On the Development of the Skull of Leptodeira hotamboia.

By

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With Plates 12 and 13 and 6 Text-figs.

Introduction.

Accounts of the development of the Ophidian skull are not numerous. Rathke as early as 1889 described the development in Coluber natrix from a macroscopic point of view. Parker (1878) gave a full description, excellently illustrated, of Tropidonotus natrix, but his work is out of date and it is evident that he was misled in several points, especially over the condition of the orbito-temporal region. He does not appreciate the reduced state of the side-wall in this region, and claims to have identified both an orbito-sphenoid and an alisphenoid. Gaupp makes many valuable contributions to the understanding of the snake skull, but, as he had only a single specimen of a Tropidonotus natrix embryo, he was unable to settle definitely the doubtful points in Parker's work. Peyer in 1912, with the intention of bringing Parker's work up to date, gave an excellent account of the stages of development in Vipera aspis, but he failed to settle the problem of the orbito-temporal region satisfactorily. De Beer (1926), in his work on the orbito-temporal region, discussed the problem of the ophidian alisphenoid in the light of the present-day understanding of that bone, but had only one specimen of Tropidonotus and one of Pseudechis at his disposal. He suggested that I should undertake a full investigation of the developmental stages. The work was begun primarily in the hope of reaching a solution to the vexed problem of the 'alisphenoid'. In the course of the investigations several interesting points have come up: the
posterior attachment of the nasal capsule, the probable absence of an extracolumella and the nature of the columella attachment to the quadrate; the homology of the fenestra cochleae.

The material for study has been a series of five different stages of embryos of *Leptodeira hotamboia*. A batch of eggs, about a month old from fertilization, was given to me by the Director of the Snake Park, Port Elizabeth, South Africa. I kept them in damp earth in a temperature warm enough to force development, and took stages every four or five days. The first four stages were taken within the second month of development, and vary from 6½ to 8 mm. in head-length. The fifth was taken after a gap of four or five weeks, a few days previous to hatching, head-length 10 mm.

Half the embryos were killed and fixed in Bouin's mixture, half in corrosive acetic mixture. The heads were stained in toto in borax carmine, sectioned, and the sections stained in picronigrosin. A blotting-paper and wax model was reconstructed from serial sections of the earliest stage.

The work has been carried out in the Department of Zoology and Comparative Anatomy, University Museum, Oxford, and I am indebted to Professor Goodrich and Mr. de Beer for their kindly advice and help, and for the loan of slides.

**Basal Plate and Occipital Region.**

In the model made from a four-week-old embryo of *Leptodeira hotamboia*, head-length 8 mm., illustrated in figs. 1 and 2, Pl. 12, the cartilaginous basal plate shows a dorsally concave floor suspended between the otic capsules, and extending from the foramen magnum posteriorly to the fenestra hypophyseos anteriorly. It is rectangular in shape; in an antero-posterior direction it inclines downwards in a steep curve so that the foramen magnum faces in a posteroventral direction. The anterior margin is thickened to form a crista sellaris, from the antero-lateral corners of which the trabeculae extend forward. The basal plate extends unusually far forward. When compared with *Lacerta* the distance between the facial foramen and the crista sellaris is exceptionally long. This portion in
Leptodeira forms a third of the whole plate. The basicranial fenestra, circular in outline, is situated entirely within this anterior third and therefore in front of the auditory capsules. Parker (1898) figures the same excessive length of the anterior end of the basal plate for Tropidonotus; Gaupp (1906) also for Tropidonotus, and Peyer (1912) for the viper, illustrate the same condition. It is probably universal for snakes.

The notochord extends forward in a ridge down the centre of the basal plate. In most of the specimens it does not extend as far as the basicranial fenestra. In Stage IV alone it was traced into the filling tissue of the fenestra.

The basal plate is continuous posteriorly with the occipital region. Its posterior margin is thickened to form a continuous crescentic condylar mass as described by Gaupp (1900) for Lacerta. Peyer's diagrams of the viper show the same structure. From the postero-lateral angles of the basal plate the occipital arches extend upwards and meet dorsally to form the tectum posterius, the whole occipital region forming a rough pentagon around the foramen magnum. The greater part of the tectum is apparently formed from the occipital region as described by Gaupp (1906, Tropidonotus), and Peyer (1912, Vipera aspis), but at its anterior end the otic capsules fuse with it, and may possibly contribute to its formation. The occipital arches are separated from the otic capsules by a posterior extension of the fissura metotica.

The foramina, through which the hypoglossal nerves pass, lie in the posterior lateral region of the basal plate. In all the specimens observed there are three foramina on each side, the most posterior lying in the occipital region. Peyer reports only two pairs of foramina in the viper. Parker (1898) says there is only one pair in Tropidonotus, but Gaupp (1900) and Chiarugi (1889) both find four. In Stage I of Leptodeira a fourth pair of foramina are present, but no nerve-roots pass through, and in the later stages they are lacking. The number of nerve-roots sometimes exceeds the number of foramina.

The vena cerebrah's posterior, as in Lacerta (Versluys, 1896, and Gaupp, 1900), passes out of the cranial cavity
between the occipital arch and the atlas, that is, through the foramen magnum, not through the fissura metotica as in mammals.

**Otic Region.**

The otic region of the skull consists primarily of paired lateral auditory capsules connected ventrally by the anterior portion of the basal plate, and dorsally by the tectum posterius. But, as already pointed out, the tectum is formed almost entirely from the occipital region. In the region of the basal plate the auditory and occipital regions are confluent. An extensive fissure, the fissura metotica, separates the posterior part of the otic capsule from the basal plate. Posteriorly, the fissure bends upwards at right angles and extends between the otic capsule and the exoccipital region. Anteriorly, capsule and basal plate are fused through the basicapsular commissure. Immediately in front of the commissure is the foramen for the facial or seventh nerve, and a very slender bridge of cartilage, the prefacial commissure, separates the foramen from the antotic incisure. Quite frequently the prefacial commissure is lacking, and the facial foramen is without an anterior boundary. The facial foramen is situated in the angle between the anterior vestibular portion of the capsule and the cochlear prominence. The cochlear prominence is of the same proportions as in *Lacerta*, encroaching slightly on the basal plate. In front of the prefacial commissure, the anterior margin of the otic capsule with the lateral margin of the basal plate forms the hind border of the wide incisura antotica. But this will be discussed under the orbito-temporal region.

In Stage I, the modelled stage, of *Leptodeira hotamboia* the external relief of the auditory capsule is already fairly well defined. On the lateral wall the three semicircular canals with their ampullae are recognizable as slight prominences. The anterior semicircular canal is the most prominent, being separated from the rest of the capsule by definite grooves and forming the dorsal margin of the capsule. On the medial wall the utricular prominence is well defined and the anterior and pos-
terior semicircular canals are again recognizable. There is no suggestion of a crista parotica on the lateral wall of the capsule.

The interior of the capsule is very similar to the condition described by Peyer (1912) for Vipera aspis, an account based on Rathke's (1889) description of Coluber natrix. There is a large vestibular cavity containing the utriculus and its recessus, the sacculus, and the endolymphatic duct. A ventral cavity is partly divided off from the vestibular cavity by a cartilaginous septum, the crista vestibuli, but there is a wide-open connexion between the two. The ventral cavity contains the cochlea. The lateral semicircular canal is separated from the general vestibular cavity for a short distance by a cartilaginous septum. The anterior semicircular canal lies in a cavity almost completely separated from the vestibular cavity by a strong septum. There is no septum between the anterior and lateral ampullae. Posteriorly, a ventral cavity is separated from the vestibular cavity and contains the posterior ampulla and the adjoining portion of the lateral canal.

The anterior and posterior acustic foramina for the branches of the eighth, or auditory nerve, open on the median surface of the capsule. The anterior opening is situated on the medio-ventral aspect of the anterior portion of the cavum vestibuli, close above its separation from the cochlear prominence. The posterior opening is in the dorso-median wall of the cochlear prominence; its projecting lower lip causes the opening to face dorsally. The two foramina are completely separate even in Stage I.

The endolymphatic foramen is a small round opening, just large enough to allow the passage of the duct; it is situated some distance dorsally and posteriorly from the acustic foramina in the median wall of the utricular prominence. At this stage there is no indication of a previous confluence with the acustic foramina.

In the dorso-posterior aspect of the capsule there is an extensive gap in the wall of the prominence of the posterior semicircular canal. It persists without change of size up to Stage IV. In Stage V the ossified capsule shows no foramen. The aperture
in the cartilaginous capsule gives access to no nerve, blood-vessel, or duct, and is evidently merely an area of retarded chondrification.

The fenestra vestibuli in the lateral wall of the cochlear prominence is oval. The foot-plate of the columella auris almost fills it, and in early stages is indistinctly separated from the wall. In later stages the fenestra vestibuli is much larger than the foot-plate, which does not nearly fill it.

The fissura metotica has already been mentioned. It extends from the posterior edge of the basicapsular commissure backwards as a separating fissure between the basal plate and the otic capsule. At the posterior margin of the capsule, the fissure bends sharply upwards and its dorsal extension separates the otic capsule from the occipital arches. This posterior portion is very narrow and is more or less filled with tissue which in the adult is replaced by bone without deposition of cartilage. The anterior end of the fissura metotica widens out considerably and forms a distinct, though small, anterior division, known as the recessus scalae tympani (Gaupp, 1900). Medially, it is separated off from the rest of the fissure by a narrow downward projection of cartilage from the wall of the otic capsule. The projection comes in very close contact with the margin of the basal plate without actually fusing. Behind the projection the posterior division of the fissura metotica is known as the jugular foramen (Gaupp, 1900). It allows for the passage of the vagus nerve but no jugular vein passes through it. The posterior cerebral vein passes out from the cranial cavity between the basal plate and the atlas, and is joined by the vena cava lateralis to form the jugular vein. But Gaupp (1900) has pointed out that the jugular foramen rightly deserves that name in reptiles, because in very early stages a vessel, corresponding to the internal jugular vein of mammals, is present. It passes out from the cranial cavity through the jugular foramen to join the vena cava lateralis; later it atrophies, and is replaced by the posterior cerebral vein of the adult. In the earliest of my stages of Leptodeira the posterior cerebral is already well established, and there is no internal jugular vein.
According to Gaupp (1900), the usual course for the glossopharyngeus nerve is through the recessus scalae tympani in reptiles, not through the jugular foramen as in mammals. In Leptodeira hotamboia it penetrates the cartilage of the basal plate immediately below the median aperture of the recessus scalae tympani. It does not actually enter the recessus but passes through a channel in the cartilage of the basal plate below it. Its exit to the exterior is in close proximity to the jugular foramen. This nerve merges into the vagus ganglion, from which a branch passes forward to the pharynx and tongue, and this leaves little doubt that it is the glossopharyngeus.

But Peyer (1912) reports that the glossopharyngeus nerve in Vipera aspis actually passes through the posterior part of the fissura metotica, the jugular foramen. He also describes an 'undetermined' nerve which passes through the aperture medialis of the recessus scalae tympani, into the cochlear capsule, and out through the apertura lateralis. Rice (1920) suggests that the 'undetermined' nerve is the true glossopharyngeus and that Peyer has mistaken a branch of the vagus for the glossopharyngeus. Möller (1905) reports an intracapsular course for the glossopharyngeus in Vipera aspis. According to Rice's summary (p. 152) an extracapsular course is much more general, the turtles being the only reptiles which regularly show an intracapsular course. I can find no nerve in Leptodeira corresponding to Peyer's 'undetermined' nerve or Möller's glossopharyngeus. The course is the normal reptilian one, through the recessus scalae tympani, the only variation being that the margin of the basal plate has surrounded it. It is conceivable that in Vipera aspis the nerve has been surrounded by the capsular wall instead of by the basal plate, thus bringing about an intracapsular position.

The recessus scalae tympani is situated immediately behind the cochlear prominence. An aperture in the posterior floor of the cochlear capsule faces into the recessus. It is the fenestra cochleae and is situated directly below the fenestra vestibuli, a narrow strip of cartilage separating the two openings.

In transverse section (fig. 21, Pl. 13) the recessus scalae
tympani appears triangular, the three points of the triangle being
the lateral and medial walls of the auditory capsule and the edge
of the basal plate. There is a median aperture from the recessus
to the cranial cavity, and a lateral aperture to the exterior,
corresponding exactly to Gaupp’s figure (1900) of *Lacerta*.
The recessus scalae tympani, then, forms a series of three com-
municating spaces:

1. from the otic cavity to the exterior, through the fenestra
cochleae and lateral aperture;
2. from the otic cavity to the cranial cavity, through the
   fenestra cochleae and medial aperture;
3. from the cranial cavity to the exterior, through the medial
   and lateral apertures.

In early stages the recessus scalae tympani is filled with
a loose embryonic tissue in which are irregular gaps; these
later coalesce to form the perilymphatic sack. The perilymphat-
ic duct of the labyrinth cavity leads out through the fenestra
cochleae into the recessus scalae tympani, where it expands into
the perilymphatic sack. It then passes through the medial
aperture of the recessus and communicates with the sub-
arachnoidal lymph-spaces of the cranial cavity. In later stages
this communication is lost. The perilymphatic sack entirely
fills the recessus, and presses outwards through the lateral
aperture against the rudimentary tympanic cavity. The
bounding wall of the perilymphatic sack, where it fills the lateral
aperture, with the bounding wall of the tympanic cavity to-
gether represent the membrana tympani secundaria of *Lacerta*
(Gaupp, 1900), which closes the aperture lateralis of the recessus
scalae tympani. But in *Leptodeira* it scarcely deserves that
name. The bounding wall of the rudimentary tympanic cavity
is not very strong and it does not combine with the wall of the
perilymphatic sack and intermediate tissue to form the stout
membrane of *Lacerta*.

The relationship between the fenestra cochleae of reptiles and
the fenestra cochleae or rotunda of mammals is an interesting
problem. Gaupp, in 1900, disagreeing with the earlier work of
Versluys (1899), put forward the conjecture that the apertures
in mammal and reptiles were homologous. Admittedly, there are differences in the condition of Lacerta and man. In the latter the opening faces laterally, in the lizard ventrally. In man it faces towards the tympanic cavity with the membrana tympani secundaria stretched across it; while in the lizard the opening is from the otic cavity into the recessus scalae tympani, and has no membrane stretched across it, the membrana tympani secundaria being stretched across the apertura lateralis of the recessus. In man the perilymphatic spaces are entirely within the otic cavity; but in the lizard the perilymphatic sack protrudes through the fenestra cochleae into the recessus scalae tympani.

Gaupp supposes that the mammalian condition is brought about by the division of the primary fenestra cochleae of the reptile, or foramen perilymphaticum as he terms it, into the definitive foramen rotundum and cochlear aqueduct of the mammal.

He says: 'In Bezug auf die Lacertilier kann aber wohl als sicher gelten, dass das in der Ohrkapsel befindliche, in den Recessus scalae tympani führende grosse Foramen, aus dem der Saccus perilymphaticus herausstritt, ganz oder doch in der Hauptsache der Fenestra cochleae s. rotunda der Säuger entspricht, und es ist nur eine Einschränkung, die möglicherweise notwendig sein wird, nämlich die, dass sich vielleicht von ihm auch die als aquaeductus cochleae bezeichnete Öffnung ableitet' (1900, p. 515).

In accordance with this theory he believes that the membrana tympani secundaria of the mammal is only physiologically, not morphologically, homologous with the membrane of the same name in the lizard. It lies across quite a different aperture, and has an entirely capsular rim instead of being stretched from capsule wall to basal plate.

Gaupp (1902) demonstrated a primitive reptilian condition in Echidna, and believed that further investigation of mammalian skull ontogeny would show the division of the primary foramen perilymphaticum into fenestra rotunda and cochlear aqueduct. E. Fischer (1903) demonstrated in an embryo Semnopithecus a dividing process springing from the
anterior margin of the foramen perilymphaticum. Voit (1909) for the rabbit, Olmstead (1911) for the dog, Macklin (1914) and Kernan (1916) for the human embryo, and Terry (1917) for the cat, all demonstrate intermediate conditions in the division of the primary foramen perilymphaticum. Voit names the process the 'processus intraperilymphaticus'.

I have been enabled to examine sections of a cat embryo which are very similar to those illustrated by Terry (1917), and also sections of a mouse embryo, a ferret, and a hedgehog, and I do not agree with Gaupp's interpretation.

I believe that the fenestra rotunda of the mammal corresponds not to a portion of the primary fenestra cochleae, or foramen perilymphaticum, but, more or less closely, to the apertura lateralis of the recessus scalae tympani in reptiles.

Text-fig. 1 A and B give a diagrammatic comparison of the condition in the reptile and mammal. They represent transverse sections through the region of the fenestra cochleae and fenestra rotunda. In A (reptile) the perilymphatic sack is seen protruding from the labyrinth cavity, through the fenestra cochleae, into the recessus scalae tympani. The bounding wall of the sack makes a circular sweep from the rim of the fenestra cochleae; stretching down to the margin of the basal plate, it forms a membrane round the whole recessus scalae tympani which closes both lateral and medial apertures of the recessus. Its lateral extent from the margin of the fenestra cochleae to the basal plate comes in contact with the wall of the tympanic cavity and these two membranes, with the intermediate tissue, form a stout membrani tympani secundaria.

In B (mammal) the perilymphatic sack lies within the cochlear capsule. It protrudes slightly through a lateral aperture in the wall of the cochlear capsule, the fenestra rotunda, pressing against the wall of the tympanic cavity and forming with it the membrana tympani secundaria. The membrane is stretched from capsular wall to capsular wall, not from capsular wall to basal plate as in the reptile (A).

Nevertheless, I consider that the fenestra rotunda in B corresponds to the apertura lateralis in A, the membrana tympani
secondaria in both being homologous. I believe that the portion of the cochlear capsule enclosing the perilymphatic sack represents the recessus scalae tympani of the reptile which has become included within the capsule.

In a model of an embryo cat, lent by Mr. de Beer, of which Text-fig. 2 B (see next page) is a diagrammatic partial representation, the fenestra rotunda faces laterally, and the plane

![Text-fig. 1.](image)

of the membrana tympani secundaria is lateral. The primary foramen perilymphaticum faces caudally; its lateral margin is in the plane of the apertura lateralis and membrana tympani secundaria, but its medial margin is situated in a more internal plane, and its aperture opens into a reduced intracapsular recessus scalae tympani. The rudimentary processus intraperilymphaticus, it is true, suggests a division of the foramen perilymphaticum into fenestra rotunda and cochlear aqueduct, as Gaupp surmised, but only in the same sense that the margin of the basal plate in the reptile separates the apertura lateralis from the apertura medialis. In those mammals, the dog (Voit) and Semnopithecus (E. Fischer), in which the processus intraperilymphaticus is completed, it must close off the fenestra rotunda from the jugular foramen (Text-fig. 2 C, and Text-fig. 3), forming a posterior support to the membrana tympani secundaria. In this sense, that is, in function, it corresponds to the
separating bar between the recessus scalae tympani and jugular foramen of the reptile, but the two structures cannot be regarded as morphologically similar.
This transformation from the reptilian to the mammalian condition can readily be understood if we suppose that the very much enlarged cochlear duct of the mammal causes the enlarging cochlear capsule to encroach backwards at the expense of the basal plate. Text-figs. 2 A, B, and C represent such a transformation. In A (reptile) the fenestra cochleae faces into the recessus scala tympani. The arrows indicate the three communicating passages of the recessus (1) from the otic capsule to the exterior, (2) from the otic cavity to the cranial cavity, and (3) from the cranial cavity to the exterior.

The area surrounded by the dotted line represents the membrana tympani secundaria.

The ventral posterior region of the cochlear capsule expands in a posterior direction carrying with it the ventral end of the fenestra cochleae, or foramen perilymphaticum, which is drawn into a semicircular shape (Text-fig. 2 B).

In C the posterior enlargement of the cochlear capsule comes almost in contact with the wall of the vestibular cavity. The margin of the basal plate has been pressed back and the recessus scala tympani is surrounded by capsule and becomes largely included within the labyrinth cavity. A projection of cartilage, the processus intraplerymphaticus, divides the fenestra rotunda from the jugular foramen and the membrana tympani secundaria is stretched across the lateral aperture. The foramen perilymphaticum, facing caudally, would be the homologue of the fenestra cochleae of the reptile.

Text-fig. 3 is an enlargement of Text-fig. 2 C, to show the relations of the fenestra perilymphaticum, fenestra rotunda, and processus intraplerymphaticus. The dotted lines A-A and B-B show the planes through which the sectional diagrams, Text-fig. 1 B, and Text-fig. 4, are taken. Text-fig. 1 B, as already described, is a transverse section through the region of the foramen perilymphaticum. Text-fig. 4 is taken in a more horizontal plane and passes through the processus perilymphaticum. Text-fig. 4 corresponds very closely with Terry's (1917) figure of the cat and also with Fischer's (1903) figure of Semnopithecus.
Although the cochlear aqueduct of the mammal is separated from the fenestra rotunda by the processus intraperilymphaticus, it is not separated from the jugular foramen, as shown in C. The separating bar between the recessus scalae tympani and jugular foramen of the reptile may have been lost. More probably the backward expansion of the cochlear capsule has obliterated the original anterior division of the fissura metotica, and the mammalian cochlear aqueduct represents the anterior limit of the original jugular foramen. Whichever be the explanation, it makes little difference to the present argument. The recessus scalae tympani of the reptile, I take it, is that part
of the fissura metotica which is occupied by the perilymphatic sack. If the enlargement of the cochlear capsule in the mammal does carry it some distance caudally along the original extent of the fissure, it still represents the recessus scalae tympani. Through its lateral aperture the bounding wall of the perilymphatic sack still comes in contact with the tympanic cavity-wall to form the membrana tympani secundaria.

With reference to this membrane Rice (1920) makes a similar statement: 'I believe that the lateral part of the membrane filling the fenestra cochleae of stage 6 of Eumeces (corresponding to the filling of the lateral aperture of the recessus scalae tympani in Lacerta and stage 5 of Eumeces) may be safely homologised with the secondary tympanic membrane of the mammal, while the median portion (corresponding to the filling of the median aperture) occupies the position of the aqueductus cochleae of the mammal' (p. 152).

I have taken the description of the typical reptile from Gaupp's description of Lacerta (1900). At this point it would be well to consider how closely the other reptilian classes conform to this typical condition. It has already been shown that Leptodeira conforms very closely. Crocodilus at first sight appears rather different. The fenestra cochleae faces laterally instead of ventrally. The margin of the basal plate has grown up dorsolaterally in a processus basicapsularis which partially covers the aperture (Shiino, 1914). A stout membrana tympani secundaria is stretched from the upper edge of the fenestra cochleae to the edge of the processus basicapsularis; that is, from capsular wall to basal plate. In this Crocodilus is essentially reptilian; the aperture closed by the membrane is similar to the apertura lateralis of Lacerta, and the fenestra cochleae is an opening into the recessus scalae tympani.

Chrysemys marginata shows an interesting variation from the typical condition. The cochlea is larger than in Lacerta and has encroached backwards slightly at the expense of the basal plate. In this way the fenestra cochleae has assumed a vertical position, facing posteriorly, or caudally, into the recessus scalae tympani, and the floor of the recessus is
partly capsular. It would appear that the condition in the turtle is intermediate between the typical reptilian and mammalian conditions.

To summarize this discussion, I consider that the fenestra cochleae of the reptile, through which the perilymphatic duct makes its exit from the labyrinth cavity, does not correspond to the fenestra rotunda of the mammal. The fenestra rotunda corresponds to the apertura lateralis of reptiles. The membranes tympani secundaria corresponds morphologically as well as functionally with that of the mammal. The fact that the membrane stretches from capsule to capsule in the mammal, while in the reptile it is from basal plate to capsule, may be accounted for by the backward encroachment of the enlarging cochlear capsule at the expense of the basal plate.

These conclusions are somewhat similar to those of Versluys (1899).

He says: 'In ihrer Function und der Hauptsache nach auch in der Lage am Schädel entspricht diese Membran demnach der Membrana tympani secundaria der Mammalia, das Foramen jugulare aber der Fenestra rotunda' (p. 353).

Versluys's investigations were on the fenestra rotunda of the bird, and he compares the condition in bird and reptile. The goose he finds differs very little from the reptile, but for the fowl he describes a condition very similar to that I have described for the typical mammal.

'Der Recessus scalae tympani des Huhns is demnach ein abgetrenntes Stück des Jugularis-Canals, die Fenestra rotunda ein Theil des Foramen jugulare externum. Dagegen entspricht der Recessus scalae tympani der Lacertilia dem ganzen Jugularis-Canal, sein äusseres hoch vollständig dem Foramen jugulare externum. . . . Es (Fenestra rotunda des Huhns) ist jedoch bestimmt nicht das Loch, durch das der Ductus perilymphaticus aus der Labyrinthhöhle in den Recessus tritt' (p. 356).

Versluys's jugular canal corresponds to the recessus scalae tympani of Gaupp's terminology. Versluys believed that in the primary reptilian condition the jugular vein passed through the
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anterior division of the fissura metotica, the same section which contained the perilymphatic sack. He called this section the jugular canal, and its lateral aperture foramen jugulare externum, Gaupp’s apertura lateralis of the recessus scalae tympani.

Thus Versluys’s conclusions on the relation between fowl and reptile are that the fenestra rotunda of the fowl does not correspond to the fenestra cochleae of the reptile but to a portion of the apertura lateralis of the recessus scalae tympani.

The Columella Auris.

The columella auris is a slender rod of cartilage; its oval foot-plate is inserted in the fenestra vestibuli of the cochlear capsule. The shaft extends outwards and slightly downwards from the side of the otic capsule. Its distal end bends sharply from the axis of the proximal end, and continues in a posterior and ventral direction. It comes in close contact with the posterior median surface of the quadrate, but may be distinguished by its procartilaginous condition when the quadrate is already well-defined cartilage. At a later stage a small nodule of cartilage differentiates from the distal end of the uniform procartilaginous rod and fuses with a projection from the quadrate. This is undoubtedly Parker’s stylohyale (1878). In the adult there is an articulating joint between the end of the columella and the stylohyale.

With the absence of a tympanic membrane no insertion plate is present, and no recognizable extracolumella. But there is a wide divergence of opinion in the literature on the ophidian columella auris as to the nature of its component parts. Gadow regarded Parker’s stylohyale as the extracolumella. Rice (1920) makes the tentative suggestion that it is in the nature of a connexion from the processus accessorius anterior of the insertion plate, similar to that described by Fuchs (1909) for Lacerta; this would be to regard the distal end of the columella rod as extracolumella. Okajima (1915) found that the extracolumella was entirely lacking, ontogenetically and morphologically, in Trigonocephalus. He states that the stylohyale is essentially a process of the quadrate, having nothing to do primarily
with the columella auris. But from my observations on Leptodeira hotamboia and on a very young night-adder embryo, I am inclined to agree with Möller (1905, on Vipera aspis) and conclude that the nodule originates from the columella auris and secondarily fuses with a projection of the quadrate. Peyer (1912) agrees that the stylohyale in Vipera aspis is a part of the columella auris in origin, and possibly an extracolumella.

The relations of the nerves and blood-vessels to the distal bent end of the columella in Leptodeira hotamboia have an important bearing upon the problem of the extracolumella. The vena capitis lateralis passes forward over the shaft of the columella auris and lies between the bent distal end and the wall of the otic capsule. The orbital artery is given off from the internal carotid artery some distance anterior to the columella. This is an interesting variation from the usual course in Reptilia, which is up and over the shaft from an origin posterior to the columella. But another unusual course is found in Sphenodon (Versluys, 1903, and Wyeth, 1924), where the orbital artery passes beneath the columella, and in Hemidactylus and other Geckones (Versluys, 1903) the orbital artery pierces the shaft, as it does in Gymnophiona and also in the mammals.

The hyomandibular branch of the facial nerve passes back over the shaft of the columella, then bends outwards and downwards below the bent distal end. The chorda tympani is given off below and posterior to the columella extremity, and runs forwards and downwards to the median side of Meckel’s cartilage. Text-fig. 5 shows the relation of the nerves and blood-vessels to the columella.

It is a well-established fact that the course of the chorda tympani in all amniotes is exceedingly uniform, and is an important factor in determining the homologies of the various parts of the ear bones. The hyomandibular branch of the facial always passes backwards over the shaft of the columella medial to the dorsal and internal processes. The chorda tympani is given off posterior to the columella, loops round the dorsal
process and passes back over the insertion plate of the extracolumella (see text-fig. 2, Goodrich, 1916).

Since in *Leptodeira hotamboia* the chorda tympani passes under the distal bent end of the columella, it cannot be an extracolumella, and therefore should not be called a stylohyale.

A further fact weighing against the recognition of an extracolumella is the complete ossification of the whole columella structure in *Leptodeira*. It is generally accepted that the medial part of the columella, the otostapes, ossifies, but the distal portion, the extracolumella or hyostapes, remains cartilaginous. Okajima found that the lateral third in *Trigonoccephalus*, the part he regards as of quadrate origin, remained cartilaginous, but Möller and Peyer both found that the whole structure ossified in *Vipera aspis*, though Peyer says the stylohyale ossifies much later than the rest.

Goodrich (1916) pointed out that the recesses of the tympanic diverticulum bear a constant relation to the columellar elements. The tympanic diverticulum of *Lacerta* has three dorsal recesses: (1) an anterior median which bends from in front over the columella shaft and is median to the dorsal and internal processes; (2) an anterior lateral; and (3) a posterior lateral.
These last two are lateral to the dorsal and internal processes; they are respectively anterior and posterior to the extracolumella shaft, and meet above it, thus encircling the shaft of the extracolumella in a ring-like diverticulum.

In all snakes the tympanic cavity is imperfectly developed and no tympanic membrane is formed. In all the stages of Leptodeira an ill-defined tympanic diverticulum is present, which extends up round the columella auris. Even the first stage, however, is too old to show the diverticulum recesses which might help in the identification of the distal process (fig. 21, Pl. 13).

It seems fairly evident, however, that the backwardly bent distal end of the columella corresponds either to a processus dorsalis or a processus internus. It lies in the loop of the chorda tympani and hyomandibular nerve and it is lateral to the vena capitis lateralis. If it be regarded as homologous with the dorsal process of Lacerta, then the nodule, Parker's stylohyale, would represent the intercalare. It is conceivable that, with the backward migration of the quadrate to facilitate the wide gape and with the absence of a processus paroticus, the intercalare loses its connexion with the otic capsule. This is paralleled in crocodiles where the dorsal process is not connected with the otic capsule, but fuses with the quadrate in the region of the otic process. Unlike crocodiles, the nodule of Leptodeira fuses with the mid-region of the quadrate, not with its most dorsal margin, where one might expect to find the otic process. This might be accounted for by the elongation and backward rotation of the quadrate. In contrast to Lacerta, this intercalare would be in connexion with the columella auris through the persistent dorsal process, but this is also the case in crocodiles (Goldby, 1925) and in Sphenodon (Versluys, 1903, and Wyeth, 1924).

If the process be regarded as homologous with the processus internus of Lacerta, there is no possible explanation of Parker's stylohyale. The relations of the nerves and blood-vessels and tympanic diverticula would be the same to the internal process as to the dorsal process, if the internal process
attached to the quadrate were swung over with the backward migration of the quadrate. The internal process in Reptilia is of much less general occurrence than the dorsal process, and in Lacterta appears much later in development. The dorsal process is possibly the more primitive structure, and I incline to homologize the distal bent end of the columella in the snake and its stylohyale with the dorsal process and intercalare of other reptiles.

Orbito-temporal Region.

The condition of the orbito-temporal region in snakes generally is very uniform. The cartilaginous skeleton is to a large extent lacking. The trabeculae of the basis cranii in Leptodeira surround the fenestra hypophyseos. They meet in front and extend forward a long way parallel to one another without fusing. There is no trace of an interorbital septum, either cartilaginous or membranous. Peyer (1912) mentions that an interorbital septum is present in Tropidonotus as thickened tissue, but does not detect any trace of it in the viper.

The cartilaginous side-wall in the anterior orbital region is entirely lacking. I find no trace of the orbito-sphenoid cartilage described by Parker (1898) for Tropidonotus. Peyer fails to find an orbito-sphenoid cartilage in the viper, and disagrees with Parker's account of Tropidonotus. The side-wall is replaced entirely by membrane which in later stages is invaded by descending processes of the parietals and frontals.

In the temporal region, also, the side-wall is lacking. A prefacial commissure may be present or the facial foramen may be confluent with the trigeminal incisure. There are no pilae antoticae or taenia marginales and the trigeminal nerve passes out through a widely open trigeminal incisure. In the lateral margin of the basal plate, ventral to the trigeminal incisure, and posterior to the crista sellaris, is an extensive gap in the cartilage of the plate. It is closed by membrane, and no nerves or blood-vessels pass through it. Gaupp (1902) describes a similar gap in the lateral margin of the basal plate in Tropidonotus, and de Beer (1926) figures the same for Pseudechis. Its
significance is unknown; it is apparently just a part of the general reduction of the cartilaginous wall of the snake-skull. As in the anterior region, the lack of cartilaginous wall is compensated by the development of a thickened tissue membrane.

From the margin of the basal plate in the region of the gap described above, a short blunt process projects outwards and slightly upwards. It projects into the thickened tissue which extends upwards to the lateral wall of the otic capsule. In this way the trigeminal ganglion is enclosed with the head vein in a cavity which is bounded mesially by the dura mater and laterally by membrane stretching from the lateral process of the basal plate, or trabecular plate it may be called in this region, to the lateral wall of the otic capsule.

In Stage IV of Leptodeira, shown in fig. 10, Pl. 13, a splinter of bone extends upwards from the edge of the cartilaginous projection of the trabecular plate into this membrane. (I hope to show that the cartilaginous process is a basitrabecular process (Goodrich) or basipterygoid process (according to previous usage); for convenience, therefore, I shall call it a basitrabecular process.)

Fig. 11, Pl. 18, shows the margin of the trabecular plate, posterior to the basitrabecular process, extending upwards in close contact with the dura mater and medial to the membrane and its bony column. A few sections further back it is continuous with the prefacial commissure. The membrane in the region of the trigeminal incisure is, therefore, though continuous with the membrane of the orbital region, definitely lateral to the line of the original skull-wall as shown by the prefacial commissure and trabecular plate margin. In Stage IV there is a noticeable gap between the bone of the descending process of the parietal and the bony column on the basitrabecular process.

In Stage V (fig. 15, Pl. 13), a month later, the whole membrane has ossified. It extends to the wall of the otic capsule, overlapping the pro-otic bone, and covering the facial foramen. Its anterior edge is in contact with the descending process of the parietal. It is lateral to and covers the profundus nerve and trigeminal ganglion. The maxillary and mandibular branches
of the trigeminal both pass out through the bone, each having a separate foramen.

Gaupp (1902) described a similar bone, separating the maxillary and mandibular branches of the trigeminal nerve, in an adult Tropidonotus and adult Dipsadomorphus, and Hallman (1887) found it in the adult Python. For convenience I shall refer to the bone as Gaupp's bone.

Peyer (1912) mentions a bone in this region, but regards it as an extension of the pro-otic bone. This will be discussed later.

Text-fig. 6 gives the relations of the chief nerves and bloodvessels to the basitrabecular process and to Gaupp's bone in its early stages (Stage IV of Leptodeira hotamboia). The mandibular and maxillary branches of the trigeminal nerve pass out over the margin of the trabecular plate posterior to the basitrabecular process. They pierce through the membrane which bounds the incisura antotica laterally. The profundus branch does not pass out through the incisura antotica. It is not included in the trigeminal ganglion, and does not even pierce the dura mater immediately, but runs forward for a short dis-
tance actually within the cranial cavity. Its position is median to the basitrabecular plate and Gaupp's bone. When it penetrates the dura mater it comes to lie in a space between the dura mater and the descending process of the parietal. It swells out into an ophthalmic ganglion.

The vena capitis lateralis passes forward over the shaft of the columella auris and continues forward lateral to Gaupp's bone. It gives off a branch which passes through the membrane of the trigeminal incisure into the space between it and the dura mater where it joins the vena capitis medialis. The vena capitis medialis passes forward in company with the profundus in the space between the dura mater and the parietal descending process. It gives off a small pituitary branch, anterior to the crista sellaris which joins its fellow of the other side. In Stage V the vena capitis medialis has disappeared. The course of the vena capitis lateralis is entirely outside the skull-wall, figs. 12 and 13, Pl. 13.

The internal carotid artery has the usual course lateral to the side-wall of the skull. It passes under the basitrabecular process, and enters the cranial cavity from a ventral direction, through a notch in the posterolateral angle of the fenestra hypophyseos, not through a separate foramen. As already mentioned, the orbital artery has its origin unusually far forward, that is, in front of the columella auris. It passes forward lateral to Gaupp's bone.

The facial nerve emerges through the facial foramen, or, when a prefacial commissure is lacking, through the same incisure as the trigeminal nerve. Its posterior branch, the hyomandibular, has already been described in connexion with the columella auris. The palatine branch runs down and forwards beneath the basitrabecular process. It accompanies the internal carotid artery in its course outside the skull-wall. It lies immediately dorsal to it and within a groove in the ventral surface of the basal plate. In Stage V the parasphenoid bone has covered them and forms the outer wall of a parabasal canal enclosing the nerve and artery.

The abducens nerve originates immediately below the trige-
SKULL OF LEPTODEIRA

It has a special canal excavated in the dorsal surface of the basal plate lateral to the crista sellaris (fig. 13, Pl. 13). The anterior opening of the canal is still within the cranial cavity. The nerve bends upwards from the opening of the canal and enters the space between the dura mater and the descending process of the parietal. It passes forward lateral to the profundus nerve, buried in the thickened tissue of the lateral wall of the space, and leaves the skull cavity round the anterior margin of the descending process of the parietal in company with the profundus. Gaupp (1902, Tropidonotus) and Peyer (1912) for the viper describe similar courses for the abducens nerve, but Gaupp regards the intracranial exit of the abducens canal as peculiar to snakes and as a result of the downgrowth of the parietal. Rice (1920), working on Eumeces and Lacerta, concludes that it is typical of reptiles. In Eumeces the abducens canal has its anterior opening in the cartilage of the basal plate within the cranial cavity, and the nerve has its exit through the foramen metopticum. This is very closely in line with the condition described for Leptodeira; the exit through the foramen metopticum in the lacertilian would correspond to the entrance of the nerve in the snake into the intermediate space bounded by the parietal descending process. The presence of this bony descending process necessitates that the final exit of the abducens nerve be through the foramen orbitale magnum (Gaupp, 1902). The trochlear and oculomotor nerves also pass forward in this intermediate space between dura mater and descending process and have their exit from the skull through the foramen orbitale magnum with the optic nerve and the abducens.

Gaupp (1902) described this intermediate space between the dura mater and the descending process of the parietal in his account of Tropidonotus. He pointed out that in the lizard the profundus, the abducens, the trochlear, oculomotor, and optic nerves pass through various separate foramina in the side-wall of the cartilaginous cranium, while in the snake the descending process of the parietal is equivalent to an additional wall outside the original cranial wall. It encloses the five nerves
in a common passage. The opening between the parietal and frontal bones through which the three eye-muscle nerves and the optic nerve make their exit, he has named the foramen orbitale magnum, and it does not correspond to the optic foramen in the lizard, which is an opening in the cartilaginous wall through which the optic nerve alone passes.

In the snake the original cartilaginous cranial wall has completely disappeared, leaving this intermediate space between the parietal and the dura mater. Gaupp regards the space as extracranial, something outside the original cranial wall, the perichondrium of which must have been in close contact with the dura mater on the medial side of the intermediate space. De Beer (1926) thinks that the space should rather be regarded as intramural, lying between the dura mater and the original cranial wall which must have been close inside the existing parietal wall. He points out that the dura mater is a long way internal to the trabeculae, the basal plate and the otic capsule which are in line with the dense mesenchyme foreshadowing the parietal downgrowth. The condition in Leptodeira hotamboia confirms de Beer’s conclusion that the space is intramural and the result of inward shrinkage of the dura mater. In early stages this intermediate space is very extensive, penetrating between the brain and the otic capsule and also inside the trabeculae. In later stages it is reduced to a lateral space inside the descending process of the parietal, and in Stage V it is almost obliterated.

However, as de Beer pointed out, whether the space be extracranial or intramural, Gaupp’s explanation of how the four eye-nerves come to have a common exit through the foramen orbitale magnum still holds good.

The cartilaginous process of the trabecular plate, my basitrabecular process, and Gaupp’s bone associated with it have been the subject of much controversy in ophidian literature. Parker’s (1878) description of Tropidonotus and Rathke’s (1839) of Coluber both mention an alisphenoid cartilage in this region. Peyer (1912) says of this structure in the viper: ‘Das Alisphenoid entsteht in der Gegend der Incisura prootica
des Primordialcraniums als Ersatzknochen mit Unterdrückung der knorpligen Präformation' (p. 607).

At one stage he found a short strip of cartilage jutting forward from the edge of the incisura antotica which he regarded as a possible vestige of a previous cartilaginous wall, but the bone he believed to be merely an extension of the pro-otic bone. The observed facts are evidently similar to those I have found in *Leptodeira*.

De Beer (1926) discusses the problem very fully. My observations on *Leptodeira* confirm his on *Pseudechis* and *Tropidonotus*. He illustrates the cartilaginous process from the trabecular plate, and *Tropidonotus* has an ossified column in close contact with the cartilaginous process. It separates the maxillary and mandibular branches of the trigeminal from the profundus, as in Stage IV of *Leptodeira*. He points out that the structure cannot be a pila antotica because it lies behind the profundus; it cannot be a pila lateralis as in *Amia*, for it is situated median to the vena capitis lateralis. He considers that it cannot be a processus ascendens, because it does not arise from and has no relations with the pterygoquadrate.

I do not consider this a serious objection. In the snake the quadrate is merely a rod of cartilage situated unusually far back. It has neither basal nor ascending process at any stage; evidently the anterior portion of the palatoquadrate cartilage has been lost or separated. The cartilaginous process has the relations of a basitrabecular process. It is a lateral projection of the trabecular plate immediately in front of the otic capsule. The palatine nerve emerges behind it and runs forward under its ventral surface. The vena capitis lateralis is dorsal to it. The bony column associated with it has the relations of an ascending process. It is lateral to the original cranial wall as shown by the prefacial commissure and basal plate and it is lateral to the vena capitis medialis. It must represent the outer wall of Gaupp's cavum epiptericum (1910). The space between the dura mater which is occupied by the vena capitis medialis and the trigeminal ganglion would be the cavum epiptericum. It is
situated in front of the maxillary and mandibular branches of
the trigeminal which pass out behind it. It separates them from
the profundus nerve which runs medially to it and passes out
anterior to it. The bone in fully developed condition, as already
described, has the relations of an epipterygoid, being external
to the profundus and tending to grow back over the pro-otic and
facial foramen. I cannot agree with Peyer that the bone is
merely an extension of the pro-otic. It appears first in contact
with the process of the trabecular plate, and there is a wide gap
between it and the otic capsule which is overgrown in later
development.

The epipterygoid bone, being an ossification of the ascending
process of the palatoquadrate, is a replacing bone, and this bone
in the snake is apparently never performed in cartilage. It is,
however, conceivable that the cartilaginous stage has been sup-
pressed and that the bone is laid down in the dense mesenchyme
which represents the cartilaginous stage. This bone is of a
different character from the descending process of the parietal.
The latter is an additional outside wall; nerves do not pierce
it, but pass round its anterior border. But this small bone in
the region of the incisura antotica is pierced by the maxillary
and the mandibular just as the replacing bone would be.

I see no serious objection to regarding this bone, Gaupp's
bone, Parker's and Rathke's alisphenoid, Peyer's pro-otic exten-
sion, and de Beer's post-profundus laterosphenoid, as the homo-
logue of the true reptilian epipterygoid.

I do not think it can be looked upon as in the nature of a
laterosphenoid. As already pointed out, observations on Leptodeira show it to be lateral to the original line of the
cranial wall, on the outer wall of the cavum epiptericum.

In reference to this problem a series of sections of a very
young night-adder embryo, still in the procartilaginous and
thickened mesenchyme stage, were very interesting. They
showed dense mesenchyme in a continuous strip lateral to the
otic capsule, from the quadrate to the trabecular plate. It
would suggest a single palatoquadrate structure.
Ethmoidal Region.

The ethmoidal region, as in snakes generally, is incomplete and delicate. The exceptionally light framework is evidently correlated with the excessive mobility of the jaws. It consists of a pair of cone-shaped cartilaginous capsules fused with the anterior extremity of the nasal septum. The nasal septum is a continuation of the fused trabecular rods, from the axis of which it inclines strongly downwards. It is a strong triangular rod of well-developed cartilage at its transition region, but rapidly narrows into a low vertical plate. Both dorsal and ventral edges are free throughout the greater part of its length. From this point forward the septum decreases rapidly in height and terminates against the premaxillary bone. It has no crista septi for the support of the septomaxillary bone, as Born (1883) reported for Tropidonotus.

The nasal capsules protrude in front of the septum, diverging from one another, and terminate in dome-shaped structures which form the end of the snout. Each capsule may roughly be divided into two regions; the posterior is rather broader than the anterior, from which it is sharply marked off by the anterior limit of the conchal infolding. The anterior half has an uninterrupted roof, but its medial wall is incomplete except for the very limited area of fusion with the nasal septum. The fenestrae superiores of Lacerta (Gaupp, 1900), Eumeces (Rice, 1920), Sphenodon (Schauinsland, 1900, and Howes and Swinnerton, 1901) are absent, nor does Peyer (1912) figure them for Vipera. In this the snakes are similar to the crocodiles and turtles. In Shiino's figures (1914) of Crocodilus there are no fenestrae superiores, but the fenestrae nariae extend dorsally into the anterior tectum nasi. I have been able to confirm this for an embryo Crocodilus (90 mm. head-length). Kunkel (1911) describes a tectum nasi uninterrupted by fenestrae superiores in Emys, and they are apparently absent in the Dermochelys, Chelone, and Chelydra investigated by Nick. In a Chrysemys embryo of 20 mm. head-length I have examined there are no fenestrae
superiores, but the fenestrae olfactoriae extend a very long way forward.

Posteriorly, the tectum nasi of Leptodeira is incomplete, a pair of very large fenestrae extending forward through half the length of the capsules. They are separated from one another medially by the nasal septum and the posterior wall of the capsule forms the posterior boundary. There are no sphenethmoidal cartilages so that each dorsal fenestra corresponds to the coalesced fenestra olfactoria and fissura orbito-nasalis of L.certa. Shiino (1914) describes a similar coalescence in the crocodile and calls the foramen the fenestra cribrosa. The olfactory nerve and ethmoidal branches of the trigeminus nerve pass in conjunction through the fenestra cribrosa into the nasal capsule.

A noteworthy and interesting condition in the snake is the fusion of the posterior wall of the capsule with the nasal septum. In Leptodeira the posterior wall broadens slightly into a vertical plate (fig. 8, Pl. 13) which must correspond to the planum antorbitale of L. certa. It is situated some distance laterally to the nasal septum, but from its medial ventral edge a narrow band of cartilage passes backwards and upwards to fuse with the dorsal margin of the nasal septum.

I have observed the same fusion in an embryo Ptyas. Peyer (1912) describes the side-wall of the nasal capsule of an embryo Vipera aspis (70 mm. head-length) as fused posteriorly with the nasal septum. From his figure this is evidently the same connexion. In an embryo of 125 mm. head-length he reports that the planum antorbitale is entirely lacking and in the figure of this later embryo the capsule is quite free from the septum nasi posteriorly. But in Leptodeira the range of embryos from about one month's age to two weeks before hatching all show complete fusion.

Other reptiles, with a single exception, are all described as showing complete freedom of the nasal capsules from the nasal septum posteriorly. Shiino (1914) describes the planum antorbitale as uniting solidly with the nasal septum in Crocodilus, but Gaupp in 1905 had reported it as free. In the single
Crocodilus I have at my disposal, the planum antorbitale is firmly wedged against the nasal septum, but the line of contact between them is distinct. Whether this contact is a process of detachment or of secondary attachment it is impossible to say from a single specimen. Apparently Shiino's twelve embryos of varying ages all showed complete fusion. He describes the nasal septum as thickened at the point of fusion and this might suggest a secondary connexion. In Dermochelys and Chelonia, Nick (1912) reports contact but no fusion between the planum antorbitale and the nasal septum, and in Chrysemys (Gaupp, 1905) and in Emys (Gaupp, 1905, and Kunkel, 1912) there is complete freedom. In the single Chrysemys I have been able to observe there is close contact without fusion.

With the exception of Shiino's crocodile the snake appears to be the only reptile in which the nasal capsule has a posterior commissure connecting it with the nasal septum. It might be a secondary attachment, an adaptation correlated with the delicate nature of the skeletal framework in the nasal region. Its persistence, however, throughout all stages of Leptodeira, with its early appearance and subsequent atrophy in the viper, suggest that it may be the primary condition.

Gaupp, however, regarded the posterior freedom of the nasal capsules from the nasal septum as the primary condition. In discussing the attachment of capsule in some mammals, he states his belief that the attached condition is a secondary modification, emphasizing the free condition of the reptilian ancestors as evidence of this (1910).

Kunkel observed that the connexion between the paraseptal cartilage and nasal septum in Emys is definitely a secondary modification, and concluded that in the primary condition the capsular wall is free from the nasal septum posterior to the zona annularis (1911).

The planum antorbitale of Leptodeira hotamboia has no maxillary processes.

The paries nasi are well developed and pass over uninterruptedly from the tectum nasi. Anteriorly there is a large
ventral gap, corresponding to the fenestra narina, but owing to the incompleteness of the capsular floor it is an open incisure, not a complete foramen. The processus alaris superior and processus alaris inferior are present as slight projections of the wall of the fenestra narina, and between them is situated the external nasal aperture.

The lateral wall in the posterior half of the capsules is complicated by the conchal infolding, which is in the form of an inverted trough open anteriorly, ventrally, and posteriorly. The extraconchal recess projects very slightly in front of the aditus conchae, so that the sulcus terminalis is very shallow. The lateral wall of the recess is complete, and there is no sign of the fenestra lateralis of Gaupp's *Lacerta* in any of my *Leptodeira* embryos.

The infolding of the paries nasi takes place early in development, and its invasion by the external gland is later. As pointed out by Rice (1920), this speaks strongly in favour of Born's theory (1879 and 1883) of the secondary relation of the gland to the concha, the folding of the olfactory epithelium being the active factor in the formation of the conchal infolding.

The nasal capsules are almost completely open basally, the entire floor being represented by the cartilaginous cup supporting Jacobson's organ. The cup is isolated from the rest of the cartilaginous skeleton. There is no anterior connexion with the cartilagines cupulares, as reported by Born (1883) for *Tropidonotus*. There is no connexion with the nasal septum. Laterally, fragments of histologically young cartilage and thickened tissue pass from the cup to the side-wall of the capsule, but there is no complete band as in *Lacerta*. This agrees with the condition found by Peyer (1912) in *Vipera*, but Born (1888) reports a continuous procartilaginous strip which later breaks down.

The isolated cup is supported by the prevomer and septomaxilla, which completely surround Jacobson's organ. The posterior portion of the cartilaginous cup protrudes up into the gland as a swollen knob, the concha. There are no paraseptal cartilages. The posterior edge of the cup is continued backwards
as a strip of cartilage which stretches to the choanae. A second cartilaginous strip runs parallel and lateral to the first process and unites with it posteriorly to form a plate of cartilage for the support of the nasal passage. The plates of the two sides approach one another very closely. Peyer describes similar cartilages in *Vipera* as the hypochoanal cartilages. Born (1888) describes them for *Tropidonotus* and *Vipera*, and identifies them with the hypochoanal cartilages of *Lacerta*. The sabre-shaped cartilages of *Python tigris* (Solger) are evidently of the same nature.

Owing to the incompleteness of the walls the foramina of the nasal capsule are not fully delimited. The fenestra narina and the fenestra cribrosa, the coalesced fenestra olfactoria, and fissura orbito-nasalis, have been described. Immediately behind its entrance into the fenestra cribrosa, the ethmoidal nerve (profundus branch of the trigeminal) divides into medial and lateral branches. The medial passes throughout the length of the capsule and emerges round the ventral anterior margin of the medial wall of the capsule (fig. 5, Pl. 13). No foramen apicale is delimited. The lateral ethmoidal emerges through a foramen epiphaniale and passes down the sulcus terminale (fig. 1, Pl. 12, and fig. 6, Pl. 13). The foramen epiphaniale is a slit-like aperture beginning slightly behind the aditus conchae. A very narrow strip of cartilage separates it from the fenestra cribrosa. If this broke down the course of the nerve would be similar to that described by Shiino for *Crocodilus* (1914). That is, the lateral ethmoidal would not enter the capsule at all but would pass over the roof of the capsule direct to the sulcus terminalis. In the same way the advehent aperture of the lateral ethmoidal, distinct from the fenestra cribrosa described by Nick (1912) for *Dermochylyis* and *Chelonia*, is probably due to an extension of the cartilaginous wall of the roof to surround the nerve behind the foramen epiphaniale.

**Mandibular Arch.**

The dorsal division of the mandibular arch, the palatoquadrate cartilage, is represented in snakes by the long slender
quadrate bar. In Stage I of Leptodeira the quadrate is a narrow vertical plate of cartilage. Its articular facet for Meckel's cartilage is saddle-shaped. Correlated with the freedom of movement of the quadrate, it has no fusion with the wall of the skull. It is ligamentously attached to the so-called squamosal bone, the supratemporal of Thyng. The quadrate has no obvious basal or ascending processes. In a previous section on the orbito-temporal region of the skull, it was assumed as probable that this region of the palatoquadrate is represented by the epipterygoid bone, the cartilaginous stage of which is suppressed.

With advance in age of the embryo the distal end of the quadrate migrates backwards, until the slender elongated bar makes a very acute angle with the ventral division of the mandibular arch, Meckel's cartilage. This slender lower jaw extends forward in a gentle curve. The anterior ends of the two rami do not meet, a wide space intervening between them. The articulating surface with the quadrate is convex. There is a large retroarticular process.

Ossified Skull.

Replacing bones.—The stages at my disposal are not favourable to the study of the replacing bones. In Stage IV there is a little ossification in the occipital region. Well-developed exoccipital bones arch over the foramen magnum, but the supraoccipital region is unossified. The basi-occipital has an ossified occipital condyle. There is an interval of four or five weeks between Stages IV and V, and in the fifth stage ossification is so far advanced in the posterior region that the individuality of the bones is lost. The auditory capsule is completely ossified but the elements, pro-otic, epiotic, and opisthotic could not be distinguished, nor was any light thrown on the problem of whether the epiotic and opisthotic are independent elements. In the side-wall of the orbito-temporal region there can be no replacing bones, beyond the possible epipterygoid, since the cartilaginous wall has all been lost. Ossification has begun in the basisphenoid region. The posterior ends of the trabeculae,
enclosed in forceps-like parasphenoid structures, have atrophied. The anterior portion of the skull, the ethmoidal region, is in Stage V still persistent cartilage.

Membrane Bones.—The secondary skull of investing bones is very strongly developed, and my observations on the membrane bones of *Leptodeira hotamboia* confirm those of Peyer on *Vipera aspis*. The bones make their appearance at a very early stage, long before any sign of ossification in the cartilaginous cranium.

There are well-developed paired parietals, but they do not at first extend far enough toward the dorsal middle line to roof over the brain. The strongest development is a longitudinal strip over the summit of the auditory capsule. It extends a short distance down the mesial surface of the capsule between it and the brain. A short projection grows out over the anterior semicircular canal. In front of the otic capsule the parietals have descending processes which form side-walls to the skull and compensate for the lack of cartilaginous wall. In Stage I the descending processes are not very extensive, but later they grow right down to the trabeculae. The anterior margin forms the posterior boundary of the foramen orbitale magnum.

A postfrontal bone is situated externally to the descending process of the parietal at its anterior end. The postfrontal inclines strongly outwards and downwards, forming a shelf over the orbit.

The frontals also are well developed, and have descending processes which form the side-walls of the anterior portion of the skull. These form the anterior margin of the foramen orbitale magnum. In the later stages of the *Leptodeira* embryos, the parietals and frontals are closely approximated in the roof of the skull, but there is a rounded gap in the middle line. They form an almost complete case for the brain in the orbito-temporal region. Each meets its fellow in the middle line. The descending processes of the frontals meet ventrally in the middle line, above the trabeculae. But between the descending processes of the parietals the parasphenoid forms the floor of the brain-case.
The prefrontal is a complicated bone. It forms a strongly convex arch over the side-wall of the cartilaginous nasal capsule. The broad base of the arch forms a strong support to the maxilla. The dorsal edge of the arch is in contact with the frontal forming a line of suture with it. In the viper Peyer describes an arch of the prefrontal extending dorsally between the nasal and frontal to meet its fellow of the other side, but in none of my Leptodeira specimens can I find such a development. Posteriorly the bone becomes outwardly concave extending under the eye.

The parasphenoid appears very much later than any other investing bone. It begins anteriorly as a vertical wedge of bone between the trabeculae. As the trabeculae separate posteriorly, the parasphenoid becomes a flattened plate of bone. Its lateral edges, forceps-shaped, enclose the trabeculae. It forms a floor over the hypophysial fenestra and extends back beneath the basisphenoid. The internal carotid artery runs forward in a channel between the parasphenoid and the basisphenoid, the parabasal canal, and enters the cranial cavity through notches in the antero-lateral corners of the crista sellaris.

The nasals penetrate deeply between the nasal capsules medianly, and in Stage V are quite large roofing bones to the capsules. The side-walls of the capsules anteriorly are unprotected by bone.

The septomaxilla and the prevomer surround Jacobson’s organ. The prevomer forms the median and ventral walls of the bony capsule, and closes it posteriorly. The septomaxilla forms the lateral and dorsal walls and closes it anteriorly. Laterally the two bones overlap, the septomaxilla being outside the prevomer. A ridge of bone rises upwards from the median surface of the prevomer; it extends back along the nasal septum (fig. 9, Pl. 13).

In close contact with the septomaxilla and the prevomer anteriorly is the wedge-shaped, unpaired premaxilla. Its median ascending process extends up between the nasal capsules to meet the descending processes of the nasals.

The maxilla is a fairly long bone situated in a lateral position.
beneath the skull. It is supported anteriorly against the prefrontal, and posteriorly it works against the transversum, or ectopterygoid. This latter is a flat bone, sloping gradually inwards to the pterygoid.

The pterygoid is an exceedingly long bone, extending from the jaw articulation forward in a medio-ventral position below the skull as far as the middle of the orbital region. In front it is loosely articulated against the palatine, a shorter bone extending beneath the nasal capsules. Posteriorly it works against the quadrate.

The maxilla, palatine, and pterygoid all bear teeth. They are all loosely articulated with one another and with the skull.

A long splint-like bone, generally known as the squamosal, develops upon the lateral aspect of the otic capsule. Anteriorly it is in close proximity to the parietal and extends back over the otic capsule between the prominences of the anterior and horizontal semicircular canals. Its ventral edge penetrates slightly between the quadrate and the wall of the otic capsule, and it does not extend over the surface of the quadrate at all. For this reason Thyng (1906) considers that it is a supratemporal and not a squamosal.

According to Thyng, the criteria for determining the homologue of the mammalian squamosal are its lateral position, overlying the otic capsule and the quadrate, and its contact with the quadratojugal. The bone in the Stegocephalia, which lies median to the squamosal and develops in close contact with the parietal, he calls the supratemporal. It is present with the squamosal in most of the primitive and extinct groups of Reptilia, but tends to be reduced in existing species. In Lacertilia it undergoes marked reduction, and in Sphenodon and Crocodilia is entirely lacking. The squamosal in all these is well developed.

According to Thyng's criteria, the bone called squamosal in the snake does more closely resemble a supratemporal. But in that case the squamosal must be entirely lacking, and this would be a unique instance in Reptilia. Snakes are peculiar
in having completely lost the temporal arcades and it is conceivable that the squamosal has disappeared with the quadratojugal, jugal, and postorbital.

Parker (1878) figured a small bone ventral to the squamosal (Thyng's supratemporal), which Thyng expected would be the true squamosal. But Gaupp failed to discover Parker's bone in his single *Tropidonotus* embryo. Peyer found it in none of his stages of the viper and I can find it in none of my stages of *Leptodeira*. But neither can I find any trace of the rest of the bones of the temporal arcades.

In the lower jaw of *Leptodeira hotamboia*, as in Gaupp's *Tropidonotus* and Peyer's *Vipera aspis*, the following investing bones may be distinguished: a dentary, a splenial, and a large composite bone. The dentary is situated dorsolaterally to Meckel's cartilage, a piece of which projects in front uncovered by bone. The splenial is a smaller strip along the medial side of Meckel's cartilage opposite the posterior portion of the dentary. The large composite bone is the posterior element extending from the dentary to the quadrate and enveloping Meckel's cartilage. In Stage I the articular element of the composite bone is unossified. A gonial and supraangular are distinguishable components of the composite bone. A wide well-defined gap in the supra-angular allows for the passage of the mandibular branch of the trigeminal into the primordial canal. The chorda tympani passes round the posterior dorsal edge of the gonial into the primordial canal. Gaupp (1911) and Peyer (1912) both find a fourth separate element in the ophidian lower jaw. Gaupp calls it an angular, but Peyer does not find a separate element in the ventral position of an angular. He distinguishes a complementary, posterior, and dorsal to the splenial.

The skull as a whole has a very different appearance from the skull of the lizard (figs. 3 and 14, Pl. 12). The cranial region is a solid bony case. It affords a firm foundation against which the slender and loosely articulated palatal and jaw structures can work. This solid case is formed for the most part of the large parietal and frontal bones and their descending processes.
Inside this framework of membrane bones, the original cranial wall has undergone great reduction. As described in a previous section, the side-walls of the orbito-temporal region are entirely lacking. In the nasal region, too, a reduction of cartilage is correlated with a strong development of membrane bones, nasals, premaxilla, prevomers, septomaxillae, and prefrontals. A certain amount of movement is possible between the nasal region and the cranial case. Instead of the nasals being firmly wedged against the frontals, there is a gap between the bones which allows a certain amount of freedom.

The maxilla finds a firm anterior support against the massive prefrontal. Temporal arches are entirely lacking so that its posterior end is free except for a movable articulation with the pterygoid through the transverse bone. The palatine and the very much elongated pterygoid are freely movable. They are situated well away from the cranial floor. Posteriorly the pterygoid is supported against the quadrates with which it is freely movable. The pterygoid is not in contact with the basitrabecular process, which is relatively insignificant. In fact Gaupp says that only the large snakes, such as the python have basitrabecular processes (basipterygoid). The python has large processes against which the pterygoids are supported.

During development the quadrates shift back along the squamosal (Thyng's supratemporal) and the posterior end of the latter is progressively raised until it forms a prominent ridge from the roof of the otic capsule. In snakes generally, the squamosal projects a long way behind the skull, but in Stage V the process has not extended beyond the otic region. The movability and length of the palatal and jaw-bones, the marked backward shifting of the quadrates and its loose articulation, and the movability of the nasal region all combine to produce a wideness of gape which enables the snake to seize and swallow comparatively large prey.

The unusual length of the temporal region, the excessive length of the basal plate between the facial foramen and crista sellaris already remarked, and the broad extent of the parietal side-wall, are probably correlated with the exceptional length
of the palatal and jaw structures, and may therefore be regarded as an adaptation to ensure a wider gape.

This account is in very close agreement with that given by Versluys (1912) for the python taken as a typical example of the snake. He classifies it as a mesokinetic type of skull, directly derivable from the condition in Amphisbaenidae, in which the movement is between frontals and parietals, not between frontals and nasals. Versluys regards the metakinetic condition of the lizard as primary, and believes that the mesokinetic character of the Amphisbaenidae and snakes is an adaptation from it for the particular habit of life and kind of food.

As described in a previous section the snake has no interorbital septum. The eyes are situated far apart outside the bony case of the parietals and frontals, and between the prefrontals and postfrontals; the eye-muscles and their nerves pass through the foramen orbitale magnum. There is no trabecula communis, but the paired trabeculae lie very close together for the anterior two-thirds of their length. This is an intermediate condition between the platybasic and the tropibasic types of skull. Gaupp (1903) and Versluys (1912) both consider that it is a secondary modification from the tropibasic reptilian condition. The eyes might be secondarily pushed apart and the trabecula communis separated into paired trabeculae with the formation of the broad cranial box.

The possibility of the secondary nature of the posterior attachment of the nasal capsules to the nasal septum has already been discussed. But the evidence in favour of the lacertilian origin of the Ophidia is debatable and insufficient to justify a dogmatic statement to that effect. It is conceivable that the highly specialized skull of the snake is fundamentally primitive and adapted from a more primitive ancestral type than the lizard. It is probable that from an investigation of the development of the less specialized snakes, such as the Typhlopidae and Glauconidae, their true nature might be read.
ABSTRACT.

The cartilaginous cranium of the snake, *Leptodeira hotamboaia*, consists of basal plate and trabeculae, otic, and nasal capsules.

The crista sellaris of the basal plate is situated exceptionally far in front of the otic capsules, and the basicranial fenestra lies entirely in an anterior pro-otic third of the basal plate.

The trabeculae converge but do not fuse in front of the fenestra hypophyseos. They run forward parallel to each other, and fuse to form the nasal septum in the nasal region.

The otic capsules show a large vestibular division and a smaller cochlear portion. Posteriorly each capsule is separated from the basal plate by the fissura metotica. This fissure is divided into a small anterior medial opening of the recessus scalae tympani and a posterior jugular foramen. The vagus nerve passes through the posterior division, but the jugular vein, as in reptiles generally, passes out through the foramen magnum.

The fenestra cochleae, an aperture of the cochlear capsule, faces towards the recessus scalae tympani.

The fenestra cochleae of the reptile is compared with the fenestra rotunda of the mammal, and it is found that the two are not homologous. The apertura lateralis of the recessus scalae tympani of the reptile is the homologue of the fenestra rotunda of the mammal. The secondary tympanic membranes in the two classes correspond morphologically as well as physiologically.

This conclusion does not confirm Gaupp’s hypothesis (1900), but is in keeping with the earlier suggestion of Versluys (1898).

The columella auris consists of foot-plate and shaft. The distal end of the shaft is bent sharply backwards, is elongated, and is in contact with the quadrate. A small nodule at the distal end ossifies separately from the columella as a process of the quadrate. This is probably an intercalare, and the distal bent end of the columella would then represent the dorsal process of the lizard.

There is no interorbital septum. The cartilaginous side-walls
in the orbito-temporal region are lacking, and are compensated for by strong downgrowths of the parietals and frontals. The eye-muscles and their nerves are gathered together in the space behind these bones and pass out through a common opening, the foramen orbitale magnum.

A small basitrabecular process projects laterally from the trabecular plate. It supports a small bone situated in the side-wall of the skull over the trigeminal incisure and the facial foramen. The bone is not performed in cartilage, but its relations to the nerves and blood-vessels show it to be an epipterygoid. This basitrabecular process and epipterygoid evidently correspond to the so-called 'alisphenoid' of Parker (1878) and Peyer (1912).

The nasal capsules are delicate and incomplete. There are large conchal infoldings. The cartilaginous cup of Jacobson's organ is isolated from the rest of the nasal skeleton. A small planum antorbitale is present, and is attached to the dorsal edge of the nasal septum by a posterior commissure.

Membrane bones are strongly developed. Parietals, frontals, and parasphenoid form a strong bony case which gives a firm foundation for the working of the slender and loosely articulated palatal and jaw structures.

**LETTERING OF FIGURES.**

*ab.*, abducens nerve; *ab.c.*, abducens canal; *a.l.*, aperture lateralis of recessus scalae tympani; *a.m.*, aperture medialis of recessus scalae tympani; *a.n.*, auditory nerve; *b.c.f.*, basicranial fenestra; *b.p.*, basal plate; *b.p.g.*, basal plate gap; *b.s.*, basisphenoid bone; *b.t.p.*, basitrabecular process; *c.a.*, columella auris; *c.aq.*, cochlear aqueduct; *c.c.*, cochlear capsule; *c.d.p.*, columella distal process; *c.f.p.*, columella foot-plate; *c.h.*, chorda tympani; *c.o.*, concha; *c.s.*, crista sellaris; *d.p.*, parietal descending process; *d.p.f.*, frontal descending process; *d.m.*, dura mater; *e.c.*, ectopterygoid; *e.t.l.*, ethmoidalis lateralis; *e.t.m.*, ethmoidalis medialis; *f.*, frontal; *f.c.*, fenestra cochleae; *f.cri.*, fenestra cribrosa; *f.ep.*, foramen epiphaniale; *f.hj.*, hypoglossus foramen; *f.hy.*, fenestra hypophyseos; *f.m.*, fissura metotica; *f.na.*, fenestra narina; *f.p.*, foramen perilymphaticum; *f.r.*, fenestra rotunda; *f.v.*, fenestra vestibuli; *G.b.*, Gaupp's bone; *g.l.n.*, glossopharyngeus; *h.y.f.*, hyomandibular nerve; *h.y.c.*, hypochoanal cartilage; *i.a.m.*, membrane of incisura antotica; *i.c.a.*, internal carotid
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artery; J.o.c., Jacobson's organ capsule; j.v., jugular vein; M.c., Meckel's cartilage; md.t., mandibular nerve; m.t., maxillary nerve; m.t.s., membrana tympani secundaria; m.x., maxilla; n., nasal bone; n.c., nasal capsule; n.s., nasal septum; o.a., orbital artery; o.c., otic capsule; o.t.n., olfactory nerve; o.u., oculo-motor nerve; op.n., optic nerve; pa., parietal bone; pal., palatine bone; p.a.i., processus alaris inferior; p.a.s., processus alaris superior; p.as., parasphenoid; p.b.c., parabasal canal; p.c., prefrontal commissure; p.f., palatine nerve; pg., pterygoid bone; pit., pituitary vein; p. intr. pmtr., processus intraperilymphaticus; p.ant., planum antorbitale; p.n.c., posterior nasal commissure; post.f., postfrontal bone; pr., pre-maxilla; pre.f., prefrontal bone; p.s., perilymphatic sack; p.t., profundus nerve; pv., prevomer bone; q., quadrate; r.s.t., recessus scalae tympani; sm., septomaxillary bone; sq., squamosal bone; st., stylohyale; t.g., trigeminal ganglion; t.n., troclear nerve; t.p., trabecular plate; tr., trabecula; ty.d., tympanic diverticulum; v., vagus nerve; v.c.l., vena capitis lateralis; v.c.m., vena capitis medialis.

EXPLANATION OF PLATES 12 AND 13.

PLATE 12.

Fig. 1.—Reconstruction of the skull of Leptodeira hotamboia—dorsal aspect. Membrane bones have been removed to show relation of nerves and blood-vessels to the cartilaginous parts.

Fig. 2.—The same—lateral aspect.

Fig. 3.—Reconstruction of the skull—ventral aspect, with the membrane bones added as they appear in Stage V.

Fig. 4.—The same—lateral aspect.

PLATE 13.

Fig. 5.—Transverse section through nasal region of Stage I, 1-3-7, showing the exit of the medial ethmoidal nerve.

Fig. 6.—Transverse section through nasal region of Stage III, 3-1-1, showing the foramen epiphaniale.

Fig. 7.—Transverse section through nasal region, Stage IV, 2-3-4, showing vestiges of zona annularis.

Fig. 8.—Transverse section through nasal region, Stage IV, 3-3-2, showing the planum antorbitale and posterior commissure.

Fig. 9.—Transverse section through nasal region of Stage V, 3-1-7, showing the relations of the membrane bones to the cartilaginous parts.

Fig. 10.—Transverse section through the region of the incisura antotica at Stage IV, 9-1-1, showing the basitrabecular process and the rudiment of Gaupp's bone.