but then go into decline. The major example of this is the edible frog, assuming that it was never native to the fen district. Certainly its final decline can be associated with the destruction of its habitat, and it may be significant that its disappearance in East Anglia coincided with changes in land management and with increasing use and pollution of the waterways, while the decline in the traditional cutting and use of reed was associated with a great silting-up process. It may be that the fading fortunes of such a species are due to its changing environment no longer remaining suitable for it.

7. Finally, the species which seem to have colonized the land successfully have either been deposited in a very suitable habitat, as in the case of the marsh frog, wall lizard (ssp. *muralis* and *nigriventris*) and some successful colonies of green treefrog : or, as with the alpine newt, midwife and yellow-bellied toads, have been fairly inconspicuous species which are not particularly specialized in their requirements. In this connection it is interesting to contrast the breeding failure of the fire-bellied toad, which lives in and around shallow water in lowland terrain, with its congener the yellow-bellied toad. This is more a creature of mountain streams, and it must have found the Devon hills to its liking.

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THE SKIN OF LIZARDS AND SNAKES

By

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Despite the fact that the scaly skin is such a characteristic reptilian feature, there is little available information on its histological structure. Lange (1931) reviewed the literature to that date, but there have been few subsequent papers and these deal only with specialized problems. Pockrandt (1936) considered the structure of the epidermis in snakes with particular reference to ophidian systematics, and Bechtel (1957) reported some histological observations on the sloughing cycle. Goslar (1958a and 1958b) described the histochemical changes associated with the sloughing cycle and discussed the hormonal control of the process. The structure of the skin as a whole has been largely neglected. In student's text-books as well as in the more specialized herpetological literature such as Bellairs' *Reptiles* (1957) and Goin and Goin's *Introduction to Herpetology* (1962), the sections dealing with the skin reflect the paucity of available information.

This article is intended to give a somewhat more detailed account of the skin of the Squamata. It is also hoped that it may serve as a basis for future more detailed studies.

In snakes and lizards, the skin consists of a series of small discrete units called scales. Generally, these scales overlap one another and form patterns which are characteristic for the species. It should be added that in some families of lizards such as the Gekkonidae and the Chamaeleontidae, the scales overlap only slightly or not at all, and may have the form of tubercles. The overlapping is also very reduced, or absent on the dorsal head surface of many forms, where each adjacent head shield is separated from the next by a shallow furrow.

The appearance of scales as a series of discrete units somewhat belies their true nature. Unlike hairs and feathers, which interrupt the continuity of the skin in a striking fashion, scales are merely localized elevations and thickenings of the skin. All the epidermal and dermal layers of each scale are continuous with those of the next*. They pass without interruption across the regions between the conspicuous elevated parts of adjacent scales, although they are thinned, and in the case of overlapping scales, folded, to form hinges. This essentially continuous character of the scales of lizards and snakes is suggested by the way in which they shed their skins, in large pieces, or as a single slough**.

The structure of a typical body scale of a lizard or snake is shown in diagrammatic section in figure 1. For purposes of description, the scale may be divided into the outer and inner surfaces and the folded hinge region. The innermost layer of the epidermis is the stratum germinativum (st. germ.) which consists of a row of cells of varying shape, flattened, cuboidal or columnar. Between the cells of the stratum germinativum on the outer scale surface there are branched pigment cells which are the epidermal melanocytes (epid. mel.).

* This statement does not, of course, apply to the separate bony plates, or osteoderms, which lie within the scales of many lizards.

** Little is known about skin-shedding in the Chelonia and Crocodilia. The structure of their skin is rather different from that of snakes and lizards, and the very small pieces which are shed, call to mind the mammalian process of desquamation, rather than sloughing.

The epidermis undergoes cyclic changes in structure which are associated with the sloughing cycle (Bechtel, 1957, Goslar, 1958a, and Maderson, in prep.). There is always a region of horny keratinized material which forms the outer surface of the body. This material consists of an outer β-layer and an inner α-layer; the former does not stain in haematoxylin and eosin sections, whereas the latter stains pink. These layers correspond to the distribution of two different types of keratin as described by Rudall (1947). On the outer scale surface, the β-layer is very much thicker than the α-layer. On the inner scale surface and in the hinge region, the α-layer predominates. The free surface of the β-layer shows the sculpturings which are characteristic of squamate keratin (Hoge and Santos, 1953), and these may be seen in section as serrations (see fig. 1).

Immediately after the animal has sloughed, the epidermis consists of the keratinized regions described above, the stratum germinativum (from which all the other epidermal layers originate), and a zone of living cells between them. Everything except for the stratum germinativum comprises what is called the outer epidermal generation (OG). This may be termed the resting condition of the epidermis (fig. 1). Although the period of time between one slough and the next may vary according to environmental conditions and the health of the animal, this resting condition persists for approximately three-quarters of that period. The lower portion of the α-layer, and the zone of living cells between it and the stratum germinativum, together make up the stratum intermedium. At the end of the resting period, the stratum germinativum undergoes a process of rapid cell division, giving rise to a new, inner epidermal generation. The newly formed cells of this undergo keratinization, so that at this stage of the cycle the epidermis contains two distinct keratinized regions, separated from each other by the stratum intermedium. The actual process of shedding is brought about by the disintegration of the stratum intermedium, so that the original outer epidermal generation is shed. The former inner generation is now exposed, becoming in its turn the outer generation. The exact way in which the disintegration of the stratum intermedium occurs is uncertain, but it has been suggested that it is due to the action of proteolytic enzymes produced by eosinophil granulocytes (Zimmermann and Pope, 1948).

Beneath the epidermal region of the scale is a core of dermis which is sub-divided into superficial and deep regions. The loosely packed connective tissue fibres of the superficial dermis appear in sharp contrast to the deep dermis, in sections of the skin. Various types of dermal pigment cell are found in the superficial dermis against the outer scale surface (see Parker, 1948). These are mainly responsible for the colour changes of chamaeleons and certain other lizards; the extensive literature on this subject has been reviewed by Parker (1948) and more recently by Waring (1963). The densely packed fibres of the deep dermis form a strand which extends up the middle of each scale. It is in this strand that the osteoderms which characterize certain families of lizards are found; these structures are absent in snakes. The deep dermal tissue is continuous around the body and sharply divides the skin from the sub-cutaneous tissue. Unlike the epidermis, the dermis does not undergo any profound changes associated with sloughing; towards the end of the resting period however, many eosinophil granulocytes appear in the blood vessels in the deep dermal strand and migrate through the dermal tissues towards the stratum intermedium of the epidermis (Bechtel, 1957 and Maderson, unpublished).

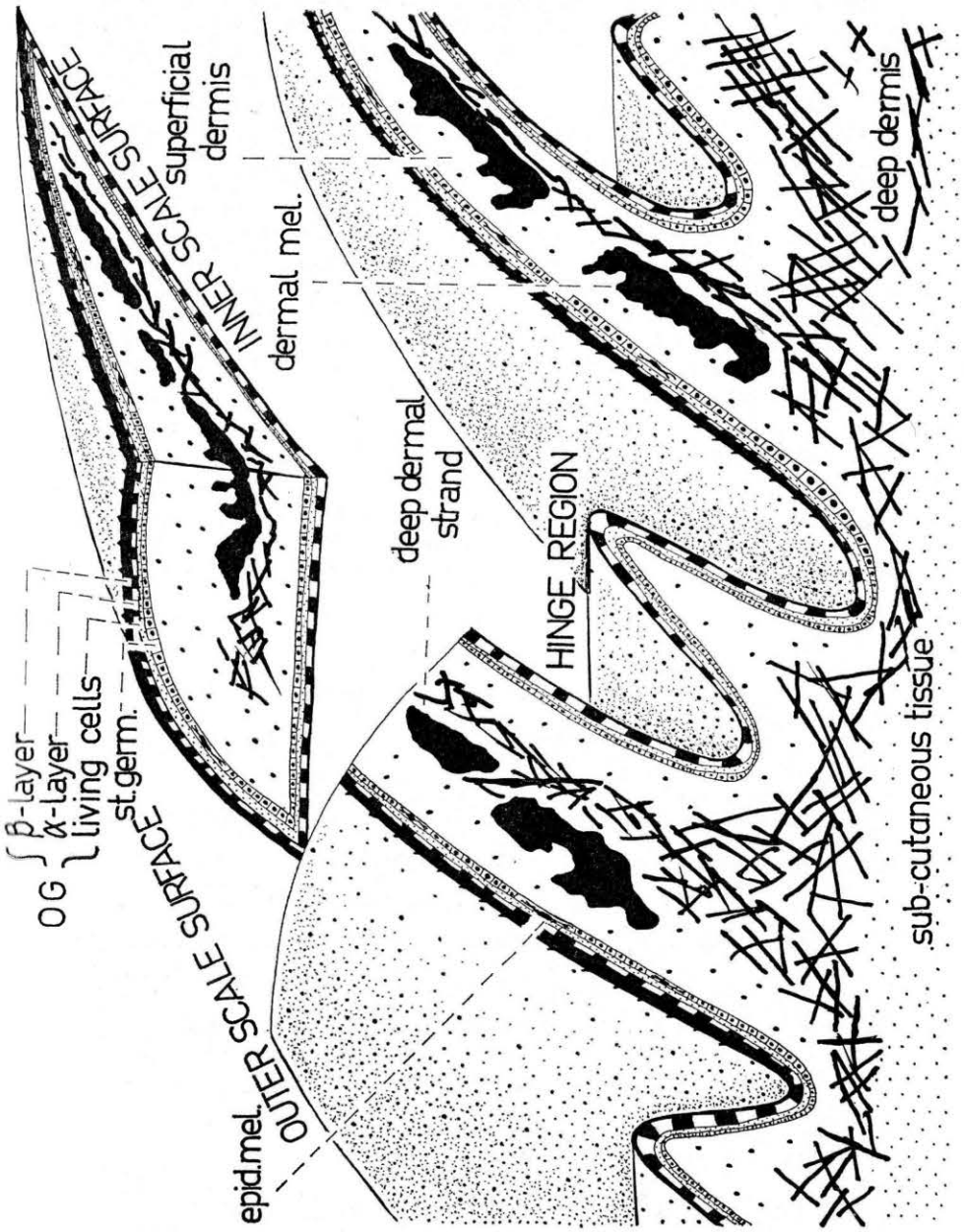

Fig. 1. Diagrammatic, partly reconstructed, longitudinal section through scale of squamate reptile. A segment has been cut out of one of the scales.

(*dermal mel., epid. mel., dermal and epidermal melanocytes*)

The presence of hinge regions between the elevated parts of the scales, where the integument is thin, makes it possible for the skin as a whole to stretch to an enormous degree. In unstretched skin, the hinge region is folded (fig. 1) and is covered by the adjacent scales. When the body is distended, the skin is stretched, the hinge regions unfold and become exposed. The keratinized portion of the epidermis is well adapted to permit this distension, in that the keratin of the inner scale surface and hinge region is predominantly of the α-type which is flexible (Mercer, 1961). The inflexible β-type, which predominates on the outer scale surface, forms the normal body surface. The ability of the skin to stretch is one of the important factors which allow snakes to swallow such relatively large prey.

Although the skin of snakes and lizards is devoid of glands, certain specialized epidermal derivatives have been studied, among which may be mentioned the femoral pores of geckos and other lizards (Taylor and Leonard, 1956), the hair-like sense organs described by Underwood (1957) in pygopodid lizards, and the sense-organs of *Typhlops braminus* described by Aota (1940).

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REARING YOUNG MEDITERRANEAN SPUR-THIGHED TORTOISES (*TESTUDO GRAECA*)

By

J. M. B. King

There appears to be little information available on the methods of rearing young tortoises, so the following details of my experiences may be helpful to others. I am of course aware that other tortoises have been raised from eggs in this country, but apart from I. & A. Noel-Hume (1954) I have found nothing published.

Five baby tortoises (*Testudo graeca*) came into my possession immediately after they hatched in October, 1960. They were the progeny of a pair which had been in the garden of Mrs. P. Meiggs in Oxford for more than four years. Seven eggs were laid in this small walled garden in early August: these were carefully dug up and incubated in a box of earth in an airing cupboard at about 70°F (21°C). They were moistened daily. Five hatched in mid-October (Appendix I).

They were then housed in a two-foot square vivarium, electrically heated, with a substrate of sand, gravel and large stones: this vivarium was placed in a greenhouse, and the daylight was supplemented by a spotlight inside the vivarium (fig. 1 and Appendix II).

The tortoises drank copiously soon after they hatched (one within 15 minutes). When placed in the vivarium on October 19th, all proceeded to eat the sand, quite deliberately: it is suggested by Noel-Hume that this is to be discouraged and that young tortoises should therefore be kept on a rubber sheet; however I did not interfere and after about a week they gave up eating sand apart from what might be taken in adventitiously on their food. To start with, they were fed on shredded lettuce, smeared with cod liver oil and wheat germ oil, and sprinkled with calcium phosphate. Pieces of cuttlebone were available which they chewed. In five days they were biting pieces from whole lettuce leaves, and after a fortnight it was hardly necessary to shred their food at all though much of it was still given shredded to avoid wastage. They were then also eating chicory, dandelion, dock, buttercup and sow-thistle, but lettuce was their undoubted favourite. No interest was shown in the soft fruits which are supposed to be eaten with relish by young tortoises, e.g. grape and apple; they were over six months before they would eat these: tomato they will not touch even at two years old. Water was available at all times in a shallow dish large enough for them to bathe in.

At the end of the first week, a powder supplement of vitamins and minerals (Vitmin, see Appendix III) was mixed in equal proportions with calcium phosphate, and this was thereafter used daily on their food. Application of cod liver oil, etc., was reduced to once a week. Vitmin contains a large amount of calcium in various forms, and is intended for feeding to birds: clearly a tortoise requires far more calcium than a bird, hence the extra calcium phosphate.

The babies grew rapidly but at markedly different rates: all hatched at about 10 grams and all were over three times their hatching weight at ten weeks: but by the eleventh month no. 2 was almost twice the weight of no. 3 (table A).

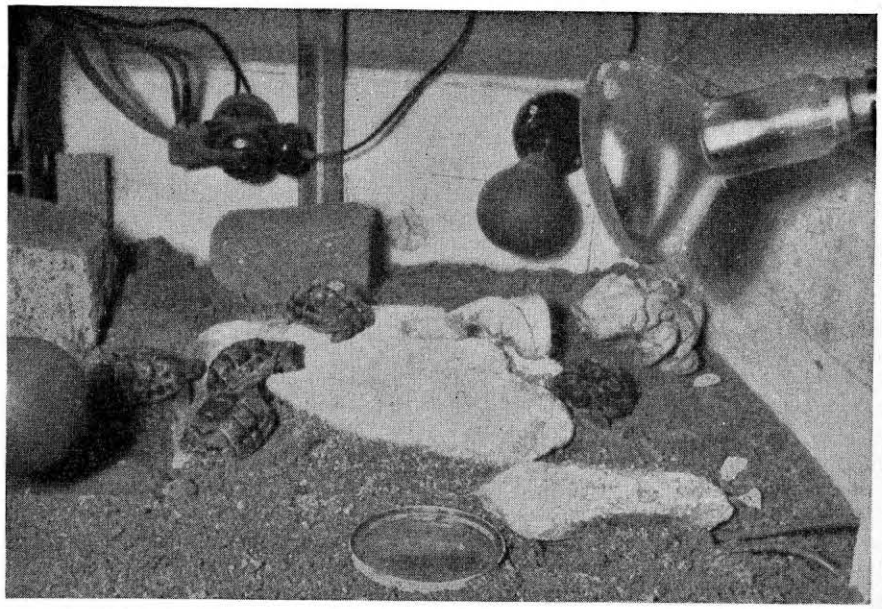

Fig. 1. General view inside vivarium, On left, thermostat is just visible behind brick, controlling socket distributing to sprayed bulbs (foreground and right background) and heating cable (partly visible on right). Spotlight is on right.

	1960				1961				1962	
	May 9	Oct. 19	Nov. 13	Dec. 30	Jan. 20	Apr. 15	Sept. 17	Oct. 19	Mar. 5	Oct. 31
A, f	55	90			97		104			147
B, f	50	95			114		147			251
1, f		9.7	15	29	35	68	115	121	179	238
2, m		10.5	18	34	41	90	169	174	260	322
3, f		11.5	16	30	36	61	92	102	150	225
4, f		9.9	16	28	35	80	130	120	166	206
5, f		10.9	16	31	38	70	111	115	160	180
Months from hatching ...		0	1	2	3	6	11	12	17	24

TABLE A

Growth by weight, shown in grams to nearest gram (except for hatching weight).

There is no explanation for loss of weight by no. 4 in Sept.-Oct. 1961. No. 5 contracted a bad cold in July 1962.

A & B are the imported ones.

1-5 are the hatchlings. f, female: m, male

	1960				1961				1962	
	May 9	Oct. 19	Nov. 13	Dec. 30	Jan. 20	Apr. 15	Sept. 17	Oct. 19	Mar. 5	Oct. 31
A, f	64	73			76		79			90
B, f	61	73			78		87			107
1, f		31.5	38	48	50	65	77	79	90	104
2, m		35.0	42	52	56	74	90	93	105	119
3, f		34.5	41	50	52	63	71	72	83	103
4, f		32.5	40	47	50	69	80	81	86	99
5, f		33.0	40	49	52	66	77	77	85	94
Months from hatching ...		0	1	2	3	6	11	12	17	24

TABLE B

Length in millimetres to nearest mm. (except hatching, to nearest .5 mm.).

On warm days (over 65°F) during the summer they were placed outside on a small sheltered rockery, but taken inside at night. They discovered some old weathered bones which they managed to chew up and eat. Since they clearly liked the taste, I offered them bone flour which they also ate;

this was therefore added to their powder supplement and has gradually replaced the calcium phosphate.

By October 1961 they were outgrowing the small vivarium and were transferred to a large enclosure on the greenhouse staging heated by a 250-watt infra-red lamp during the day, with a heated box into which they retired at night. This arrangement they shared with two large Brazilian Tortoises (*T. denticulata*).

The young tortoises were over eighteen months old before it was possible to sex them with certainty as one male and four females. Small male tortoises show no concavity of the plastron. At this stage (summer 1962) the male became very active, charging all other tortoises which were around and mounting those which he could. This activity was probably precocious.

During the same period I had two imported young tortoises of the same species. I had selected them in May 1960 as being heavy, healthy specimens, and they were of course much larger than the hatchlings in October 1960. They were kept in similar conditions. The five hatchlings grew faster so that all overtook one of the imported babies and by two years old no. 2 (the male) was larger than either. But both the imported ones were female (tables A and B).

None of these tortoises has been hibernated, since this can be a risky proceeding and is hardly essential to their well-being. Their growth rate appears reasonable and is in line with some figures quoted by Noel-Hume. It is interesting that the male has grown so much faster than the other four; one would like to know if this is normally the case. Most sexually active male tortoises are smaller than females, and it remains to be seen whether this one's growth now slows down and his sisters overtake him.

I wish to express my gratitude to Mrs. P. Meiggs of Holywell Manor, Oxford, for allowing me to watch and record the hatching process in her sitting room and then giving me the baby tortoises; and to Johnson's Veterinary Products Ltd. of Sutton Coldfield for giving permission to quote the constituents of their Vitmin powder.

SUMMARY

Five tortoises hatched from seven eggs and were reared in a heated vivarium: they were fed on a varied diet supplemented by a wide range of artificially added vitamins and minerals. They hatched weighing about 10 gm. ($\frac{1}{3}$ oz.) and being about 33 mm. ($1\frac{1}{4}$ in.) long: at two years old they varied from 180 gm. (6 oz.) and 94 mm. ($3\frac{3}{4}$ in.) to 322 gm. ($11\frac{1}{4}$ oz.) and 119 mm. ($4\frac{3}{4}$ in.).

REFERENCE

Noel-Hume, I. & A. (1954). Tortoises, terrapins and turtles. Foyle, London.

APPENDIX I

INCUBATION AND HATCHING

Aug. 1th—10th.	7 eggs laid. Incubated in airing cupboard. Temperature on Oct. 18th-19th varied between 65-72°F (18-22°C). Moistened daily, but earth not damp.		
Oct. 15th.	1st egg hatched		6 p.m. Incubation period 10 weeks.
	2nd	,,	7 p.m.
16th.	3rd	,,	12 noon.
19th.	4th	,,	10-11.30 a.m. Had a leg out at 10.0, free at 11.30.
	5th	,,	10-12.30 a.m. Just cracked shell at 10.0, free at 12.30 p.m.

Identification of individuals was made by record of plastron pattern, supplemented later by photographs.

APPENDIX II

DETAILS OF VIVARIUM

Wooden box 24″ square, 12″ high, with one glass side and glass top held $\frac{1}{2}$″ above sides of box to allow ventilation.

Heating by (1) 125-watt Ekco soil heating element fixed to baseboard and covered by 1-2″ of sand. Two 60-watt colour-sprayed bulbs. All controlled by Constat QK thermostat at 70°F (21°C).

(2) 100-watt mirror-backed spotlight switched on through a time switch for 9 hours daily, controlled by thermostat at 80°F (27°C).

During the summer, the day temperature frequently rose to 90° or 100°F (32-38°C) due to sun heat in the greenhouse. During such hot spells, the top glass had been removed, and a shaded portion was provided.

APPENDIX III

Composition of Vitmin, manufactured by Johnson's Veterinary Products Ltd. (available in powder or liquid form).

Calcium gluconate BP $12\frac{1}{2}$%, Calcium phosphate BP 10%, Calcium carbonate BP 14%, Ferri phosphate BP, Copper sulphate BP, Cobalt lactate BP, Light mag carb BP, Manganese phosphate BP, Sodium iodide BP. Vitamins A, B1, B2, B6, B12, C, D3, E.

This is a supplement manufactured for feeding to cage birds; it was used because it is readily available. It must not be assumed that all these constituents are essential to tortoises.

23 Brock Street, Bath, Somerset.

NOTES ON THE SUCCESSFUL CROSS BREEDING OF *ELAPHE LAETA* WITH *ELAPHE OBSOLETA LINDHEIMERI*

By

D. RICHARDSON

The two snakes concerned came into my possession in 1957 both as young snakes of approximately 1 foot long. The female of *Elaphe laeta* was collected in Mexico while the male *Elaphe obsoleta* was collected in Texas, U.S.A.

HOUSING

The two snakes were first housed in separate cases but after some twelve months they were placed together in a glass-fronted case, the floor of which was covered in fine gravel. A large earthenware seed pan with a piece cut out of the rim is kept in the case rim side down to afford some cover for the snakes. A temperature of 70°F is maintained throughout the year.

BREEDING.

1961. Preliminary chasing was noticed on May 2nd and 3rd. Actual mating took place on May 4th. Mating first took place in the centre of the case, and was later continued under the seed pan. One large egg was

laid on June 29th followed by seven smaller ones on June 30th. The eggs were placed in damp rotten wood in a large unglazed earthenware bulb bowl, which was stood in a large saucer which was kept filled with water. A sheet of glass was placed over the top of the bowl to help prevent too rapid evaporation. The temperature of the rotten wood was maintained at 75°F the whole of the time. On August 9th it was found that the seven small eggs had collapsed and were going mouldy. As the remaining egg had not hatched by September 26th it was cut open. It contained a dead but fully formed young snake and from the slight odour of decomposition it was estimated the snake had not been dead very long. In colouration and marking it resembled very closely *Elaphe obsoleta lindheimeri.*

1962. Chasing took place on June 17th; the actual mating was not seen, but it was assumed to have taken place on the night of June 17th. On August 3rd it was seen that one large egg had been laid and this was shortly followed by five smaller ones. The same method of incubation was again used but the temperature throughout was raised to 82°F. On August 24th the five small eggs were discarded as they had collapsed and gone mouldy. The remaining egg was first noticed to be split on October 12th but full emergence did not take place until some 24 hours later. Shortly after full emergence the snake was removed to a small case where it fed on a small mouse. The egg tooth was shed on October 23rd and the first slough took place on October 25th. The estimated length at birth was nine inches. To date the snake continues to thrive and is some two feet long closely resembling *Elaphe laeta* in markings and colouration.

1963. No chasing or mating was observed but it was noticed in June the female appeared to be carrying eggs. On July 5th seven eggs were laid in the following order: One small egg at 7.50 a.m., two large eggs at 7.55 a.m., three small eggs at 8.20 a.m. and a further small egg at 12.30 p.m. The same method of incubation was used; the temperature throughout was maintained at 85°F. The five small eggs were discarded on July 17th as they had collapsed and gone mouldy. Of the two remaining eggs, one hatched on September 6th, the snake emerging some 24 hours after the slit was first noticed. It sloughed on September 16th and was found dead on September 20th. Although offered food it never fed. In markings and colouration it closely resembled *Elaphe laeta.* On September 18th a slit was noticed in the other egg but no movement could be discerned in the shell. As emergence had not taken place 24 hours later the egg was carefully cut open to reveal an apparently fully formed but dead snake. A large yolk was still attached to it by the cord. The cord was tightly wound twice round the snake in the region of the umbilical slit, and in such a way that it would have been impossible for the snake to free itself.

CONCLUSION

It will be noticed that in all three instances only the large eggs appear to be fertile and that these are the first eggs to be laid. It is thought that the large number of infertile eggs may be due to the difference in size of the snakes, the male being about twice as large as the female. As the young snake bred in 1962 appears to be a male it is intended to try and breed it back to the female when it reaches maturity.

—"Far Hills", 52 Knowsley Road, Macclesfield, Cheshire.

YOUNG ADDERS (*VIPERA BERUS*) FEEDING IN CAPTIVITY

By

BERNARD GOOCH

Many herpetologists have stated that young adders feed on invertebrates. For example, M. Smith (The British amphibians and reptiles, 1954, Collins, 2nd ed., 248) writes "Insects, spiders and worms probably form the main diet of the very young". This was tested on eight young born in captivity on September 3rd, 1962; they sloughed their skins within 24 hours of birth. They ignored earthworms, grasshoppers, slugs, spiders, wood-lice and beetles during their first three weeks of post-natal life.

Young adders born in the autumn will survive without food until the following spring. Their ability to do this may be due to the fact that the yolk remaining at birth is withdrawn into the body, where it is presumably available for nutrition at the beginning of post-natal life (R. Bellairs, *et al.,* Nature, 1955, *176,* 657). Nevertheless, the young do sometimes feed before their first hibernation. A specimen the same length as the captives (6½ inches) which was taken in the wild had clearly swallowed large prey.

The captive snakes, when 20 days old, were given a young lizard (*Lacerta vivipara*) some 3 inches long. Three or four of the snakes saw it but ignored it; another, slightly larger than the rest, seized it by the middle and quickly swallowed it head first. This snake and the others which fed later were removed to a second cage.

The hungry juveniles that had not yet eaten were now left in their cage with no more than the scent of a lizard, but active hunting continued, the snakes carefully nosing their way along the rock or over the small stones on which the (already dead) lizard had been lying while it was being swallowed. They also nosed the glass side of the vivarium against which for a little while the lizard's body had been pressed. Indeed several of them, opening their mouths wide as they pressed their snouts against the glass, made two or three deliberate attempts each to bite the glass. While this was going on, scuffling sounds suggested that "fighting" had broken out under cover of a rock. Within the next few minutes six attacks were observed; in each case the snake had been seized by the middle of the body or the neck by another and broke free only after a struggle. Fortunately these snakes appear to be immune to one another's poison.

The last attack seen showed how some of these "fights" may have started. It appears that the snakes' heads quickly became covered with lizard scent as they followed the trail, for after a while they started nosing each other's heads and necks whenever two or three happened to be investigating the same patch of herbage. As I watched a snake with its widely opened mouth pressed against the glass, another slightly smaller individual came up, put its nose against the other's head and then slowly and deliberately took the first snake's head in its mouth: this time I do not think the fangs were erected. The snake could not open its jaws—they were held tightly shut by its attacker—and it began to look as if it was going to be engulfed head first as the attacker manouevred it into position. However, being the stronger and larger of the two, it broke free after a struggle.

On September 27th, when the snakes were twenty-four days old, an adult viviparous lizard was placed in the first vivarium with the snakes that had not yet eaten. This was a powerful lizard, of considerable girth, some four or five inches long. The snakes were in hiding because the sun

was too hot; but they came out into the open when the cage was partially shaded, and hunting began. Almost at once the lizard was struck in the tail, but it quickly shed this appendage and made good its escape. The tail leaped about so actively, however, that the two juveniles that were watching it hesitated to go very near, though one of them quickly seized it once it had begun to quiet down, swallowing it by the thick or proximal end first.

Despite its size the adult lizard was evidently regarded by these snakes as acceptable prey. It was struck four or five times in rapid succession and presumably succumbed much more rapidly than it would have done had it been bitten once only by a single juvenile in the wild; it was not certain, however, how many minutes it took to die. Once it was immobilized, attempts were made by three snakes to swallow it, one seizing it by the tail stump, but soon giving up; another twice took hold of it for a little while by the neck, while the third took hold of the nose and immediately began to engulf its prey. Swallowing took seventeen minutes, the snake becoming enormously distended as it swallowed a lizard considerably larger than itself. Even nine days later it was still very distended and very active.

After this initial success, attempts were made to see whether any other available vertebrate prey was acceptable. The adders completely ignored new-born slow-worms (*Anguis fragilis*) born in the same cage, or presented to them, and young Warty or Crested Newts (*Triturus cristatus*) which shared the same accommodation. As the mother accepted small mammals (swallowing dead shrews and showing great interest in dead voles), a dead Bank Vole (*Clethrionomys glareolus*) was given to the snakes. Because of its size it was cut up into suitable pieces after the gut and liver had been removed. The snakes that had still not eaten (owing, I believe, solely to the supply of lizards having run out) were offered the fur-covered portions but did not appear interested.

The mother, before swallowing a shrew or examining a vole, applied its nose to the animal's anus. It seemed possible therefore that the young snakes might be interested in the viscera, such as the heart and intestine, and these were offered to the snakes which had already eaten lizards. Within a few minutes two snakes took hold of opposite ends of the gut and a tug-of-war began. The pair retreated beneath a rock after unsuccessful attempts to separate them and it was impossible to observe them closely. The stomach, heart and liver of the vole were eaten, however, although the gut, originally seized, was not swallowed.

These young adders, which were later released, were kept warm indoors; whether they have similar feeding habits in the wild is not known.

—Chesilhay, West Bexington, Dorchester, Dorset.

EGG LAYING AND INCUBATION OF THE STRIPED MOUNTAIN LIZARD *PHOLIDOBOLUS MONTIUM* (TEIIDAE) WITH NOTES ON AN INCUBATOR

By

ROBERT BUSTARD

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INTRODUCTION

Pholidobolus montium and its habitat have been briefly described by Copping (1957). A small species, measuring in total length about five inches, it is very active and a good climber. It is reminiscent of *Lacerta vivipara,* and, in my opinion, closely resembles small specimens of *Gerrhosaurus flavigularis.*

I received a dozen of these lizards from Ecuador on September 29th, 1955. They were installed in a metal vivarium 20″ x 20″ x 20″ with a glass front. A 2″ layer of damp (but not wet) soil and damp moss as a base, and small branches and a water dish were added. Their large appetites were satisfied with bluebottles on which they thrived. They can stand a wide range of temperature with no ill effects, but are, naturally, much more active at higher temperatures. In the vivarium the sole source of heat was a pearl electric light bulb of 40 watts which provided a temperature of about 75°F (Bustard, 1958). This was switched on between the hours of 9 a.m. and 9 p.m. It was observed that the lizards were active whenever the light was put on in the morning and throughout most of the day, but they were almost all absent by the early evening, resting under the moss.

THE EGGS

In transit one specimen had laid a clutch of two eggs which, however, soon dried up due to lack of suitable conditions en route. Several females were clearly gravid and an attempt was made to watch them. During October three clutches of eggs were laid, each of two eggs. One clutch was not noticed in time and had commenced to dry up when found, and a second clutch developed fungoid growths after about two months. The remaining clutch was laid on October 22nd, 1955.

When laid the eggs are fairly large (10-2 mms. x 6-7 mms.) and are creamy white. Copping (1957) states that *P. montium* lays hard-shelled eggs but this is certainly not my experience; the four clutches that I examined all had parchment-like shells.

INCUBATION

The eggs were placed in an incubator, which consisted of a tin about 7″ x 4″ x 4″ with a 2″ layer of damp sand. A layer of damp moss was added, then the eggs, covered by more damp moss. The tin was placed on top of a metal vivarium which had a light bulb suspended near its roof, so that the heat reached the tin from below. This method of incubation has been found most successful for reptile eggs. The heat causes the moisture in the soil to evaporate but when it reaches the lid it condenses to drip back through the moss. The lid of the incubator had a few small holes in it to allow excess humidity to escape. Using this method it is possible to ignore the eggs for long periods of time once one gets to know just how much moisture is required. By this technique—in which the eggs are kept in a humid environment and moistened almost automatically by an evapora-

tion cycle—I have been able to incubate eggs when I have been away from home for considerable periods. Formerly such absences were usually fatal to developing eggs.

The temperature of the incubator was between 80-90°F during the day, but fell to about 60°F at night when the light bulb in the vivarium below was switched off. Under these conditions eggs of *Anolis carolinensis* hatch with a high degree of success in about eight weeks.

When possible the eggs were examined regularly and any that had shrivelled up, gone bad, or been attacked by fungoid growths were removed. It is an advantage if the constituents of the incubator can be sterilized before use although at this stage sterilization was not part of my procedure. Wilson (1959) suggests the use of "Germstroyd" disinfectant to discourage the growth of fungi or bacteria. It is interesting to compare the methods used by White (1957) to hatch the eggs of *Lacerta viridis* and those used by Wilson (1959) to try to incubate the eggs of *Naja melanoleuca* which include an adaptation from those of White.

When placing the eggs in the incubator it is important to keep the egg in the position in which it was found, i.e., the egg must not be rotated. If this takes place the egg will not hatch as the embryo will be killed (unlike the situation with birds' eggs, whereby the embryo is automatically maintained on top of the yolk when the egg is rotated).

By January only one egg remained. During the incubation period the egg had swollen to nearly double its original size as do many snakes' eggs and indeed those with soft shells generally.

On the evening of May 25th at 9 p.m. a lizard was found on the floor of the reptile building. It measured 5 cms. overall and was the newly hatched *P. montium* which had escaped from the incubator. It was put in a special vivarium by itself and fed on *Drosophila* and other small insects. It was a perfect replica of the adults. The incubation period was, therefore, 216 days, or about 31 weeks, which is, in my experience, a very long period under such conditions. During this lengthy time occasional re-dampening of the incubator was required, but was not a time-consuming process because water was just run down the side of the soil and the evaporation-condensation cycle did the rest.

SUMMARY

Four clutches of eggs of *Philodobolus montium* were laid in the vivarium, each of which consisted of two eggs with parchment-like shells. The eggs were large, measuring 10-12 mms. x 6-7 mms. and creamy white. An incubator, which is almost self-dampening is described. It uses cycles of evaporation and condensation to keep up the humidity in the moss containing the eggs.*

* After writing the above I have noticed an article by Butler (1948) who also used this system of moist air passing through the moss containing the eggs to hatch many clutches of *Natrix natrix* eggs.

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Wilson, D. (1959). The hatching and rearing of the cobra (*Naja melanoleuca*). Brit. J. Herpetol. **2.** 159.

UN EMBRYON ECTOPIQUE CHEZ LE LEZARD VIVIPARE (*LACERTA VIVIPARA* JACQUIN)

By

JEAN-PIERRE DUFAURE

Des oeufs et des embryons ectopiques ont été trouvés chez différents Reptiles ovovivipares :

1°) chez des Serpents, par W. T. Neill (Copeia, 1948, n° 2, p. 139), chez *Natrix* et *Thamnophis,* par S. A. Minton (Herpetologica, 1949, t. 5, n° 4, p. 96) chez *Coluber,* et par A. d'A. Bellairs (Brit. Journ. Herpetol. 1949, t. 2, p. 55) chez *Vipera berus.*

2°) chez des Lézards par L. de Walsche (Ann. Soc. Zool. Belge, 1925, t. 56, p. 99) et par F. Hochstetter (Anz. Akad. Wiss. Wien, 1946, t. 83, p. 37) chez *Lacerta vivipara.*

Nous avons observé un cas semblable de gestation anormale chez une femelle de *Lacerta vivipara* Jacquin récoltée dans le Massif Central (France) au mois de juin 1962.* A la dissection la femelle présentait deux oviductes contenant chacun quatre embryons à un stade peu avancé du développement (stade 16 à 17 de la table de Dufaure et Hubert). En outre nous avons découvert dans la cavité abdominale un petit lézard mort. Il était enfermé dans une capsule formée de matériel cellulaire provenant de la mère. Cette enveloppe mince et souple n'était pas calcifiée comme dans les cas rapportés par Neill et Bellairs. Sa position exacte était la suivante: il était allongé sur le côté droit de la femelle, entre l'oviducte et la paroi du corps, sa tête dirigée vers la région antérieure de la mère et la queue repliée le long du corps. L'étude morphologique indique qu'il s'agit d'un Lézard arrivé normalement au terme de son développement. La dissection a permis de reconnaître tous les organes, notamment l'appareil génital qui est du sexe femelle. L'étude histologique a montré que les différents organes et tissus sont encore parfaitement reconnaissables : leur position et leur structure sont normales mais les cellules qui les constituent sont plus ou moins nécrosées; cependant dans le mésonéphros où les cellules sont peu nécrosées, certains noyaux cellulaires présentent encore une structure reconnaissable (le nucléole est visible); signalons aussi que les fibres musculaires striées ont une allure tout à fait typique.

Sachant que le Lézard vivipare ne se reproduit qu'une fois par an et que le développement était rélativement peu avancé pour l'ensemble des femelles récoltées en juin 1962, il est incontestable que cet individu provenait d'une gestation de 1961. Il faut donc remarquer que ce Lézard est resté un an dans la cavité abdominale maternelle sans se putréfier et que sa présence n'a pas empêché une nouvelle gestation. Contrairement à L. de Walsche et en accord avec d'autres auteurs et notamment M. Panigel (Ann. Sc. Nat. Zool., 1956, t. 18, p. 569) qui a particulièrement bien étudié la gestation du Lézard vivipare, nous ne pensons pas qu'il s'agisse d'une gestation abdominale mais d'une anomalie survenue lors de la parturition.

SUMMARY

An ectopic embryo, recovered from the abdominal cavity of a pregnant *Lacerta vivipara* is described. It was enclosed in a capsule formed of cellular material of maternal origin; some of its internal organs were still recognizable histologically. It is thought that this embryo was the product of the previous year's gestation and it is of interest that its presence had not prevented a subsequent pregnancy.

—Faculté des Sciences de Clermont-Ferrand, France.

*Un autre cas a été rencontré en 1963 pendant l'impression de cette note

ABILITY OF *TESTUDO ELONGATA* BLYTH TO WITHSTAND EXCESSIVE HEAT

By

R. J. Swindells and F. C. Brown

On the afternoon of Saturday, March 2nd, 1963, a specimen of *T. elongata* in our collection was found to be moving about in its cage with great rapidity. It appeared to be in great distress since it continually banged its head against the sides of its cage from which cause it had badly rubbed its nose. The sides of its head and neck were also red and sore as if the capillaries just under the skin had burst. Vapour was issuing from its mouth and it was continually gasping. It appeared, also, to be sweating, as moisture was observed on its head, neck and limbs.

When the tortoise was bathed in tepid water a hissing noise was clearly audible. After being thoroughly dried it was removed to another cage where it remained very quiet and moved very little for the rest of the day. At the time our chief concern was for the welfare of the tortoise and we neglected to find out the air temperature in its cage. However, the air temperature of the conservatory in which the cage was situated was 90°F.

We thought afterwards that a record of the temperature reached in the cage would be interesting, and on the following Monday (two days later) the cage was set up again under, as far as possible, the same conditions as on the previous Saturday. The cage is an ordinary glass-sided, angle-iron framed aquarium with a floor space of 24" by 12" and a height of 15". The floor is covered with fine gravel to a depth of about 1½", and the top is three-quarters open to the air. Heating and lighting is by means of a 150-watt infra-red dull emitter (ceramic type) and a 75-watt pearl lamp. (The temperature range for January and February had been approximately 60° to 80°F.

Saturday, March 2nd, was one of the first fine days after a long cold spell during which snow was on the ground for nine weeks. The air temperature, therefore, was relatively high and since the cage in which the tortoise was housed was immediately adjacent to the conservatory window the temperature of the air in the cage rose proportionately.

The weather on the following Monday was much the same as on the Saturday. The cage was set up as described and the maximum temperature recorded during the day was 120°F.

It seems almost certain then that our specimen of *T. elongata* withstood a temperature of approximately 120°F. This ordeal does not appear to have had any adverse effect on it as it has continued to eat satisfactorily and increased in weight from 3 lb. 8 oz. on February 28th to 3 lb. 10 oz. on March 16th.

Our experience with *T. elongata* would seem to be in accord with the account of Mr. K. G. Gairdner as recorded by Smith (1931) in which he (Smith) states that Gairdner "often found it crawling about on the open hill-sides in Siam during the day, when the heat of the ground was so great that the hand could hardly bear to touch it".

Reference

Smith, M. A. "Fauna of British India including Ceylon and Burma, Reptilia and Amphibia, Vol. I, Loricata, Testudines." London, 1931.

—6 Osmond Gardens, Wallington, Surrey.

OBSERVATIONS ON THE DEFENSIVE ATTITUDE OF A SOUTHERN TOAD (*BUFO TERRESTRIS*)

By

John Oliver Truitt

While in the process of feeding a collection of captive snakes, I had occasion to observe a unique defensive display by a Southern Toad (*Bufo terrestris*). Upon being introduced into the cage containing a common Hog-nosed Snake *Heterodon platyrhinos platyrhinos*), the toad observed the snake and almost immediately stood high on its legs and danced back and forth, very similar to the stance and movements of a crab. It would charge at the snake, moving sideways in this crablike fashion, stopping inches from its head and would then retreat rapidly. This defensive "dance" went on for some minutes and to the complete bewilderment of the snake. It was later observed that the toad would kick sand at the snake's head prior to the rapid retreat. This defensive activity continued for some 15 to 20 minutes until the toad was captured and consumed by the snake.

It is interesting to note that in 15 years of having Hog-nosed Snakes in the collection and using toads as food for these specimens, I have never before nor since observed this interesting and unusual defensive attitude on the part of a toad.

—808 Almeria Avenue, Coral Gables 34, Florida, U.S.A.

REVIEWS

INTRODUCTION TO HERPETOLOGY: By Coleman J. Goin and Olive B. Goin. W. H. Freeman and Company, publishers, San Francisco and London, 1962, pp. v-ix, 1-341, illust., price $8.00/.

This textbook has been written especially for a one semester course in herpetology and for students having at least one year of biology.

Chapter one deals very briefly with the zoological position of amphibians and reptiles, systematics and taxonomy, nomenclature, and history of herpetology. The section on history is restricted to very early workers and only those recent students who are deceased. This, perhaps, is the only fair way to handle such an area, but it is disappointing not to see any references to the prominent living herpetologists.

Chapters 2 to 6 are concerned with structure, origin and evolution, and reproduction and life history, with the two classes (Amphibia and Reptilia) considered separately under these topics.

The next four chapters (7 to 11) relate to both groups, the subject matter being: Relation to environment, behaviour, mechanisms of speciation, and geographic distribution.

The final six chapters cover the classification and characteristics of the higher categories. Except for various genera and species given as examples, the coverage is at the family or subfamily level and above.

There are two appendices, both of which should prove useful. The first is a list of classification to the family level, including fossil groups; the second is a list of the number of chromosomes for those species of amphibians and reptiles for which such information is known.

Two deviations from most recent literature should, perhaps, be noted. The authors have placed the genera *Siren* and *Pseudobranchus* in a separate

order Trachystomata. They have placed the family Typhlopidae in the lizard suborder Lacertilia, a group which has most often in the past been placed with the snakes.

The only real, and perhaps invalid, criticism I have is the briefness of the book, and especially on the sections covering classification. Otherwise, the book fills a very real need and should be widely used wherever a course in herpetology is taught. The method of coverage is such that there is no geographical limitation imposed as to its use.

Those herpetologists "waist deep" in research should take a moment to applaud these two colleagues, who have taken time from their work to write an adequate and useful text on the subject.

KENNETH L. WILLIAMS,
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REPTILES OF AUSTRALIA: by ERIC WORRELL. Angus & Robertson, Ltd., Australia and London, 1963. 207 pp., 328 photographs (69 in colour) and 12 pp. of drawings.

When I reviewed Worrell's previous book "The Song of the Snake" a few years ago (B.J.H., Vol. 2, No. 8, September, 1959), I thought he was a good field herpetologist but did not imagine that he would be altogether at home in the museum. This was a mistake, as since then he has made a great impact on the taxonomical classification of his country's reptiles, earning the disapproval of some authorities in the process but undoubtedly setting the pace for a much-needed reappraisal of many genera and species. The present book reflects the author's all-round ability by its excellent balance between field and museum study.

Short chapters are devoted to a general introduction to reptiles, a glossary of scientific terms and a check-list of Australian reptiles, but the main bulk of the book deals with the individual species. The excellent descriptions and photographs ensure that this work will be referred to by anyone wishing to identify Australian species, especially so since it is the first time that all the reptiles of Australia have been included in one volume. A great deal of information is also given on the habits of many species, much of it resulting from the author's own observations both on extensive expeditions to remote areas and in the Australian Reptile Park at Gosford.

Since this is clearly a book destined for several editions, the rather large number of minor printing errors will undoubtedly be put right in the next revision. I am sure that many museum workers throughout the world would appreciate it if at the same time the check-list could be expanded to include all the more important synonyms applied in the past to various species, and for my part I would like to see the rather general descriptions of distribution amplified by a series of range maps, extending outside Australia where applicable.

This, however, is merely trying to gild the lily. The book is a most welcome addition to the world's herpetological literature, in a form which will make it of great value to many of the world's herpetologists. Those especially interested in the reptiles of Australia will find it indispensible.

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11, Churchill Road, St. Albans, Herts.

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