

# SKULL OF *VARANUS MONITOR* (LINN.).

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## 1. INTRODUCTION.

The skull of *Varanus* forms a very suitable type of the Lacertilian skull and has therefore been figured in several current books on the comparative anatomy of vertebrates. For example, Bütschli (3, p. 274) figures the ventral, lateral and posterior aspects of the skull of *Varanus salvator*, but his description deals only with some of the leading features of the skull of Lacertilia as a whole as compared with the skulls of other reptiles. Similarly, Shimkewitsch (8, p. 122) gives the dorsal and ventral views of the skull of *Varanus niloticus*, but his description is very brief and includes only a few of the important characters of the skull. Amongst English authors, Reynolds (7, pp. 195 and 290) figures the dorsal, ventral and lateral views and also a longitudinal section of the skull of *Varanus varius*, but he too does not describe this skull as such, although he gives adequate descriptions of the skull of a chelonian and that of a crocodilian. Similarly, Thomson (11, p. 695) gives a diagram of the roof of the skull of a Varanid from a specimen, but his diagram is incompletely and even wrongly labelled and his description

is equally incomplete. Boulenger (1, p. 160), in the first edition of the *Fauna of British India* (Reptiles and Amphibia), gave rough sketches of the skull of *Varanus griseus*, which have been reproduced unaltered by Malcolm Smith (10, p. 396) in the second edition. These sketches are hardly complete and at places give a misleading idea of the relationships of bones and cartilages. Lastly, Goodrich (5, pp. 343 and 344), in his masterly work on the structure and development of vertebrates, gives the diagrams of Reynolds, but his account of the lacertilian skull is necessarily comparative and is based chiefly on that of *Lacerta*.

In all the first five books<sup>1</sup>, the diagrams are original, i.e., they have been specially drawn for each of these books. There are no standard diagrams in any memoir, from which they could be taken. Unfortunately, therefore, the diagrams vary and all of them are incomplete in several respects and even incorrect in some cases. As all these diagrams have apparently been made from dried skulls, the omission of important cartilaginous and even small bony parts of the complete skull is a specially weak feature of these diagrams. Further, no attention altogether has been paid to the large number of foramina through which the blood vessels and nerves pass.

In almost all the Indian Universities, *Varanus* is studied as a type of the Lacertilia; even where smaller types like *Calotes*, *Uromastix* or *Mabuia* are used for dissection, the skeleton studied is always that of *Varanus*. I began this work originally to identify the large number of foramina in the skull, but when I found that there was no satisfactory account of the skull, I decided to describe the complete skull, as I felt, firstly, that a description of the foramina alone would not be so useful as that of the whole skull, and, secondly, that I could correct and improve upon the diagrams which are extant in the commonly used text-books.

I have selected *Varanus monitor* (syn. *Varanus bengalensis*) as the type, as this species is the commonest and most extensively distributed throughout India, Ceylon, Assam and the greater part of Burma (10). In size it is the second largest species, the head and body being 750 mm. and the tail 1000 mm. The largest species is *Varanus salvator* (head and body 1000 mm. and tail 1500 mm.), but it is not found in the peninsula of India except in the extreme north-east, Eastern Bengal and the Eastern Himalayas (10). As the work involved a number of dissections and preparations displaying blood vessels and nerves, I have included a number of diagrams showing the relations of the bones with these structures in the hope that they would prove useful. Further, wherever possible, comparisons have been made with the skulls of *Sphenodon*, *Lacerta* and *Uromastix*.

I am indebted to Professor E. S. Goodrich of Oxford for kindly lending me Siebenrock's valuable paper on the skull of *Lacerta* from his private library. My best thanks are due to Mr. M. L. Bhatia who has rendered valuable assistance in the preparation of illustrations. Prof. A. H. Siddiqui has very kindly helped me in the dissections of some of the muscles.

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<sup>1</sup> I have not attempted to make an exhaustive search of all the books dealing with skull of *Varanus*, but have quoted these six only as representative examples.

## 2. THE SKULL.

## I.—General characteristics.

The skull of *Varanus monitor* is pyramidal in shape, each of the dorsal, ventral and lateral surfaces being more or less triangular in outline; the posterior surface is also more or less triangular and forms, so to speak, the base of the pyramid, the apex being formed by the anterior pointed snout (united premaxillae). The skull is well ossified, although there are several tracts of cartilage even in the adult. It is a strong, compactly built structure, very well buttressed along its posterior and lateral aspects. The sutures between different bones remain clearly visible even in the adult, unlike these in *Lacerta* where they become obliterated in the adult skull.

The *cranium* or brain-box forms the axial part of the posterior two-thirds of the skull and is disposed, like the enclosed brain, in an obliquely elongated direction, higher in front and lower behind. The posterior part of the cranium enclosing the mid-brain and the hind-brain is more or less completely ossified but the anterior part surrounding the cerebral hemispheres and the diencephalon is ossified only dorsally, remaining partly membranous and partly cartilaginous along the greater part of its ventral and lateral aspects. At the extreme anterior end, however, the olfactory stalks are again enclosed completely in a bony tube. The *auditory capsules* are completely ossified and are intimately united with the occipital region of the cranium. The *orbits* are large and are well protected by bones; they are separated from each other by an extensive *inter-orbital septum*, which is largely cartilaginous but partly membranous. This septum lies beneath the anterior part of the cranial cavity all along its length and even extends forwards as the *internasal septum*. The *olfactory capsules* are also large and lie immediately in front of the cranial cavity; they are partially surrounded by bones latero-posteriorly but are mainly enclosed in large cartilaginous capsules along the greater part of their extent. The united pre-maxillae form the rostrum.

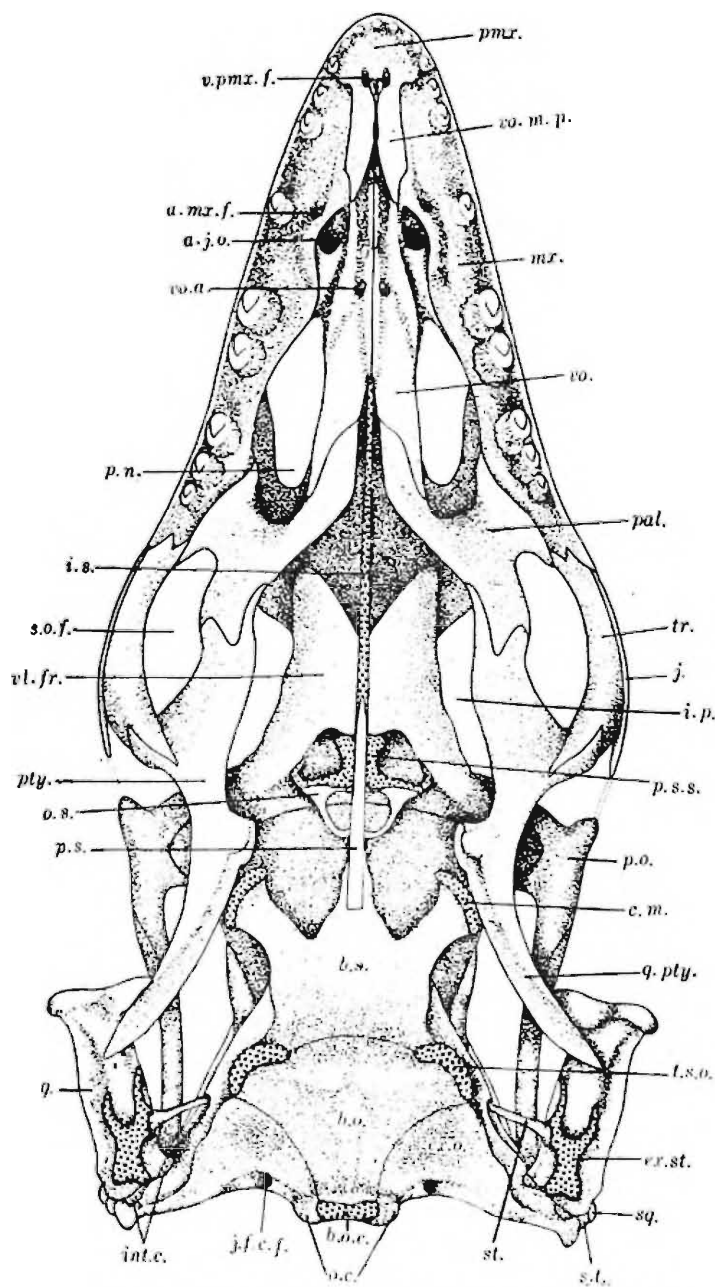
## II.—The Cranium.

(a) *The Occipital Region.*

The *occipital region* is almost completely ossified and lies dorsally at a lower level than the parietal and frontal regions in front. It consists of four bones, (a) the basi-occipital, (b) the paired ex-occipitals, and (c) the supra-occipital, all of which remain distinct and take part in surrounding the foramen magnum. The single median *occipital condyle* (figs. 1, 6) is crescentic in outline and is distinctly tripartite, the median piece being formed by the posterior end of the basi-occipital and the two lateral pieces by the posterior ends of the two ex-occipitals. The median basi-occipital piece of the condyle (*pars condyloidea*) is the smallest and is covered over by a thin, scale-like, elliptical piece of calcified cartilage which has a smooth surface and a milk-white appearance. The only other cartilage present in this region is the *cone-shaped cartilage* (*processus ascendens*) at the anterior border of the supra-occipital (*vide infra*). All

the four bones of the occipital region are ossifications of the chondrocranium (replacing bones).

The median *basi-occipital* (fig. 1) forms a more or less triangular flat plate, broad in front but narrow and pointed behind. Its anterior border,



TEXT-FIG. 1. A ventral view of the skull of *Varanus monitor* ( $\times ca. 2$ ).

*a.j.o.*, aperture for the Jacobson's organ; *a.mx.f.*, anterior maxillary foramen; *b.o.*, basi-occipital; *b.o.c.*, basi-occipital cartilage; *b.s.*, basisphenoid; *c.m.*, cartilaginous meniscus at the end of the basiptyergoid process of the basisphenoid; *ex.o.*, ex-occipital; *ex.st.*, extra-stapes (proportionately much enlarged); *int.c.*, intercalary cartilage; *i.p.*, incisura piriformis (interptyergoid fissure); *i.s.*, ventral border of the interorbital septum; *j.*, jugal; *j.f.c.f.*, combined jugular and condylar foramen; *mx.*, maxilla; *o.c.*, occipital condyle; *o.s.*, orbitosphenoid; *pal.*, palatine; *pmx.*, premaxilla; *p.n.*, position of the posterior nares; *p.o.*, postorbital; *p.s.*, parasphenoid; *p.s.s.*, septum (planum) supra-septale; *pty.*, pterygoid; *q.*, quadrate; *q.pty.*, quadrate process of the pterygoid; *s.o.f.*, sub-orbital fossa; *sq.*, posterior end of squamosal; *s.t.*, posterior end of supra-temporal; *st.*, stapes; *tr.*, transverse; *t.s.o.*, tuberculum spheno-occipitale; *vl.fr.*, ventro-lateral process of the frontal; *vo.*, vomer; *vo.a.*, vomerine aperture; *vo.m.p.*, vomero-maxillary process of the premaxilla; *v.pmx.f.*, ventral premaxillary foramen. Cartilages are shown with uniformly thick dots.

forming the base of the triangle, is crescentic in outline, being convex from side to side, and fits against the basisphenoid in front and the pro-otic on each side; the two lateral borders forming the two sides of the triangle are concave in outline and fit against the ex-occipital of each side; the posterior end of the bone corresponding to the apex of the triangle forms the median piece of the occipital condyle and also a very small part of the ventral boundary of the foramen magnum. The dorsal surface of the basi-occipital is depressed to form an oval area for the accommodation of the ventral surface of the medulla oblongata; in fact, the bone in this oval area is thin and appears translucent against transmitted light, the remaining portion of the bone being thick and opaque. On each of the two antero-lateral borders of the basi-occipital, between it and the pro-otic, there is a kidney-shaped cartilaginous tuberosity wedged in between these bones on each side: this is called the *tuberculum spheno-occipitale* (figs. 1 and 13). On this are inserted, on each side, strong tendons of two muscles, (1) the *musculus longus colli* and (2) the *musculus transversalis cervicis*<sup>1</sup>.

The paired *ex-occipitals* (figs. 1, 2 and 3) of the adult are irregularly shaped bones, each formed by a fusion of the ex-occipital proper with the opisthotic of its own side; each is, therefore, a compound bone, and, since it forms not only the side-wall of the cranial cavity but also a part of the auditory capsule and a prominent lateral process, the *paroccipital process*, it has been named by different workers as *pleuro-occipital*, *lateral occipital* or *oto-occipital*.

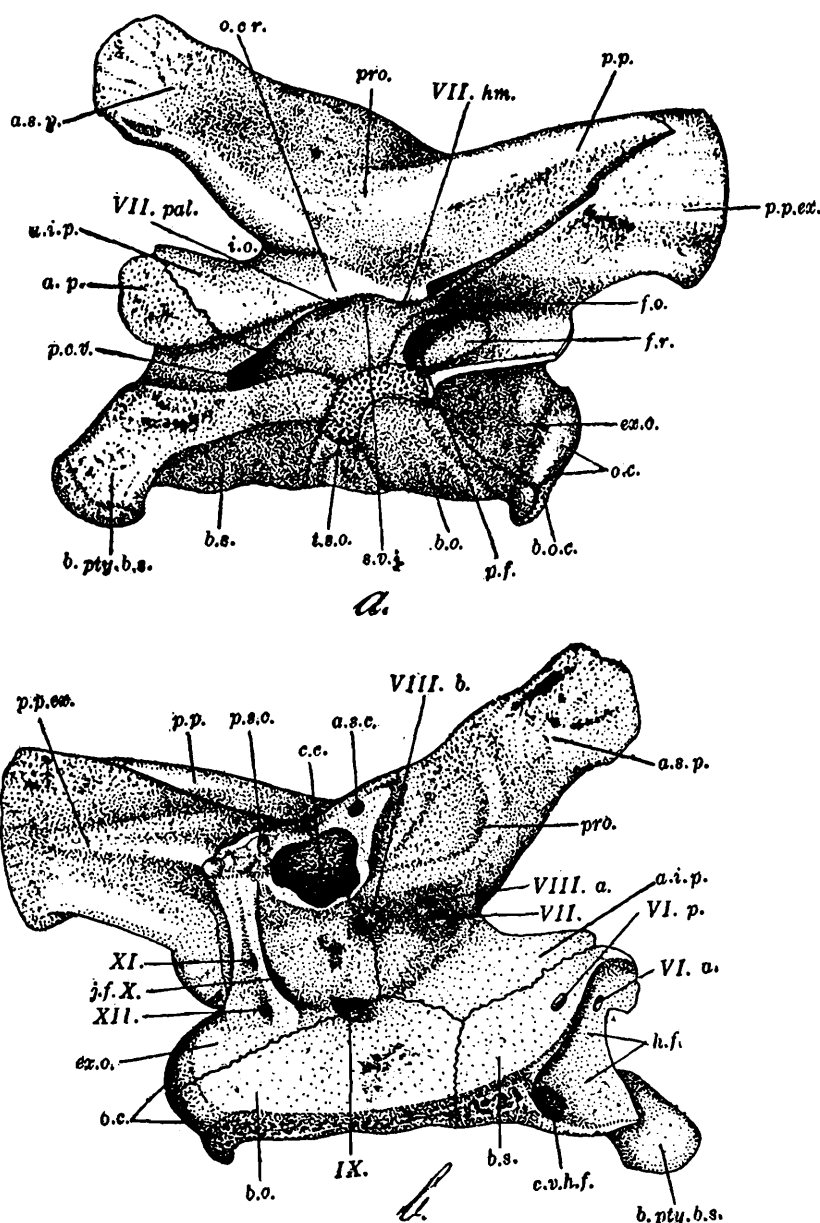
The ex-occipital proper is the small triangular plate lying ventrolaterally on each side of the basi-occipital (fig. 1), while the remaining larger part of the bone lying on the dorsal and outer side almost at a right angle to the ex-occipital proper represents the opisthotic. The ex-occipital part of the bone fits all along its inner border against the basi-occipital, while the opisthotic part fits anteriorly and externally against the pro-otic and dorsally against the posterior half of the supra-occipital. The ventral surface of the ex-occipital is depressed and forms the place of insertion of the *musculus rectus capitis inferior*. This muscle lies immediately above the *musculus longus colli* and arises from the hypophysial processes of the first four cervical vertebrae. The muscle-fibres are inserted directly on the ex-occipital without the formation of a tendon.

The boundary between the ex-occipital and opisthotic parts of the bone is clearly indicated on the *inner surface of the cranium* (seen in a

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<sup>1</sup> As the nomenclature of these two muscles is uncertain, I am giving here their origin, extent and insertion. The *musculus longus colli* of each side is an elongated elliptical muscle inserted by a distinct tendon on the inner part of the tuberculum spheno-occipitale. The bodies of the two muscles lie closely pressed together in the neck, one on each side of the mid-ventral line, immediately dorsal to the oesophagus and ventral to the cervical vertebrae. Their fibres originate from the hypophyses of the first seven vertebrae. The *musculus transversalis cervicis* is inserted by a distinct tendon on the outer part of the tuberculum, but this tendon continues on its outer side into an aponeurosis inserted on the entire outer border of the ventral part of the ex-occipital. The body of the muscle itself consists of two parts: (1) a short anterior part which originates from the second vertebra and a part of the third, and (2) a long posterior part which originates from a part of the third and the fourth and fifth vertebrae. The muscle is attached to the outer surface of each neural arch along the line joining the pre- and post-zygapophyses.

longitudinal section) by a large crescentic slit-like aperture, the *jugular foramen* or *foramen lacerum posterius* (fig. 2 b), which lies between



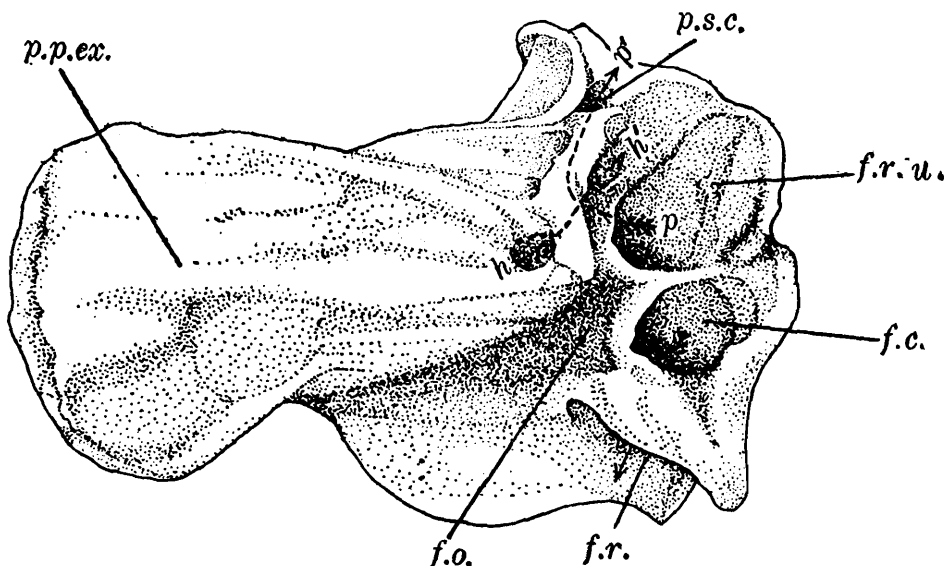
TEXT-FIG. 2. Two views of the basi- and ex-occipitals, the basisphenoid and the pro-otic. Cartilages are shown with uniformly thick dots ( $\times ca. 3$ ).

a. ventro-lateral view; b. in longitudinal section.

*a.i.p.*, anterior inferior process, *a.p.*, alar process; *a.s.c.*, channel for the anterior vertical semi-circular canal; *a.s.p.*, anterior superior process of the pro-otic; *b.o.*, basi-occipital; *b.o.c.*, basi-occipital cartilage; *b.s.*, basisphenoid; *b.pty.b.s.*, basi-ptyergoid process of the basisphenoid; *c.c.*, cavum capsularis in which is lodged the membranous labyrinth of the inner ear; *c.v.h.f.*, opening of the canalis vidianus into the hypophyseal fossa (foramen caroticum internum) through which the intra-cranial branch of the internal carotid enters the cranial cavity; *ex.o.*, ex-occipital; *f.o.*, fenestra ovalis, into which fits the inner end of the *columella auris*; *f.r.*, fenestra rotunda, which is covered over in life by the *membrana tympani scundaria* and through which the glossopharyngeal nerve leaves the skull; *h.f.*, hypophyseal fossa; *i.o.*, incisura otosphenoida for the Vth nerve; *j.f.x.*, jugular foramen for the exit of the jugular vein and the tenth cranial nerve; *o.c.*, occipital condyle; *o.cr.*, otosphenoidal crest; *p.c.v.*, posterior opening of the *canalis vidianus* through which the palatine branch of the facial nerve and the sympathetic and the internal carotid artery enter the basisphenoid bone; *p.f.*, perilymphatic foramen; *p.p.*, posterior process of the pro-otic; *p.p.ex.*, paroccipital process of the ex-occipital; *pro.*, pro-otic; *p.s.c.*, channel for the posterior vertical semi-circular canal; *s.v.f.*, sulcus venae jugularis; *t.s.o.*, tuberculum spheno-occipitale; *VI.a.*, anterior foramen for the exit of the sixth cranial nerve out of the basisphenoid; *VI.p.*, posterior foramen through which the VIth cranial nerve enters the basisphenoid bone; *VII.*, facial foramen through which the VIIth nerve leaves the cranial cavity; *VII.hm.*, posterior facial foramen for the exit of the hymomandibular division of the VIIth nerve; *VII.pal.*, anterior facial foramen through which the palatine branch of the VIIth nerve leaves the skull; *VIII.a.*, foramen acusticum anterius; *VIII.b.*, foramen acusticum posterius; *IX.*, foramen perilymphaticum or glossopharyngeal foramen; *XI.*, foramen for the exit of the spinal accessory nerve; *XII.*, foramen for the exit of the hypoglossal nerve.

the two parts of the bone in such a manner that the anterior wall of the foramen is formed by the opisthotic and its posterior wall by the ex-occipital. The jugular foramen transmits the vagus nerve (X), the *vena cerebialis posterior branch* of the internal jugular vein and the *occipital branch* of the occipito-vertebral artery. Immediately behind the jugular foramen lie two small rounded foramina (fig. 2 b), one above the other, on the inner surface of each ex-occipital: the lower of these two transmits the *hypoglossal nerve* (XII), while the upper lets through the *spinal accessory nerve* (XI). On piercing the cranial wall internally, these two foramina open into the large jugular foramen, so that on the outer surface of the cranium there is a single large oval foramen lying just outside the occipital condyle at the root of each paroccipital process. This is, therefore, the combined *foramen lacerum posterius (jugular foramen)* + the *condylar (hypoglossal) foramen* of the mammalian skull and also that of *Sphenodon* and lets through the internal jugular vein (*vena cerebialis posterior branch*) and the Xth, XIth and XIIth cranial nerves and lets in the *occipital branch* of the occipito-vertebral artery (figs. 1, 2 and 13).

The opisthotic part of the bone forms (1) the posterior part of the auditory capsule, and (2) a stout horizontal process, the *paroccipital process*, directed outwards and slightly backwards. This process on each side supports the supra-temporal above and the quadrate below. On the dorsal surface of the opisthotic part, at the root of the paroccipital process, there is a small foramen (figs. 2 b, 3 and 10) leading above and below into the passage for the *posterior vertical semi-circular canal* of the internal ear; while on the anterior vertical surface of the paroccipital process, at its root, lies the foramen leading behind and



TEXT-FIG. 3. Fronto-lateral view of the ex-occipital ( $\times ca. 7$ ).

*f.c.*, fenestra cochleae leading below into *f.r.*, the fenestra rotunda, the passage being shown by an arrow; *f.o.*, the posterior wall of fenestra ovalis; *f.r.u.*, recessus utriculi; *h-h'*, arrow passing through the channel for the horizontal semi-circular canal; *p-p'*, arrow passing through the channel for the posterior semi-circular canal; *p.p.ex.*, paroccipital process of the ex-occipital; *p.s.c.*, opening for the posterior semi-circular canal.

in front into the passage for the *horizontal semi-circular canal*. These two foramina can only be seen in the disarticulated bone (fig. 3);

in the complete skull the first foramen is covered over by the supra-occipital and the second by the pro-otic. The anterior end of each opisthotic is excavated to form a fossa which extends upwards into the supra-occipital, and is continuous with a similar fossa on the postero-internal surface of the pro-otic, the fossae on these three bones together forming the cavity (*cavum capsularis*) of the auditory capsule (figs. 5 and 10) in which is lodged the membranous labyrinth of the internal ear. These fossae also can be seen separately only in a disarticulated skull.

The fossa of the opisthotic part of the auditory capsule presents a central recess, a large foramen on the inner and ventral side and another small one on the outer and dorsal side (fig. 3). The central recess lodges the *recessus utriculi* and the *ampulla posterior* leading into the posterior semi-circular canal; the outer and dorsal foramen leads into the passage for the horizontal semi-circular canal, while the inner and ventral foramen (*fenestra cochleae* or *perilymphatica*) provides for the passage of the *aqueductus perilymphaticus* into the *recessus scalae tympani* of the *fenestra rotunda*<sup>1</sup>. The *fenestra rotunda* (fig. 2 a), is a large, more or less elliptical, opening with an arched roof, lying on the outer lateral surface of the skull, between the outer convex border of the ex-occipital below and the *fenestra ovalis* above. It is closed in life by a thick membrane, the *membrana tympani secundaria*, which is really the outer wall of the *saccus perilymphaticus*, lying in a short space within the *fenestra rotunda*. This space is called the *recessus scalae tympani* and opens above through the *fenestra cochleae* into the *cavum vestibulare* (inner middle region of *cavum capsularis*) and inwards through the *aqueductus perilymphaticus* passing through the *perilymphatic foramen* into the subarachnoid spaces beneath the brain in the cranial cavity. The *glossopharyngeal nerve* leaves the cranial cavity through the *foramen perilymphaticus* (fig. 2b), runs along the posterior wall of the *recessus scalae tympani* imbedded in the wall of the perilymphatic membrane and emerges out of the *fenestra rotunda* into the cavity of the middle ear. The greater part of the *fenestra rotunda* is formed by the ex-occipital, which forms a process resembling an arched bridge, only the antero-ventral end being formed by the *tuberculum sphenoccipitale* (fig. 2 a). Similarly, the posterior part of the *fenestra ovalis*, lying immediately above the *fenestra rotunda*, is formed by the opisthotic, being closed anteriorly by the pro-otic. It should be noted that both the *fenestra ovalis* and *fenestra rotunda* lie at the bottom of a shallow pit bounded ventrally by the free lateral border of the ex-occipital and dorsally by the pro-otic and the paroccipital process: this pit is the inner part of the middle ear, which has a wide communication with the pharynx below, and across which runs the *columella auris* from the *fenestra ovalis* to the tympanic membrane on the outside (figs. 1, 6 and 13).

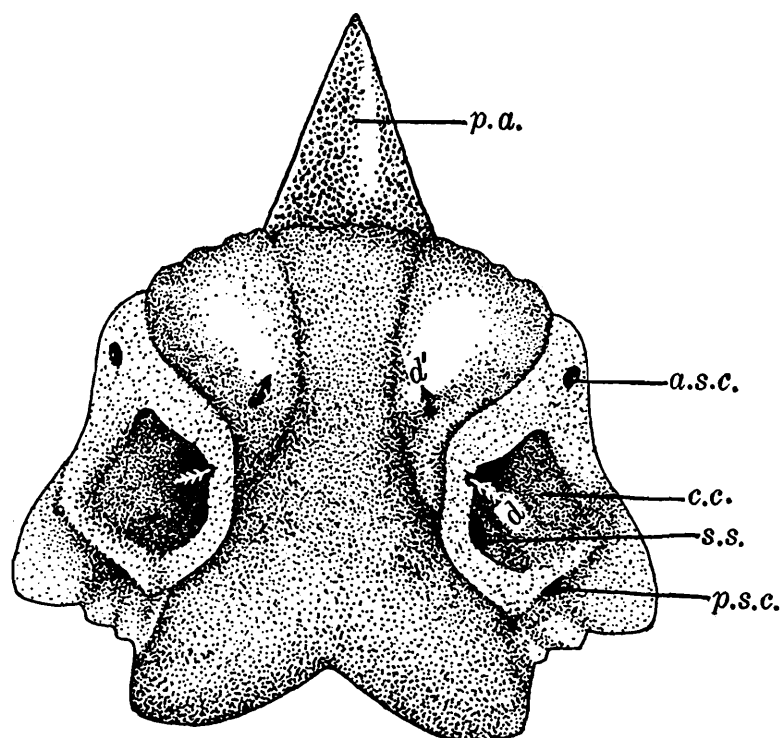
The median *supra-occipital* (figs. 3, 4, 5 and 6) forms the roof of the occipital segment and also that of the auditory capsule on each side. Dorsally, it lies at a lower level behind the parietals and slopes in an antero-posterior direction as well as laterally on each side. Looked

<sup>1</sup> In *Sphenodon*, as in the *Chelonia*, *Ophidia* and *Anser* (*Aves*), there is no *fenestra rotunda* and no *membrana tympani secundaria* either.





from the anterior border of the supra-occipital and fits closely into a deep funnel-shaped depression (*parietal fossa*) into the posterior border of the parietal in the median line (fig. 5). Bradley (2, p. 482) regards this cone-shaped cartilage as corresponding to the *processus ascendens tecti synotici* of the cartilaginous cranium. There is thus a "peg and socket" joint between the supra-occipital and the united parietals which would obviously allow only a limited range of movement between these two bones. This joint is an important feature of the Lacertilian skull and forms an essential factor in the *kinetism*<sup>1</sup> of the skull (*vide infra*). The two antero-lateral borders of the supra-occipital fit against the pro-otics on each side, the postero-lateral borders against the ex-occipitals, while the posterior border with the notch is free and forms the roof of the foramen magnum (fig. 6). Along its mid-dorsal line runs an inconspicuous *occipital ridge* or *crest* and the bone slopes down on each side of this crest to meet the ex-occipital behind and the pro-otic in front. The disarticulated supra-occipital resembles in shape the neural arch of a vertebra with thick lateral walls; its ventral aspect (fig. 5) gives the appearance of a deep gutter with thick and expanded but hollowed walls. Each of these thick walls forms the roof of the auditory capsule and is hollowed out into a central fossa which lodges the dorsal portion of the membranous labyrinth. Deep down on the inner wall of the fossa, there is a rounded aperture leading into a narrow tube which lodges the *sinus*

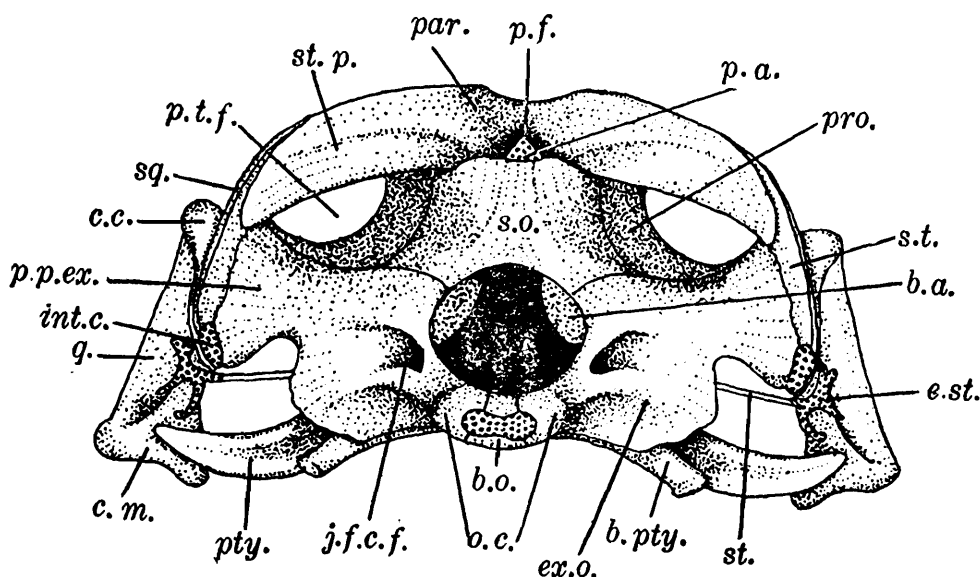


TEXT-FIG. 5. Ventral view of the supra-occipital ( $\times ca. 6$ ).

*a.s.c.*, channel for the anterior semi-circular canal; *c.c.*, the dorsal part of the cavum capsularis; *d-d'*, arrow passing through the aqueductus endolymphaticus which lodges the ductus endolymphaticus; *p.a.*, *processus ascendens* (cartilaginous); *p.s.c.*, channel for the posterior semi-circular canal; *s.s.*, channel for the sinus superior leading into the channel for the anterior semi-circular canal in front and the channel for the posterior semi-circular canal behind.

<sup>1</sup> The fronto-parietal region of the skull is movable upon the occipito-sphenoidal part.

*superior* of the membranous labyrinth; this tube leads into minute hair-like tunnels both anteriorly and posteriorly which can be seen as extremely minute apertures on the outer wall, one lying anteriorly and the other posteriorly to the fossa; these tunnels accommodate the upper parts of the *anterior* and *posterior vertical semi-circular canals* (fig. 5). A third hair-like tunnel pierces the inner wall of the fossa a little above and anterior to the aperture for the sinus superior; it leads into the cranial cavity by a minute aperture (*aqueductus vestibuli*) lying on the antero-lateral surface of the inner wall of the supra-occipital as seen from the ventral side (fig. 5); this tunnel lodges the *ductus endolymphaticus*, which opens into the cranial cavity.



TEXT-FIG. 6. Posterior view of the skull of *Varanus monitor* ( $\times$  ca. 3).

*b.a.*, bulging of the auditory capsule into the cranial cavity; *b.o.*, basi-occipital with the elliptical basi-occipital cartilage attached to its posterior end; *b.pt.*, basipterygoid process of the basisphenoid; *c.c.*, condylus cephalicus; *c.m.*, condylus mandibularis; *e.st.*, cartilaginous extra-stapes; *ex.o.*, ex-occipital; *int.c.*, intercalary cartilage; *j.f.c.f.*, combined jugular and condylar foramen for the exit of the Xth, XIth and XIIth nerves and the vena cerebialis posterior branch of the internal jugular vein and for the entrance of the occipital branch of the occipito-vertebral artery; *o.c.*, occipital condyle; *p.a.*, processus ascendens cartilage fitting into the parietal fossa; *par.*, parietal; *p.f.*, parietal fossa; *p.p.ex.*, paroccipital process of the ex-occipital; *pro.*, pro-otic; *p.t.f.*, post-temporal fossa; *pty.*, pterygoid; *q.*, quadrate; *s.o.*, supra-occipital; *sq.*, squamosal; *s.t.*, supra-temporal; *st.*, stapes; *st.p.*, supra-temporal process of the parietal.

The supra-occipital forms the roof of the bun-shaped cerebellum disposed in an obliquely dorso-ventral direction and the medulla oblongata (hind-brain). The anterior border and the dorsal surface of the supra-occipital form the place of insertion for the occipito-vertebral muscles (*rectus capitis*, *obliquus capitis* and *spinalis capitis muscles*). These muscles form a thick pad covering the supra-occipital in such a way that, on removal of the integument, the occipital segment appears on the same level with the parietal.

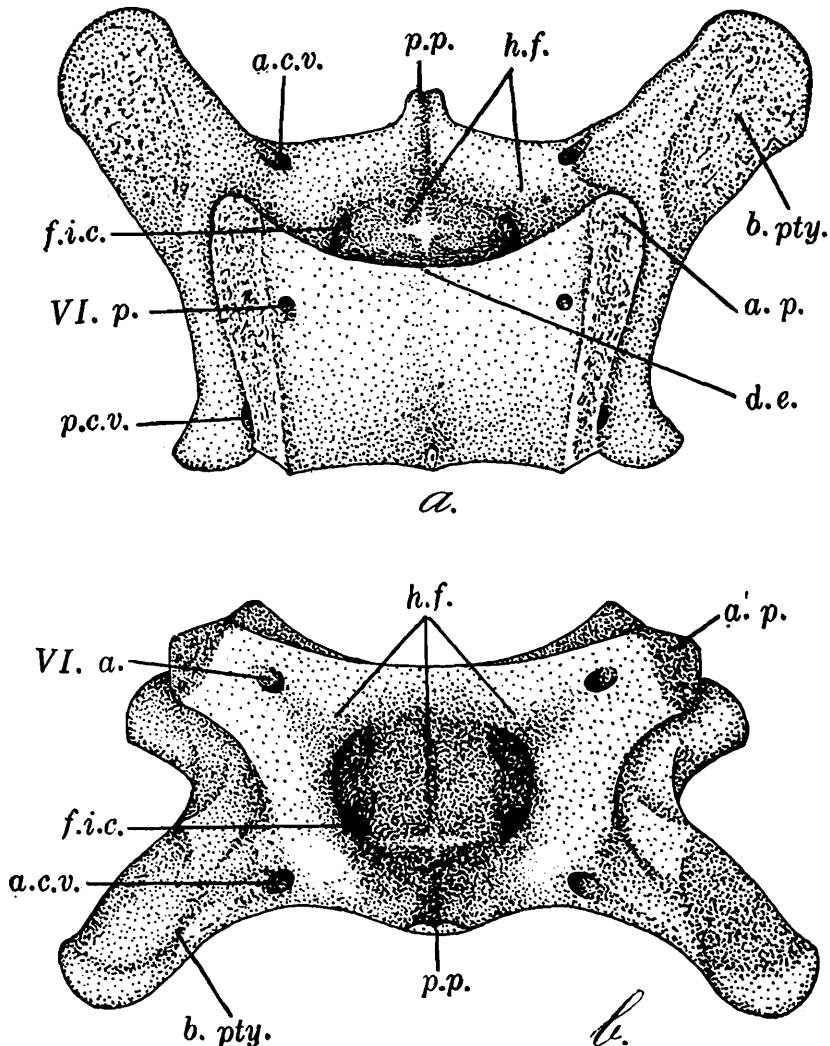
In *Sphenodon*, the external jugular foramen transmits the IXth Xth and XIth nerves and the vena cerebialis posterior branch of the internal jugular, while there is a separate foramen for the XIIth nerve. In *Lacerta*, there are two separate foramina for the XIIth nerve and another for the Xth. The IXth nerve also comes out separately and not from the *fenestra rotunda* as it does in *Varanus*.

In *Lacerta* (9, p. 9), the *processus ascendens* of the supra-occipital is bony and is only tipped with cartilage, but in *Varanus* the process is wholly cartilaginous and fits into the hinder and not on the under surface of the parietal.

(b) *The Parietal Region.*

The *parietal region* consists of the united parietals above and the median basisphenoid below. There are no alisphenoids, the side-walls of the cranium in this region being formed by the pro-otics behind and thick membranous walls in front. The basisphenoid is a chondrocranial ossification but the parietals are dermal bones.

The *basisphenoid* (figs. 1 and 7) is more or less quadrangular in shape and lies immediately in front of the basi-occipital, forming the floor of the cranial cavity beneath the mid-brain and a part of the hind-



TEXT-FIG. 7. Two views of the basisphenoid ( $\times ca. 6$ )

a. dorsal; b. anterior.

a.c.v., anterior opening of canalis vidianus; a.p., alar process; b.pty., basipterygoid process; d.e., dorsum ephippii; f.i.c., foramen caroticum intercum; h.f., hypophyseal fossa; p.c.v., posterior opening of canalis vidianus; p.p., parasphenoid process; VI.a., anterior foramen for the abducens nerve; VI.p., posterior foramen for the abducens nerve.

brain. Its posterior border is straight and single, fitting closely and immovably against the basi-occipital, but the anterior border is double,

there being a *dorsal anterior border* (*dorsum ephippi*) and a *ventral anterior border* formed as a result of the presence at the anterior end of a large and deep depression called the *hypophysial fossa* (*sella turcica*), which lodges the *recessus infundibularis* and the *hypophysis* of the diencephalon. The dorsal anterior border is concave and is produced laterally on each side into a very short conical process (fig. 7) corresponding to the *alar process* in *Sphenodon*. The ventral anterior border gives off a short and stumpy median bifid process with which the parasphenoid articulates in front; this median process is therefore called the *parasphenoid process* (*processes trabeculae inferiores* of Siebenrock). On each side of this process, the bone is produced antero-laterally into a thick stout process, the *basipterygoid process*<sup>1</sup>, which is expanded at its extremity and articulates with the pterygoid, there being a cartilaginous meniscus (figs. 1 and 13) at the point of articulation. It should be noted that this articulation is movable like that between the supra-occipital and the parietal and forms another essential factor in the kinesis of the skull. Just as there are two anterior borders, similarly there are two lateral borders on each side, a *dorsal lateral border* and a *ventral lateral border* separated by a longitudinal groove (*sulcus venae jugularis*) between the two; the dorsal border articulates all along its length with the pro-otic, while the ventral border is free.

The dorsal surface of the basisphenoid is concave from side to side and is higher in front than behind; the concavity of the two bones (the basi-occipital and the basisphenoid) together forms a shallow depression into which fits the ventral convex surface of the brain behind the pituitary body. In the anterior third of the dorsal surface lie two small foramina (fig. 7a), one on each side, for the exit of the VIth (*abducens*) nerve<sup>2</sup>. This nerve perforates the bone at the base of each alar process, runs through a very short canal and comes out into the dorsal part of the hypophysial fossa (fig. 7b), wherefrom it runs outwards to innervate the external rectus muscle of the eye. The base of the basipterygoid process of each side is tunnelled through by the *canalis vidianus*<sup>3</sup> (fig. 7a), through which pass the *palatine branch of the internal carotid artery* and the *palatine branch of the facial nerve*. These two structures run close together side by side along the lateral wall of the basisphenoid in the groove between its dorsal and ventro-lateral borders and then pass together through the *canalis vidianus* and even on coming out run close together on the palate. The posterior opening of the *canalis vidianus* lies on the lateral wall of the basisphenoid just in front of its posterior end; the anterior opening of the canal, however, lies at the base of the basipterygoid process, on each side, on the outer side of the median parasphenoid process. About the middle of its course, the *canalis vidianus* passes through the extreme lateral boundary of the

<sup>1</sup> The basipterygoid process of the basisphenoid represents an ossification of a part of the greatly reduced palato-quadrato cartilage (5, p. 428).

<sup>2</sup> Siebenrock (9, pp. 11 and 12) mentions this foramen as *foramen internum* in *Lacerta* and says that it transmits a branch of the internal carotid. According to his description, the position of the *foramen internum* is the same as that of the foramen for the VIth nerve in *Varanus*. I think Siebenrock mistook the nerve for a branch of the internal carotid; at any rate, his statement on this point needs confirmation.

<sup>3</sup> The palatine branch of the facial nerve, as it joins the sympathetic branch from the IXth is called the *vidian nerve* (5, p. 271).

hypophysial fossa. The hypophysial fossa itself is a funnel-like pit, the base of which extends laterally on each side and communicates through an aperture with the canalis vidianus. Through this aperture (foramen caroticum internum, figs. 3, 8, 9 and 11), the cranial branch of the internal carotid enters the sella turcica from the canalis vidianus and becomes completely intra-cranial; it then runs laterally to the hypophysis and mounts upwards to supply the latero-ventral wall of the brain.

The united *parietal* (fig. 4) forms a more or less quadrangular bony plate, narrow in the middle but expanded both anteriorly and posteriorly. It articulates in front with the paired frontals through a more or less straight transverse suture, but is produced behind into two long, stout and laterally compressed processes, the *supra-temporal processes*—*processus parietales* of Siebenrock—(fig. 6), which diverge and run outwards and backwards to articulate behind with the supra-temporal on each side through an obliquely running suture. Laterally, between the supra-occipital and the pro-otic on one side and the parietal on the other, there is always a small area which is unossified and in a dry skull looks like a triangular fissure. It is covered in life with a thick fibrous membrane and provides a loose movable connection between the parietal and the pro-otic, so that the whole of the occipital segment, the basisphenoid and the pro-otic move as one piece on the parietal (Kinetism).

Each of the two concave lateral borders of the parietal is bevelled off all along its length to form a narrow ledge (fig. 4) slanting outwards; these bevelled ledges serve chiefly for the attachment of the adductor mandibulae medius muscles. The *parietal process* (*anterior superior process*) of the *pro-otic* articulates movably with each of these bevelled borders about the middle of its length.

The dorsal surface of the united parietal is evenly flat like that of the frontals, but the ventral surface is slightly concave from side to side, forming a shallow depression into which fits the dorsal surface of the fore-brain and the mid-brain. In the anterior half of the bone, right in the median line, lies the oval *parietal foramen*, into which fits the parietal organ. Between the roots of the supra-temporal processes, the posterior border of the parietal is excavated in the median line to form a deep funnel-like pit, the *fossa parietalis* (fig. 6), which in the entire skull is hidden by the anterior border of the supra-occipital. Into the fossa parietalis is inserted the cone-shaped cartilaginous projection<sup>1</sup> from the anterior border of the supra-occipital, forming a "peg and socket" joint (p. 142).

The basisphenoid of *Varanus* presents important differences from that of *Sphenodon*. The alar processes are very short and there is no median dorsal process of the *dorsum ephippii*. Further, the anterior openings of the canalis vidianus are paired and not median and common as in *Sphenodon*, and the canalis vidianus transmits both the palatine artery and nerve and not the palatine artery alone as it does in

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<sup>1</sup> The processus ascendens tecti synotici cartilage.

Besides these bones, there are several cartilaginous and membranous tracts which complete the wall of the reduced cranial cavity of this region. The brain-cavity is confined here to the dorsal part of the skull and lodges only the anterior part of the cerebral hemispheres and the olfactory stalks, the remaining greater part of the brain having been

pushed back behind the large eyes into the parietal and occipital regions. The brain is obliquely placed: the olfactory stalks are lodged in the narrow tubular cavity formed by the ventro-lateral extensions of the frontals, the cerebral hemispheres are covered by the frontals above and are supported by cartilage and thick fibrous membrane below, while the optic chiasma is surrounded by the minute orbitosphenoid bones. The *inter-orbital septum* extends forwards from the median parasphenoid process of the basisphenoid, and lies below the narrow cranial cavity between the two large orbits, continuing forwards into the olfactory chamber as the *inter-nasal septum* (fig. 8b). As the cranial cavity is very much reduced between the large eyes and is largely replaced by the inter-orbital septum, the skull is almost completely *tropibasic*.

The *parasphenoid* (figs. 1 and 8b) is a long narrow bone flattened dorso-ventrally and resembling in shape the blade of a bayonet. It underlies the ventral border of the inter-orbital septum in the mid-ventral line just in front of the basisphenoid, articulating behind with the median parasphenoid process of the basisphenoid and terminating in front at a point about half the length of the inter-orbital septum (fig. 8b). Posteriorly, the parasphenoid protects the infundibulum of the diencephalon and even forms part of the hypophysial fossa, while along the greater part of its length it forms the ventral support of the posterior half of the inter-orbital septum. In a freshly prepared skull, the parasphenoid is more or less horizontal in position, being only slightly bent upwards anteriorly; but in a dried skull, as the inter-orbital septum shrivels up, the parasphenoid gets bent upwards, but its anterior end never reaches the frontal as is shown by Reynolds (7) in his diagrams.

The parasphenoid of *Varanus* is very much reduced and corresponds only to the *rostrum parasphenoides* (*processus cultriformis*) of *Sphenodon*, the main body of the parasphenoid corresponding to the hinder wing-like processes, the middle shield and the transverse processes of the parasphenoid of *Sphenodon* being absent.

The paired *frontals* (fig. 4) are elongated bones, narrow in front but broad behind. They articulate with each other through a long and straight median suture and with the parietals behind through a more or less straight transverse suture. Anteriorly each frontal presents a shallow concavity and a cleft, into which is wedged in one of the two posterior processes of the united nasals, while along the anterior half of its outer lateral border, there is a triangular depression for articulation with the pre-frontal of its own side. Dorsally, the frontals are evenly flat and lie at the same level with the parietals, but laterally each is inflected downwards and inwards to form a latero-ventral process (fig. 8b), which meets the corresponding process of the other side, enclosing a more or less complete bony canal (*canalis olfactorius*<sup>1</sup>), in which are lodged the elongated olfactory stalks. Ventrally these inflected processes enclose between them the dorsal membranous border of the inter-orbital septum.

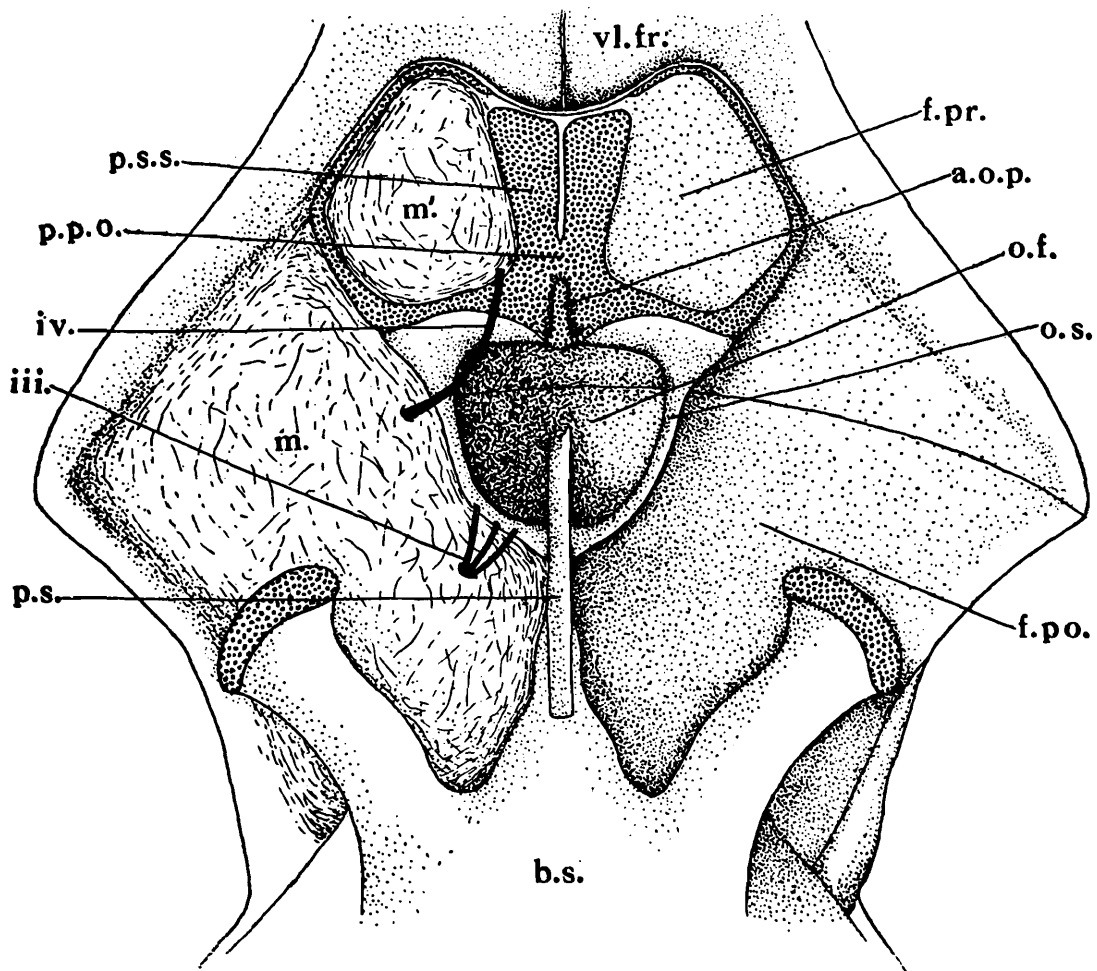
The ventro-lateral walls of the cranial cavity (fig. 9) enclosing the fore-brain are formed partly of calcified and hyaline cartilage, partly

<sup>1</sup> In *Lacerta*, the *canalis olfactorius* is mainly membranous.



of a thick fibrous membrane and partly by the paired *orbitosphenoid* bones. The cartilaginous portion is represented by the *planum (septum) supra-septale* or *pila preoptica* and its lateral extensions. The *planum supra-septale* (figs. 1 and 9) rests anteriorly against the ventral part of the posterior border of the *canalis olfactorius* and is divided into two longitudinal strips along the greater part of its length by the insertion of the dorsal border of the *inter-orbital septum*. The posterior part of the cartilage is undivided; it forms the anterior boundary of the *optic fenestra* and gives off an obliquely directed median ventral process, the *anterior optic process* (fig. 9) and two long narrow *lateral processes* which extend upwards and reach the *frontals* above, and then run forwards along their postero-ventral borders (figs. 8b and 9).

The *orbitosphenoids*<sup>1</sup> (figs. 1, 8b and 9) are two minute, curved, and flattened bones which are connected anteriorly with the *pila*



TEXT-FIG. 9. The orbitosphenoids and the connected cartilages and membranes from the ventral side ( $\times ca. 4\frac{1}{2}$ ).

*a.o.p.*, anterior optic process; *b.s.*, basisphenoid; *f.po.*, fenestra postoptica; *f. pr.*, fenestra preoptica; *m.*, membrane covering the fenestra postoptica; *m'*, membrane covering the fenestra preoptica; *o.f.*, optic fenestra; *o.s.*, orbitosphenoid; *p.p.o.*, pila preoptica; *p.s.*, parasphenoid; *p.s.s.*, planum supra-septale; *vl.fr.*, ventro-lateral process of the frontal; *iii.*, the three branches of the oculomotor nerve; *iv.*, trochlear nerve.

<sup>1</sup> Reynolds (7) shows the orbitosphenoids in a longitudinal section hanging vertically downwards from the junction of the parietal and frontal bones in *V. varius*. His diagram does not seem to be correct, as it is extremely unlikely that both could be seen in a longitudinal section. In *Varanus monitor*, they lie in a vertical position, one on each side of the middle line, between the septum supra-septale above and the posterior end of the inter-orbital septum below, as shown in fig. 8.

*preoptica* and posteriorly with the vestigial *pila postoptica*. The orbitosphenoids represent the reduced vestiges of the sphenethmoid ossification of some primitive extinct reptiles (5). Each is a slender bone, broader at its dorsal than at its ventral end and forms the antero-lateral, lateral and posterior boundary of the optic fenestra (fig. 9).

On either side of the planum supraseptale, bounded behind and laterally by its lateral extensions and in front by the frontals, there is a large oval area covered by membrane: this is the *fenestra preoptica* (fig. 12). On either side of the orbitosphenoids, there is a similar *fenestra postoptica*. The fourth nerve (pathetic) leaves the cranial cavity at the inner border of this fenestra, while the three branches of the third nerve come out a little behind the fourth (fig. 9).

The vertical *inter-orbital septum* is chiefly cartilaginous all along its length but a small dorsal part of it lying immediately below the *canalis olfactorius* of the frontals is membranous (fig. 8*b*). The optic fenestra enclosed by the two orbitosphenoids is single when looked at from the dorsal side, but as the inter-orbital septum runs vertically below it, it is seen to be divided into two when looked at from the ventral side, each of the two fenestrae providing an exit for the optic nerve of its own side. In dried skulls, the cartilages and membranes of the region and the minute orbito-sphenoid bones are lost and therefore the orbits are seen to open widely into each other.

In *Lacerta* also, the inter-orbital septum is partly membranous and partly cartilaginous. Siebenrock (9) applies the name inter-orbital septum only to the upper membranous part, while the lower cartilaginous part is distinguished by him as the *pre-sphenoid*.

### III. The Sense-Capsules.

Of the three sense-capsules, the auditory and the olfactory are closely connected with the skull, but the optic capsule is free although it is supported and protected by a number of bones of the skull.

#### (a) *The Auditory Capsules.*

The *auditory capsules* are closely associated with the occipital region of the cranium and are formed on each side by the pro-otic, the opisthotic part of the ex-occipital and the supra-occipital. Each auditory capsule bulges inwards into the cranial cavity as the *auditory bulla* (fig. 6), which is easily seen on each side through the foramen magnum. All the three bones taking part in the formation of the auditory capsules are chondrocranial ossifications.

The ex-occipitals and the supra-occipital have already been described. We shall, therefore, describe the pro-otic only here.

The *pro-otic (otosphenoid)* is an irregularly triradiate bone on each side (figs. 2*a*, 2*b*, 8*a*, 8*b* and 10), forming the anterior and antero-ventral parts of the auditory capsule. One of its radii (the *anterior inferior process*) is flat and stumpy and articulates ventrally with the upper lateral border of the basisphenoid in front and with the tuberculum speno-occipitale behind. Another radius (the *anterior superior*

*process* or the *parietal process*<sup>1</sup>) articulates moveably against the lateral bevelled edge of the parietal internally and against the dorsal end of the epipterygoid externally, while the third conical radius (the *posterior process*) fits against the outer surface of the paroccipital process of the ex-occipital. The central part of the bone where the three radii meet is hollowed out and fits posteriorly against the opisthotic part of the ex-occipital, completing the floor and side-walls of the auditory capsule, the roof of the capsule being formed by the supra-occipital, with the anterior half of which the pro-otic articulates dorsally. The outer surface of the dorsal part of the bone is deeply concave, while the inner surface is strongly convex.

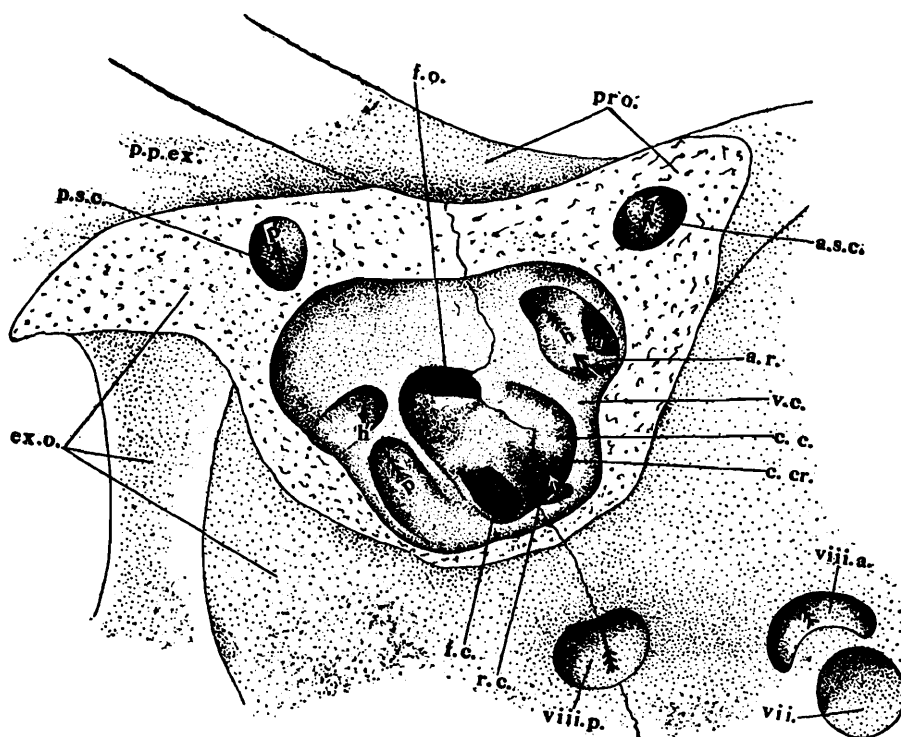
Looked at from the side (fig. 2a), the anterior superior and anterior inferior processes meet at an angle and enclose between them a triangular space covered over in life with a membrane. This membrane is perforated by a large aperture through which the trigeminal nerve (Vth) leaves the cranial cavity. This triangular space corresponds to the "incisura otosphenoida" (Siebenrock) of *Sphenodon* and *Lacerta*. The root of the anterior superior process is perforated dorsally by the *anterior vertical semi-circular canal* of the internal ear, the remaining part of which lies in the corresponding portion of the supra-occipital. The greater part of the *horizontal semi-circular canal* lies within the pro-otic in a canal-like perforation of its outer wall, the remaining part of this canal lying in the opisthotic part of the ex-occipital (fig. 10). The hollow excavation of the central part of the bone extends deep into the anterior superior process forming the anterior ampullary recess and accommodating both the *ampulla anterior* and the *ampulla horizontalis* of the membranous labyrinth (fig. 10).

On the outer surface of the bone close to its ventral border, there is a groove overhung by an elongated crest which extends forwards even on the basisphenoid; the crest is called the *otosphenoidal crest* (fig. 2a), while the groove is named the *sulcus venae jugularis*. In this groove, there are two foramina: the anterior one provides for the exit of the *palatine branch*, while the posterior lets through the *hyomandibular branch* of the facial nerve. Immediately below and behind the foramen for the hyomandibular branch of the 7th nerve lies the *fenestra ovalis* (fig. 2) for the insertion of the inner end of the columella auris. The anterior and posterior facial foramina lead into a common canal within the body of the bone and open internally into the cranial cavity by a common aperture, the *facial foramen* (figs. 2b, and 10), lying immediately behind the "incisura otosphenoida" and below the anterior auditory foramen. The inner surface of the pro-otic bears three foramina: the facial foramen and the anterior and posterior auditory foramina. The facial foramen provides exit for the facial (VII) nerve, while the anterior auditory foramen lets through the anterior division of the auditory nerve. The posterior auditory foramen lies at the junction of the inner wall of the pro-otic with that of the ex-occipital and lets through the posterior division of the auditory nerve.

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<sup>1</sup> *Ala otosphenoida* of Siebenrock.

The *cavum capsularis* (fig. 10) or the cavity of the auditory capsule lodging the internal ear is a more or less spherical space lined by the



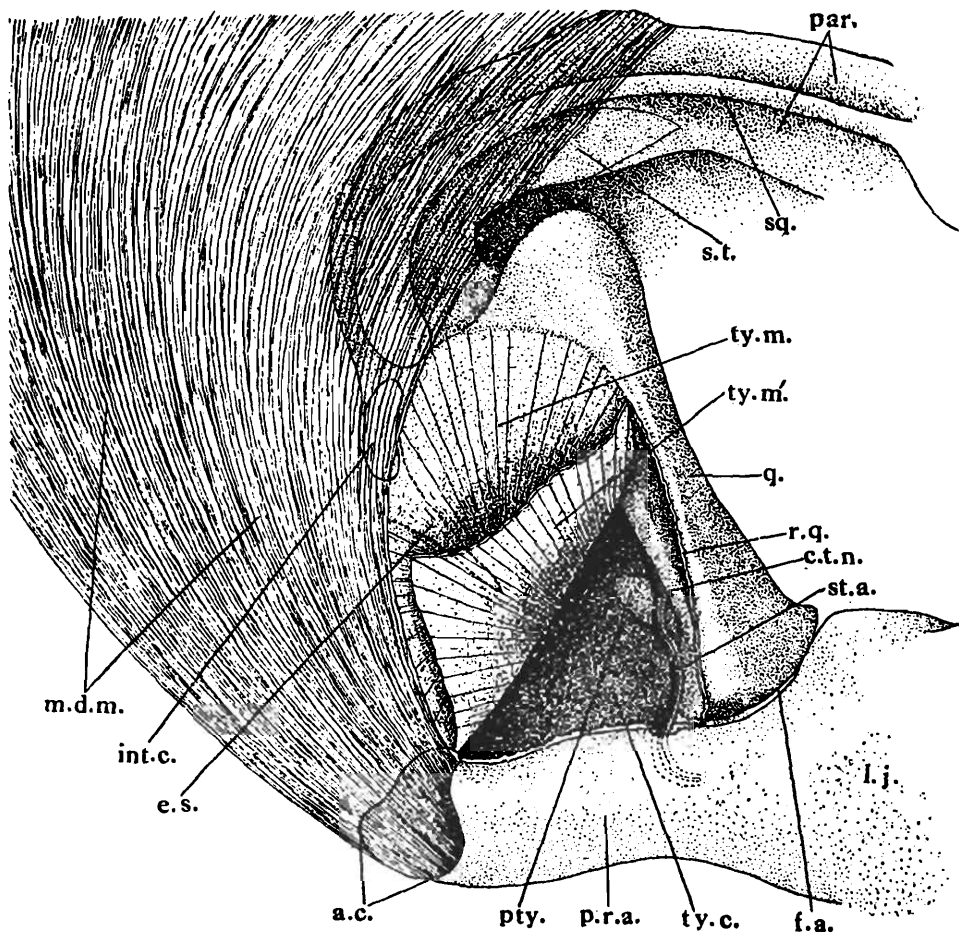
TEXT-FIG. 10. Dorsal view of the *cavum capsularis* after removal of the supra-occipital. The flat upper border with crooked lines and dots represents the place of articulation with the supra-occipital ( $\times ca. 10$ ).

*a-a'*, arrow passing through the channel for the anterior semi-circular canal; *a.r.*, anterior ampullary recess; *a.s.c.*, opening for the anterior vertical semicircular canal; *c.c.*, cochlear cavity; *c.cr.*, cochlear crest; *ex.o.*, ex-occipital; *f.c.*, fenestra cochleae; *f.o.*, fenestra ovalis; *h.h'*, arrow passing through the channel for the horizontal semi-circular canal; *p.p.ex.*, paroccipital process of the ex-occipital; *p.p'*, arrow passing through the channel for the posterior vertical semi-circular canal; *pro.*, pro-otic; *r.c.*, recessus cochlearis; *v.c.*, vestibular cavity; *vii.*, facial foramen; *viii.a.*, foramen through which the *nervus acusticus anterior* leaves the cranial cavity; the arrow represents the course of the nerve, which enters the anterior ampullary recess *a.r.* to supply the anterior part of the membranous labyrinth; *viii.p.*, foramen through which the *nervus acusticus posterior* leaves the cranial cavity; the arrow represents the course of the nerve which enters the inner wall of the vestibular cavity just above the recessus cochlearis.

perilymphatic membrane and enclosed by the ex-occipital, pro-otic and supra-occipital bones. It is divided into an upper large *vestibular cavity* containing the utricle and the saccule, and a lower small egg-shaped *cochlear cavity* lodging the cochlea and the legena, the two cavities being separated by a ridge called the *cochlear crest* (fig. 10). At the anterior end of the vestibular cavity lies the *anterior ampullary recess*, into which are lodged the *ampulla anterior* and *ampulla horizontalis* leading into the anterior vertical and horizontal semi-circular canals, and into which enters the *anterior auditory nerve* through a small aperture on its inner face. Along the posterior wall of the vestibular cavity lie: (1) the *posterior ampullary recess* into which is lodged the *ampulla posterior* leading into the posterior vertical semi-circular canal, and (2) the opening for the posterior end of the horizontal semi-circular canal. Along the inner wall of the vestibular cavity lies the aperture for the posterior auditory nerve. This aperture and the anterior

ampullary recess lie in the pro-otic bone, while the posterior ampullary recess and the posterior aperture for the horizontal canal lie in the ex-occipital.

The cochlear cavity presents a deep, funnel-shaped pit a long its inner wall just below the aperture for the posterior auditory nerve; this is called the *recessus cochlearis* and lodges the cochlear portion of the membranous labyrinth. Immediately behind the recessus cochlearis lies a fissure called the *fenestra cochleae* which leads below into the fenestra rotunda and through which the perilymphatic sac passes into the recessus scalae tympani. Along the outer edge of the cochlear



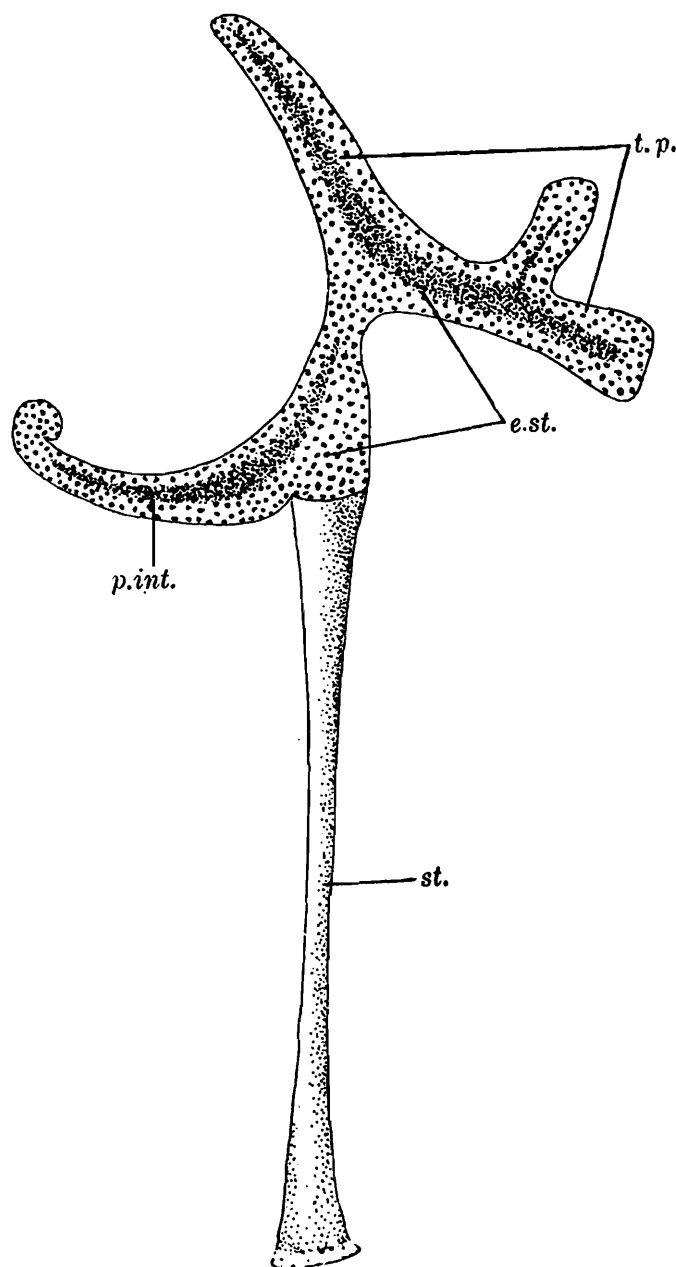
TEXT-FIG. 11. A dissection of the postero-lateral part of the head showing the tympanic membrane and its relations. The lower part of the membrane has been detached and reflected ( $\times ca. 3$ ).

*a.c.*, position of the articular cartilage; *c.t.n.*, chorda tympani nerve; *e.s.*, position of the extra-stapes lying immediately beneath the tympanic membrane; its outline is shown in broken lines; *f.a.*, fovea articularis; *int.c.*, intercalary cartilage; *l.j.*, lower jaw; *m.d.m.*, musculus depressor mandibulae, to which is attached the posterior border of the tympanic membrane; *par.*, parietal; *p.r.a.*, processes retro-articularis, to which is attached the ventral border of the tympanic membrane; the wavy line represents the cut border of the tympanic membrane; *pty.*, posterior end of the pterygoid; *q.*, quadrate; *r.q.*, outer ridge of the quadrate to which is attached the dorsal and anterior border of the tympanic membrane; *sq.*, squamosal; *s.t.*, supra-temporal; *st.a.*, stapedial artery (arteria auricularis); *ty.c.*, tympanic cavity; *ty.m.*, tympanic membrane in position; *ty.m'*, tympanic membrane cut and reflected.

cavity lies another fissure which opens into the fenestra ovalis and through which the inner end of the stapes fits against the perilymphatic

membrane of the internal ear. The recessus cochlearis lies in the pro-otic bone, the fenestra cochleae perforates the ex-occipital, while the fissure leading into the fenestra ovalis lies between the ex-occipital and the pro-otic. Fig. 10 represents the cavum capsularis and the associated chambers and canaliculi in relation to the different parts of the membranous labyrinth.

The *columella auris* (figs. 1 and 12) extends from the fenestra ovalis to the tympanic membrane across the cavity of the middle ear. It consists of two distinct parts: (a) a long proximal bony rod called the *stapes* or *columella*, with a small cartilaginous piece at its inner end embedded in the membrane closing the fenestra ovalis; the outer



TEXT-FIG. 12. The columella auris ( $\times ca. 14$ ).

*e.st.*, extra-stapes; *p.int.*, internal or ventral process; *st.*, stapes; *t.p.*, tympanic process.

end of the stapes reaches the level of the upper end of the quadrate bone where it (the stapes) is connected with the base of the *processus*

*internus* of the extra-columella; and (b) a distal cartilaginous triradiate part called the *extra-stapes* or *extra-columella*, which consists of a thick elongated concave piece or *body* pressed obliquely against the upper half of the tympanic membrane (fig. 11) and a *processus internus* or *ventralis* (*quadrate process*) which is slightly curved and runs downwards and forwards along the posterior surface of the quadrate. A *processus dorsalis* is absent. The forked end of the body of the extra-stapes rests against the quadrate while the other pointed end reaches about the centre of the tympanic membrane (fig. 11). A strong ligament passes from the "intercalary" (a meniscus of cartilage wedged in between the quadrate and the paroccipital process of the ex-occipital ventro-internally) to the outer side of the body of the extra-stapes, between it and the tympanic membrane; another ligament from the intercalary passes directly across the anterior surface of the extra-stapes and is inserted along the anterior surface of the *processus internus* (fig. 13).

The *chorda tympani nerve* (figs. 11 and 13) branches off from the hyo-mandibular division of the VIIth along the posterior wall of the cavity of the middle ear, close to the upper end of the quadrate, and runs forwards and downwards along the ridge on the posterior surface of the quadrate, between it and the *processus internus* of the extra-columella, towards the lower end of the quadrate, where it crosses over to the outer side of the pterygo-quadrate articulation (fig. 13) and then runs downwards to enter into the foramen on the dorsal surface of the post-articular process of the mandible.

We may note here that the anterior and dorsal borders of the tympanic membrane are supported by the outer elongated ridge (tympanic crest) and the upper end of the quadrate and that the ventral border of the tympanic membrane is supported by the post-articular process of the mandible of the lower jaw, while its posterior border is supported by the *musculus depressor mandibulae* (fig. 11).

#### (b) *Bones in Relation with the Optic Capsules.*

The *optic capsule* proper (the eye-ball) remains free from the skull and retains its usual mobility. It is not bony by itself but is protected by a number of bones of the skull, which are described at this place as a matter of convenience.

The *supra-orbitals* (fig. 4) are a pair of triangular bones, each of which is attached by its broad base to the outer upper border of the pre-frontal of its own side, but is free along its other two sides and also at its apex. The bone is more or less flattened and strongly curved backwards, so that its inner border is strongly concave while the outer border is slightly convex. The detached bone strongly resembles a large tooth of a shark. The supra-orbital undoubtedly affords a strong protection to the antero-dorsal part of the eye-ball and forms the anterior and incomplete outer boundary of the *supra-orbital fossa*.

The paired *pre-frontals* (fig. 8a) are capsule-shaped bones, each with an elongated conical process, which forms a sort of handle to the capsule and articulates with the antero-lateral border of each frontal. The capsular body of the bone articulates directly with the lacrymal on the outside and with the maxilla in front, and through a small inter-

vening area of cartilage with the palatine below. The triangular supra-orbital is loosely attached to its antero-lateral border and often gets detached. The posterior surface of the pre-frontal forms the anterior wall of the orbit, while its anterior cup-shaped surface together with the lacrymal forms the hind-wall and part of the lateral wall of the olfactory chamber. The outer border of the pre-frontal with the inner border of the lacrymal encloses a large oval aperture, the *orbito-nasal canal*.

The *lacrymal* (fig. 8a) on each side is a small irregular bone wedged in between the pre-frontal on the inside and the posterior border of the maxilla on the outside. The anterior end of the bone is produced into a small triangular process which articulates with the inner surface of the maxilla and forms part of the lateral wall of the olfactory chamber. Posteriorly also, the bone is produced into a short but broad triangular process which is prominently seen at the anterior border of the orbit, just below the base of the supra-orbital (fig. 8a). The inner surface of the bone is concave and forms the entire outer border of the orbito-nasal canal. The ventral part of the bone articulates with the jugal and the maxillary process of the palatine and is perforated by a small oval foramen, the *lacrymal foramen*, which provides a passage for the *lacrymal canal*.

The *post-orbitals* (post-frontals of Siebenrock) are a pair of elongated bones, each with a clasp-shaped process on the inner side of its anterior half (fig. 4). The elongated posterior bar of the bone articulates with the squamosal behind and forms the anterior half of the supra-temporal arcade. The outer anterior end of the bone is curved downwards and forms a short thick conical process, the *orbital process*, which is connected by means of a cartilaginous bar with the posterior end of the jugal, thus forming the outer posterior boundary of the orbit. The anterior and inner clasp-shaped process has a deeply concave inner border and closely grips within it the antero-lateral border of the parietal and the postero-lateral border of the frontal bone.

There is a single post-orbital on each side unlike the case in some species of *Lacerta* in which there are two on each side, described by Siebenrock (9) as post-frontal 1 and post-frontal 2.

The paired *jugals* (fig. 8a) are slender curved bones forming with the lacrymals the outer ventral boundary of the orbit. Anteriorly each of them is thickened and is triangular in cross-section, but posteriorly it becomes slender and pointed. It articulates anteriorly with the maxilla and the lacrymal, laterally with the transverse, while posteriorly it is connected with the post-orbital through a slender cord of cartilage. Its anterior part articulating with the maxilla is called the *maxillary process*, while its posterior part leading towards the post-orbital is called the *temporal process*. A quadrato-jugal is absent in the skull of the *Lacertilia*. The loss of this bone evidently leads to a greater mobility of the jaws.

All these four bones are dermal in origin (*investing bones*).

The free bony shields (*lamina superciliaris* and *schläfenpanzer* of Siebenrock) covering the orbit from above and also the temporal region in *Lacerta* are absent in *Varanus*. Thus, the *scuta supraocularia* and the *scuta superciliaria* are absent and so are the *scuta temporalia*.



(c) *Bones in Relation with the Olfactory Capsules.*

The *olfactory capsules* are two fairly large oblong structures occupying the greater part of the facial portion of the skull. They lie in front of the cranial cavity, one on each side of the middle line, and are formed almost completely of cartilage partially protected by bones. Each is bounded behind by the pre-frontal and the lacrymal, and laterally by the lacrymal and the maxilla ; the roof is covered over chiefly by the integument of the face and only partially by the united nasals behind, while the floor is formed by the flat rostral portion of the maxilla and the septo-maxillary in front, and the vomer and the vomerine process of the palatine behind. The two capsules are separated from each other and bounded internally by the nasal process of the pre-maxilla and the cartilaginous nasal septum which extends below and behind this bony nasal process, and continues behind into the inter-orbital septum.

Each olfactory capsule is horse-shoe-shaped in outline and consists of two parts : (1) the *vestibule*, corresponding to the outer limb of the  $\cap$ , which begins behind with the external narial aperture and leads forwards right up to the junction of the pre-maxilla and maxilla ; and (2) the *olfactory chamber* corresponding to the inner limb of the  $\cap$  and lying parallel and internal to the vestibule and leading backwards to open into the buccal cavity through the *internal nares* or *choanae*. The vestibule and the olfactory chamber are continuous with each other at the extreme anterior end just behind the pre-maxilla, but are separated from each other along the remaining parts of their lengths by an obliquely vertical cartilaginous partition called the *concha*. The external nares are funnel-shaped ; each is bounded behind by the slightly flattened and gradually ascending anterior border of the maxilla and leads forwards into the vestibule, which extends right up to the pre-maxilla and then turns round on the inner side of the concha to continue into the olfactory chamber. The concha extends forwards and inwards from the posterior border of each external nare along the outer edge of each septo-maxillary, as seen from the dorsal surface.

The united *nasals* (fig. 4) form an elongated, more or less triangular, bone lying immediately anterior to the frontals. The two bones are fused together along the greater part of their length and form a more or less flat plate, but their laterally compressed and conical anterior fourths remain separate, enclosing between them the posterior end of the median nasal process of the pre-maxilla, which extends behind to meet the frontals ventrally beneath the nasals (fig. 11). Posteriorly the nasals present a short median cleft and are produced into two small lateral wing-like processes, each of which closely fits into the concavity and cleft at the anterior end of each frontal. The nasals form a very small part of the roof at the posterior end of each olfactory chamber, the greater part of which is covered by the thick integument of the face. The cartilaginous *inter-nasal septum* is attached to the ventral surface of the frontals and the nasal process of the pre-maxilla in the middle line, the nasals remaining on the dorsal surface of the skull (fig. 11).

The paired *septo-maxillaries* (*turbinals* of Siebenrock) are two small, more or less triangular bones, lying one on each side of the nasal process of the pre-maxilla, between it and the maxilla on the outside (fig. 4).

Dorsally each of these bones is seen to lie just behind the flat rostral portion of the maxilla. A disarticulated bone has the shape of an inverted watch-glass, the hollow being directed ventralwards so as to overlie the anterior part of the vomer and enclose the Jacobson's organ within. The latter communicates with the anterior part of the buccal cavity through a triangular aperture on the roof of the mouth, between the maxilla and the vomer (fig. 1). Along the whole length of its inner border, each septo-maxillary presents a narrow groove, along which runs the *ramus frontalis ophthalmici nerve* (V). At the anterior conical end of the bone this nerve gives off a branch which passes through a *foramen* (the *anterior septo-maxillary foramen*) and runs outwards along the antero-lateral border of the bone and then penetrates inwards to innervate the mucous membrane of the Jacobson's organ.

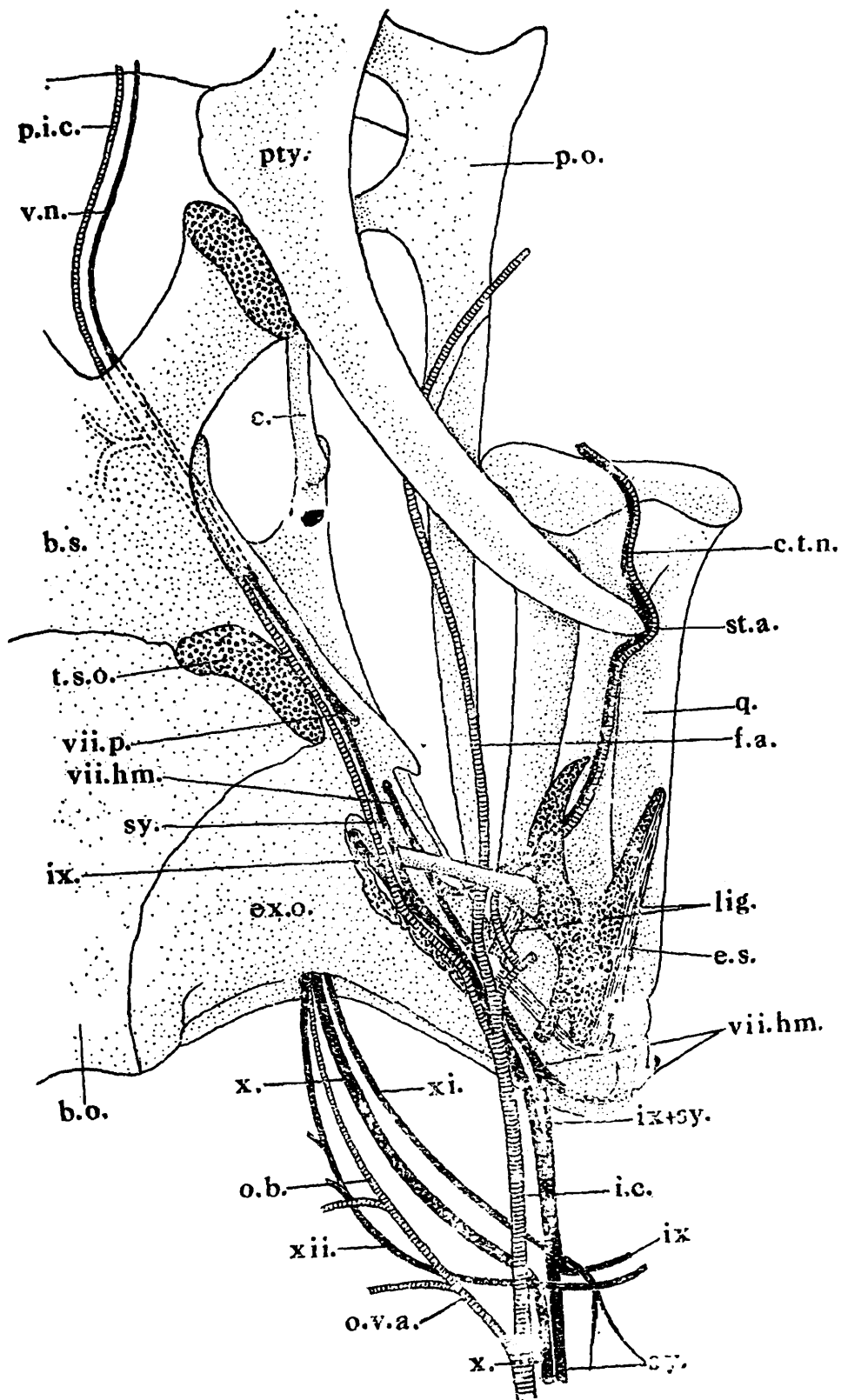
All the bones in relation with the olfactory capsule are dermal investing bones.

#### IV. The Suspensorium.

The *suspensorium* is formed on each side by the stout pillar-like quadrate, the ventral end (*condylus mandibularis*) of which forms the articular surface for the lower jaw, while the dorsal end is supported and strengthened by the squamosal, the supra-temporal and the paroccipital process of the ex-occipital (fig. 8a).

The palatoquadrate cartilage is very much reduced in the Amniota, the only parts remaining being the processus ascendens and the basal process articulating with the basitrabecular process and the quadrate cartilage. The former ossifies as the epipterygoid bone and the basipterygoid process of the basisphenoid and the latter as the quadrate bone (5, p. 440).

The *quadrate* is a stout pillar-like bone forming the posterior boundary of the side-wall of the skull and the anterior and outer boundary of the middle ear. It is disposed in an obliquely dorso-ventral direction, the dorsal end being directed backwards and the ventral end slightly forwards. The upper dorsal end (*condylus cephalicus*) is expanded antero-posteriorly and articulates above with the squamosal, the supra-temporal and the paroccipital process of the ex-occipital (fig. 8a). Between the articular surface of the quadrate and the paroccipital process, there is a small meniscus of cartilage called the "intercalary cartilage" (*supra* p. 155). This cartilage provides for the movement of the quadrate on the paroccipital process (*streptostylism*). In front of the articulation with the squamosal, there is a more or less rounded facet covered with cartilage for the insertion of the adductores mandibulae externus and medius muscles. The lower end is expanded laterally to form the articular surface for the lower jaw. Close to this articular surface, along its internal border, the quadrate bears a facet for articulation with the pterygoid. Along both of its outer and inner borders, the quadrate is produced into thin elongated ridges, to the outer of which (*tympanic crest*) is attached the anterior margin of the tympanic membrane. The anterior and posterior surfaces are broad; the anterior gives attachment to the adductores mandibulae externus and medius muscles, while the whole of the posterior surface forms part of the cavity of the middle ear.



TEXT-FIG. 13. Ventral view of the left half of the posterior part of the skull showing the relations of the nerves and arteries with the bones ( $\times ca. 4\frac{1}{2}$ ).

b.o., basioccipital; b.s., basisphenoid; c., columella cranii; c.t.n., chorda tympani nerve; e.s., extra-stapes; ex.o., ex-occipital; f.a., facial artery; i.c., internal carotid artery; lig., two ligaments, first, between the outer surface of the extra-stapes and the tympanic membrane originating from the intercalary cartilage; the second also originates from the same cartilage and goes towards the *processus ventralis* of the extra-stapes on which it is inserted; o.b., occipital branch of the internal carotid artery; p.i.c., palatine branch of the internal carotid; p.o., post-orbital; pty., pterygoid; q., quadrate; st.a., stapedial artery (arteria auricularis); sy., sympathetic nerve; t.s.o., tuberculum spheno-occipitale; v.n., vidian nerve consisting of the palatine branch of the VIIth nerve and the sympathetic; vii.p., palatine branch of the VIIth nerve; vii.hm., hyomandibular branch; ix., glossopharyngeal; ix+sy., combined ninth and sympathetic nerve; x., vagus nerve; xi., spinal accessory; xii., hypoglossal nerve.

The paired *epipterygoids* (*columella cranii*) are slender rod-shaped bones (figs. 8a and 8b) which are disposed in an obliquely dorso-ventral direction, the ventral end lying distinctly anterior to the dorsal end. The dorsal and ventral ends of the bone are slightly flattened; the dorsal end fits against the parietal process of the pro-otic, while the ventral fits into a depression (*fossa columellae*) on the dorsal surface of the pterygoid at about the middle of its length.

The *squamosal* (fig. 8a) is a thin elongated bone curved posteriorly into a comma-like shape, the head of the comma fitting on to the dorsal end of the quadrate and against the outer surface of the supra-temporal. The anterior end of the bone forming the tail of the comma is directed forwards and fits against the outer surface of the hinder end of the post-orbital, the two bones together (squamosal and post-orbital) forming the superior temporal arcade.

The *supra-temporal* (figs. 4 and 8a) is a small bone resembling in shape the *Kukri* (short sword) of the Gurkha soldier. It is curved like the squamosal and its lower hinder end fits on to the dorsal end of the quadrate. Its anterior blade-like portion is sickle-shaped and covers externally the hinder end of the supra-temporal process of the parietal, while its posterior curved end is wedged in between the squamosal externally and the paroccipital process of the ex-occipital internally.

The quadrate and the epipterygoid are endochondral ossifications of the palatoquadrate cartilage but the squamosal and the supra-temporal are dermal bones

## V. The Palate and the Upper Jaw.

The palate and the upper jaw are formed of the pterygoids, ectopterygoids (transpalatines), palatines and vomers and the pre-maxillae and the maxillae. All these are dermal (investing) bones.

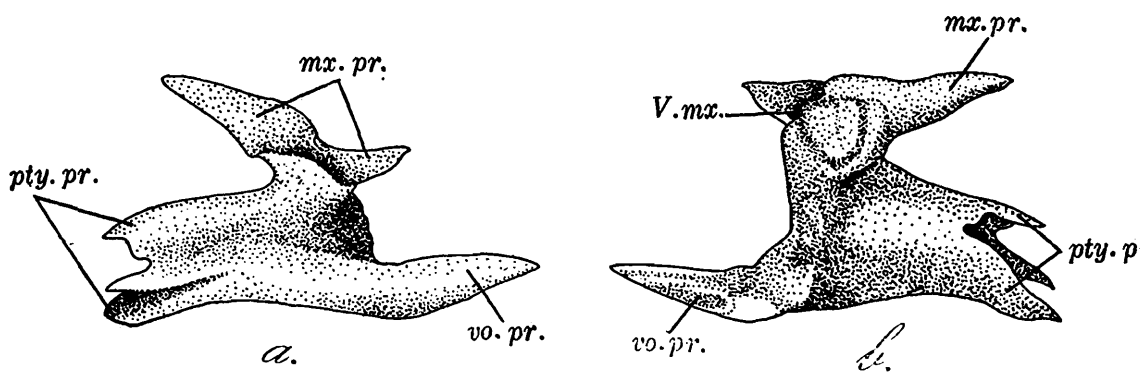
The *pterygoid* (figs. 1 and 8) is an elongated, slightly curved bone, which forms a more or less flat plate in front and a long outwardly directed rod-like process behind. The flat plate is produced in front into an expanded *palatal process* articulating with the palatine, and externally into a conical *transverse process* articulating with the ectopterygoid (transverse). These two processes enclose between them a space which forms the posterior part of the *sub-orbital fossa* (fig. 1). The rod-like *quadrate process* is the longest and rests posteriorly against the inner border of the quadrate, close to its lower end, in such a way that the articulation is movable, the pterygoid sliding on the quadrate. On the dorsal surface, at the junction of the quadrate and palatal processes, lies a slightly elongated but deep pit, the *fossa columellae*, into which fits the lower end of the *epipterygoid* (*columella cranii*); on the inner surface of the pterygoid, about the middle of its length, supported below by a small conical tubercle, lies the articular facet for the basiptyergoid process of the basisphenoid. As in *Sphenodon*, there is a cartilaginous meniscus between the basiptyergoid process of the basisphenoid and the pterygoid. This meniscus is prominent in the adult *Varanus* and Broom holds that it corresponds to the mesopterygoid of Fishes. The pterygoid in *Varanus* does not articulate with the vomer as it does in *Sphenodon*, *Uromastix*, the Crocodilia and some

Chelonia. Unlike the case in *Lacerta*, the pterygoids of *Varanus* bear no teeth.

Between the pterygo-palato-vomerine bar on the outside and the ventral border of the inter-orbital and inter-nasal septum in the middle line, there is an elongated space called the *incisura piriformis* or the *lacuna pterygo-vomerina* of Siebenrock (fig. 1).

The *transverse* (*ectopterygoid* or *transpalatine*) is a small curved bone (fig. 1), the inner and posterior end of which embraces the transverse process of the pterygoid, while the anterior end fits against the maxilla and the maxillary process of the palatine. The internal concave border of the bone forms the outer boundary of the sub-orbital fossa, while its outer and dorsal convex border articulates all along its length with the jugal.

The *palatine* (figs. 1 and 14) is roughly H-shaped in appearance and has an irregular outline, with *three* differently shaped articulating processes : (1) the anterior process is narrow and elongated ; it is directed antero-mesially and articulates with the vomer in front ; it is therefore called the *vomerine process* ; (2) the posterior process is broad



TEXT-FIG. 14. Palatine of the right side ( $\times ca. 3$ ).

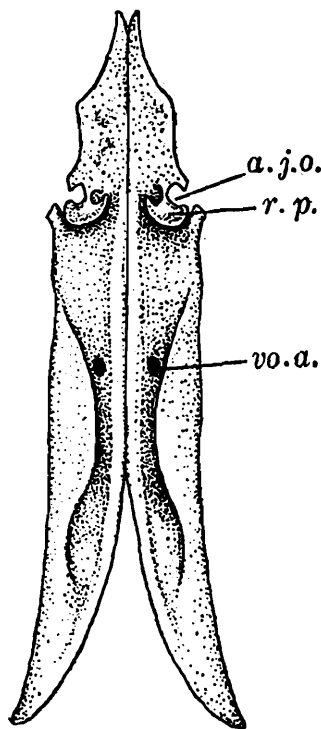
a., ventral view ; b., dorsal view.

mx.pr., maxillary process ; pty.pr., pterygoid process ; V.mx., foramen for the maxillary division of the Vth nerve ; vo.pr., vomerine process.

and is directed backwards and slightly outwards ; it is produced at its distal end into three small conical projections, which articulate immovably with the pterygoid behind ; this process is called the *pterygoid process* ; (3) the third or the outer lateral process is narrow at its origin but is expanded antero-posteriorly at its distal end, which forms an elongated articular surface for the maxilla on the outside ; the pointed posterior end of the process joins the jugal and transverse bones ; this outer process may be called the *maxillary process*. It is perforated by a foramen (*the maxillary or palatine foramen*), through which the *superior alveolar nerve* (maxillary branch of the Vth nerve) along with the *inferior orbital artery* and the *vena maxillaris* passes into the long bony canal (*canalis alveolaris superior*) of the maxilla. On the dorsal surface, the anterior concave border joining the vomerine and maxillary processes is produced into a shallow ridge on which are seated the pre-frontal and lacrymal bones. The palatines bear no teeth.

The upper surface of the palatine with the pterygoid behind forms the floor of the orbit, while the anterior smaller portion of the palatine with the vomer forms the floor of the nasal chamber,

The paired *vomers* (figs. 1 and 15) lie, one on each side of the middle line, in front of the palatines, and together form the median part of the roof of the anterior region of the buccal cavity. Looked at from the dorsal surface (fig. 15), the posterior two-thirds of each vomer appears like an open drain-pipe, the outer wall of which is higher than the inner and is slightly curved inwards. Along this drain-pipe canal of the vomer run the *dorsal palatine artery* and the *ramus frontalis ophthalmici* of the *Vth* nerve and the branch of the olfactory nerve going to the Jacobson's organ. Anteriorly each vomer at first flattens and then becomes pointed at the extreme anterior end, which articulates with and is covered over by the palatal process of the pre-maxilla. At about one-fourth of its length from the anterior end, each bone gives off a very small and slender rod-like process expanding into a small kidney-shaped outgrowth at its end (fig. 15), the process and its outgrowth being so thin and delicate as to be broken off in prepared skulls. In a whole skull this outgrowth projects into the ventral hollow concavity of the septo-maxillary and forms in life a ventral ingrowth into the cavity of the Jacobson's organ. Just behind this process, on each lateral border, there is an articular facet for articulation with the maxilla of each side. Posteriorly each vomer diverges from the middle line and articulates with the palatine of each side, while dorsally the greater part of the vomer is covered over by the septo-maxillary of each side and the nasal process of the premaxilla in the median line.



TEXT-FIG. 15. Dorsal view of the vomers ( $\times ca. 3$ ).

*a.j.o.*, aperture for the Jacobson's organ; *r.p.*, reniform or kidney-shaped process of each vomer which projects upwards into the cavity of the Jacobson's organ; *vo.a.*, vomerine aperture.

On the ventral surface, the anterior part of the vomers bears a low median ridge flanked by two long oblique ridges, one on each side. Enclosed between the posterior ends of these oblique ridges, there are

two minute foramina, the *vomerine apertures* (figs. 1 and 15), one on each side. Through each of these foramina comes out a small vein from the posterior part of the Jacobson's organ and enters the *sinus palatinus medius* lying immediately beneath the mucous membrane of the roof of the mouth at this place. About half an inch in front of these foramina, there are two large triangular apertures, each enclosed between the vomer and maxilla of its own side, just in front of the articular facet of the vomer fitting against the maxilla; these are the *openings of the Jacobson's organs* (fig. 1) into the buccal cavity.

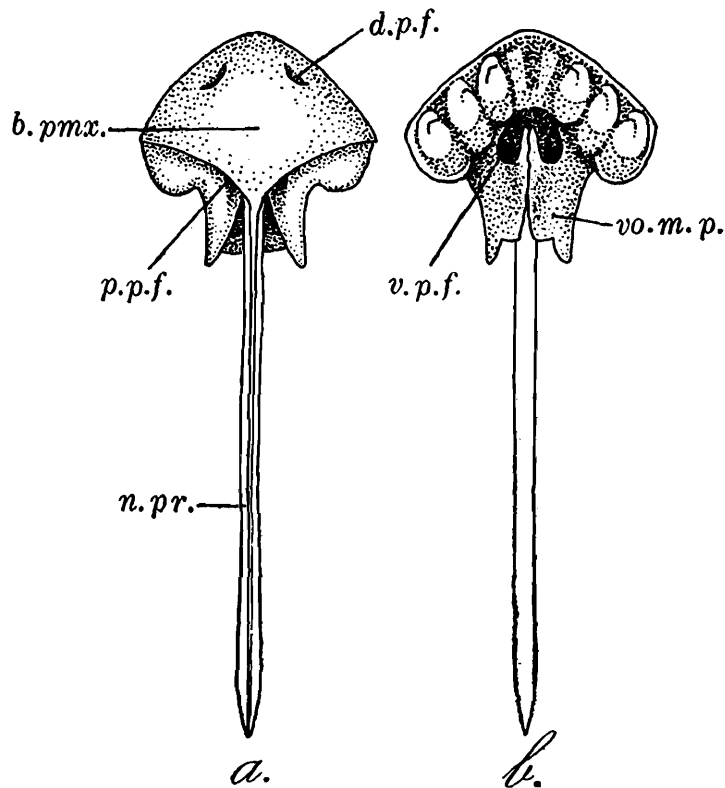
The vomers bear no teeth.

The paired *maxillae* (fig. 8a) are extensive bones, more or less triangular in outline, which form the greater part of the face of the lizard, with narrow alveolar and palatal portions. Each maxilla articulates in front with the pre-maxilla, mesially with the septo-maxillary and the vomer and through a piece of cartilage with the nasal process of the pre-maxilla, and posteriorly with the pre-frontal, the lacrymal, the jugal, the transverse and the maxillary process of the palatine. The anterior part of each maxilla is made up of a narrow vertical facial portion and a flattened nasal or rostral portion lying on each side of and in front of the septo-maxillary; this nasal portion forms the floor of the vestibule of the olfactory capsule. The posterior part of the maxilla is chiefly facial in position and forms a high lateral wall on the outer side of the hinder part of the olfactory chamber. The anterior concave border of the high lateral wall forms the posterior border of the anterior nares on each side. The alveolar portion of the maxilla is narrow except at its anterior end and at its junction with the vomer, where it forms flat palatal processes.

The alveolar portion of the bone is tunnelled through by the *canalis alveolaris superior*, which lodges the *superior alveolar nerve* and the *arteria maxillaris* (p.) 161. The cutaneous branches of this nerve come out through several (8-10) fine openings which lie in a long row, a little above the base of the outer facial part of the bone. Another aperture on the palatal surface between the first group of two teeth and the other group of six or seven transmits the palatal branch of the superior alveolar nerve.

The *pre-maxillae* (figs. 1, 4, 8a and 16) of the two sides are united to form a single median *pre-maxilla*, which forms a triangular rostral *body* at the anterior end of the skull and gives off posteriorly a long median laterally compressed sabre-shaped process, the *nasal process*. The posterior end of the nasal process is wedged in between the nasals and extends behind to meet the frontals beneath the nasals, while along the greater part of its length, it divides the two septo-maxillaries from each other and supports the cartilaginous inter-nasal septum behind. The median rostral portion (*body*) gives off on the ventral surface a short *vomero-maxillary process* on each side; these two processes meet in the middle line and form the anteriormost part of the hard palate, articulating behind with the vomers and laterally with the maxilla of each side. At the junction of the two vomero-maxillary processes in the mid-ventral line, each process is produced into a ridge, the two ridges together forming

a double median ridge projecting in front and overhanging the ventral pre-maxillary foramina.



TEXT-FIG. 16. Pre-maxilla ( $\times ca. 3$ ).

a., dorsal view : b., ventral view.

b.pmx., body of the pre-maxilla ; d.p.f., dorsal pre-maxillary foramen ; n.pr., nasal process of the pre-maxilla ; p.p.f., posterior pre-maxillary foramen ; v.p.f., ventral pre-maxillary foramen ; vo.m.p., vomeromaxillary process.

Three pairs of foramina are seen on the united pre-maxillae. A pair of transversely elongated slit-like foramina perforate the dorso-lateral surfaces of the pre-maxillae. These *anterior dorsal pre-maxillary foramina* look like anterior nasal apertures and lead behind into the two *posterior pre-maxillary foramina*, lying one on each side of the root of the nasal process on the pre-maxilla. At the extreme anterior end of the hard palatal vomeromaxillary processes, there are a pair a *ventral pre-maxillary foramina* which also lead into the posterior pre-maxillary foramina. The ventral foramina transmit the anterior small branches of the arteria maxillaris, while the anterior and posterior foramina transmit the *ramus frontalis ophthalmici* branch of the Vth nerve.

The united premaxillae generally carry 8 small teeth on the inner side of their margin.

## VI. The Lower Jaw.

The *lower jaw* (fig. 17) consists of two long slightly curved rami, which are united together at their anterior ends through a bony symphysis. Each ramus consists of six bones : the *articular* (+*pre-articular*), the *angular*, the *supra-angular*, the *splénial*, the *coronoid* and the *dentary*. The *articular*, with which is united the pre-articular, forms the *hinder*



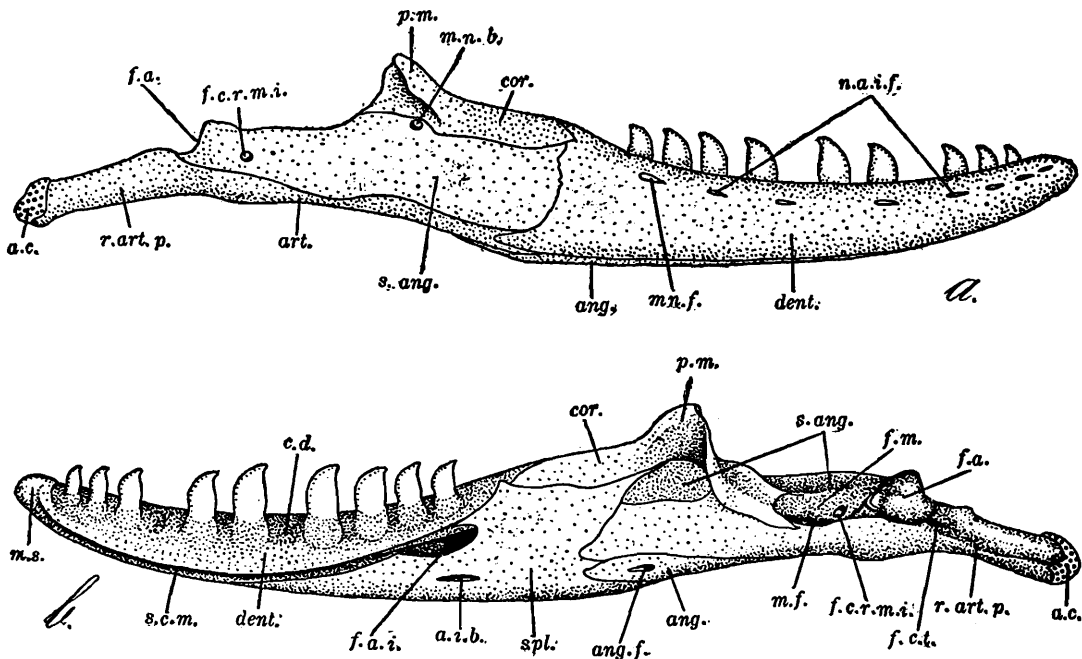
proximal end of the mandible. It is an elongated bone, the posterior part of which is strong and stout, while the anterior part is thin and vertical. The posterior stout part bears on its dorsal surface a transversely concave facet (*fovea articularis*) for articulation with the lower end of the quadrate. The part of the bone behind the articular facet is called the *post-articular process* (*processus retro-articularis*). The outer upper border of this process forms the ventral boundary of the tympanic membrane (fig. 11), while its dorsal surface behind the fovea articularis is depressed to form a shallow *fossa retro-articularis*, at the anterior end of which there is an aperture for the entrance of the *chorda tympani nerve*. The posterior end of the articular is tipped with a piece of cartilage on which is inserted the *musculus depressor mandibulae* (fig. 11). The thin vertical anterior part of the articular fits against the inner surface of the ventral part of the supra-angular. The articular extends over half the length of the mandible on the inner side, and is, in fact, the longest of all the bones of the lower jaw.

Closely fitting against the part of the articular lying in front of the fovea articularis is the *supra-angular*, visible chiefly on the outer surface of the mandible, although partially visible also on the inner and dorsal surfaces. This is a stout laterally compressed bone which expands posteriorly to form a depressed surface, and grips the vertical surface of the articular immediately below and in front of the fovea articularis. About the middle of its length, the supra-angular is produced dorsally into a flat triangular process which fits into the coronoid and is, therefore, called the *coronoid process*.

The supra-angular bears a number of foramina. Close to its posterior end, running through the thickness of the bone from the inner to the outer surface, there is a canal-like perforation into which enters, from the inner surface, the *nervus cutaneus recurrens maxillae inferiores* branch of the mandibular division of the Vth nerve. This nerve comes out on the outer surface almost opposite the leading-in foramen and supplies the skin of this region. Just in front of this foramen, on the inner surface of the mandible, bounded ventrally and internally by the articular, and dorsally and externally by the supra-angular, there is a large elliptical fossa, the *fossa Meckelii*, at the anterior end of which lies the *mandibular foramen*, through this foramen the main trunk of the *mandibular division* of the Vth nerve and the mandibular artery enter the lower jaw, while the mandibular vein comes out of this foramen. The mandibular nerve gives off several branches: one of them comes out through a foramen on the outer surface of the coronoid process of the supra-angular; another branch canalises the supra-angular all along its length, but the main trunk of the nerve runs in a ventral canal formed by the apposition of the articular and the supra-angular as the *nervus alveolaris inferior*.

When the articular and supra-angular are fitted together, there remains an elongated cleft between the anterior thirds of their ventral borders; this cleft is filled up in the complete lower jaw by the *angular*, which is a short and thin splint-like bone, being, in fact, the smallest of the six bones of the mandible. The greater part of the angular is wedged in between the articular and the supra-angular, while a

small anterior part lies in between the dentary on the outside and the splenial on the inside. About the middle of its length, the angular bears a foramen which leads into the *canalis alveolaris inferior*, and transmits the angular branch of the *nervus alveolaris inferior*.



TEXT-FIG. 17. The mandible ( $\times ca. 2$ ).

a. from the outer side; b. from the inner side.

a.c., articular cartilage; a.i.b., foramen for a branch of the *nervus alveolaris inferior*; ang., angular; ang.f., angular foramen; art., articular; c.d., crista dentalis; cor., coronoid; dent., dentary; f.a., fovea articularis; f.a.i., foramen for the main trunk of the *nervus alveolaris inferior*; f.c.r.m., foramen for the cutaneous recurrens maxillae inferiores branch of the mandibular division of the Vth nerve; f.c.t., foramen for the chorda tympani branch of the VIIth nerve; f.m., fossa Meckelii; m.f., mandibular foramen for the entrance of the mandibular division of the Vth nerve and the mandibular artery; m.n.b., foramen for a branch of the mandibular nerve; mn.f., mental foramen; m.s., surface of the mandibular symphysis; n.a.i.f., foramina for the branches of the *nervus alveolaris inferior* (mandibular division of the Vth nerve); p.m., processus messetericus; r.art.p., processus retro-articularis; s.ang., supra-angular; s.c.m., sulcus cartilaginis Meckelii; spl., splenial.

The *dentary* forms the greater part of the distal half of the mandible. Its inner surface is partially covered by the *splenial*, while on its outer surface it is fully exposed and presents a long row of eight foramina, the most posterior of which is called the *mental foramen* for the exit of the *mental branch* of the inferior alveolar nerve. The bone is canalised all along its length by the *nervus alveolaris inferior*, which gives off several branches, each coming out of one of the eight foramina of the row. The upper inner border of the dentary, called the *crista dentalis*, bears nine teeth. Along its ventral and inner border runs an open channel, narrow in front but wide behind, called the *sulcus cartilaginis Meckelii*, into which fits the persistent part of the *Meckel's cartilage*. The anterior end of the dentary is slightly flattened on its inner surface and fits against a similar surface of the dentary of the other side to form the *symphysis mandibularis*. The posterior end of the dentary has a concave border and a deep notch into which fits the anterior end of the supra-angular.

The *splénial* consists of a thin vertical quadrangular part and an elongated horizontal splint-like part. The vertical part partially covers internally a part of each of the articular, supra-angular, coronoid and dentary bones and serves to hold all these bones together, while the lower horizontal part forms the inner surface of the ventral border of the mandible and serves to hold the angular in position. On the inner surface of the mandible, between the anterior border of the splénial and the lower border of the dentary, there is a large elliptical notch, the greater part of which lodges the posterior end of the Meckel's cartilage, while at the bottom of the notch there is a foramen through which the *inferior alveolar nerve* enters the dentary.

The *coronoid* is an elongated triangular bone which is slightly twisted and is seated on the coronoid process of the supra-angular. It articulates posteriorly with the articular and the supra-angular and anteriorly with the splénial and the dentary. Along its ventral border, it presents a shallow groove into which fits the upper border of the coronoid process of the supra-angular. The posterior end of the bone forms the anterior boundary of the mandibular foramen in the fossa Meckelii, while the vertex of the bone in the complete skull projects upwards into the lateral temporal fossa to form the *processus messetericus*. The outer posterior border of the coronoid along with the upper border of the supra-angular serves for the attachment of the adductores mandibulae externus and medius muscles.

Of the six bones of the lower jaw, the articular alone is an endochondral ossification, while the other five are dermal bones.

## VII. Temporal arcades and fossae and other large vacuities.

The temporal region of the skull is strongly built and bears a lateral bridge or arcade called the *superior temporal arcade* (figs. 3 and 8a), formed by the post-orbital and the squamosal; a second arcade, the *inferior temporal arcade*, formed by the jugal and quadrato-jugal in *Sphenodon* and the Crocodilia amongst recent reptiles, is absent in *Varanus*, there being no quadrato-jugal in *Varanus*. We get three fossae in the temporal region: (1) a more or less triangular *superior temporal fossa* (figs. 4 and 10) on the roof of the skull on each side, bounded externally by the superior temporal arcade and internally by the parietal and supra-temporal; (2) a confluent *lateral* and *inferior temporal fossa* bounded above by the superior temporal arcade, below by the pterygoid and behind by the quadrate; and (3) a *post-temporal fossa* (*foramen retro-temporale* of Siebenrock) on the posterior aspect of the skull (fig. 6), which is more or less triangular in outline and is bounded above by the post-temporal process of the parietal and below by the supra and ex-occipitals and the pro-otic. In life, these temporal fossae are filled in by the adductor mandibulae muscles and the extensor muscles of the head.

Lying in front of each superior temporal fossa is the incomplete *supra-orbital fossa* (fig. 3) on each side, bounded by the supra-orbital and pre-frontal in front and the frontal and post-orbital internally and behind. It is incomplete on its outer and hinder aspects, as there

is no bony connection between the supra-orbital and the post-orbital, the two being joined only by a cartilaginous bar.

On the ventral surface of the skull in its posterior region, there is a large quadrangular vacuity on each side, bounded internally by the outer edge of the floor of the cranium and externally by the quadrate and the quadrate process of the pterygoid. In the living condition, the tympanic membrane stretches across the hinder part of this vacuity, which is really the *cavity of the middle ear*. In front of these two vacuities, lying beneath the optic capsules, there are two elongated oval apertures, one on each side, surrounded by the pterygoid, transverse and palatine bones. These are the *sub-orbital fenestrae*. In the middle, there are two large cavities lying one on each side of the parasphenoid and the inter-orbital septum in the mid-ventral line, and bounded externally by the pterygoids and palatines: these (fig. 1) are called the *incisura piriformis* (*inter-ptyergoid fissures*). In front of these fissures there are a pair of large elongated elliptical openings, the posterior portions of which form the *choanae* or the *internal nares* (fig. 1).

### VIII. The Foramina of the Skull.

#### (a) Dorsal Surface (fig. 4).

1. The *dorsal pre-maxillary foramina* are a pair of small slit-like apertures, one on each side of the middle line, on the dorso-lateral surfaces of the body of the united pre-maxillae. In a dry skull they look like a pair of external nostrils. Through these emerge two short terminal branches of the *ramus frontalis ophthalmici* of the deep ophthalmic division of the Vth nerve to supply the skin of the snout.

2. The *posterior pre-maxillary foramina* are a pair of small apertures, one at each angle between the median nasal process of the pre-maxilla and the body of the pre-maxilla. These apertures lead through very short canals within the united pre-maxillae to the dorsal pre-maxillary foramina. The *ramus frontalis ophthalmici* enters the pre-maxilla through each of these two apertures.

3. The *anterior septo-maxillary foramina* are a pair of apertures, at the anterior end of each septo-maxillary. Each of these transmits a lateral twig of the *ramus frontalis ophthalmici* along with a small vein.

4. The *dorsal septo-maxillary foramina* are a pair of small apertures as shown in fig. 4. They also transmit a branch of the *ramus frontalis ophthalmici* of the Vth nerve.

5. The *posterior septo-maxillary foramina* are a pair of small apertures, each at the posterior end of each septo-maxillary. The *ramus frontalis ophthalmici* enters this foramen to run forwards along the inner border of the septo-maxillary all along its length.

6. The *anterior narial openings* are a pair of oval apertures, one on each side on the maxillae. Each is bounded anteriorly by cartilage and posteriorly by the ascending anterior border of the maxilla. These openings lead forwards on each side into the vestibule which turns backwards into the olfactory chamber proper, opening behind into the choanae or internal nares. In a dry skull, therefore, the posterior end alone of the place for the olfactory chamber represents anterior nares proper (fig. 4).

7. The *parietal foramen* is a prominent median aperture lying in the middle line of the united parietals. It lodges the parietal organ.

(b) *Ventral Surface* (fig. 1).

1. The *ventral pre-maxillary foramina* lie on the ventral surface of the pre-maxilla on each side of the anterior end of the median ridge. A branch of the *arteria maxillaris* comes out of each of these foramina to supply the mucous membrane of this region.

2. The *apertures for the Jacobson's organs* are two large triangular apertures, one on each side, between the anterior part of each vomer and the palatal process of the maxilla. The Jacobson's organs communicate through these apertures with the buccal cavity, the apertures on the mucous membrane of the roof of the mouth in a whole specimen being slit-like in appearance.

3. The *anterior maxillary foramina* are a pair of apertures, each situated just on the outside of the aperture for the Jacobson's organ. Through this aperture, the *superior alveolar nerve* and the *arteria maxillaris* leave the alveolar canal of the maxilla and run forwards supplying branches to the mucous membrane of the anterior region of the hard palate.

4. The *vomerine apertures* are a pair of apertures on the vomers lying one on each side of the middle line. A venule from the Jacobson's organ comes out through each of these apertures and enters the *sinus palatinus medius*.

(c) *Lateral Surface* (figs. 2a, 3 and 7a).

1. The *fenestra ovalis* is a small aperture, lying at the antero-lateral end of the ex-occipital and bounded anteriorly by the pro-otic. It lies immediately above the fenestra rotunda being separated from it by a narrow bony ridge. The inner end of the stapes fits into the fenestra ovalis. In dry skulls, the fenestra ovalis is seen to open internally into the cavity of the internal ear but sometimes the inner cartilaginous end of the stapes remains and clogs the fenestra.

2. The *fenestra rotunda* is a large elliptical aperture which lies immediately below the fenestra ovalis and is bounded by the ex-occipital except at its anterior end where it is closed by the *tuberculum spheno-occipitale* cartilage. The aperture leads into a small space the *recessus scalae tympani*, in which lies the *saccus perilymphaticus*, the outer wall of which forms the *secondary tympanic membrane* closing the fenestra rotunda. On the posterior wall of this fenestra runs the *glossopharyngeal nerve* (IXth) which leaves the fenestra at its posterior end.

3. The *posterior facial foramen* is a very small aperture lying in front of the fenestra ovalis at a slightly higher level. It perforates the pro-otic bone and is overhung by the backwardly directed conical process of the pro-otic (*otosphenoidal crest*). The *hyomandibular division of the facial* (VIIth) nerve leaves the skull through this foramen.

4. The *anterior facial foramen* is also a small aperture lying in front of the posterior facial foramen and perforating the pro-otic bone. Through it the *palatine branch of the facial nerve* leaves the skull.

5. The *canalis vidianus (ductus caroticus)* is a short canal which perforates the basisphenoid bone on each side. Its posterior opening lies in front of the anterior facial foramen at a slightly lower level. Through it the *palatine division of the facial nerve* and the *internal carotid artery* perforate the basisphenoid bone to run forwards. During their passage through the *canalis vidianus*, the internal carotid gives off an *intra-cranial branch* which enters the cranial cavity through the hypophysial fossa, while the palatine branch of the internal carotid and the palatine branch of the facial come out through the anterior opening of the vidian canal to run forwards on the roof of the mouth. The palatine branch of the seventh nerve receives a *sympathetic branch from the ninth nerve* (fig. 13) and is, therefore, called the *vidian nerve*, which gives the name *canalis vidianus* to the passage through the basisphenoid.

6. The *optic fenestrae* (figs. 2a, 8a and 9) are two large oval apertures, one on each side, for the exit of the optic nerves. The two minute orbito-sphenoids enclose the optic chiasma between them, but as the inter-orbital septum lies in the middle line immediately below these bones, the common optic fenestra above is seen to be divided into two fenestrae ventro-laterally, each providing an exit for the *optic nerve* of its own side. Each optic fenestra is thus bounded by the orbito-sphenoid externally and the inter-orbital septum internally.

7. The *orbito-nasal canal* is a large oval aperture bounded internally by the pre-frontal and externally by the lacrymal. It lies at the extreme anterior angle of the orbit and is hidden from the lateral surface by the outer conical process of the lacrymal. Through this aperture, the orbit is placed in communication with the nasal chamber.

8. The *lacrymal foramen* is a small aperture perforating the ventral part of the lacrymal bone and lying below the orbito-nasal canal.

9. The *maxillo-palatine foramen* lies below the lacrymal foramen and perforates the outer maxillary process of the palatine bone. Through this aperture, the *maxillary division of the trigeminal nerve* enters the upper jaw and continues forwards into the bony canal of the maxilla as the *superior alveolar nerve*, giving off branches all along its length to the skin on the outside of the maxilla through a row of minute apertures all along the outer surface of the lower border of the maxilla.

#### (d) *Posterior Surface* (fig. 6).

1. The *foramen magnum* is the large median aperture, almost circular in outline, at the posterior end of the skull. It is bounded by the four occipital bones and forms an important landmark where the medulla oblongata of the brain passes out into the spinal cord.

2. The *foramen lacerum posterius + hypoglossal foramen* is an obliquely oval aperture on each side of the foramen magnum perforating the ex-occipital. It transmits the *pneumogastric* or *vagus* (X),

*spinal accessory* (XI) and *hypoglossal* (XII) nerves and the *vena cerebialis posterior branch* of the *internal jugular vein* and the *occipital branch* of the *internal carotid artery*.

(e) *Longitudinal Section* (figs. 2b, 8b, 10 and 13).

1. The *hypoglossal foramen* is a small rounded foramen situated on the ex-occipital a little in front of its posterior border. It lets through the *hypoglossal nerve* and opens externally into the jugular foramen or foramen lacerum posterius.

2. The *foramen for the spinal accessory nerve* is a very small foramen lying just above the hypoglossal foramen. This foramen, like the hypoglossal, opens into the jugular foramen and transmits the *spinal accessory nerve*.

3. The *jugular foramen* is a large dorso-ventrally elongated aperture situated just in front of the hypoglossal and spinal accessory foramina. The *vagus nerve* and the *vena cerebialis posterior branch of the internal jugular vein* leave the cranial cavity and the *occipital branch of the occipito-vertebral artery* enters through this foramen. The hypoglossal and spinal accessory foramina open into the jugular foramen and consequently the foramen on the posterior surface of the skull is a combined foramen lacerum posterius and hypoglossal foramen (*vide supra*).

4. The *foramen perilymphaticus* or *glossopharyngeal foramen* is a fairly large oval foramen at the junction of the pro-otic, opisthotic part of the ex-occipital and the basi-occipital. Through it, the *glossopharyngeal nerve* leaves the cranial cavity, while the *ductus perilymphaticus* enters the cranial cavity.

5. The *foramen acusticum posterius* lies about a quarter of an inch above the foramen perilymphaticus at the junction of the pro-otic and opisthotic bones. It transmits the *ramus acusticus posterior* division of the auditory nerve.

6. The *foramen acusticum anterius* is a small foramen on the inner wall of the pro-otic lying anterior to and at the same level with the *foramen acusticum posterius*. This foramen transmits the *ramus acusticus anterior* division of the auditory nerve.

7. The *facial foramen* is a small aperture lying below and slightly anterior to the *foramen acusticum anterius*. The *facial nerve* (VII) leaves the cranial cavity through this foramen and divides within the bone into two branches which emerge separately on the outside of the skull through the anterior and posterior facial foramina.

8. The *foramen for the abducens nerve* lies on the dorsal surface of the anterior part of the basisphenoid bone. This nerve perforates the base of each alar process by a very short canal and comes out through a *foramen* in the dorsal part of the hypophysial fossa.

9. The *hypophysial fossa* appears in a longitudinal section as a triangular pit, in the dorsal part of which opens the foramen for the abducens nerve, while laterally there is a large *foramen leading into the*

*canalis vidianus* through which the intra-cranial branch of the internal carotid enters the hypophysial fossa and in which is lodged one of the two lateral diverticula of the recessus infundibularis.

### 3. STREPTOSTYLISM AND KINETISM.

Stannius applied the term *streptostylic* to describe those skulls in which the quadrate was freely movable. The Lacertilian skull shows a typical streptostylic condition in that "the bony quadrate is isolated from the epipterygoid (*columella cranii*) and is only connected somewhat loosely to the pterygoid below and the parotic process above by ligament" (5, p. 433). In *Varanus*, the inner border of the lower end of the quadrate is movably articulated with the pterygoid, while dorsally the quadrate is joined to the squamosal and supra-temporal above and the paroccipital process of the ex-occipital behind in such a manner as to render movement possible. Further, the lower end of the quadrate (*condylus mandibularis*) articulates movably with the mandible. The quadrate, therefore, is movable at all its joints with the other bones and consequently the skull is truly *streptostylic*.

In addition to streptostylism, the skull of *Varanus*, like that of other Lacertilia, shows "a certain degree of looseness and consequent power of motion between the dermal roofing bones (parietals and frontals) and the posterior brain-case." This phenomenon has been termed *kinetism* of the skull by Versluys *et al* (6). We have already seen that the occipital bones (supra-occipital, ex-occipitals and the basi-occipital) are immovably articulated with the basi-sphenoid and the pro-otic. These six bones form a compact rigid structure which moves as one piece and is termed, for convenience, the *occipital segment* (posterior brain-case). The remaining part of the skull consisting of the quadrate, squamosal, supra-temporal, parietal and frontal on the one hand, and the pterygoid, palatine, transverse, maxilla, and pre-maxilla, on the other, together constitutes the *maxillary segment*. These two segments move on each other at various places.

The junction between the supra-occipital and the parietal is formed of fibrous tissue and thus forms a loose vertically movable joint, the movement being limited only by the cone-shaped processus ascendens tecti synotici cartilage which fits closely into the parietal fossa. Similarly, the anterior superior process of the pro-otic is connected loosely with the lateral bevelled border of the parietal. The basipterygoid processes of the basisphenoid are movable on the pterygoids, as the articulation through the cartilaginous meniscus forms a synovial joint. Lastly, the paroccipital process of the ex-occipital is movably articulated with the quadrate and the supra-temporal through the intercalary cartilage. It must, further, be noticed that in front of the "occipital segment" the lateral walls and floor of the cranium, as well as the inter-orbital septum are composed only of cartilage and membrane; these structures are therefore not rigid and would permit of a slight movement.

It is thus clear that there are *four* places (not *three* as stated by Edgeworth, (4, p. 62) at which the occipital segment is movable



on the maxillary segment. The movement is brought about by the action of the protractor pterygoidei, pterygo-sphenoidalis posterior and pterygo-parietalis muscles (5, p. 434) and consists, as pointed out by Bradley (2, p. 484), of a movement of elevation and depression of the maxillary segment on the occipital segment which itself remains fixed. The kinesis, therefore, is very marked in *Varanus* and such a skull is termed *metakinetic*.

#### 4. SUMMARY.

1. The skull of *Varanus* is well ossified, although there are important cartilaginous structures, chief of which are the olfactory capsules, the planum supra-septale and its lateral extensions, the tuberculum sphenoccipitale and the intercalary cartilage.

2. The muscles inserted on the basi- and ex-occipitals and also on the tuberculum sphenoccipitale are described. Similarly, the origin and insertion of the adductor mandibulae and depressor mandibulae muscles have been included.

3. All the foramina of the skull have been listed, and the nerves and blood-vessels entering or coming out of these foramina have been identified and described.

The foramen internum of Siebenrock has been identified and it has been shown that it transmits the VIth nerve and not a branch of the internal carotid artery, as he believed.

4. The different bones have been compared with those of *Lacerta* and *Sphenodon* and the differences noted. The orbito-sphenoids and their exact relationship with contiguous cartilages have been described and sketched, these having been incorrectly represented by Reynolds.

5. The diagrams of previous authors have been critically examined and corrected and new standard diagrams of the skull have been provided.

6. The streptostylism and metakinesis of the skull have been described.

#### 5. LIST OF REFERENCES.

1. Boulenger, G. A.—*Reptilia and Batrachia in the Fauna of British India* (London : 1890).
2. Bradley, O. Charnock—The muscles of mastication and the movements of the skull in Lacertilia. *Zool. Jahrb. Anat. Abth.* XVIII, 1903.
3. Bütschli, Otto—*Vorlesungen über vergleichende Anatomie*, Lieferung 1, (Berlin : 1910).
4. Edgeworth, F. H.—*The Cranial Muscles of Vertebrates* (Cambridge : 1935).
5. Goodrich, E. S.—*Studies on the Structure and Development of Vertebrates* (London : 1930).
6. Ihle, Kampen, Nierstrasz und Versluys—*Vergleichende Anatomie der Wirbeltiere* (Berlin : 1927).
7. Reynolds, S. H.—*The Vertebrate Skeleton* (Cambridge : 1913).

8. Schimkewitsch, W.—*Lehrbuch der vergleichenden Anatomie der Wirbeltiere*, (Stuttgart: 1921).
9. Siebenrock, F.—Skelet der Lacerta. *Sitz. AK.wiss. Wien*, CIII, 1894.
10. Smith, Malcolm A.—Reptilia and Amphibia, II, in the *Fauna of British India*, (London: 1935).
11. Thomson, J. A.—*Outlines of Zoology* (Oxford: 1929).
12. Wettstein, Otto von.—Rhynchocephalia in Kükenthal and Krumbach, *Handbuch der Zoologie* (Berlin und Leipzig: 1932).