OBSERVATIONS ON THE SNOUT OF *VARANUS*, AND A COMPARISON WITH THAT OF OTHER LIZARDS AND SNAKES

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INTRODUCTION

The family Varanidae comprises the single genus of monitor lizards which are widely distributed throughout the tropical and subtropical regions of the Old World. This genus includes the largest of all living lizards; the different species are conservatively modified in adaptation to terrestrial, partly arboreal and partly aquatic habits. *Varanus* occupies a somewhat isolated position among the living members of the order Sauria; it has generally been recognized as an ally of the extinct mosasaurs (Williston, 1925; Camp, 1923, 1940), and has also been regarded as related to the ancestors of snakes (Camp, 1923; Romer, 1945). In spite of the interest of the group, however, no systematic investigation of the chondrocranium of *Varanus* has yet been made, although several studies of the bones and other cranial structures are available. Kesteven (1940) has made some observations on the development of the skull in *V. varius*, but these are restricted to the base of the cranium. Pratt (1948) has described and figured the nasal and vomeronasal organs of *V. monitor* and *V. niloticus*; his account, however, is necessarily brief as it forms part of a general survey of the nasal region throughout the Sauria. It was therefore thought desirable to attempt a more detailed study of the anatomy of the snout in this genus, and to compare conditions present in *Varanus* with those in other lizards and snakes. Since no general description of the snout of any reptile is available, it was also hoped that this account might be of wider interest.

This investigation is principally based on serial sections through the nasal region of a juvenile example of each of the following species: *V. monitor* (Linn.), (*syn. V. bengalensis*), *V. salvator* (Laurenti) and *V. niloticus* (Linn.). I am much indebted to Mr C. W. M. Pratt for the loan of his sections of *V. niloticus*, and also for opportunities for discussing my results with him. The graphic reconstructions and most of the sections figured are based on the specimen of *V. monitor*, which was sectioned at $14\,\mu$ and stained with haematoxylin and eosin. This specimen measured approximately 240 mm. from snout to tail-tip (head-length 25 mm.) and was obtained near Meiktila in central Burma. Other *Varanus* material included the head of an adult specimen of *V. salvator*, a skull assigned to the same species, a juvenile skull of *V. monitor* and another of *V. niloticus*. I am indebted to Mr H. W. Parker and Dr Malcolm Smith of the British Museum of Natural History, and to Dr R. E. Rewell and the Zoological Society of London for the gift or loan of these latter specimens. My thanks are also due to Mr W. Warwick James for the young specimen of *Tupinambis teguixin* from which the sections shown in Text-fig. 11 C and Pl. 1 B were prepared.

TERMINOLOGY

In a monograph on the snout of Crossopterygian fishes and lower gnathostomes in general, Jarvik (1942) has pointed out the shortcomings of the nomenclature usually employed in describing the structures in this region. In particular, he draws attention to the fact that inadequate distinction is usually made between cavities and the structures, both skeletal and non-skeletal, which enclose them. Since Jarvik's terminology seems to be an advance on any previously used and may, with certain modifications, be applied to vertebrates in general, it has been employed as far as possible throughout this account.

The endocranial skeleton of the nasal region is termed the nasal capsule. Inside this lie the nasal sacs which can be subdivided into various regions, as described by Beecker (1903) and Pratt (1948). Each nasal sac communicates with the outside by means of an anterior nasal tube opening by an anterior external nostril, and with the mouth or pharynx by an internal nasal or choanal tube. The nasal and oro-pharyngeal openings of each choanal tube are termed the inner and outer choanae respectively, following the usage of Born (1879), who gave the first comprehensive description of this region in Sauria. Both anterior and internal nasal tubes pass through fenestrae, first in the endocranial and then in the dermal skeleton; the fenestrae for the anterior nasal tubes are termed the fenestra endonarina anterior and fenestra exonarina anterior respectively, while those for the choanal tubes are termed fenestra endochoanalis and fenestra exochoanalis respectively. The posterior nasal tubes and posterior external nostrils of fishes are regarded by Jarvik as homologous with the lachrymal ducts and puncta of tetrapods. In the case of Squamata the term lachrymal duct is preferable to the more familiar naso-lachrymal of mammalian anatomy, since in the former group its anterior opening is more closely related to the mouth than to the nasal sac in many forms.

Since the variations in the saurian palate, which have been almost entirely neglected in the English literature, appear of considerable importance in a general understanding of palatal morphology in amniotes, the terminology of this region has also received some attention. An attempt has been made to apply the principles of Jarvik's nomenclature to the palate, which may be defined as all those tissues which lie between the nasal sacs above, and the mouth or pharynx below. These tissues may be subdivided into:

(*a*) The floor of the nasal capsule, which is conveniently described by the usual terminology of the chondrocranium.

(*b*) The dermal skeleton, here called the bony palate.

(*c*) The soft tissues lying between the bony palate and the oral and pharyngeal cavities; the term superficial palate has been arbitrarily applied to these.

The duct of Jacobson's organ passes through these palatal tissues in all adult Squamata, and opens into the oral cavity, its epithelium becoming continuous with that of the superficial palate. The fenestrae in the endocranial and dermal skeletons traversed by this duct have therefore been called the fenestra vomeronasalis interna and fenestra vomeronasalis externa respectively.

CONDITIONS IN *VARANUS*

(1) Bones

The skull bones of *Varanus* have been thoroughly described by Bahl (1937) with special reference to the individual bony elements and nerve foramina, and by Mertens (1942) who devoted much attention to interspecific variations. The bony skull has not, therefore, been treated in detail in the present account, although some attention has been given to certain features which have previously received little notice. No attempt has been made to make graphic reconstructions of the bones, but these elements have been drawn in from a dried skull of another juvenile specimen, so that their relationship with the chondrocranium may be appreciated (Text-figs. 1 A, 2 A and 3). The levels of the individual bones in these drawings have been checked as far as possible to correspond with those in the sections on which the reconstructions of the chondrocranium have been based; in some cases slight alterations in the outlines of these bones have been made. The specific features of the bony skull described have been included with the accounts of the non-bony structures related to them, while the palate has been dealt with in the comparative section.
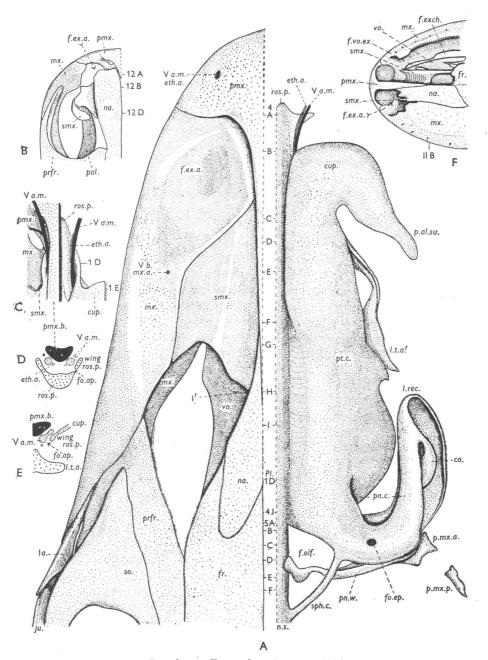
(2) Nasal capsule

The general morphology of the saurian chondrocranium is now well known from the work of Born (1879), Gaupp (1900), Rice (1920), de Beer (1937) and others; it is, therefore, only necessary to describe in detail the features which are particular to this genus. The reconstructions given (Text-figs. 1 A, 2 A and 3) agree in the main with that of Pratt. The nasal capsule is narrow and elongated, corresponding with the contours of the head. As in all living reptiles it remains unossified throughout life.

The unfenestrated nasal septum is low and terminates anteriorly in a flattened rostral process which is expanded into lateral wings. These wings are upturned, especially in *V. salvator* (Text-fig. 1 D) and support the medial ethmoidal nerves and vessels. In *V. monitor* the wings taper off behind into the central part of the rostral process, which widens out again further back as the lamina transversalis anterior. The medial ethmoidal nerve and terminal branch of the ethmoidal artery run

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Legend to Text-fig. 1

Text-fig. 1. A. *Varanus monitor*, subadult. Reconstruction of chondrocranium (right), and bones of snout (left), seen from above. (Bones in Text-figs. 1 A, 2 A and 3 drawn from dried skull.) Levels of sections in Text-figs. 4, 5 and Pl. 1 D are shown. B. *Xenopeltis unicolor*, subadult. Dorsal view of bones of front of snout (drawn from dried skull). Levels of some sections in Text-fig. 12 are shown. C. *Varanus salvator*, subadult. Reconstruction of part of snout showing relationship of ethmoidal nerves and vessels to the skeleton. The main nerve branches only are shown. The right half of the premaxillary bar has been removed. In this species the medial ethmoidal nerve does not enter the premaxilla before dividing into its terminal branches, as in *V. monitor*, but runs forwards in a groove on the dorsal surface of the bone. A lateral branch passes downwards through a large foramen between the premaxilla and maxilla, while medial branches run through a foramen between the premaxillary bar and the lateral part of that bone. The foramina for the corresponding nerve branches are differently situated in *V. monitor*, and study of the figures shown by Mertens (1942) suggests that the precise relationships exhibited by the structures in this region are liable to considerable interspecific variation. D, E. *V. salvator*. Transverse sections through rostral process and premaxillary bar at levels shown in C above. F. *Tarentola mauretanica*, adult. Dorsal view of bones of front of snout, drawn from a dried skull. The nasal and part of the maxilla have been removed on one side to expose the septomaxilla and bony palate. Level of section in Text-fig. 11 B is shown. (A, × 13; B, × 5; C, × 12; D, E, × 10; F, × 3·7.)

Text-fig. 1. (For explanation see p. 118.)

forwards between the medial edge of the anterior cupola and the rostral process, so that there is no distinct foramen apicale (Text-figs. 1 A, 2 A, 3 and 4 A, B). In *V. salvator* and *V. niloticus* these relationships are slightly different. The wings join the medial edge of the anterior cupola behind, and the nerves and vessels pass through an elongated foramen apicale between the wings and central part of the rostral process (Text-fig. 1 C–E).
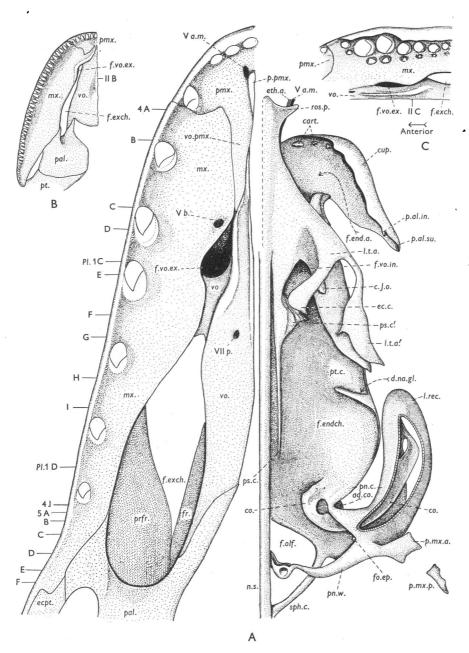
According to Pratt, the roof and sides of the nasal capsule are developed from two morphologically distinct elements—a medial element, the dorsal plate, which runs the whole length of the capsule roof on either side of the midline, and a lateral element which includes the parietotectal and paranasal cartilages which are continuous with each other. The line of junction between these medial and lateral elements cannot be determined accurately in the adult, but Pratt claims that it is indicated by the positions of the foramina for the branches of the ethmoidal nerve, and by the sites of the fenestrae superior and lateralis in those forms where they are present. In *Varanus* these fenestrae do not occur and it is only possible to infer approximately what the relative extent of these different elements may have been in the embryo. The labelling of the different regions of the capsule roof must therefore be regarded as provisional.

The front part of the capsule roof forms the large anterior cupola which lies above the curved part of the anterior nasal tube. The cupola is continuous laterally with the processus alaris superior, beneath which the anterior nasal tube passes inward to reach the nasal sac. A small projection from the cupola side wall beneath the processus alaris superior is interpreted as an inferior alar process (Text-figs. 3, 4 D). The fenestra endonarina anterior curves round above this small projection, behind and beneath the processus alaris superior (Text-figs. 2 A, 3).

Behind the anterior cupola the roof of the nasal capsule forms an uninterrupted covering for the elongated anterior chamber of the nasal sac. Owing to the characteristic incompleteness of the dermal skeleton of the varanid snout, this part of the capsule roof, together with the cupola, is exposed in the gap between the maxilla laterally and the narrow premaxillary bar in the midline (Text-figs. 1 A, 3 and 4 A–H). The nasal capsule is therefore covered dorsally only by skin and connective tissue in this region.

The middle part of the tectum nasi is expanded both laterally and dorsally to accommodate the olfactory chamber of the nasal sac (Text-figs. 4 I–J, 5 A, B). Behind this level the roof is continuous laterally with the dorsal wall of the capsule of the lateral recess. The foramen epiphaniale is situated in the transverse segment which joins the main part of the roof of the capsule with that of the lateral recess (Text-figs. 1 A, 5 C). The sphenethmoid commissures arise from the free posterior borders of the capsule roof (Text-figs. 1 A, 5 D); the olfactory lobes project over the commissures into the fenestrae olfactoria.
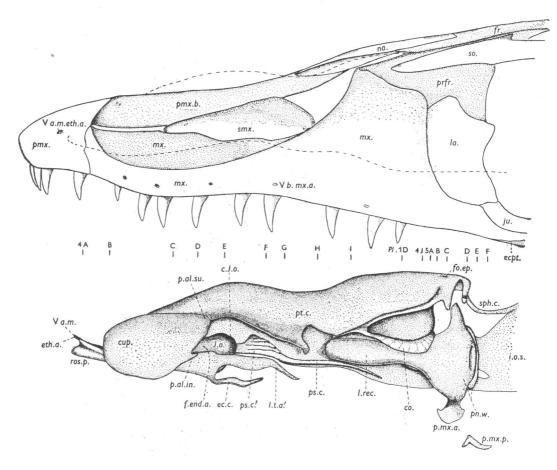
Behind the region of the anterior cupola, the lateral wall of the nasal capsule only extends down as far as the upper part of the nasal septum. No zona annularis is present, and the cartilage of Jacobson's organ and the whole length of the paraseptal cartilage are exposed in lateral view (Text-fig. 3). Two processes project downwards from the free edge of the lateral wall. The first of these, situated about on level with the tip of the lamina transversalis anterior, marks the termination of the lateral part

Text-fig. 2. A. *Varanus monitor*, subadult. Reconstruction of chondrocranium (right) and bones of snout (left), seen from below. Levels of sections in Text-figs. 4, 5 and Pl. 1 C, D are shown. A window has been cut in the lateral recess capsule to expose the nasal concha. B. *Tarentola mauretanica*, adult. Ventral view of right side of bony palate showing paleochoanate condition. (Drawn from dried skull.) Level of section in Text-fig. 11 B is shown. C. *Tupinambis nigropunctata*, adult. Ventral view of right side of bony palate showing incomplete neochoanate condition. (Drawn from dried skull.) Level corresponding to section in Text-fig. 11 C is shown. (A, × 13; B, × 4; C, × 2·2.)

of the floor of the nasal capsule which runs to a point posteriorly (Text-fig. 2A). The second process lies farther back at the level of the front of the lateral recess capsule. The duct of the nasal gland (Text-figs. 4I, 10C) hooks medially round this process before entering the nasal sac.

Text-fig. 3. *Varanus monitor*, subadult. Reconstruction of chondrocranium (below) and bones of snout (above), seen from the side. Outline of roof of nasal capsule and lower edge of nasal septum is shown by interrupted lines in upper drawing. Levels of section in Text-figs. 4, 5 and Pl. 1D are shown. The prefronto-maxillary contact in the specimen drawn is unusual; in most specimens of *V. monitor* the contact runs obliquely downwards from in front, and the maxilla sends up a spur which articulates also with the frontal and tip of the supraorbital. (× 12.)

The posterior third of the lateral wall is modified in relation to the conchal infolding and the formation of the capsule of the lateral recess.* The morphology of this region was found to differ considerably in the three species of *Varanus* examined.

*This structure, which is present in many other lizards (see later) has usually been termed the cavum extra-conchale or extra-conchal recess. Since the nasal concha extends into it in *V. monitor*, however, the term lateral recess has been thought more appropriate.

In *V. salvator* the lateral recess capsule is joined with the lateral wall of the main nasal capsule, and the concha is not continued round into the recess (Text-fig. 10 A). In *V. niloticus* conditions appear to be intermediate between those in *V. salvator* and *V. monitor*; the lateral recess is more extensive than in the former species and its anterior part is cut off from the rest of the nasal sac by a separate medial wall.

In *V. monitor* the lateral recess reaches its greatest development, and is completely cut off from the rest of the nasal sac for most of its length by a separate medial wall and floor (Text-figs. 4 I, J, 5 A, B and 10 B, C). The extent of the concha inside the main part of the nasal capsule is relatively small; it continues laterally, however, and runs down most of the length of the lateral recess capsule, to the medial wall of which it is attached (Text-figs. 4 I, J, 5 A, B and 10 B). As the roof of the recess capsule is only partly complete the anterior part of the concha is exposed from above (Text-fig. 1 A).

The lateral recess capsule may be regarded as a continuation of the main nasal capsule bent round laterally, so that the medial wall of the former is continuous with the lateral wall of the latter, which in this region is derived from paranasal cartilage. It therefore seems probable that the greater part of the recess capsule is of paranasal origin, with perhaps a dorsal plate contribution to the region behind the foramen epiphaniale. The relations of the paranasal cartilage and concha to the nasal sac in *V. salvator* and *monitor* are shown diagrammatically in Text-fig. 10 A, B.

The floor of the nasal capsule, in contrast with the roof, is very incomplete. Anteriorly, three small nodules of cartilage lie beneath the front edge of the anterior cupola (Text-figs. 2 A, 4 B). Towards the midline the rostral process sweeps backwards and laterally to become continuous with the lamina transversalis anterior. The latter structure does not join the parietotectal cartilage to form a zona annularis, but runs backwards for some distance to a free posterior tip. The cartilage of Jacobson's organ projects upwards from the lamina transversalis (Text-figs. 4 D, E, 9 A).

Pratt has stated that paraseptal and ectochoanal cartilages are absent in *Varanus*. Examination of further material, however, indicates that these are present in the usual saurian position. Both cartilages are more extensive in *V. monitor* than in *V. salvator* and *V. niloticus*. Near its root the paraseptal cartilage is much swollen and fragmented to form a cartilaginous network through which the vomeronasal nerve bundles pass on their way backwards from Jacobson's organ (Text-figs. 3, 9 B). The ectochoanal cartilage is directed medially and extends beneath the swollen part of the paraseptal, partly enclosing the fenestra vomeronasalis interna (Text-fig. 9 A). Above the ectochoanal cartilage and lamina transversalis anterior, the side wall of the nasal capsule is bent round and lies beneath the lateral part of the anterior chamber of the nasal sac (Text-figs. 4 F, G) so that the floor of the capsule is duplicated in this region.

Behind the level of the ectochoanal cartilage, the floor of the nasal capsule is absent, so that the fenestra endochoanalis is very extensive. In the complete skull, however, this vacuity is partly closed by the vomer and the palatal process of the maxilla. The floor of the lateral recess capsule is continuous with the paranasal cartilage; the interpretation of this region has already been discussed. The lateral recess capsule lies against the concave inner aspects of the maxilla and prefrontal, and

is separated from the inwardly projecting maxillary shelf by the lachrymal ducts (Text-figs. 4I, J, 5A,B).

The postnasal wall (Jarvik 1942: planum antorbitale, other writers) passes from the transverse segment connecting the capsule of the main nasal sac with that of the lateral recess to the edge of the nasal septum. It is in contact with the latter, but is not fused with it. Near the septum its lower edge is continuous with a small anteriorly directed process, which, by analogy with other forms, probably represents a detached caudal rudiment of the paraseptal cartilage (Text-figs. 2A, 5E). The anterior face of the postnasal wall is slightly folded, accommodating small extensions from the antorbital space of the nasal sac. Behind the postnasal wall the prefrontal swings medially to form a rigid bony wall at the back of the nasal capsule (Text-fig. 6).
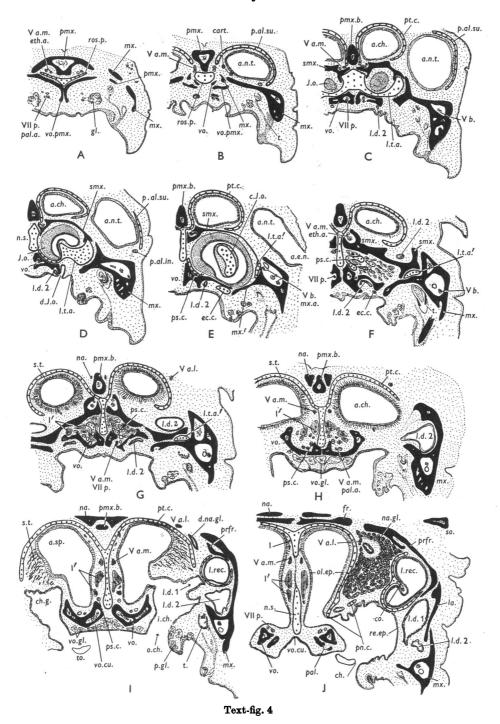
(3) *Nasal sac*

My reconstruction of the nasal sac of *V. monitor* (Text-fig. 10D) agrees closely with those shown by Wegner (1922) and Pratt (1948). The anterior external nostril is longer and situated relatively farther forward in this species than in *V. niloticus* and *V. salvator* (Text-fig. 10A,B). The anterior nasal tube is also more elongated and curved in *V. monitor*. It is possible that these differences have an adaptive significance, for *V. monitor* is a partly deserticolous form, whereas the other two species have amphibious tendencies (see Wegner, 1922: Mertens, 1942).
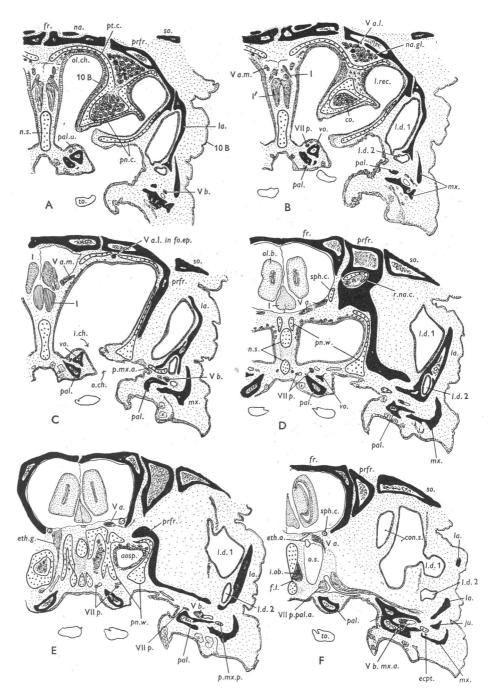
The anterior nasal tube passes medially to become continuous with the very elongated anterior chamber of the nasal sac. The latter is partly surrounded by spongy sinusoidal tissue (Text-fig. 4G–I). Bruner (1907) has shown that this tissue is present in many lizards, and suggests that its intumescence provides a mechanism for closing the nasal passages without interfering with the other functions of the head. The anterior chamber leads backwards into the olfactory chamber, the point of entry of the nasal gland duct indicating the region of transition between the two. The most anterior part of the olfactory chamber is known as the anterior space (Beecker, 1903), and extends ventrally, coming into relationship with the front of the choanal groove (Text-fig. 4I). The anterior space passes back into the conchal zone which is divided by the projecting concha into dorsal and ventral parts (Text-figs. 4J, 5A,B). The ventral part of the conchal zone leads downwards through the opening of the inner choana into the choanal tube, which communicates with the mouth at the outer choana (Text-fig. 10C). Behind the choanal region the nasal sac ends in a small blind pocket, the antorbital space (Text-fig. 5D,E).

The lateral recess of the nasal sac communicates posteriorly with the main olfactory chamber (Text-fig. 5A,B) and may be regarded as a continuation of it. The variations in the extent of the lateral recess in the different species of *Varanus* studied have already been described; it seems possible that these may also be related to differences in habits.

The anterior chamber is lined by squamous stratified epithelium which continues back on to the roof of the anterior space. The floor of the latter, however, is covered by ciliated epithelium of respiratory type and this extends backwards over the walls of the ventral conchal zone to the region of the choanal tube. Here the respiratory epithelium is replaced by the stratified squamous epithelium of the palate (Text-
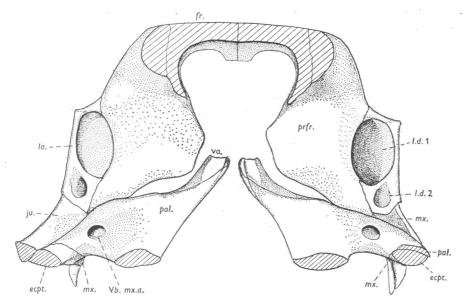
Text-fig. 4

Text-figs. 4, 5. *Varanus monitor*, subadult. Transverse sections through snout at levels shown in Text-figs. 1–3. (×11.)

Text-fig. 5. (For explanation see p. 125.)

fig. 10 C). The sensory olfactory epithelium of *Varanus* is more limited in extent than in many other lizards. It is apparently confined to the dorsal surface of the conchal projection and to the roof and medial wall of the conchal zone, giving way to respiratory epithelium medially, above the inner choana (Text-fig. 10 C). The olfactory fibres arise from the sensory cells of the olfactory chamber and pass medially until they reach the side of the nasal septum. They become arranged into fibre bundles which run back dorsal to the vomeronasal nerves to enter the tip of the olfactory bulb (Text-figs. 4 I, J, 5 A, B).

Text-fig. 6. *Varanus niloticus,* subadult. Transverse section of bony snout just in front of orbits, seen from behind. (Drawn from a dried skull.) The canal for lachrymal duct 2 penetrates the lachrymal bone; that for *l.d.* 1 passes between the lachrymal and prefrontal. Cf. Text-fig. 5 E, F for relationships of non-bony structures. The jugal is missing on the right side. (× 6.)
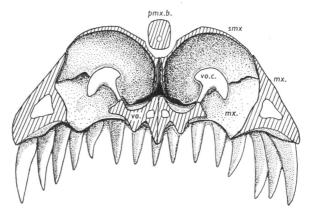
The appearance of the epithelium lining the lateral recess (Pl. 1 D) varies considerably in different places. At the tip of the concha there is a small patch of respiratory type epithelium containing mucous cells. The remainder of the recess is lined by epithelium of transitional type which on the dorsal surface of the concha approaches sensory olfactory epithelium in appearance. The sensory nature of this area might be expected if the dorsal part of the recess is regarded as a continuation of the main dorsal conchal zone. No nerve fibres were, however, observed to arise from the epithelium of this or any other part of the lateral recess.

(4) *Organ of Jacobson*

The vomeronasal organs (Text-figs. 4 D, E, 8; Pl. 1 C) are relatively larger than in most lizards. Experimental evidence based on other squamate types (e.g. Noble & Kumpf, 1936) has shown that odorous particles are conveyed to the duct of Jacobson's organ or to the neighbouring parts of the palate by the tips of the tongue. The

presence of a long bifid retractile tongue in *Varanus*, together with the large size of Jacobson's organs, suggests that the vomeronasal sense plays as important a part in the behaviour of these lizards as has been shown to be the case in snakes.

In their general morphology the vomeronasal organs of *Varanus* conform to the usual squamate pattern as described by Pratt. Each organ possesses a large dorsal dome lined by sensory epithelium, and a mushroom body which is invaginated into the lumen from in front and below. This structure is covered by non-sensory ciliated epithelium, beneath which is a layer of rather dense connective tissue. This is supported by the cartilage of Jacobson's organ which projects upwards and backwards from the lamina transversalis anterior. The cartilage in turn rests on the vomerine concha which is carried on a stalk from the dorsal surface of the vomer (Text-figs. 7, 8 and 9).
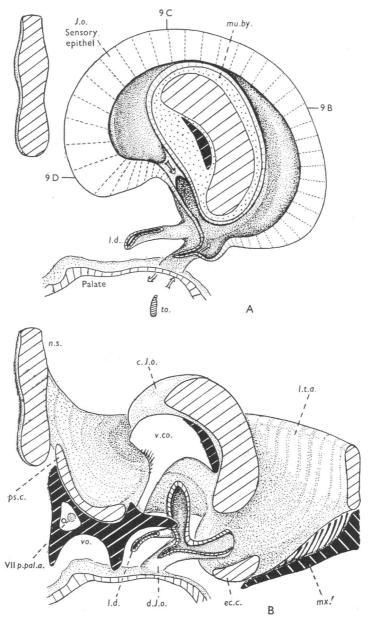

Text-fig. 7. *Varanus niloticus*, subadult. Anterior part of bony snout in transverse section seen from behind, showing chamber for Jacobson's organ. (Drawn from a dried skull.) The vomerine concha (*vo.c.*) supports the mushroom body of Jacobson's organ. Cf. Pl. 1C and Text-figs. 4E, 8 for relationships of non-bony structures. (× 6.)

The spiral duct of Jacobson's organ (Text-figs. 8, 9) has a crescentic opening into the lumen beneath the posterior part of the mushroom body, and passes downwards and forwards to lead into the mouth. The lachrymal duct opens into its medial aspect as it traverses the tissues of the superficial palate. The existence of a ciliary mechanism by which odorous particles are carried into the lumen of Jacobson's organ along the lateral aspect of its duct, over the mushroom body and back into the mouth down the medial aspect of the duct has been suggested by Pratt. The direction of this one-way circuit is indicated by arrows in Text-fig. 8A. Since the duct of Jacobson's organ is lined by stratified epithelium, it would seem that odorous particles would have to be inserted into the lumen of the organ by the tongue tips before they could come under the influence of the cilia on the mushroom body.

The vomeronasal nerves are more numerous than the olfactory nerves. Their fibres arise from the sensory epithelium of the dorsal dome of Jacobson's organ and pass back over the concave upper surface of the vomer, between this bone and the septomaxilla. In this part of their course the fibres traverse the cartilaginous network formed by the swollen fragmented parts of the paraseptal cartilage (Text-

figs. 4 F, 9 B). The nerves then become arranged into several large bundles which run back along the side of the nasal septum to reach the accessory olfactory bulb. The vomeronasal nerves, especially near their origin from Jacobson's organ, are richly
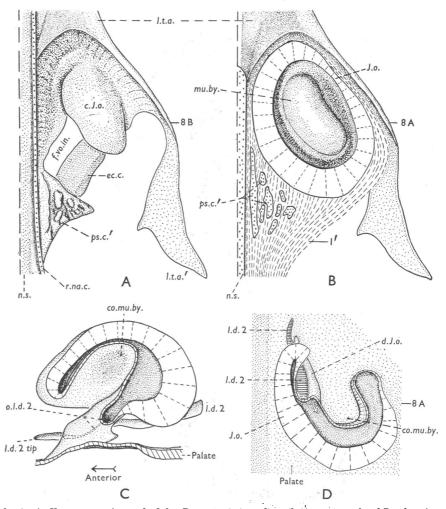
Text-fig. 8. A. *Varanus monitor*, subadult. Reconstruction of right organ of Jacobson seen in transverse section from behind. Level of section shown in Text-fig. 9 B, D. Arrows indicate probable direction of flow of particles. B. *V. monitor*. Reconstruction of cartilaginous capsule and duct of Jacobson's organ seen in transverse section from behind. Level of section as in Text-fig. 8 A; level also shown in Text-fig. 9 A. Some bones are included. The lachrymal duct *l.d.* figured is (l.d.) 2. (A, B, × 50.)

vascularized, each of the main fibre bundles containing a dozen or more visible arterioles in any single cross-section.

Each organ of Jacobson is almost completely surrounded by a skeletal investment from which it is separated by a layer of loose connective tissue containing many

Text-fig. 9. A. *Varanus monitor*, subadult. Reconstruction of cartilaginous capsule of Jacobson's organ seen from above after removal of roof of nasal capsule (cut edge shown). B. *V. monitor*. Reconstruction of right organ of Jacobson and cartilaginous capsule seen in horizontal section from above at level shown in Text-fig. 8 A. The mushroom body is shown intact. C. *V. monitor*. Reconstruction of right organ of Jacobson seen in longitudinal section from lateral side. Level of section shown in Text-fig. 8 A. Cartilage not included. D. *V. monitor*. Reconstruction of right organ of Jacobson seen in horizontal section from above at level shown in Text-fig. 8 A. Cartilage not included. (All × 23.)

blood-vessels. This investment consists of an inner cartilaginous and an outer bony capsule (Text-figs. 7, 8 and 9). The cartilaginous capsule is incomplete dorsally. Its floor is formed by the hollowed posterior edge of the lamina transversalis anterior

with its projecting cartilage of Jacobson's organ, and farther back by the paraseptal and ectochoanal cartilages which extend posteriorly from the lamina. The latter cartilage projects downwards outside the bony capsule, passing between the vomer and the palatal process of the maxilla, and coming to lie in the superficial palate (Text-fig. 4 E, F). The medial wall is formed by the nasal septum, while an incomplete lateral wall is provided by the free lateral extension of the lamina transversalis anterior.

The bony capsule (Text-fig. 7) is more complete, and encloses the organ of Jacobson and its cartilaginous capsule. The septomaxilla arches across the dorsal dome of the organ, separating it from the floor of the nasal sac. Laterally the septomaxilla is in contact with the vertical part of the maxilla, but medially and in front there is a gap between the septomaxilla and the dorsal surface of the vomer which is occupied by the nasal septum and the lamina transversalis anterior. These pass forwards out of the bony capsule to become continuous with the rostral process. At the posterior aspect of the bony capsule there is also a small vacuity between the septomaxilla and vomer through which pass the vomeronasal nerves.
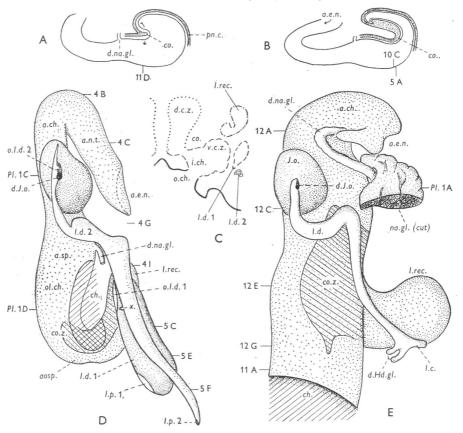
The floor of the capsule is formed by the lateral extension from the vomer and the palatal process of the maxilla: the duct of Jacobson's organ passes down between these structures (Text-fig. 8 B) through the fenestra vomeronasalis externa. Posterior to this level the lateral margin of the vomer and the maxillary palatal processes come into apposition so that the fenestra vomeronasalis is completely separated from the fenestra exochoanalis. This feature will receive further attention when the palate of *Varanus* is compared with that of other types.

(5) *Lachrymal apparatus*

V. monitor (and also probably *V. salvator* and *V. niloticus*, though the condition of the sections in this region made it impossible to confirm this with certainty) differs from all other lizards examined in that there are two separate lachrymal ducts on each side. Each duct arises at a separate punctum from the medial aspect of the lower eyelid; the punctum for the upper of the two ducts (lachrymal duct 1) is placed considerably in front of that for the lower duct (*l.d.* 2) (Text-fig. 5 F: Bellairs & Boyd, 1947). *l.d.* 1 is wider and much shorter than *l.d.* 2; it passes forward to enter the snout through a foramen between the prefrontal and lachrymal bones (Text-fig. 6) and passes into an elongated gutter which opens into the ventral conchal zone of the nasal sac, above the inner choana (Text-figs. 4 I–J, 5 A–F; Pl. 1 D). From its origin to about the level where it enters its bony canal, *l.d.* 1 is lined by stratified epithelium which is continuous with that of the palpebral conjunctiva; in the anterior part of its course, however, its epithelium is of ciliated respiratory type, similar to that of the ventral conchal zone into which the duct opens.

Lachrymal duct 2 passes back beneath the punctum for *l.d.* 1 (Text-fig. 5 F) and enters the snout through a foramen in the lachrymal bone (Text-fig. 7). It then runs forwards on the inner surface of the vertical part of the maxilla, resting on the bony shelf formed by the maxillary palatal process (Text-fig. 4 H–J). In this situation it reaches a level a little posterior to Jacobson's organ (Text-fig. 4 H), and then curves sharply inwards and downwards, passing transversely across the concave posterior border of the septomaxilla to open into the medial aspect of the duct of Jacobson's

organ. The angular part of the duct shows a marked dilatation which bulges forwards on to the dorsal surface of the septomaxilla (Text-figs. 4F, G, 10D). Anterior to this level the diameter of the duct undergoes marked reduction; its opening into the duct of Jacobson's organ is elongated in the antero-posterior direction but is compressed from above downwards, so that its orifice has the form of a long narrow slit (Pl. 1D; Text-figs. 9C, 10D). The lachrymal duct continues forwards for some distance anterior to the level at which it opens into the duct of Jacobson's organ, ending blindly about the level of the front of the organ (Text-fig. 1C).

Text-fig. 10. A, B. Diagrams showing horizontal section of nasal sac in (A) *Varanus salvator* (plane of section shown in Text-fig. 11D), and (B) *V. monitor* (plane of section shown in Text-fig. 5A). (Partly based on personal communication from C. W. M. Pratt.) Conditions in these two species illustrate the development of the lateral recess and the corresponding changes in the concha and paranasal cartilage (stippled). C. *V. monitor*. Diagram showing different types of epithelium lining nasal sac etc., at level of Text-fig. 4J. Stratified epithelium of palate shown in thick black lines; sensory epithelium over dorsal conchal zone (*d.c.z.*) in dots; ciliated epithelium with mucous cells (respiratory type) over ventral conchal zone (*v.c.z.*), upper part of choanal tube, tip of lateral recess concha and lachrymal duct 1, shown by interrupted lines; transitional epithelium with cilia but few mucous cells over most of lateral recess, shown by interrupted lines and dots; columnar non-ciliated epithelium (*l.d.* 2 only) in double lines. D, E. Diagrammatic reconstruction of nasal sac, organ of Jacobson and lachrymal ducts seen from below in (D) *V. monitor* and (E) *Xenopeltis unicolor*. Extent of choanal tube is indicated by slanting lines; conchal zone (*co.z.*) shown by slanting lines and dots. Levels of some sections in Text-figs. 4, 5, 11, and 12 and in Pl. 1A, C, D are shown.

At one point in its course, below the anterior opening of the upper duct, *l.d.* 2 communicates with the ventral conchal zone by means of a short transverse channel (Pl. 1 D); this channel has a small tortuous diverticulum leading from it. In this region a small invagination of epithelium and connective tissue projects into the main lumen of the duct. The significance of these features is obscure.

In the anterior part of its course *l.d.* 2 is lined by stratified epithelium. Around the level of the front of the lateral recess this is replaced by columnar non-ciliated epithelium which becomes continuous with the respiratory epithelium of the ventral conchal zone at the transverse communication (Pl. 1 D). In the posterior part of its course, behind the lachrymal foramen, the epithelium again changes to the stratified type, as in the posterior part of *l.d.* 1.

The curious relationship of the two lachrymal ducts to the prefrontal and lachrymal bones (Text-fig. 6) was first described by Mertens (1942), and is apparently constant for all species of *Varanus*. In all species the upper duct (*l.d.* 1) is wider than the lower, but the relative disparity in size of the two ducts varies considerably.

(6) *Glands and teeth*

The nasal (lateral nasal, Fahrenholz, 1937) gland is smaller than in many lizards and is situated in the aditus conchae, between the paranasal cartilage and the medial wall of the lateral recess capsule. Its duct leads forwards, hooking medially round the posterior of the two projections from the capsule roof, to open into the nasal sac around the level at which the anterior chamber becomes continuous with the anterior space (Text-figs. 4 I, J, 5 A, B and 10 D). Its acini are mainly mucous in character.

The distribution of the palatal glands follows the usual saurian pattern (Fahrenholz, 1937). A median vomerine group of glands lies along the lower border of the vomerine cushion, while the more scattered acini of the palatine group are situated farther laterally (Text-fig. 4 I). The superior labial glands are represented only by a few isolated acini along the medial aspect of the dental lamina. The glands of the palate appear to be mainly serous in character.

The pleurodont teeth of *Varanus* vary in appearance, depending on the age and species of the individual. In many cases they are sharp and recurved: in mature specimens, particularly of *V. niloticus* and *V. exanthematus*, they may be blunt and rounded (Mertens, 1942). It is possible that the diet, which ranges from small vertebrates to insects and crabs (Cowles, 1930), may also be associated with the form of the teeth. No study of the histology or mode of tooth succession was made; a review of the relevant literature is given by Peyer (1937).

(7) *Nerves*

The topography of the cranial nerves has been described by Fischer (1852) in *Varanus bengalensis* and by Watkinson (1906) in *V. bivittatus*, while Bahl (1937) has enumerated the nerve foramina in the bony skull of *V. monitor*. A more detailed account of the cranial nerves of a lizard has been given by Willard (1915) for the iguanid *Anolis carolinensis*. My own findings largely confirm those of the workers cited, but in the absence of selectively stained material it has not been possible to investigate the distribution of nerve endings, or ganglionic connexions. The following account is based mainly on serial sections of *V. monitor*.

Apart from the nerves of special sense, the snout receives its innervation from three sources: the ophthalmic and maxillary divisions of the trigeminal, and the palatine branch of the facial nerve. The two branches of the fifth nerve probably carry fibres which are mainly somatic sensory in nature; the extensive communication between these two nerves and the palatine nerve, however, renders it likely that some autonomic fibres are also distributed with the two trigeminal branches. The palatine nerve is probably composed in the main of pre- and post-ganglionic parasympathetic fibres which are distributed to the glands and blood vessels of the snout. Sympathetic and visceral afferent fibres may also be present (Willard, 1915; Adams, 1942).

The ophthalmic nerve passes along the medial aspect of the orbit on either side of the interorbital septum, and enters the snout through the orbitonasal fissure, between the septum and the sphenethmoid commissure (Text-fig. 5F), where it becomes the ethmoidal nerve. As it lies in the fissure it possesses a swelling in which many ganglion cells can be seen. This swelling corresponds with the ethmoidal ganglion described by Willard in *Anolis*, and communicates with the palatine nerve by a band of fibres which runs vertically downwards behind the postnasal wall (Text-fig. 5E).

Slightly anterior to the ethmoidal ganglion the nerve divides into its lateral and medial rami (Text-fig. 5D). The lateral ramus passes forwards beneath the roof of the nasal capsule for a short distance, and then leaves the capsule through the foramen epiphaniale (Text-fig. 5C). It then breaks up into numerous branches among the acini of the nasal gland (Text-fig. 5B, etc.) and probably supplies the latter (see Gaupp, 1888) as well as the skin and tissues of the snout.

The medial branch of the ethmoidal nerve passes forwards at the side of the nasal septum where it is closely related to the olfactory and vomeronasal nerves (Text-figs. 4, 5A–C). It enters a groove along the medial edge of the septomaxilla and runs forwards in this situation (Text-fig. 4D–G), escaping through a foramen at the front of the bone (Text-fig. 4B, C). Anterior to this level it lies between the rostral process and roof of the nasal capsule (Text-fig. 4B), and in front of this again, between the rostral process and premaxilla; the slightly different condition in *V. salvator* has been described. The nerve then enters the posterior premaxillary foramen (of Bahl) and divides into dorsal and ventral branches which emerge from the dorsal and ventral premaxillary foramina respectively (Text-figs. 1A, 2A) to supply the tip of the snout. No branches supplying the nasal sac or the organ of Jacobson could be identified, although the existence of such branches seems probable.

The maxillary nerve passes along the ventrolateral aspect of the orbit and enters the snout through a canal in the palatine bone (Text-figs. 5F, 6). During its course through the orbital region it has two principal communications with the palatine nerve: one near the back of the orbit and another just anterior to the orbit. After the nerve has left the palatine canal (Text-fig. 5E) it enters the maxillary canal after giving off several small branches which are probably distributed to the glands and epithelium of the palate. At intervals throughout its course in the maxillary canal the nerve supplies the teeth, and also sends branches laterally which pass through small foramina in the bone and are distributed to the side of the jaw. A few rami also pass medially through the palatal process of the maxilla to reach the palate. One rather large branch emerges from the easily recognizable anterior maxillary foramen (Bahl) which lies lateral to the fenestra vomeronasalis externa (Text-

fig. 2A); Another large branch also passes upwards and medially through a foramen in the dorsal aspect of the maxilla (Text-figs. 1A, 4E), and is apparently distributed to the anterior nasal tube. The main nerve trunk finally escapes through a foramen near the anterior extremity of the maxilla and breaks up into branches in the superficial tissues of the snout.

The palatine branch of the facial nerve leaves the parabasal canal and passes forwards beneath the orbit at first medial to the pterygoid and then dorsal and lateral to it. In this situation, a little behind the midorbital region, it communicates with the infraorbital (maxillary) nerve, and bears a swelling containing ganglion cells. This swelling corresponds in position with the palatine ganglion in *Anolis*, and with the sphenopalatine ganglion figured by Adams (1942) in *Lacerta viridis*. Anterior to this level the nerve continues above the palatine bone, sending branches to the superficial palate. At the front of the orbit the nerve swings medially and enters the snout near the lower edge of the interorbitonasal septum (Text-fig. 5F). In this situation the nerve carries another ganglionic swelling which is connected with both the ethmoidal ganglion above and the maxillary nerve laterally; a small bundle of fibres joins the maxillary nerve and passes with it into the maxillary canal (Text-fig. 5E). This anterior ganglion probably corresponds with the structure described by Haller v. Hallerstein (1937) in *Anguis fragilis*. After giving off several lateral branches to the superficial palate the main trunk of the nerve passes forwards above the vomeropalatine articulation (Text-fig. 5A–D) and then over the concave upper surface of the vomer (Text-fig. 4G–I). In the region of Jacobson's organ it becomes completely enclosed in a canal in the medial part of the vomer, from which it sends at least one branch downwards through the bone to reach the superficial palate (Text-fig. 4G), probably supplying the palatine glands and epithelium (Gaupp, 1888). Anteriorly the nerve leaves the vomerine canal and breaks up into fine branches in the premaxillary region of the superficial palate.

No fibres from the trigeminal (or facial) nerve supplying Jacobson's organ could be identified, nor have any been described by Watkinson, nor by Willard in *Anolis*. It seems likely, however, that Jacobson's organ receives some sensory trigeminal innervation; it is unfortunate that in *Anolis*, the only form of which selectively stained preparations have been studied, the organ of Jacobson is smaller and less conspicuous than in most lizards. The nervus terminalis could not be identified in *Varanus*.
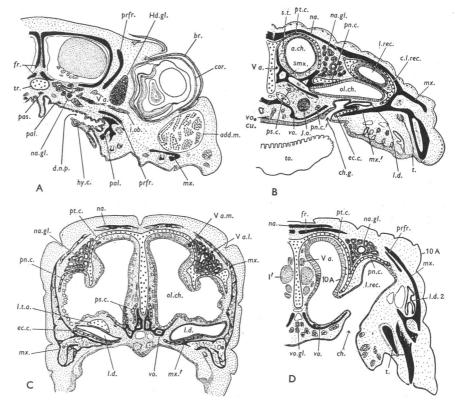
(8) *Blood vessels*

The vascular system of *V.* ('*Psammosaurus*') *griseus* was studied by Corti (1847), but he hardly deals with the vessels of the snout. Subsequent descriptions of the blood supply of the snout in lizards have been given by Bruner (1907), who dealt only with the veins, and by Hafferl (1933) in the Bolk Handbook, while O'Donoghue (1920) has described the condition in *Sphenodon*.

The arterial supply of the snout is derived from three main vessels which all stem ultimately from the internal carotid: the supraorbital, infraorbital and palatine arteries.

The supraorbital artery in *Varanus* seems to be smaller than in *Sphenodon*. It arises from the temporal artery behind the orbit and passes forwards above the eye, lying at first lateral to the taenia marginalis and then running downwards and medially on the lateral aspect of the downgrowth from the frontal bone. It enters

the snout through the orbitonasal fissure in proximity to the ethmoidal nerve, and becomes the ethmoidal artery (Text-fig. 5 F). The artery then breaks up into a large number of dorsal and ventral branches behind the postnasal wall which run forwards to supply the nasal sac and the spongy tissue around the anterior chamber. One large ventral branch runs downwards and laterally to anastomose with the palatine

Text-fig. 11. A. *Xenopeltis unicolor*, subadult. Transverse section through orbital region at level indicated in Text-figs. 10, 13, showing ductus nasopharyngeus. B. *Tarentola mauretanica*, adult. Transverse section of snout through posterior part of Jacobson's organ at level indicated in Text-figs. 1 F, 2 B, showing paleochoanate type of palate. C. *Tupinambis teguixin*, subadult. Transverse section through snout behind Jacobson's organ at level indicated in Text-fig. 2 C, showing incomplete neochoanate type of palate. D. *Varanus salvator*, subadult. Transverse section through snout at level corresponding with that shown in Text-fig. 4 J of *V. monitor*. The lateral recess is not closed off in *V. salvator*, and *l.d.*1 is not seen at this level. Plane of Text-fig. 10 A shown. (A, × 13·5; B, × 18; C, × 7; D, × 9.)

and maxillary arteries (Text-fig. 5 E, F). Some of the dorsal branches appear to supply the tips of the olfactory bulbs as well as the olfactory nerves. A large branch on each side passes forwards to enter the septomaxillary canal with the medial ethmoidal nerve, and is distributed with it (Text-fig. 4 F).

The infraorbital artery also arises from the temporal artery and runs forwards on the ventrolateral aspect of the orbit, near the infraorbital (maxillary) nerve. At the front of the orbit it receives anastomotic connexions from the palatine and ethmoidal arteries and enters the maxillary canal with the maxillary nerve, being distributed

with it to the teeth, jaws, palate and sides of the snout and, through its dorsal branch, to the spongy tissue around the anterior chamber of the nasal sac.

The palatine artery arises directly from the internal carotid and passes along the roof of the mouth near the palatine nerve. In the snout it sends numerous branches to supply the palatine glands and epithelium. A large branch on each side runs forwards to enter the vomerine canal with the palatine nerve. This sends many large branches to supply the organ of Jacobson and vomeronasal fibre bundles (Text-fig. 4G, etc.).

The complicated system of venous sinuses in the saurian head has been thoroughly described by Bruner (1907) in *Lacerta agilis* and other forms: it was not possible to make any critical investigation of these structures in my own material. Bruner's observations show that almost all the venous drainage of the snout passes through an extensive series of nasal and palatine veins into the large orbital sinus (Text-fig. 5F), and ultimately into the internal jugular veins.

COMPARISON WITH OTHER LIZARDS

A detailed survey of the saurian snout and the extensive literature concerned with it is beyond the scope of this account; it is only possible, therefore, to touch on those features which seem relevant to the affinities of *Varanus*, or appear of general morphological interest.

The curiously incomplete condition of the dermal skeleton of the varanid snout does not seem to occur in other living lizards. In most forms the fenestra exonarina anterior is relatively small, and is bounded medially and in front by the premaxilla, and laterally by the maxilla which conceals the septomaxilla almost entirely. Such a condition is present in the gecko *Tarentola mauretanica* (Text-fig. 1F). In *Varanus* the maxilla does not conceal the septomaxilla in this way and the greater part of the latter bone is exposed in the huge fenestra exonarina when the nasal capsule has been removed (Text-fig. 1A). The only forms which seem to approach the varanids in this respect are the Cretaceous mosasaurs. This region has been clearly described and figured by Camp (1940) in *Kolposaurus*, where the long slender premaxillary bar and the exposed septomaxillae are highly reminiscent of the varanid condition. The septomaxilla is, however, narrower and more elongated in the mosasaur, and it may be supposed that the bony chamber for Jacobson's organ was less spacious in the sea lizard than in *Varanus*.

The palate of *Varanus* is remarkable for the completeness of both its bony and superficial components. In an extensive study of the bony palate of Sauria, Lakjer (1927) has shown that three main varieties may be distinguished. In the first type the palate is only complete as far back as the anterior margin of the fenestra vomeronasalis externa which is confluent with the fenestra exochoanalis. This type (called by Lakjer paleochoanate) is present in forms such as agamids, iguanids and geckos (e.g. *Tarentola*, Text-figs. 2B, 11B). It is regarded as the most primitive variety of saurian palate, and approximates to the condition in *Sphenodon* and the early eosuchian reptiles. An advance on this type of palate is shown by the incomplete neochoanate condition which occurs in forms such as skinks, lacertids and teiids (e.g. *Tupinambis*, Text-figs. 2C, 11C). Here the fenestra vomeronasalis externa is partly cut off from the fenestra exochoanalis by the palatal process of the

maxilla, which extends medially beneath the lateral margin of the vomer (Text-fig. 11 C). The final complete neochoanate condition is found only in the genus *Varanus*, where the palatal process of the maxilla is still more extensive, and actually contacts the vomer for a short distance behind the fenestra vomeronasalis, separating it from the fenestra exochoanalis (Text-figs. 2 A, 4 E–G).*

These variations correspond more or less closely with the condition of the superficial palate, which forms the subject of a most extensive German literature (see Barge, 1937, for review). In the paleochoanate and incomplete neochoanate forms the choanal tube is continuous anteriorly with a long choanal groove which passes upwards towards the nasal sac, separating the median vomerine part of the palate (vomerine cushion: see Text-fig. 11 B) from the lateral maxillary portion. In many forms the lachrymal duct discharges into the choanal groove, but in others, such as *Varanus* (Pl. 1 C) and *Tupinambis* (Pl. 1 B) it opens directly into the duct of Jacobson's organ. These relationships are to a large extent dependent upon the degree of fusion between the frontonasal and maxillary processes during ontogeny. It is hoped that some account of the embryological processes involved, together with the numerous variations in this region which occur throughout the Sauria, will be given in greater detail elsewhere.

Pratt (1948) has suggested that the presence of these choanal grooves provides a mechanism for the filling of Jacobson's organ, and that particles deposited in them by the tongue tips are carried forwards by ciliary action into the lumen of the organ. In *Varanus* these choanal grooves are relatively short, and do not extend forwards to reach the duct of Jacobson's organ. It is, therefore, assumed that the particles are inserted inside the orifice of the duct, or actually into the lumen of the organ. This mechanism, which probably also occurs in snakes where the anatomical relationships are very similar, is reputed to be more effective than the method which is dependent on the action of cilia in the choanal grooves. It may be noted that the long retractile tongue of *Varanus*, which has been regarded as suggesting affinities with snakes, is also present in the large American teiid *Tupinambis*. Although the bony palate of this form is incompletely neochoanate, the morphology of the superficial palate, with short choanal grooves and the lachrymal duct opening directly into the duct of the organ of Jacobson (Pl. 1 B) approaches the varanid condition. A rather similar state is also present in some of the Amphisbaenidae, a group of specialized burrowing reptiles usually classified with the Sauria.

The general appearance of the nasal capsule, with its elongated form, incomplete floor and (in *Varanus monitor*) enormous lateral recess bears a certain resemblance to the condition in *Eumeces quinquelineatus* as described by Rice (1920), and perhaps also to that in certain agamids (e.g. *Agama atricollis*, Pratt, 1948). It would be rash, however, to suggest that these features have any great systematic value in view of the striking interspecific differences within the genus *Varanus*.

The long rostral process with its lateral wings extending forward of the nasal cupola, and the low anterior part of the nasal septum are unusual. The absence of

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* It may be noted that the small 'secondary palate' formed in this way differs from the condition in crocodiles and in mammals. In these forms the secondary palate is derived entirely from the lateral bones (maxillae, palatines, etc.) which fuse in the midline, displacing the vomers upwards in relation to the nasal septum.

a discrete foramen apicale in *V. monitor* and the relationships of this foramen in *V. salvator* are also noteworthy.

Another feature of interest is the disposition of the paraseptal cartilage and the way in which the ectochoanal cartilage runs backwards and medially to extend beneath it. In many lizards (e.g. *Lacerta agilis*, Gaupp, 1900; *Eumeces quinquelineatus*, Rice, 1920) the ectochoanal cartilage projects backwards and outwards. Its inward direction in *Varanus* almost encloses the fenestra vomeronasalis interna, separating it from the fenestra endochoanalis in the same way as the vomeromaxillary contact separates the fenestra vomeronasalis externa from the fenestra exochoanalis.

The significance of the fragmentation of the paraseptal cartilage into a network surrounding the vomeronasal nerves is obscure. This feature was present in all the three species of *Varanus* studied, and also occurs in the genus *Gerrhosaurus* (Malan, 1941), in *Tupinambis teguixin*, and, to a lesser extent, in *Lacerta vivipara*.
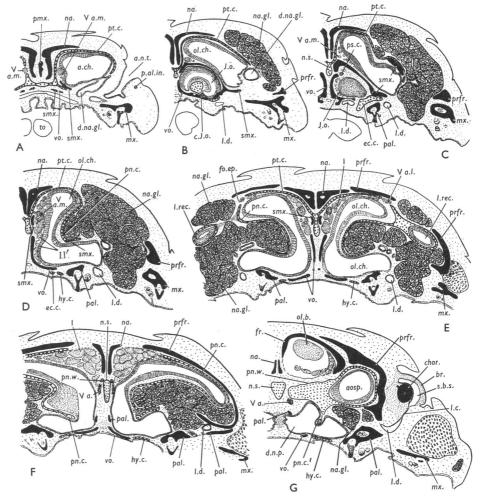
COMPARISON WITH SNAKES

The Sunbeam snake, *Xenopeltis unicolor* Reinwardt (fam. Xenopeltidae), has been selected for comparison with *Varanus*. Two series of sections through the nasal region of this primitive and comparatively generalized ophidian have been available for study; for the specimens from which these have been prepared I am indebted to Dr Malcolm Smith, and to Mr M. W. F. Tweedie of the Raffles Museum, Singapore.

The snout of *Xenopeltis* is shorter and wider than is the case with most lizards, and contrasts particularly with the elongated snout of *Varanus*. The dorsal surface of the skull (Text-fig. 1B) shows a large fenestra exonarina anterior in which the septomaxilla is widely exposed. The relationships of the bones are so different from those in *Varanus*, however, that the latter feature can hardly be regarded as suggesting affinity between the two forms.

The bony palate of *Xenopeltis* (Text-fig. 13) differs even more strikingly from the saurian condition. The premaxillae form a rounded arcade which is in contact with the anterior tip of the maxilla on each side. This condition is found only among the most primitive snakes, and in more advanced forms such as the colubrids and vipers the premaxillae are much reduced and are not in contact with the maxillae. In all non-viperine snakes* the lateral extent of the maxilla is reduced and the bone has the form of a narrow rod which is separated from the vomer and palatine medially by a considerable gap in which the septomaxilla is widely exposed. The fenestra vomeronasalis externa lies between the septomaxilla laterally and the vomer medially, instead of between the maxilla and the vomer, as in *Varanus* and other lizards. A peculiar feature in *Xenopeltis* is the presence of a long slender process which runs forward from the main part of the palatine bone and lies above the vomer in the medial wall of the ductus nasopharyngeus (Text-figs. 11A, 12F, G and 13). The position of the fenestra exochoanalis in *Xenopeltis*, as in snakes generally, is very different from that in Sauria. In the latter the fenestra occupies a large part of the bony palate and is situated between the maxilla and the vomer, with the palatine behind (Text-fig. 2A, B, C). In snakes the fenestra is directed backwards from above the posterior part of the vomer (Text-fig. 11A) and is hardly visible from the ventral

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* In the vipers the maxilla is short and highly specialized in association with the mechanism of fang erection.

aspect. The fenestra vomeronasalis externa is therefore separated by the greater part of the length of the vomer from the fenestra exochoanalis. An extensive bony 'secondary palate' is therefore present, but this lies only beneath the medial part of the nasal sac which extends laterally across the gap between the vomer and the palatine.
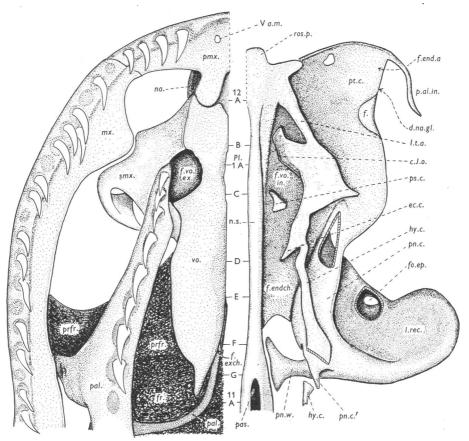
Text-fig. 12. *Xenopeltis unicolor*, subadult. Transverse sections through snout at levels shown in Text-figs. 10 E and 13. (× 15.)

The appearance of the nasal sac in *Xenopeltis* with its short anterior nasal tube and poorly differentiated lateral recess is shown in Text-fig. 10 E. As in all snakes the choanal tube is drawn out into an elongated ductus nasopharyngeus which lies dorsal to the posterior part of the vomer (Text-fig. 11 A). A ductus nasopharyngeus is also present in many skinks and certain other lizards, but here the bony relationships are very different (see Lakjer, 1927; Barge, 1937).

The most striking similarity between *Varanus* and the snakes is shown by the

condition of Jacobson's organ, by the relationship of its duct to the lachrymal system, by the morphology of the superficial palate, and by the presence of a slender bifid tongue. These structures, together with the eye glands which provide the secretion in which the odorous particles deposited by the tongue tips are carried through Jacobson's organ, constitute a functional 'vomeronasal unit' which seems to have reached its greatest development among Squamata in the varanid lizards and the snakes. In the latter a single lachrymal duct only is present. It will be seen, however

Text-fig. 13. *Xenopeltis unicolor*, subadult. Reconstruction of chondrocranium (right) and bones of snout (left) seen from below. (Bones drawn from dried skull.) Levels of section in Text-figs. 11 and 12 are shown. Windows have been cut in the paranasal cartilage and lateral recess capsule and a segment of the hypochoanal cartilage has been removed. (× 25.)

(Text-fig. 10E), that the relationships of the anterior part of this structure, with its dilated angular portion behind the organ of Jacobson, and its direct opening into the duct of the latter organ, are essentially similar to those of the long lachrymal duct 2 of *Varanus*. The posterior (orbital) end of the lachrymal duct system is markedly different in *Varanus* and *Xenopeltis*, however, conditions in the former following the usual saurian pattern with the lachrymal puncta arising from the conjunctival space on the deep aspect of the lower eyelid (see Bellairs & Boyd, 1947).

The nasal capsule of *Xenopeltis* differs little from that of more advanced and 'typical' snakes such as *Natrix* (*Tropidonotus*) *natrix* (Bäckström, 1931). Characteristic ophidian features are the high anterior cupolae joined by a flattened rostral process which runs back into the low nasal septum, the long processus alaris inferior and the extensive conchal infolding which is exposed from below by the almost complete absence of the true capsule floor. The ectochoanal cartilage is connected with a long hypochoanal cartilage which runs back to support the ductus nasopharyngeus. As in snakes generally, the sphenethmoid commissures are absent.

Perhaps the only feature in the nasal capsule of *Xenopeltis* which can be regarded as primitive is the presence of a small nodule of cartilage on each side of the nasal septum behind the fenestra vomeronasalis interna (Text-figs. 12 C, 13). From its position and relationship to the vomeronasal nerves, this nodule appears to represent a rudiment of the paraseptal cartilage of lizards. No similar structure has been reported in other snakes, nor have I found anything resembling it in sections of other forms usually regarded as primitive (e.g. *Cylindrophis*, *Eryx*, *Constrictor*).

DISCUSSION

In assessing the affinities of any form it is always a matter of difficulty to distinguish between those resemblances with other types which are indicative of true phylogenetic relationship, and those which result from parallel evolution. This is particularly the case with a group like the Squamata, where extensive parallel evolution has occurred in association with a host of divergent specialized trends. It is, therefore, unwise to attempt even a provisional assessment of the relationships of *Varanus* without some consideration of a wider range of characters than has been described in this account.

The striking differences between the snout of *Varanus* and that of other lizards can be matched with certain peculiarities shown by other regions of the body. The presence of cartilage canals in the epiphyses of the long bones, a feature unique among reptiles (Haines, 1941), together with other characters listed by Camp (1923) are suggestive of a long evolutionary history distinct from other living saurian families. Relationship with the mosasaurs, however, is indicated by numerous features of cranial morphology (see Camp, 1940).

In spite of its peculiarities, the basic morphology of the varanid snout, as exemplified by such structures as the bony palate and nasal capsule, are essentially saurian rather than ophidian in nature. Apart from the slightly ophidian appearance of the anterior part of the nasal septum and its relationship with the nasal cupolae and site of exit of the ethmoidal nerves, the few absolutely characteristic features of the ophidian nasal capsule are not shown, or even approached, in *Varanus*. Such typical ophidian features are the long processus alaris inferior, the presence of the hypochoanal cartilage, and the absence (or marked reduction) of the paraseptal cartilage.

The undoubted resemblances between the varanid superficial palate and vomeronasal apparatus do not seem of great phylogenetic significance. The fact that these resemblances involve the soft parts only, and are superimposed upon skeletal structures of a very different type, is suggestive of parallel evolution associated with the development of a highly efficient vomeronasal sense. The similarity between the

vomeronasal organs and palate of *Varanus* and those of at least two very distinct squamate genera, *Amphisbaena* and *Tupinambis*, lends further support to this view.

An investigation of the endocranial brain-case in reptiles shows that one of the most clearly marked distinctions between the cranial anatomy of lizards and snakes lies in the disposition of the trabeculae in the orbital region, and in the presence or absence of sphenolateral cartilages. The varanid brain-case with its high interorbital septum and fenestrated sphenolateral is essentially similar to that of such generalized lizards as *Eumeces* and *Lacerta*, and is in striking contrast with the platytrabic condition of snakes where the sphenolateral cartilages are absent in the adult state. Other features of the varanid skull such as the presence of the lachrymal and jugal bones and the structure of the ear seem to show that, on grounds of cranial morphology at least, there is no reason to regard *Varanus* as having any specially close affinities with the snakes. Indeed, certain other saurian groups appear to show a closer resemblance to snakes in many important respects (see Bellairs, 1949).

On the classification devised by Camp (1923) the Varanidae appear as the closest living relatives of snakes, and this concept has been expressed more emphatically by Romer (1945), who writes that the snakes are 'obviously derived from varanid types'. Camp's original view seems to have been mainly based on the structure of the hemipenes and vertebrae, together with certain cranial features, which, as I hope to show elsewhere, are open to a different interpretation. I do not feel that this view has been adequately substantiated by the study of cranial morphology, which has so far failed to reveal any significant resemblances between *Varanus* and the snakes which cannot as readily be explained on grounds of parallel evolution. It is therefore suggested that further evidence is required before a specially close relationship between the Varanidae and the snakes can be established.

SUMMARY

1. The anatomy of the snout of *Varanus* is described, largely from serial sections of the species *monitor, salvator* and *niloticus*. The nasal capsule, nasal and vomeronasal organs, lachrymal apparatus and palate are described in some detail, and an account is also given of some features of the bony snout, and the distribution of the main nerves and arteries. The terminology devised by Jarvik (1942) for the different parts of the ethmoidal region of anamniotes has been applied and extended. The most important features shown by *Varanus* are listed below.

2. The nasal capsule is incompletely covered by dermal bones on the dorsal surface of the snout. The fenestra exonarina anterior is very large, with the septomaxilla widely exposed in it. (Condition approached by mosasaurs.)

3. The nasal capsule is elongated with an unfenestrated roof. The nasal septum ends anteriorly in a flattened rostral process which extends forwards in front of the cupolae. The floor of the nasal capsule is largely incomplete and the zona annularis is absent. Paraseptal and ectochoanal cartilages are present and almost enclose the fenestra vomeronasalis interna. There is an extensive separate capsule for the lateral recess of the nasal sac in *V. monitor*. (This feature is present in some other lizards such as *Eumeces*, but is less well developed in *Varanus salvator* and *V. niloticus*.)

4. The anterior nasal tube is long and curved and the anterior chamber of the nasal sac is elongated. The olfactory chamber is limited in extent. The nasal concha

extends into the lateral recess in *V. monitor* only. The choanal opening is limited to the posterior part of the nasal sac, but is not drawn out to form a ductus naso-pharyngeus as in some lizards and all snakes.

5. The organ of Jacobson is very large and its duct opens into the mouth and receives the anterior orifice of lachrymal duct 2.

6. There are two separate lachrymal ducts on each side. Lachrymal duct 1 (arising from the superior punctum) is short and discharges into the olfactory chamber of the nasal sac after passing between the prefrontal and lachrymal bones. Lachrymal duct 2 is long and passes through a foramen in the lachrymal bone to discharge into the medial aspect of the duct of the organ of Jacobson. The relations of lachrymal duct 2 somewhat resemble those of the single lachrymal duct of snakes.

7. The bony palate is completely neochoanate, with the fenestra vomeronasalis externa separated from the fenestra exochoanalis by the vomeromaxillary contact. The superficial palate is remarkably complete, with short choanal grooves.

8. A brief description of some of the features of the snout of the primitive snake *Xenopeltis unicolor* is given. Except for the presence of a nodule interpreted as a rudimentary paraseptal cartilage, conditions are very similar to those in more advanced snakes such as *Natrix*. The most striking differences from the saurian condition are shown by the morphology of the bony snout, especially the palate, and by certain features of the nasal capsule.

9. A comparison between *Varanus* and other lizards suggests that its isolated systematic position within the suborder Sauria is fully in accord with the findings described.

10. A comparison with snakes shows that, in spite of its peculiarities, the genus *Varanus* conforms in all essential respects to the saurian rather than to the ophidian pattern. On the evidence cited in this paper, and on a consideration of certain other cranial features, it is suggested that a close relationship between the Varanidae and the Serpentes cannot yet be regarded as firmly established.

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REFERENCES

ADAMS, W. E. (1942). Observations on the lacertilian sympathetic system. *J. Anat., Lond.*, 77, 6–11.

BÄCKSTRÖM, K. (1931). Rekonstruktionsbilder zur Ontogenie des Kopfskeletts von *Tropidonotus natrix*. *Acta Zool., Stockh.*, 12, 83–144.

BAHL, K. N. (1937). Skull of *Varanus monitor* (Linn). *Rec. Indian Mus.* 39, 133–174.

BARGE, J. A. J. (1937). Mundhöhlendach und Gaumen. In *Handbuch der Vergleichenden Anatomie der Wirbeltiere* (ed. L. Bolk), 3. Berlin und Wien: Urban und Schwarzenberg.

BEECKER, A. (1903). Vergleichende Stilistik der Nasenregion bei den Sauriern, Vögeln und Säugetieren. *Morph. Jb.* 31, 565–619.

BELLAIRS, A. D'A. (1949). The anterior brain-case and interorbital septum of Sauropsida. *J. linn. Soc.* (*Zool.*). In the Press.

BELLAIRS, A. D'A. & BOYD, J. D. (1947). The lachrymal apparatus in lizards and snakes. I. The brille, the orbital glands, lachrymal canaliculi and origin of the lachrymal duct. *Proc. zool. Soc. Lond.* 117, 81–108.

BORN, G. (1879). Die Nasenhöhlen und der Thränennasengang der amnioten Wirbelthiere. *Morph. Jb.* 5, 62–140.

BRUNER, H. L. (1907). On the cephalic veins and sinuses of reptiles, with a description of a mechanism for raising the venous blood-pressure in the head. *Amer. J. Anat.* 7, 1–118.

CAMP, C. L. (1923). Classification of the Lizards. *Bull. Amer. Mus. nat. Hist.* **48**, 289–482.

CAMP, C. L. (1940). California mosasaurs. *Mem. Univ. Calif.* **13**, 1–68.

CORTI, A. (1847). *De systemate vasorum Psammosauri grisei.* Vindobonae.

COWLES, R. B. (1930). The life history of *Varanus niloticus* (Linnaeus). *J. Ent. Zool.* **22**, 3–31.

DE BEER, G. R. (1937). *The Development of the Vertebrate Skull.* Oxford University Press.

FAHRENHOLZ, C. (1937). Drüsen der Mundhöhle. In *Handbuch der Vergleichenden Anatomie der Wirbeltiere* (ed. L. Bolk), **3**. Berlin und Wien: Urban und Schwarzenberg.

FISCHER, J. G. (1852). Die Gehirnnerven der Saurier anatomisch untersucht. *Abh. Naturw. Hamburg,* **2**, 109–212.

GAUPP, E. (1888). Anatomische Untersuchungen über die Nervenversorgung der Mund- und Nasenhöhlendrüsen der Wirbelthiere. *Morph. Jb.* **14**, 436–489.

GAUPP, E. (1900). Das Chondrocranium von *Lacerta agilis.* Ein Beitrag zum Verständnis des Amniotenschädels. *Arb. anat. Inst., Wiesbaden (Anat. Hefte),* **15**, 435–592.

HAFFERL, A. (1933). Das Arteriensystem. In *Handbuch der Vergleichenden Anatomie der Wirbeltiere* (ed. L. Bolk), **6**. Berlin und Wien: Urban und Schwarzenberg.

HAINES, R. W. (1941). Epiphyseal structure in lizards and marsupials. *J. Anat., Lond.,* **75**, 282–294.

HALLER VOM HALLERSTEIN, V. (1937). Zerebrospinales Nervensystem (Zentralnervensystem). In *Handbuch der Vergleichenden Anatomie der Wirbeltiere* (ed. L. Bolk), **2**. Berlin und Wien: Urban und Schwarzenberg.

JARVIK, E. (1942). On the Structure of the Snout of Crossopterygians and Lower Gnathostomes in General. *Zool. Bidr. Upsala,* **21**, 235–675.

KESTEVEN, H. L. (1940). The osteogenesis of the base of the Saurian cranium and a search for the parasphenoid bone. *Proc. Linn. Soc. N.S.W.* **66**, 447–467.

LAKJER, T. (1927). Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und primitiven Sauropsiden. *Zool. Jb.* (Anat. Abt.), **49**, 57–356.

MALAN, M. E. (1941). The cranial anatomy of the genus *Gerrhosaurus.* *S. Afr. J. Sci.* **37**, 192–217.

MERTENS, R. (1942). Die Familie der Warane (Varanidae). *Abh. senckenb. naturf. Ges.* **462**, 1–116; **465**, 117–234.

NOBLE, G. K. & KUMPF, K. F. (1936). The function of Jacobson's Organ in Lizards. *J. gen. Psychol.* **48**, 371–382.

O'DONOGHUE, C. H. (1920). The blood vascular system of the Tuatera, *Sphenodon punctatus.* *Philos. Trans.* B, **210**, 175–252.

PEYER, B. (1937). Zähne und Gebiss. In *Handbuch der Vergleichenden Anatomie der Wirbeltiere* (ed. L. Bolk), **3**. Berlin und Wien: Urban und Schwarzenberg.

PRATT, C. W. M. (1948). The morphology of the ethmoidal region of *Sphenodon* and lizards. *Proc. zool. Soc. Lond.* **118**, 171–201.

RICE, E. L. (1920). The development of the skull in the skink, *Eumeces quinquelineatus.* *J. Morph.* **34**, 120–216.

ROMER, A. S. (1945). *Vertebrate Paleontology.* University of Chicago Press.

WATKINSON, G. B. (1906). The cranial nerves of *Varanus bivittatus.* *Morph. Jb.* **35**, 450–472.

WEGNER, R. N. (1922). Der Stützknochen, Os nariale, in der Nasenhöhle bei den Gürteltieren, Dasypodidae, und seine homologen Gebilde bei Amphibien, Reptilien und Monotremen. *Morph. Jb.* **51**, 413–492.

WILLARD, W. A. (1915). The cranial nerves of *Anolis carolinensis.* *Bull. Mus. comp. Zool. Harv.* **59**, 17–116.

WILLISTON, S. W. (1925). *The Osteology of the Reptiles.* Harvard University Press.
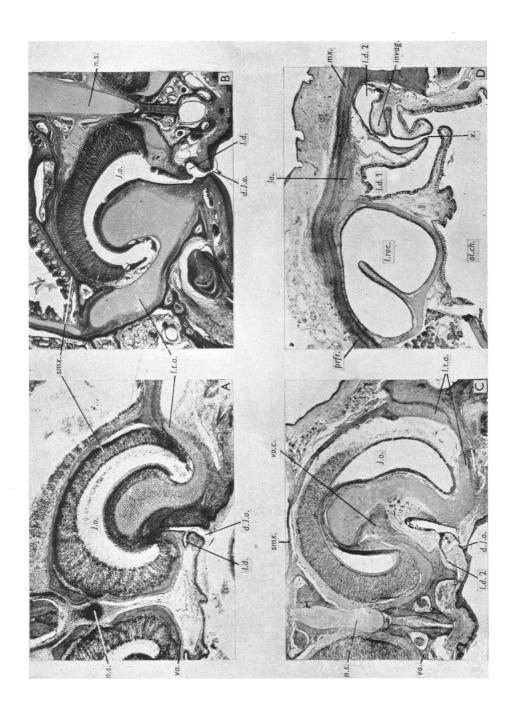
Abbreviations to Text-figures and Plate

a.ch.	anterior chamber of nasal sac.	*ch.*	choanal tube.
ad.co.	aditus conchae.	*ch.g.*	choanal groove.
add.m.	adductor mandibulae muscle.	*chor.*	choroid.
a.e.n.	anterior external nostril.	*c.J.o.*	cartilage of Jacobson's organ.
a.n.t.	anterior nasal tube.	*c.l.rec.*	capsule of lateral recess.
aosp.	antorbital space of nasal sac.	*co.*	nasal concha.
a.sp.	anterior space of nasal sac.	*co.mu.by.*	concavity for mushroom body.
br.	brille (spectacle).	*con.s.*	conjunctival space.
cart.	nodules of cartilage beneath anterior cupola.	*cor.*	cornea.
		co.z.	conchal zone of nasal sac.

cup.	anterior cupola.		*o.l.d.* 1, *o.l.d.* 2.	openings of lachrymal ducts 1 and 2.
d.c.z.	dorsal conchal zone.		*ol. ep.*	olfactory epithelium.
d.Hd.gl.	duct of Harderian gland.		*o.s.*	orbital sinus.
d.J.o.	duct of Jacobson's organ.		*pal.*	palatine.
d.na.gl.	duct of nasal gland.		*pal.a.*	palatine artery.
d.n.p.	ductus nasopharyngeus.		*p.al.in.*	processus alaris inferior.
ec.c.	ectochoanal cartilage.		*p.al.su.*	processus alaris superior.
ecpt.	ectopterygoid.		*pas.*	parasphenoid.
eth.a.	ethmoidal artery.		*p.gl.*	palatine gland.
eth.g.	ethmoidal ganglion.		*pmx.*	premaxilla.
f.	flange of cartilage.		*p.mx.a.*	processus maxillaris anterior.
f.end.a.	fenestra endonarina anterior.		*p.mx.p.*	processus maxillaris posterior.
f.endch.	fenestra endochoanalis.		*pmx.b.*	premaxillary bar.
f.ex.a.	fenestra exonarina anterior.		*pn.c.*	paranasal cartilage.
f.exch.	fenestra exochoanalis.		*pn.c.′*	separated part of *pn.c.*
f.l.	fenestra in nasal septum.		*pn.w.*	postnasal wall (planum antorbitale).
f.olf.	fenestra olfactoria.		*p.pmx.*	palatal process of *pmx.*
fo.ap.	foramen apicale.		*prfr.*	prefrontal.
fo.ep.	foramen epiphaniale.		*ps.c.*	paraseptal cartilage.
fr.	frontal.		*ps.c.′*	fragmented part of *ps.c.*
f.vo.ex.	fenestra vomeronasalis externa.		*pt.*	pterygoid.
f.vo.in.	fenestra vomeronasalis interna.		*pt.c.*	parietotectal cartilage.
gl.	gland.		*r.na.c.*	roof of nasal capsule.
Hd.gl.	Harderian gland.		*re.ep.*	respiratory epithelium.
hy.c.	hypochoanal cartilage.		*ros.p.*	rostral process.
i.ch.	inner choana.		*s.b.s.*	sub-brillar space (closed conjunctival space).
invag.	invagination of wall of lachrymal duct 2 in *Varanus.*		*smx.*	septomaxilla.
i.ob.	inferior oblique muscle.		*so.*	supraorbital.
i.o.s.	interorbital septum.		*sph.c.*	sphenethmoid commissure.
J.o.	Jacobson's organ.		*s.t.*	spongy tissue round anterior chamber of nasal sac.
ju.	jugal.			
la.	lachrymal.		*t.*	tooth and dental lamina.
l.c.	lachrymal canaliculus.		*to.*	tongue.
l.d.	lachrymal duct.		*tr.*	trabecula communis.
l.d. 1, *l.d.* 2.	lachrymal ducts 1 and 2 in *Varanus.*		*v.co., vo.c.*	vomerine concha.
l.p. 1, *l.p.* 2.	lachrymal puncta 1 and 2.		*v.c.z.*	ventral conchal zone of nasal sac.
l.rec.	lateral recess of nasal sac.		*vo.*	vomer.
l.t.a.	lamina transversalis anterior.		*vo.cu.*	vomerine cushion.
l.t.a.′	free posterior end of *l.t.a.*		*vo.gl.*	vomerine gland.
mu.by.	mushroom body.		*vo.pmx.*	vomerine process of *pmx.*
mx.	maxilla.		*x.*	connexion between *l.d.* 2 and cavity of nasal sac in *Varanus.*
mx.′	palatal process of *mx.*			
mx.a.	maxillary artery.		I.	olfactory nerve.
na.	nasal.		I′.	vomeronasal nerve.
na.gl.	nasal gland.		V *a.*	ophthalmic and ethmoidal nerve.
n.s.	nasal septum.		V *a.m.*	medial ethmoidal branch of V *a.*
o.ch.	outer choana.		V *a.l.*	lateral ethmoidal branch of V *a.*
o.d.J.o.	opening of duct of *J.o.*		V *b.*	maxillary nerve.
ol.b.	olfactory bulb.		VII *p.*	palatine branch of facial nerve.
ol.ch.	olfactory chamber of nasal sac.			

EXPLANATION OF PLATE

A. *Xenopeltis unicolor*, subadult. Transverse section through right organ of Jacobson showing relationship of lachrymal duct to duct of Jacobson's organ. (*c.* × 260.) B. *Tupinambis teguixin*, subadult. Transverse section through left organ of Jacobson. (*c.* × 20.) C. *Varanus monitor*, subadult. Transverse section through right organ of Jacobson. The relationship of the lachrymal duct to Jacobson's organ is similar in A, B and C. (*c.* × 36.) D. *Varanus monitor*, subadult. Transverse section through side of snout showing ending of lachrymal duct 1, and connexion (*x*) between lachrymal duct 2, and cavity of nasal sac. (*c.* × 36.)