



THE CRANIAL ANATOMY OF COECILIA OCHROCEPHALA COPE. (FURTHER CONTRIBU-
TIONS TO THE CRANIAL MORPHOLOGY OF THE GYMNOPTIONA).



TIONS TO THE CRANIAL MORPHOLOGY OF THE GYMNOPHIONA.

The cranial morphology of the Neotropical genera of the Gymnophiona has received but little attention in the past. Of the six genera confined to South America, two species of the genus *Coecilia* and one of *Siphonops* were investigated by Wiedersheim (1879); of the other no data exist at all. Of the genera *Dermophis* and *Herpele*, represented in both South America and Africa, two species of the former were investigated by the author (1938).

Wiedersheim's work on the two species of *Coecilia* is not very complete, as he did not give any details regarding the cranial nerves and ganglia; he did, however, give complete descriptions of the olfactory organs and the general cranial topography. His work was of great assistance, as the species *Coecilia ochrocephala* was found to be highly specialised in certain respects, and comparison with Wiedersheim's data was therefore very important.

In this paper I intend giving details of the olfactory organ, the suspensorial region, and of the cranial nerves and bloodvessels, and to compare them with data supplied by Wiedersheim in particular, and also with those concerning other genera, such as *Dermophis*.

Material and Technique.

The material used consisted of two specimens of *Coecilia ochrocephala*, put at my disposal by Mr. Loveridge of the Museum of Comparative Zoology at Harvard University. The material was found to be very well fixed, and no maceration of the mucous membrane of the nasal cavities had occurred. It was decalcified, in Ebner's solution for one week; bulk-stained in haemalum for two days and counterstained on slides with eosin. The staining was on the whole, very good.

Own Investigations.

The nasal organ of *Cocilia ochrocephala*.

The narial apertures are situated dorso-laterally near the tip of the rounded snout, which is occupied by numerous large mucous glands with and connective tissue and nerve fibres ramifying between them. These mucous glands, found all over the head, are more numerous than in other genera examined by me, such as *Dermophis* and *Ichthyophis*. The small narial apertures are surrounded by a cartilaginous ring, constituting the anterior part of the nasal capsule; it is, however, soon replaced by the nasopremaxillary, forming a complete ring around the anterior portion of the nasal sac (Fig. 1). The *cavum nasale principale*, at its anterior end, is a simple tube with a slight dorso-lateral indentation, formed rostrad by the cartilage mentioned above, and caudad by the nasopremaxillary (Figs. 1 and 2). This indentation was also described for *Dermophis* (the author, 1938), and for *Ichthyophis*, *Cocilia* and *Siphonops* by Wiedersheim (op. cit.). It is comparatively deep rostrad, but becomes weaker caudad and soon disappears. The ventral indentation in the *cavum nasale principale* described for *Dermophis*, *Siphonops* and *Ichthyophis*, is formed in these genera by a process of the nasopremaxillary rostrad, and by the vomer and mesethmoid caudad, and it divides the *cavum nasale principale* into two parts: a lateral respiratory and a medial olfactory part. In *Cocilia rostrata* Wiedersheim found a very slight indentation formed by a process of the vomer (Fig. 52, T. 5), but in *Cocilia ochrocephala* no such process, either of mesethmoid, vomer or nasopremaxillary, is present. No division of the *cavum nasale principale* therefore occurs, and in only a small dorsal portion of the nasal sac olfactory epithelium is absent. In the rest of the *cavum nasale principale* the olfactory epithelium is

only a few layers thick (Fig. 3). The main nasal sac is anteriorly more or less pear shaped (Figs. 1 and 2), as a result of the ventro-lateral concave shape of the nasopresaxillary. This bone has this shape in order to accommodate the tentacle, which on moving inwards, comes to lie ventro-laterally next to the nasopresaxillary, before it is enclosed in a maxillo-palatine canal (Fig. 1). The *cavum nasale principale* remains pear shaped, until the appearance of the "Nebennase" lateral to it (Fig. 3), when it takes on an oval shape, and the olfactory epithelium then becomes only two cell layers in thickness (Fig. 4).

The "Nebennase" begins as a blind canal, lateral to the *cavum nasale principale*, and not in the same cavity, but in a cavity in the maxillo-palatine, which as in the genus *Dermophis*, remains a separate bone (Fig. 2). Anteriorly the two nasal cavities are separated by means of two bony lamellae: the lateral portion of the nasopresaxillary and the medial portion of the maxillo-palatine (Fig. 2). These lamellae, however, soon disappear, the former before the latter, and the two nasal cavities become confluent (Figs. 3 and 4). The "Nebennase" gland lies between the "Nebennase" and the *cavum nasale principale* (Fig. 3). This condition is also described by Wiedersheim for *C. lumbricoides* and *C. rostrata*. Wiedersheim further describes a thick separating membrane between the two cavities after the disappearance of the two bony lamellae. This membrane, he states, remains between the two cavities throughout their entire length. In *C. ochrocephala* connective tissue fills the spaces in the nasal cavities, and is also present between the two nasal sacs, but a definite separating "membrane" is not found.

Upon the communication of the "Nebennase" canal with the main nasal cavity, the *cavum nasale principale* becomes compressed laterally, and its walls thinner. The "Nebennase" on its first appearance is a circum-

lar structure (Fig. 3), but then stretches obliquely into the main nasal cavity, ventral to the main nasal sac, and is then sausage shaped with a narrow lumen and very thick walls consisting of olfactory epithelium (Fig. 4). Caudal the "Nebennase" becomes shortened from its lateral side and ends posteriorly as a small tubular structure, which opens into the main nasal sac on its^t medio-ventral side (Fig. 5). This opening is present in a few sections only, and lies medial and not lateral in the main nasal sac, as in other genera (cp. author for *Dermophis*). This may account for the fact that Wiedersheim failed to find the communication between the two nasal sacs in the species of *Coeccilia* described by him. He also failed to demonstrate the communication in *Ichthyophis* which we know to exist because of the work of the Sarasins (1880); in the specimens of *Ichthyophis* examined by me, the communication is also present. Wiedersheim described the "Nebennase" as opening into the choana (Fig. 54, T. 5), after its olfactory epithelium lining has been replaced by large cylindrical epithelial cells (op. cit., p. 42).

The "Nebennase" (Tastnase) according to Laubmann (1927) develops as a ventro-lateral outgrowth of the *cavum nasale principale*. In *Ichthyophis* larvae I found the development taking place in this way, and in a juvenile form the "Nebennase" communicates through its whole length with the main nasal sac. Later in the development, it presumably is restricted off from the main nasal sac, only a small communication being left between the two sacs. In all genera described, with the exception of *Ichthyophis* and *Coeccilia* (Wiedersheim) and *Hypogeophis* the communication is present, although it is usually limited to the posterior part of the "Nebennase". This shortening of the opening between the two nasal sacs is probably due to specialisation, and because *Coeccilia* and *Dermophis* show a greater degree of specialisation than *Ichthyophis* (such as degenera-

tion of the eye, development of the "Nebennase" and fusion of the cranial bones), it seems improbable that the former two will retain the communication and the latter lose it. In *Hypogeophis*, Marcus and Laubmann describe the "Nebennase" as follows: "Neben dieser Hauptnase existiert eine Nebennase, die sich hinten aus einem ventro-lateralen Blindsack entwickelt und durch zwei dickwandige Rörchen mit der Aussenwelt kommuniziert, indem sie in dem Tentakelsack münden" (Marcus, 1930, p. 662). The persistence of the communication in the adult may also be regarded as a neotenic characteristic, or, as I have mentioned above, the complete separation may arise as a result of the large development of the tentacle as the only sense organ, in corroboration with the almost complete degeneration of the eye. This latter suggestion seems to me the most likely, as in *C. ochrocephala* the "Nebennase" is highly specialised. It lies in its own cavity, it receives its own nerve supply, separate from the rest of the nerves of the nasal region (see below), and the eye has disappeared almost completely. The tentacle is the only sense organ; the two thick walled tentacle canals, opening at their distal ends into the tentacle groove, proceed caudad and mediad; they perforate the lateral wall of the maxillo-palatine, and enter the cavity containing the "Nebennase". Here they do not join to form a single duct before opening into the "Nebennase", as is described by Wiedersheim for *C. lumbricoideus*, but open separately into the "Nebennase". Wiedersheim believed these two canals to be the ducts of the tentacle glands. As I have pointed out previously, these two ducts open into the "Nebennase" of the genera *Dermophis* and *Ichthyophis*, and they definitely do not act as ducts for the tentacle gland ("Nebennase" gland), the latter being a nasal gland and opening into the "Nebennase".

When the "Nebennase" disappears from section, it is replaced by

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a mass of connective tissue with small mucous alveoli. In this mass of tissue an opening appears (Fig. 5), which widens caudad to form a cavity situated ventral to the main nasal sac, which latter has dwindled to a small circular cavity with very ~~small~~ thin walls. These two cavities are continued caudad for a short way before communicating with each other, a short distance anterior to their joint opening into the buccal cavity (Fig. 6). Their epithelial lining becomes continuous with the epithelium of the buccal cavity. This ventral sac is the homologue of the "Choanen-schleimbeutel" described by the Sarasins for Ichthyophis, and for the two species of Dermophis by the author. This sac is not described by Wiedersheim for Coccilia; he mentions, however, that the "Nebennase" at its posterior end contains large columnar epithelial cells instead of olfactory epithelium, and that it opens into the choana. It therefore seems probable that he did not notice that the sac lined by columnar epithelium, and the "Nebennase" lined by olfactory epithelium are two separate cavities. It is not necessary that the "Nebennase" should open into the choana, as it apparently has nothing to do with respiration at all, but acts as a highly specialised sense organ in co-ordination with the tentacle and tentacle canals. This is also the chief reason for the almost complete separation between "Nebennase" and main nasal sac, and the enclosure of the former in its own bony cavity. According to Wiedersheim then, the "Nebennase" is blind at its anterior end, and opens into the choana at its posterior end. It cannot serve as a respiratory organ without an anterior opening too, and it seems impossible that it could function as an olfactory ~~opening~~ organ, as the entrance of fluid into the "Nebennase" via the choana is prevented by the epithelial folds in the latter (see below). Under conditions existing in *C. ochrocephala*, the "Nebennase" ~~x~~

can definitely act as an olfactory organ, because it communicates with the exterior by means of two tentacle canals, and also through its opening in the main nasal sac, which latter according to Wiedersheim's description for *Coecilia*, ends blindly posteriorly, and communicates with the exterior through the external narial apertures at its anterior end. This cavity, therefore, cannot serve as a respiratory organ, and *Coecilia* cannot breathe through its nose. Wiedersheim must have missed the communications between the different sacs as described above for *C. ochrocephala*. The reader is referred to Wiedersheim's Figs. 46- 54 on Table 5, and it will then become clear that the relations he described are physiologically impossible. In *Ichthyophis* and *Siphonops* he describes the "Nebennase" as opening into the choana together with the main nasal sac, and in both species I have found his conclusions to be erroneous. Wiedersheim, throughout, mistook the "Choanenschleimbeutel" for the posterior part of the "Nebennase". The former does actually open into the choana together with the main nasal sac.

In *C. ochrocephala* an epithelial fold divides the anterior part of the choana into two portions: the "Choanenschleimbeutel" opening on the medial side of the fold and the main nasal sac on the lateral side (Fig. 6). This fold was described by Laubmann as a "Dachfalte", of which he found two in the choana of *Hypogeophis* (Fig. 13, S. 632). In relation to the choana he says: "Seitlich davon erheben sich am Munddach zwei Falten, die beiden dem ausmündenden Nasenabschnitt anliegen". In *C. ochrocephala* the medial fold appears far back in the choana, and persists for a very short distance only. Both folds end near the posterior end of the choana.

The most important features of the nasal organ of *C. ochrocephala* as contrasted with the nasal organ of other *Gymnophiona*, are the following:

(i) The slight dorso-lateral indentation, thusfar described for all other Gymnophiona investigated, is present.

(ii) A ventral indentation, formed by the nasopremaxillary, vomer and mesethmoid, is absent, so that the division of the main nasal sac into lateral respiratory and medial olfactory parts is not evident. The presence of this division in all Gymnophiona thusfar described gave rise to the idea that it was typical of all Gymnophiona. Its absence in *Coeccilia* is obviously due to specialisation, as the whole of the ~~main of the~~ main nasal sac seems to be used as a respiratory organ, the olfactory epithelium being very poorly developed and the olfactory sense being confined to the "Nebennase", which is already enclosed in its own cavity in the maxillo-palatine.

(iii) The "Nebennase" retains its opening into the main nasal sac, although Wiedersheim failed to notice this in species of *Coeccilia* investigated. The progressive separation between the "Nebennase" and the main nasal sac is probably due to specialisation of the former as the sole, highly developed sense organ.

(iv) The "Choanenschleimbeutel", containing numerous mucous alveoli in its walls, occupies the same position in relation to "Nebennase" and main nasal sac and choana as in *Dermaphis* (author) and *Ichthyophis* (Serasins). Wiedersheim obviously mistook it for the posterior part of the "Nebennase", and he also missed its opening into the posterior end of the main nasal sac. In a 3.5 cm. *Ichthyophis* embryo, the "Choanenschleimbeutel" is present as a small cavity lateral to the posterior end of the "Nebennase". Its development has not been described, but it appears to arise as an excavation of the connective tissue lateral to the main nasal sac, and its epithelium might be derived from the buccal epithelium.

its only function seems to be to supply mucus at the choana, as its walls contain large numbers of mucous alveoli.

The nasal glands. There are two main nasal glands: the first is the "Nasendrüse" described by Wiedersheim, the Saracins, Laubmann and the author for Ichthyophis, Siphonops, Coccilia, Hypogaeophis and Dermophis. The alveoli of this gland open into the main nasal sac. The gland differs in size in the various genera. In *C. ochrocephala* it is a large structure, with one long duct running[~] rostrad almost to the anterior end of the main nasal sac, below the dorso-lateral process of the nasopremaxillary (Figs. 1 and 2). This duct is accompanied by a large bloodvessel, shown in the text figures, and it opens into the anterior end of the main nasal/sac. On the appearance of the "Nebennase" the duct enters the nasal gland, which rapidly increases in size and is situated dorso-lateral on the main nasal sac (Figs. 3 and 4). At the posterior end of the "Nebennase", where it opens into the main nasal sac, the latter dwindles to a small tube and the nasal gland fills about one third of the nasal cavity. It then diminishes in size, and near its posterior end, the place of the large clear alveoli is taken by a few smaller darkly staining alveoli, which open directly into the main nasal sac. It would appear, therefore, that the nasal gland consists of two parts: A larger anterior part with large clear alveoli, which possess^{ses} one duct opening into the anterior portion of the main nasal sac, and a smaller posterior portion, consisting of small alveoli, with granular cytoplasm and darkly stained nuclei; these alveoli open directly into the main nasal sac. The significance of the division into two parts is not clear, as no comparative data exist, and the development of the gland has not been described in much detail. Wiedersheim found that the gland was absent in *C. rostrata*, and con-

sidered it to be replaced by the large number of glands of Bowman (op. cit., p. 42).

The "Tentakeldrüse" of Wiedersheim, or "Nebennasedrüse" of the Sarasins, is present in *Coecilia ochrocephala*, and Wiedersheim also described it for both species of *Coecilia* he examined. This gland is definitely a nasal gland, and not a tentacle gland as Wiedersheim suggested, because the tentacle canals have no connection with it at all. This gland appears simultaneously with the "Nebennase" and is also situated in the maxillo-palatine canal. It does not lie dorso-laterally on the "Nebennase" as in other genera, but medially to the "Nebennase", between the latter and the main nasal sac. It never attains to large proportions, and disappears from section before the posterior end of the "Nebennase" is reached.

The olfactory epithelium in the main nasal sac contains numerous small glands of Bowman (Figs. 1 and 2). The "Choanenschleimbeutel" has many large mucous alveoli in its anterior part (Fig. 5). Posteriorly no alveoli are present, and the walls contain columnar epithelial cells only. A choanal gland, consisting of a few large alveoli, is situated medially to the choana. A similar gland was also described for the genus *Dermophis*. Two of these alveoli are shown in Fig. 6.

The nasal capsule. The bones taking part in the formation of the nasal capsule are the same as those described for other genera, with this difference that they are more firmly applied, thus giving the nasal capsule a stronger build, which is admirably suited to a burrowing mode of life. The nasopremaxillary is the first bone to appear in section. It contains numerous small grooves and canals. In a dorsal groove a number of nerve fibres, ramifying between the mucous glands of the snout, accu-

ulate; they belong to the ramus ophthalmicus V. The nasopremaxillaries are situated medially in the anterior part of the snout. A mass of cartilage cells appear dorso-laterally; it becomes hollow, and a crescent-shaped cartilaginous band is formed surrounding the anterior elongation of the nasal sac, and also the external nasal apertures. The lateral part of the crescent is then replaced by connective tissue, leaving a dorsal and ventral cartilaginous bar, with the nasopremaxillary in a median position. The nasopremaxillary now gives two laterally projecting processes; one ventral and one dorsal to the nasal sac; as they expand laterad the cartilaginous bars become shortened and ultimately disappear altogether. The dorsal arm of the nasopremaxillary extends as far as the dorso-lateral indentation only. The ventral bar stretches laterad, then curves upwards to form the lateral wall of the nasal capsule, and finally turns inwards to complete the dorsal wall. A few nerve fibres separate the dorsal and ventral arms of the nasopremaxillary for a short distance, they then unite, and a complete ring is formed around the nasal sac. In Fig. 1 the medial wall of this ring is being broken up by the appearance of a piece of cartilage in it; this cartilage is the anterior elongation of the mesethmoid. This bone, therefore, appears far back for the first time, in contrast to other genera such as *Dermophis* and *Ichthyophis*, where the cartilaginous anterior part of the mesethmoid is continued between the two nasopremaxillaries almost to the anterior ends of the latter. Furthermore the mesethmoid in *O. ochrocephala* is not situated between the nasopremaxillaries, but its anterior end is forked, and each limb is incorporated in the medial portion of the nasopremaxillary, as is clearly indicated in Fig. 1. The connective tissue separating the two limbs is soon replaced by cartilage, so that the mesethmoid is present in the form of a cartilaginous hexangle, fused with the nasopre-

maxillaries. Slightly further caudad ossification appears in the mesethmoid, and it becomes separated off from the nasopremaxillaries by means of connective tissue.

The vomer appears in section as a small bone, ventral to the mesethmoid, and its anterior end fits into a fork of the ventral portion of the nasopremaxillary (Fig. 2). The maxillo-palatine has also made its appearance in the form of a small bone lateral to the nasopremaxillary; it increases rapidly in size, and becomes hollowed out so that a cavity is formed, in which the "Nebennase" and "Nebennase" gland are situated, as described above. The lateral portion of the nasopremaxillary now disappears, and shortly afterwards the medial portion of the maxillo-palatine, with the result that the cavities containing the nasal sacs become confluent. A second canal is now formed in the maxillo-palatine. It starts as a groove into which the tentacle sac moves (Fig. 2). This groove soon closes to form a canal, ventro-lateral to the "Nebennase" canal, and with several branches of the ramus maxillaris V and bloodvessels accompanying the tentacle sac in it (Fig. 3).

Meanwhile the ventral portion of the nasopremaxillary becomes shortened from both sides, and soon disappears from section, the maxillo-palatine and vomer then form the floor of the nasal capsule (Fig. 4). The frontal has already appeared in section below the dorsal portion of the nasopremaxillary, which then becomes shortened from its lateral side (Fig. 3). The mesethmoid is a thin bony bar situated medially, with two ventral processes stretching laterad. The dorsal part of the mesethmoid remains hidden between the nasopremaxillaries, but at the posterior end of the latter, the mesethmoid appears on the dorsal surface (Fig. 4). In Fig. 4 three canals are already found in the mesethmoid; and two deep grooves, which latter close to form canals, are present in the ventral

portion of the bone. Branches of the olfactory nerves are located in these canals.

The vomer is very small in comparison with that of other *Gymnophiona*. It is situated along the medial half of the floor of the nasal cavity (Fig. 4), and takes part in the formation of the floor. The vomer contains the ramus palatinus VII and the a. carotis interna in a vomerine canal, typical in the *Gymnophiona* (Fig. 4). Near the posterior end of the "Nebennase" the mesethmoid is a massive structure, containing five canals, whereas in other genera such as *Dermophis*, only four canals are present. All five canals contain branches of the olfactory nerve, which will be described below. They join the olfactory lobes, which are enclosed in a mesethmoid canal, as is also the case in *Dermophis gregorii*. The lobes stretch rostrad beyond the "Choanenschleimbeutel". Immediately behind the nasal capsule, the dorsal portion of the mesethmoid disappears from section and the frontal takes its place dorsal to the olfactory lobes. A long process of the mesethmoid appears on the dorsal surface between the posterior ends of the nasopremaxillaries and the frontals. On a level with the posterior end of the main nasal sac, a small triangle of cartilage appears between the orbital gland and the nasal gland (Fig. 5). Further caudad it joins the dorso-lateral side of the mesethmoid, becomes ossified, and the r. ophthalmicus V is enclosed in a canal within it (Fig. 6). In Fig. 6 the choana is also shown, with the small vomer on its medial side and the large maxillo-palatine on the lateral side. The basal bone has made its appearance between the two vomers.

The bones in the nasal region of *C. lumbricoides* and *C. rostrata*, especially those of the former, as described by Wiedersheim, are similar to those of *C. ochrocephala*. In both the nasopremaxillaries end posteriorly as two narrow, dorsally situated processes, and the mesethmoid

appears on the dorsal surface between their posterior ends and also between the frontals. In *C. rostrata* the mesethmoid appears on the dorsal surface between the anterior ends of the parietals only. The frontals in the former two retain a dorsal position, due to the large expansion of the maxillo-palatines on to the dorsal surface, whereas in *C. rostrata* the frontals reach down over the lateral sides of the skull (Wiedersheim, op. cit., p. 28). The posterior part of the frontal in *C. ochrocephala* also stretches down on the lateral side. The orbit of *C. lumbricoides*, enclosed in the maxillo-palatine only, resembles a nerve foramen, according to Wiedersheim. In *C. ochrocephala* an orbital opening is completely absent, although a small rudiment of the eye still remains (Fig. 8). In genera such as *Dermophis* and *Ichthyophis*, the paraquadrate also takes part in the formation of the rim of the orbital opening, but in *C. ochrocephala* and *C. lumbricoides* the paraquadrate is shortened considerably, due to the maxillo-palatine which stretches very far caudad. The canals in the maxillo-palatine are similar in *C. ochrocephala* and *C. lumbricoides*. Wiedersheim describes the vomer as a smaller bone in *Coccilia* than in *Ichthyophis* and *Siphonops* (op. cit., p. 30), and this is also the case in *C. ochrocephala*. It takes part in the formation of the choana in *C. ochrocephala* and *C. lumbricoides*, whereas in *C. rostrata* the maxillo-palatine is the only bone surrounding the choana, the vomer reaching only as far as the anterior edge of the choana (Wiedersheim, op. cit., p. 30).

The nerves of the nasal region. The fact that *Gymnophiones* possess two pairs of olfactory nerves, has been attested by all workers on the group. According to Wiedersheim the presence of two pairs of olfactory nerves is due to a physiological reason, namely so as to assure a diffuse distribution of the fibres throughout the olfactory epithelium (op. cit.,

p. 80). In both species of *Cocilia* described by him, he found the dorsal nerve to be the real continuation of the olfactory lobe, while the ventral one arises from the ventro-lateral bulblike process of the lobe (op. cit., p. 59). In *C. ochrocephala* there are three pairs of olfactory nerves. The dorsal pair becomes enclosed in the dorsal portion of the mesethmoid (Fig. 4), and the fibres are distributed to the walls of the main nasal sac, especially to the dorsal and medial walls. The remaining two pairs correspond to the ventral nerves of other genera. The most ventrally situated pair consists of large nerves, supplying the "Nebennase" only (Fig. 4). The nerve is enclosed in a canal in the ventral portion of the mesethmoid. Anterior to the entrance of these latter nerves into the mesethmoid, two small branches of a few fibres each enter a small canal in the medial portion of the mesethmoid, nearer the ventral surface. These branches supply the main nasal sac. It therefore seems possible that they belong to the ventral olfactory nerve, a view which is strengthened by the fact that they join the ventro-lateral bulblike process of the olfactory lobe, together with the large ventral nerves. On the left side in one of the specimens, this small branch enters its own canal, but on the right side, although it is separate from the large ventral olfactory, it enters the canal of the latter. The reason for the division of the ventral olfactory into two distinct branches, must be looked for in the large development of the "Nebennase" as the most important sense organ of the animal. It therefore has its own branch of the olfactory nerve, as well as being situated in its own bony canal. Branches of the r. maxillaris V, the r. ophthalmicus V and r. palatinus VII are also present in the nasal region. No anastomoses are formed between these nerves and the olfactory nerves.

In this description of the nasal region of *C. ochrocephala* the following points of specialisation and degeneration seem to be important: The "Nebennase" is a very well-developed sense organ, and it lies partly in its own cavity in the maxillo-palatine; it also has its nerve supply completely separated off from the nerves of the rest of the nasal sacs. The specialisation of the "Nebennase" is associated with the degeneration of the main nasal sac. The latter is not divided into respiratory and olfactory parts, and its walls contain a few layers of olfactory epithelium only. The communication between "Nebennase" and main nasal sac is limited to the extreme posterior end of the former; this also indicates specialisation of the "Nebennase". The glands are well-developed; especially the nasal gland and the mucous alveoli in the walls of the "Choanenschleimbeutel". The bones of the nasal capsule are strongly ossified and firmly applied to one another. The maxillo-palatine is a large bone and limits the development of the vomer and the frontals. The forked anterior end of the mesethmoid is incorporated in the nasopremaxillaries, and the mesethmoid appears on the dorsal surface between the nasopremaxillaries and the frontals. All these points indicate specialisation and adaptation to a burrowing mode of life. Most of the specialised features are in some way connected with the highly developed "Nebennase".

The tentacle and eye of *Cuscilia ochrocephala*.

The tentacle is situated on the side of the snout, below the external narial apertures in a horse shoe shaped tentacle groove. Two small tentacle canals, with thick connective tissue walls and an epithelial lining (Fig. 1), open into the anterior end of the tentacle groove. They are continued caudad in the connective tissue, and finally, after

performing the maxillo-palatine (Fig. 2), they open into the "Nebennase". Distally the tentacle has a free end projecting from the tentacle groove. It is continued caudad through the connective tissue, and is surrounded by a thin connective ^{tissue} sheath. The tentacle consists of an epithelium lined sac invaginated laterally by a connective tissue strand, which is replaced further caudad by the retractor muscle of the tentacle (Fig. 2). Posteriorly the tentacle sac lies against the latero-ventral portion of the nasopremaxillary. The maxillo-palatine appears dorsal to the tentacle sac; it then reaches over the lateral side of the latter and finally encloses the latter in a canal, ventral to the canal of the "Nebennase" in the same bone. Large bloodvessels and branches of the r. maxillaris V accompany the tentacle sac in this canal.

The epithelium lined tentacle sac then divides into several smaller canals, and the epithelial cells become more columnar in shape. These small canals are surrounded by the alveoli of the orbital gland, and they act as ducts of the latter. The secretion of the orbital gland therefore enters the tentacle sac and is carried into the tentacle groove and on to the lateral side of the head. The alveoli of the orbital gland appear dorsal and lateral to the retractor muscle (Figs. 4 and 5), and finally surround the muscle completely; it is a well developed gland, as shown in Fig. 7. Posteriorly the maxillo-palatine decreases in size; laterally it is replaced by the paraquadrate, and dorsally by the frontal, which now reaches over the sides of the skull (Fig. 7), whereas rostrad it is confined to a dorsal position.

The compressor muscle of the orbital gland appears dorsal of the orbital gland; it then stretches laterad, and curves inward to surround the gland completely (Fig. 7). As the gland decreases in size, the com-

pressor muscle increases, and forms a large circular muscle surrounding the retractor muscle. The latter has shifted mediad, and finally lies pressed against the trabecula as a very small muscle with the n. abducens enclosed within it. The compressor muscle inserts on the trabecula only, and is replaced by the m. adductor mandibulae externus major, which arises dorsally from the frontal and then extends ventrally (Figs. 7 and 8). Medio-ventrally a few fibres of the compressor muscle separate off to form a small muscle belly, which is continued much further caudad than the rest of the muscle. This muscle belly shifts laterad and lies pressed against the ventral side of the m. adductor mandibulae externus major, and inserts on the tendon of the latter.

Important is the innervation of the different parts of the tentacle. The n. abducens, supplying the retractor muscle, can be located in the posterior part of the muscle. After leaving the muscle it lies closely applied to the lateral wall of the neurocranium. Its further course will be described below. The innervation of the large compressor muscle could not be demonstrated at all. A few nerve fibres were seen in the muscle belly described above, but they could not be traced to any of the nerves. The large orbital ^{gland} ~~muscle~~ also indicates specialisation of the "Nebennase" and the tentacle. Its secretion is probably used as a lubricant and cleanser of the tentacle, tentacle groove and the skin surrounding the latter. The compressor ~~muscle~~ muscle was believed to assist the gland in pouring its secretion into the tentacle groove. It therefore seems strange that in this species, where all these structures are highly developed, the nerve supply of the compressor muscle could not be demonstrated. In *Dermophis*, where both gland and muscle are so much smaller, a strong ramulus of Vb innervates the muscle, as is also the case in

Scolecormorphus and *Boulengerula* (de Villiers) and in *Ichthyophis* (Engelhardt). No nerve fibres innervating the connective tissue tentacle sheath were found, and although three branches of Vb accompany the tentacle, they do not send any fibres to the latter.

The eye of *Coecilia ochrocephala* has almost completely degenerated. It is present in a few sections only as a small mass of pigment, situated on the lateral side of the orbital gland (Fig. 6). The lens is entirely absent, as well as an orbital opening. The eye is covered completely by the maxillo-palatine. Wiedersheim described the orbital opening in *C. lumbricoides* as resembling a small nerve foramen. In *Herpele*, a South American and African genus, Nieden (1918) described the eye as covered by cranial bones. With the exception of the retractor muscle and the n. abducens, all the eye muscles and nerves have disappeared completely.

Suspensorium of *Coecilia ochrocephala*.

The skull of a Gymnophione, such as *Hypogeophis*, is hyostylic and kinetic, as is clearly explained by H. Marcus in "Der kinetische Schädel von *Hypogeophis* und die Gehörknöchelchen" (1935). The palatoquadrate has four processes: (a) The anterior process arising on the ventral surface, articulates with the basal bone and is the p. pterygoideus palatoquadrati; (b) the p. ascendens is a slightly convex bony squame underlying the paraquadrate, and it reaches the cartilage between the paraquadrate and the parietal; (c) the p. columellaris proceeds caudad and articulates with the stapes forming the quadrate-stapedial articulation; (d) the fourth process is a conical one fitting into the articulating socket of the lower jaw, and is the p. articularis (op. cit., p. 162-163, and Fig. 13).

In *C. ochrocephala* all four processes of the palatoquadrate are present. A separate pterygoid is absent, and the p. pterygoideus reaches rostrad as far as the anterior end of the trabecula. It lies wedged in between the trabecula and the maxillo-palatine, which is here reduced to a ventrally situated squame. The p. pterygoideus forms the quadrato-basal articulation with the basal bone. The synovial cavity is very small, and for the greater part the two articulating surfaces are closely pressed against each other (Fig. 10), so that the power of mutual movement seems in the process of degeneration. In *Dermophis* the p. pterygoideus in forming the articulation lies lateral to the basal process, but in *C. ochrocephala* it has a more dorsal position (Fig. 9). The m. levator quadrati, stretching between the lateral wall of the neurocranium and the p. pterygoideus (Fig. 9), is very small, and no innervation could be demonstrated. This supports the suggestion that the quadrato-basal articulation is degenerating. The p. pterygoideus joins the body of the palatoquadrate immediately after the r. mandibularis V has passed laterally over it on its way to the lower jaw.

The dorsally directed p. ascendens almost reaches the parietal, the bones being separated by a narrow strip of connective tissue only (Figs. 8 and 9). The paraquadrate, covering the p. ascendens, also reaches the parietal (Fig. 9), so that the skull is definitely stegokrotaphic. The paraquadrate is shortened rostrad by the maxillo-palatine; it does not reach the eye, whereas in *Dermophis* it takes part in the formation of the orbital opening. No movement seems possible between the paraquadrate and the p. ascendens, as they are firmly bound together by means of a narrow strip of dense connective tissue (Fig. 9).

The p. articularis, articulating with the lower jaw, is a sharp

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conical process fitting into the V-shaped socket in the lower jaw (Fig. 10). At the level of the jaw articulation, the paraquadrate has reached its posterior end, and the palatoquadrate then forms the outer wall of the skull (Fig. 10). The latter lies pressed against the neurocranium, so that the quadrate-cranial passage is almost obliterated, whereas in genera such as *Dermophis*, *Ichthyophis* and *Siphonops*, its position is broadly laterad, so that a large cranio-quadrate passage is formed, and the skulls are consequently much broader. This condition in *Coeccilia* was also noticed and described by Wiedersheim. With the disappearance of the quadrate-cranial passage the bloodvessels, ganglia and nerves of this region are pressed into the cranial cavity (see below).

Posterior to the jaw articulation, the palatoquadrate rapidly decreases in size until a small posteriorly projecting process, the p. columellaris, alone remains. This process articulates with the stapes in *Hypogeophis*, *Ichthyophis*, *Siphonops* and *Boulengerula*. In *Dermophis* this articulation is in the process of being lost: the synovial cavity is present, but the two components undergo a certain amount of fusion. In *Cochrocephala* the synovial cavity is present in two sections only marking the boundary between the stapes and the palatoquadrate. In Fig. 11 the quadrate and stapodial components are cartilaginous and continuous, and the small synovial cavity is shown. In the next section the synovial cavity is obliterated and the stapes is ossified. The articulation is therefore almost completely lost, being indicated in two sections only.

Together with the synovial cavity, the footplate of the stapes appears as a small bone fixed by means of cartilage to the side wall of the neurocranium (Fig. 11). A few sections further caudad the footplate is in actual bony continuation with the skull for a short distance. The

style then joins the footplate, very near its anterior end. The fenestra ovalis is continued right to the anterior end of the otic capsule and the footplate fills the entire fenestra. In some sections only one cell layer of connective tissue separated the footplate from the lips of the fenestra, so that movement is practically impossible, as is also indicated by the circumstance that the footplate is in bony and cartilaginous continuity with the wall of the neurocranium. Where the style joins the footplate, it is directed laterad, but dorsally, and encloses a small cavity next to the neurocranium, in which the r, hyomandibularis VII and the a. stapediae are continued. The style then becomes shorter, but these structures retain their dorsal position with respect to it. Movement between the palatoquadrate and the neurocranium is therefore impossible, and the skull is definitely akinetic. The degeneration of the articulations is much further advanced than in *Dermophis*, in which the quadrate-basal articulation and the m. levator quadrati are still well developed.

The muscles and the remaining cranial bones.

Caudad of the nasal capsule the basal bone enlarges rapidly, and finally replaces the mesethmoid in the floor of the skull. The lateral portion of the mesethmoid is reduced to two cartilaginous bars: the dorsal taenia marginalis and the ventral trabecula. Va lies between them, and the retractor maxillae and compressor muscles are situated laterad in relation to them. The basal bone then extends upwards and incorporates the taenia and trabecula, so that the floor and the side walls of the neurocranium are formed by the basal bone (Fig. 8). No other bones appear in these parts, except the palatoquadrate, which forms the lateral wall of the skull at the foramen preoticum, as is described above.

The frontals overlap the parietals for a considerable distance. The paraquadrates reach the frontal and the parietal laterally, so that the skull is stegokrotaphic. After the appearance of the paraquadrate in section, the p. ascendens still remains in contact with the parietal which is a large bone, reaching well over the sides of the skull. The dorsal portion of the mesethmoid appears for a short distance between the two parietals, which, however, soon meet in the middorsal line, and the mesethmoid is continued beneath then for a short way; it ends caudad beyond the incorporation of the trabacula and taenia into the basal bone.

The basal bone has two important foramina anterior to the otic capsule: a ventral one for the a. carotis interna immediately behind the quadrato-basal articulation (Fig. 10), and a large lateral foramen prooticum, which is covered laterally by the palatoquadrate. The otic capsule is formed by the basal bone, which at the anterior end of the capsule, extends on to the dorsal surface below the parietals. Behind the latter, the basal bone closes in the middorsal line and forms a pronounced ridge for a short distance; the basal bone is therefore the only bone posterior to the otic capsule.

The muscles do not differ much from those of other genera. The m. adductor mandibulae externus major arises from the frontal and is situated dorsal to the compressor muscle and orbital gland (Fig. 7). The muscle retains this dorsal position for a short distance, and then extends ventrally over the lateral side of the compressor muscle. As the latter decreases in size, the m. adductor mandibulae externus major increases in size and finally fills almost the entire temporal groove (Fig. 8). At the anterior end of the muscle, another arises from the taenia marginalis, and the two muscles are separated dorsally by a large blood-

vessel, and ventrally by the r. maxillaris V (Fig. 8). This medially situated muscle is the m. pseudotemporalis, also described by Luther for *Cocillia* (1914). Both muscles insert on the lower jaw. Behind the small m. pseudotemporalis, its place is taken by the small m. levator quadrati, described above (Fig. 9). On the level of the m. levator quadrati, the m. pterygoideus arises from the ventral surface of the p. pterygoideus, and inserts on the medial surface of the lower jaw (Fig. 8). Rostrad it is a small muscle, but caudad it is large.

Laterally, near the posterior end of the m. adductor mandibulae externus major, the m. adductor mandibulae externus minor arises from the inner surface of the p. ascendens palatoquadrati. It is small, and inserts on the lower jaw. Ve on its way to the lower jaw passes between these two muscles (Fig. 8).

The m. cephalo-dorso-maxillaris arises from the outer surface of the paraquadrata p. and caudad from the frontal and parietal; it inserts on the lower jaw (Figs. 9, 10 and 11). The innervation of these muscles will be discussed below with the nerves.

The cranial nerves of *Cocillia ochrocephala*.

The olfactory nerve has already been discussed above; important is its division into three branches. The optic, oculomotor and trochlear nerves have degenerated completely with the degeneration of the eye and its muscles. The n. abducens is present as a very fine nerve, innervating the retractor muscle of the tentacle. It enters the muscle near its posterior end next to the trabecula. The nerve could only be located in the posterior part of the muscle. It is continued caudad in this ventral position, and at the anterior end of the quadrato-basal articulation the n. abducens, the r. ophthalmicus V (Va) and the r. palatinus VII lie me-

die-dorsal of the articulation (Fig. 8). The anterior end of the large foramen prooticum now appears, and Va enters the anterior elongation of its ganglion (Fig. 9). The n. abducens also enters the ganglion of Va at its ventral end, and then disappears completely. It was impossible to trace the nerve fibres through the ganglion into the brain. In a juvenile *Ichthyophis* I found the n. abducens leaving the cranial cavity ventral to the ganglion of Va; de Villiers described the same relations in *Scolecophorus* (op. cit., p. 22). In both specimens of *C. ochrocephala* and on either side of the head, the entrance of the n. abducens into the ganglion of Va was noted, and its further course could not be demonstrated.

The palatoquadrate as described above, lies pressed against the lateral wall of the neurocranium, and at the posterior end of the paracquadrate it is pressed so closely to the neurocranium, that the quadrate-cranial passage is completely obliterated (Fig. 10), with the result that the ganglia, nerves and bloodvessels of this region are shifted into the cranial cavity. The anterior end of the ganglion of Va and a small part of the maxillo-mandibular (Vb+c) ganglion are the only parts remaining outside the cranial cavity. Another important point is the fusion of the ganglia to a very great extent. In *Dermophis*, as described by the author, the following ganglia are present: (i) a geniculate ganglion for the facial nerve; in *Dermophis mexicanus* this ganglion is forked, indicating a separate ganglion for the r. palatinus VII, a point which became clear on studying a juvenile *Ichthyophis*, where the ganglion of the r. palatinus VII is completely separate; (ii) Two separate ganglia for the n. trigeminus, one for the maxillo-mandibular branch and one for the ophthalmic branch of the nerve. Between the ganglia of the facial and trigeminal nerves a commissure consisting of a few fine fibres was described for *Dermophis*.

gregorii and on one side only for *Hermophis mexicanus* (op. cit., pp. 332 and 333).

On making reconstructions of the ganglia in *C. schrocephala*, it was found that the ganglia have fused to a considerable extent. The ganglion of the acoustic nerve, situated in the cranial cavity, lies pressed against the inner wall of the otic capsule, and three branches are seen passing through three separate foramina into the inner ear (Fig. 13). The two posterior ones pass through ventrally situated foramina, the anterior one enters the extreme anterior end through a more dorsally situated foramen. The root of the facial nerve leaves the brain slightly anterior to the root of the acoustic, and the dorsal fibres of the root enter the anterior end of the acoustic ganglion (Fig. 13), these fibres leave the cranial cavity immediately anterior to the otic capsule through the posterior end of the large foramen prooticum, and form the r. hyomandibularis VII, which passes backward against the lateral wall of the neurocranium (Fig. 12). The ventral fibres of the facial root do not attain any connection with the acoustic ganglion, but they enter the anterior end of the large maxillo-mandibular ganglion (Fig. 13), which appears in section immediately anterior to the acoustic ganglion. These fibres form the r. palatinus VII, and they leave the ganglion of Vb+c when the Vb+c portion of the trigeminal nerve root enters the ganglion. The r. palatinus VII is continued in the cranial cavity ventral to the ganglion of Vb+c, and then lateral to the ganglion of Va, and it leaves the cranial cavity together with this ganglion, and is then continued rostrad together medio-dorsal to the quadrato-basal articulation (Figs. 8 and 9). The root of the trigeminal nerve divides into two portions in the cranial cavity: the maxillo-mandibular portion enters the maxillo-mandibular ganglion;

the other portion is the ophthalmic root and is continued rostrad in the cranial cavity for a considerable distance before entering the ophthalmic (Va) ganglion (Fig. 13). The r. maxillaris V (Vc) is the first to leave the ganglion of Vb+c, and is continued rostrad towards the lower jaw. The anterior end of the ganglion of Vb+c lies outside the cranial cavity (Fig. 9), and Vb leaves it and is continued downwards between the muscles in the temporal groove (Fig. 8). The anterior part of the ganglion of Va also lies outside the cranial cavity, medio-dorsal to the quadrato-basal articulation (Fig. 9), and it is separated from the rest of the structures in the temporal groove by the m. levator quadrati (Fig. 9). Behind the m. levator quadrati, the two ganglia of the trigeminal nerve lie close against each other, but no connection exists between them. These ganglia are similar to those of *Dermophis*, and separate trigeminal ganglia were also described for *Boulengerula* by de Villiers.

The absence of a separate facial ganglion is interesting. The only possible explanation seems to be the following: The ganglion of the r. hyomandibularis VII, corresponding to the geniculate ganglion of a juvenile *Ichthyophis*, has fused with the acoustic ganglion, and the ganglion of the r. palatinus VII, corresponding to the ganglion pro nerve palatino of a juvenile *Ichthyophis*, has fused with the ganglion of Vb+c. The fusion of the ganglia may be due to their being crowded into the cranial cavity, and in the limited space fusion resulted. It is unfortunate that Wiedersheim did not give a description of these ganglia of the two species of *Coccolia* he investigated, as he did notice the fact that the palatoquadrate is pressed against the neurocranium. As it is, no comparative data exist, and the condition cannot be absolutely clear unless the development is investigated. Important also, is the presence of one

large foramen prooticum, whereas in *Dermophis* Va and Vb+c each have separate foramina, and the facial also has its own foramen. These separate foramina were interpreted as an attempt to strengthen the skull for a burrowing life. In the nasal region of *Coeccilia* the bones are strongly ossified and fused for a burrowing life. The weakening of the skull due to the presence of the large prootic foramen is probably remedied by the alkinetic palatoquadrate, which is pressed against the skull; it forms adequate protection in the region of the foramen prooticum.

The further course of the fifth and seventh cranial nerves.

The n. facialis. (i) The r. hyomandibularis VII, after leaving the cranial cavity, is situated in a canal bounded by the stapediale style and the lateral wall of the neurocranium, together with the a. stapediale and the v. jugularis interna (Fig. 12). The first branch of the r. hyomandibularis VII consists of a few fibres proceeding laterad and then dipping down between the m. cephalo-dorso-maxillaris and the m. pterygoideus towards the inner surface of the lower jaw. They enter a canal in the lower jaw, and are the chorda tympani, which is continued rostrad in the lower jaw dorsal to Meckel's cartilage (Figs. 10 and 12). It forms an anastomosis with a branch of Vc, and leaves the lower a short distance in front of the mental symphysis to innervate the tongue and its epithelium. The remaining fibres of the r. hyomandibularis VII pass backwards, and divide into two branches: The outer one innervates the m. cephalo-dorso-maxillaris, and the final termination of the other could not be traced. The r. hyomandibularis VII has the same relations in *Dermophis* (op. cit., p. 337).

(ii) The r. palatinus VII after leaving the cranial cavity, is

continued rostrad in a ventral position together with the a. carotis interna. Ventral to the posterior end of the compressor muscle it divides into two branches: one remains in its original position, the other proceeds laterad (Fig. 7), and passes ventral to the r. maxillaris V which has passed down between the m. pseudotemporalis and the m. adductor mandibulae externus major from a dorsal to a ventral position. Here the branch of the r. palatinus VII enters a small ganglion, present in five sections only. After the nerve has emerged from the ganglion, it is continued rostrad together with Vb for a considerable distance before fusing with the latter, thus forming an anastomosis. Before this anastomosis is effected, Vb gives off a small branch which proceeds mediad and forms an anastomosis with the ventrally situated branch of the r. palatinus VII. There are therefore, two anastomoses between Vb and the r. palatinus VII, a condition also described by Engelhardt for *Ichthyophis*. In *Dermophis* and *Scolecophorus* only one anastomosis is present. The small ganglion mentioned above is present on both sides of the head and in both specimens examined. The r. palatinus VII is continued rostrad between the vomer and the mesethmoid, and finally comes to lie in a vomerine canal. Its fibres innervate the buccal epithelium, and the nerve is accompanied throughout its course by the a. carotis interna.

The n. trigeminus. (i) The r. mandibularis (Vc) leaves the ganglion of Vb+c laterally, and immediately gives off a branch passing laterally over the p. pterygoideus palatoquadrati and entering the m. pterygoideus. Two other small branches are then given off: one remains in a dorsal position and ultimately enters the m. adductor mandibulae externus major, while the other passes laterad and innervates the m. adductor mandibulae externus minor (Fig. 9). Vc then enters the lower jaw and divides

into three branches: one passes right through the lower jaw and innervates the *m. intermandibularis*. The second small one forms an anastomosis with the chorda tympani, which is then continued rostrad dorsal to Meckel's cartilage, and the third branch remains in a canal in the lower jaw and gives off small branches innervating the lateral and ventral skin.

(ii) The *r. maxillaris V (Vb)*. Two branches of Vb leave the ganglion of Vb+c before Vc does so. The dorsal one passes through the parietal and innervates the dorsal skin. This branch corresponds to the ridge-like branch described for *Dermophis*, *Scopelomorphus* and *Boulengerula*. The other branch passes laterad and innervates the *m. adductor mandibulae externus major*; it was also described for *Dermophis*. The main trunk of Vb leaves the ganglion at its anterior end and passes down between the *m. pseudotemporalis* and the *m. adductor mandibulae externus major* (Fig. 3). Immediately after leaving the ganglion, Vb gives off a small branch which remains in a dorsal position (Fig. 3), and finally forms an anastomosis with a branch of Va, given off just before it (Va) enters a canal in the lateral portion of the mesethmoid. This fused branch of Va and Vb is continued far rostrad and it gives off fibres to the skin on the lateral and dorsal sides of the head.

The main trunk of Vb after attaining a ventral position, forms the anastomoses with the *r. palatinus VII*, referred to above. Vb then divides into two branches: one moves laterad and the other mediad; both enter a canal in the maxillo-palatine, and are continued far rostrad in these canals and subsequently in the cavity containing the tentacle structures in the same bone. The medial branch finally enters a canal in the nasopremaxillary. These branches of Vb innervate the skin on the lateral and ventral sides of the head. No branch of Vb innervating the compressor

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muscle could be traced. In *Dermophis* and *Ichthyophis* a large branch of Vb innervates this muscle. A small ^{nerve} located in the muscle could not be traced to any of the rami of the trigeminal nerve.

(iii) The r. ophthalmicus V (Va) is a large nerve, leaving its ganglion anterior to the quadrate-basal articulation. At first it is situated in a ventral position, but then moves upwards against the lateral wall of the neurocranium (Fig. 7), and gives off a small branch which fuses with a branch of Vb as described above. This composite nerve is continued in a canal in the frontal and in the tentacular canal in the maxillo-palatine and it innervates the dorsal skin. The main trunk of Va passes into the nasal cavity through a canal in the lateral portion of the mesethmoid (Fig. 8). In the nasal cavity it ~~splits~~ divides into two branches: one lies embedded in the nasal gland (Fig. 3), and the other one proceeds mediad and is situated dorsal to the nasal sac (Fig. 4). Both branches ultimately enter a canal in the nasopremaxillary; the lateral branch innervates the dorsal skin, while the medial branch leaves the canal in the nasopremaxillary and lies between the medial surfaces of the two nasopremaxillaries, sending out branches to the dorsal and ventral portions of the skin. Va as was previously stressed for *Dermophis*, is a purely sensory nerve, innervating mainly the skin in the snout region. The anastomosis existing between Va and Vb, is absent in *Dermophis* and *Ichthyophis*, but de Villiers found in one specimen of *Boulengerula* no less than three anastomoses between these two rami. Vb contains a motor and a sensory component; the former consists of a branch innervating the m. adductor mandibulae externus major; no branch innervating the compressor muscle could be demonstrated. The remaining fibres form the cutaneous component. Va also contains a motor and a

sensory component. The motor part consists of three branches innervating the m. adductor mandibulae externus minor, the m. pterygoideus and the m. intermandibularis. The sensory component consists of one large branch running rostrad in the lower jaw, and fibres are sent out to the skin.

The nerves of *Cocilia ochrocephala* therefore do not differ very much from those of other genera. The ganglia and foramina, however, differ to a great extent. The most important features of the cranial nerves are the following:

(i) The fusion of the facial ganglia with the acoustic and maxillo-mandibular ganglia.

(ii) Separate trigeminal ganglia are present, without any commissure connecting them.

(iii) These ganglia are situated in the cranial cavity, and the nerves leaving them pass through one large prootic foramen, which is covered laterally by the palatoquadrate.

(iv) Two anastomoses are formed between the r. palatinus VII and Vb; one between Vb and Va and one between Vc and the chorda tympani.

(v) Va is a purely sensory nerve, and Vb has one motor branch only, the other fibres are sensory; Vc has three motor branches. The r. palatinus VII innervates the buccal epithelium, and the r. hyomandibularis VII has a motor branch innervating the m. cephalo-dorso-maxillaris.

(vi) The innervation of the following muscles could not be demonstrated: the m. levator quadrati, the m. pseudotemporalis and the large compressor muscle of the orbital gland. According to Luther the m. levator quadrati is supplied by a branch of Vc and the latter two by branches of Vb.

The cephalic bloodvessels.

A. The arteries. The a. stapedialis is a branch of the a. carotis interna, given off at the posterior end of the skull, where the artery has acquired a ventral position. The a. stapedialis runs upwards and reaches the ventral side of the r. hyomandibularis VII, which it accompanies rostrad together with the v. jugularis interna. As in *Dermophis*, *Scolecophorus* and *Boulengerula*, the a. stapedialis supplies the cranial nerves. The first branch given off is a small one accompanying the chorda tympani into the lower jaw. The artery does not pierce the stapes, but is first situated dorsal and then medial to the stapedial footplate (Figs. 11 and 12). In the posterior part of the quadrato-cranial passage it is pushed into the cranial cavity together with the veins and nerves of this region. The two small branches of Vb leaving the ganglion of Vb+c, each have a small branch of the a. stapedialis accompanying them, and a larger branch passes dorsally over the main trunk of Vc and enters the lower jaw with the latter; here it divides into three small branches, one for each branch of Vc.

The main branch of the a. stapedialis moves down between the m. pseudotemporalis and the m. adductor mandibulae externus major with Vb (Fig. 8), and divides into two branches: one accompanying Vb, and the other runs upwards and supplies the branch of Vb effecting the anastomosis with Va. Where this anastomosis takes place, the branch of the a. stapedialis divides into two: one branch going towards the main trunk of Va, and the other one remaining with the fused Va and Vb branches. The branch accompanying the main trunk of Vb divides into two when the nerve divides into medial and lateral branches, and these arteries accompany the nerves throughout their entire course. The a. stapedialis

is therefore clearly an artery supplying the fifth and seventh cranial nerves.

The a. carotis interna retains a ventral position throughout. It gives off the a. stapediales, and is then continued rostrad as an unbranched vessel together with the v. palatina between the roof of the buccal cavity and the skull, until the posterior end of the quadrate-basal articulation is reached. It then enters the cranial cavity through a canal in the basal bone (Fig. 10). Here it divides into two branches: one supplying the brain and the other one continues rostrad in the cranial cavity for a considerable distance before it leaves through the anterior end of the foramen prooticum. This branch accompanies the f. palatinus VII through its entire course, and enters a vomerine canal with it. After leaving this latter it supplies the buccal epithelium with blood. It is a comparatively unbranched vessel.

B. The veins. The veins form large sinuses, and are much more branched than the arteries, forming large sinusoidal networks characteristic of the Gymnophiona. Large veins arising in the anterior part of the snout between the mucous glands and from the buccal epithelium, enter the maxillo-palatine cavity in which the tentacle structures are situated. Three of these vessels enter the cavity, each one accompanying a branch of Vb, which also occupies the cavity (Fig. 3). In the nasal cavity a large vein, arising in the anterior part of the nasal sac, is continued caudad with the large duct of the nasal gland, and finally opens into the v. capitis lateralis. Two of the vessels in the maxillo-palatine canal unite to form a dorsally situated vessel, the v. capitis lateralis, which forms a very large network between the m. pseudotemporalis and the m. adductor mandibulae externus major (Fig. 3). This

sinus is joined by a vein arising in the m. adductor mandibulae externus major.

The v. jugularis arises as a plexus in the buccal epithelium; it runs upwards and finally lies pressed against the ventral side of the ganglion of Va, medio-ventral to the m. pseudotemporalis (Fig. 8). It gives off a branch which passes close against the wall of the neurocranium through the insertion of the m. pseudotemporalis, and forms an anastomosis with the v. capitis lateralis (Fig. 8). When the anterior part of the foramen prooticum is reached, the v. jugularis is pressed into the cranial cavity together with the ganglion of Va. The v. capitis lateralis is also pressed into the cranial cavity together with the ganglion of Vb+c, after it has been joined by a vessel from the m. adductor mandibulae externus minor, and one from the dorsal skin. The two veins then join to form one large venous channel lying lateral to the trigeminal ganglia (Fig. 10). A large bloodvessel continued rostrad ventrally in the cranial cavity from the posterior part of the otic capsule, here joins the large venous channel on its ventral side, and this vessel is the only cephalic branch (Figs. 11 and 12). At the anterior end of the otic capsule, the venous channel, which has fallen into a network, again forms one vessel, which is continued caudad with the r. hyomandibularis VII. This vein is joined caudad by a large venous channel leaving the cranial cavity through the foramen jugulare. The v. palatina forms a network in the buccal epithelium and is continued caudad together with the a. carotis interna (Fig. 12).

The large venous channel surrounding the trigeminal ganglia, and the one vein continued caudad lateral to the otic capsule, were also described for *Dermophis* (the author). In that genus there are, however,

three cephalic branches joining the venous channel, and they have their own foramina separate from those of the cranial nerves, whereas the vessel in *Cocilia* joins the venous channel in the cranial cavity. One communication is present between the v. capitis lateralis and the v. jugularis anterior to the formation of the large venous channel; in *Scolecormorphus* de Villiers described three of these communications (op. cit., p. 17). The vein escaping through the foramen jugulare was also described by de Villiers for *Scolecormorphus* and for *Dermophis* by the author.

General conclusions.

Cocilia ochrocephala is a highly specialised species, and agrees in many ways with the two species of the same genus described by Wiedersheim. The various points of specialisation and degeneration have been fully discussed above, and a brief summary will suffice.

(i) The nasal region is highly specialised: the "Nebennase" has its own cavity in the maxillo-palatine and its own separate nerve, so that the olfactory nerve is divided into three portions.

(ii) The main nasal sac shows degeneration, as it performs a respiratory function only, the "Nebennase" taking over the olfactory function.

(iii) The tentacle is well developed, and has a very large retractor muscle, orbital gland and compressor muscle. The tentacle and the "Nebennase" therefore form a highly developed sense organ.

(iv) The eye is represented by a small pigment mass, and an orbital opening is absent.

(v) The bones of the nasal region are firmly applied to one another so that a rigid structure results.

(vi) The skull is completely akinetic. The quadrate-stapedial articulation has degenerated, and the quadrate-basal^{articulation} has progressed much further in degeneration than in the genus *Dermophis*. The stapes is in bony and cartilaginous continuity with the otic capsule.

(vii) The ganglia of the cranial nerves have fused to a great extent, a separate ganglion for the facial nerve being absent, and the ganglia and bloodvessels of the quadrate-cranial passage are forced into the cranial cavity through the one large foramen prooticum, which latter is roofed over laterally by the palatoquadrate.

(viii) The nerves do not differ much from that of other genera. Two anastomoses between Vb and the r. palatinus VII are present, and one between Vb and Va.

(ix) The arteries and veins do not show any important features; the a. stapedialis supplies the fifth and seventh cranial nerves. Only one cephalic branch of the v. capitis lateralis is present, and it joins the venous channel in the cranial cavity.

The general impression made by the skull is that of very considerable specialisation and of almost complete degeneration of certain parts. The cranial bones are firmly fused and applied to one another, and the skull is akinetic, so that it is eminently suited for a burrowing mode of life.

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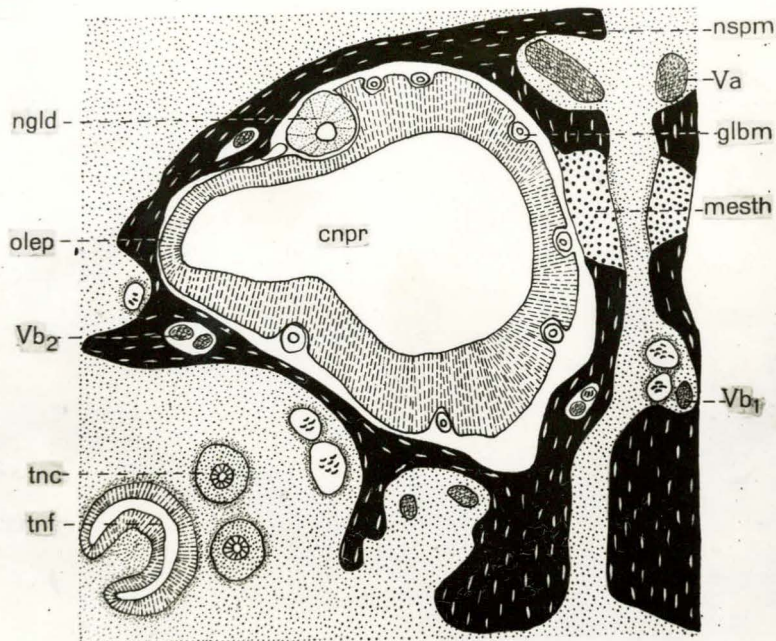


Figure I.

Figure 1. A transverse section through the anterior part of the nasal region. cnpr cavum nasale principale; glbm gland of Bowman; mesth mesethmoid; ngld duct of the nasal gland; nspm nasopremaxillary; olep olfactory epithelium; tnc tentacle canal; tnf tentacle fold; Va ramus ophthalmicus trigemini; Vb1 medial branch of the ramus maxillaris trigemini; Vb2 lateral branch of the ramus maxillaris trigemini.

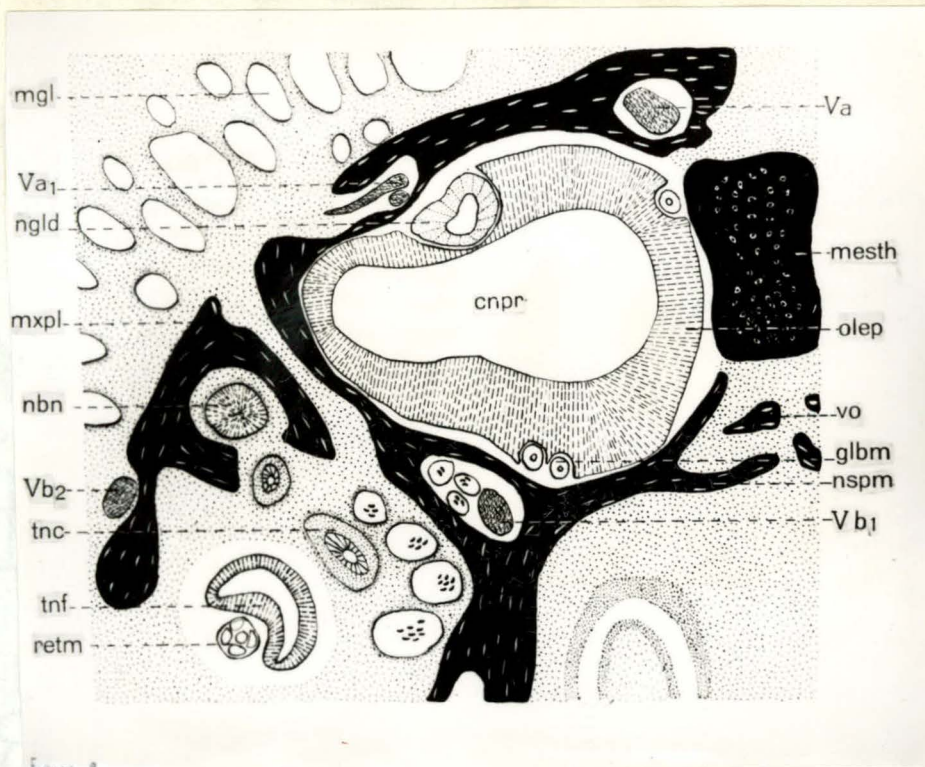


Figure 2. A transverse section through the anterior end of the "Neben-nase". agl mucous gland; mxpl maxillo-palatine; nbn "Nebennase"; retm retractor muscle of the tentacle; vo vomer; Va1 a branch of the r. ophthalmicusV. Other abbreviations as for Figure 1.

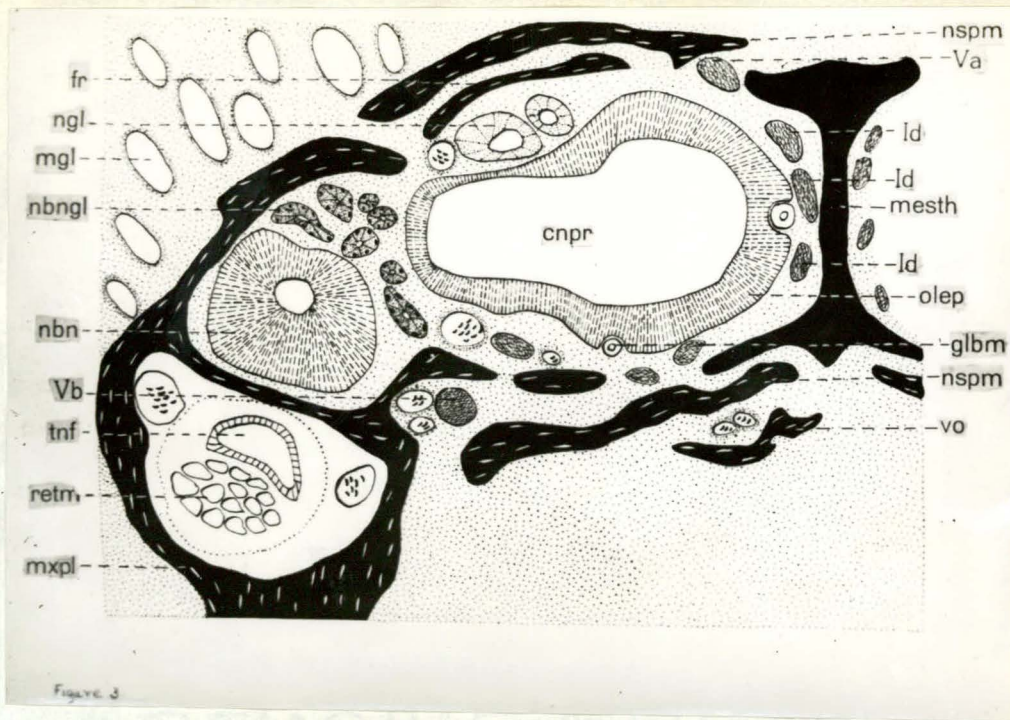


Figure 3. A transverse section through the nasal region showing the cavities in the maxillo-palatine. fr frontal; nbngl "Nobornase" gland; ngl nasal gland; ld dorsal olfactory nerve. Other abbreviations as for previous figures.



Figure 4. A transverse section through the nasal region showing the relative size of the "Nobanase" and the cavum nasale principale. acarin arteria carotis interna; bas basal bone; orgl orbital gland; rpalVII ramus palatinus of the 7th facial nerve; Iv ventral olfactory nerve; Iva branch of the ventral olfactory nerve supplying the cavum nasale principale. Other abbreviations as for previous figures.

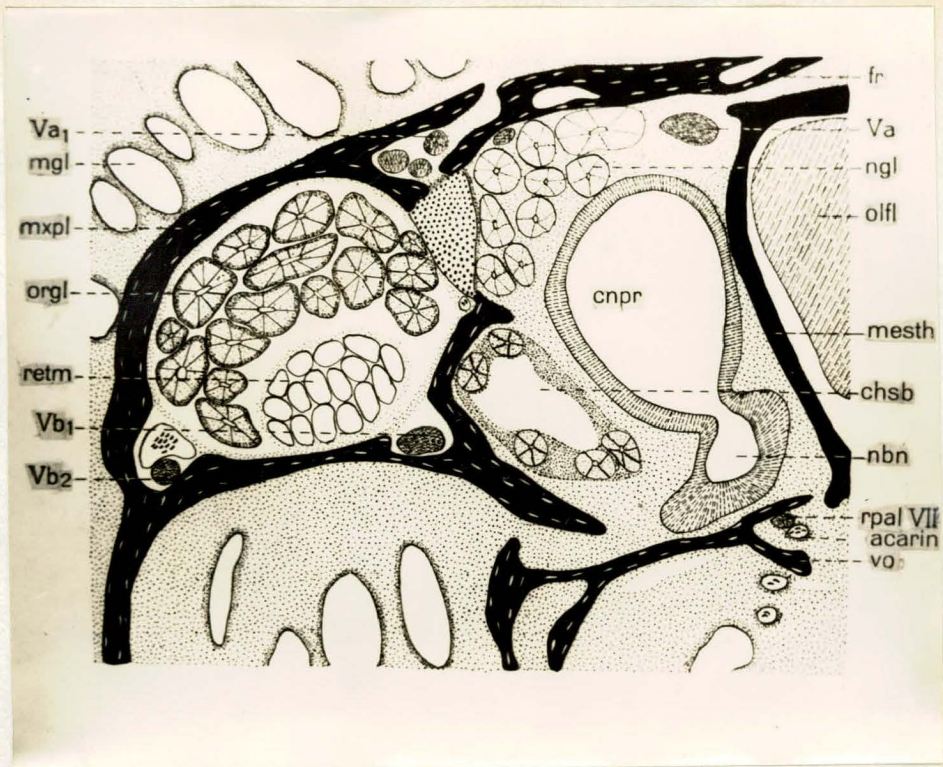


Figure 3. A transverse section through the nasal region showing the communication between the "Nebennase" and the cavum nasale principale, and the "Choanenschleimbeutel". chsb "Choanenschleimbeutel"; olfl olfactory lobes; Other abbreviations as for previous figures.

Figure 6. A section through the posterior part of the nasal region, showing the communication between the "Choanenschleimbeutel" and the cavum nasale principale and the choana. ch choana; chgl choanal gland; reye remains of the degenerated eye. Other abbreviations as for previous figures.

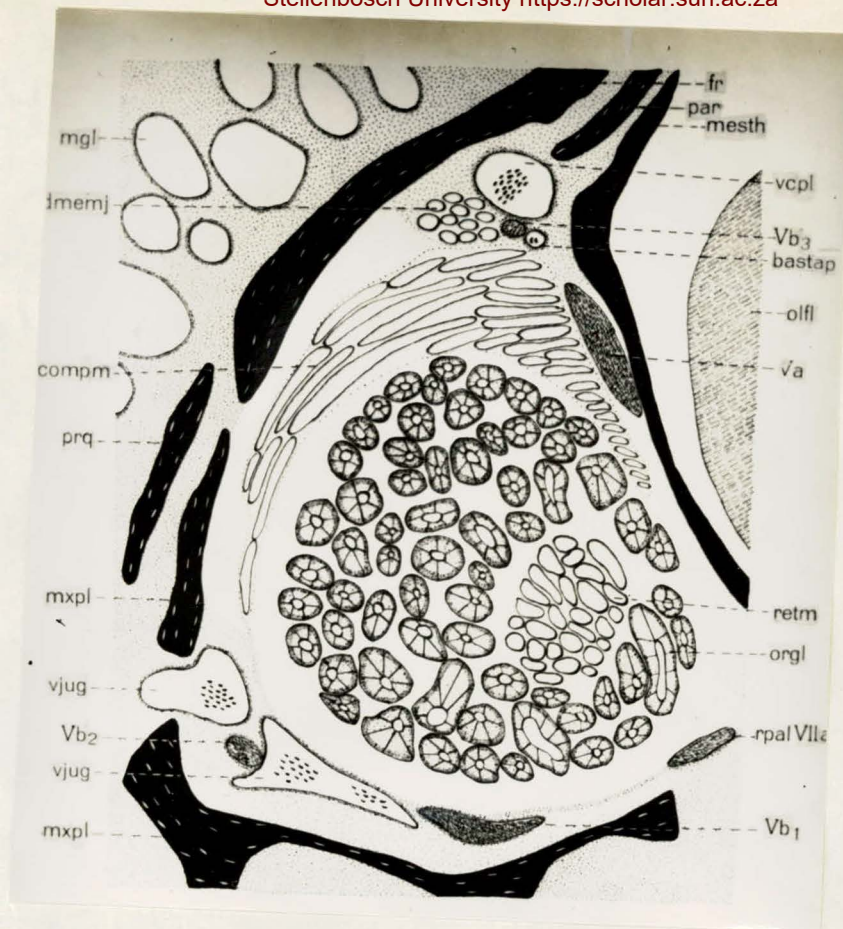


Figure 7. A transverse section just behind the nasal region to show the large orbital gland and compressor muscle in the anterior part of the orbit. bastap branch of the arteria stapediale accompanying the r. mandibularis V; compm compressor muscle of the orbital gland; madmemj musculus adductor mandibulae externus major; par parietal; rpal VIIa a branch of the r. palatinus VII forming an anastomosis with the medial branch of the r. maxillaris V; vcpl vena capitis lateralis; vjug vena jugularis interna; Vb3 branch of the r. maxillaris V forming an anastomosis with Va. Other abbreviations as for previous figures.

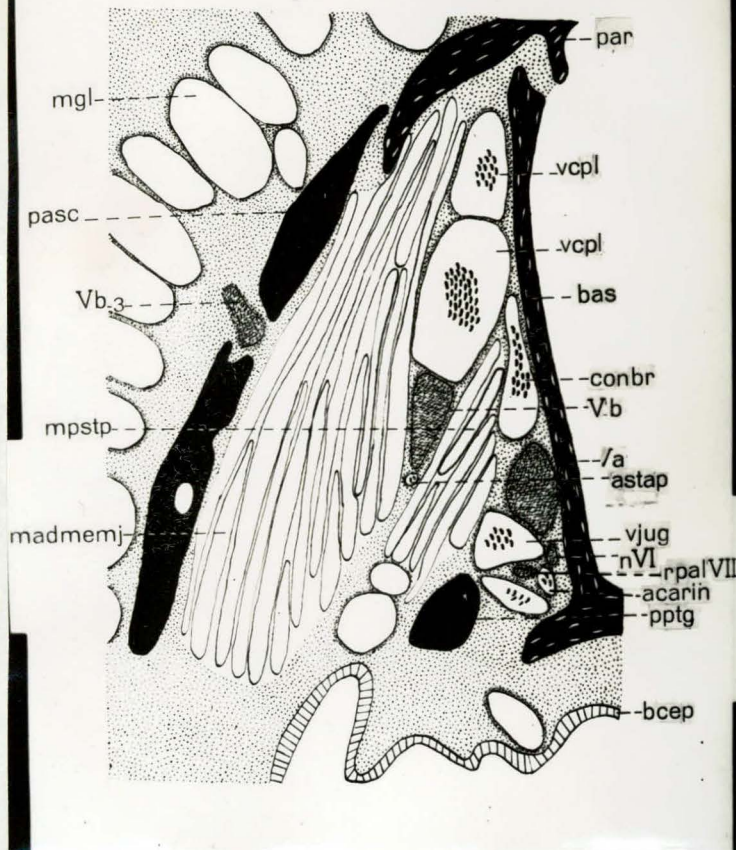


Figure 8. A section through the temporal groove to show the muscles. astap arteria stapedia; bcep buccal epithelium; conbr connecting branch between the v. capitis lateralis and the v. jugularis interna; mpstp musculus pseudotemporalis; nVI nervus abducens; pasc processus ascendens palatoquadrati; pptg p. pterygoideus palatoquadrati; Vb ramus maxillaris of the trigeminal nerve. Other abbreviations as for previous figures.

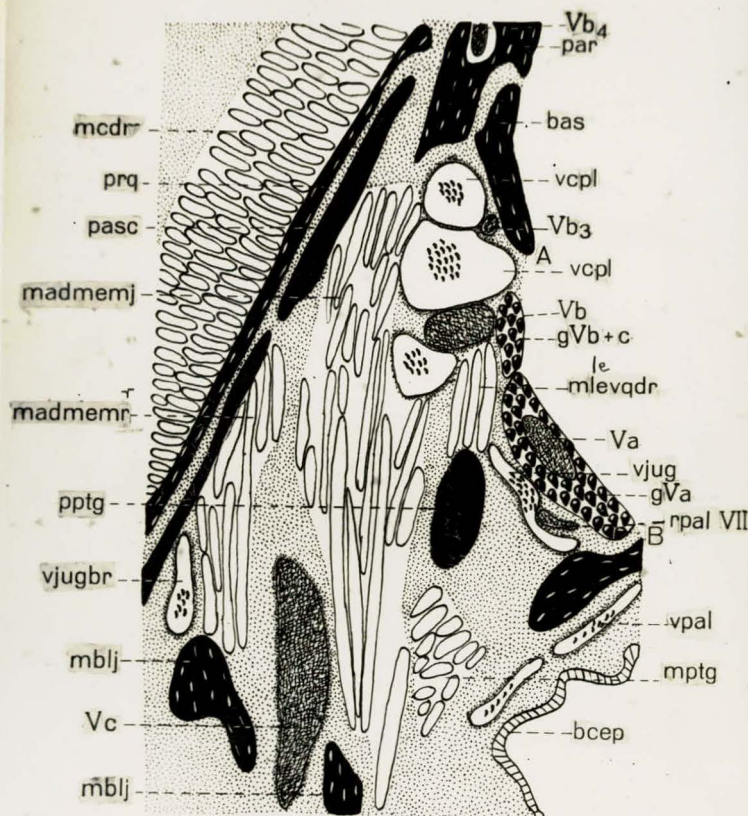


Figure 9. A transverse section through the anterior part of the foramen prooticum. gVa ganglion of the ophthalmic portion of the trigeminal nerve; gVb+c ganglion of the maxillo-mandibular portion of the trigeminal nerve; madmemr musculus adductor mandibulae externus minor; mblj mixed bone of the lower jaw; mcdm m. cephalo-dorso-maxillaris; mlevqdr m. levator quadrati; mptg m. pterygoideus; prq paraquadratus; vpal vena palatina; vjugbr branch of the v. jugularis interna; Vb4 dorsal ridge-like branch of the r. maxillaris innervating the dorsal skin; Vc ramus mandibularis of the trigeminal nerve. Other abbreviations as for previous figures.

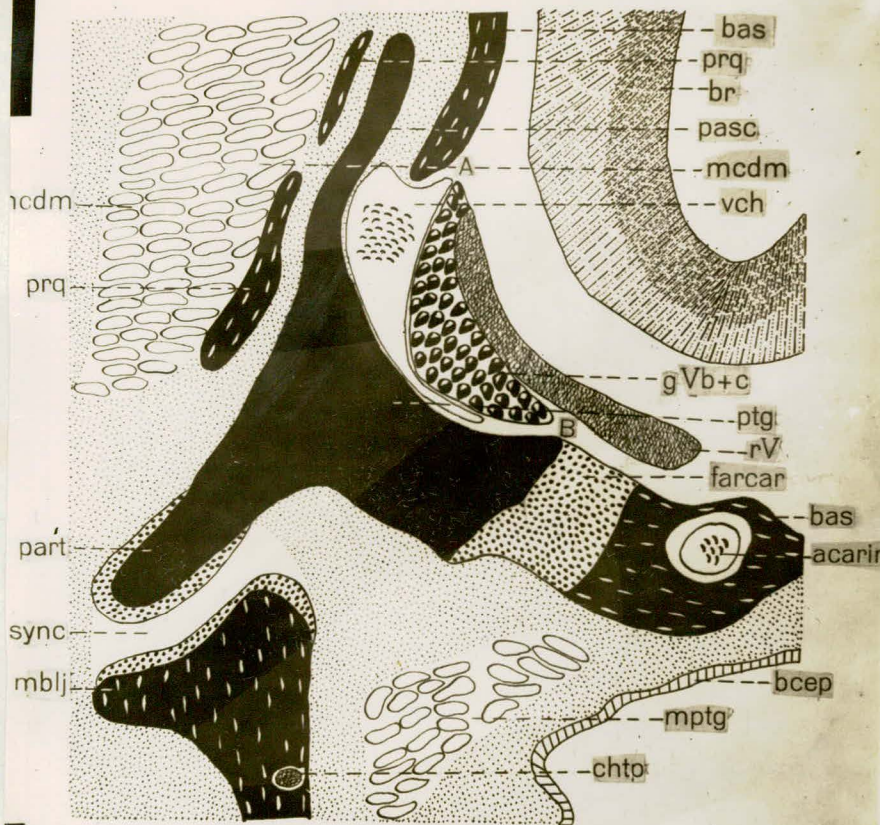


Figure 10. A transverse section through the posterior part of the quadrato-basal articulation to show the degeneration of the articulation. br brain; chtp chorda tympani; farcar fused articulation cartilages of the quadrato-basal articulation; part p. articularis palatoquadrati; ptg palatoquadrate; rV root of the trigeminal nerve; sync synovial cavity; vch venous channel formed by the v. vagitis lateralis and the v. jugularis interna; Other abbreviations as for previous figures.

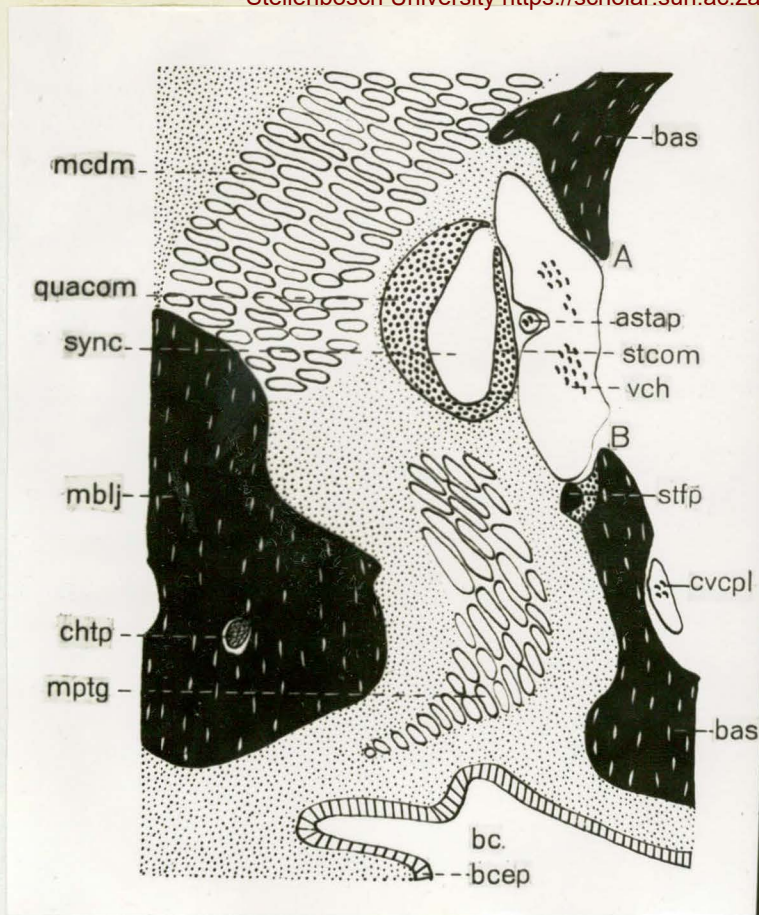


Figure 11. A transverse section to show the degeneration of the quadrate-stapedial articulation. bc buccal cavity; cvcpl cephalic branch of the v. capitis lateralis; quacom quadrate component of the quadrate-stapedial articulation; stcom stapedial component of the quadrate-stapedial articulation; stfp stapedial footplate. Other abbreviations as for previous figures.

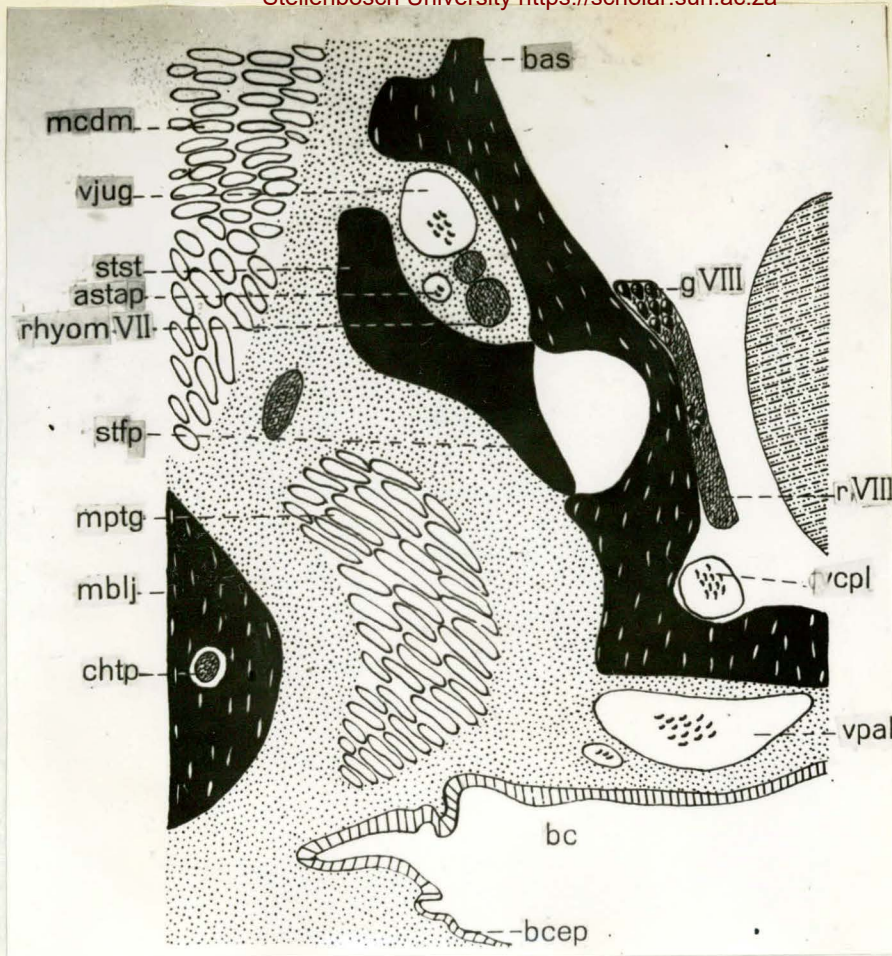


Figure 12. A transverse section through the anterior part of the otic capsule. g.VIII ganglion of the acoustic nerve; rhyom.VII ramus hyomandibularis of the facial nerve; r.VIII root of the acoustic nerve; stst stapedial style. Other abbreviations as for previous figures.

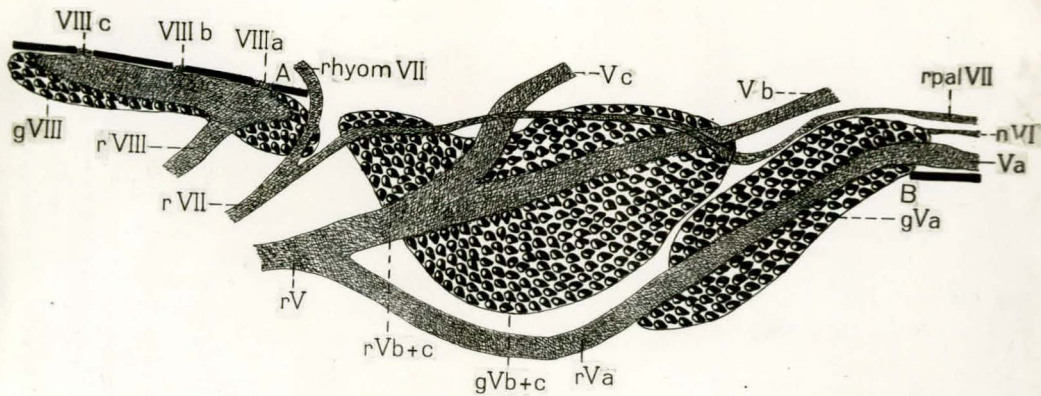


Figure 13.

Figure 13. A schematic graphic reconstruction of the ganglia of the fifth, seventh and eighth cranial nerves. rVII root of the facial nerve; rVa ophthalmic portion of the trigeminal nerve root; rVb+c maxillo-mandibular portion of the trigeminal nerve root; VIIIa, VIIIb and VIIIc branches of the acoustic nerve entering the labyrinth cavity through separate foramina. Other abbreviations as for previous figures.

SOME POINTS IN THE DEVELOPMENT OF THE STAPES OF *ICHTHYOPHIS GLUTINOSUS*.

SOME POINTS IN THE DEVELOPMENT OF THE STAPES OF ICHTHYOPHISGLUTINOSUS.

By E.F.J. de Jager.

Various stages in the development of the Gymnophione stapes have been described by Peter (1898), Winslow (1898) and Marcus (1909 and 1935). It will be necessary to give a brief summary of the findings of these authors, before a description is given of the development of the stapes of *Ichthyophis glutinosus*. According to Peter the stapes of *Ichthyophis glutinosus* develops from the primordial "Grundlage" with ossification setting in during embryonic life. The footplate (operculum) shows ossification prior to that of the style (columella), and in the adult the distal end of the style and the rostral end of the footplate remain cartilaginous. In the embryo the footplate is a narrow bar of cartilage which increases in size in the later development, and in the adult it represents a comparatively broad, oval structure filling the fenestra ovalis (op. cit., p. 42). In the youngest embryos examined by him, Peter^{found} the procartilaginous anlage of the stapes to be continuous with the procartilage of the otic capsule (op. cit., p. 18). The stapes and palatoquadrate are intimately connected during the development with a thin connective tissue membrane separating them. Signs of a synovial cavity between the stapes and the palatoquadrate could not be demonstrated in these young embryos. Because of the separating membrane between the stapes and palatoquadrate the stapes cannot be considered as a palatoquadrate derivative, but of the otic capsule.

Winslow (1898) in his description of the development of the *Ichthyophis* skull, referred briefly to the development of the stapes, and he

states the following: " The stapes is continued forward into a process which reaches the posterior surface of the quadrate. The stapes is perforated in a dorso-ventral direction for the arteria perforans stapedia" (op. cit., p. 176).

Marcus traced the development of the stapes from very young embryos to the adult form in the genus *Hypogeophis*. In his work on the development of the head (1909) he gave a very clear picture of the relations between the stapes, hyoid arch and the otic capsule blasteme. In the early development of the stapes and the hyoid the blastemes are continuous, and the otic capsule blasteme is definitely separated from the continuous stapes and hyoid blasteme. " Man sieht nämlich vom Ohrkapselblastem völlig getrennt durch einen hellen zellarmen Streifen die Stapesanlage in kontinuierlichem Zusammenhang mit dem Hyoidbogenvorknorpel" (op. cit., p. 145). Marcus' statement that the stapes is a hyoid derivative is proved conclusively by the details given of the development of the stapes and also by the evidence afforded by a study of the relations of nerves and bloodvessels to the hyoid arch and stapes.

In 1935 Marcus investigated the development of the stapedial footplate in larvae in which the otic capsule is already largely ossified, and in these stages of the development he was able to show that the otic capsule takes part in the formation of the stapedial footplate. The footplate is at first a narrow cylindrical bar of cartilage which ossifies perichondrally, and does not fill the large fenestra ovalis. A portion of the otic capsule dorsal to the stapes separates off in a cranio-caudal direction and fuses with the stapedial footplate to form a broad oval plate filling the fenestra ovalis completely (op. cit., pp. 144 and 145, and Figs. 2 and 3). Marcus,

therefore, comes to the following conclusion: " Mir scheint, der Schluss ist zwingend, dass ein Teil der Ohrkapsel mit dem viszeralen Abschnitt des Stapes verwächst und die Fussplatte bildet" (op. cit., p. 145). In another contribution (1935) Marcus, Stimmelmayer and Porsch, give further details regarding the development of the stapes. In a 2.5 cm. *Hypogeophis* embryo they describe the stapes as a cylindrical cartilaginous bar lying close to the quadrate and directed towards the trabecula, without, however, reaching the latter. In older embryos the cartilaginous stapes fuses with the palatoquadrate and also with the trabecula. The reader is referred to Fig. 9 on p. 415 of their publication. In a 6.8 cm. larva the connection between the stapes and the trabecula is lost, and the synovial cavity has been formed between the stapes and the palatoquadrate. The palatoquadrate is therefore suspended from the otic capsule by means of the stapes which is a hyoid derivate: the *Gymnophione* skull is therefore hyostylic as Marcus pointed out.

I had the opportunity of studying the development of the stapes of *Ichthyophis glutinosus* in longitudinal and transverse serial sections of two 3.5 cm. embryos kindly sent by Mr. Ramaswami to the Zoological Institute of the University of Stellenbosch. One 7 cm. and one 8 cm. larvae were already available, and later Professor van der Hoerst of the Witwatersrand University provided another 3.5 cm. embryo. I owe Mr Ramaswami and Professor van der Horst my sincere thanks for putting the valuable material at my disposal. Two of the 3.5 cm. embryos were stained with iron haematoxylin, the other 3.5 cm. embryo was bulk-stained in haemalum and counterstained on slides with van Gieson's solution. The 7 and 8 cm. larvae were bulkstained in haemalum and

counterstained on slides with eosin. An 11 cm. juvenile form, bulk-stained in haemalum and counterstained on slides with eosin was also available.

In the longitudinal sections of the 3.5 cm. embryo the stapes is a cylindrical cartilaginous bar with its rostral end touching the posterior surface of the cartilaginous palatoquadrate. The stapes is separated from the palatoquadrate by means of a thin connective tissue membrane, two cell layers in thickness (Fig. 1). The quadrate portion of the palatoquadrate is also separated from Meckel's cartilage by means of a thin membrane. The stapedia artery passes through the stapes in a dorso-ventral direction, close to the connection of the stapes with the palatoquadrate. The stapes comprises a long thin bar of cartilage lying parallel to the otic capsule and it fits into the fenestra ovalis, a long ventro-lateral foramen in the otic capsule. The anterior end of the stapedia footplate becomes incorporated in the neurocranial cartilage where the otic capsule goes over into the trabecula (Fig. 2), immediately posterior to the place where the ramus palatinus of the facial nerve leaves its ganglion. At this level the trabecula has a small laterally directed process which is perforated by the r. palatinus VII. The fusion of the stapes with the trabecular cartilage where the latter goes over into the otic capsule, corresponds to the fusion of the stapes with the trabecula as described by Marcus for *Hypogeophis*, and in both genera this fusion occurs simultaneous with the close connection of the stapes and the palatoquadrate.

In both the transversely sectioned 3.5 cm. embryos the palatoquadrate and Meckel's cartilage are separated by a thin membrane. Ventral to the anterior end of the otic capsule the trabecula also shows

the laterally projecting process, through which the r; palatinus VII passes from its ganglion on its way to the roof of the buccal cavity. The otic capsule already shows signs of ossification in some parts. The palatoquadrate, caudad to its connection with Meckel's cartilage represents a round bar of cartilage (Fig. 3). This bar proceeds mediad, the stapedial artery passes through it in a dorso-ventral direction and it ultimately fits into the fenestra ovalis. This caudad portion of the palatoquadrate must therefore represent the stapes. No separation between the stapes and the palatoquadrate could however be demonstrated: they have fused completely to form one continuous bar of cartilage connected at one end with Meckel's cartilage and fitting into the fenestra ovalis at its other end. The stapes does not fill the fenestra ovalis: dorsal and ventral to it a large opening remains. The connection between the stapes and the trabecula is less clearly indicated than in the longitudinal sections. In one of the transversely sectioned 3.5 cm. embryos a small group of cartilage cells is seen on the lateral side of the trabecula, as indicated in Fig. 3. Rostrad these cells are continuous with the trabecular cartilage; they then separate off and fuse with the stapes slightly further caudad. In the other 3.5 cm. embryo a connection between the stapes and trabecula is absent on one side, and dense connective tissue separates them. On the other side, however, the connection is still present, although connective tissue is already growing in between them.

Transverse sections of a 7 cm. larva furnished the following interesting points. After the processus ascendens palatoquadrati projecting rostrad beyond the body of the palatoquadrate and connected with the lateral wall of the neurocranium by means of dense connective tissue, and the p. pterygoideus palatoquadrati situated immediately

dorsal to the small pterygoid bone, have joined the body of the palatoquadrate, the latter forms the jaw articulation. At the jaw articulation the palatoquadrate is almost entirely ossified, but slightly further caudad it is almost entirely cartilaginous, and it is connected with the ventro-lateral surface of the basal bone by means of strong connective tissue. The stapes appears in section as a small piece of cartilage applied to the (here) cartilaginous palatoquadrate by means of a narrow strip of dense connective tissue. Caudad the stapes increases in size and in two sections a small cavity is present between the stapes and the palatoquadrate. Still further caudad the stapes shows perichondral ossification and fits into the fenestra ovalis. In Fig. 5 the small cavity separating the stapes and the palatoquadrate is shown. Medio-dorsal to the stapes the geniculate ganglion is situated, and the foramen for the root of the facial nerve lies dorsal to the stapediaal style. The connection between the stapes and the trabecula has degenerated completely and, as described above, the intimate connection between the stapes and the palatoquadrate is in the process of being lost. The stapediaal footplate now fills the fenestra ovalis completely and the otic capsule is almost entirely ossified. Unfortunately stages of development showing the increase in size of the stapediaal footplate were not available, so that it cannot be stated whether the otic capsule takes part in the stapediaal footplate, as is the case in *Hypogeophis* (Marcus, 1935).

In the 8 cm. larva the synovial cavity between the stapes and the palatoquadrate is much better developed, and in the 11 cm. juvenile form the quadrato-stapesial articulation is completely formed. In both the 8 and 11 cm. specimens the stapediaal artery perforates the

stapes.

In the above description the following points in the development of the stapes of *Ichthyophis glutinosus* merit special attention.

(1) In the 3.5 cm. embryos the stapes is completely separated from the hyoid arch but it has attained intimate relations with the palatoquadrate. In two of the available specimens the stapes cartilage is continuous with the palatoquadrate cartilage and in the other specimen a very thin connective tissue membrane separates the two elements.

(2) The stapes is fused with the trabecula in one 3.5 cm. embryo, and in the other two indications of such a fusion are present.

(3) In the 7 cm. larva a synovial cavity is beginning to appear between the stapes and the palatoquadrate, and becomes fully developed in the 8 and 11 cm. specimens. The quadrato-stapedial articulation is therefore absent in the earlier stages of development.

(4) In the 3.5 cm. embryo the stapedial footplate fits into the fenestra ovalis but does not fill it. In the 7 cm. larva the stapedial footplate does fill the fenestra ovalis, but because intervening stages could not be obtained, the increase in size of the stapedial footplate could not be traced.

(5) In all the stages examined, the stapedial artery perforates the stapes.

(6) In all the later stages of development in which ossification has started, such ossification is perichondral. The stapes, palatoquadrate and trabecula in the 7 and 8 cm. specimens represent cartilaginous structures ensheathed in perichondrally ossified bone. This was also noted by Marcus for *Hypogeophis*.

In conclusion it may be added that the development of the stapes

of *Ichthyophis glutinosus*, after its separation from the hyoid blasteme does not differ from that of *Hypogeophis* as described by Marcus, Stimmelmayer and Porsch, and that the above description affords corroborative evidence in favour of the conclusions arrived at by Marcus and his students. Developmental material of the *Gymnophiones* continues to be somewhat of a rarity: a very much to be regretted admission, since the recent work by Prof. Marcus and his students in Munich, and that of Prof. de Villiers and the author at Stellenbosch have accentuated the morphological and phylogenetic importance of the *Gymnophiona*.

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Alphabetical list of abbreviations showing the number of the figure where
they were first introduced.

acin 3; astp 1; bas 3; bc 3; br 3; ctu 1; fov 2; ggen 5; gel 2;
g VIII 3; hya 2; lc 1; m₂ 1; medm 3; otc 1; par 3; plq 1; rpl VII
2; stp 1; tr 3.

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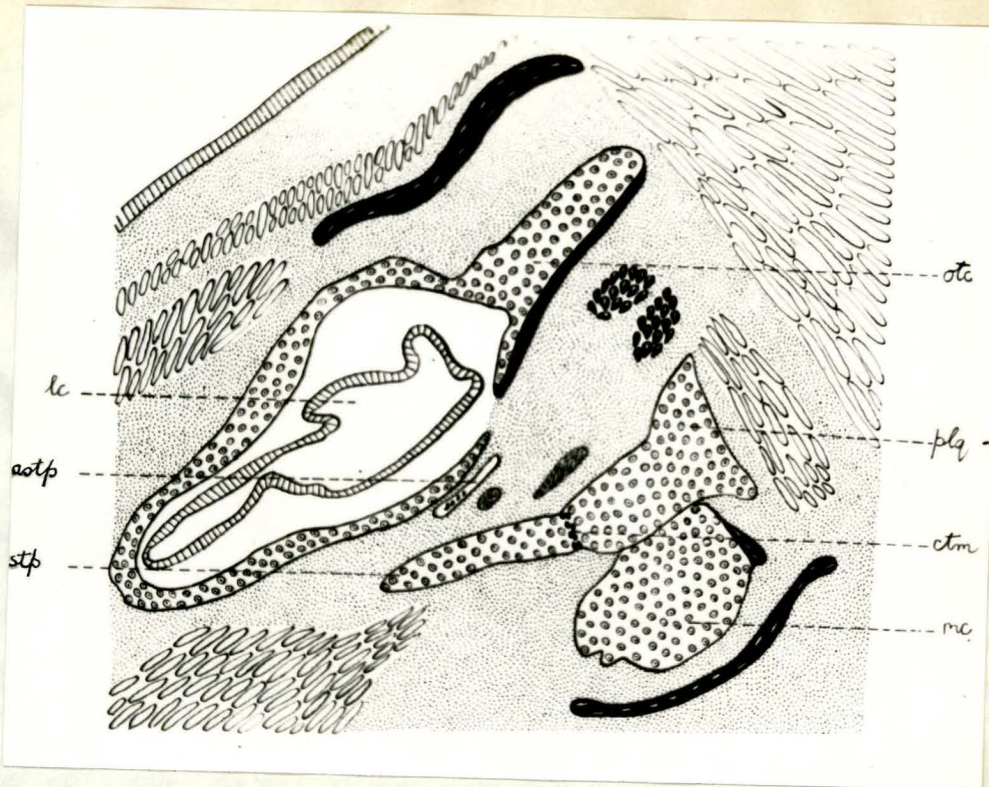


Figure 1. Longitudinal section through the head of a 3.5 cm *Ichthyophis glutinosus* embryo, showing the stapes separated from the cartilaginous palatoquadrate by means of connective tissue. astp arteria stapedialis; ctm connective tissue separating the stapes and palatoquadrate; lc labyrinth cavity; ml Meckel's cartilage; otc otic capsule; plq palatoquadrate; stp stapes.

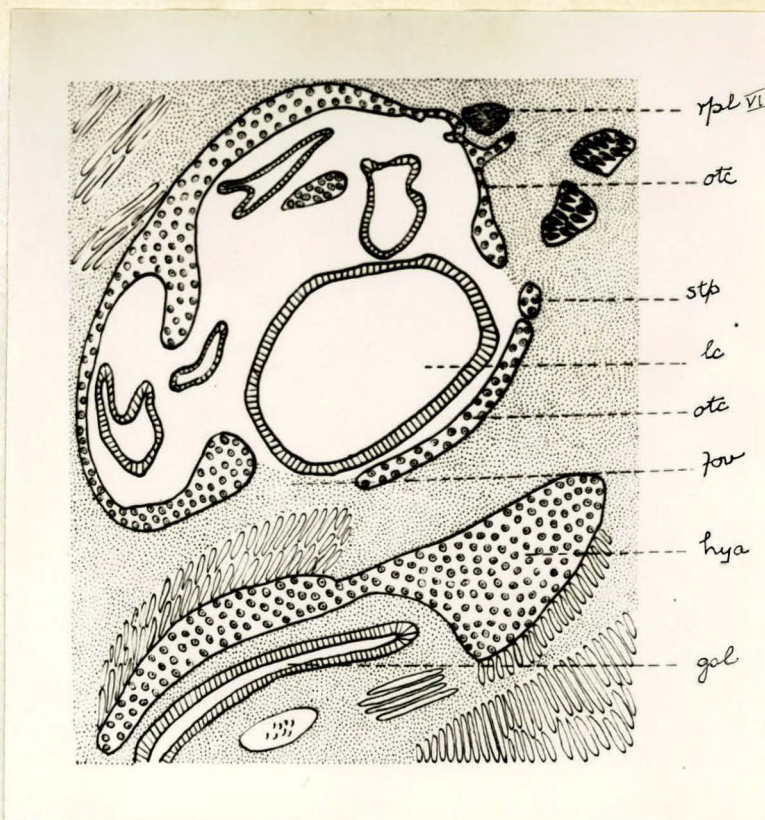


Figure 2. Longitudinal section through the head of a 3.5 cm *Ichthyophis* embryo, showing the anterior tip of the stapedial footplate, which fuses with the trabecular cartilage. fov fenestra ovalis; gsl gill slit;hya hyoid apparatus; rpl VII ramus palatinus of the facial nerve. Other abbreviations as for Figure 1.

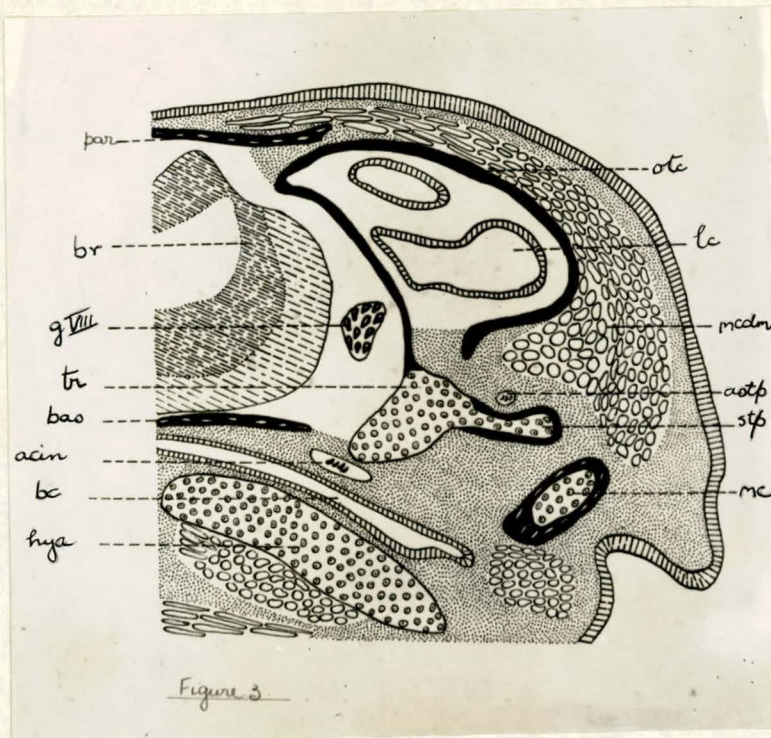


Figure 3. Transverse section through the head of a 3.5 cm *Ichthyophis* embryo, showing the stapes fused to the trabecula. acin arteria carotis interna; bc buccal cavity; bs basal bone; br brain; g VIII ganglion of the acoustic nerve; mcdm m. cephalo-dorso-maxillaris; par parietal; tr trabecula. Other abbreviations as for previous figures.

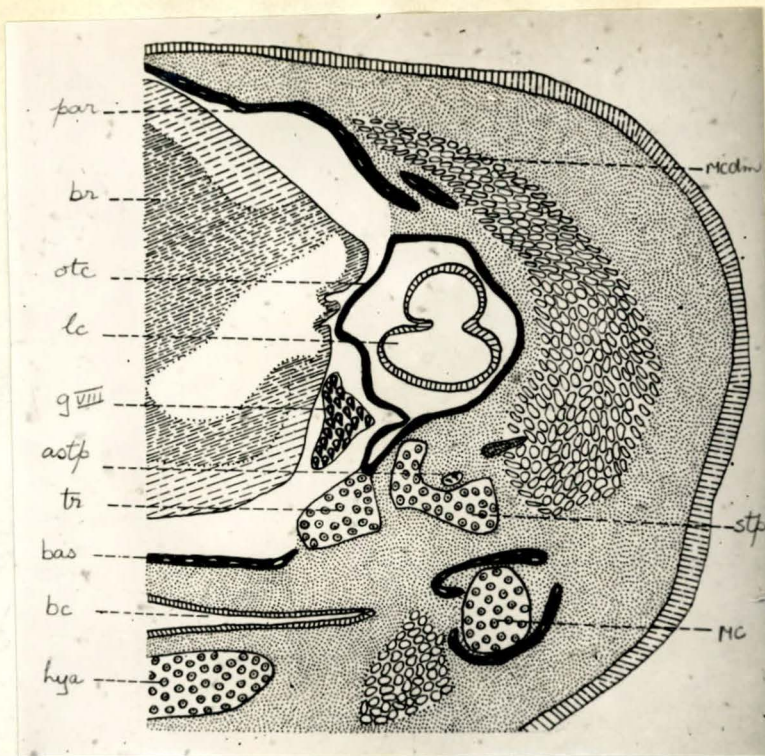


Figure 4. Transverse section through the head of a 3.5 cm *Ichthophis* embryo, showing the stapes separated from the trabecula. Abbreviations as for previous figures.

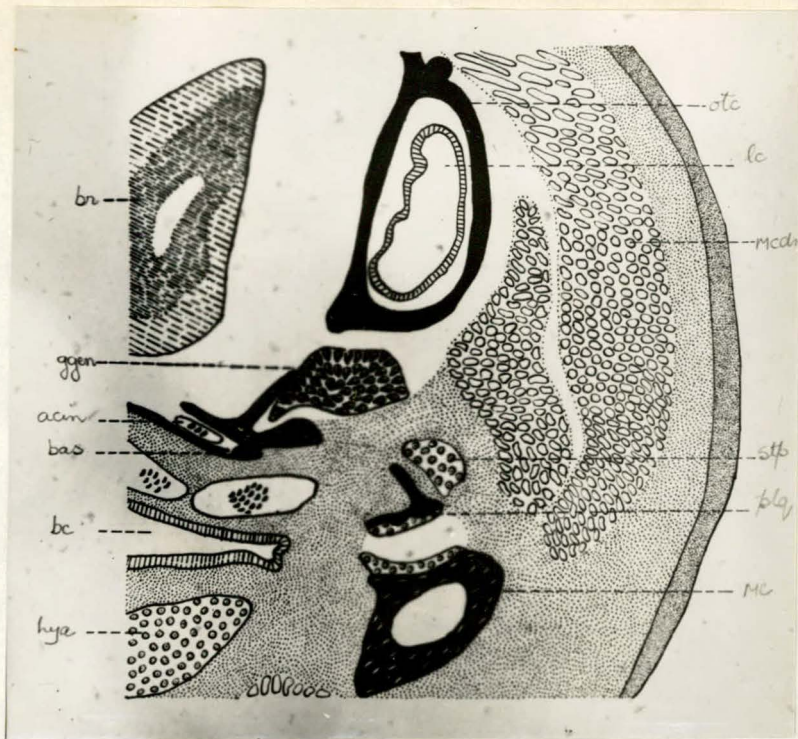


Figure 5. Transverse section through the head of a 7 cm *Ichthyophis* embryo, showing the stapes separated from the palatoquadrate by means of connective tissue. ggen geniculate ganglion. Other abbreviations as for previous figures.

THE CRANIAL MORPHOLOGY OF SIPHONOPS ANNULATUS WAGLER.
CONTRIBUTIONS TO THE CRANIAL ANATOMY OF THE GYMNOPTERON.

THE CRANIAL MORPHOLOGY OF SIPHONOPS ANNULATUS WAGLER.
CONTRIBUTIONS TO THE CRANIAL ANATOMY OF THE GYMNOPHIONA.

After having studied the cranial morphology of the greatly specialised Neotropical genus *Coecilia*, I considered it advisable to study an additional Neotropical genus in detail, with a view to obtaining comparative data. Wiedersheim (1879) investigated two species of the genus *Coecilia*; his conclusions were discussed in detail by the author in a previous paper (1939). Of *Siphonops annulatus* he described the nasal organ and cranial bones, but gave very little information regarding the cranial nerves and bloodvessels. These latter proved to be of great interest in *Coecilia*, and in this paper they will be described in detail together with other cranial features. The data obtained will be compared with those for *Coecilia* and *Dermophis*, which latter is represented in both South America and Africa, and was investigated by the author in 1938 and 1959. It may be mentioned here that the genus *Siphonops* proved to be very similar to *Dermophis*, but differs widely from *Coecilia*.

The genus *Siphonops* was first described by Wagler in 1828. There are five species, all confined to South America. The stegokrotaphic condition of the skull, the visibility of the eyes through the skin and the position of the tentacle immediately in front of and below the eye, are given as distinguishing features by Nieden (1915).

Material and Technique.

The material consisted of one specimen of *Siphonops annulatus*, kindly placed at my disposal by Mr. Loveridge of the Museum of Comparative Zoology at Harvard University. The material was decalcified for one week in Eimer's solution and was then bulk-stained in haemalum and coun-

terstained on slides with eosin. The fixation was extremely good, and resulted in clear histological details.

Own Investigations.

The olfactory organ consists of three main divisions: (a) a main nasal sac, which, as in *Dermophis* (the author) is divided into two portions by a process formed by the nasopremaxillary, vomer and the mesethmoid; (b) a "Nebennase" opening into the main nasal sac, and (c) a "Choanense_hleimbeutel" which also opens into the main nasal sac.

The main nasal sac, at its anterior end, is a pearshaped structure with the external narial aperture at its extreme anterior end. The walls of the sac here consist of thick olfactory epithelium, except for a small lateral portion. A ring of small glands of Bowman is present around the anterior elongation of the main nasal sac. In the dorso-lateral wall of the anterior portion of the sac, the cartilage surrounding the external narial aperture, forms an indentation, which slightly further caudad is situated more laterad. Immediately dorsal to the indentation a large duct, lined with large cylindrical epithelial cells, is located. It opens into the anterior end of the sac, runs backwards and becomes imbedded in the nasal gland.

For a considerable distance caudad the main nasal sac remains a simple tube, before an indentation in its floor is formed by a longitudinal ridge on the dorsal surface of the ventral portion of the nasopremaxillary. This ridge pushes the floor of the nasal sac upwards, thus producing a separation into lateral and medial portions. Posteriorly, the nasopremaxillary ridge is replaced by the vomer, which stretches from \nearrow medio-ventral to latero-dorsal, and the lateral edge of the vomer forms the in-

3.

dentation. The lateral end of a ventral process of the mesethmoid forms a cap over the lateral end of the vomer, and also takes part in the formation of the ventral indentation (Fig. 1). The "Nebennase", arising lateral to the main nasal sac and stretching mediad ventral to the latter, opens into the main nasal sac immediately lateral to the ventral indentation (Fig. 1). The "Choanenschleimbeutel" arises between the posterior portion of the "Nebennase" and the main nasal sac (Fig. 1), and is continued caudad with the latter. At its posterior end the main nasal sac is divided into three portions: the medial olfactory portion separates off and becomes enclosed within a canal in the ventral portion of the mesethmoid. This canal lies ventral to the canal in which the ventral olfactory nerve is situated (Fig. 2). This portion of the main nasal sac ends blindly. The remaining portion is then divided into two parts by a laterally projecting ventral process of the mesethmoid and by a process of the maxillo-palatine, which forms a deep indentation in the nasal sac and finally effects complete division of the latter into two separate portions (Fig. 2); the dorsally situated portion ends blindly. The ventrally situated portion, representing the respiratory portion of the main nasal sac, opens into the "Choanenschleimbeutel" (Fig. 2) and these two together open into the buccal cavity at the choana (Fig. 3). A small epithelial fold indicates the boundary between the "Choanenschleimbeutel" and the main nasal sac.

The "Nebennase" appears lateral to the main nasal sac at the level of the anterior end of the ventral indentation. It is enclosed in the same bony capsule as the main nasal sac, and stretches mediad ventral to the latter (Fig. 1). Its walls consist of thick olfactory epithelium, and it communicates with the main nasal sac lateral to the ventral indentation. The opening, therefore, lies in the floor of the main nasal sac (Fig. 1).

Two tentacle canals open into the posterior portion of the "Nebennase" (Fig. 1).

The following nasal glands are present: a nasal gland, a "Nebennase" gland, a choanal gland and a large number of small glands of Bowman. These glands are also present in other genera investigated, but the size of the glands differs in the various genera. The nasal gland in *Siphonops annulatus* is a long tract, very large in the posterior portion of the nasal cavity and lying dorso-lateral to the main nasal sac (Figs. 1 and 2). It has a long duct running forward and opening into the anterior end of the main nasal sac, as described above. The alveoli are formed by large clear cells; similar ones, present on the ventral side, open singly into the main nasal sac. Between these ventral alveoli and the dorso-laterally situated nasal gland there is connective tissue connection.

The "Nebennase" gland is situated between the "Nebennase" and the main nasal sac (Fig. 1). Its alveoli do not open into the "Nebennase", but a number of them unite to form a large duct which widens to form the "Choanenschleimbeutel". Caudad, several further "Nebennase" glandular alveoli appear on the lateral and medial sides of the "Choanenschleimbeutel" (Fig. 2), and they also open into the latter. The choanal gland is situated medial to the choana and consists of a few large alveoli which open into the choana (Fig. 3). The glands of Bowman are confined to the anterior part of the nasal cavity where they form a ring around the main nasal sac.

In comparing the anatomical points discussed above with those given by Wiedersheim for the same species, the following points deserve attention: Wiedersheim mentions the division of the main nasal sac into two portions by the nasopremaxillary, vomer and mesethmoid (op. cit., p. 14), but he does not mention the absence of olfactory epithelium in the lateral

portion. He describes a thick membrane present between the nasal gland and the main nasal sac, but could not demonstrate the openings of the alveoli into the nasal sac (op. cit., p. 35). The membrane, as described by Wiedersheim, is absent in my specimen, and the duct leading from the nasal gland into the anterior end of the main nasal sac, has been described above. The presence of gland alveoli on the ventral side of the main nasal sac, exactly similar to those of the nasal gland, is not mentioned by Wiedersheim,

The "Nebennase" gland is described by Wiedersheim as a "Tentakeldrüse", and he considers the tentacle canals as ducts leading from this gland (op. cit., p. 35). Actually, however, they open into the "Nebennase" in Siphonops, as well as in Ichthyophis, Hypogeophis, Coecilia and Dermophis (Barasins, Laubeann and the author). In Siphonops annulatus the "Nebennase" gland alveoli do not open into the "Nebennase", but the alveoli unite to form a large duct which is continued caudad as the "Choanenschleimbeutel". Similar relations of the "Nebennase" gland to the "Choanenschleimbeutel" were described by the author for the two species of Dermophis (op. cit., pp. 195, 201).

The "Nebennase" of Siphonops annulatus, according to Wiedersheim, opens into the main nasal sac and also into the buccal cavity (op. cit., p. 36). As I have pointed out in a previous paper on the genus Coecilia (1939), Wiedersheim constantly mistook the "Choanenschleimbeutel" which does open into the choana, for the posterior part of the "Nebennase". The division of the posterior part of the main nasal sac into three divisions, two of which end blindly and a third which opens into the "Choanenschleimbeutel" and the choana, is not mentioned by Wiedersheim.

The nasal sacs of Dermophis and Siphonops show many similarities.

6.

The opening of the "Nebennase" into the main nasal sac in the two genera is situated lateral to the ventral indentation, whereas this opening lies medially against the internasal septum at the extreme posterior end of the "Nebennase" in *Cocilia*. The relations of the "Nebennase" gland to the "Choanenschleimbeutel" and the position of the gland are similar in *Dermophis* and *Siphonops*. In *Cocilia*, the "Nebennase" gland lies lateral to the "Nebennase" and is confined to the "Nebennase" space in the maxillo-palatine (the author). In both *Cocilia* and *Siphonops* the nasal gland is provided with a large duct which runs rostrad and opens into the main nasal sac. In *Dermophis* no such duct is present, and the alveoli open separately into the main nasal sac (the author). In both *Dermophis* and *Siphonops* the olfactory portion of the main nasal sac separates off from the lateral respiratory portion of in front of the choana and ends blindly. In *Siphonops* a portion of the lateral part of the main nasal sac is also separated off and it too ends blindly. In neither of these genera does the olfactory ^{portion} of the main nasal sac open into the buccal cavity. In *Cocilia* the olfactory epithelium in the main nasal sac is very poorly developed and there is no division of the latter into an olfactory and respiratory portion; the whole main nasal sac opens into the buccal cavity. Two epithelial folds are present in the choana of *Cocilia* (the author) and in *Hypogeophis* (Laubmann). In *Siphonops annulatus* only one such fold is present.

The small glands present in the roof of the buccal cavity should be mentioned here. In both *Dermophis* and *Cocilia* these glands were noted, and in *Siphonops annulatus* they are present in large numbers. They consist of single alveoli which open singly into the buccal cavity. In Figs. 1, 2 and 4 these glands have been sectioned.

The nasal capsule of *Siphonops annulatus*.

The bones taking part in the formation of the nasal capsule are firmly applied to one another, thus forming a strong structure. The following bones are present in the nasal capsule: nasopremaxillary, vomer, maxillo-palatine, mesethmoid and that portion of the frontal forming part of the roof of the nasal capsule.

The nasopremaxillary forms a complete ring around the anterior part of the nasal sac; only in the region of the external narial aperture is the bone replaced by cartilage surrounding the external narial aperture. Many foramina are present in the lateral and ventral portions of the bone in the anterior region. Nerve fibres coming from the skin of the snout enter small canals in the nasopremaxillary through these foramina. Such nerve fibres gather into two large bundles: (a) a dorsal one constituting a branch of the r. maxillaris V (Vb), and (b) a ventral bundle constituting a branch of the r. ophthalmicus V (Va).

The median portion of the nasopremaxillary is continued backward for a short distance only. It forms with the mesethmoid (which is here cartilaginous) the anterior portion of the internasal septum. Behind the median portion of the nasopremaxillary the mesethmoid alone forms the internasal septum. The lateral portion of the nasopremaxillary forms the lateral wall of the nasal capsule as far as the anterior end of the "Nebennase", and its place is then taken by the maxillo-palatine. The ventral portion of the nasopremaxillary forms the entire floor of the nasal capsule in the anterior region. It bears on its dorsal surface a ridge forming the ventral indentation in the main nasal sac. Immediately in front of the "Nebennase" the vomer and the maxillo-palatine replace the ventral portion of the nasopremaxillary, and form the floor of the nasal capsule, with the vomer occu-

pying a medial position and the maxillo-palatine a lateral position (Fig. 1). The dorsal portion of the nasopremaxillary, extending further caudad than the ventral portion, forms the greater part of the roof of the nasal capsule (Fig. 1). The frontal, stretching rostrad below the nasopremaxillary, forms the roof behind the latter (Fig. 2). Branches of Va and Vb are located in canals in the nasopremaxillary, as mentioned above. Va leaves its canal in the dorsal portion of the nasopremaxillary immediately in front of the frontal and runs caudad in the nasal cavity dorsal to the main nasal sac (Figs. 1 and 2). Vb leaves the ventral portion of the nasopremaxillary and enters a canal in the maxillo-palatine (Figs. 1 and 2).

The vomer is a large bone, consisting of a broad middle portion with two long narrow processes: the anterior one extending far rostrad above the ventral portion of the nasopremaxillary, and the posterior one forming a small portion of the median wall of the choana (Fig. 3). In the broad portion, forming part of the floor of the nasal capsule, a short canal is present (Fig. 1), which, beginning caudad as a deep groove on the dorsal surface of the vomer, ends rostrad as a deep groove on its ventral surface. The dorsal groove is roofed over by a cap-like process of the mesethmoid (Fig. 1). The ramus palatinus VII and a branch of the arteria carotis interna run forward in the canal and the grooves. The posterior narrow process of the vomer extends caudad beyond the choana.

The maxillo-palatine is a large bone with several processes taking part in the formation of the nasal skeleton. The body of the bone is situated laterally immediately behind the lateral portion of the nasopremaxillary; from the body a narrow process extends rostrad in a ventro-lateral position, and a ventral one extends mediad to form the lateral portion of the floor of the nasal capsule (Fig. 2). The two tentacle canals pierce the latter

process, and open into the post_{er}ior part of the "Nebennase"(Fig. 1). Immediately behind the "Nebennase" the laterally situated maxillo-palatine, which is here very thick, becomes excavated from the outside, until only a thin bone is left separating the nasal sacs from the orbital gland and the retractor muscle, which latter structures are located lateral to it (Fig. 2). A third process of the maxillo-palatine is sectioned in the region of the choana. This process is made up of two portions: caudad it consists of a broad bone extending from the dorsal surface of the maxillo-palatine body above the posterior parts of the nasal sacs. From the medial edge of this first portion another process extends downward and forward on the medial side of the nasal sacs (Fig. 2). The posterior portions of the main nasal sac and the "Choanenschleimbeutel" are therefore situated in a deep groove formed by the maxillo-palatine and its curved process (Fig. 3). The maxillo-palatine and its processes form the/walls of the choana, behind which the groove in the maxillo-palatine becomes shallower and finally disappears completely, the maxillo-palatine then occupying a ventral position only. Behind the nasal capsule the bone forms the floor of the orbit for a short way; behind the eye it becomes reduced laterad, and a large medio-palatine fenestra is formed between it and the base of the neurocranium. Slightly further caudad it also becomes reduced laterally, and another fenestra, the basitemporal fenestra, is formed on its lateral side. The maxillo-palatine is thus reduced to a very narrow process separating the large medio-palatine and basitemporal fenestrae. The bone is pierced by numerous canals through^{which} ramuli of the r. maxillaris V pass. The nasopre-maxillaries, vomers and maxillo-palatines are all teeth bearing bones.

The mesethmoid consists of a body surrounding the anterior ends of the olfactory lobes. From it a long medio-dorsal process, which appears

on the dorsal surface between the nasopremaxillaries and the frontals, extends caudad almost to the anterior end of the otic capsule (Figs. 1 and 2). At the level of the choana two broad processes extending laterad are present on the lateral side of the body: a dorsal process lying above the main nasal sac and extending rostrad almost to the anterior end of the nasal capsule (Figs. 1 and 2), and a ventral process reaching farther forward than the dorsal one. The dorsal and ventral olfactory nerves become incorporated in the dorsal and ventral processes respectively. The lateral edge of the ventral process bears a narrow process extending far rostrad and forming a cap-like process over the ~~fixx~~ vomer. Both the vomer and this cap-like process form the ventral indentation in the main nasal sac behind the ventral portion of the nasopremaxillary.

At their posterior ends, the dorsal and ventral processes each bear a narrow cartilaginous process attached to their lateral edges. These unite to form a single process extending laterad over the nasal sacs and fusing with ^{the} inner surface of the body of the maxillo-palatine (Fig. 1). In front of the olfactory lobes, the body of the mesethmoid is continued rostrad as a thin bony lamella forming the internasal septum (Fig. 1). Its anterior end is cartilaginous and is continued between the medial portions of the nasopremaxillaries almost up to the anterior end of the nasal capsule.

Behind the nasal capsule the mesethmoid forms the lateral and ventral walls of the neurocranium. The ventral portion is covered below by the vomers and behind these latter by the basal bone, which stretches far rostrad as a narrow process between the posterior portions of the vomers. On either side, the lateral portion of the mesethmoid dwindles to two cartilaginous bars: a dorsal taenia marginalis and a ventral trabecula, with a thick mem-

brane between them. These two bars become incorporated in the basal bone which extends upwards laterally to form the side walls of the neurocranium. In Fig. 4 the cartilaginous trabecula can be seen enclosed within the basal bone.

The nasal capsule of *Siphonops annulatus* is very similar to that of *Dermophis*. In both genera the nasal sacs are situated in a common cavity surrounded by the nasopremaxillaries, vomers, maxillo-palatines and mesethmoid, whereas in *Coeccilia*, the "Nebennase" has its own cavity in the maxillo-palatine. In *Coeccilia*, *Siphonops* and *Dermophis gregorii* the caudad directed medio-dorsal process of the mesethmoid appears on the dorsal surface between the posterior extensions of the nasopremaxillaries and the frontals. In *Dermophis mexicanus*, however, the mesethmoid does not appear on the dorsal surface (op. cit., p. 201). The deep groove in the ventral portion of the maxillo-palatine of *Siphonops*, in which the posterior portions of the "Choanenschleimbeutel" and main nasal sac are situated, is absent in both *Dermophis* and *Coeccilia*. In all three genera the vomer reaches caudad as far as the choana, and takes part in the formation of the medial wall of the latter.

The tentacle and associated structures.

The tentacle is situated immediately in front of and below the degenerate eye, which is visible through the skin. The eye is surrounded by the paraquadrate which extends rostrad beyond it into the nasal region. The two tentacle canals open into the tentacle groove at their distal ends, and into the posterior part of the "Nebennase" at their proximal ends. The large retractor muscle of the tentacle and the orbital gland, with its numerous alveoli surrounding the retractor muscle, are situated in the orbit

behind the eye (Fig. 3), whence they extend backward into the temporal groove. The retractor muscle inserts on the ventral trabecula. One large duct, leading from the anterior end of the orbital gland, opens into the tentacle sac. The tentacle itself does not vary in structure from that of *Ichthyophis* and *Dermophis* as described by Engelhardt (1924) and the author. The compressor muscle of the orbital gland appears in section far back in the temporal groove; it surrounds the posterior portions of the retractor muscle and the orbital gland. The compressor muscle is closely applied to the ventral surface of the *musculus adductor mandibulae externus major*, and posteriorly it dwindles to a small muscle belly inserting on the tendon of the *m. adductor mandibulae externus major*. The compressor muscle is smaller *than* that of *Coecilia*, in which it is particularly large.

According to Wiedersheim, *Siphonops* possesses two small openings in the region of the tentacle groove, instead of a single one as is the case in *Dermophis* and *Coecilia*. He maintains that they are not the openings of the tentacle canals, because upon removal of the skin perforated by the two openings, the tentacle canal openings and the tentacle papilla could be seen. Wiedersheim therefore concludes that the tentacle papilla cannot be freely moved in and out of the tentacle groove, as in other genera (op. cit., p. 46). In the specimen examined by me, however, the relations of tentacle groove and tentacle papilla are quite similar to those of *Dermophis* and *Coecilia*.

Structures in the temporal groove.

Temporal groove

The ~~tentacle~~ is a posterior continuation of the orbit and is completely roofed over by the paraquadrate, except for the posterior region where a small slit is present between the parietal and the paraquadrate (Figs. 4 and 5). The skull is therefore very slightly zygomorphic. The processus ascen-

dens palatoquadrati lies below the paraquadrato, and forms the side wall of the skull behind the latter; it does not reach the side wall of the neurocranium, since a small cleft is present between it and the parietal (Figs. 4 and 5).

In the anterior portion of the temporal groove the reflector muscle of the tentacle and the orbital gland are situated in a ventral position, as described above. The m. adductor mandibulae externus major arising in a cranio-caudal direction from the paraquadrato, p. ascendens palatoquadrati, frontal and parietal, fills almost the entire temporal groove (Fig. 4). It is therefore very large and extends rostrad into the nasal region dorsal to the nasal sacs (Figs. 2 and 3). The muscle passes through the basitemporal fenestra and inserts on the inner surface of the lower jaw. The m. adductor mandibulae externus minor is located lateral to the m. adductor mandibulae externus major in the posterior part of the temporal groove (Fig. 4). It is very small and also inserts on the inner surface of the lower jaw. A third small muscle is present in the posterior part of the temporal groove. This is the m. levator quadrati, which arises from the lateral wall of the neurocranium and inserts on the dorsal surface of the p. pterygoideus palatoquadrati where the latter forms the quadrato-basal articulation (Fig. 5). The muscle separates the anterior portions of the ophthalmic and maxillo-mandibular ganglia of the trigeminal nerve (Fig. 5). The m. cephalo-dorso-maxillaris and the m. pterygoideus are also present in the temporal region. The former arises from the outer surface of the paraquadrato and the p. ascendens palatoquadrati (Figs. 4 and 5), and the latter from the ventral surface of the p. pterygoideus palatoquadrati (Fig. 5), and inserts on the inner surface of the lower jaw.

The three rami of the trigeminal nerve pass through the temporal

groove. The course of these rami will be described below. The skull is very broad in the temporal region, the paraquadrate and the p. ascendens palatoquadratii lying far out to the side so that the temporal groove is very wide (Fig. 4).

The bones in the suspensorial region.

The jaw articulation lies far out to the side. The palatoquadrate has three processes: the p. pterygoideus and p. ascendens which project rostrad beyond the body of the bone (Fig. 4), and the p. columellaris which which forms an articulation with the stapes (Fig. 6). Between the anterior end of the p. pterygoideus palatoquadratii and the posterior end of the maxillo-palatine a small bone is inserted (Fig. 4). Wiedersheim also described this small bone in *Siphonops annulatus* and *Coeccilia rostrata*, and he considers it to be homologous with the postpalatine described by Parker for the Urodela. Upon considering the position of the bone and comparing the palate of *Siphonops annulatus* with that of certain *Stegocephalia*, it was noticed that this so-called postpalatine corresponds in position to the ectopterygoid or transversum of the Stegocephalia. In many *Stegocephalia* the ectopterygoid is absent, in others it is well developed, and again in some it is much reduced. The postpalatine of *Siphonops annulatus* is obviously vestigial, and is absent in all other *Gymnophiona* investigated except in *Coeccilia rostrata*, where it is also a very small bone according to Wiedersheim. The presence of a transversum in the *Gymnophiona* will be of immense phylogenetic importance, as a transversum is absent in all modern *Amphibia*, but present in some *Stegocephalia*, as pointed out above. The presence of a transversum in the *Gymnophiona* is important evidence for the standpoint of Marcus, who maintains that the *Gymnophiona* are closely related to the *Stegocephalia*, in

fact, that they can be considered as living Stegocephalia. Embryological material of Siphonops is an absolute necessity in order to study the development of the bone.

The *p. pterygoideus palatoquadrati* forms a well developed quadrato-basal articulation with a broad ventro-lateral process of the basal bone (Fig. 5). As described above, the *p. ascendens palatoquadrati* is a bony squame underlying the paraquadrato. It forms the side wall of the skull behind the paraquadrato and does not reach the parietal. The *p. ascendens* and the *p. pterygoideus palatoquadrati* join the body of the palatoquadrato at the suspensorium. The palatoquadrato and its two processes enclose a wide passage against the side wall of the neurocranium. This is the cranio-quadrato passage which is continued caudad to the anterior end of the otic capsule. The passage is filled with ganglia of the trigeminal nerve and several veins and arteries (Fig. 5), which will be described below.

In front of the otic capsule, the palatoquadrato and its two processes dwindle rapidly, and only a small process, the *p. columellaris palatoquadrati*, remains. This latter lies far laterad (Fig. 6), and forms a quadrato-stapedial articulation with the distal cartilaginous end of the stapedial style (Fig. 6). The geniculate ganglion, vena jugularis interna and the arteria stapedialis lie between the quadrato-stapedial articulation and the side wall of the neurocranium (Fig. 6). The stapedial style joins the extreme anterior end of the stapedial footplate, projecting rostrad beyond the otic capsule, and attached to the lateral wall of the neurocranium by means of cartilage immediately ventral to the foramen for the facial nerve root (Fig. 7). The stapedial footplate fits into the fenestra ovalis, and fills it completely. The stapes is not perforated by the *a. stapedialis*, which

retains a position dorsal to the stapes (Fig. 7).

The otic capsules are not independent structures, but are incorporated in the basal bone. In the otic region the basal bone also expands on to the roof of the skull below the parietals, and in the occipital region it is the only bone present, and there forms the two occipital condyles.

In comparing the temporal and suspensorial regions of *Siphonops* with those of *Coecilia* and *Dermophis*, the following points should be noticed:

(a) The *m. pseudotemporalis*, present in *Dermophis mexicanus* and *Coecilia*, is absent in *Siphonops*.

(b) The *m. levator quadrati* is a comparatively large muscle in *Siphonops* and *Dermophis*, whereas it is represented by a few muscle fibres only in *Coecilia*. The state of development of this muscle obviously corresponds to the state of development or degeneration of the quadrato-basal articulation, as was pointed out before. In *Coecilia* the articulation has almost entirely degenerated and a well developed *m. levator quadrati* would therefore be superfluous: the muscle therefore is disappearing in *Coecilia*.

(c) *Dermophis* and *Siphonops* both show slight *zygokrotaphy*, whereas *Coecilia* is definitely *stegokrotaphic*.

(d) The presence of a transversum in *Siphonops annulatus* and *Coecilia rostrata* may prove to be of prime importance. It is absent in *Dermophis* and *Coecilia ochrocephala* (described by the author).

(e) As regards the suspensorium, *Siphonops* and *Dermophis* are very similar. The quadrato-basal articulation is clearly defined in both, but in the former the quadrato-stapedial articulation is better developed than in the latter, where the articulation is degenerating. In *Coecilia ochrocephala* both these articulations have almost completely disappeared as the result of fusion, and the skull is monimostylic, whereas in *Siphonops* it is strepto-

stylic. According to Wiedersheim, *Siphonops annulatus* does not possess a quadrate-stapedial articulation: "Diese geräht mittelst eines straffen, fibrösen Bandes mit dem hinteren Umfang des Quadraternes in Contact" (op. cit., p. 17).

(f) The cranio-quadrate passage of *Siphonops* and *Dermophis* is wide and the skull is broad in this region. In *Cœcilia* the passage is almost entirely obliterated and the ganglia and bloodvessels have shifted into the cranial cavity. The skull of *Cœcilia* is therefore much narrower in the suspensorial region than in *Siphonops* and *Dermophis*.

The above mentioned points indicate that the cranial anatomy of *Siphonops* presents on the whole a much more primitive picture than *Cœcilia*. *Dermophis* and *Siphonops* are more directly comparable as regards most of the cranial features, although *Siphonops* shows a few primitive features, absent in *Dermophis*.

The ganglia and branches of the trigeminal, facial and acoustic nerves.

The roots of the seventh and eighth cranial nerves are not applied to each other. The root of the latter nerve enters the anterior end of the long acoustic ganglion, which is situated within the cranial cavity and is pressed closely against the inner wall of the otic capsule (Fig. 7). The four branches of the acoustic nerve enter the labyrinth cavity through separate foramina: the two anterior branches effecting an entrance through foramina situated ventrally in front of the foramen endolymphaticum, and the two posterior ones through foramina situated ventrally in front of the foramen for the perilymphatic duct.

The root of the facial nerve, as mentioned above, is distinct from the root of the acoustic nerve, but it is closely applied to the ventral surface of the anterior elongation of the acoustic ganglion (Fig. 7). It leaves

the cranial cavity through a ventrally situated foramen located immediately below the anterior end of the otic capsule and dorsal to the rostral end of the stapedial styx footplate, which latter is here connected with the lateral wall of the neurocranium by means of cartilage (Fig. 7). It then enters the small ^{ic} geniculate ganglion situated dorsal to the stapedial style. The first branch of the facial nerve to leave the geniculate ganglion, is the ramus hyomandibularis VII, which runs backward against the side of the skull. Shortly after leaving its ganglion, it gives off the small chorda tympani, running laterad and forward, and entering a canal in the lower jaw. It is continued rostrad in the lower jaw dorsal to Meckel's cartilage for a considerable distance before forming an anastomosis with a small branch of the ramus mandibularis V (Vc). A few ganglionic cells are present at the point of anastomosis. Rostrad of the anastomosis, the chorda tympani divides into several ramuli: two of these innervate the epithelium and a third the muscles of the tongue, whereas two small ramuli, evidently containing the trigeminal fibres, innervate the ventral skin in the region of the mental symphysis.

The main trunk of the r. hyomandibularis VII runs caudad and divides into two branches, one of which innervates the m. cephalo-dorso-maxillaris, while the termination of the second branch could not be traced.

The geniculate ganglion extends rostrad into the cranio-quadrate passage from its position on the medial side of the quadrate-stapedial articulation (Fig. 6). It is accompanied by the a. stapedialis and the v. jugularis interna. In the cranio-quadrate passage the geniculate ganglion enlarges considerably, and the maxillo-mandibular (Vb+c) portion of the trigeminal nerve root enters this enlarged ganglion at the same level at which the r. palatinus VII emerges from the ganglion on the ventral side. The

geniculate ganglion is therefore continuous with the maxillo-mandibular ganglion. Ventral to the ganglion for Vb+c the large ophthalmic (Va) ganglion is situated (Fig. 5). Posteriorly the two trigeminal ganglia are closely applied, with only a thin connective tissue membrane separating them; anteriorly they are separated by the m. levator quadrati, and are therefore nowhere continuous (Fig. 5).

The root of the trigeminal nerve divides into two portions in the cranial cavity: the Vb+c portion leaving the cranial cavity through a dorsally situated foramen, and the Va portion leaving through a more ventrally situated foramen. The Va portion of the trigeminal nerve root enters the ganglion for Va which lies pressed against the lateral wall of the neurocranium immediately above the ventro-lateral process of the basal bone forming the quadrate-basal articulation (Fig. 5).

Vc, Vb as well as several independent ramuli of Vb leave the Vb+c ganglion. Vc, a strong ramus, leaves the ganglion on its lateral side, and passes laterad through the temporal groove towards the lower jaw (Fig. 5). Its course lies lateral to the p. pterygoideus palatoquadrati and the m. pterygoideus, and medial to the m. adductor mandibulae externus minor. Immediately after leaving the ganglion, Vc gives off three ramuli: one, given off on the ventral side of the main trunk of Vc, innervates the m. pterygoideus, and two others, given off on the median dorsal side of the main trunk, innervate the m. adductor mandibulae externus major and the m. adductor mandibulae externus minor respectively. The main trunk of Vc enters the lower jaw and divides into three branches, one of which leaves the lower jaw on its lateral side to innervate the skin on the side of the head. The medial branch of the two remaining in the lower jaw, forms an anastomosis with the chorda tympani as described above. The remaining laterally situated branch

sends out a number of ramuli into the skin of the side of the head, and at the mental symphysis it also gives off small branches innervating the skin of the ventral side.

Three small branches of Vb leave the ganglion of Vb+c before the main trunk of Vb. The most posterior of the three ramuli, Vb₁, leaves the ganglion dorsally and pierces the parietal; it innervates the skin on the dorsal side. Slightly further caudad two other ramuli ^{leave} the ganglion, one on either side of the first one. The more medially situated of the two ramuli, Vb₂, also pierces the parietal and innervates the skin on the dorsal side. The laterally situated branch, Vb₂, runs laterad for a considerable distance in the m. adductor mandibulae externus major against the under surface of the p. ascendens palatoquadrati. In front of the latter, Vb₂ enters a canal in the paraquadrate, in which it runs backwards for a short distance before passing into the skin on the lateral side.

The main trunk of Vb leaves the ganglion at its anterior end, and runs downwards medial to the m. adductor mandibulae externus major (Fig. 4). A small ramulus of Vb, given off after the nerve has left the ganglion, runs along with the main trunk of the nerve and finally enters the small muscle belly of the compressor muscle of the orbital gland; it is the only motor branch of Vb.

Two anastomoses are formed between Vb and the r. palatinus VII. The latter, after leaving the geniculate ganglion, runs forward in a position latero-ventral to the ganglion of Va (Fig. 5). It remains dorsal to the quadrato-basal articulation, and in front of the latter it assumes a situation in the medio-palatine fenestra (Fig. 4). A branch of the r. palatinus VII now runs laterad and fuses with the main trunk of Vb. At the point of anastomosis ganglionic cells appear, and a small branch piercing the maxillo-

palatine and innervating the buccal epithelium, is given off, by the main trunk of Vb where the anastomosis takes place. Caudad to the anastomosis of the r. palatinus VII with Vb described above, the latter gives off a small branch, running rostrad for a short distance, passing through the compressor muscle of the orbital gland and forming an anastomosis with the r. palatinus VII.

Before entering a canal in the maxillo-palatine, Vb gives off four small branches: three of these perforate the maxillo-palatine and innervate the teeth, while the fourth runs laterad and upward, pierces the paraquadrate, and innervates the skin on the lateral side. From the canal in the maxillo-palatine, Vb sends out several branches: one into the buccal roof and several into the skin on the lateral side of the head. Vb leaves the maxillo-palatine near the anterior end of the bone, and enters a canal in the ventral portion of the nasopremaxillary. The nerve then passes from a lateral to a medial position in the premaxillary. It forms an anastomosis with Va and then breaks up into small branches innervating the skin on the lateral side, but the nerve does not extend to the anterior end of the snout. Va alone is responsible for the innervation of the skin of the extreme anterior portion of the snout.

The r. palatinus VII, after forming the double anastomosis with Vb, runs forwards on the floor of the orbit. In the posterior part of the nasal region it runs between the mesethmoid and the maxillo-palatine (Fig. 3), and divides into four branches. One of these perforates the maxillo-palatine, and innervates the buccal epithelium in the region of the choana. Two of the remaining pass through the vomer into the buccal roof, and the fourth divides into two branches running forwards in a deep groove on the dorsal surface of the vomer. The groove is roofed over by a cap-like process of

the mesethmoid; rostrad it deepens, and the two branches pass through the vomer and appear on the ventral surface. One proceeds mediad, the other laterad in the buccal roof, of which they innervate the anterior portion.

Va, after leaving its ventrally situated ganglion, runs upwards against the lateral wall of the neurocranium and then occupies a more dorsal position. In the orbital region it lies pressed against the membranous lateral wall of the neurocranium, between the taenia marginalis and the trabecula. It remains an unbranched nerve until, it reaches the posterior part of the nasal region, where it lies above the cartilaginous mesethmoid process (Fig. 3). Here Va gives off a small ramulus piercing the frontal and supplying the skin on the dorsal side of the head. Va then passes into the nasal cavity where it is situated in a medial position, dorsal to the main nasal sac (Figs. 1 and 2). Another small branch is given off passing laterad over the nasal gland (Figs. 1 and 2), and running rostrad before piercing the nasopremaxillary to supply the skin of the sides of the head.

The dorsal olfactory nerve (Id), upon leaving its canal in the dorsal portion of the mesethmoid, lies pressed against the main trunk of Va. The fibres of the two adjacent nerves are histologically completely different. A small ramulus of Va separates off from the main trunk and fuses with Id; this is, however, a temporary anastomosis., because the Va ramulus soon separates from Id, runs downwards against the internasal septum, which latter is formed here by the ossified mesethmoid, and forms a temporary anastomosis with the ventral olfactory nerve (Iv). Iv is accompanied for a short distance by the Va ramulus, which then separates off and enters a canal in the ventral portion of the nasopremaxillary, where it forms an anastomosis with the anterior portion of Vb, and innervates the skin of the ventral side.

The main trunk of Va, after giving off the ramulus forming the anas-

tomosis with Id, Iv and Vb, enters a canal in the dorsal portion of the mesonasopremaxillary, from where it sends several branches to the skin on the dorsal side. Near the anterior end of the snout, Va runs downwards in a long canal in the medial portion of the nasopremaxillary; a strong branch runs backwards in the ventral portion of the nasopremaxillary and supplies the ventral skin of the snout anterior to the final terminations of Vb. The remaining fibres of Va proceed rostrad and several ramuli pierce the nasopremaxillary and innervate the skin of the tip of the snout. Va is therefore a purely sensory nerve innervating the skin on the dorsal side of the head, and especially the skin of the snout; Vb supplies the skin on the lateral sides of the head and a portion of the ventral skin of the snout; Vc supplies the skin of the lower jaw.

Two pairs of olfactory nerves are present as in all Gymnophiona: the dorsal one innervating the dorsal and medial walls of the main nasal sac, and the ventral nerve innervating the "Nebennase" and a small portion of the ventral wall of the main nasal sac.

In the above description the following points should be noted:

(a) The two ganglia of the trigeminal nerve are in no way connected even as in *Dermophis* and *Coeccilia*, but the geniculate ganglion and the ganglion of Vb+c are continuous. In *Dermophis* these two ganglia are not continuous, but they are connected by means of a thin strand of connective tissue; in *Coeccilia* a separate ganglion for the facial nerve is absent, as was described in detail in a previous paper. The condition in *Coeccilia* was interpreted as indicative of specialisation.

(b) The roots of the acoustic, facial and trigeminal nerves are not connected. The root of the facial nerve is merely applied to the acoustic ganglion, this being the only connection between the facial and acous-

tic nerves.

(c) The roots of Va, Vb+c and the facial nerve have separate foramina, as in *Dermophis*. In *Coecilia*, however, these three nerve roots pass through one large prootic foramen.

(d) The following anastomoses are present: (i) an anastomosis between Va and the chorda tympani (also described for *Dermophis* and *Coecilia*); (ii) two anastomoses between Vb and the r. palatinus VII. (In *Coecilia* the same condition obtains, but in *Dermophis* only one is present); (iii) A temporary anastomosis between a branch of Va and Id and Iv, and a permanent anastomosis between the same branch of Va and Vb. In both *Coecilia* and *Dermophis* these ^{to Tr}anastomoses are absent, although in the latter, Va possesses a branch which runs down the internasal septum and forms an anastomosis with Vb without forming anastomoses with the two olfactory nerves.

(e) Va, as in *Dermophis* and *Coecilia*, is a purely sensory nerve. Vb contains only one small motor branch innervating the compressor muscle of the orbital gland, whereas Vc has several motor branches as well as a large number of cutaneous branches.

On the whole the cranial nerves of *Dermophis* and *Siphonops* are very similar. The nerves of both these genera present a much more primitive picture than those of *Coecilia*.

As mentioned before, Wiedersheim gave a very incomplete description of the cranial nerves of *Siphonops*, and the only other description of its brain and nerves was done by Waldschmidt (1886). Apart from failing to describe several branches of the cranial nerves, he describes several other features which could not be demonstrated in the specimen studied by me. As instances may be cited the presence of an optic and oculomotor nerve, with an anastomosis between the latter and Vb; an anastomosis between Va and the

ganglion Gasseri (ganglion of Vb+c) and an anastomosis between the ganglion of Vb+c and the geniculate ganglion. Features which he failed to notice are two separate ganglia of the trigeminal nerve, and the various branches of the facial nerve. Of the latter, he described one branch running forwards; this is evidently the chorda tympani. He missed the r. hyomandibularis VII and although he noticed a small nerve pressed against the floor of the skull, described as a palatine nerve, he could not trace its origin or its final terminations. He could not demonstrate an acoustic nerve.

The cranial veins and arteries.

Owing to the size of the blood corpuscles and the thick walls of the vessels it was comparatively easy to trace the arteries in the head. The anterior branches of the internal carotid artery, however, could not be traced, as these are lost among the large number of small veins in the snout region. The veins are extensively branched to form large networks. It was extremely difficult to trace the veins, as their walls were frequently broken and the vessels had collapsed in many parts.

The arteries of the head.

The a. stapediales, a branch of the a. carotis interna, runs rostrad lateral to the posterior part of the skull accompanied by the r. hyomandibularis VII. The artery gives off two branches in the otic region: one accompanying the branch of the r. hyomandibularis innervating the m. cephalo-dorso-maxillaris, and the other accompanying the chorda tympani into the lower jaw. The a. stapediales does not pierce the stapes, but retains a position dorsal to the stapediale style (Fig. 7). In the quadrato-cranial passage, where it runs lateral to the trigeminal ganglia (Fig. 5), the a. stapediales divides into two branches, one accompanying Vc and dividing into as many

branches as there are ramuli of the nerve; these small branches of the artery accompany the nerve ramuli to their final terminations. The other branch remains close to the ganglion of Vb+c, and sends small branchlets to the three ramuli of Vb leaving the ganglion of Vb+c before the main trunk of Vb does. The main stem of the artery runs along with Vb, and at the anterior end of the m. levator quadrati it gives off a branch running mediad then rostrad with Va. The branch running rostrad with Vb divides into numerous branchlets accompanying the ramuli of Vb to the roof of the buccal cavity and to the skin on the dorsal and lateral sides of the head (Figs 2 and 3). The branch of the artery accompanying Va also gives off branchlets which accompany the ramuli of the nerve to the dorsal, lateral and ventral skin of the head and snout region (Fig. 2).

In Siphonops therefore, more so than in Coecilia, it becomes clear that the a. stapediale is an artery supplying the ramuli of the fifth and seventh cranial nerves and the various structures innervated by these nerve ramuli.

The a. carotis interna, as in other Gymnophiona, is an unbranched artery. It runs rostrad ventral to the neurocranium, and at the anterior end of the otic capsule it enters the cranial cavity through a foramen situated immediately below the stapediale footplate where the latter is attached to the neurocranium by means of cartilage (Fig. 7). The foramen for the facial nerve root is situated at the same level dorsal to the stapes. In the cranial cavity the artery gives off a large branch supplying the brain. The main stem of the artery runs rostrad in the cranial cavity and leaves it again through a foramen situated in the lateral wall of the neurocranium immediately below the foramen for the ophthalmic root of the trigeminal nerve. It runs forwards with the r. palatinus VII and the v. jugularis in-

terna (Figs. 3, 4 and 5), and gives off branches which accompany the ramuli buccal of the r. palatinus VII into the buccal cavity. Beyond the termination of the r. palatinus VII the course of the artery could not be traced. The cranial veins, as mentioned above, are much branched and were difficult to trace.

The vena jugularis interna. In the snout region a large number of small branchlets, coming from the skin on the dorsal and ventral sides, are present. They join to form the v. jugularis interna running caudad in a ventral position. It is joined by branches from the buccal cavity, and in the orbit it is accompanied by the r. palatinus VII and the a. carotis interna (Fig. 3). In the posterior part of the temporal groove it is a large network, and in the quadrato-cranial passage it forms with the v. capitis lateralis a network around the ganglia of the trigeminal nerve (Fig. 5). In the temporal groove the m. levator quadrati separates the v. jugularis interna from the v. capitis lateralis (Fig. 5).

The vena capitis lateralis is formed by the junction of a large number of small veins arising in the nasal sac. The vein runs caudad, and is joined by several veins emerging from the m. adductor mandibulae externus major (Fig. 4). In the quadrato-cranial passage it forms a large network with the v. jugularis interna. From this network one large venous channel runs caudad (Figs. 6 and 7), and is joined by two cephalic veins leaving the cranial cavity. The ventral cephalic vein passes through a short canal in the lateral wall of the neurocranium immediately above the stapedial footplate, at the level of the entrance of the a. carotis interna into the cranial cavity. The dorsal cephalic vein leaves the cranial cavity above the posterior end of the ganglion of Vb+c. From here one vessel alone is continued caudad lateral to the otic capsule; it accompanies the r. hyomandibularis VII and the a. stapedialis. The number of cephalic veins as well as their means of exit from the cranial cavity varies in the different zono-

ra,. In *Dermophis gregorii* two and in *Dermophis mexicanus* three cephalic vessels were described by the author. In *Coecilia* only one is present.

General Conclusions.

The various points of importance have already been discussed in detail above, and a brief summary will therefore suffice. The investigation on Siphonops was undertaken with the view of obtaining comparative data, especially as the classification of the Gymnophiona is by no means settled as yet. Morphological data will therefore be of great value to the systematist.

In comparison with a highly specialised genus like *Coecilia*, *Siphonops* is a primitive form. It does not differ much from *Dermophis*, but it possesses several primitive features which are in the process of degeneration in *Dermophis*. The nasal sacs are very similar to those of *Dermophis*: the main nasal sac is divided into a lateral respiratory and a medial olfactory portion, as in *Dermophis*, and the opening of the "Nebennase" into the main nasal sac is similarly situated in the two genera. In both the olfactory portion of the main nasal sac becomes completely separated off from the respiratory portion in front of the choana, so that the "Choanenschleimbeutel" communicates with the respiratory portion only. In *Coecilia* the main nasal sac remains undivided, and the opening of the "Nebennase" into the main nasal sac is situated medially and ^{not} laterally as in *Dermophis* and *Siphonops*. Another important similarity between *Dermophis* and *Siphonops* is the relation of the "Nebennase" gland to the "Choanenschleimbeutel". In both the gland opens into the "Choanenschleimbeutel", and not into the "Nebennase" as in *Coecilia*.

There is one important difference in the structure of the nasal cap-

sules of *Dermophis* and *Siphonops*: the posterior portions of the main nasal sac and the "Choanenschleimbeutel" of *Siphonops* are situated in a deep groove in the ventral portion of the maxillo-palatine. The internal nares are therefore roofed over by bone. This condition does not obtain in either *Dermophis* or *Coecilia*. In *Coecilia* the "Nebennase" is situated in a separate cavity in the maxillo-palatine, and not in the main nasal cavity together with the main nasal sac. In both *Dermophis* and *Siphonops* the "Nebennase" and the main nasal sac share the same cavity.

The structure of the tentacle and the position of the tentacle groove are similar in *Dermophis* and *Siphonops*. The eye, in both these genera, is visible through the skin and is surrounded by the paraquadrate. The innervation of the retractor muscle could not be demonstrated in either of these two. The absence of the nerve is probably a sign of degeneration of the tentacular apparatus. In *Coecilia*, however, the abducent nerve innervating the retractor muscle of the tentacle, is present.

The absence of the *m. pseudotemporalis* in *Siphonops* cannot be regarded as of great importance. The view was maintained in a previous paper that this muscle is a muscle belly of the *m. adductor mandibulae externus major*, separated off from the latter by *Vb*. Its importance is therefore negligible. The innervation of the *m. levator quadrati* could not be traced in *Siphonops* and this also points to degeneration.

As regards the cranial kinesis, *Siphonops* retains a more primitive condition than either *Dermophis* or *Coecilia*. The quadrate-basal articulation shows no signs of degeneration, and the quadrate-stapedial articulation is well developed. In *Dermophis* the former articulation is well developed, but the latter is degenerating, whereas in *Coecilia*, both articulations show an advanced stage of degeneration. Movement between the *p. ascendens*

palatoquadrati and the paraquadrate seems to be impossible in all three genera. The skull of Siphonops is slightly zygokrotaphic, a specialised condition, and the p. ascendens palatoquadrati does not reach the lateral wall of the neurocranium.

In the palate of Siphonops, two large fenestrae, the medio-palatine and the basitemporal, are present. The vomer ^{ends} a little way caudad of the choana, as in Dermophis and Coecilia. An important feature of Siphonops is the presence of a small bone between the p. pterygoideus palatoquadrati and the maxillo-palatine. The bone, as pointed out above, corresponds in position to the transversum of some Stegocephalia, and its presence is therefore of great phylogenetic significance.

The cranial nerves of Siphonops differ slightly from those of Dermophis. The ganglionic masses of the facial nerve and the maxillo-mandibular portion of the trigeminal nerve are continuous in Siphonops, whereas only a thin commissure is present between the geniculate ganglion and the ganglion of Vb+c in Dermophis. Siphonops possesses two anastomoses between Vb and the r. palatinus VII, whereas in Dermophis only one is present between these two nerves. A branch of Va forms an anastomosis with Id, Iv and Vb, as described above. In Dermophis such a branch of Va is also present, but it forms an anastomosis with Vb only. In Coecilia these anastomoses are completely absent, Vb in Siphonops contains only one small motor branch in comparison to several in Dermophis. The cranial nerves and ganglia differ widely from those of Coecilia, and the significance of these differences were discussed in detail in a previous paper. Dermophis and Siphonops, on the other hand, show great similarity as regards cranial nerves and also as regards the general cranial morphology.

Alphabetical list of abbreviations to show the number of the figure
where they were first introduced.

astp 1; bas 2; bc 6; bep 3; br 2; carin 1; chg 3; csb 2; dp 2;
fr 1; ggen 6; gVa 5; gVb+c 5; gVIII 7; mamj 2; ~~mam~~n 4; mblj 6;
medm 4; mg 1; mlq 4; mns 1; mptg 5; msth 1; mxpl 1; nbg 1;
nbn 1; nsg 1; nspm 1; o~~h~~g 2; olp 1; otc 7; par 5; pasd 4; pbp
5; pl 3; pmsth 2; pptg 4; prq 2; qua 6; ret 3; rp 1; rpl VII 1;
rtm 2; rVII 7; sfp 7; sst 6; sync 5; tnc 1; tr 4; tvs 4; wepl 4;
vjug 3; vo 1; vp 2; vpl 5; Id 1; Iv 1; Va 1; Vb 1; Vb₁ 5; Vb₂ 5;
Vb₃ 5; Vc 5.

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Figure 1. Transverse section through the nasal region of Siphonops, showing the main nasal sac and "Nebennase". astp arteria stapediaлис; carin arteria carotis interna; fr frontal; mg mucous glands in the buccal roof; mns main nasal sac; msth mesethmoid; mxpl maxillo-palatine; nbg "Nebennase" gland; nbn "Nebennase"; nsg nasal gland; nspm nasopremaxillary; rp respiratory portion of the main nasal sac; olp olfactory portion of the main nasal sac; rpl VII ramus palatinus of the facial nerve; tnc tentacle canals; vo vomer; Id dorsal olfactory nerve; Iv ventral olfactory nerve; Va ramus ophthalmicus of the trigeminal nerve; Vb ramus maxillaris of the trigeminal nerve.

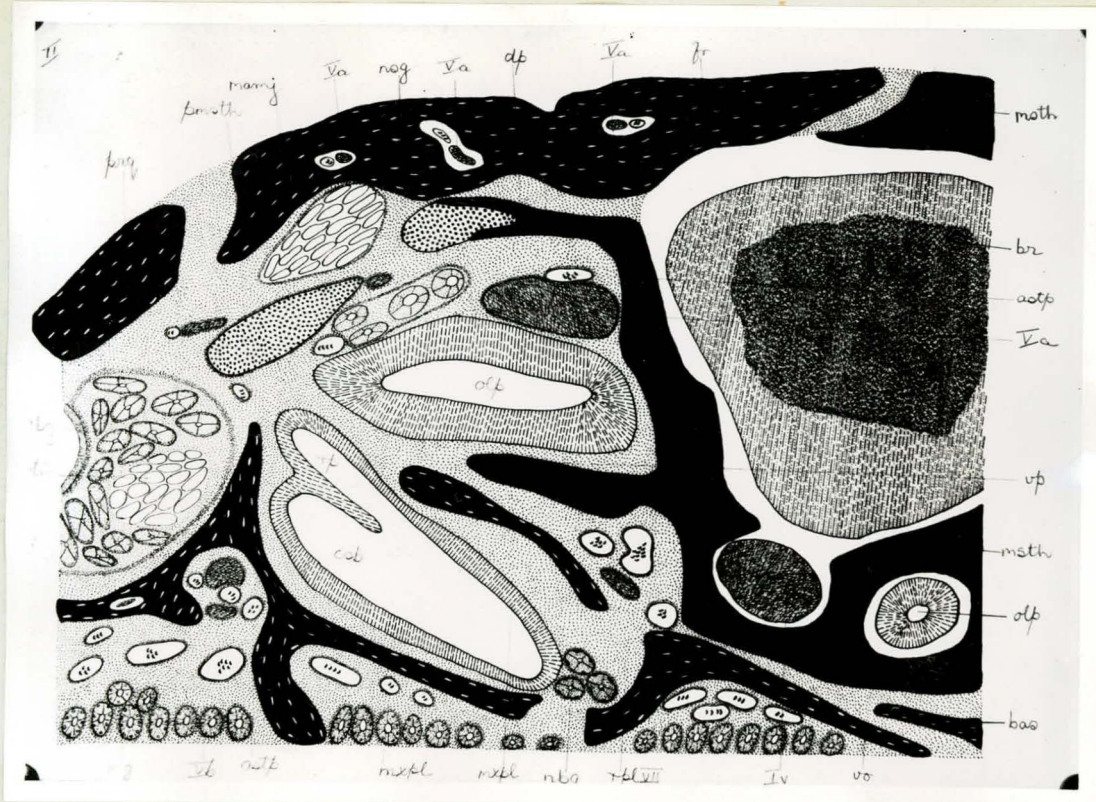


Figure 2. Transverse section through the nasal region immediately in front of the choana. bas os basale; br brain; csb "Choanenschleimbeutel"; dp dorsal process of the mesethmoid; mamj musculus adductor mandibulae externus major; obg orbital gland; pmsth cartilaginous process of the mesethmoid; prq paraquadrate; rtm retractor muscle of the tentacle; vp ventral process of the mesethmoid. Other abbreviations as for Figure 1.

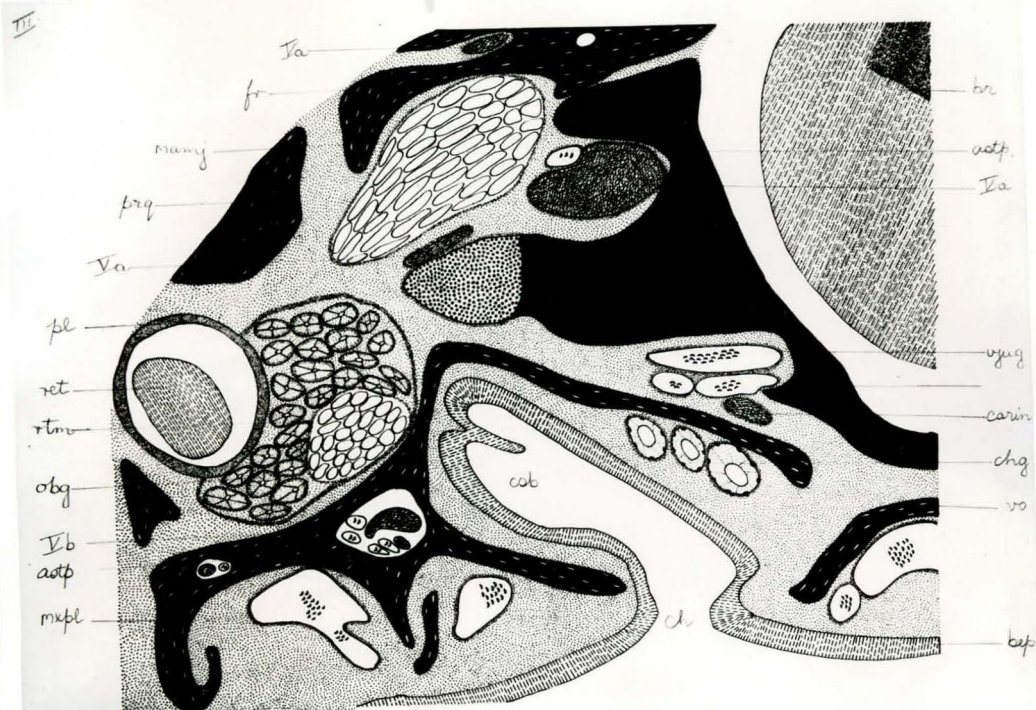


Figure 3. Transverse section through the choanal region, also showing the eye and the tentacle structures. bep buccal epithelium; chg choanal gland; pl pigment layer of the optic cup; ret retina; vjug vena jugularis interna. Other abbreviations as for previous figures.

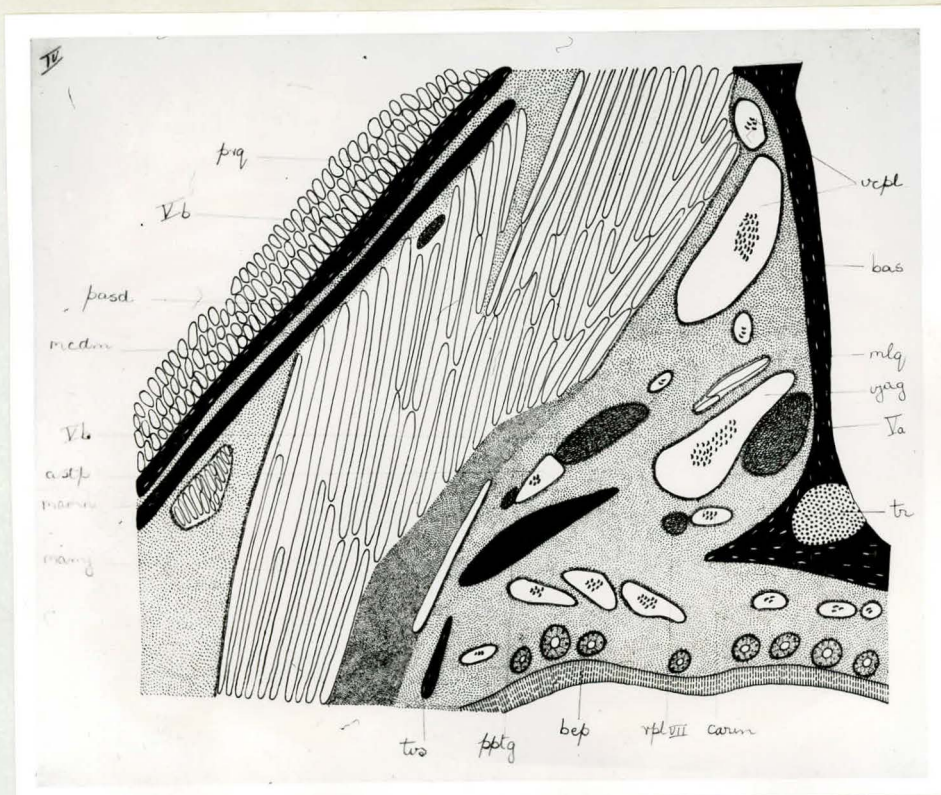


Figure 4. Transverse section through the temporal region, showing the muscles in the temporal groove. *mamm m.* adductor mandibulae externus minor; *medm m.* cephalo-dorso-maxillaris; *mlq m.* levator quadrati; *pasd* processus ascendens palatoquadrati; *pptg p.* pterygoideus palatoquadrati; *tr* trabecula; *tvs* transversum; *vcpl* vena capitis lateralis. Other abbreviations as for previous figures.

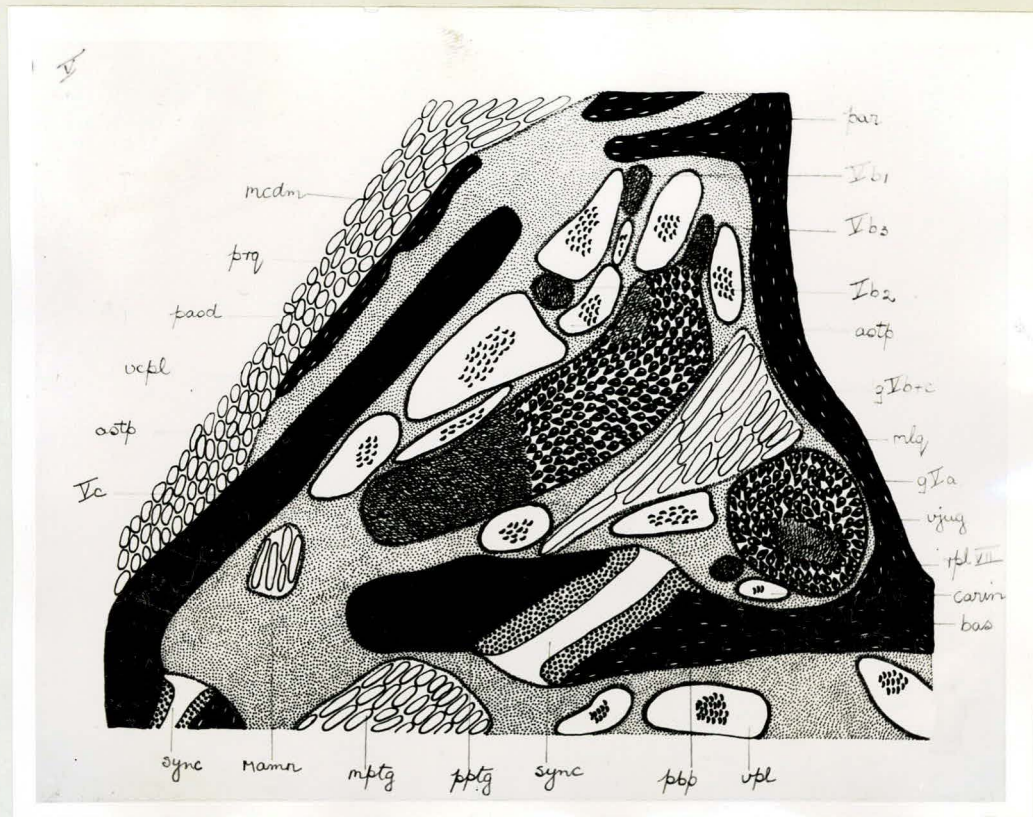


Figure 5. Transverse section through the anterior part of the quadrato-cranial passage showing the ganglia and bloodvessels in it and the quadrato-basal articulation. gVa ganglion ophthalmicum of the trigeminal nerve; gVb+c ganglion maxillo-mandibulare of the trigeminal nerve; mptg m. pterygoideus; par parietal; pbp processus basipterygoideus of the basal bone; sync synovial cavity; vpl vena palatina; Vb₁, Vb₂ and Vb₃ branches of the r. maxillaris V leaving the ganglion of Vb+c; Vc ramus mandibularis of the trigeminal nerve. Other abbreviations as for previous figures.

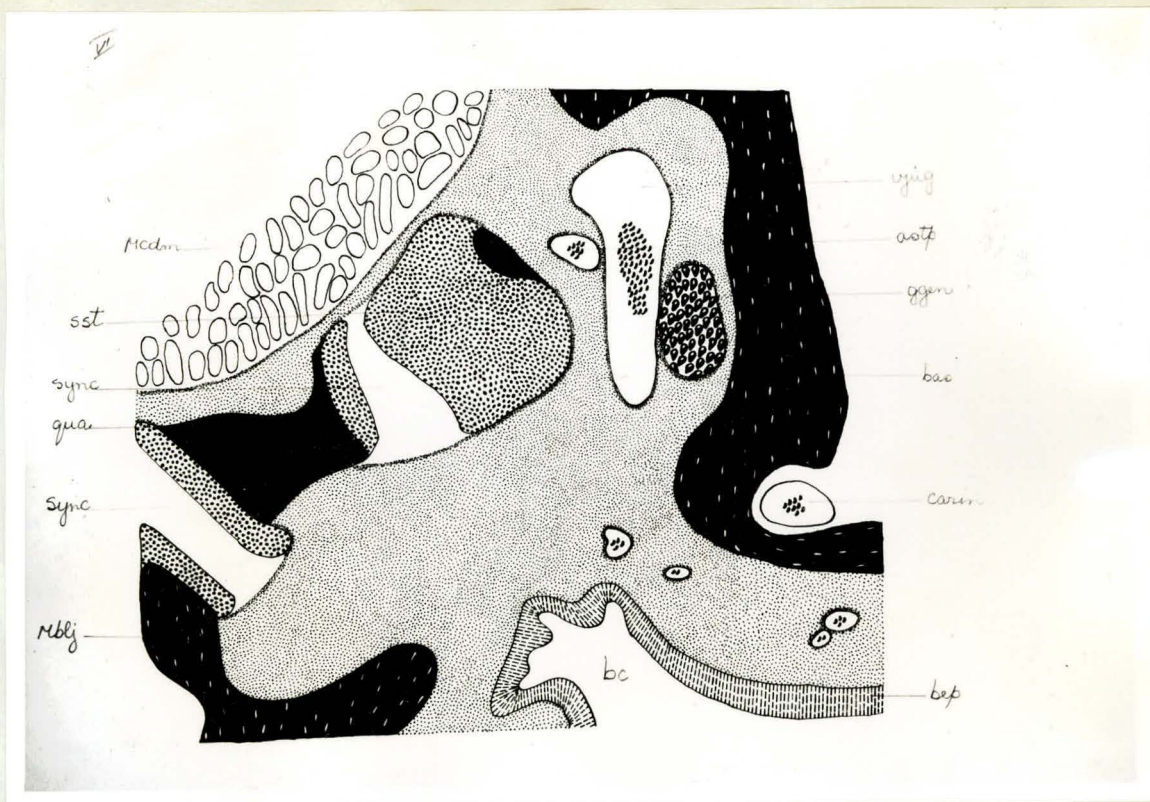


Figure 3. Transverse section immediately in front of the otic capsule showing the quadrato-stapedial articulation. bc buccal cavity; ggen geniculate ganglion; mblj mixed bone of the lower jaw; qua portion of the palatoquadrate forming the jaw articulation; sst stapedial style. Other abbreviations as for previous figures.

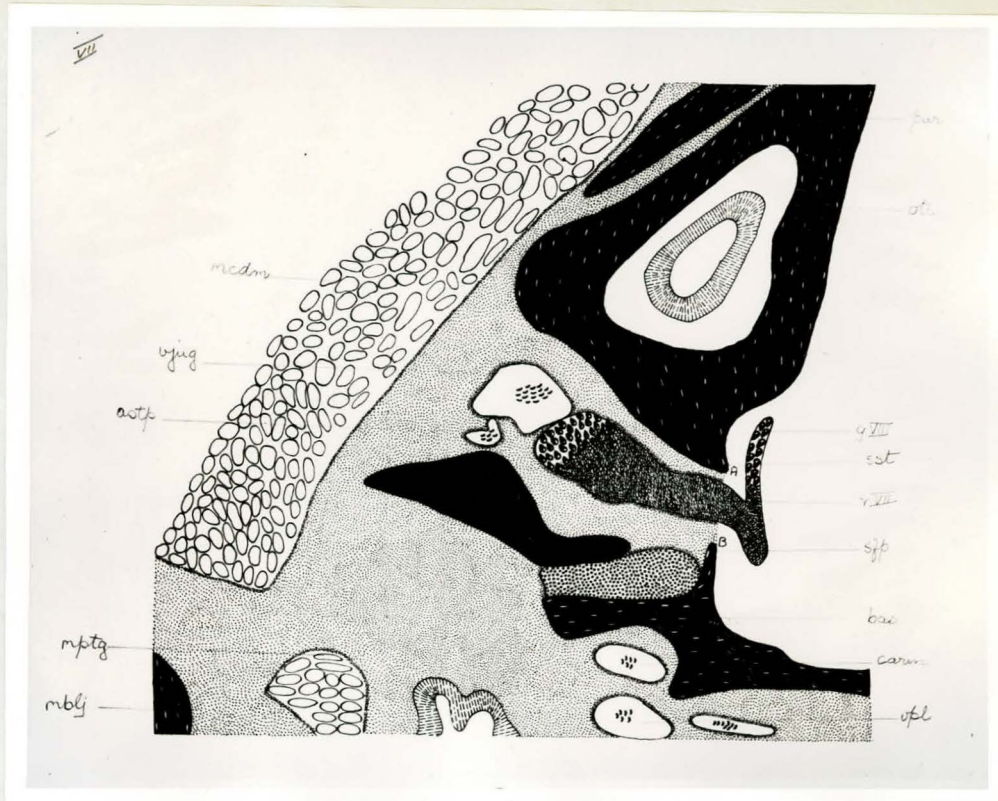


Figure 7. Transverse section through the anterior tip of the otic capsule, showing the foramen for the facial nerve root and the stapedial footplate attached to the wall of the neurocranium by means of cartilage. gVIII ganglion of the acoustic nerve; otc otic capsule; rVII root of the facial nerve; sfp stapedial footplate. Other abbreviations as for previous figures.

CONTRIBUTIONS TO THE CRANIAL ANATOMY OF THE GYMNOPTIONA.
THE NASAL REGION AND TENTACLE OF BOULENGERULA BOULENGERI AND
SCOLECOMORPHUS ULUGURENSIS.

CONTRIBUTIONS TO THE CRANIAL ANATOMY OF THE GYMNOPHONA.THE NASAL REGION AND TENTACLE OF BOULENGERULA BOULENGERI AND SCOLECOMORPHUS ULUGURENSIS.

Some cranial features of the two East African genera, Boulengerula and Scolecomorphus were described by de Villiers (1938). Details of the nasal organ and capsule were not given, and these structures as well as the tentacle and its associated structures will be described in this paper. As regards the suspensorial region, Boulengerula compared well with genera such as Dermophis, Ichthyophis and Siphonops, whereas Scolecomorphus differed profoundly from all the above mentioned genera. The absence of the quadrate-stapedial articulation, the stapes and the musculus levator quadrati, as well as the position of the quadrate-basal articulation (much more dorsal and nearer the neurocranium) were some of the striking features in the Scolecomorphus skull. These features, coupled with the persistence of separate nasals, and premaxillaries, indicate a neotenic condition in Scolecomorphus, as was pointed out by de Villiers (op. cit., p. 24).

In Coecilia, Dermophis and Siphonops (the author), the anatomy of the nasal organ and its associated structures were considered as indicative of the degree of specialisation attained by the animals. The nasal organ of a presumably neotenic genus like Scolecomorphus, and that of Boulengerula, which conforms to the general Gymnophione plan, should therefore be of considerable interest. Considering the widely different suspensorial regions of the two genera, it was not surprising to find that their nasal structures show hardly any similarities. That the nasal organ of Boulengerula and the very specialised Neotropical genus Coecilia would show any similarities was unexpected, as

Apart from the nasal organ and the nasal capsule, the tentacle and its associated structures will also be described in this paper. The structure of the tentacle is almost identical in the various genera studied by the author. The only points of variation were usually to be found in the position of the tentacle and the relative size of its associated structures, which latter variations could usually be correlated with the degree of degeneration of the eye and the relative importance of the tentacle and the "Hebamase" as the chief sense organs. (See here the discussion under *Cocilia*).

1 The nasal organ of *Boulengerula boulengeri*.

In *Boulengerula boulengeri* the nasal region is broad but very low, with the result that the nasal sacs are oblong in shape. The main nasal sac can be considered as consisting of three portions.. There is

a short anterior portion, oval shaped, with a small dorso-lateral indentation, formed by the tissue surrounding the external narial aperture. The dorso-lateral indentation was found to be present in every genus studied by the author. The anterior portion of the main nasal sac is followed by the median portion, which constitutes the greatest part of the main nasal sac. In *Dermophis* and *Siphonops* (the author 1938 and 1940) and in *Ichthyophis* (Wiedersheim, 1879), the median portion has a deep ventral indentation in its floor. The indentation is formed cranio-caudad by a ridge on the ventral portion of the nasopremaxillary, the lateral edge of the vomer and a process of it and a ventral, winglike process of the mesethmoid. These processes divide the main nasal sac into a medial olfactory portion and a lateral respiratory portion lacking the olfactory epithelium. *Coecilia* (the author and Wiedersheim) is the only genus so far described, in which the main nasal sac remains an undivided sac. In *Boulengerula* there is just the slightest trace of such an indentation, but to speak of a division into medial and lateral portions is out of the question (Fig. 1). *Boulengerula* and *Coecilia* therefore agree as far as the undivided condition of the main nasal sac is concerned, but the olfactory epithelium in the main nasal sac of the former is very well developed, except in the short lateral wall where it is absent. In the latter, however, the olfactory epithelium is poorly developed, and the main nasal sac presumably performs a respiratory function only (see Fig. 4 of the *Coecilia* paper). The third or posterior portion of the main nasal sac of *Boulengerula* is ^a more or less circular tube, and is much narrower than the median portion. In *Dermophis* the posterior portion of the main nasal sac divides into two portions, one of which communicates with the "Choanenschleimbeutel", and the other

(the olfactory portion) ends blindly (op. cit., p. 200). In *Siphonops* it divides into three portions, two of which end blindly, and the third (the respiratory portion), communicates with the "Choanenschleimbbeutel" and opens into the buccal cavity. In *Boulengerula*, as in *Cocilia*, the posterior portion of the main nasal sac does not divide into separate portions as described above, but dwindles to a small circular tube which opens into the buccal cavity together with the "Choanenschleimbbeutel". The nasal gland consisting of a fairly large number of alveoli, occupies a position on the lateral half of the roof of the nasal sac (Fig. 2). Alveoli are present throughout the nasal cavity with the exception of the extreme anterior portion, and they open separately into the main nasal sac, a large duct leading from the gland into the anterior part of the main nasal sac as in *Cocilia* and *Siphonops* being absent.

The walls of the "Nebennase", as in all genera described, consist of very thick olfactory epithelium, and the "Nebennase" lies in the same cavity as the main nasal sac. Its anterior portion is oblong in shape and it lies ventral to the main nasal sac, being almost as wide as the latter (Fig. 1). The medial half of the main nasal sac is separated from the anterior portion of the "Nebennase" by a laterally projecting process of the mesethmoid (Fig. 1). This mesethmoid process corresponds to the ventral winglike process forming the ventral indentation in *Siphonops* and *Dermophis*, but it is very much smaller and lacks the dorsally projecting portion found in the latter genera. Near its posterior end, the "Nebennase" is reduced to a small circular tube lying medially against the floor of the main nasal sac. It then opens into the posterior portion of the main nasal sac, and the commu-

nicating opening is situated ventrally in the medial wall of the latter (Fig. 2). *Coecilia* is the only other genus described, in which the communication is similarly situated (See Fig. 5 in the *Coecilia* paper). In genera such as *Dermochphis*, *Siphonops* and *Ichthyophis* where the deep ventral indentation is present, the communication between the "Nebennase" and the main nasal sac lies lateral to the ventral indentation, i.e. the "Nebennase" communicates with the lateral respiratory portion of the main nasal sac. In both *Coecilia* and *Boulengerula* the ventral indentation is absent, and the "Nebennase" opens into the medial wall of the main nasal sac. This similarity in the position of the communicating opening is probably due to the absence of the processes forming the ventral indentation.

The two tentacle canals perforate the maxillo-palatine laterally, and join just before opening into the anterior portion of the "Nebennase" (Fig. 1). The alveoli of the "Nebennase" gland are concentrated mainly on the lateral side of the "Nebennase", but a few are also present on its medial side. These alveoli all open into the "Choanenscheimbeutel", which appears in section immediately behind the lateral portion of the "Nebennase", occupying the same position as the latter in relation to the main nasal sac (Fig. 2). The "Choanenschleimbeutel" opens into the posterior portion of the main nasal sac, and the two sacs have a common opening into the buccal cavity. An epithelial fold indicating the boundary between the main nasal sac and the "Choanenschleimbeutel" is present, and is obviously homologous with one of the "Dachfalten" described by Laube for *Hypogeothis* and by the author for *Dermophis* and *Coecilia*.

The nasal capsule of Boulengerula.

The bones forming the nasal capsule are fused to a considerable extent, so that there are no separate nasals, premaxillaries, maxillaries or palatines, but just two large bones, the nasopremaxillary and the maxillo-palatine, as is also the case in genera such as *Dermophis*, *Siphonops* and *Coccolia*. The nasopremaxillary surrounds the anterior oval portion of the main nasal sac completely, except in the region of the external narial aperture. The anterior portion of the internasal septum is formed by the medial portions of the nasopremaxillaries with the cartilaginous mesethmoid between them. The mesethmoid alone forms the greater part of the internasal septum, and is ossified except for its short anterior portion lying between the nasopremaxillaries. The vomers, occupying a medial position on the floor of the nasal capsule (Fig. 1), extend very far rostrad, their anterior portions being covered ventrally by the nasopremaxillaries. The maxillo-palatine occupying a lateral position, extends rostrad as far as the anterior limit of the "Nebennase", and at about this level it takes the place of the nasopremaxillary on the lateral half of the floor and at the side of the nasal capsule (Fig. 1). Its lateral portion is here perforated by the two tentacle canals on their way to the "Nebennase". The vomer now replaces the remaining portion of the nasopremaxillary on the floor of the nasal capsule. The frontal extending rostrad below the dorsal portion of the nasopremaxillary, appears on the dorsal surface at the level of the anterior end of the "Nebennase" and forms the roof of the nasal capsule (Figs. 1 and 2). The mesethmoid forming the internasal septum is a narrow perpendicular lamina between the anterior portions of the nasal cavities. At the level of the anterior end of the "Nebennase"

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dorsal and ventral ends of the perpendicular lamina enlarge considerably. In the broad dorsal portion, which appears on the dorsal surface between the two frontals (Fig. 1), the two dorsal olfactory nerves lie in a common canal, and in the large ventral pedestal of the septum the ventral olfactory nerves are situated in two separate canals (Fig. 1). On either side of the pedestal of the septum a narrow laterally projecting process, lying between the medial portion of the main nasal sac and the "Nebennase", is present (Fig. 1).

The main nasal sac and the "Nebennase" are situated in the same oblong cavity formed by the bones mentioned above. The cranial cavity extends rostrad between the posterior parts of the two nasal cavities (Fig. 2), ^h thus reducing them from oblong cavities to more or less circular cavities. The vomer also becomes reduced to a narrow process lying ventral to the mesethmoid (Fig. 2). At the level of the choana the nasal cavity is reduced still further by the enlarged cranial cavity, and only a narrow cavity remains in which the posterior portions of the nasal sacs are situated. The choana is bound laterally by the maxillo-palatine and medially by the vomer.

The vomer extends caudad beyond the choana for a very short distance only (Fig. 3). The maxillo-palatine, on the other hand, extends mediad behind the choana and reaches the mesethmoid and basal bone forming the floor of the neurocranium (Fig. 3). The maxillo-palatine, therefore, forms a complete floor for the anterior part of the orbit. It does not remain such a broad bone for any considerable distance, but narrows from its medial side, thus allowing a medio-palatine fenestra between the base of the neurocranium and the maxillo-palatine. The

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medio-palatine fenestra is, however, very much narrower than in Siphonops and Dermophis. In the latter two the maxillo-palatine also forms a firm pal^ate behind the choana for a short way. In Boulengerula the anterior portion of the basitemporal fenestra ² is also much narrower than in the other genera mentioned above. The maxillo-palatine ends caudad immediately in front of the quadrate-basal articulation. The paraquadrate also extends into the nasal region; it reaches rostrad as far as the posterior end of the "Nebennase", where it occupies a lateral position. Together with the maxillo-palatine it here forms a canal in which the tentacle and its associated structures are situated (Fig. 2).

The most important points in the above description of the nasal organ and capsule of Boulengerula boulengeri are the following: The main nasal sac^b an undivided sac, the ventral indentation found in Ichthyophis, Dermophis and Siphonops is absent, Coecilia being the only other genus in which this is the case; and secondly the main nasal sac does not divide into two or more separate portions immediately in front of the choana, as happens in Dermophis and Siphonops.

The "Nebennase" opens into the main nasal sac, but the opening does not lie ventro-lateral as in Ichthyophis, Dermophis and Siphonops, but ventro-medially as in Coecilia. Boulengerula and Coecilia therefore have two important features in common as far as the nasal sacs are concerned, but as was stressed above, the main nasal sac of the former is a well-developed olfactory organ, whereas in the latter it is mainly a respiratory organ, with the "Nebennase" as main olfactory organ. In Coecilia the absence of the ventral indentation and the undivided condition of the main nasal sac in front of the choana can be explained

on the grounds of specialisation of the "Hebennase" and the tentacle as the only sense organs. In *Boulengerula*, where the eye is even more degenerate than in *Coecilia*, the "Hebennase" and some of the tentacle structures are not so specialised as in *Coecilia* (see below), and *Boulengerula* can therefore be considered as an intermediate stage between *Dermophis* and *Siphonops* (representing the general *Gymnophione* plan), and *Coecilia* (a very specialised genus).

As regards the nasal capsule, the only interesting fact is the absence of elaborate processes attached to the mesethmoid and the maxillo-palatine. In *Siphonops* these bones bear many processes. The mesethmoid of *Coecilia* ^{is} also a simple structure and does appear on the dorsal surface as in *Boulengerula*. In these ^{two} genera the maxillo-palatine forms a firm palate behind the choana.

The tentacle with its associated structures and the
eye of *Boulengerula boulengeri*.

The tentacle groove is situated laterally midway between the external narial aperture and the degenerate eye. The two tentacle canals, opening into the tentacle groove at their distal ends, perforate the maxillo-palatine laterally to open into the anterior end of the "Hebennase". The structure of the tentacle itself does not differ at all from that of *Ichthyophis*, as described by the Sarasin (1896). The epithelial tentacle sac indented by connective tissue to form the tentacle fold, the connective tissue tentacle sheath surrounding the tentacle sac, and the free tentacle papilla, are exactly similar to that of *Ichthyophis*. The reader is referred to the description given by the Sarasin (op. cit., pp. 195--197).

The retractor muscle taking the place of the connective tissue in the tentacle fold, is present as in other genera described. It is divided anteriorly into two portions by the orbital gland alveoli, which latter surround the tentacle sac and fold, and they possess a few large ducts opening into the tentacle sac. In the nasal region, the tentacle structures, i.e. retractor muscle and orbital gland, are situated in a deep lateral groove in the lateral portion of the maxillo-palatine (Fig. 2). This groove is covered laterally by the paraquadrate, which extends into the nasal region. Throughout the nasal region the tentacle structures are separated from the nasal sacs by the maxillo-palatine. The anterior portion of the orbit which has a bony floor formed by the maxillo-palatine, is filled by the retractor muscle and the orbital gland. The latter is a large structure, although not quite as well developed as in *Cocilia ochrocephala*. The orbit of *Boulengerula* is covered laterally by the paraquadrate, and there is no orbital opening, as was already noted by Peter (1903). *Cocilia* is another genus where an orbital opening is completely absent. The eye of *Boulengerula* is therefore covered by bone and has degenerated almost completely. In only seven sections a small bundle of pigment cells situated laterally in the orbital gland, is present. The compressor muscle of the orbital gland is small, and appears in section for the first time in the anterior part of the orbit. Posteriorly in the orbit it is closely applied to the dorsal surface of the retractor muscle, and the two muscles here lie pressed against the lateral membranous wall of the neurocranium between the tania marginalis and the trabecula, on to which the retractor muscle inserts. At its posterior end the compressor muscle

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forms a small medio-ventrally situated muscle belly, which caudad stretches laterad and inserts on the tendon of the musculus adductor mandibulae externus major.

The structure of the tentacle of *Boulengerula* is similar to that of genera such as *Dermophis* or *Ichthyophis*. The retractor muscle is well developed, but no innervation could be traced, whereas in *Cocilia* (the author) and in *Scolecophorus* (de Villiers) this muscle is supplied by the abducent nerve. The orbital gland is well developed, although not quite as large as in *Cocilia*, and the compressor muscle of the latter is an immense structure, while in *Boulengerula* it is a fairly small muscle. These two genera both lack an orbital opening, and the eyes in both have degenerated much more than in *Dermophis* or *Siphonops*, where a lens is still present and where the eye can be seen through the skin. In these latter ^{genera} the tentacle structures, especially the orbital gland, are not nearly as well developed as in *Boulengerula* or *Cocilia*. In the latter two, together with the marked development of the tentacle structures and the marked degeneration of the eye, the nasal sacs also show several differences from those of the former genera. These differences have been discussed above, and they indicate degeneration of the main nasal sac as an olfactory organ and the specialisation of the "Nebennase" as the main olfactory organ. In both these genera we therefore find a progressive development of the tentacle structures which, together with the progressive developed "Nebennase", form the main sense organ. *Boulengerula* and *Cocilia* therefore show many similar specialised features, although the latter has progressed much further in this line of specialisation, as was pointed out above.

The nasal sacs of *Scolecophorus ulugurensis*.

The nasal sacs of *Scolecophorus* differ very much from those of *Boulengerula* and resemble those of genera such as *Dermophis* and *Siphonops* much more, although they give the impression of being more elaborately folded and indented. The reason for this is probably the shape of the nasal cavity, which is almost as high as it is wide, the nasal sacs being therefore more or less circular. The main nasal sac opens to the exterior anteriorly at the external narial aperture, which is situated laterally. The anterior portion of the main nasal sac is oval in shape with a small dorso-lateral indentation formed by the lacrymal (see below). Many small glands of Bowman are situated medial and ventral to the anterior portion of the main nasal sac. Behind the anterior portion, the median portion shows a deep ventral indentation formed throughout by a process of the mesethmoid (Figs. 4 and 5). The anterior portion of this process is circular and cartilaginous, and is fused to the premaxillary and the maxillo-palatine (Fig. 4). Further caudad the process separates off from the above mentioned bones, and lies much more dorsally: about half way up the nasal cavity (Fig. 5). The process is connected with the vomer by means of connective tissue, and a considerable distance further caudad it extends downwards and connects up with a laterally projecting ventral process of the internasal septum, here formed by a perpendicular lamina of the mesethmoid. Because of the height of the nasal cavity and the mesethmoid process reaching half way up, the main nasal sac is divided into two portions which are bent almost at right angles: a medial portion lying vertically and a lateral portion lying almost horizontally (Fig. 5). The epithelium in the lateral portion is thinner than in the medial portion, but the former still

contains olfactory epithelium. At the level at which the "Nebennase" opens into the main nasal sac, the medial portion of the latter separates off completely from the lateral portion and becomes enclosed in a canal in the ventral portion of the mesethmoid (Fig. 6). The nasal gland consisting of a large number of alveoli, lies dorsally on the roof of the main nasal sac (Figs. 5 and 6). Its alveoli open separately into the latter.

The "Nebennase" is a straight circular tube lying ventral to the mesethmoid process forming the ventral indentation in the main nasal sac, and it actually occupies the angle between the medial and lateral portions of the latter (Fig. 5). Its walls consist of thick olfactory epithelium, and it opens into the lateral portion of the main nasal sac after the medial portion has separated off (Fig. 6). The communicating opening lies in the medial wall of the lateral portion, lateral to the mesethmoid process forming the indentation. The opening is therefore situated more or less as in *Dermophis* and *Siphonops*, although in these latter the medial portion of the main nasal sac separates off after the "Nebennase" has opened into the lateral portion. The "Nebennase" of *Scolecormorphus* is a circular cavity (Fig. 5), whereas in all genera investigated by the author it is a sausage shaped structure. In *Scolecormorphus* it never extends laterad as in these forms, and is therefore a much smaller structure.

The "Nebennase" gland consists of a few alveoli lying lateral to the "Nebennase" (Fig. 5), and they join to form the "Choanenschleimbeutel". The latter lies ventral to the lateral portion of the main nasal sac (Fig. 6), into which it opens, forming a triangular sac opening into the buccal cavity. The nasal sacs are very vascular, with numerous small vessels surrounding them.

The nasal capsule of *Scolecophorus ulugurensis*.

As was stated in the introduction, the bones forming the nasal cavity are not fused as in most of the other genera. Apart from separate nasals, premaxillaries and maxillo-palatines, another small bone is present, described by Peter (1895) for *Scolecophorus kirkii* as a lacrymal. Between the extreme anterior ends of the nasal sacs the nasals form a short internasal septum, which is formed caudad by the mesethmoid alone, and the nasals are then confined to a dorsal position (Fig. 4). They form the roof as far as the anterior end of the "Nebennase" and are then replaced by the frontals.

At the level of the external apertures the premaxillary appears on the ventral surface, and forms the medial portion of the floor as far as the anterior end of the "Nebennase". The premaxillary is therefore a short, ventrally situated bone occupying a medial position (Fig. 4). Behind the premaxillary the vomer forms the medial portion of the floor of the nasal capsule. The vomer extends very far rostrad above the premaxillary, and forms the floor below the medial portion of the main nasal sac (Figs. 5 and 6). The lateral portion of the floor below the "Nebennase" and the lateral portion of the main nasal sac is formed by the maxillo-palatine which bears a long dorsally directed process in the anterior region of the nasal capsule (Fig. 5). This process extends caudad only a short way and separates the tentacle structures from the nasal sacs, and is perforated by the tentacle canals. At the level of the posterior end of the "Nebennase" the maxillo-palatine process shortens and finally disappears, so that the tentacle structures come to lie in the lateral portion of the nasal cavity (Fig. 6), and the maxillo-palatine is then limited to a ventral position.

At the choana both the vomer and the maxillo-palatine are reduced to thin spiky processes lying on the medial and lateral sides of the choana respectively.

In front of the choana the vomer and maxillo-palatine are not closely applied to each other, but there is a definite opening between them (Fig. 6). For none of the bones present in the nasal region are there any definite sutures present, but slitlike openings, as was also noted by Peter for *Scolecormorphus kirkii* (op. cit., p. 7).

The premaxillary, vomer and maxillo-palatine are all tooth bearing bones, and they do not take part in the formation of the ventral indentation in the main nasal sac. The lateral wall of the nasal capsule is formed by two bones. Immediately behind the external nasal aperture a small appears on the lateral side of the main nasal sac, filling in the gap between the dorsally situated nasal and the ventrally situated premaxillary and maxillo-palatine (Fig. 4). This bone is also present in *Scolecormorphus kirkii*, and Peter described it as a lacrymal. The foramen described by Peter as being present in the lacrymal, is simply a small nerve foramen through which a branch of the r. maxillaris V passes on its way to the skin on the lateral side of the head. In one of the available specimens the lacrymal fuses at its posterior end with the maxillo-palatine, but in the other it remains a separate bone, and is reduced to a narrow process at its posterior end. Immediately behind the lacrymal the prefrontal appears occupying the same position as the former (Fig. 5). It is a large bone, as is also the case in *Scolecormorphus kirkii* (op. cit., p. 8), and it extends laterad over the tentacle structures, which then lie between the dorsally directed pro-

cess of the maxillo-palatine and the prefrontal. On the disappearance of the former process, the cavity containing the tentacle structures becomes confluent with the nasal cavity and the prefrontal then forms the lateral wall of the nasal capsule (Fig. 6). The prefrontal is nowhere very closely applied to the maxillo-palatine, a fairly broad slit separating them (Fig. 6). The prefrontal restricts the development of the maxillo-palatine on to the dorsal surface, and the latter is therefore confined to a ventral position.

Between the greater portions of the two nasal cavities the mesethmoid forms a perpendicular lamina, which is cartilaginous at its anterior end. As in *Boulengerulus* the perpendicular lamina bears a broad dorsal portion, in which the two dorsal olfactory nerves are situated in two separate canals; slightly further caudad these canals fuse to form a single cavity which is the anterior elongation of the cranial cavity containing the olfactory lobes (Fig. 6). The latter extend rostrad beyond the communication of the "Nebennase" with the main nasal sac. The mesethmoid also bears the short ventral process mentioned above. This process has a dorsally directed portion, from the dorsal tip of which a long thin process extends rostrad to form the ventral indentation in the main nasal sac, as described above. The medial portion of the main nasal sac, after its separation from the lateral portion, lies in a small canal in the ventral portion of the mesethmoid together with the ventral olfactory nerve (Fig. 6). At the level of the choana the ventral olfactory nerve joins the olfactory lobe, and the mesethmoid then forms the floor and sides of the enlarged cranial cavity, with the frontal forming the roof. The mesethmoid does not appear on the dorsal surface, as Peter also described for *Scolecophorus*

kirkii (op. cit., p. 4). The paraquadrate can be seen as a small process lying lateral to the prefrontal at the level of the choana; it therefore does not extend as far rostrad as in Boulengerula.

The vomer, extending caudad a short way beyond the choana, is throughout its whole length a narrow medially situated bone. The maxillo-palatine does not attain to large proportions, and is confined to a ventral position by the prefrontal. Behind the choana of which it forms the lateral wall, the maxillo-palatine does not extend mediad as in Boulengerula, Coecilia and Dermophis (see above), but is a narrow process attached to the ventral rim of the prefrontal. Between it and the base of the neurocranium there is therefore a large medio-palatine fenestra not separated at all from the basitemporal fenestra. The palate behind the choana is therefore not a firm structure as in other genera mentioned above, but is broken by a wide fenestra, in which the tentacle structures are situated.

In the above description it becomes clear that Scolecomorphus differs very much from Boulengerula and Coecilia, the two specialised genera (see above discussion), and also from Dermophis and Siphonops which present the general Gymnophione plan. As far as the nasal cavities are concerned, the main nasal sac is divided into medial and lateral portions, but in the latter olfactory epithelium is much better developed than in Siphonops and Dermophis, and the whole main nasal sac can be considered as an olfactory organ. The ventral indentation is formed by the mesethmoid alone, whereas in other genera where it is present, it is formed by the nasopremaxillary, vomer and mesethmoid. The "Nebennase" is a much smaller structure than in any of the other genera described by the author: it is confined to a medial position, and never

extends laterad to become a sausage shaped structure. The "Nebennase" is therefore not so well developed, while the main nasal sac is a much better developed olfactory organ than in these other genera. To understand the significance of the position of the "Nebennase" and the absence of goblet cells in a large part of the lateral portion of the main nasal sac, we must go back to the development of the nasal sacs. The development was first described by the Sarasins and later by Laubmann (1927). The former authors described the development in *Ichthyophis*, and the following points are of importance: the "Nebennase" (named an organ of Jacobson/by the Sarasins) develops from a medially situated evagination of the main nasal sac. This evagination later in the development, is replaced to a lateral position by the rotation of the main nasal sac. The whole "Nebennase" therefore comes to lie laterally, but its posterior portion retains its medial position, and later, when the "Nebennase" separates off from the main nasal sac, its opening into the latter is always at its posterior medially situated end. The following is a quotation from the description given by the Sarasins: "Was aber trotz aller Veränderungen dauernd sich erhält, das ist die mediale Stellung der Einmündung des Jacobson'schen Organs (Nebennase) in die Nasenhöhle, ein Verhältniss, das auch beim ausgewachsenen Thier noch bedeutsam genug auf die Entstehung die^ser^s Organe als einer ursprünglich medialwärts gerichteten Ausbuchtung des Geruchsackes hinweist" (op. cit., p. 184). In the early development the lateral respiratory part of the main nasal sac is very small, and only when the larva is ready to leave the water does the lateral portion increase in size (op. cit., p. 184). The "Nebennase" of *Scolecormorphus* retains a medial

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position as was pointed out above, and although the main nasal sac is divided into medial and lateral portions by the ventral indentation, the lateral portion is not a well developed olfactory organ containing goblet cells only, but still has fairly well developed olfactory epithelium. These conditions correspond to that of an embryo, as described by the Saracins for *Ichthyophis*, and they can be considered as neotenic features. In *Ichthyophis* the ventral indentation appears late in the development, and in *Scolecocomorphus*, although the ventral indentation is well developed, only one of the bones forming the nasal capsule takes part in the formation of the indentation, whereas in genera such as *Dermophis* and *Siphonops* it is formed by at least three of the bones forming the nasal capsule (see above).

In addition to separate nasals and premaxillaries, there are also a lacrymal and prefrontal present in the nasal capsule of *Scolecocomorphus ulugurensis*; the same was described for *S. kirkii* by Peter. Peter also stressed the weak cranial structure in *S. kirkii*: in *S. ulugurensis* the nasal bones are not only unfused as pointed out above, but they are not even firmly applied to one another, there being definite slitlike openings present between the various bones. The weak cranial structure is also evident in the structure of the palate behind the choana: here there is a large fenestra between the base of the neurocranium and the maxillo-palatine, whereas in genera such as *Boulengerula* and *Coccolia* the palate is here formed by a bony plate of the maxillo-palatine. Peter considered the weak cranial structure and the unfused condition of the bones in the nasal region as indicative of a primitive condition (op. cit., p. 10). De Villiers, on the other hand, pointed out that these features point to neoteny, a view which is now

strengthened by the meiotic condition of the nasal sacs.

The tentacle with its associated structures and the
eye of *Scolecophorus ulugurensis*.

The structure of the tentacle varies slightly from that of other genera. A short distance behind the external nasal aperture, two small grooves ^{appear} in section ventro-laterally in the skin of the head. In the subcutaneous connective tissue the tentacle sac surrounding the tentacle papilla lying free in the sac, appears. A few sections further caudad the two tentacle canals open into the tentacle sac, which then opens to the exterior between the two grooves mentioned above, thus forming the tentacle groove, in which the tentacle papilla lies as a free structure. A short distance further caudad the epithelium clothing the papilla becomes continuous with that of the skin of the head between the two grooves (Fig. 5). The tentacle sac is also indented by a mass of connective tissue with which the papilla is continuous. At the level of the anterior end of the "Hebennase" the tentacle with the tentacle fold lies laterally to the dorsally directed process of the maxillo-palatine, and the prefrontal is here confined to a dorsal position. In the connective tissue of the tentacle fold at this level, the remains of the degenerate eye appears: the eye therefore lies at the level of the anterior end ~~of the tentacle fold~~ of the "Hebennase" and indents the tentacle sac, thus occupying the position of the connective tissue in ~~the~~ the tentacle fold (Fig. 5). As the prefrontal here occupies a dorsal position, the eye is not covered by bone; it appears in ten sections, and its place in the tentacle fold is then taken by the retractor muscle surrounded by the alveoli of the orbital gland. The prefrontal then

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extends downwards and covers the tentacle structures laterally. On the disappearance of the dorsally situated maxillo-palatine process, the tentacle structures come to lie in the lateral portion of the nasal cavity, and are separated from the nasal sacs by connective tissue (Fig. 6). The orbital gland is very small in comparison with that of *Cocilia* and *Boulengerula*, and its alveoli open into the tentacle sac. The retractor muscle is large and is innervated by the abducent nerve as was pointed out by de Villiers (op. cit., p. 22). The compressor muscle of the orbital gland is not very large, but it appears far rostrad at the level of the choana and forms a complete ring around the orbital gland. Behind the choana the tentacle structures occupy a ventral position in the large medio-palatine fenestra in the palate. The two muscles are continued very far caudad into the temporal groove, where the retractor muscle inserts on the lateral side of the basal bone immediately below the ganglion of the trigeminal nerve (See Fig. 6 in de Villiers' paper).

The position of the eye in *Scolecormorphus* seems to have caused some confusion. The following is a quotation from Peter's description of *S. kirkii*: "Bei unserem Apoden sind es die Praefrontalia, welche, sich ungemein entwickelnd, den Processus frontalis des Oberkiefers zum Schwinden brachten und das Auge unter sich borgen" (op. cit., p. 6). Thanks! According to Peter therefore the eye is covered by the pre-frontal. According to de Villiers the eye in *S. ulugurensis* is covered laterally by the paraquadrate and lies on the ventral rim of the m. adductor mandibulae externus major (op. cit., p. 5). The real position of the eye in *S. ulugurensis* has been described above: it is not covered by bone and lies very far rostrad surrounded by the tentacle

sac. This was found to be the case in both available specimens. The eye has degenerated considerably, more than in *Dermophis* and *Siphonops*.

If we compare the tentacle and its structures with that of other genera described, we find that it differs slightly in structure, and that moreover the ~~maxillary~~ orbital gland and compressor muscle are not so well developed as in *Cecilia* or *Boulengerula*. In all genera studied by the author the tentacle structures are included in the maxillo-palatine and are separated from the nasal sacs. In *Scolecormorphus* the tentacle structures are not included in the maxillo-palatine or in any other bone, and in the posterior part of the nasal region they are situated in the lateral portion of the nasal cavity. Behind the choana they are not protected ventrally by bone as in these other genera, but lie in the large medio-palatine fenestra. The associated tentacle structures are therefore not greatly developed and they are not protected by bone. Peter doubted whether *Scolecormorphus* had a burrowing mode of life, and from the above description several features, such as the weak cranial structure, the unprotected eye and tentacle structures, seem to indicate that it is not a burrowing animal.. According to Loveridge both *Boulengerula* and *Scolecormorphus* live in mud and are not burrowing animals at all.

Summary.

De Villiers described the suspensorial regions and the cranial nerves of the two East African genera, *Boulengerula* and *Scolecormorphus*. As far as these features are concerned, *Boulengerula* proved to be very similar to genera such as *Dermophis* and *Siphonops* (described by the author), while *Scolecormorphus* proved to be completely different. The

nasal region, tentacle and eye of the two East African genera have been described above, and all the points of importance have been discussed, so that a brief summary of the conclusions arrived at will suffice.

In *Boulengerula* the main nasal sac with its well developed olfactory epithelium, lacks a ventral indentation, and the large "Nebennase" opens medially into the undivided posterior portion of the latter former. *Cocilia*, a very specialised genus as far as cranial nerves and suspensorial region are concerned (see author on *Cocilia*), has nasal sacs exactly similar to those of *Boulengerula*, with the exception that the olfactory epithelium in the main nasal sac is not so well developed. The two genera also possess a very degenerate eye covered laterally by the paraquadrate, well developed tentacle structures, a strong nasal capsule and a firm bony palate behind the choana. The suspensorial region and the cranial nerves of *Boulengerula* are, however, not so specialised as in *Cocilia*. *Boulengerula* can therefore be considered as a genus which, although it is not quite so specialised as the Neotropical genus *Cocilia*, shows many secondary characteristics in common with the latter genus, but absent in *Dermophis* and *Siphonops*, which are less specialised.

Scolecormorphus, on the other hand, shows marked degeneration of the eye, and other degenerate features such as the absence of the quadrate-stapedial articulation, the stapes and the m. levator quadrati (see de Villiers on *Scolecormorphus*). In its nasal region it has features common to embryos of the Gymnophiona: such as the separate nasals, premaxillaries, lacrymals and prefrontals; the "Nebennase" is confined to a medial position, and the lateral portion of the main nasal sac is a poorly developed respiratory organ, as goblet cells are almost entirely

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absent. All these features are present in the *Gymnophione* embryo described by the Sarasin, and we can reasonably assume that they point to neoteny, as was also pointed out by de Villiers.

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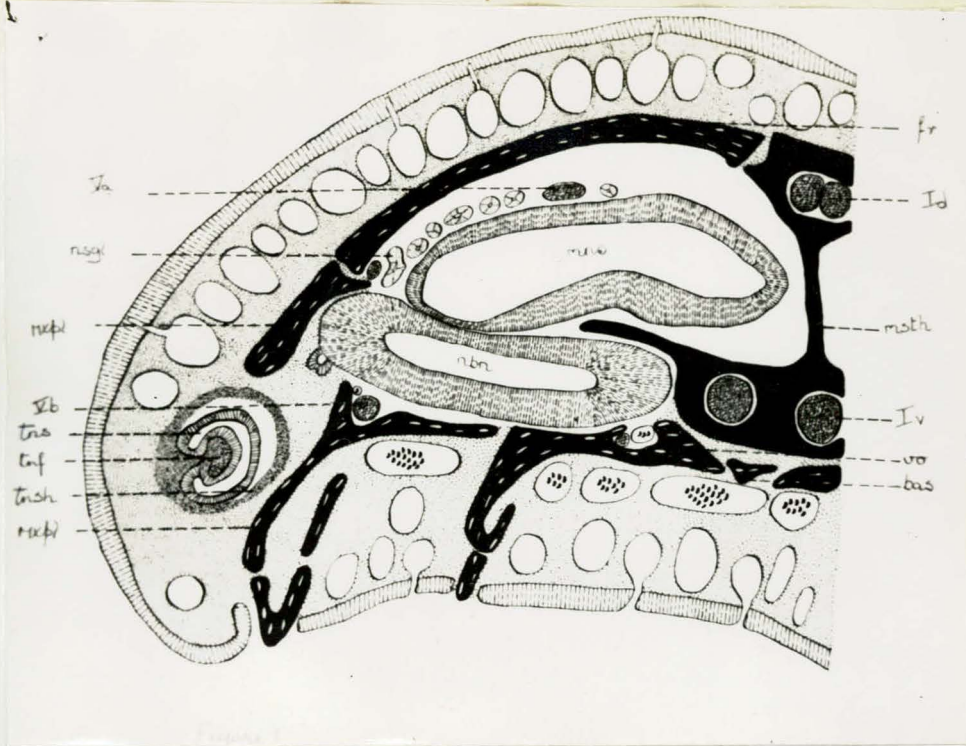


Figure 1

Figure 1. Transverse section through the nasal region of *Boulengerula boulengeri*, showing the main nasal sac and the "Nebennase".

bas os basale; fr frenal; mns main nasal sac; math mesethmoid; mxpl maxillo-palatine; nbn "Nebennase"; nsgl nasal gland; tnf tentacle fold; tas tentacle sac; tnsh tentacle sheath; vo vomax; Id dorsal olfactory nerve; Iv ventral olfactory nerve; Va ramus ophthalmicus of the trigeminal nerve; Vb r. maxillaris of the trigeminal nerve.

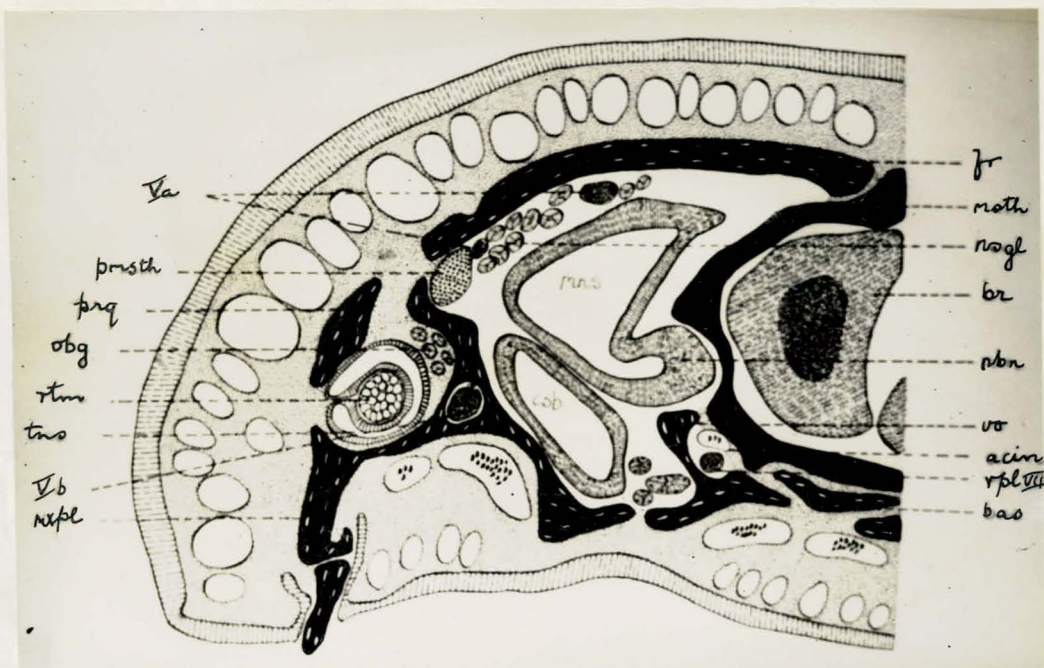


Figure 2. Transverse section through the nasal region of *Boulengerula boulengeri*, showing the "Nebennase" opening into the main nasal sac. acin arteria carotis interna; br brain; csb "Choanenschleimbeutel"; obg orbital gland; pmsth cartilaginous process of the mesethmoid; prq paraquadrate; rpl VII ramus palatinus of the facial nerve; rtm retractor muscle of the tentacle. Other abbreviations as for previous figures.

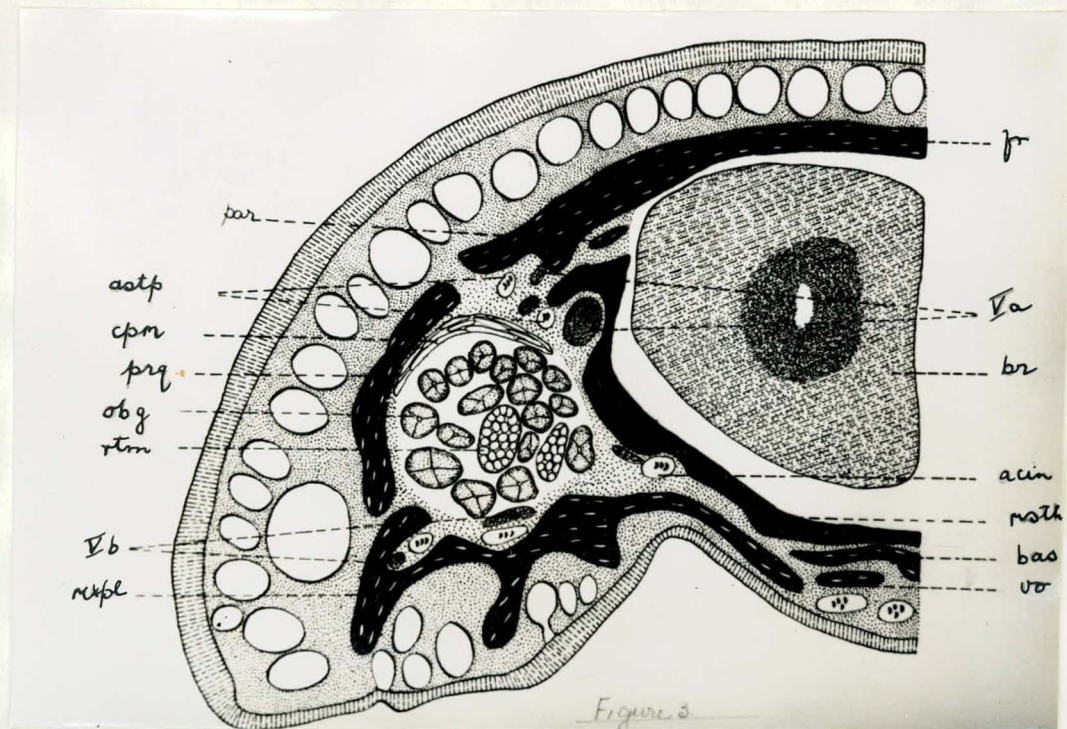


Figure 3. Transverse section through the anterior part of the orbit of *Boulengerula boulengeri*., showing the bony palate. astp arteria stapedialis; cpm compressor muscle; par parietal. Other abbreviations as for previous figures.

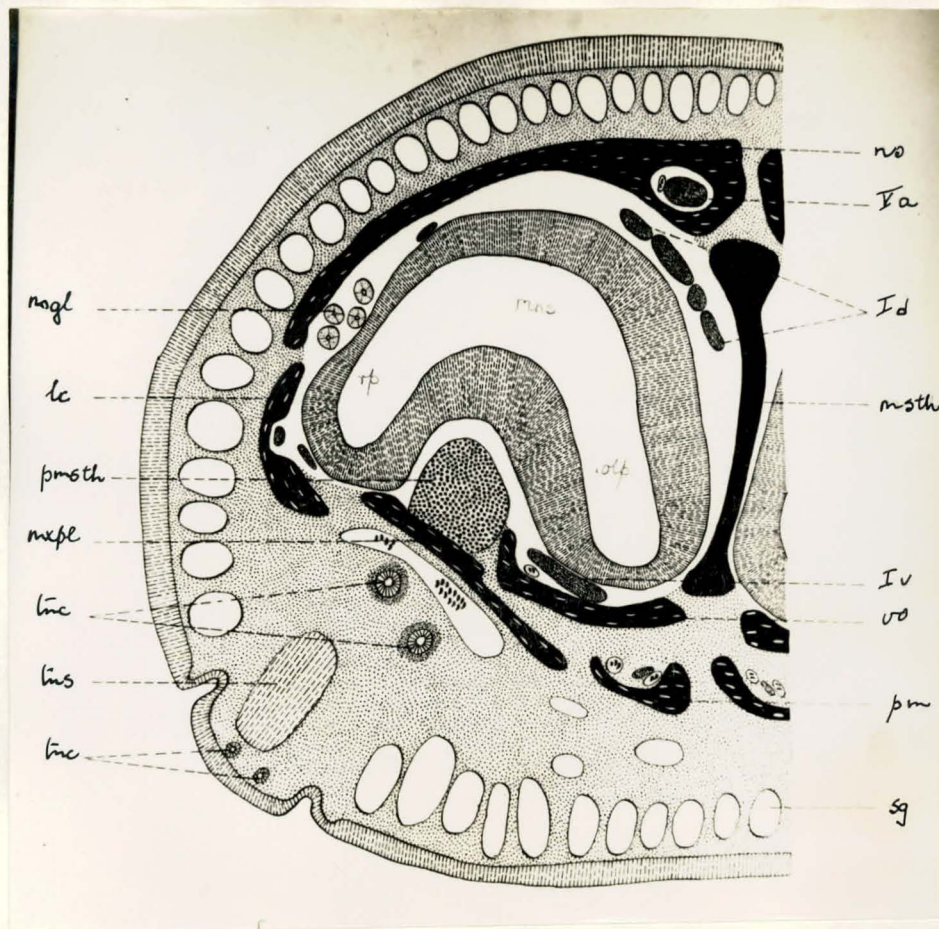


Figure 4. Transverse section through the anterior part of the nasal region of *Scolecomorphus ulugurensis*; showing the indented main nasal sac. lc lacrymal bone; ns nasal bone; olp olfactory portion of the main nasal sac; pm premaxillary; rp respiratory portion of the main nasal sac; sg skin glands; tnc tentacle canals. Other abbreviations as for previous figures.

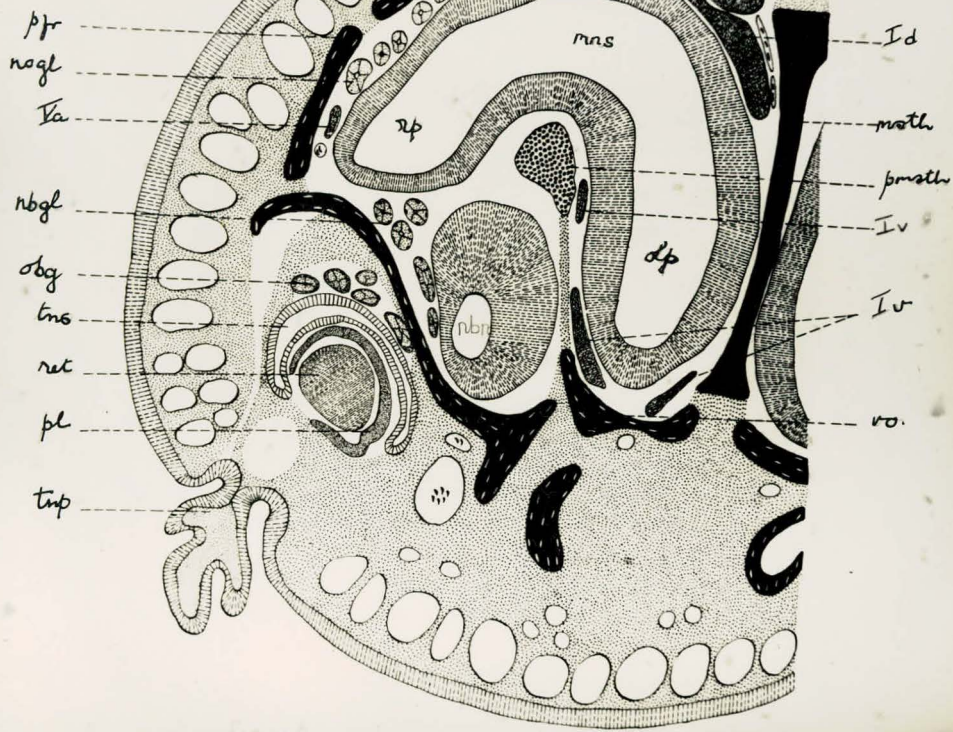


Figure 5. Transverse section through the nasal region of *Scolecomorphus ulugurensis*, showing the "Nebennase" and the tentacle structures. nbgl "Nebennase" gland; pfr prefrontal; pl pigment layer of the optic cup; ret retina; tnp tentacle papilla; Other abbreviations as for previous figures.

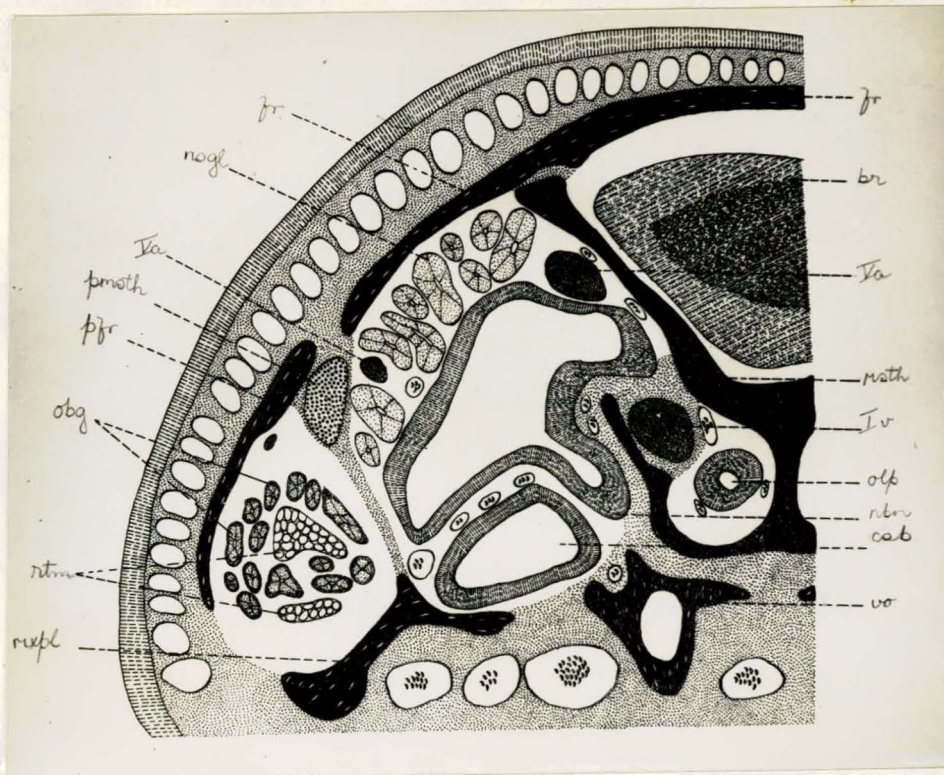


Figure 6. Transverse section through the posterior part of the nasal region of *Scolecomorphus ulugurensis*, showing the opening of the "Nebennase" into the main nasal sac. Abbreviations as for previous figures.

THE CRANIAL MORPHOLOGY OF THE WEST AFRICAN GYMNOPTERIS
PETERSII. CONTRIBUTIONS TO THE CRANIAL ANATOMY OF THE GYMNOPTERIS.

THE CRANIAL MORPHOLOGY OF THE WEST AFRICAN GYMNOPTERES: GEOTRYPETES
PETERSII. CONTRIBUTIONS TO THE CRANIAL ANATOMY OF THE GYMNOPTERES.

In this series of contributions to the cranial morphology of the Gymnopteres, three East African genera, Boulengerula, Scolecomorphus and Dermophis gregorii, as well as three South American genera, Dermophis mexicanus, Coecilia and Siphonops, have been studied. In addition to these it was thought necessary to study a West African genus, before a résumé of the various points of phylogenetic and taxonomic importance could be given. It was ⁱⁿpossible to obtain any other Oriental genera besides Ichthyophis, which has been described in great detail by the Sarasin (1880). Marcus and his students have given a very full account of the genus Hypogeophis represented in the Seychelles, so that with the inclusion of Geotrypetes, representatives from every locality have been studied.

The procedure followed in the previous contributions in describing the cranial morphology, will also be adopted in this paper. From the previous studies of the above mentioned Gymnoptere genera, it became clear that these latter could be grouped in two distinct groups. The one group, of which Dermophis and Siphonops are examples, is characterised by the possession of a fairly well developed eye, visible through the skin, the position of the tentacle groove near the eye, and a stegokrotaphic or very slightly zygotrotaphic skull. In this group the nasal sacs consist of an indented main nasal sac, and a well developed "Nebennase" opening into the lateral respiratory portion of the main nasal sac. The articulations in the skull of representatives of this group are well developed, the quadrato-stapedial articulation showing slight signs of degeneration in some of them. The second group consisting of genera such as Coecilia and Boulengerula, shows a marked

degeneration of the eye which is covered by bone; and with this degeneration the nasal sacs undergo a compensating specialisation; especially the "Nebennase" undergo a marked development. The tentacle structures also show greater development in this second group, and the articulations in the skull progress much further in the line of degeneration indicated in some of the genera of the first group.

It was rather difficult to decide to which of the two groups *Geotrypetes* belongs, as it possesses several features common to one or the other of the above groups. The eye, for example, is well developed, and visible through the skin: a feature of the one group. On the other hand, parts of the nasal sacs present a specialisation common to the second group. Taking all the features into consideration, however, it seems reasonable to group *Geotrypetes* with *Dermophis* and *Siphonops*. The various features and their significance will be discussed below.

Nieden (1913) gives the visibility of the eyes through the skin, the position of the tentacle below and behind the external narial aperture and the xygokroptaphic condition of the skull as distinguishing features of the *Geotrypetes* skull.

Material and Technique.

Two specimens of *Geotrypetes petersii* were sent to me by Mr. Loveridge of the Museum of Comparative Zoölogy at Harvard University. I desire to extend to Mr. Loveridge my very sincere thanks for putting the valuable material at my disposal. Both specimens were bulkstained in haemalum; one was counterstained on slides with eosin, the other with van Gieson's solution. Unfortunately the head of one specimen was

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was severely damaged; especially the soft parts were broken. The fixation was extremely good, and as was mentioned before, the histology of the Gymnophiona is astonishingly clear.

Own Investigations.

The nasal organ and its glands.

As was pointed out in Boulengerula, the main nasal sac can be considered as consisting of three portions: a short anterior portion with thick olfactory epithelium, a median portion constituting the greatest part of the main nasal sac and possessing a deep ventral indentation^{present} in all genera described with the exception of Boulengerula and Coecilia, and lastly a short posterior portion communicating with the buccal cavity. These three portions with their associated structures will be considered separately.

(a) The anterior portion is very short and opens to the exterior latero-dorsally at its anterior tip, thus forming the external narial aperture. This portion is circular at its anterior end, and then becomes oval and bears a short dorso-lateral indentation. The latter was found to occur in all genera studied by the author. The olfactory epithelium forming the walls is very thick, and is absent in the short lateral wall only, where respiratory epithelium is present. Numerous small glands of Bowman are present especially on the medial side of the anterior portion. Immediately behind the dorso-lateral indentation, at the junction of respiratory and olfactory epithelia, a large duct opens into the main nasal sac. The duct runs caudad for a short distance before entering the anterior portion of the nasal gland. In Siphonops and Coecilia the nasal gland possesses a similar duct, whereas the al-

veoli of the nasal gland open separately into the main nasal sac in genera such as *Dermophis* and *Boulengerula*.

(b) Behind the short anterior portion, the median portion of the main nasal sac widens and becomes more oblong in shape (Fig. 1). Through its whole length the median portion is divided into lateral and medial portions by a deep ventral indentation. In *Dermophis* and *Siphonops*, where the indentation is also present, the medial and lateral portions are of more or less equal size. In *Geotrypetes*, however, the indentation is situated more laterally, with the result that the respiratory portion is about half the size of the olfactory portion (Fig. 2), except in the posterior region where the two portions are of more equal size. The ventral indentation is formed cranio-caudad by a ridge on the ventral portion of the nasopremaxillary, the vomer and a process of the mesethmoid. The "Nebenhase" opens into the posterior part of the median portion, immediately lateral to the ventral indentation.

(c) The posterior portion of the main nasal sac is very short, even as the anterior portion. In one of the available specimens, it remains undivided and opens into the "Choanenschleimbeutel" immediately in front of the choana. In the other, however, a small medial portion separates off and becomes enclosed in a mesethmoid canal, where it ends blindly; the remaining portion opens into the "Choanenschleimbeutel" and into the buccal cavity. Whereas olfactory epithelium forms the greater part of the walls of the anterior and median portions of the main nasal sac, respiratory epithelium gradually replaces the olfactory epithelium in the posterior.

Besides the numerous glands of Bowman mentioned above, a nasal

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gland is also associated with the main nasal sac. It comprises only a few alveoli in the anterior half of the nasal cavity, where it occupies a position dorso-lateral on the main nasal sac (Figs. 1 and 2). In the posterior half of the nasal cavity, it enlarges rapidly and extends mediad over the whole nasal sac (Fig. 3). The duct leading from the gland has been described above.

The main nasal sac and the nasal gland occupy the main nasal cavity enclosed medially by the mesethmoid, ventrally by the nasopremaxillary and vomer, dorsally by the nasopremaxillary and frontal, and laterally for a short distance in the anterior region by the lateral portion of the nasopremaxillary. The dorsal olfactory nerve and a branch of the ventral olfactory nerve innervate the main nasal sac, which latter is definitely an olfactory organ with very well developed sensory epithelium.

At the anterior level of the ventral indentation, the maxillo-palatine is a small laterally situated bone. In it two canals occur; the dorsally situated one is very short and opens anteriorly on the outer surface of the maxillo-palatine. Caudad it widens rapidly and opens on the medial surface of the bone immediately behind the short lateral portion of the nasopremaxillary, with the result that the main nasal cavity and this maxillo-palatine canal are without bony separation (Fig. 2). The canal in the maxillo-palatine can be described as a "Nebennase" cavity, and corresponds to the same cavity in the maxillo-palatine of *Cocilia* (the author). The "Nebennase" gland, a particularly large structure in *Geotrypetes*, fills the anterior portion of the "Nebennase" cavity. In the dorso-lateral corner of the latter, the

"Nebennase" appears in section as a small circular tube; into its anterior end the two tentacle canals open. The "Nebennase" is therefore separated from the main nasal sac by the large "Nebennase" gland (Fig. 2). The latter gradually becomes smaller as the "Nebennase" enlarges until it is finally reduced to a few alveoli situated between the two nasal sacs. Although the bone separating the anterior elongation of the "Nebennase" cavity and the main nasal cavity disappears from section very far posteriorly, the two cavities do not actually become confluent, as a thick connective tissue ^{mem}brane remains between them (Fig. 2). The maxillo-palatine alone forms the walls around the "Nebennase" cavity.

For the greater part of its length, the "Nebennase" is a laterally situated tube, circular in cross-section; very near its posterior end it extends mediod ventral to the respiratory portion of the main nasal sac, and at the same level the "Nebennase" cavity becomes very much reduced and the maxillo-palatine then forms the lateral wall of the main nasal cavity. The "Nebennase" extends mediod as far as the ventral indentation and it opens into the main nasal sac immediately lateral to the mesethmoid process forming the ventral indentation (Fig. 5). At this level the olfactory epithelium in the main nasal sac becomes very thin, and the respiratory epithelium begins spreading further mediod especially in the dorsal wall of the main nasal sac. A large branch of the ventral olfactory nerve innervates the "Nebennase", and remains separate from the other branch of the same nerve innervating the main nasal sac for a very considerable distance. In Fig. 3 the two branches have joined.

Immediately behind the "Nebennase" the "Chancen-schleimbeutel" appears in section lateral to the main nasal sac. It is surrounded here

by the connective tissue separating the main nasal sac and the "Nebennase" (Fig. 5). The "Choanenschleimbeutel" enlarges rapidly to form a thin-walled sac which opens into the posterior part of the main nasal sac, and the two sacs have a common opening into the buccal cavity. The alveoli of the "Nebennase" gland do not open into the "Choanenschleimbeutel" as in Siphonops and Dermophis; the gland actually ends caudad a little way in front of the "Choanenschleimbeutel". A few of the alveoli of the "Nebennase" gland could be seen opening into the anterior portion of the "Nebennase". Both the "Nebennase" and its gland are well-developed structures, and are situated in a separate cavity surrounded by the maxillo-palatine, and separated from the main nasal cavity by a thick connective tissue membrane.

In comparing the data given above with those available for other genera, the following points are important:

- (a) The main nasal sac of *Geotrypetes* is very similar to that of *Dermophis* and *Siphonops*, with a clearly defined ventral indentation. The latter lies more laterad than in the other two genera, so that a larger portion of the main nasal sac is clothed with olfactory epithelium several layers in thickness. The main nasal sac is therefore a well-developed olfactory organ.
- (b) The nasal gland is present as in all genera described, and it has a long duct opening into the anterior portion of the main nasal sac as in *Siphonops* and *Coeclilia*.
- (c) The "Nebennase" is an olfactory organ with very thick olfactory epithelium. It opens into the lateral respiratory portion of the main nasal sac, lateral to the ventral indentation, as in genera such

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as *Dermophis*, *Siphonops* and *Ichthyophis* where the ventral indentation is present. The "Nebennase" gland is a much bigger structure than in any other genus studied by the author. Some of its alveoli open into the "Nebennase".

(d) The "Nebennase" and its gland are situated in a wide cavity in the maxillo-palatine, and are separated throughout from the main nasal cavity by means of thick connective tissue. The branch of the ventral olfactory nerve innervating the "Nebennase" is also separated from the rest of the nerve for a very considerable distance. In *Cocilia* the separation of the "Nebennase", its gland and the nerve innervating it, from the rest of the nasal structures, has proceeded further than in *Geotrypetes*, and this condition in *Cocilia* was interpreted as indicative of specialisation of the "Nebennase"; the only sense organ. In *Cocilia* the main nasal sac undergoes degeneration: the ventral indentation is absent and the olfactory epithelium is very poorly developed. In *Geotrypetes*, however, although the "Nebennase" shows the same specialisation as in *Cocilia*, the main nasal sac does not show a corresponding degeneration, but remains a well developed olfactory organ as in *Dermophis* and *Siphonops*, where the "Nebennase" and its gland do not undergo a marked development.

(e) The "Choanenschleimbeutel" has the same relations to the posterior part of the main nasal sac and the buccal cavity as in the other genera mentioned above.

(f) In *Dermophis*, *Siphonops* and *Ichthyophis*, where the main nasal sac is an important olfactory organ, the medial portion of the main nasal sac separates off from the lateral portion in front of the choana. In *Cocilia* and *Boulengerula* the main nasal sac remains undi-

vided and opens into the buccal cavity. In one specimen of *Geotrypetes*, the main nasal sac remains undivided and the olfactory epithelium in the posterior portion is replaced by respiratory epithelium. In the other specimen, only a portion of the olfactory portion separates off, in the remaining olfactory portion respiratory epithelium replaces the olfactory epithelium. And this condition in the posterior part of the main nasal sac is the only sign of a possible decrease of olfactory importance of the main nasal sac.

The nasal capsule of *Geotrypetes*.

The bones in the nasal capsule of *Geotrypetes* fit firmly together. As in all the genera investigated by the author, with the exception of *Scolecormorphus*, the nasopremaxillaries, maxillo-palatines, the vomers and the mesethmoid are the only bones present in the nasal region. The nasopremaxillary forms a complete ring around the anterior portion of the main nasal sac, and is incomplete on the lateral side at the external nares only. Behind the anterior portion of the main nasal sac, the medial portion of the nasopremaxillary disappears from section, and the internasal septum is then formed by the mesethmoid alone. The latter is continued rostrad to the anterior end of the nasal capsule as a cartilaginous rod between the two nasopremaxillaries. The ventral portion of the nasopremaxillary forms the whole of the floor of the nasal capsule for a short distance only, as the vomer, which is continued very far rostrad as a narrow process below the cartilaginous process of the mesethmoid, appears medially on the ventral surface, and the nasopremaxillary is then reduced laterad. The vomer forms the median half of the floor of the nasal capsule up to the choana. On the ventral por-

tion of the nasopremaxillary a ridge forming the anterior portion of the ventral indentation is present, and behind this ridge, the vomer forms the indentation. The lateral portion of the floor of the nasal capsule is formed by the nasopremaxillary as far as the anterior end of the "Nebennase" and is then replaced by the maxillo-palatine (Fig. 2).

Very far rostrad, in the region of the anterior portion of the main nasal sac, the maxillo-palatine appears in section as a small process situated above the tentacle and tentacle canals. The bone enlarges rapidly, and in Fig. 1 two deep grooves can be seen on its lateral side. The dorsally situated groove has been described in detail above; it becomes a canal in which the "Nebennase" and its gland are situated. This canal continues caudad almost to the posterior end of the nasal region. In the more ventrally situated groove the tentacle and tentacle canals are located (Fig. 1). This groove also becomes converted into a canal which runs ventro-laterally through the whole length of the nasal region and it contains the various structures associated with the tentacle (Figs. 2 and 3). Behind the "Nebennase" the maxillo-palatine forms the lateral wall of the main nasal cavity; anterior to that it forms the walls around the "Nebennase" and its gland. The roof of the main nasal cavity is formed by the dorsal portion of the nasopremaxillary (Fig. 2). At the level of the anterior end of the "Nebennase" the frontal appears in section between the nasopremaxillary and the maxillo-palatine (Fig. 2); it extends mediad below the former and forms the roof of the nasal capsule behind the dorsal portion of the nasopremaxillary (Fig. 3).

The vomer, as mentioned above, extends very far rostrad, and forms the medial half of the floor of the nasal capsule; in it a long

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canal is present. The r. palatinus VII and the arteria carotis interna run caudad in this canal, and in the anterior part of it a branch of the ramus ophthalmicus V is present (Figs. 1 and 2).

The mesethmoid is completely ossified, except for a short anterior process lying between the nasopremaxillaries. As far as the anterior end of the "Nebennase" the mesethmoid is a simple perpendicular lamina forming the internasal septum. At the level of the anterior end of the "Nebennase" it bears a ventral process which is directed laterad. At its lateral end this process turns upwards and forms the ventral indentation in the main nasal sac behind the vomer (Fig. 3). The ventral olfactory nerve becomes enclosed in a canal in the dorsally directed portion of this process (Fig. 3). At the level of the posterior end of the "Nebennase" the dorsal tip of the perpendicular lamina enlarges to form a broad plate appearing on the dorsal surface between the frontals (Fig. 3), and the two dorsal olfactory nerves are located in two canals in the dorsal portion of the mesethmoid.

Behind the "Nebennase", the "Nebennase" cavity disappears completely and the maxillo-palatine then forms the lateral wall of the main nasal cavity. With the decrease in size of the "Nebennase" cavity, the canal containing the tentacle structures enlarges and at the same time shifts more dorsad (Figs. 2 and 3). Immediately in front of the choana, the maxillo-palatine extends further mediad on the floor of the nasal cavity, and the vomer becomes correspondingly narrower; these two bones surround the choana. The vomer ends caudad immediately behind the choana, but the maxillo-palatine extends even further mediad behind the choana and reaches the basal bone which has already appeared in sec-

tion, to form a bony floor for the anterior part of the orbit (Fig. 4). At the level of the posterior part of the "Nebennase" the canal containing the tentacle structures opens laterally (Fig. 3), and behind the choana the remaining lateral portion of the maxillo-palatine also shortens and disappears from section, so that at this level the maxillo-palatine is reduced to a ventrally situated bony plate.

In the above description of the nasal capsule of *Geotrypetes*, the following points should be stressed:

- (a) There are two separate nasal cavities: a main nasal cavity and a "Nebennase" cavity in the maxillo-palatine.
- (b) Besides the "Nebennase" cavity in the maxillo-palatine, a canal containing the tentacle structures is also present in the same bone.
- (c) The vomer is a fairly broad bone, and ends caudad immediately behind the choana. The vomerine canal, characteristic of all the other genera described, is also present.
- (d) The mesethmoid appears on the dorsal surface between the two frontals, and bears a ventral process forming the posterior part of the ventral indentation.
- (e) Behind the choana the maxillo-palatine extends mediad and forms a bony floor for the anterior portion of the orbit. The lateral portion of the bone is reduced completely behind the choana, and a large orbital opening is therefore formed.

The tentacle, its associated structures and the eye.

The tentacle groove is situated ventro-laterally immediately behind the external nares. The tentacle papilla lies free in the ten-

tacle groove, and the two tentacle ^{canals} grooves open into the latter. The epithelial tentacle sac opens into the tentacle groove, and in the former the tentacle papilla appears as a structure which is free as far as the anterior end of the "Nebennase". The epithelium clothing the papilla then becomes continuous with the an epithelial fold in the tentacle sac (Fig. 3). In all other genera studied by the author this happens immediately behind the tentacle groove, and *Geotrypetes* is the only one so far investigated where the papilla lies free in the tentacle sac (Figs. 1 and 2). The epithelial tentacle sac is surrounded by a connective tissue sheath (Figs. 1, 2 and 3).

In the nasal region the tentacle sac and papilla are situated in a canal in the maxillo-palatine, as described above. Branches of the r. maxillaris V (Vb) run rostrad in this canal, and several small ramuli pierce the maxillo-palatine laterally to innervate the skin on the lateral side of the head (Fig. 3). A short distance in front of the choana, the tentacle sac becomes divided into two large ducts (Fig. 3), which in turn divide into several smaller ones entering the orbital gland. Some of the ducts scattered amongst the alveoli of the latter can be seen in Fig. 4. Immediately behind the choana the connective tissue in the tentacle papilla is replaced by the retractor muscle, a comparatively large structure, and the alveoli of the orbital gland appear grouped around this muscle (Fig. 4). These tentacle structures are continued into the orbit where they lie above the broad ventral portion of the maxillo-palatine. The orbit, as was mentioned above, has a large orbital opening (Fig. 4). In the ocular cavity the compressor muscle appears on the medial side of the orbital gland and the eye on the lateral side. The latter consists of a well-developed optic cup with

a lens, and the connective tissue covering the eye is fairly thin, so that is clearly visible through the skin (Fig. 4). The eye is no here covered by bone. The paraquadrate/ does appear in section as a small process above the eye, but it extends downwards behind the latter only. The orbital gland never attains to large proportions and decreases in size as the compressor muscle gradually extends round the retractor muscle. In Fig. 5 it can be seen surrounding the retractor on three sides; the latter is well-developed, and the abducent nerve innervating it could be traced throughout the entire length of the muscle. These two muscles extend backwards through the orbit into the temporal groove, and the compressor ends caudad just in front of the quadrato-basal articulation, while the retractor extends still further caudad and inserts on the basal bone forming the lateral wall of the neurocranium immediately above the basipterygoid process of the basal bone.

In the posterior part of the orbit the maxillo-palatine, which forms a complete floor for the anterior portion of the orbit, becomes shortened from its medial side, and a large medio-palatine fenestra is formed in the palate. In this fenestra the tentacle structures can be seen (Fig. 5). The m. adductor mandibulae externus major extends into the orbit, where it arises from the ventral surface of the frontal, and it covers the tentacle structures laterally.

The tentacle and the eye of *Geotrypetes* therefore show the following interesting features:

(a) The tentacle papilla lies as a free structure inside the tentacle sac for a very considerable distance before its epithelium becomes continuous with the epithelium of the latter.

(b) The orbital gland and the compressor muscle are comparative-

ly small structures when compared with those of *Boulengerula* and *Cecilia*. The retractor muscle, on the other hand, is a large structure and its innervation was very clear.

(c) Both muscles are continued much further caudad than in other genera studied by me. The retractor muscle reaches caudad beyond the quadrato-basal articulation.

(d) The eye is represented by a well-developed optic cup and a lens, and lies very close to the surface with only a very thin layer of connective tissue covering it. The orbital opening is much larger than in genera such as *Dermophis* and *Siphonops* where the eye is also fairly well-developed and visible through the skin.

The cranial bones and muscles behind the nasal region.

Behind the nasal region the mesethmoid forms the floor and side walls of the neurocranium, with the frontal forming the roof. In the posterior part of the orbital region the basal bone replaces the mesethmoid on the floor, and at the sides the mesethmoid becomes reduced to two cartilaginous bars: the dorsally situated taenia marginalis and the ventrally situated trabecula. Between them the latter two the large foramen in the side wall of the neurocranium is closed by means of a connective tissue membrane. This foramen extends well into the temporal region (Fig. 5), before the basal bone which has incorporated the trabecula, extends upwards to incorporate the taenia marginalis. The r. ophthalmicus V (Va) and the tentacle muscles are pressed against the membranous side wall (Fig. 5). In the temporal region one large foramen is present in the side wall of the neurocranium; through it the roots of the trigeminal nerve leave the cranial cavity.

the maxillo-palatine, as was mentioned above, shortens laterad in the orbital region, so that a large medio-palatine fenestra is formed between it and the base of the neurocranium. Slightly further caudad the maxillo-palatine also shortens from its lateral side and a basitemporal fenestra is formed between it and the paraquadrates, which has now extended downward from its position above the eye (Fig. 5). The maxillo-palatine is therefore reduced to a narrow process, and above it the p. pterygoideus palatoquadrati appears in section (Fig. 5). The paraquadrate extends downward behind the eye and forms a long laterally situated bony squame. Between it and the parietal a large fossa is present in which the m. adductor mandibulae externus major is intercalated; the skull is therefore zygokrotaphic (Figs. 5 and 6).

The m. adductor mandibulae externus major fills the lateral half of the temporal groove completely and is particularly large. It arises cranio-caudad from the frontal and parietal and passes through the basitemporal fenestra to insert on the inner surface of the lower jaw (Figs. 5 and 6). In the posterior third of the temporal groove the m. levator quadrati arises from the lateral wall of the neurocranium and inserts on the dorsal surface of the p. pterygoideus palatoquadrati where the latter forms the quadrato-basal articulation with a laterally directed process of the basal bone (Fig. 6). The m. levator quadrati is covered laterally by the m. adductor mandibulae externus major and separated from it by the anterior maxillo-mandibular (Vb+c) ganglion, and it separates the anterior portion of the ganglion of Vb+c from the posterior portion of the ophthalmic (Va) ganglion. The latter extends rostrad beyond the quadrato-basal articulation. At the same level as the m. levator quadrati, the m. pterygoideus arises from the ventral surface of

the *p. pterygoideus palatoquadrati*, immediately behind the maxillo-palatine (Fig. 5), and it inserts on the medial surface of the lower jaw. The *m. cephalo-dorso-maxillaris* extends far rostrad and arises from the outer surface of the paraquadrate (Figs. 5 and 6).

The quadrate-basal articulation is well developed with a large synovial cavity and strong synovial membranes (Fig. 6). At the level of the articulation, the *p. ascendens palatoquadrati* appears in section against the inner surface of the paraquadrate (Fig. 6); it too is separated from the side wall of the neurocranium by the large temporal fossa. In the posterior portion of the temporal groove the *m. adductor mandibulae externus minor* arises from the inner surface of the *p. ascendens palatoquadrati* and passes through the posterior extension of the basitemporal fenestra to insert on the inner surface of the lower jaw immediately behind the insertion of the *m. adductor mandibulae externus major*. The *m. adductor mandibulae externus minor* is a comparatively large muscle in *Geotrypetes* (Fig. 6). The *r. mandibularis V (Vc)* passes downward towards the lower jaw against the medial border of the muscle.

The quadrate-cranial passage formed between the ~~xxxxxxxxxxxx~~ palatoquadrate and the side wall of the neurocranium, is ^every short and widely open on the dorsal side as a result of the agkretaphic condition of the skull and the failure of the *p. ascendens palatoquadrati* to meet the parietal. The passage is filled with large bloodvessels and the posterior elongation of the ganglion of *Vb+c*. The jaw articulation is formed immediately behind the quadrate-basal articulation. The palatoquadrate dwindles caudad to a short *p. columellaris palatoquadrati*, which is cartilaginous at its posterior tip. This latter process reaches

the anterior cartilaginous end of the stapediai style, and a certain amount of fusion takes place between them; a synovial cavity is, however, still present. The quadrato-stapedial articulation is therefore in the process of being lost, even as in *Dermophis* and *Boulengerula*.

The stapediai footplate extends rostrad beyond the otic capsule and the quadrato-stapedial articulation, and is here fused to the side wall of the neurocranium by means of cartilage (Fig. 7). Immediately above this anterior elongation of the stapediai footplate, the foramen for the root of the facial nerve is situated, and below it in the floor of the neurocranium is a large foramen through which the *arteria carotis interna* enters the cranial cavity. The latter is the only foramen in the basis cranii behind the nasal capsule. The stapediai style joins the stapediai footplate near the anterior end of the latter, which then fits into the fenestra ovalis, a long foramen in the lateral wall of the otic capsule. The latter is not a separate structure but has coalesced with the basal bone. In the otic region the basal bone also extends on to the dorsal surface of the neurocranium; in the occipital region it is the only bone present, and it forms the two occipital condyles. In front of each condyle, a large jugular foramen is present, and through it a large vein as well as the roots of the ninth and tenth cranial nerves leave the cranial cavity. In the otic and occipital regions the *m. cephalo-dorso-maxillaris* is a very large structure, and the *m. pterygoideus* also enlarges considerably.

The following points are of particular interest in the above description:

(a) The skull is distinctly *oxyekrotaphic*, the large temporal fossa stretching over the whole of the temporal region.

(b) The quadrato-basal articulation and the *m. levator quadrati* and the *m. pterygoideus*, the two muscles associated with it, are well developed, as in all genera studied by the author with the exception of *Cocilia*, where both the articulation and the *m. levator quadrati* itself are degenerating.

(c) The quadrato-stapedial articulation is degenerating even as in *Dermophis* and *Cocilia*, but has not reached such an advanced stage of degeneration as in the latter. Slight movement between the stapes and the *p. columellaris* may be considered possible.

(d) As in *Dermophis*, *Cocilia* and *Siphonops*, the stapedial footplate overlaps the rim of the fenestra ovalis and is connected with the side wall of the neurocranium by means of cartilage. Movement of the stapedial footplate in the fenestra ovalis is therefore impossible. The *p. ascendens palatoquadrati* is firmly connected with the paraquadratus by means of dense connective tissue; movement, if any, in the quadrato-stapedial articulation is very slight, so that the well-developed quadrato-basal articulation seems to be superfluous. As was pointed out before, *Cocilia* is the only genus studied, in which the quadrato-basal articulation is degenerating, probably as a result of the loss of the quadrato-stapedial articulation and the fusion of the stapedial footplate with the side wall of the neurocranium.

(e) The muscles in the temporal region are the same as those of *Dermophis* and *Siphonops*. The *m. adductor mandibulae externus minor* is bigger than in any other genus studied by me, and the *m. pseudotemporalis* is absent as in *Dermophis*, *Boulengerula* and *Scolecophorus*.

(f) The quadrato-cranial passage is very short, and the quadrato-basal articulation is situated further caudad than in other genera studied by me, with the result that the ganglion of *Va* extends rostrad

far beyond the articulation.

(g) The palate is very similar to that of genera such as *Dermophis*, *Siphonops* and *Coccolia*. As in these latter, two large fenestrae separated by the posterior elongation of the maxillo-palatine, are present. And behind the choana the maxillo-palatine forms a complete floor for the anterior portion of the orbit. *Scolecocomorphus* is the only genus so far investigated, in which the maxillo-palatine remains a small laterally situated process behind the choana.

The cranial nerves and their ganglia in Geotrypetes.

Reconstructions of the cranial nerves of both specimens were made, and only a few differences were noted between them. The fifth and seventh cranial nerves with their ganglia represent such the same picture as in *Dermophis* and *Siphonops*, especially the latter.

The facial nerve has three important branches: the r. hyomandibularis VII running caudad against the otic capsule; the chorda tympani running rostrad in a canal in the lower jaw, and the r. palatinus VII running rostrad in a ventral position against the neurocranium. These three branches are present in *Dermophis*, *Siphonops* and *Coccolia* (the author), but in both *Boulengerula* and *Scolecocomorphus* the chorda tympani is absent and in *Boulengerula* the r. palatinus VII is absent as well. The foramen for the root of the facial nerve is situated in front of the otic capsule immediately above the anterior elongation of the stapedial footplate (Fig. 7). The foramen occupies the same position in *Dermophis* and *Siphonops*, but in *Coccolia* the trigeminal and facial nerve roots share a large prootic foramen. The facial nerve root enters the posterior end of the geniculate ganglion, which extends into the quadrate-cranial

passage where it is surrounded by large venous networks. In the quadrato-cranial passage the ganglion of Vb+c appears in section lateral to the geniculate ganglion in both specimens; in one of them the two ganglia then fuse to form one large ganglionic mass; in the other specimen although they are very closely applied, there is only connective tissue connection between them and no actual fusion. In *Siphonops* the geniculate ganglion and the ganglion of Vb+c are also continuous.

The r. hyomandibularis VII leaves the geniculate ganglion at its posterior end and runs caudad above the stapedial style accompanied by the a. stapedialis and the v. jugularis interna. Immediately behind the stapedial style it gives off a small twig innervating the m. cephalo-dorso-maxillaris. Slightly further caudad the nerve divides into two branches: the medially situated of the two branches runs further caudad without dividing and its terminations could not be traced; the laterally situated branch gives off the chorda tympani as well as another branch into the m. cephalo-dorso-maxillaris. The latter therefore receives two branches from the r. hyomandibularis VII, and this was found to be the case in both specimens. The chorda tympani runs laterad against the ventral rim of the m. cephalo-dorso-maxillaris and at the level of the quadrato-stapedial articulation it enters a canal in the lower jaw, from the medial side of the latter. A small branch of the a. stapedialis accompanies the chorda tympani later and runs forwards with the latter in the lower jaw (Fig. 7). The further course of the chorda tympani will be described below with the trigeminal nerve.

The r. palatinus VII runs forwards in the geniculate ganglion and then in the fused geniculate and maxillo-mandibular ganglionic mass, and leaves the latter when the root of Vb+c enters it. In the other

specimen in which the two ganglia do not fuse, the r. palatinus VII does not enter the ganglion of Vb+c, but runs forwards ventral to it, and in both specimens it lies pressed against the dorsal surface of the basipterygoid process of the basal bone (Fig. 6).

The ganglion of Vb+c is large and extends from the quadrato-cranial passage into the temporal groove. The anterior tip of the ganglion is sectioned in Fig. 6. One long foramen in the side wall of the neurocranium serves the passage of both the Va and Vb+c portions of the trigeminal nerve root. The root of Vb+c passes through the posterior portion of ^{the} foramen, and the n. abducens slips through with it, and then runs rostrad together with the r. palatinus VII. (Fig. 6). At the level at which the root of Vb+c enters the ganglion of Vb+c, the latter is surrounded by large venous channels, dorsal to it the m. adductor mandibulae externus major is situated, and lateral to it the m. adductor mandibulae externus minor. Vc leaves the ganglion of Vb+c on its ventral side, and at the same level a small branch of Vb leaves the ganglion on its dorsal side. The latter branch passes upwards against the medial surface of the m. adductor mandibulae externus major (Fig. 6), and innervates the skin on the dorsal side of the head. Vc passes downwards against the medial surface of the m. adductor mandibulae externus minor (Fig. 6), and on its way to the lower jaw gives off two branches, a lateral one innervating the m. adductor mandibulae externus minor, and a medial branch innervating the m. pterygoideus (Fig. 6). Upon entering the lower jaw, Vc divides into three branches, one of which passes through the lower jaw and innervates the m. int. mandibularis as well as the skin on the ventral side of the head. The other two branches remain in the lower jaw. The medially situated of these two forms an anastomosis

with the chorda tympani and runs above Meckel's cartilage for a considerable distance before branching. It then gives off several branches innervating the teeth of the lower jaw as well as a few small twigs innervating the mucous membrane of the tongue. Immediately in front of the mental symphysis it divides into small twigs innervating the skin. The laterally situated branch of Vc runs rostrad in the lower jaw and sends numerous ramuli into the skin and a few to the teeth of the lower jaw. This branch runs forwards to the mental symphysis where it innervates the skin. Vc is therefore a mixed nerve, with sensory fibres predominating. The motor branches to the m. adductor mandibulae externus minor and the m. pterygoideus are very small.

At the level where Vc leaves the ganglion of Vb+c, the m. levator quadrati appears in section on the medial side of the latter. The muscle arises from the basal bone above the anterior elongation of the large foramen for the trigeminal nerve roots. The ganglion of Va appears in section on the ventral side of the m. levator quadrati, and the latter therefore separates the anterior portion of the ganglion of Vb+c from the ganglion of Va. The two trigeminal ganglia are therefore in no way connected. The root of Va passes through the anterior portion of the foramen pro nervo trigemino (Fig. 6).

The n. abducens and the r. palatinus VII both enter the ganglion of Va and run rostrad in it for a short distance. The n. abducens then leaves the ganglion and enters the retractor muscle, which as was stated above, continues caudad beyond the quadrate-basal articulation where it lies ventral to the ganglion of Va. The r. palatinus VII leaves the ganglion and runs forwards accompanied by the a. carotis interna. The ganglion of Va reaches rostrad beyond the quadrate-basal articulation, and

Va emerging from the anterior end of the ganglion then lies pressed against the side wall of the neurocranium (Fig. 5). Throughout the temporal region and the posterior part of the orbit Va remains an unbranched nerve.

Vb, on the other hand, branches several times on its way through the temporal groove and the orbit. After emerging from its ganglion, Vb runs forwards between the m. levator quadrati and the m. adductor mandibulae externus major, immediately above the anterior elongation of the p. pyriformis palatoquadrati. In front of the m. levator quadrati, the compressor and retractor muscles of the tentacle lie medial to Vb, while the r. palatinus VII lies ventral to these muscles in the medio-palatine fenestra (Fig. 5). Vb here gives off a tiny branch into the m. adductor mandibulae externus major, and another bigger branch running mediad below the compressor muscle. The latter branch divides into two twigs, one entering the compressor muscle, and the other forming an anastomosis with the r. palatinus VII. The nerve in the compressor muscle can be seen in Fig. 5. The r. palatinus VII gives off a small branch running laterad and forming an anastomosis with the main trunk of Vb, before it fuses with the above mentioned branch of Vb. These two anastomoses between Vb and the r. palatinus VII could be demonstrated in both specimens, but only in one could the innervation of the compressor muscle be demonstrated.

From its position in the medio-palatine fenestra the r. palatinus VII sends a few branches into the epithelium of the buccal roof. In the anterior part of the orbit the nerve shifts more mediad (Fig. 4), and in the choanal region it runs between the vomer and the mesethmoid. It then enters a long canal in the vomer and is here accompanied by the a. carotis interna and a small branch of the v. jugularis interna. The

r. palatinus VII leaves the vomerine canal near the anterior end of the buccal cavity and divides into several ramuli innervating the buccal epithelium.

Vb runs through the temporal groove just above the p. pterygoideus palatoquadrati. In the orbit it shifts further laterad, and divides into three branches, one of which splits up into several small ramuli piercing the maxillo-palatine and the paraquadrata and innervating the skin on the lateral side of the head. The other two branches run rostrad above the maxillo-palatine (Fig. 4). The medially situated of the two branches sends small twigs through the ventral portion of the maxillo-palatine into the teeth, and at the level of the posterior end of the "Nebennase" it enters a canal in the maxillo-palatine (Fig. 3). The laterally situated branch sends tiny ramuli into the skin on the lateral side of the head, and it continually shifts more laterad, so that in the nasal region it lies lateral to the tentacle structures in the large canal in the maxillo-palatine (Figs. 2 and 3). From here it sends its final branches into the skin. In Fig. 2 the medial branch can be seen also inside the tentacle cavity in the maxillo-palatine, and it runs rostrad on the medial side of the tentacle structures. It sends six branches into the skin surrounding the tentacle groove, and the remaining fibres are distributed to the skin on the ventral and lateral sides of the head snout. Vb is therefore a mixed nerve, but with only a few visceromotor fibres forming two branches, one into the m. adductor mandibulae externus major and the other to the compressor muscle. The sensory fibres of Vb mainly innervate the skin on the lateral sides of the head.

Va, as was stated above, remains unbranched until it reaches the anterior end of the orbit, where it is situated in a deep groove on the

lateral side of the mesethmoid (Fig. 4). Here it gives off a branch running laterad and dividing into four smaller ramuli, three of which innervate the skin on the dorsol side of the head, and the fourth can be traced far rostrad and innervates the connective tissue tentacle sheath. In the nasal region, Va runs against the mesethmoid in the nasal cavity, in the posterior part of which it gives off a branch running far laterad (Fig. 3) and then rostrad between the nasal gland and the "Nebennase" gland (Fig. 2); this branch then divides into several small twigs piercing the maxillo-palatine dorsally and innervating the skin on the dorsal side. The main stem of Va, however, remains in a medial position against the internasal septum (Fig. 3). At the level of the anterior end of the "Nebennase" the dorsal olfactory nerve leaves its canal in the dorsal portion of the mesethmoid and for a short distance Va and Id form one nerve trunk (Fig. 2). The fibres of the two nerves are histologically completely different and easily distinguishable from each other. From the common nerve trunk, Va gives off a branch running down against the internasal septum (Fig. 2), and entering the vomerine canal which was previously occupied by the r. palatinus VII (Fig. 1). Va then separates from Id and enters a canal in the dorsal portion of the nasopremaxillary (Fig. 1), from where it sends several branchlets into the skin on the dorsal side of the head. Near the tip of the snout a long canal forms in the medial portion of the nasopremaxillary and Va extends downwards in it and sends branches to the skin of the snout. The branch of Va in the vomerine canal innervates the skin on the ventral side of the snout. Va is therefore a sensory nerve, innervating especially the skin on the dorsal side of the head and the skin of the snout. It forms a temporary anastomosis with the dorsal olfactory nerve.

The ganglion of the acoustic nerve lies pressed against the inner wall of the otic capsule, and from it three branches enter the labyrinth cavity, through three foramina. Two of the latter are situated ventrally whereas the third occupies a more dorsal position. There is no connection whatsoever between the roots of the acoustic and facial nerves.

The distribution of the cranial nerves of *Geotrypetes* is almost identical with that of *Siphonops*, and very similar to that of *Dermophis*. The two ganglia of the trigeminal nerve are completely separate in these three genera, and the geniculate ganglion and the ganglion of Vb+c are continuous in *Siphonops* and *Geotrypetes*. The facial nerve root has its own foramen immediately anterior to the otic capsule, even as in *Dermophis* and *Siphonops*, but only one foramen for the two portions of the trigeminal nerve root is present in *Geotrypetes*, whereas two separate foramina are present in *Dermophis* and *Siphonops*. The roots of the trigeminal, facial and acoustic nerves are separate in these three genera.

The anastomosis between the chorda tympani and a branch of Vc, is present as in *Dermophis*, *Siphonops* and *Cocilia*, as well as the double anastomosis between the r. palatinus VII and Vb even as in the latter two genera. In *Siphonops* the branch of Va running down against the internal septum, forms a temporary anastomosis with Id, Iv and a permanent anastomosis with a branch of Vb. In *Geotrypetes* this branch of Va is also present, but it forms no anastomoses; the main trunk of Va, however, forms a temporary anastomosis with Id.

Va is a sensory nerve in all genera studied by the author; Vb has a few motor fibres and Vc also. In all these genera Va innervates mainly the skin on the dorsal side of the head and the skin of the snout; Vb innervates the skin on the lateral side of the head, and Vc innervates

the skin on the ventral side. The n. abducens is present as in *Scolecophorus* and *Coccolis*. It leaves the cranial cavity together with the root of Vb+c, runs forwards for a short distance in the ganglion of Va and then enters the retractor muscle.

The cranial arteries and veins of *Gectrypetes*.

The arteria stapediale is a branch of the a. carotis interna, given off from the latter in the occipital region. The a. carotis interna is here situated ventral to the neurocranium and runs rostrad in this position as far as the anterior end of the otic capsule, where it enters the cranial cavity through a foramen in the base of the neurocranium. In the cranial cavity it gives off one large branch supplying the brain, and the main stem of the artery runs forwards in the cranial cavity for a short distance and achieves an exit through a foramen situated ventral to the foramen for the trigeminal nerve roots. In Fig. 6 the artery can be seen lying in the basal bone. It then runs rostrad with the r. palatinus VII (Figs. 3, 4 and 5). Immediately behind the nasal region it gives off a branch supplying the roof of the buccal cavity, and in the nasal region the a. carotis interna and the r. palatinus VII enter a canal in the vomer (Fig. 2). From this canal, two branches of the artery are given off into the nasal cavity, one supplying the "Nebennase" and the other the main nasal sac. Another large branch is then given off into the buccal epithelium. Near the anterior end of the vomer, the a. carotis interna leaves the latter, and forms an anastomosis with the artery from the other side, and then divides into several small branches supplying the snout region.

The a. stapediale, as is mentioned above, is a branch of the a.

carotis interna. In the occipital and otic regions, it runs along with the r. hyomandibularis VII and the v. jugularis interna (Fig. 7). Its first branches are two small twigs accompanying the chorda tympani into the lower jaw, and a branch of the r. hyomandibularis VII into the m. cephalo-dorso-maxillaris. The main stem of the artery runs forwards through the quadrato-cranial passage with the ganglion of Vb+c and in the temporal groove it gives off a branch accompanying Vc into the lower jaw. This branch divides into as many twigs as there are ramuli of Vc, and they accompany the latter to their final terminations. The main stem of the artery divides into two branches: one accompanying Va and the other Vb. These two branches also divide into numerous smaller twigs supplying the various ramuli of Va and Vb. In all the figures the branches of the a. stapedialis can be seen as tiny vessels accompanying the branches of the trigeminal nerve.

The cranial veins, especially the v. jugularis interna, are much branched vessels as in all genera studied by me. The v. capitis lateralis arises in the nasal region as a network of small vessels above the nasal sacs. Behind the nasal region, the vein accompanies Va (Fig. 4) and in the temporal groove it receives branches from the m. levator quadrati, the m. adductor mandibulae externus major and the m. adductor mandibulae externus minor, as well as a large branch from the ganglion of Vb+c. It then runs caudad above the ganglion of Vb+c and in the quadrato-cranial passage it forms a large sinusoidal network.

The v. jugularis interna arises in the snout as a large network of small vessels. It receives branches arising as a network in the buccal roof and around the tentacle structures (Figs. 1, 2 and 3), and

in the orbital region the vein accompanies the r. palatinus VII and the a. carotis interna. Immediately in front of the m. levator quadrati it forms an anastomosis with the v. capitis lateralis. In the temporal region the v. jugularis interna runs below the ganglion of Vb+c, and it also forms a large network in the quadrate-cranial passage. One large venous channel arises from the venous networks formed by the v. jugularis interna and the v. capitis lateralis, and it is joined by one vessel emerging from the cranial cavity through a foramen situated immediately above the foramen for the facial nerve root. In the occipital region it is joined by a large vessel leaving the cranial cavity through the jugular foramen together with the roots of the ninth and tenth cranial nerves.

General conclusions.

As was pointed out in the introduction, *Geotrypetes* is very similar to genera such as *Dermophis* and *Siphonops*, although it possesses a few features also encountered in *Coeccilia*, a genus showing many specialised features. The various points of importance in the cranial morphology of *Geotrypetes* have been discussed in detail above, and only a brief summary will be given here.

The bones in the nasal region have fused to the same extent as in the other genera mentioned above, and the main nasal sac presents the same plan as in *Dermophis* and *Siphonops*. The ventral indentation is present, and the main nasal sac is a well-developed olfactory organ. The "Nebennase" and its gland are better developed than in *Dermophis* and *Siphonops*, and resemble those of *Coeccilia* more closely. As in the latter genus, the "Nebennase" is already enclosed in its own cavity separate from the main nasal cavity, even and even the ventral olfactory nerve

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shows signs of becoming divided into two portions, one for the main nasal sac and the other for the "Nebennase". The main nasal sac, however, shows no signs of degeneration as in *Coecilia*.

The tentacle structures are well-developed, but the orbital gland and the compressor muscle are not nearly as large as in *Coecilia*. The innervation of the retractor muscle could be traced: the tentacular apparatus therefore shows no signs of degeneration. The eye of *Geotrypetes* consists of a well-developed optic cup and lens, and a large orbital opening is present, so that the eye is clearly visible through the skin. The eye is therefore just as well developed as in *Dermophis* and *Siphonops*, whereas in *Coecilia* and *Boulengerula*, the eye has degenerated to a tiny pigment mass and is completely covered by bone.

The trigeminal musculature is similar to that of other genera studied by me. The *m. pseudotemporalis* is absent as in *Siphonops*, *Boulengerula* and *Dermophis*. The quadrato-basal articulation and the two muscles associated with it, show no sign of degeneration at all even as in *Dermophis* and *Siphonops*, whereas the articulation and the *m. levator quadrati* are degenerating in *Coecilia*. The quadrato-stapedial articulation on the other hand, shows signs of degeneration, but the degeneration has not progressed nearly as far as in *Dermophis* and *Coecilia*. In the latter the stapedial style and the *p. columellaris palatoquadrati* have fused completely, while in *Siphonops* no degeneration has taken place. The stapedial footplate ~~is~~ fused to the side wall of the neurocranium and the *p. ascendens palatoquadrati* is firmly applied to the paraquadrato by means of dense connective tissue. The palatoquadrato therefore seems to be unable to move at all and the well-developed quadrato-basal arti-

ulation seems to be superfluous.

The cranial nerves and their ganglia, as pointed out above, show hardly any differences from those of Siphonops. The geniculate ganglion and the ganglion of Vb+c are continuous in both genera, and a sensory anastomosis between the olfactory nerves and Va is present in both. The double anastomoses between the r. palatinus VII and Vb and the anastomosis between the chorda tympani and Vc are described for both genera. The ganglia of the cranial nerves of Coecilia are entirely different from those of Geotrypetes, Siphonops and Dermophis.

As regards the bloodvessels of the head, the a. stapediale divides into numerous branches accompanying the branches of the trigeminal nerve, as in Siphonops and Coecilia. The a. carotis interna could be traced to its final terminations. At their anterior ends the two arteries form an anastomosis with each other. Branches of the artery could be traced to the nasal sacs and to the buccal epithelium. The v. jugularis interna and the v. capitis lateralis are not different from those of other genera, but only one cephalic branch emerging from the cranial could be demonstrated. The number of cephalic branches and their means of exit from the cranial cavity vary very much in the different genera. The large branch passing through the jugular foramen is present in Geotrypetes as in all genera studied by the author.

Taking into consideration all the various cranial features discussed above, it seems reasonable to class Geotrypetes with such genera as Dermophis, and Siphonops representing the general Gymnophione plan. It does, however, show specialisation of certain parts of the nasal sac as in Coecilia, which latter differs profoundly from Geotrypetes, Dermophis and Siphonops as regards most of the cranial features.

Alphabetical list of abbreviations to show the number of the figure
where they were first introduced.

acin 1; astp 1; bas 5; bc 6; bep 6; br 4; cpm 4; csb 5; cts 1; ctym 7;
dobg 4; fr 2; ggen 7; gVa 6; gVb+c 6; ls 4; mamj 5; mann 6; mblj 6;
medm 5; mem 1; memp 3; mg 1; mlq 6; mns 1; mptg 6; mxpl 1; nbg 1; nbn 2;
ng 1; npm 1; n VI 6; obg 4; olans 3; otc 7; par 5; pasd 6; pbas 6;
pl 4; pptg 5; prq 5; qua 7; ret 4; rpl VII 2; rpans 3; rtm 4; r Va 6;
r Vb 6; r VII 7; sfp 7; sg 1; sync 6; vch 7; vcpl 5; vjug 1; vo 1;
Id 1; Iv 1; Va 1; Vb 1; Vc 6.

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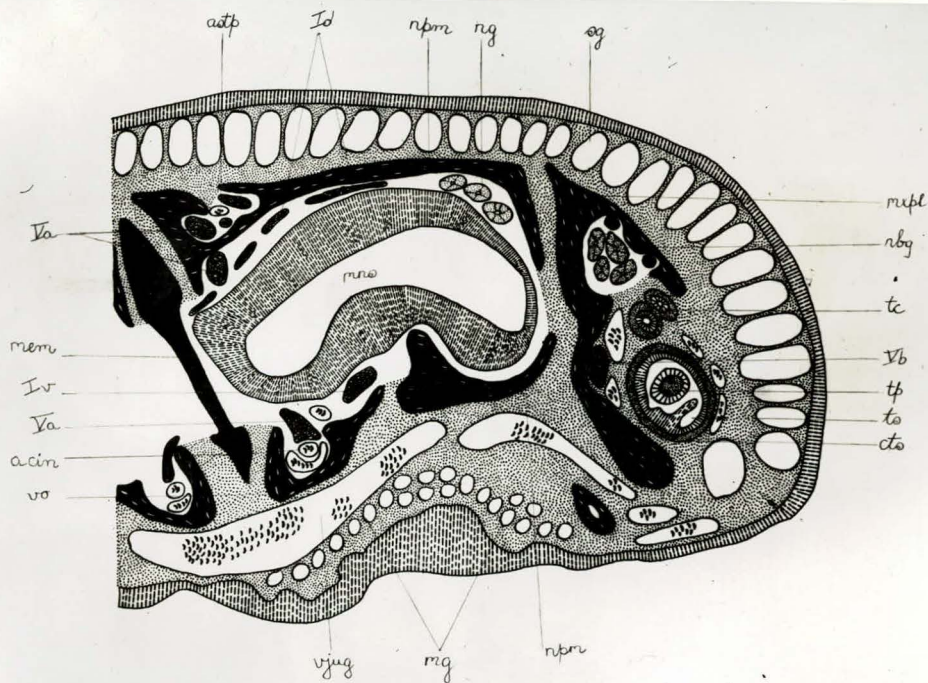


Figure 1.

Figure 1. Transverse section through the anterior part of the nasal region. acin arteria carotis interna; astp arteria stapediale; cts connective tissue tentacle sheath; mem mesethmoid; mg mucous secreting glands; mns main nasal sac; mxpl maxillo-palatine; nbg "Nebennase" gland; ng nasal gland; npm nasopremaxillary; sg skin glands; tc tentacle canals; tp tentacle papilla; ts tentacle sac; vjug vena jugularis interna; vo vomer; Id dorsal olfactory nerve; Iv ventral olfactory nerve; Va ramus ophthalmicus of the trigeminal nerve; Vb ramus maxillaris of the trigeminal nerve.

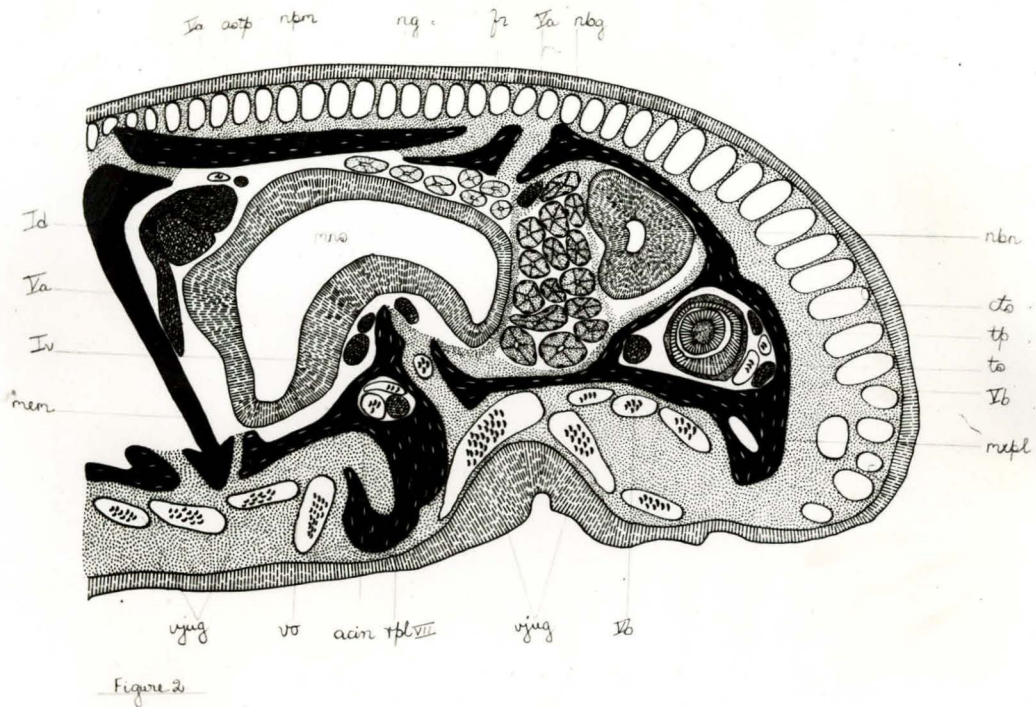


Figure 2. A transverse section through the anterior part of the "Nebennase"; showing the "Nebennase" cavity in the maxillo-palatine.
fr frontal; nbn "Nebennase"; rpl VII ramus palatinus of the facial nerve. Other abbreviations as for paxx Figure 1.

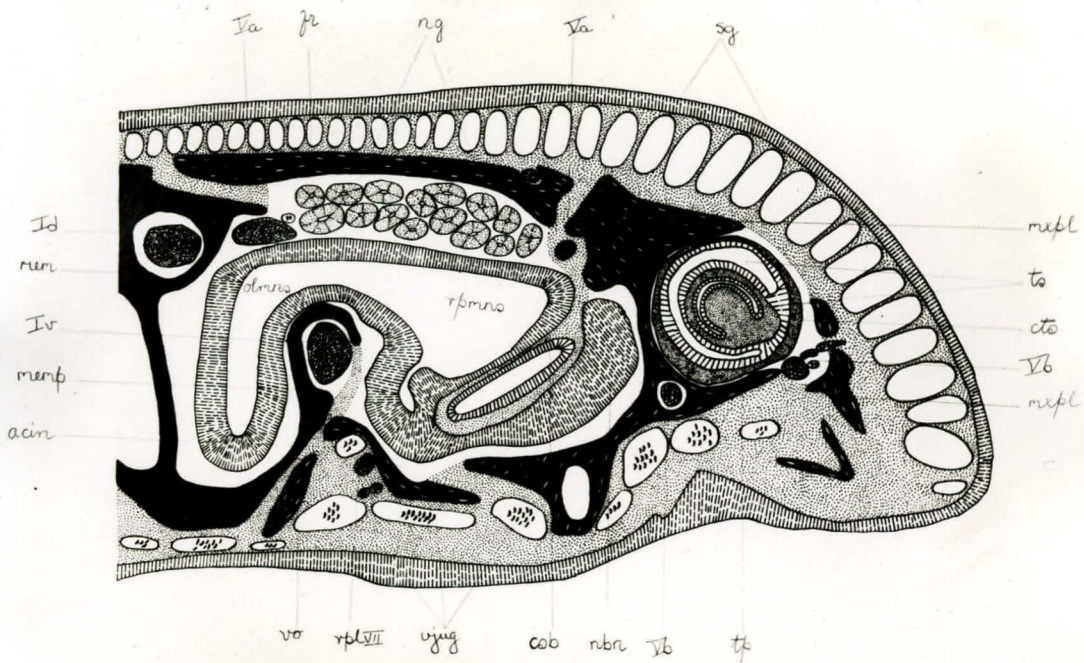


Figure 3

Figure 3. Transverse section through the nasal region, showing the "Nebennase" opening into the main nasal sac. csb "Choanenschleimbeutel"; memv ventral process of the mesothoid forming the ventral indentation; olans olfactory portion of the main nasal sac; rpnas respiratory portion of the main nasal sac. Other abbreviations as for previous figures.

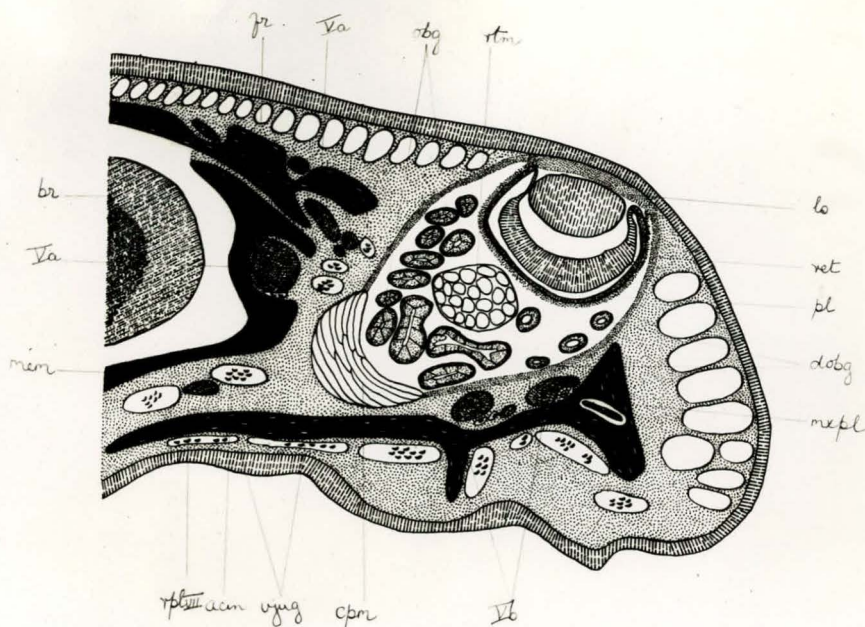


Figure 4. Transverse section through the orbital region, showing the eye and the tentacle structures. br brain; c-pr compressor muscle of the orbital gland; dobg ducts of the orbital gland; pl pigment layer of the optic cup; ret retina; rtm retractor muscle of the tentacle. Other abbreviations as for previous figures.

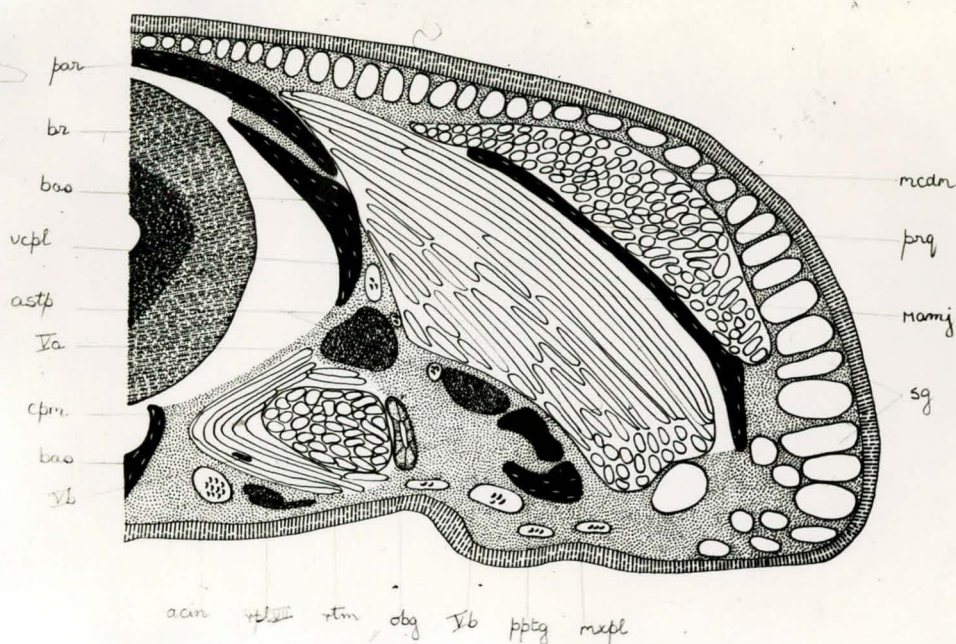


Figure 5

Figure 5. Transverse section through the temporal region, showing the muscles in this region and the zygokretaphic condition of the skull. bas on basale; mamj m. adductor mandibulae externus major; mcdm m. cephalo-dorso-maxillaris; par parietal; pptg processus pterygoideus palatoquadrate; prq paraquadrate; vcpl vena capitis lateralis. Other abbreviations as for previous figures.

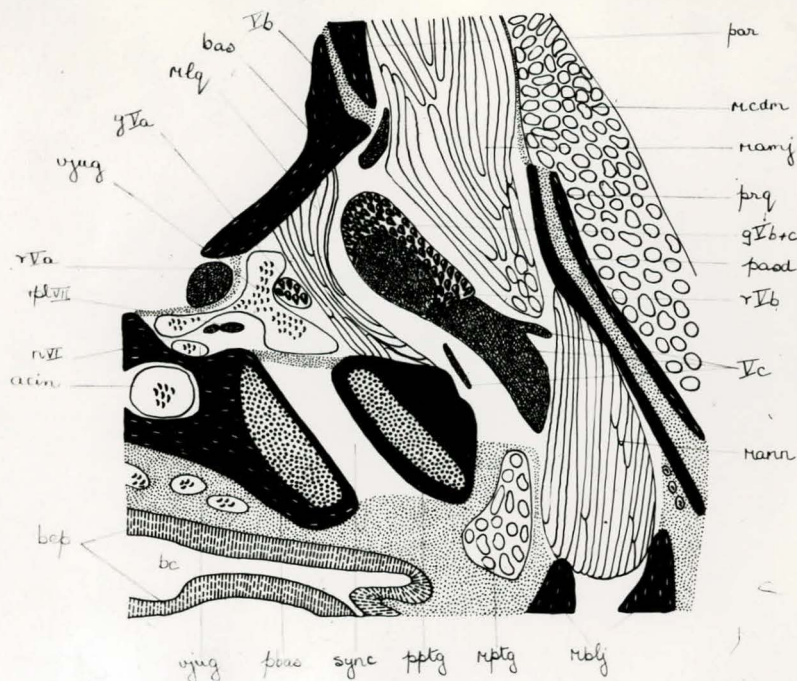


Figure 6

Figure 6. Transverse section through the posterior part of the temporal groove. bep buccal epithelium; bc buccal cavity; gVa ganglion ophthalmicum of the trigeminal nerve; gVb+c ganglion maxillo-mandibulare of the trigeminal nerve; mam m. adductor mandibulae externus minor; mlq m. levator quadrati; mb mixed bone of the lower jaw; mptg m. pterygoideus; nVI nervus abducens; pasd p. ascendens palatoquadrati; pbas p. basipterygoideus of the basal bone; rVa ophthalmic portion of the trigeminal nerve root; rVb maxillary portion of the trigeminal nerve root; sync synovial cavity; Vc ramus mandibularis of the trigeminal nerve. Other abbreviations as for previous figures.



Figure 7

Figure 7. Transverse section through the anterior tip of the otic capsule. ctym chorda tympani; ggen geniculate ganglion; otc otic capsule; qua portion of the palatoquadrate forming the jaw articulation; rVII root of the facial nerve; sfp stapedial footplate; vch venous channel formed by the v. jugularis interna and the v. capitis lateralis. Other abbreviations as for previous figures.

**A SUMMARY OF THE CRANIAL FEATURES OF THE GYMNOPTERID GENERA THUS FAR
DESCRIBED.**

A SUMMARY OF THE CRANIAL FEATURES OF THE GYMNOPTERID GENERA THUS FAR
DESCRIBED.

In the series of contributions to the cranial morphology of the Gymnoptera, genera from several localities have been studied by the author. The following genera were investigated by various workers: *Ichthyophis glutinosus*, an Oriental form, was studied in great detail by Wiedersheim (1879) and the Sarasin (1890). The data given by the latter will be referred to in the summary given below. K. Peter (1898) described in some detail the macroscopic anatomy of the skulls of *Boulengerula* and *Scolecophorus*, two East African genera. De Villiers (1938) and the author (1940) have, however, studied the skulls of these two genera microscopically. H. Marcus and his students in a long series of contributions (1909-1935), described the anatomy and development of the *Hypogeophis* skull; this genus occurs in the Seychelles. In 1938-1939 the author investigated two species of *Dermophis*; one represented in South America and the other in East Africa. Wiedersheim and the author (1929) described the cranial morphology of two South American genera: *Coccolia* and *Siphonops*. In addition to these a West African genus, *Geotrypetes*, has recently been studied by the author (1940).

A summary of the cranial features of the above mentioned eight genera will be given below, and an attempt will be made to sort out the various points of phylogenetic and taxonomic importance. The ontogeny of only two genera has been studied so far: that of *Ichthyophis* by the Sarasin and Peter (1898), and of *Hypogeophis* by Marcus and his students. The various cranial structures will be treated separately in the summary given below.

2.

The nasal organ and capsule.

The Gymnophione skull is a very small and compactly built structure, with the various organs very closely packed. Considering the small space occupied by the nasal sacs, the latter show a considerable amount of variation in the various genera. The variations shown by the nasal sacs in certain genera were considered as indicative of a compensatory development for the degeneration of the eye. An interesting fact noted in genera in which the nasal sacs do reach marked development, is that the development of the tentacle and its associated structures keeps pace with the development of the nasal sacs.

The general plan of the main nasal sac as found in genera such as *Dermophis*, *Siphonops*, *Geotrypetes* (author) and *Ichthyophis* (Sarasins), is the following: It consists of three portions, a short anterior portion with a dorso-lateral indentation and with walls formed by thick olfactory epithelium, a large median portion divided by a ventral indentation into ^amedial olfactory and a lateral respiratory portion, and a short posterior portion dividing into an olfactory portion ending blindly and a lateral portion opening into the buccal cavity. The other genera studied differ from the above plan. In *Scolecophorus* the ventral indentation is present, but olfactory epithelium is present also in the lateral portion, whereas in the above mentioned genera the lateral portion is clothed by indifferent respiratory epithelium. In *Hypogeophis*, according to Laubmann, olfactory epithelium is present in both lateral and medial portions with indifferent epithelium separating the two portions. Judging from the illustrations given by Laubmann and ^{Marcus} ~~Laubmann~~, the ventral indentation is not

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nearly as deep in *Hypogeophis* as in the above mentioned genera; they also describe the dorso-lateral indentation in the anterior portion of the main nasal sac, but do not mention any division of the posterior portion of the main nasal sac into ~~xxxxxx~~ an olfactory portion ending blindly and a lateral portion opening into the buccal cavity. In *Boulengerula* a ventral indentation is only slightly indicated, and the main nasal sac cannot be considered as consisting of medial and lateral portions. Olfactory epithelium is well developed in the main nasal sac, and its posterior portion remains undivided as in *Hypogeophis*. In *Cocilia* the main nasal sac is definitely not indented and the olfactory epithelium is very poorly developed; the main nasal sac is a straight tube with a presumably exclusively respiratory function. From the above it therefore becomes clear that in *Dermophis*, *Siphonops*, *Gecryptes* and *Ichthyophis* the main nasal sac is divided into olfactory and respiratory portions by a ventral indentation; in *Hypogeophis* and *Scolecophorus*, although a ventral indentation is ~~very~~ present, olfactory epithelium is found throughout the whole of the main nasal sac, and in the former genus the ventral indentation is very slight in comparison with that of other genera. In *Cocilia* and *Boulengerula* the division of the main nasal sac into respiratory and olfactory portions is not represented at all, and in the former genus the olfactory epithelium is very poorly developed in the main nasal sac.

Besides the main nasal sac, there is also a "Nebennase" which has developed as an evagination of the main nasal sac, as described by the Sarasin's for *Ichthyophis* and by Laubmann for *Hypogeophis*. Its walls consist of very thick olfactory epithelium, and it lies ^{lateral} ~~ventral~~ to the main nasal sac, except at its posterior end where it lies ventral to it, and it opens into the lateral portion of the latter. These conditions

4.

apply to the "Nebennase" of *Dermophis*, *Siphonops*, *Geotrypetes*, *Ichthyophis* and *Hypogeophis*. In *Scolecocomorphus* the "Nebennase" lies ventral to the main nasal sac throughout its whole length, but it opens into the main nasal sac as in the above mentioned genera. In *Boulengerula* and *Coecilia*, it lies lateral to the main nasal sac at its anterior end, but at its posterior end it extends mediad as far as the internasal septum and has its opening in the medial wall of the undivided posterior portion of the main nasal sac. In all the genera with the exception of *Hypogeophis*, *Coecilia* and *Geotrypetes*, the "Nebennase" lies in the same cavity as the main nasal sac. In the three genera mentioned above, the "Nebennase" has its own cavity in the maxillo-palatine. The "Nebennase" cavity and the main nasal cavity are separated by bone at their anterior ends and by connective tissue further caudad. Into the anterior blind end of the "Nebennase" of all the genera described, two tentacle canals open. They open at their distal ends into the tentacle groove situated between the external narial aperture and the eye. The "Nebennase" is found in the Gymnophiona only, and is a highly developed sense organ functioning in conjunction with the tentacle. The animal can therefore not only smell by inhaling through its external narial aperture, but also by inhaling through the tentacle canals into the "Nebennase", and can probably locate odours in this way, as pointed out by Laubmann.

A small sac, the "Choanenschleimbeutel", lying behind the "Nebennase" and opening into the posterior portion of the main nasal sac, is apparently represented in all genera, except *Hypogeophis*. The "Choanenschleimbeutel" is devoid of olfactory epithelium and opens into the buccal cavity together with the main nasal sac. Laubmann did not find

this sac in *Hypogeophis*, but describes a dorsally situated organ of Jacobson, absent in all the other genera. It was not possible for the author to procure material of *Hypogeophis* for comparison.

A nasal gland lying on the roof of the main nasal sac, is described for all genera. Its alveoli either open singly into the main nasal sac, or it has a long duct opening into the anterior portion of the main nasal sac, as in *Coecilia*, *Siphonops* and *Geotrypetes*. Laubmann describes a similar gland for *Hypogeophis*, as well as another one on the ventral side of the main nasal sac. In *Siphonops* the author also found several alveoli on the ventral side, but not such a well developed gland as in *Hypogeophis*. A "Nebennase" gland is also present, and is a fairly well developed structure in most genera, with the exception of *Dermophis gregorii* in which a few alveoli present in the wall of the "Choanenschleimbeutel", are the only indication of the gland. The alveoli of this gland open into the "Nebennase" of *Ichthyophis*, *Hypogeophis*, *Coecilia* and *Geotrypetes*. In *Dermophis*, *Siphonops*, *Boulengerula* and *Scalacomorphus* the author found the alveoli opening into the "Choanenschleimbeutel".

Two pairs of olfactory nerves are present in all genera: a dorsal olfactory nerve innervating the medial portion of the main nasal sac, and a ventral olfactory nerve innervating the "Nebennase" and the lateral portion of the main nasal sac. The larger number of fibres of the ventral nerve innervate the "Nebennase", and in *Coecilia* the ventral nerve was found to be divided into two separate portions immediately after emerging from the olfactory lobe, with the larger portion supplying the "Nebennase"; in *Geotrypetes* the division of the ventral olfactory nerve has progressed almost as far as in *Coecilia*. In *Hypogeophis*

6.

and Geotrypetes the r. ophthalmicus of the trigeminal nerve (Va) forms an anastomosis with the dorsal olfactory nerve, and in Siphonops with the ventral nerve as well. According to Laubmann this sensory anastomosis may well indicate the presence of a n. terminalis.

The nasal capsule.

The nasal capsule of all the genera with the exception of Ichthyophis and Scolecophorus, is formed by the nasopremaxillaries, the vomers, maxillo-palatines, the mesethmoid and the frontals, which latter form part of the roof of the nasal capsule. The nasopremaxillary of Hypogeophis is described as being formed by the fusion of the nasal, premaxillary and the septomaxillary (Marcus). It surrounds the anterior part of the main nasal sac completely and is perforated by the external narial aperture. The vomers are wedged in between the ventral portions of the nasopremaxillaries and form the medial portion of the floor of the nasal capsule. They end caudad just beyond the choanae of which they form the medial rim. The vomer, when looked at from the ventral side, is not flat, but slightly arched, and a long canal is present in it. The a. caretis interna and the r. palatinus of the facial nerve run rostrad in this canal. At their anterior ends the vomers overlap the anterior prolongation of the basal bone.

The maxillo-palatine is situated laterally and extends very slightly ^{to} on the dorsal surface where it forms a suture with the dorsal portion of the nasopremaxillary and behind the latter with the frontal. It also extends on to the ventral surface, and forms a suture with the ventral portion of the nasopremaxillary and with the vomer. The maxillo-palatine is perforated laterally by the two tentacle canals, and in it

is a long groove for the tentacle structures. This groove opens into the anterior end of the ocular cavity. In *Hypogeophis*, *Coeccilia* and *Geotrypetes*, there is also another large groove in the maxillo-palatine for reception of the "Nebennase". In all the genera the maxillo-palatine forms the lateral rim of the choana, and in the orbital region it forms the bony floor for the anterior part of the orbit and then becomes reduced to a narrow process extending caudad to the anterior end of the p. pterygoideus palatoquadrati. This posterior process separates two large fenestrae in the palate: the medio-palatine and basitemporal fenestrae. In *Hypogeophis*, *Dermophis*, *Siphonops* and *Geotrypetes*, the maxillo-palatine also forms the anterior rim of the orbital opening. In *Coeccilia* and *Boulengerula* an orbital opening is absent and the maxillo-palatine is therefore not ~~in~~ incomplete on its lateral side as in these former genera, but in the orbital region of the latter two genera the maxillo-palatine is overlapped by the paraquadrato, which occupies its position posteriorly.

The mesethmoid is a very complicated bone. It consists of a transversely disposed bone lamella, the lamina praecerebralis (Marcus), separating the cranial from the nasal cavity. The lamina praecerebralis bears two horizontal processes: a short dorsal and a long ventral one. The latter forms the posterior part of the ventral indentation in genera in which this is present. It also bears a perpendicular lamina forming the internasal septum and ending rostrad as a cartilaginous process between the two nasopremaxillaries. Caudad the lamina praecerebralis bears three processes: there is a mid-dorsal process appearing on the dorsal surface between the two frontals in *Coeccilia*, *Boulengerula*, *Siphonops* and *Dermophis gregorii*. In the remaining genera it

lies below the frontals and covers the median suture of the latter bones ventrally. Then there are two lateral processes forming the lateral walls of the neurocranium in the orbital region, and ending on either side as two cartilaginous processes: a dorsal taenia marginalis and a ventral trabecula, and between these is a large optic foramen covered by a thick membrane. This description of the mesethmoid can be applied to all the genera with the exception of *Cocilia* and *Boulengerula*. The mesethmoid in these two genera differs from that of the others, in that the two horizontal processes are very short. The dorsal one is barely developed, and the ventral one is present in the anterior third of the nasal region only, and is very much shorter than in the other genera. The lamina praecerebralis in all the genera is perforated by large foramina for the two pairs of olfactory nerves.

In *Ichthyophis* and *Scolecormorphus* the bones in the nasal region have not fused as in the other genera. There are separate nasals, premaxillaries, vomers, maxillo-palatines and prefrontals forming the side walls of the nasal capsule behind the maxillo-palatines, and in both genera a small bone lying laterally between the dorsal nasal and the ventral premaxillary. This bone was termed a turbinal by the Sarasin for *Ichthyophis*, and a lachrymal by Peter and the author (for *Scolecormorphus*); it surrounds the external nasal aperture. The mesethmoid has the same structure as in other genera and does not appear on the dorsal surface. In *Scolecormorphus* the bones in the nasal region do not form sutures; there are actual slitlike openings between them, and the maxillo-palatine is a very small bone in comparison with that of other genera. It does not extend on to the ~~lateral~~ lateral side of the head, where its place is taken by the prefrontal; behind the choana it is a

narrow process attached to the ventral rim of the prefrontal. The prefrontal forms the side wall of the skull in the orbital region, and it is not perforated by an orbital opening. In *Ichthyophis* the orbital opening is surrounded by a separate bone, the postfrontal.

The tentacle, its associated structures and the eye.

The structure of the tentacle and its associated structures varies very little in the various genera studied. The tentacle consists of an epithelial sac opening at one end into the tentacle groove, situated on the side of the head between the external narial aperture and the eye. The position of the groove in relation to the narial aperture and the eye varies in the different genera. The tentacle sac is indented on the one side by a mass of connective tissue thus forming a tentacle fold. At the distal end of the sac the connective tissue becomes surrounded by epithelium and projects into the tentacle groove as a free tentacle papilla. In the nasal region the connective tissue in the tentacle fold is replaced by the retractor muscle of the tentacle. This muscle is continued caudad into the orbit and temporal groove where it inserts on the lateral wall of the neurocranium. The tentacle sac is surrounded by a connective tissue tentacle sheath. In the nasal region the tentacle sac lies in a deep groove or canal in the maxillo-palatine, and this groove opens into the anterior part of the orbit, from which an orbital or Harderian gland extends forwards into the maxillo-palatine groove, where the gland alveoli open into the tentacle sac. The orbital gland surrounds the retractor muscle in the ocular cavity, and the gland in its turn is surrounded by a compressor muscle of the orbital gland. The compressor muscle extends into the temporal

groove. In all the genera studied, the tentacle structures are related to one another as described above; *Scolecormorphus* is the only genus in which they are situated within the nasal cavity. In the anterior half of the nasal region they lie lateral to the maxillo-palatine, but in the posterior half they lie within the nasal cavity, and are separated from the nasal sac by means of thick connective tissue. The innervation of the retractor muscle could be demonstrated in *Scolecormorphus*, *Coccolia*, *Geotrypetes* and *Ichthyophis*: it is innervated by the n. abducens. The compressor muscle is innervated by the r. maxillaris of the trigeminal nerve (Vb), which therefore cannot be a purely pretrematic dorsal nerve, but must be partly visceromotor as well.

In all the genera with the exception of *Scolecormorphus*, the eye lies in the orbit lateral to the tentacle structures. In *Ichthyophis*, *Hypogeophis*, *Dermophis*, *Siphonops* and *Geotrypetes*, it consists of an optic cup with a pigment layer and retina, and a lens; and in these genera a large orbital opening is present. In *Coccolia* and *Boulengerula* the eye has degenerated to a small mass of pigment and an orbital opening is absent. In *Scolecormorphus* the eye lies in the nasal region and is situated in the tentacle fold immediately anterior to the retractor muscle. The anterior rim of the orbital opening in these genera in which it is present, is formed by the maxillo-palatine, and the rest of the rim by is formed by the paraquadrata, except in *Ichthyophis* in which the orbital opening is surrounded by the postfrontal.

The tentacle and structures are similar in all the various genera studied: the only important variation being the relative size of the various structures. In the genera *Coccolia* and *Boulengerula*, in which the eye has degenerated almost completely, the orbital gland, re-

The remaining cranial bones.

The bones in the nasal region have already been discussed, the only remaining ones are the basal, parietal, frontal, paratracheate, palatoquadrato and the stapes. The basal bone is a large structure, formed by the fusion of the exoccipitals, the parietal bones, probably an alisphenoid and the parasphenoid (Marcus). In all the genera studied it surrounds the foramen magnum and forms the two large occipital condyles. It incorporates the two otic capsules and forms the floor and side walls of the neurocranium in the orbital and temporal regions. In front of the otic capsule it is perforated laterally by a foramen for the root of the facial nerve, except in *Cocilia* where a separate foramen for the latter is absent. In front of this, a large foramen for the trigeminal nerve root is present in the lateral portion of the basal bone. This latter foramen may be subdivided, so that the ophthalmic and maxillo-mandibular portions of the trigeminal nerve root have separate foramina as in *Dermophis* and *Siphonops*. In front of the otic capsule the basal bone is also perforated ventrally by a foramen for the a. carotis interna; a pituitary foramen is absent. In the temporal region the bone bears a ventral process directed laterad: the basipterygoid process forming an articulation with the p. pterygoideus palatoquadrati (see below). In the orbital region the lateral portion of the basal bone is

continued as two cartilaginous bars, the taenia marginalis and the trabecula. These two cartilages, as mentioned above, are also continuous with the lateral portion of the mesethmoid. According to Marcus, the optic foramen between the taenia and trabecula is very small in Hypogeophis; in all the other genera it is large, especially so in Geotrypetes. Ventrally the basal bone forms the floor of the neurocranium; in the choanal region it becomes narrower and is continued very far rostrad into the nasal region as a narrow process lying above the vomers.

The frontals and parietals form the roof of the skull behind the nasal capsule. The former projects far rostrad below the nasopremaxillaries, and the mesethmoid appears on the dorsal surface between them, in some genera (see above). The parietals lie behind the frontals and reach caudad as far as the posterior end of the otic capsule; the basal bone then extends on to the roof of the skull.

The paraquadrates forms the side wall of the skull behind the maxillo-palatine, and between it and the lateral portion of the basal bone a large temporal groove is enclosed, open on the ventral side. The large opening is divided into a medio-palatine and a basitemporal fenestra by the posterior elongation of the maxillo-palatine and the anterior portion of the p. pterygoideus palatoquadrati. Through the basitemporal fenestra the masticatory muscles innervated by the trigeminal nerve pass to the lower jaw where they are inserted. In genera with an orbital opening the paraquadrate forms its posterior, dorsal and ventral rims. In Coecilia, Boulengerula and Scolecomorphus, where an orbital opening is absent, the paraquadrate is continued far rostrad, especially in Boulengerula where it extends far into the nasal region. The paraquadrate reaches the parietal in only two of the genera studied. Hypogeophis

and *Coecilia* are the only truly stegokrotaphic genera with the paraquadrate effecting contiguity with the parietal. *Dermophis*, *Boulengerula*, *Scolecormorphus* and *Ichthyophis* are slightly zygekrotaphic with a narrow slit separating the paraquadrate and parietal, and in *Siphonops* and *Geotrypetes* the skulls are much more zygekrotaphic. Especially in the latter genus the temporal fossa is very wide. The paraquadrate ends caudad in front of the otic capsule.

The palatoquadrate, in all genera with the exception of *Scolecormorphus*, is a fairly large bone with four processes: a p. articularis forming the jaw articulation, a p. pterygoideus given off from the ventral side of the bone and extending far rostrad, a p. ascendens underlying the paraquadrate and a p. columellaris arising from the posterior surface of the bone, and forming the quadrate-stapedial articulation. The p. pterygoideus palatoquadrati forms the quadrate-basal articulation with the basipterygoid process of the basal bone. Anterior to the articulation, the p. pterygoideus palatoquadrati is a narrow process lying between the medio-palatine and basitemporal fenestrae and it reaches the posterior end of the maxillo-palatine (see above). In *Ichthyophis* a quadrate-basal articulation is not formed, although the two processes approach each other closely; only a connective tissue connection is present between them. In *Coecilia* the two processes forming the articulation have fused with each other to a fair extent; the articulation in this genus is therefore in the process of being lost. In the remaining genera the articulation is well developed.

The p. ascendens palatoquadrati is a broad bony plate, with its anterior portion covered by the paraquadrate, and the two bones firmly cemented to each other with only a thin layer of dense connective tissue

separating them. According to Marcus some movement is possible between these two bones in *Hypogeophis*, although in most genera studied by the author it can only be very slight. In *Hypogeophis* and *Coeccilia* the *p. ascendens palatoquadrati* reaches the parietal; in the other genera it is separated from the parietal by the temporal fossa. The *p. columellaris palatoquadrati* is short and reaches the anterior end of the stapedial style in all the genera except in *Scolecophorus*. The two bones form a quadrato-stapedial articulation which is well developed in *Ichthyophis*, *Hypogeophis* and *Siphonops* only. In the other genera a certain amount of fusion takes place between them, and in *Coeccilia* this fusion is almost complete. The quadrato-stapedial articulation is therefore also in the process of being lost. With the loss of this articulation the skull becomes *akinetik*.

The stapes consists of a footplate fitting into the fenestra ovalis, and in all the genera studied with the exception of *Hypogeophis* and *Ichthyophis* the footplate is synchondrotically fused to the side wall of the otic capsule; movement of the stapes in the fenestra ovalis is therefore impossible. The style forms the quadrato-stapedial articulation, as mentioned above. In *Scolecophorus* a stapes is completely absent, and with it, of course, the quadrato-stapedial articulation.

The pterygoid is absent as a separate bone in most of the genera studied. According to Luther (1914) and Marcus, the pterygoid remains separate in some genera, whereas in others it fuses either with the *p. pterygoideus palatoquadrati* or the maxillo-palatine. In *Siphonops*, *Coeccilia*, *Ichthyophis* and *Hypogeophis* a separate ^{pterygoid} was described by the above mentioned authors. In *Siphonops* the author described a small bone between the *p. pterygoideus palatoquadrati* and the maxillo-palatine, and

it was suggested that this obviously degenerating bone could be considered as a transversum.

The muscles of the suspensorial region.

The muscles were described in detail by Luther, Marcus and the author for various genera. The following are encountered in the suspensorial region: the *m. levator quadrati*, *m. adductor mandibulae externus major*, *m. adductor mandibulae externus minor*, *m. pseudotemporalis*, *m. pterygoideus* and the *m. cephalo-dorso-maxillaris*. The *m. levator quadrati* arises from the lateral wall of the neurocranium in the region of the foramen for the trigeminal nerve root and separates the two ganglia of the trigeminal nerve. The muscle inserts on the dorsal surface of the *p. pterygoideus palatoquadrati* where the latter forms the quadrate-basal articulation. It is fairly well developed in most genera, but is completely absent in *Scälecomorphus* and only a few fibres remain in *Coccolia*. In the former genus the absence of the muscle points to a loss of kinesis of the skull, and in the latter it degenerates with the quadrate-basal articulation: i.e. its degeneration equally points to the loss of kinesis. The innervation of the muscle could not be traced in any of the genera studied by the author, but according to Marcus and Luther, it is innervated by a branch of the r. mandibularis V (Vc). Professor de Villiers informs me that he had the opportunity of seeing the innervation in one of Professor Marcus' frontal series of *Hypogeophis* at Munich in 1935.

The *m. adductor mandibulae externus major* is large in all the genera studied and fills the greater part of the temporal groove. It arises from the parietal, frontal and paraquadrate, and extends very far

rostrad in some genera; in Siphonops for example it extends into the nasal region. It is separated from the m. levator quadrati by the ganglion maxillo-mandibulare of the trigeminal nerve and by Vb, and it passes through the basitemporal fenestra to insert on the lower jaw. The m. pseudotemporalis, described by Marcus and Luther for *Lichthyophis*, *Siphonops* and *Hypogeophis*, and by the author for *Dermophis mexicanus*, lies medial to the m. adductor mandibulae externus major. In *Scolecocorpus*, *Boulengerula* and *Geotrypetes* the muscle is absent.

The m. adductor mandibulae externus minor arises partly from the p. ascendens palatoquadrati and partly from the paraquadratus. It is small in most genera, and large in *Geotrypetes* only. It lies lateral to the m. adductor mandibulae externus major, and is separated from the latter by Vc. It also passes through the basitemporal fenestra to insert on the lower jaw behind the insertion of the m. adductor mandibulae externus major. These visceromotor muscles mentioned so far are situated in the temporal groove and are innervated by branches of Vc, although a branch of Vb has been traced by the author into the m. adductor mandibulae externus major in *Dermophis*, *Geotrypetes* and *Siphonops*.

The m. pterygoideus appears in section at the same level as the m. levator quadrati; it arises from the ventral surface of the lower jaw, and p. pterygoideus palatoquadrati and inserts on the medial surface of the lower jaw; and is also innervated by Vc. The m. cephalo-dorso-maxillaris is a large structure arising from the outer surface of the paraquadratus, p. ascendens palatoquadrati and the parietal, and it is innervated by visceromotor fibres of the r. hyomandibularis VII.

The cranial nerves and their ganglia.

The facial and trigeminal nerves have been studied in detail in most of the above mentioned genera. The facial nerve root leaves the cranial cavity through a foramen situated immediately in front of the otic capsule in all the genera except in *Cocilia*, where it leaves the cranial cavity together with the root of the trigeminal nerve. The geniculate ganglion in *Dermaphis mexicanus*, *Boulengerula* and *Scolecocomorphus* is forked, and there is in these genera an indication of a separate ganglion for the ~~sensory~~ viscerosensory fibres of the r. palatinus VII. In an *Ichthyophis* embryo a separate ganglion pro ramo palatino VII was found to be present, so that in the above mentioned genera the significance of the forked geniculate ganglion becomes clear. In *Siphonops* and *Geotrypetes* the geniculate ganglion and the ganglion maxillo-mandibulare (Vb+c) have fused to form a large ganglionic mass. In *Cocilia* a separate geniculate ganglion is completely absent, the sensory fibres of the facial nerve passing through the ganglion of Vb+c and the motor fibres being applied to the ganglion of the acoustic nerve, which is therefore theoretically a ganglion acustico-faciale.

The facial nerve has three main branches: the r. hyomandibularis VII running caudad against the otic capsule and innervating the m. cephalo-dorso-maxillaris; a chorda tympani (= a pretrematic ramus mandibularis VII) running forwards in the lower jaw and forming an anastomosis with Vc, and the r. palatinus VII₂ containing the viscerosensory fibres of the facial nerve and innervating the epithelium of the buccal roof. The chorda tympani was found to be absent in both *Scolecocomorphus* and *Boulengerula*; it is present in all the other genera. The r. palati-

nus VII runs rostrad in all genera, with the exception of *Boulengerula* where the nerve forms a commissure between the geniculate ganglion and the ganglion of Vb+c and ends in the latter ganglion. The r. palatinus VII and Vb form two anastomoses, except in *Dermophis* and *Scolecormorphus*, in which only one anastomosis is formed.

The trigeminal root divides in the cranial cavity into the ophthalmic (Va) and the maxillo-mandibular (Vb+c) portions. In *Dermophis* and *Siphonops* the two roots leave through separate foramina, in the other genera only one large trigeminal foramen is present. With the exception of *Scolecormorphus* and *Ichthyophis*, two separate trigeminal ganglia are present, and they are in no way connected with each other. In *Scolecormorphus* only one ganglion is present (de Villiers), and in *Ichthyophis*, although only one ganglion is present, Engelhardt could distinguish two separate portions of it: a posterior portion for the Vb+c portion of the root and an anterior portion for the Va portion of the trigeminal root. According to Waldschmidt the two trigeminal ganglia develop separately, and fusion of the two ganglia indicate a secondary condition. The ophthalmicus profundus is frequently considered as not belonging to the dorsal nerve of the mandibular segment, but to that of the degenerated preoral one.

The Vc branch of the trigeminal nerve passes into the lower jaw after giving off the visceromotor branches supplying the muscles in the temporal groove (see above). Its somatic sensory fibres supply mainly the skin on the ventral side of the head. Vc forms an anastomosis with the chorda tympani in the lower jaw. Vb forms one or two anastomoses with the viscerosensory r. palatinus VII and innervates the compressor muscle of the orbital gland as well as the skin on the lateral side of the head. Va, remaining separate from Vb+c in all the genera

ra except in *Ichthyophis* and *Scolecormorphus*, is a purely somatic-sensory nerve, supplying the skin on the dorsal side of the head and the skin of the snout. In *Hypogeophis* and *Geotrypetes* it forms an anastomosis with the dorsal olfactory nerve, and in *Siphonops* with the ventral olfactory nerve as well. In the other genera these sensory anastomoses are absent.

The abducent nerve could be traced in *Ichthyophis*, *Coecilia*, *Geotrypetes* and *Scolecormorphus*. It supplies the retractor muscle of the tentacle, and runs for a short distance in the ganglion of Va after having emerged from the cranial cavity together with the roots of the trigeminal nerve.

The bloodvessels of the head.

The bloodvessels are described in all the genera studied by the author, and in *Scolecormorphus* and *Boulengerula* by de Villiers. The a. carotis interna runs against the floor of the neurocranium in the posterior part of the skull. In front of the otic capsule it enters the cranial cavity through a foramen in the floor of the neurocranium. In the cranial cavity a large branch supplying the brain is given off, the remaining branch of the artery leaving the cranial cavity through a foramen situated ventral to the ~~large~~ foramen for the roots of the trigeminal nerve. It then runs rostrad with the r. palatinus VII, and sends branches into the buccal roof, the nasal sacs and finally into the snout. The a. stapediale is a branch of the a. carotis interna; it divides into three main branches accompanying the three rami of the trigeminal nerve, and these three branches again divide into many smaller ones accompanying the ramuli of the trigeminal nerve.

The v. jugularis interna and the v. capitis lateralis form large venous networks in the skull. The former begins as a network in the snout and the buccal roof, and the latter as a network in the nasal cavity. The v. jugularis interna runs caudad in a ventral position and forms a large network in the quadrato-cranial passage; the v. capitis lateralis runs caudad in a dorsal position and also forms a network in the quadrato-cranial passage. From these one large vessel emerges and is joined by one, two or three veins coming out of the cranial cavity; their number vary in the different genera. The vessel then runs caudad against the otic capsule together with the a. stapediaalis and the r. hyomandibularis VII and is joined by a large vein leaving the cranial cavity through the jugular foramen together with the root of the vagus nerve.

Features of taxonomic importance.

1. The amount of fusion of the bones in the nasal region: We know from the work of the Sarasin and Marcus, that in the development separate nasals, premaxillaries, septomaxillaries, maxillaries and palatines are present. In most of the genera these bones have fused to form a nasopremaxillary and a maxillo-palatine. When they are still found separate as in *Ichthyophis* and *Scolecormorphus*, // neoteny// is indicated.
2. The structure of the palate: In all the genera with the exception of *Scolecormorphus*, the maxillo-palatine forms a broad plate behind the choana, and then tapers down to a narrow process separating the medio-palatine and basitemporal fenestrae. In *Scolecormorphus*, however, the maxillo-palatine behind the choana is confined to a lateral position, and represents a narrow process attached to the ventral rim of the prefrontal. The basitemporal and medio-palatine fenestrae are therefore

continuous. This condition may be a neotenic feature or it may be the result of degeneration of the bones in the palate.

3. The part played by the vomer in the formation of the palate and the choana: In a personal communication, Dr. Dunn stressed the part taken by the vomer in the forming the choana and the palate as an important taxonomic feature. In all the genera studied by me, the vomer is a medially situated bone, slightly wider in some genera than in others, it forms the medial rim of the choana and ends caudad immediately behind the latter. The vomer, therefore, has similar relations in all the genera studied, and does not appear to have any significance as a taxonomic feature.

4. The presence of a small pterygoid: In some genera, for example *Cocilia*, *Siphonops* and *Hypogeophis*, there is a small bone present between the maxillo-palatine and the p. pterygoideus palatoquadrati. This bone was called a pterygoid by Luther and Marcus; the author suggested that it may be a transversum with the pterygoid fused to either the maxillo-palatine or the p. pterygoideus palatoquadrati. Whatever the homologies of the bone may be, its presence seems to be of taxonomic importance and probably implies a primitive condition.

5. The zygokrotaphic condition of the skull: As was pointed out by various authors, the skull of the Gymnophiona is primarily stegokrotaphic. A zygokrotaphic condition therefore indicates degeneration of the temporal bones. Various degrees of zygokrotaphy were met with in the different genera studied.

6. The position of the palatoquadrate in relation to the neurocranium: In most genera studied a large quadrate-cranial passage is enclosed between the palatoquadrate and the neurocranium, that is, the

palatoquadrate is situated far out to the side. In *Coeccilia* the latter bone lies much nearer the neurocranium, and the quadrato-cranial passage is almost obliterated. This can reasonably be considered as a secondary feature.

7. The articulations in the skull: The presence of a well-developed quadrato-basal articulation, a well-developed quadrato-stapedial articulation and a p. ascendens palatoquadrati moveable against the paraquadrate, are necessary for a truly kinetic condition of the skull. In *Hyposcaphis* and *Siphonops* these conditions are present, and the skulls of these animals can therefore be said to be kinetic. In the other genera, however, a loss of the quadrato-stapedial articulation is in progress, the stapedial footplate is firmly attached to the side wall of the neurocranium, the p. ascendens palatoquadrati and the paraquadrate seem to allow very little movement, if any, against each other, so that the skull becomes akinetic. The degree of degeneration of the articulations varies in the different genera; in *Coeccilia* the degeneration has progressed much further than in any of the other genera. The kinetic condition of the *Gymnophiona* skull is the primary condition, so that the akinesis of the skull is a secondary feature and of great taxonomic importance. There seems, moreover, to be very little doubt that *Amphibia* as a class are, or were, characterised by cranial kinesis.

8. The development of the nasal sacs. A main nasal sac divided in to a medial olfactory and a lateral respiratory portion by a deep ventral indentation, and a "Nebennase" lying in the same cavity as the main nasal sac and opening into the lateral portion of the latter, seem to represent the primary plan of the nasal organ of the *Gymnophiona*.

Departures from this primary plan must be considered of importance. For example, the absence of the ventral indentation and the degeneration of olfactory epithelium in the main nasal sac, the higher development of the "Nebennase" and its inclusion in a cavity of its own in the maxillo-palatine, must be considered as secondary features indicating specialisation of the "Nebennase" as a sense organ.

9. The development of the tentacle structures: ^A | especially large orbital gland with well developed retractor and compressor muscles, indicates increasing importance of the tentacle. This increased development of the tentacle structures is found in genera in which the "Nebennase" is also undergoing marked development, and the differentiation of the tentacular apparatus together with the "Nebennase" as the sense organ of the animal.

10. The degree of degeneration of the eye. In some genera the eye is represented by a well-developed optic cup and lens; even an orbital opening may be present. In others the eye has degenerated to a small mass of pigment and is completely covered by bone: that is, the orbital opening is absent. Together with the greater degeneration of the eye is usually found an increased development of the tentacle structures and the "Nebennase".

11. The development of the m. levator quadrati. The m. levator quadrati plays a part in raising the palatoquadrate towards the neurocranium in the quadrato-basal articulation; it therefore plays a part in the kinesis of the skull. The degree of degeneration of this muscle will therefore be an index to the degree of akinesis of the palatoquadrate. In *Coscilia* in which the quadrato-basal articulation is degenerating and in which the skull is definitely akinetic, the muscle has degenerated almost completely.

12. The ganglia of the fifth and the seventh cranial nerves:

The normal Gymnophione condition of these ganglia seems to be the presence of two completely separate trigeminal ganglia and a smaller separate geniculate ganglion. Fusion of the two constituent trigeminal ganglionic masses or of the geniculate ganglion with the ganglion maxillo-mandibulare indicates a secondary condition. The presence of a forked geniculate ganglion, indicating the presence of a separate ganglion for the palatine nerve, possibly indicates a neotenic condition; it should however, be kept in mind that such a ganglion might reasonably represent a ganglion epibranchiale associated with the point of bifurcation of the ramus ventralis into the r. pharyngeus and the ramus more particularly associated with the hyoid gill cleft.

13. The absence of certain branches of the cranial nerves: The absence of the chorda tympani or the r. palatinus VII are indicative of a degeneration of these branches, and is therefore a secondary feature.

If the data available for the various genera are studied with the above features of taxonomic importance in mind, we find that Coecilia is the genus showing the greatest number of secondary and degenerating features. The nasal sacs depart from the general Gymnophione plan: the main nasal sac lacks a ventral indentation, the "Nebennase" lies in its own cavity in the maxillo-palatine; the tentacle structures are exceptionally well developed, the eye has degenerated almost completely and an orbital opening is absent. The skull is definitely akinetic: the quadrate-basal articulation and the m. levator quadrati are degenerating, the quadrate-stapedial articulation has disappeared almost completely, and the p. ascendens palatoquadrati is very firmly applied to the para-

quadrate. The ganglia of the cranial nerves also depart much from the primitive condition: a geniculate ganglion separate from the ganglion acusticum is absent and a quadrate-cranial passage is almost completely obliterated. *Coecilia* therefore shows many degenerate features and at the same time many specialised or secondary features. It can be considered as the most specialised of the *Gymnophione* genera studied.

Boulengerula shows almost the same features of specialisation and degeneration as *Coecilia*, but has not progressed as far from the primary condition as *Coecilia* has. For example, the skull is akinetic, but the articulations have not degenerated nearly as much as in *Coecilia*. The main nasal sac lacks a ventral indentation, but the "Nebennase" and the tentacle structures have not attained to the same degree of specialisation as in *Coecilia*. The eye, however, has degenerated even more than in the latter genus.

In Hypogeophis, judging from illustrations given by Marcus and Laubmann, the ventral indentation is not so well developed as in *Dermophis* and *Siphonops* and the "Nebennase" already lies in its own cavity in the maxillo-palatine. The eye is well developed and an orbital opening is present. The skull is stegokrotaphic and kinetic: both primary features. Except for the position of the "Nebennase", the skull represents the general plan very closely.

Ceotrypetes shows the "Nebennase" in its own cavity, but has a well developed main nasal sac with a ventral indentation, a well developed eye with a large orbital opening, and has normally developed tentacle structures. The skull is, however, xygokrotaphic and the animal is already losing its cranial kinesis, as the quadrate-stapedial articulation is in the process of being lost and the paraquadrates and the p.

ascendens palatoquadrati are very closely applied. Geotrypetes therefore shows more degenerate features than Hypogeophis, and must be considered as having progressed further from the primary plan than the latter.

Dermophis has a nasal organ exactly similar to that represented in the general plan. There is a well developed main nasal sac with a deep ventral indentation and a "Nebennase" lying in the same cavity as the main nasal sac and opening into the lateral portion of the latter. The eye is well developed as in Hypogeophis and Geotrypetes, and an orbital opening is present. The quadrato-stapedial articulation is degenerating and the p. ascendens palatoquadrati is firmly applied to the paraquadrate, the skull therefore becomes akinetic. The cranial nerves represent the primary condition, and a separate ganglion pro ramo palatino is indicated in the presence of a forked geniculate ganglion.

Siphonops has a nasal organ like that of Dermophis, the eye represents the same stage of development as in the latter and the tentacle structures show no sign of increased accentuation. The cranial nerves are like those of Dermophis with a few small differences; a small pterygoid is present in the adult animal, the articulations in the skull are well developed, and the skull is slightly kinetic.

These six genera can therefore be arranged as follows, starting with the genus departing least from the primary plan:

Siphonops

Dermophis

Hypogeophis

Geotrypetes

Boulengerula

Cocclia.

Ichthyophis and Scolecormorphus are the two presumably neotenic genera, with bones in the nasal region still unfused, and with the nasal sacs in Scolecormorphus also representing a neotenic condition; these latter in Ichthyophis resemble those of Dermophis and Siphonops closely. In Ichthyophis the quadrato-stapedial articulation is present as in Siphonops, but the quadrato-basal articulation has not developed; in Scolecormorphus the stapes together with the quadrato-stapedial articulation is absent. These conditions may be considered as neotenic. The two components of the trigeminal ganglion in both genera have fused. Ichthyophis on the whole differs very little from Siphonops and Dermophis except in the few instances mentioned above. But Scolecormorphus shows several more differences, such as the position of the quadrato-basal articulation, the position of the eye and the structure of the palate. Ichthyophis can therefore be placed near ~~//~~ Siphonops and Dermophis in the above list, but it is not quite clear where Scolecormorphus should be fitted in; not enough embryological data is available to determine its position in relation to the other genera.

The suppositious neotenic status of some genera as noted by Prof. de Villiers and the author are put forward as tentative; a final conclusion can only be reached upon the ontogenesis of the genera in question becoming known. Apart from the series of researches of Marcus and his pupils upon the Seychelles genus Hypogeophis, very little data regarding the later ontogeny of the Gymnophiona are available.

There is no point in comparing the skulls of adult living genera with apodal Stegocephalia such as the Aistopoda, since Marcus has proved that progressive ankylosis of the bones is a feature of the Gymnophiona cranial ontogeny.

In conclusion it may be pointed out that the tentative anatomical linear grouping of the genera investigated ~~finds~~ follows very closely that advocated by Marcus' pupil Tonutti (1932) who based his conclusions upon the conditions obtaining in the phallosome and associated muscles in the service of the copulatory apparatus.

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