SOME ASPECTS OF THE CRANIAL MORPHOLOGY OF URAEO-TYPHLUS NARAYANI SESHACHAR (APODA).

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(Plates IV-VI.)

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INTRODUCTION.

The genus Uraeotyphlus was originally included under Caecilia (part) Dum. & Bibr. until it was shown by Peters (1879) how Uraeotyphlus differed from the other genera; Peters, therefore, erected the new genus Uraeotyphlus to accommodate the three species known at the time. Nieden (1913), who followed Peters, included the three species of Caecilia,—C. malabaricus, C. oxyuris and C. seraphini under Uraeotyphlus; but the last species of Uraeotyphlus has subsequently been shown to belong to Geotrypetes by Parker (1927). Two more species were added later, namely, U. menoni and U. narayani, making in all four Oriental species. The last one was recently described by Seshachar (1939).

The important difference between the commonly occurring South Indian genera Ichthyophis and Uraeotyphlus in the arrangement of cranial bones is that in the former the parietal and squamosal approximate together dorsally (stegokrotaphy) while in the latter, a gap separates them (zygokrotaphy). The genera Dermophis, Hypogeophis, Caecilia, Cryptopsophis, Amphiumophis, Herpele, Gymnopis, Typhlonectes, Siphonops, Boulengerula and Gegenophis are related to Ichthyophis in regard to the arrangement of the parietal and squamosal while the remaining genera Rhinatrema, Geotrypetes, Praslinia, Bdellophis, Chthonerpeton and Scolecomorphus conform to the Uraeotyphlus plan. Recently Parker (1936) described a new genus from Cameroon, South Africa,—Idiocranium; in this also the parietal is not separated from the squamosal by a wide gap.

Wiedersheim (1879) having examined a single specimen of Caecilia oxyura (U. oxyurus) came to the conclusion that anatomically it was not very different from C. lumbricoides (C. gracilis) and C. rostrata (Hypogeophis rostratus), and remarked that the latter two species could very well be treated together. I reproduce his sentence (p. 27) here, for it chiefly concerns the genus Uraeotyphlus which is discussed in the present paper:

"Caecilia lumbricoides und Caecilia rostrata. Beide Arten zeigen nur so geringe Abweichungen dass sie fuglich zusammen abgehandelt werden konnen. Dasselbe gilt auch C. oxyura, insoweit er mit gelungen ist, an dem einem mir zu gebote stehenden Examplare ins klare zu kommen."

The cranial morphology of a large number of Apodan members was described by Wiedersheim, viz., I. glutinosus, C. lumbricoidea (C. gracilis), C. rostrata (H. rostratus), C. oxyura (U. oxyurus), Siphonops annulatus, Siphonops indistinctum (Chthonerpeton indistinctum); of these the accounts of the skull, hyoid apparatus, olfactory and auditory organs, the tentacle, the brain and its nerves chiefly concern us. It should be noted, however, that he described a species of Uraeotyphlus (U. oxyurus) as belonging to the genus Caecilia and similarly his two other examples C. rostrata and S. indistinctum are now regarded as species of the genera Hypogeophis and Chthonerpeton respectively.

¹ Bdellophis is merged with Scolecomorphus, see Barbour and Loveridge, 1928,

Peters (1881) noted that the skull of Uraeotyphlus closely resembled that of Ichthyophis, and, therefore, both differed considerably from that in the other genera. He described the gross morphology of the skull of U. oxyurus, having studied two specimens and remarked that the founding of the genus was definitely established. Describing the skull of U. oxyurus, he recorded the occurrence of separate intermaxillaria (premaxilla), a side piece on either side of the nasal (septomaxilla), a prefrontal, an orbital (postfrontal) and a pterygoid. The skull of Uraeotyphlus closely resembles that of Ichthyophis both coming from the same locality (South India)¹ except that the prefrontal does not reach the detached nasale (septomaxilla), and there is a gap between the squamosal (squamosojugale of Peters) and parietal. It is, however, significantly pointed out by Peters that these features may be individual variations or due to differences in age.

My object has been to describe in detail the morphology of the head of *U. narayani* and try to compare the anatomical details of this species with what has been described for other genera and finally to decide whether the erection of the new genus is justifiable.

MATERIAL AND METHODS.

The heads of larval and adult specimens of *I. glutinosus* and *U. narayani* secured from the Western Ghats were fixed in suitable fixatives (Bouin, Formol) and decalcified in a mixture of 70 per cent. alcohol containing 3 per cent. con. nitric acid (with phloroglucin). Alizarin transparencies of larval and adult animals were made for checking the skull preparations obtained by maceration. Sections were stained in Haematoxylin-eosin, Pasini, boraxcarmine-picro-indigocarmine and mucicarmine.

The entire lengths of the larval forms of I. glutinosus and of a juvenile specimen of U. narayani studied were as follows:

I. glutinosus: 3.8 (embryo), 7.0, 8.3, 10.0 and 12.7 cm.

U. narayani: 9.0 cm.

A single adult head of *Ichthyophis monochrous* was also sectioned for comparison. Heads of *Dermophis gregorii* Blgr., *Herpele ochrocephala* Cope, *Scolecomorphus uluguruensis* Barb. and Lov., and *Boulengerula boulengeri* Torn. were also sectioned and studied.

OBSERVATIONS.

The skull.—It is customary to study the skull by dividing it into regions, viz., frontal, parietal, occipital, palate and upper jaw, suspensorium and bones in association with the sense-capsules. But in the apodan skull where some of the bones fuse with adjacent ones, a

¹ Sarasins (1890) remark that one species of *Uraeotyphlus*, *U. africanus* (*U. seraphini*, Nieden 1913) is found in Africa, while there is not even a single record of the occurrence of an *Ichthyophis* from the Ethiopian Continent; Parker (1927), however, correctly referred this species of *Uraeotyphlus* to *Geotrypetes* and thus removed a distributional anomaly.

narration based on this classification would entail a repetition of certain parts and therefore, I have adopted the following mode of description:

NASO-ETHMOID REGION:

(bones in association with the olfactory capsule). The nasal capsule). The septomaxilla

The sphenethmoid.

The cartilages of the nasal region.

ORBITO-TEMPORAL REGION:

The frontal

The parietal

The pre- and post-frontal

(the frontal, pre- and post-frontals belong to the orbit; the parasphenoid and pleurosphenoid which belong to this region are described under the occipito-auditory region).

OCCIPITO-AUDITORY REGION:

The os Basale

The stapes.

THE UPPER JAW, PALATE AND SUSPENSORIUM:

The premaxilla

The maxillopalatine

The pterygoid

The prevomer

The squamosal

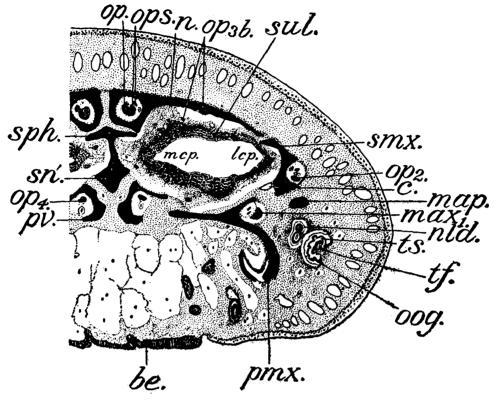
The quadrate

The only cartilage bones in the skull of Apoda are the os Basale, the stapes, and the quadrate.

Naso-ethmoid region.

The nasal (paired).—The nasals appear anteriorly as two vertical pieces of bone on either side of the prenasal prong. Posteriorly (see text-figs. 1, 8, 9, n) a horizontal piece is noticed dorsally to the olfactory chamber and the two (vertical and horizontal of each side) unite to enclose the main trunk of the ophthalmicus profundus nerve. feature of the roofing bone (Pl. IV, fig. 1) is noticed till we reach the frontal which appears underneath the nasal and a few sections posteriorly the nasal disappear.

The septomaxilla (paired).—(Nariale, Marcus, Stimmelmayr and Porsch 1935). The septomaxilla (Pl. IV, fig. 1, text-fig. 1, smx.) which is noticed anteriorly to the appearance of the maxillopalatine in sectional views gives exit (through foramen epiphaniale?) to a branch of the ophthalmicus profundus (op_2) nerve and is not united with the nasal (n.) above or with the premaxilla (pmx.) below. The contour of the bone in Uraeotyphlus differs slightly from that in Ichthyophis. A figure of a model of the septomaxilla is given by Sarasins (1890) where an upper, an external and an internal lamella are delineated. In U. narayani it appears posteriorly to the anterior paris as a small 1-shaped bone clasping the lateral portion of the olfactory sac; the dorsal limb extends towards the nasal, while the lower limb is in contact with a cartilage (c). Anterior to the appearance of the prefrontal, the septo-



Text-fig. 1.—Uraeotyphlus narayani Seshachar.

Transverse section in the septomaxilla region, posterior to fig. 8: ×33.

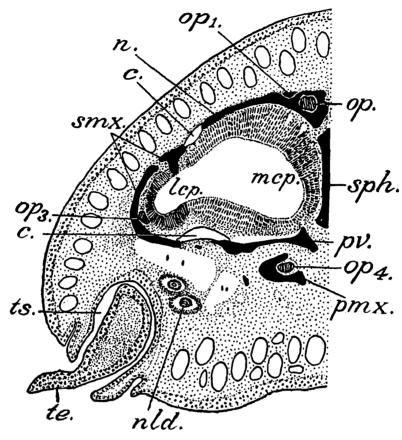
be., buccal epithelium; c., nasal cartilage; lcp., lateral cavum nasale principale; map., maxilloplatine bone; $max_1.$, medial division of r. maxillaris V; mcp., median cavum nasale principale; n., nasal bone; nld., nasolacrimal duet; oog., opening of orbital gland; op., r. ophthalmicus profundus V; op., branch of r. ophthalmicus profundus; op., branches of op., branches of op., branches of op., prevomer; smx., septomaxilla; sn'., ossified septum nasi; sph., sphenethmoid; sul., sulcus; tf., tentacular fold; ts., tentacular sac.

maxilla disappears from sections. In the juvenile specimen of *Uraeotyphlus* that I have examined, the septomaxilla has not reached the maximum development noticed in the adult, but the adult configuration and the passage of the nerve (op_2) can be clearly made out.

In Scolecomorphus (text-fig. 2, smx.) anterior to the external naris the septomaxilla appears as a small piece of bone on the ventral aspect of the olfactory sac externally to the premaxilla; in the plica which depends into the cavum nasale principale, a portion of the bone is noticed which however, in posterior sections, unites with the limb situated below the cavum nasale principale after the latter bone gives exit to a branch of the ophthalmicus profundus (op_3) . The septomaxilla forms a horseshoe-shaped bone in the hollow of which the lateral part (lcp.) of the cavum nasale is located. The bone disappears in the region where the eye and prefrontal appear in sections.

The sphenethmoid.—This bone starts in the nasal septum (text-fig. 1, sph.) and invades the preoptic roots also. Anteriorly the bone appears as a median pillar and on the dorsolateral aspects of which the broad internal portion of each nasal rests. Ventrally the sphenethmoid

is slightly broadened with a cartilaginous tip (see cartilages of the nasal region). Posteriorly the sphenethmoid encloses the dorsal and ventral olfactory divisions of the nervous olfactorius (text-figs. 3, 9, don, von.)



TEXT-FIG. 2.—Scolecomorphus uluguruensis Barbour & Loveridge.

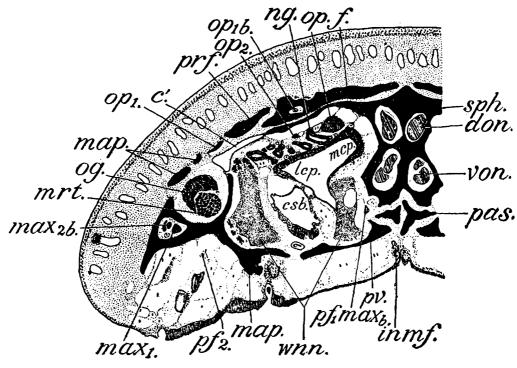
Transverse section in the septimaxilla region: ×55.

c., nasal cartilage; lcp., lateral cavum nasale principale; mcp., median cavum nasale principale; n., nasal bone; nld., nasolacrimal duct; op_1 , op_2 , op_4 ., branches of r. ophthalmicus profundus; pmx., premaxilla; pv., prevomer; smx., septomaxilla; sph., sphenethmoid; te., tentacle; ts., tentacular sac.

and in a slightly prechoanal region, five canals can be made out; two dorsal for the dorsal olfactory nerves, two ventral for the two ventral olfactory nerves and a median one (sce text-fig. 9, von_b) in which a branch of the right ventral olfactory nerve runs. In text-fig. 3, a large bony extension running dorsally to the olfactory chamber on each side is given off and in this region, only four canals can be seen in the sphenethmoid. The gap between the lateral extension of the sphenethmoid and a dorsal limb of the maxillopalatine is bridged by a piece of cartilage (c'.). In the region of the olfactory lobes, the sphenethmoid shows the typical girdle shape with the lateral extension still persisting. Dorsally an infrafrontal (interfrontale?) extension of the sphenethmoid is also noticed as described in Hypogeophis by Marcus, Stimmelmayr and Porsch (1935), and this point is indicated by these authors when they say that (p. 414):

Die bei Siphonops noch das Schädeldach bildende Deckplatte, die bei Hypogeophis von den Stirnbeinen verdeckt wird, wurde als Dermethmoidale bezeichnet und der dorsale ebenfalls der male Fortsatz des Processus interfrontalis.

The ophthalmicus profundus branch is enclosed in the dorsolateral wall of the sphenethmoid in posterior sectional views of *Uraeotyphlus*. In



Text-fig. 3.—Uraeotyphlus narayani Seshachar.

Transverse section, posterior to fig. $9: \times 30$.

c', c''., nasal cartilages; csb., "choanenschleimbeutel"; don., dorsal olfactory nerve; f., frontal bone; inmf., intermaxillary gland of Fahrenholz; lcp., lateral cavum nasale principale; map., maxillopalatine; max_1 ., medial division of r. maxillaris V; max_2b ., branches of max_2 ; mcp., median cavum nasale principale; mrt., m. retractor tentaculi; ng., nasal gland; og., orbital gland; op., r. ophthalmicus profundus V; op_1 , op_2 ., branches of r. ophthalmicus profundus; op_1b ., branch of op_1 ; pas., parasphenoid portion of os Basale; pf_1max_b ., palatinus facialis plus a branch of r. maxillaris V; pf_2 ., lateral division of palatinus facialis; prf., prefrontal bone; pv., prevomer; sph., sphenethmoid; von., ventral olfactory nerve; wnn., wall of "Nebennase".

the optic region, the sphenethmoid becomes incomplete midventrally and forms only the ventrolateral boundary for the brain; further in this region the ophthalmicus profundus is not enclosed in a bony canal. The infrafrontal sphenethmoid persists. The foramen opticus (plus oculomotorius) appears and the sphenethmoid is noticed only dorsally and ventrally as rounded pieces of bone. However, posteriorly cartilage appears in these two portions representing the orbital (dorsal) and trabecular (ventral) cartilages.

In Hypogeophis, the ethmoidal region, which I have designated as the sphenethmoid following de Beer (1937), is composed of an anterior mesethmoid or presphenoid (arising in nasal septum), a dorsal dermethmoid and in the sides by the sphenethmoid (pleurethmoid plus sphenorbital) and a preethmoid (in connexion with the prevomer). However, de Beer considers that the sphenethmoid represents the presphenoid and orbitosphenoid bones.

The formation of an eminentia olfactoria (processus conchoides, Sarasins 1890) is characteristic of only some genera of Apoda. In *I. glutinosus* and *I. monochrous* an eminentia olfactoria is formed by the prevomer and sphenethmoid. A ventrolateral extension of the

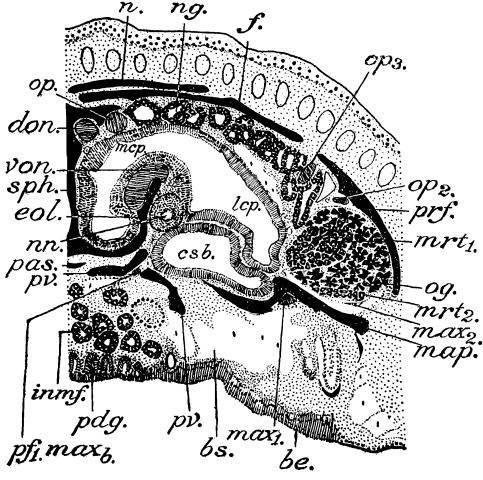
sphenethmoid projects into the nasal sac along with a portion of the prevomer so much so the cavity of the olfactory chamber is divided into a lateral and an inner (median) portion. A similar arrangement is also seen in Geotrypetes and Dermophis (Norris and Hughes 1918). However, in the latter animal the nasopremaxilla and the prevomer give rise to the elevation in the olfactory chamber anteriorly while in the posterior sections, the prevomer and the sphenethmoid contribute to it. Similarly in the case of Ichthyophis, the maxillopalatine sends a small projection on the external aspect of the prevomer. The formation of the eminentia olfactoria is totally wanting in Herpele, Caecilia and Hypogeophis (Wiedersheim 1879; Norris and Hughes 1918; Marcus, Stimmelmayr and Porsch 1935). In U. narayani also an eminentia olfactoria is absent and therefore a lateral chamber of the nasal sac, as described by Sarasins (1890) for I. glutinosus, is also absent.

In the investigated examples like Boulengerula, the degenerate eye is covered by squamosal while in Caecilia and Herpele the eye is covered by maxillopalatine and the eye muscles and eminentia olfactoria are absent, whereas in Ichthyophis, Dermophis and Geotrypetes an eminentia olfactoria is developed and the eye is not covered by bone. Scolecomorphus the eye is degenerate and is not covered by any bone, U. narayani forms a but an eminentia olfactoria is well developed. good link between Boulengerula, Caecilia and Herpele on the one hand and Ichthyophis, Dermophis and Geotrypetes on the other and it is noticed that the eye in Uraeotyphlus is not covered, the eye muscles are well developed with an optic nerve, but an eminentia is absent. might be thought that there is a correlation between the degeneration of the eye consequent upon covered nature of it as in Herpele and Boulengerula, etc., and the absence of an eminentia, but the presence of a well developed eye and the absence of an eminentia in Hypogeophis and Uracotyphlus and the presence of a degenerate eye and the possession of an eminentia in Scolecomorphus (see text-fig. 4, eol.) rules out any such relation.

The cartilages of the nasal region.—The prenasal prong appears as a thin cartilaginous structure between the premaxillae. In the region where the cartilaginous nasal septum (see text-fig. 8, sn.) which gives rise to the prong anteriorly widens to give rise to short tectal (tn.) and solum (son.) cartilages, it is noticed that the lateral sinus of the olfactory chamber (cavum nasale principale) is bounded externally by a crescentic cartilage (cc.) from which a short projection is noticed to enter the plica (pl.). In sections anterior to the nares, this crescentic cartilage forms a part of the roof and also the floor of the cavum nasale The ventral cartilaginous limb of this in posterior sections lies between the lower limb of the septomaxilla and the premaxilla (text-fig. 1, c.) and further posteriorly is seen in between the inner portion of the maxillopalatine and prevomer and joins the bony solum of the sphenethmoid bone. Quite independently of the cartilages mentioned above, there appears a cartilage (see text-fig. 9, c.') between the prefrontal and frontal and spreads posteriorly between the maxillopalatine and the sphenethmoidal tectum (text-fig. 3, c'.) and fuses with

¹ See The olfactory organ and associated glands.

the latter; in other words it is an anterior cartilaginous extension from the tectum.



Text-fig. 4.—Scolecomorphus uluguruensis Barbour & Loveridge.

Transverse section showing eminentia olfactoria: ×55.

be., buccal epithelium; bs., blood sinus; csb., "choanenschleimbeutel"; don., dorsal olfactory nerve; eol., eminentia olfactoria; f., frontal bone; inmf., intermaxillary glands of Fahrenholz; lcp., lateral cavum nasale principale; map., maxillopalatine; max₁., medial division of r. maxillaris V; max₂., lateral division of r. maxillaris V; mcp., median cavum nasale principale; mrt_1 ., mrt_2 ., two parts of m. retractor tentaculi; n., nasal bone; ng., nasal gland; nn., "Nebennase"; og., orbital gland; op., op₂., op₃., r. ophthalmicus profundus (op) and its branches; pas., parasphenoid portion of os basale; pdg., postdental gland; pf_1max_b ., palatinus facialis plus a branch of r. maxillaris V; prf., prefrontal; pv., prevomer; sph., sphenethmoid; von., ventral olfactory nerve.

In the region where the anterior portion of the "Choanenschleimbeutel" (text-fig. 3, csb.) is noticed between the two portions of the "Nebennase", a horseshoe-shaped cartilage clasps the choanal chamber; posteriorly a bit of this cartilage (c''.) is noticed dorsally to the maxillopalatine bone and this finally disappears.

ORBITO-TEMPORAL REGION.

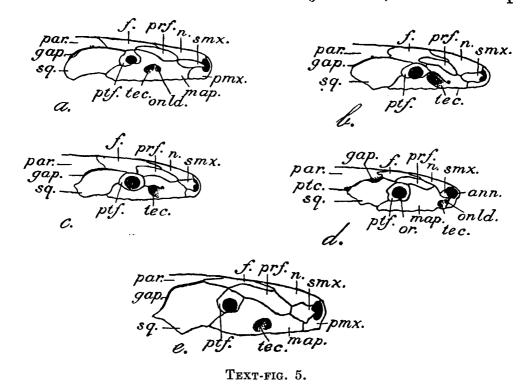
The frontal (paired).—(text-figs. 3, 9, f.) The frontals meet each other in a close suture (Pl. IV, fig. 1) so that the sphenethmoid is not visible externally, a feature also noticed in Gymnopis (Peters 1879), Hypogeophis (Marcus, Stimmelmayr and Porsch 1935), Ichthyophis and Chthonerpeton. In Siphonops (Wiedersheim 1879) between the nasopremaxilla, the frontals and parietals of either side, the sphenethmoid

is visible as a diamond-shaped area; in Herpele squalostomum, Peters (1879) shows the sphenethmoid in two areas, viz., between the naso-premaxilla and the frontals and between the latter bones and parietals. Parker (1936) who reproduced a figure of the same species of Herpele for purposes of comparison with Idiocranium, indicates the sphenethmoid as visible externally only between the nasopremaxilla and the frontals; this probably is a variable feature. In Scolecomorphus (Peters 1895) the roofing bones approximate and, therefore, a part of the sphenethmoid is not visible externally, a point also confirmed by de Villiers (1938). In Boulengerula (Peter 1908), the bone is visible mainly between frontals. From the figures of Norris and Hughes (1918) it can be concluded that the sphenethmoid is visible dorsally owing to the incomplete approximation of the nasopremaxilla and the frontals in Dermophis and also in Herpele.

The parietal (paired).—(text-fig. 10, par.) They appear underneath the frontals and posteriorly form not only the roof but a part (dorsal) of the side, articulating with the os Basale (the pleurosphenoid, prootic and exoccipital parts).

The pre- and post-frontal (paired).—These two bones may be considered together. In Ichthyophis and Uraeotyphlus only these two bones are present, in all other Apoda they are absent, except in Scolecomorphus (Peter 1895, 1908) in which only a prefrontal is noticed (textfig. 4, prf.). In the South Indian genera studied by me, the prefrontal (described as Preorbital by J. Müller) is bounded by the nasal and maxillopalatine anterolaterally and posterolaterally by the frontal and prefrontal. In the case of I. glutinosus, the figures of Sarasins (1890) show that the anterior tip of the prefrontal reaches the posterior border of the septomaxilla. In some of the skulls that I have examined this is not so, for the prefrontal is separated from the septomaxilla by the juxtaposed portions of the nasal and maxillopalatine. The sectional views of well grown adults of both I. glutinosus and U. narayani also exhibit the latter feature. A side view (see text-figs. 5a, 5c and 5e) depicts the condition enumerated above where the maxillopalatine and the nasal are not separated by the septomaxilla or prefrontal.

The exact contour of the postfrontal differs in individuals. case of I. qlutinosus, Sarasins remarked that the bone was always 'halfmoon '-shaped confirming the observation of J. Müller. Wiedersheim (1879) noted that the bone was ring-like normally and the crescentic nature of it was due to injury and Peters (1879) also remarked the same In the figure drawn by Nieden (1913, p. 3), a ringabout the bone. like postfrontal (see text-fig. 5c, ptf.) has been shown following Wiedersheim and Peters. In U. narayani, only one type is found, i.e., the circular. In one series of sections of a large animal the postfrontal is ring-like while in another (of a smaller size) it is crescentic with the gap towards the maxillopalatine. In the juvenile specimen of U. narayani (9 cm.), which I have studied, it is crescentic. The skulls of large specimens that have been prepared by maceration show a ring-like post-It is therefore abundantly clear that in *U. narayani*, the cresfrontal. centic nature of the postfrontal is noticed in smaller animals while in the well grown adults, a ring-like postfrontal is present. In my figures (Pl. IV, fig. 1 and text-fig. 5d) I have shown the bone ring-like. Having examined a large number of skulls of *I. glutinosus*, the crescentic post-



Ichthyophis glutinosus (Linn.). Skull, lateral aspect.

a. (after Sarasins, 1890): $\times 4.5$.

b. original: $\times 4.5$.

c. (after Nieden, 1913 modified): $\times 4.5$.

Uraeotyphlus narayani Seshachar. Skull, lateral aspect, $d. \times 4.5$.

Ichthyophis monochrous (Bleek.). Skull, lateral aspect, e. ×4.5.

ann., anterior nares; f., frontal; gap., fossa between squamosal and parietal; map., maxillopalatine; n., nasal; onld., opening of nasolacrimal duet; or., orbit; par., parietal; pmx., premaxilla; prf., prefrontal; ptc., pteroccipital cavity; ptf., postfrontal: smx., septomaxilla; sq., squamosal; tec., tentacular canal.

frontal is noticed in a majority of them while the presence of a circular one is not uncommon. In my preparations the ring-like postfrontal belongs to one which is easily the biggest among the macerated skulls and since Sarasins (1890) have shown a crescentic postfrontal in an equally large skull the shape of the bone is obviously subject to varia-On the other hand, in *U. narayani*, the shape of the postfrontal is always circular in well grown individuals. Peculiarly there is another feature of variation met with in these South Indian apodan genera to which reference has been made briefly already. In the figures by Sarasins (1890) of I. glutinosus, the septomaxilla and prefrontal (text-fig. 5a) meet each other; in I. monochrous (text-fig. 5e) the topographical relationship of bones is exactly like that in I. glutinosus. But in the skulls of I. glutinosus studied by me, in some where the postfrontal is crescentic the prefrontal and septomaxilla are separated by the extension of nasal and maxillopalatine. The other type where the postfrontal is circular, the close apposition of the prefrontal and septomaxilla is also seen. I do not like to establish any correlation between the

shape of the postfrontal and the nature of approximation of prefrontal and septomaxilla without examining the other species, but it may be remarked that among all the skulls of *I. glutinosus* examined by me not one was noticed to possess a circular postfrontal and with prefrontal and septomaxilla separated from each other. In this connexion, the statement of Peters (1881) based on an examination of two skulls of Caecilia oxyura (U. oxyurus) that if the prefrontal reached the 'losgelosten nasale' (septomaxilla), it would closely approximate to the condition delineated for *I. glutinosus* is rather significant. This condition, i.e., the separated prefrontal and septomaxilla particularly characterises all the skulls of *U. narayani* examined by me.

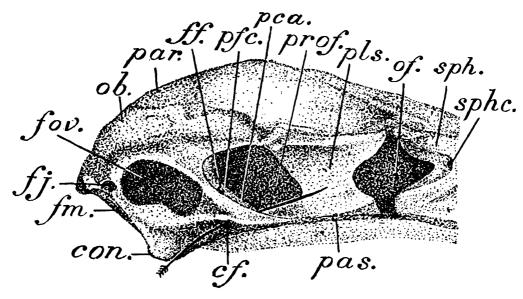
In Scolecomorphus kirkii (Peter 1895, 1908) and in S. uluguruensis (de Villiers 1938) there is a separate prefrontal but a postfrontal is absent; in Hypogeophis (Marcus, Stimmelmayr and Porsch 1935) a prefrontal appears in the larval stages but in the adult it fuses with the frontal and lachrymal and the composite bone is called a temporal.

OCCIPITO-AUDITORY REGION.

The os Basale.—Under this term, Sarasins (1890) described the composite skeletal framework formed by the fusion of parasphenoid with its anterior rostrum (Pl. IV, fig. 2, r.) (called processus cultriformis in Hypogeophis) between the prevomers, basioccipital, supraoccipital and otic ossification and the pleurosphenoid,—the latter forming the lateral wall of the cranium posterior to the optic (plus oculomotor) foramen. According to Marcus, Stimmelmayr and Porsch (1935) the os Basale is contributed by nine different bones, viz., basi-, pleuro-, supra-, and infra-occipitals, an epiotic, a pleurosphenoid, two parasphenoids and otic capsule.

A similar os Basale is also found in *U. narayani* and on its ventral face, orifices for the carotid artery (Pl. IV, fig. 2, cf.) and jugular foramina are located. In the lateral aspect of the cranium (text-fig. 6), the side wall reveals the optic (plus oculomotor) (of.), prootic (prof.) and facial (ff.) foramina. Roughly the position of some bones which have fused may be made out. Posterior to the optic (plus oculomotor) foramen is the pleurosphenoid bone (pls.) which commences from the anterior margin of the prootic foramen. The prootic (prof.) and facial (ff.) foramina are accommodated in the prootic region. A separate foramen for the oculomotor nerve is not seen, and in those forms where the third nerve is described in the adult, it enters the cranium along with the second nerve through the optic foramen. In the larval stages also there is no separate foramen in the cartilaginous wall and therefore, a pila metoptica is absent. As suggested by de Beer (1937) the cartilaginous wall which separates the optic and trigeminal foramina is a pila antotica produced far anteriorly. The trigeminal (prof.) and facial (ff.) foramina are separated by a bony bridge,—the prefacial commissure (pfc.) both in Ichthyophis and Uraeotyphlus.

The parasphenoidal portion of the os Basale gives rise to the basipterygoid process (Pl. IV, fig. 2, bp.) with which the processus pterygoideus (ppt.) of the quadrate is united syndesmotically and since this joint is identical with the basal articulation found in other Apoda being situated anteriorly to the facial nerve, it must be called a basal joint while in others it is a basal articulation of the cartilaginous facets of the processus pterygoideus and basipterygoid process.



Text-fig. 6.—Uraeotyphlus narayani Seshachar.

Side view of cranium showing nerve foramina: $\times 15$.

cf., carotid foramen; con., condyle; ff., facial foramen; fj., jugular foramen; fm., foramen magnum; fov., foramen ovale; ob., os Basale; of., optic plus oculomotor foramen; par., parietal; pas., parasphenoid portion of os Basale; pca., palatine canal; pfc., prefacial commissure; pls., pleurosphenoid portion of os Basale; prof., protoic foramen; sph., sphenethmoid; sphc., sphenethmoidal canal for r. ophthalmicus profundus.

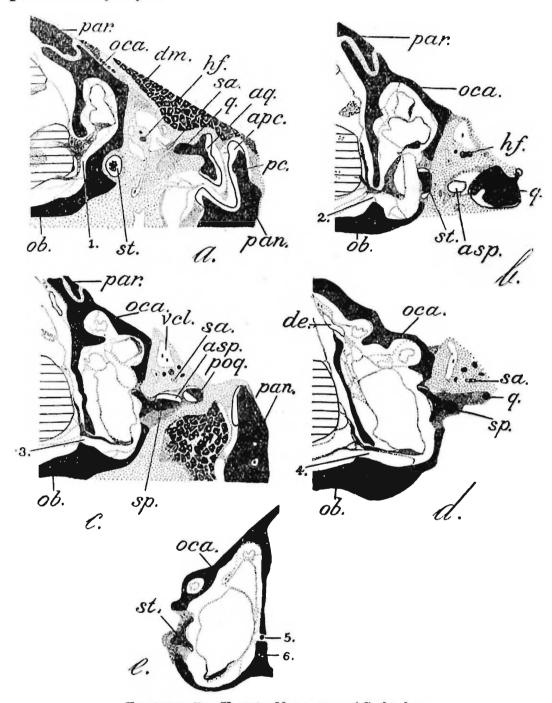
There is a well formed depression (sella turcica), in the os Basale for the accommodation of the pituitary body in *Uraeotyphlus*, *Dermophis*, *Scolecomorphus*, *Boulengerula* and *Herpele*, but in *Ichthyophis* it was not seen.

The stapes (text-fig. 7 a-d, st.).—(ossified operculum) with its stapedial process (sp.) is bony as in other Apoda and invariably the stapedial process articulates by its cartilaginous facet (asp.) with a similar facet of the processus oticus. The operculum is, however, stated to be absent by Wiedersheim (1879), Kingsley and Ruddick (1899), Kingsley (1900), M. Fürbringer (1922) and Stadtmüller (1936). The absence of the middle ear is ascribed to a borrowing mode of life by Versluys (1927, 1931). However, in Scolecomorphus (de Villiers 1938) there is no stapedial articulation since the stapes is absent (see page 19). In Dermophis (de Jager 1939) the stapedial process unites with the processus oticus which, however, is not seen in my preparations.

As in *Ichthyophis*, the stapedial artery in *Boulengerula* passes through a canal in the stapes before entering the cranioquadrate passage thus simulating the condition noticed in *Ranodon*, Geckones and mammals.

Marcus (1933) has pointed out that the stapes in *Hypogeophis* is in blastematous continuity with the hyoid in early stages of development and therefore it is a hyoid derivative. If this is proved for other

apodan genera also, then the suspension of the pterygoquadrate or quadrate is hyostylic.



Text-fig. 7.—Uraeotyphlus narayani Seshachar.

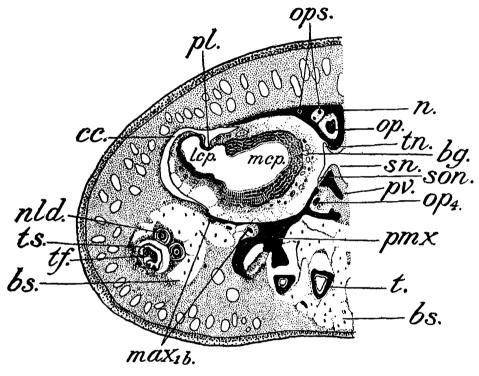
a-e., consecutive transverse sections in the auditory region: $\times 22$.

apc., articular facet of the processus condyloides; aq., articular facet of the quadrate; asp., articular process of stapes; de., ductus endolymphaticus; dm., M. depressor mandibulae; hf., r. hyomandibularis facialis; ob., os Basale; oca., otic capsule; pan., pseudoangular; par., parietal; pc., processus condyloides; poq., processus oticus of quadrate; q., quadrate; sa., stapedial artery; sp., stapedial process; st., stapes; vcl., vena capitis lateralis; l., auditory orifice for the utricular nerve; l., l.

THE UPPER JAW, PALATE AND SUSPENSORIUM.

The premaxilla (paired).—The first bony structure one meets with in the sectional views of the anterior narial region is the premaxilla

(Pl. IV, figs. 1, 2 and text-fig. 8, pmx.). The premaxilla of either side is noticed to be pierced by blood vessels and branches of ophthalmicus profundus nerve. It is also seen that there is an oval cartilage of the sphenethmoid between the premaxillae of either side and in embryos, this cartilage projects as the prenasal prong (Peter 1898, de Beer 1937). Posteriorly, the premaxilla forms partly the internal boundary of the olfactory organ and a principal branch of ophthalmicus profundus (text-fig. 8, op_4) and a ramulus from the median branch of maxillary V run within it before gaining exit. In the region where the anterior portion of the "Nebennase" is met with, the premaxilla disappears from sections.



Text-fig. 8.—Uraeotyphlus narayani Seshachar.

Transverse section anterior to fig. 1: \times 33.

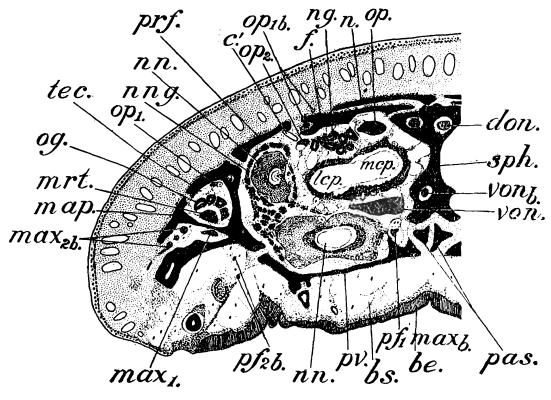
bg., Bowman's gland; bs., blood sinus; cc., crescentic cartilage; kcp., lateral cavum nasale principale; mcp., median cavum nasale principale; max_{1b} , branches of max_{1} ; n., nasal; nld., nasolacrimal duct; op., op_{4} , op., ophthalmicus profundus and branch respectively; ops., branches of op to skin; pl., plica; pmx., premaxilla; pv., prevomer; son., solum nasi; sn., septum nasi; t., tooth; tf., tentacular fold; tn., tectum nasi; ts., tentacular sac.

The fusion of the premaxilla with the nasal and septomaxilla to form a nasopremaxilla is a common feature of the apodan genera. In Hypogeophis, Caecilia, Herpele, Gymnopis, Chthonerpeton, Siphonops, Boulengerula (Peter 1908), Dermophis (Norris and Hughes 1918, de Jager 1939), Idiocranium (Parker 1936) a fused nasopremaxilla is noticed. In I. glutinosus, I. monochrous, U. narayani and Scolecomorphus (Peter 1908) the nasals, premaxilla and septomaxilla are always separate though de Beer (1937) points out that these bones fuse in I. glutinosus.

The maxillopalatine (paired).—The anteriormost part of the maxillopalatine is met with in sections behind the anterior nares (Pl. IV

¹ See The olfactory organ and associated glands,

figs. 1, 2 and text-fig. 1, map.). In the region where the two nasolacrimal ducts enter into the "Nebennase" the outer portion of the maxillopalatine is seen as a horseshoe-shaped structure enclosing the "Nebennase" In the choanal region the lateral branch of the palatinus facialis passes through a foramen in this bone and runs ventrally to it. Further posteriorly where the tentacular canal (text-fig. 9, tec.) in the maxillopalatine (map.) is noticed dorsally, the lateral (max_{2b}) and medial (max_1) maxillary branches run ventrally in the bone separated from each other. Dorsally to the tentacular canal, the ophthalmicus profundus branch (op_2) runs in the maxillopalatine. In the optic region, the two passages for the maxillary ramuli are lost and post-optically, it is noticed that the anterior end of the pterygoid articulates with the posterior tip of the maxillopalatine by means of connective tissue (see text-fig. 10, pt., map.).



Text-fig. 9 .- Uraeotyphlus narayani Seshachar.

Transverse section posterior to fig. 1: \times 33.

be., buccal epithelium; bs., blood sinus; c'., nasal cartilage; don., dorsal olfactory nerve; f., frontal; lcp., lateral cavum nasale principale; map., maxillopalatine; max₁., medial division of r. maxillaris V; max_{2b}., branches of max₂; mcp., median cavum nasale principale; mrt., M. retractor tentactori; n., nasal; ng., nasal gland; nn., "Nebennase"; nng., glands of "Nebennase"; og., orbital gland; op., op₁, op_{1b}, op₂., r. ophthalmicus profundus and branches; pas., parasphenoid portion of os Basale; pf, max_b., palatinus facialis plus a branch of r. maxillaris V; pf_{2b}., branch of the lateral division of palatinus facialis; prf., prefrontal; pv., prevomer; sph., sphenethmoid; tec., tentacular canal; von., ventral olfactory nerve; von_b., branch of von.

In Boulengerula, it is noticed by de Villiers (1938) that the suture between the posterior portion of the premaxilla of the nasopremaxilla and the maxillopalatine is lost and therefore the maxillopalatine also fuses with the anterior bones,—an instance of further consolidation of the bones of the maxillary segment.

In Hypogeophis (Marcus, Stimmelmayr and Porsch 1935) the maxillo-palatine is formed by the fusion of maxilla, palatine and lachrymal and probably in Ichthyophis, the first two go to form the composite bone.

Two rows of teeth can be distinguished; an outer and an inner. While the outer row is borne upon the premaxilla and the maxillopalatine, the inner row is carried by the prevomer and the maxillopalatine. Between the two rows of teeth, there is a large interdental area and glands occupy this region and these are described separately (see The glands of buccal cavity). However, the second row of maxillopalatine teeth may form an incomplete row. In Scolecomorphus and Boulengerula (Peter 1908) the teeth of the second row are absent near the choana, while anteriorly and posteriorly the prevomer and maxillopalatine are dentigerous.

The pterygoid (paired).—This bone (Pl. IV, fig. 2 and text-fig. 10, pt.) which is situated between the posterolateral aspect of the maxillopalatine and the basipterygoid process of the os Basale, does not fuse with the quadrate to form a pterygoquadrate in I. glutinosus, I. monochrous and *U. narayani*. The pterygoid (Pl. IV, fig. 2, pt.) and the os Basale are separated by a large vacuity,—the mediopalatinal cavity (mpc.) which is filled with connective tissue in the living animal. posterior sectional views where the articular facet of the os Basale (basipterygoid process) is met with, the anterior portion of the processus pterygoideus of the quadrate is noticed dorsally to the pterygoid In Chthonerpeton (Peters 1879), Ichthyophis (Sarasins 1890), Idiocranium (Parker 1936) and in I. monochrous and Uraeotyphlus¹ the pterygoid is an independent bone. In the other genera investigated a pterygoquadrate has been described, this is surmised to be formed by the fusion of the pterygoid and quadrate, though developmentally it is not substantiated. In Boulengerula (Peter 1908, de Villiers 1938), Scolecomorphus (de Villiers 1938), Dermophis (de Jager 1939), and also in Herpele, a pterygoquadrate is seen. Wiedersheim (1879) was not able to discover a pterygoid in Siphonops, Chthonerpeton, Hypogeophis rostratus and Caecilia and he referred the "doubtful bones" in between the maxillopalatine and the processus pterygoideus as Jugale (?) or postpalatine (?). Luther (1914) in his figures 4B and C shows a well marked pterygoid in Siphonops (dentigerous) while in Caecilia, a posterior portion of the maxillopalatine is shown as pterygoid. It is just possible that the processus pterygoideus of the pterygoquadrate reaches the maxillopalatine with no definite bone in between. In Hypogeophis alternans an independent quadrate or the formation of a pterygoquadrate is described by Marcus, Winsauer and Hueber (1933) and is depicted in their figures 3, 19 and 23.

The prevomer (paired).—The prevomer (Pl. IV, fig. 2 and text-figs. 1, 3, 8, 9, pv.) which forms the roof of the palate anteriorly is bounded by the premaxilla or the premaxillary part of the nasopremaxilla anteriorly, the maxillopalatine laterally and the parasphenoidal rostrum

¹ Peter (1908) was not able to discover the nature of the pterygoid (united with quadrate or free) in *Uraeotyphlus* and *Scolecomorphus*.

² Parrington and Westoll (1939) remark that the term prevomer is synonymous with vomer and must be dropped,

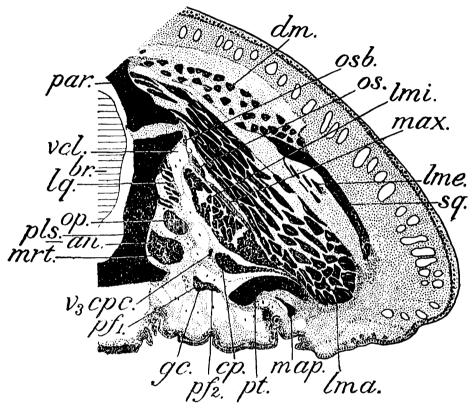
of the os Basale mesially. This rostrum may or may not be visible externally in macerated skulls. In *Ichthyophis*, the prevomers of either side meet each other mesially, and only a very small portion of the rostrum is seen; the internal portion lies between the prevomers and the base of the sphenethmoid. In *U. narayani*, the prevomers are wide apart and between these bones the rostrum is seen. In one specimen of *U. narayani* whose sections are figured, the rostrum is double, but in the juvenile one and the other adults there is only a single one.

The second row of teeth belonging to the upper jaw is arranged as an arc of a circle on each prevomer. In the majority of cases the prevomer forms the anteromedian boundary of the choana (Ichthyophis, Uraeotyphlus, Scolecomorphus, etc.), while in Dermophis (D. thomensis, D. seychellensis, D. mexicanus, Parker 1936) and Boulengerula (Peter 1908) the prevomer lies far distant from the choanal opening. It has already been remarked that the prevomer contributes to the formation along with a limb of the sphenethmoid of an eminentia olfactoria, as in I. glutinosus, I. monochrous, Dermophis (Norris and Hughes 1918), Geotrypetes and Scolecomorphus (see Wiedersheim 1879, Figs. 32-34 and 37-40). The bone is pierced in Uraeotyphlus by the ventral ramulus of the ophthalmicus profundus nerve (op_4) anteriorly and posteriorly by the palatinus facialis (pf_1max_b) as in other Apoda. In the choanal region the prevomer articulates with the rostrum referred to above and the bone disappears a few sections posteriorly to the choana.

The squamosal (paired).—(Paraquadrate Gaupp., Peter., Marcus, Winsauer and Hueber., Marcus, Stimmelmayr and Porsch., Jugale Sarasins., Squamosojugale Peter., Peters).

It has already been remarked that the stegokrotaphic nature or zygokrotaphy of squamosal and parietal is utilised for purposes of taxonomy and the presence of a large gap between the parietal and squamosal in Uraeotyphlus (Pl. IV, fig. 1, gap.) separates it from its South Indian congener Ichthyophis. However, in Ichthyophis, a thin cleft is figured by Sarasins between the above named bones; but Wiedersheim (1879) does not show any cleft thereby making it a typically stegokrotaphic cranium. Peter (1908) refers to this feature as probably a variation. This is not an individual variation or due to differences in growth as Peters (1881) imagined it to be, for, having studied a large number of skulls of Ichthyophis and Uraeotyphlus, I notice a thin cleft in the former and a big one in Uraeotyphlus, and therefore the presence or absence of a cleft is certainly comparative.

In sectional views, the squamosal is noticed posteriorly to the postfrontal and is disposed laterally to the frontal and parietal, and in anterior sections dorsally to the maxillopalatine. In the posterior region of the optic (plus oculomotor) foramen the brain is covered over by the parietal and on the sides the anterior portion of the pleurosphenoid encloses the reminiscent orbital cartilage; the floor is formed by the os Basale (parasphenoid portion). Between the side wall of the cranium and the squamosal (Pl. IV, fig. 2 and text-fig. 10, sq.) in the lower temporal fossa (ltf.), the MM. levator mandibular anterior (lma.), levator mandibular externus (lme.), levator mandibulae internus (cp., lmi.), the ophthalmicus profundus (op.) and maxillary (max.) branches of the trigeminal nerve and the head vein (vcl.) are noticed. Posteriorly the squamosal gives rise to a shelf-like projection towards the cranium (seen only in a few sections) free from any muscle insertions as in Boulengerula. Where the quadrate (Pl. IV, fig. 2, q.) appears as a bone closely applied to the inner face of the squamosal (sq.) separated by a thin connective tissue lamella, the insertion of the fibres of M. levator mandibulae externus is noticed on the former bone; the apposition of the bones persists in a large number of sections, and posteriorly to the trigeminal foramen, the squamosal disappears.



Text-fig. 10.— $Uraeotyphlus\ narayani$ Seshachar. Transverse section in the squamosal region : $\times 33$.

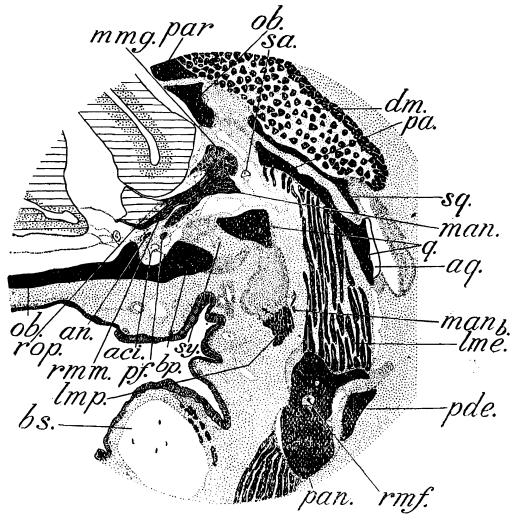
an., abducens nerve; br., brain; cp., "Caput preorbitale" of M. l. m. internus; dm., M. depressor mandibulae; gc., ganglion cell; lma., M. levator mandibulae anterior; lme., M. levator mandibulae externus; lmi., M. levator mandibulae internus; lq., M. levator quadrati; map., maxillopalatine; max., r. maxillaris V; mrt., M. retractor tentaculi; op., r. ophthalmicus profundus V; os., r. ophthalmicus superficialis VII; osb., branch of r. ophthalmicus superficialis; par., parietal; pls., pleurosphenoid portion of os Basale; pf_1 , pf_2 ., median and lateral divisions of r. palatinus facialis respectively; pt., pterygoid bone; sq., squamosal; vcl., vena capitis lateralis; v_3 cpc., branch of r. mandibularis V to "Caput preorbitale" and M. compressor orbitalis.

[In figures 14, 15, 18, 20-25 and 28 Norris and Hughes (1918) label a bone in a precise topographical position of the squamosal as 'post-frontal' The disposition of the bone and the muscular attachment conclusively prove when compared with other forms that it is a squamosal and not a post-frontal, for notice in figure 28, the post-frontal lying externally to the anterior portion of the 'pterygoquadrate', an anomalous position, and moreover, in the species examined by them, a post-frontal is absent.]

The quadrate (paired) or Suspensorium of Sarasins.

On the inner aspect of the squamosal appears the anterior portion of the quadrate (Pl. IV, fig. 2, q.) as an elongated bone separated by

some connective tissue. We can distinguish three processes given off anteriorly from the quadrate bone; a processus ascendens (processus



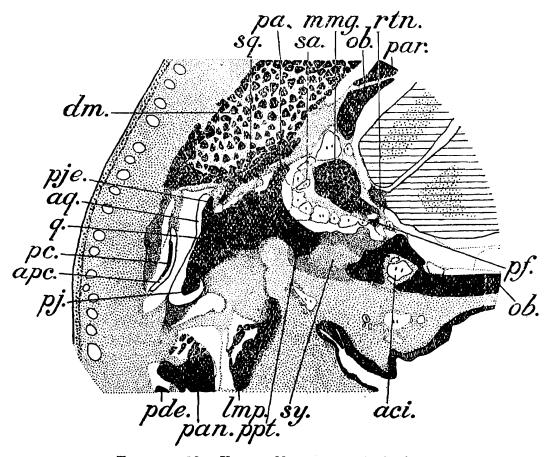
Text-fig. 11.—Uraeotyphlus narayani Seshachar.

Transverse section in the region of gasserian ganglion: $\times 33$.

aci., arteria carotis interna; an., abducens nerve; aq., articular facet of the quadrate; bp., basipterygoid process; bs., blood sinus; dm., M. depressor mandibulae; lme., M. levator mandibulae externus; lmp., M. levator mandibulae posterior; man., r. mandibularis V; manb., branch of r. mandibularis V; mmg., maxillomandibular part of gasserian ganglion; ob., os Basale; pa., processus ascendens; pan., pseudoangular; par., parietal; pde., pseudodentary; pf., r. palatinus facialis; q., quadrate; rmf., ramulus mandibularis internus facialis (chorda tympani); rmm., root of maxillomandibular nerve; rop., root of ophthalmicus profundus nerve; sa., stapedial artery; sq., squamosal; sy., syndesmotic connection.

squamosus, Sarasins 1890) (Pl. IV, fig. 2 and text-figs. 11, 12, pa.), a processus pterygoideus (Pl. IV, fig. 2 and text-fig. 12, ppt.) which articulates with the basipterygoid process (Pl. IV, fig. 2 and text-figs. 11, 12; bp.) of the os Basale by connective tissue (syndesmosis) (sy.), and a processus jugalis (text-fig. 12, pj.). Posteriorly, the quadrate gives rise to a fourth process,—the processus oticus (processus columellaris) (Pl. IV, fig. 2; see also text-fig. 7b, poq.) whose cartilaginous tip articulates with the cartilaginous portion of the stapedial process. the external aspect of the short processus jugalis (text-fig. 12, pj.), a process is given off which articulates with the lower tip of the squamosal sq.) by means of connective tissue. I have called this the processus

jugalis externus (text-fig. 12, pje.). In the region of the articulation of the lower jaw, the quadrate bears a processus articularis (Pl. IV, fig. 2 and text-fig. 12; see also text-fig. 7a., aq.) with which the pseudo-angulare articulates.



Text-fig. 12.—Uraeotyphlus narayani Seshachar.

Transverse section in the region of the Quadrate: ×33.

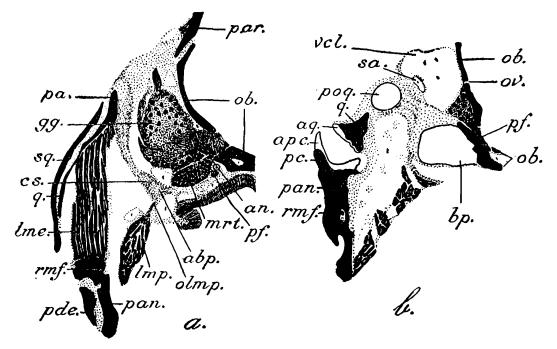
aci., arteria carotis interna; apc., articular facet for the processus condyloides; aq., articular facet of the quadrate; dm., M. depressor mandibulae; lmp., M. levator mandibulae posterior; mmg., maxillomandibular part of gasserian ganglion; ob., os Basale; pa., processus ascendens; pan., pseudoangular; par., parietal; pc., processus condyloides; pde., pseudodentary; pf., r. palatinus facialis; pj., processus jugalis; pje., processus jugalis externus; ppt., processus pterygoideus; q., quadrate; rtn., root of trigeminal nerve; sa., stapedial artery; sq., squamosal; sy., syndesmotic connection.

In *Ichthyophis*, the processus jugalis is longer than in *Uraeotyphlus* and Peter (1898) discovered a quadratojugal bone in it.

The articulation of the processus pterygoideus of the quadrate (or the pterygoquadrate where the pterygoid is not discoverable as an independent bone) with the basipterygoid process of the os Basale is a characteristic feature of Apoda. In *Ichthyophis* and *Uraeotyphlus* the articulation is by syndesmosis; in the former even in the larval condition, the quadrate does not develop a basal process¹ and therefore the quadrate is syndesmotically connected with the basitrabecular or basipterygoid process. This may apply also to *Uraeotyphlus*. In other forms that have been studied, viz., Dermophis (Norris and Hughes

¹ However, Edgeworth (1925, p. 235) mentions in his table that 'basal process' forms a joint with the 'basal plate' in *Ichthyophis* and Peter (1898) also referred to a rudimentary processus basalis palatoquadrati.

1918, de Jager 1938, 1939), Herpele (Norris and Hughes 1918), Boulengerula (de Villiers 1936) the articulation is by the cartilaginous facets of the basipterygoid process and the processus pterygoideus of the quadrate. A basal process has been described in a Siphonops brazieliense larva (7 cm. long), which is continuous with the basitrabecular process by Edgeworth (1925, 1935) but in the same sized larva, Goodrich (1930, Fig. 509) shows a joint. In Hypogeophis also (Marcus, Stimmelmayr and Porsch 1935) a basal process of the quadrate is formed which develops into the adult palatobasal articulation with the basipterygoid process. In Scolecomorphus (de Villiers 1938, p. 9) it is noted that "Although Scolecomorphus lacks a quadratostapedial articulation, it retains the pterygoquadratobasal one which is situated much more dorsally and much more closely to the side of the neurocranium than in Boulengerula", but again on page 11, the author states that "There is of course just a possibility of Scolecomorphus being neotenic in which case the absence of basopterygoquadrate and of a loose attachment of the outer wall of the otic capsule may not be due to degeneration My own sections show that there is a connective tissue strand arising from the processus ascendens (text-fig. 13a, pa.) and proceeding towards the anterior portion of the basipterygoid process where the ligament of the M. 1. m. posterior (lmp.) is also inserted. However, in posterior sections (text-fig. 13b) arising from the processus pterygoi-



Text-fig. 13.—Scolecomorphus uluguruensis Barbour & Loveridge.

a. Transverse section in the suspensorial region: ×ca. 40.

b. Transverse section posterior to $a: \times ca.$ 40.

abp., anterior face of the basipteryogoid process; an., abducens nerve; apc., articular facet of the processus condyloides; aq., articular facet of the quadrate; bp., basipterygoid process; cs., connective tissue strand from ascending to basipterygoid process; gg., gasserian ganglion; lme., M. levator mandibulae externus; lmp., M. levator mandibulae posterior; mrt., M. retractor tentaculi; ob., os Basale; olmp., origin of M. levator mandibulae posterior; ov., orifice for a branch of vena capitis lateralis in the wall; pa., processus ascendens; pan., pseudoangular; par., parietal; pc., processus condyloides; pde., pseudodentary; pf., r. palatinus facialis; poq., processus oticus of quadrate; q., quadrate; rmf., ramulus mandibularis internus facialis; sa., stapedial artery; sq., squamosal; vcl., vena capitis lateralis.

deus is a cartilaginous facet with which a similar facet of the basiptery-

goid process (bp.) articulates as in Boulengerula.

The processus oticus (processus columellaris of Marcus, Winsauer and Hueber 1933) articulation of the quadrate with the stapedial process is another characteristic feature of Apoda. In Ichthyophis, Uraeotyphlus (Pl. IV, fig. 2, poq.), Boulengerula, (de Villiers 1938) and in Herpele, it is present; in Siphonops and Caecilia a rudimentary one is recorded (Stadtmüller 1936) while in Scolecomorphus (de Villiers 1938) it is absent along with the stapes. In Dermophis (de Jager 1939) the processus oticus palatoquadrati is fused with the stapedial style and according to her this loss of quadratostapedial kinesis has taken place within recent times. It is of interest to note that in the case of Hypogeophis larva (Marcus, Stimmelmayr and Porsch 1935) the processus oticus of the quadrate enters into a temporary fusion with the stapedial process. In *Ichthyophis* embryo (Goodrich 1930) there is a processus oticus (rudimentary according to Stadtmüller 1936) which does not establish any connection dorsally while in Siphonops larva (Goodrich 1930, Fig. 509) the otic process establishes contact with the auditory capsule. Edgeworth (1925, 1935) however, differs from Goodrich; he does not find an otic process in his larva of Ichthyophis measuring 2.85 cm, but his Fig. 88 of Siphonops larva resembles exactly the reconstructed figure 509 of Goodrich where the otic process of the latter author corresponds with the processus ascendens articulating by means of a joint with the pleurosphenoid region. Incidentally, it may be remarked here that the bone labelled by Goodrich in his figure as 'f' (frontal) should be read as parietal.

A brief reference may be made to the connection of the processus ascendens with the orbital cartilage (taenia marginalis). The connection of the processus ascendens with the orbital cartilage has been recorded by Winslow (1898) and Edgeworth (1925, 1935) in I. glutinosus embryos, but Peter (1898) who also studied early embryonic stages While Edgeworth records the size of the embryo (2.85 cm.) the other two authors do not; Edgeworth, however, mentions that his embryo is slightly smaller than the one modelled by Peter. is just a chance that the processus ascendens connection might have been formed previously and lost in Peter's stage. De Jager (1939a) refers to a similar connection (between pleurosphenoid and processus ascendens cartilage) in a 11 cm. larva of I. glutinosus, and further remarks that had Peter examined a similar stage he would have discovered it since he did not study stages between 10 and 16 cm. in length, while Stadtmüller (1936) mentions only a partial connection in a 10 cm. larva of I. glutinosus. When I referred this point to Prof. Goodrich he informed me that this difference in the behaviour of the processus ascendens connection may be due to the fact that the authors were examining embryos of different species of Ichthyophis. This is not so, for, both Winslow and Peter secured their material from Dr. F. Sarasin, and unless it be that Sarasin's collection itself consisted of two races, it is difficult to reconcile the observations of Edgeworth and Winslow on the one hand and Peter on the other. De Jager's account may not

¹ Though de Villiers refers in the text to the absence of a stapes yet in his figure 4 (p. 14), a stapes is indicated.

be taken into consideration since she describes it in a larval form and also since the time of appearance of these cartilaginous structures varies. I have not been able to secure early embryonic stages, but in the stages examined by me of *I. glutinosus*, no connection was noticed. Therefore it may be that as suggested above, Edgeworth and Winslow were examining a stage where a connection is present and Peter, a slightly older one (as recorded by Edgeworth) where the connection is lost or if not, it is a case of variation.

THE GLANDS OF THE BUCCAL CAVITY.

Recently two memoirs have been published on buccal cavity glands; one on Anura (Müller 1932) and another on Urodela (Seifert 1932). Leydig (1868) and Wiedersheim (1879) described the glands of the buccal cavity of some apodan genera. In Ichthyophis glutinosus, Sarasins (1890) described a set of glands between the two rows of teeth in the upper jaw and a set behind the second row of teeth. are designated by them as the palatal glands (Gaumendrüse). (1935) working on Hypogeophis labelled the glands present in between the dental rows as the "interdental" glands while those behind the second row of teeth as the "intermaxillary" glands. But Fahrenholz¹ (1934) described in Uraeotyphlus menoni, a few glands distributed almost mediolongitudinally starting slightly anteriorly to the choana as the intermaxillary glands comparable with those found in Anura and Urodela; this set is obviously in addition to the set found in between the teeth rows and that behind them. He did not refer to the "Gaumendrüse" in U. menoni but suggested that an examination of the "zwischenkieferdrüse" in other apodan genera would be very desir-In the case of I. monochrous and also in I. glutinosus, the intermaxillary glands as described by Fahrenholz for Uraeotyphlus are absent (Mahadevan 1936). In U. narayani (text-fig. 3, inmf.) and U. menoni, an extra set is added on in the palate which opens into the buccal cavity in a median groove as described in some Urodela (Seifert 1932). Mang (1935) however, did not refer to this gland in Hypogeophis and obviously it is absent and as already pointed out, the second set corresponding to the "Gaumendrüse" of Sarasins, is labelled by him in Hypogeophis as intermaxillary glands. The nomenclature I have adopted is as follows:

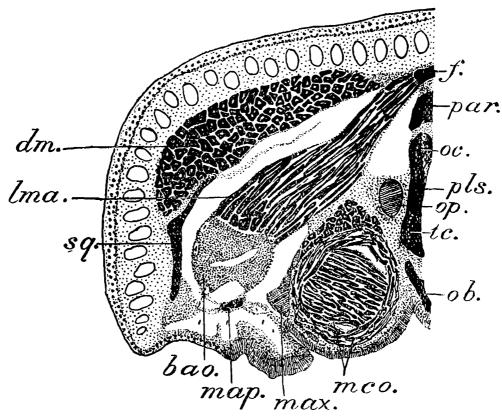
I. glutinosus (Sarasins 1890).		••	Gaumendrüse 1. bet ween teeth row		Gaumendrüse 2. be hind second teet		No intermaxillary of Fahrenholz.
I. monochrous (Mahadevan 1936).	••	••	upper jaw. Interdental glands	••	row. Intermaxillary glar	nds	Absent.
U. menoni (Fahrenholz 1934).	••	••	No reference	• • •	No reference .	•	Present.
U. narayani (Ramaswami).	••	••	Interdental glands	••	Postdental glands.	• •	Present.
H. ochrocephala	• •		Ditto		Ditto		Absent.
S. uluguruensis	••	••	Ditto	• '•	Ditto	••	Present; differs from that in Uraeotyphlus.
B. bowengeri	••		Ditto		Ditto .		Absent.
D. gregorii	••	••	Ditto	••	Ditto .	•	Absent.

¹ Fahrenholz does not unfortunately mention the source of his material, and if it was from South India, it is just possible that both of us have been dealing with the more commonly occurring species, *U. narayani* which for a long time the authorities of the Biological Supplies, Kottayam, S. India were supplying under the name of *U. menoni*.

Both the interdental and postdental glands resemble each other in histological details and the name suggested therefore is more for topographical convenience than for histological differentiation. However, the intermaxillary glands of U. menoni and U. narayani differ considerably from the other sets described above. A comparision of the interdental or postdental of I. monochrous or U. narayani (Pl. VI, fig. 1, indg., pdg.) with the intermaxillary of U. narayani (see text-fig. 3, inmf.) reveals at once the points of difference. As in U. menoni, each gland in U. narayani also is composed of single layered glandular epithelium and opens into the buccal cavity by a convoluted duct. While in the younger specimen examined the duct is short and opens directly from the gland above into the mouth, in aged individuals the gland is enlarged and the duct follows an oblique course.

In Scolecomorphus (Pl. V, fig. 4 and text-fig. 4, inmf.) a well developed set of glands is present between the sphenethmoid region and the postdental glands (pdg.) resembling the dorsal glands (ng.). These open into the buccal cavity posteriorly and are topographically comparable with the intermaxillary glands of Fahrenholz, and I have therefore designated them as the intermaxillary glands.

The true palatal glands (Palatinaldrüse Mang 1935, Rachendrüse of Anura, Oppel 1900) described as occurring behind the choanae in Hypogeophis are absent in I. glutinosus, I. monochrous and U. narayani. No reference is made to these glands in U. menoni by Fahrenholz (1934).

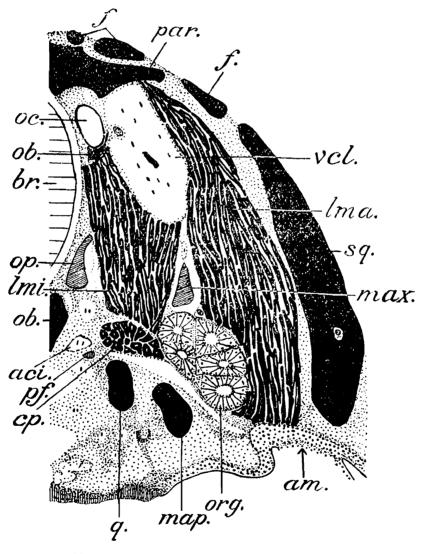


Text-fig. 14.—Scolecomorphus uluguruensis Barbour & Loveridge. Transverse section showing Bursa angularis oris: $\times 55$.

bao., Bursa angularis oris; dm., M. depressor mandibulae; f., frontal; lma., M. levator mandibulae anterior; map., maxillopalatine; max., r. maxillaris V; mco., M. constrictor orbitalis; ob., os Basale; oc., orbital cartilage; op., r. ophthalmicus profundus V; par., parietal; pls., pleurosphenoid portion of os Basale; sq., squamosal; tc., trabecular cartilage.

The choanal glands (Choanendrüse, Sarasins 1890) in *U. narayani* (Pl. VI, fig. 6, chg.) open into the choana as in *I. glutinosus* and *I. monochrous*. Again no reference is made to this in *U. menoni* (Fahrenholz 1934). The presence of this gland is recorded by de Jager in *D. mexicanus* and not in *D. gregorii*. In *Herpele*, opening into the choana there are a few choanal glands; in *Scolecomorphus* the choanal glands are similar to the intermaxillary glands of Fahrenholz and open into the posterior portion of the choana and *Boulengerula* also possesses a set of choanal glands.

The dental and sublingual glands (dentaldrüse, sublingualdrüse Mang 1935) are disposed in *U. narayani* (Pl. VI, fig. 1, slg.) as in *Hypogeophis*.



Text-fig. 15.—Herpele ochrocephala (Cope).

Transverse section showing oral mucous glands: ×55.

aci., arteria carotis interna; am., angle of mouth; br., brain; cp., "caput preorbitale" of M. l. m. internus; f., frontal; lma., M. levator mandibulae anterior; lmi., M. levator mandibulae internus; map., maxillopalatine; max., r. maxillaris V; ob., os Basale; oc., orbital cartilage; op., r. ophthalmicus profundus V; org., oral gland; par., parietal; pf., r. palatinus facialis; q., quadrate; sq., squamosal; vcl., vena capitis lateralis:

The bursa angularis oris (Fuchs 1931).—The occurrence of a bursa angularis oris has already been noted among Anura and in some am-

niote examples (Fuchs 1931). I have already noted (1934) that this structure is absent in *Ichthyophis* and *Uraeotyphlus*. In *Scolecomorphus* (text-fig. 14, bao.), however, it appears as a lymphocytic accumulation between the anterior end of the squamosal (sq.) and the compressor muscle of the orbital gland (mco.) and soon a cavity is noticed in it when the M. levator mandibulae anterior (lma.) is situated dorsally to it. The cavity of the gland (?) does not communicate with the buccal cavity as in anuran examples. Posteriorly, this structure disappears at the angle of the mouth.

In Herpele, a set of mucous glands appears in between the M. levator mandibulae internus (text-fig. 15, lmi.) and the "Caput preorbitale" (cp.) of the same and the M. levator mandibular anterior (lma.) just above the maxillopalatine bone (map.). Posteriorly they open into the buccal cavity. These are different histologically from the bursa angularis oris, but their anterior position and their opening into the buccal cavity are rather significant. These are obviously mucous glands of the skin which have migrated far internally.

THE TONGUE.

The apodan tongue is a padlike \mathbf{n} -shaped structure in the anterior portion of the floor of the mouth and is incapable of eversion as in Anura. The earliest reference made to the apodan lingual organ is by J. Müller (1831) where he referred to the bilobed papillae in *Ichthyophis*. Sentzen described the tongue of *Caecilia tentaculata*, while Widersheim (1879) referred briefly to the elevated lateral portions of the tongue of *C. lumbricoides* (*C. gracilis*).

Teipel (1932) gave a complete account of the development of the tongue of *Hypogeophis* and also its adult structure. Both Marcus (1932) and Teipel remark that in a transverse sectional view the tongue of *Hypogeophis* is roughly divisible into lateral and median parts. The median part is highly vascular and glandular while the raised lateral parts are free from glands but the genioglossus muscle is inserted into them aiding the animal in respiratory activities.² This exclusive differentiation of the tongue into a median glandular and a lateral muscular part is disproved by Mang (1935) for he says (p. 304):

Vier Querschnitte dieser Serie sind in der Zungenarbeit von Teipel in der Abb. 3 veroffentlicht. Auch in seiner Abb. 2 ist eine a graphische Horizontalrekonstruktion der Zunge von dieser Serie gemacht, um zu ziegen, dass die mittlere Zunge nur vorn von Drüsen erfullt ist, und wie sich die Drüsen erst weiter hinten und beim erwachsenen Tier auch auf die seitlichen Zungenteile erstrecken. Dabei muss diese Zeichnung fur die Drüsen als unvollstandig bezeichnet werden, da seitlich die Drüsen sich uber die Zunge hinaus erstrecken.

However, it must be pointed out that the few scattered glands to which Mang refers appear only posteriorly to the insertion of the muscle in the lateral part.

¹ Quoted by Teipel (1932).

² Marcus has informed me (in. litt.) that he does not agree with the views of Kallius (1901) and Gegenbaur (1894) that the glandular activity was the primary cause of the muscularisation of the tongue.

In the case of I. glutinosus, I. monochrous (Mahadevan 1936), U. menoni (Chatterjee 1936) and U. narayani, the pad-like tongue observes the shape of an inverted U. Further, the tongue in Ichthyophis (Pl. V, fig. 3) and Uraeotyphlus (Pl. VI, fig. 2) is not divisible into median glandular and lateral muscular parts, but the two lateral limbs of the n-shaped tongue project posteriorly. The tongue proper is covered over by stratified epithelium (se.) on the surface of which open a large number of glands (Pl. V, figs. 2, 3, lg.) and the latter are not supplied with sphincter muscles as in Hypogeophis (Teipel 1932). glands are larger and are more vertically elongated in I. monochrous (Pl. V, fig. 3, lq.) than in I. qlutinosus and U. narayani. These tongue glands show quantities of mucus which can be stained by mucicarmine and obviously this secretion keeps the surface of the tongue moist, probably aiding the animal in deglutition. In U. narayani, the anterior tip reveals in sectional views (Pl. VI, fig. 1) a large number of blood vessels in the ventral aspect and a set of glands (lg.) dorsally; in the prechoanal portion, the lateral parts (Pl. VI, fig. 2, t.) of the tongue are separated by the mesial ciliated pharyngeal portion. Buccal glands (pg.) occur in this middle portion (the postlingual glands of Mang) and thus a transverse section gives the spurious appearance of the tongue being divided into lateral muscular and mesial glandular parts. consider this mesial section as a part of the tongue for, it correctly belongs to the pharyngeal region. Further, I am inclined to believe that the central glandular part described by Teipel (1932) in Hypoqeophis tongue is really the pharyngeal part with its glands. the lingual muscle,—M. genioglossus appears (M. hyoglossus being absent from the tongue of Apoda so far examined), the major portion of this enters the lateral part as in Hypogeophis while a few fibres proceed to the median part also.

The mucous glands referred to above in the tongue make their appearance only in late larval life of I. quatinosus. Mang (1935) points out that in his preparations of stages 48 and 49 of Hypogeophis the tongue is lined by simple epithelium (single layered; he does not mention if it is ciliated as in Ichthyophis), but the epithelial cells are loaded with vitreous mucus. At any rate the glands seem to make their appearance in the next stage, 50 (7 cm. long larva),—a stage where the external gills are still persisting. According to him an invagination appears in the determined area and the cells commence to secrete mucus. In I. glutinosus on the other hand, it is the embryonic stage which is branchiate as already remarked, measures 6-7 cm. in length and obviously the time of development of the glands does not follow that in Hypogeophis. I have examined in this connection a young stage of U. narayani that I have with me (9 cm.), in this all the adult features have already made their appearance but only they have not grown to their maximum size. The tongue and the associated glands and the glands of the buccal cavity including the intermaxillary (though feebly) have made their appearance. Uraeotyphlus as compared to Ichthyophis, has a greatly abbreviated larval life, for the appearance of most of the characters like the tentacle, nasolacrimal ducts and the complete development of the eye muscles which only develop in late

larval life of *Ichthyophis*, are compressed into the very early larval life or they may even appear in the embryonic condition. I am inclined to believe that the embryonic life of *U. narayani* is very short and most of the characters enumerated above are heralded in this stage and when the larva is hatched, it is supplied with the full complements of an adult individual, only not so completely. This point can be confirmed only after examining embryos and as more material becomes available, I hope to study the early development of this interesting apodan type.

In *D. gregorii*, the lingual organ is well developed and in the choanal region (Pl. VI, fig. 3) the entrance of a few fibres of the genioglossus muscle into the central pharyngeal region can be made out. The glands are uniformly distributed in the tongue.

In H. ochrocephala, anterior sectional views reveal the presence of large sublingual glands and the tip of the tongue appears as a projection. Photomicrograph (Pl. VI, fig. 4) shows the lateral muscular portion (lt.) free from glands and the central cilited pharyngeal region full of glands (pg.). It can also be seen that a few fibres of the genioglossus muscle enter the middle portion. Posteriorly, in the middle of the pharyngeal region, a groove appears into which the glands open.

In Scolecomorphus, since the second row of teeth is absent in the lower jaw, the anterior sections reveal a large number of sublingual glands extending between the jaws. The tongue no doubt observes the shape of an inverted U, but is not raised above the level of the jaw. The muscles (Pl. V, fig. 4) are inserted into the lateral aspect while the glands occupy the central ciliated area. In Boulengerula also (Pl. VI, fig. 7) the same features are noticed.

The study of the tongue in the Apoda reveals that the distribution of the lingual glands is rather interesting. In the tip (i.e., at the anterior end of the n-shaped tongue) a set of glands is always present. In the lateral portions of the tongue, the genioglossus muscle is predominantly noticed; the absence of glands from this part is noticed in Uraeotyphlus, Herpele, Scolecomorphus, Boulengerula and Ichthyophis, while in Dermophis glands are also seen in the lateral parts.

According to Teipel (1932), three nerves enter into the tongue. The hypoglossal (XII) innervates the genioglossus muscle and the glossopharyngeal (IX) enters the median portion of the tongue. A ramulus from the united mandibular nerve (chorda tympani VII plus ramus mandibulari internus V) passes into the tongue as ramus lingualis. The lingual innervation by a branch of the chorda tympani is an important feature, for in this feature the Apoda simulate the higher tetrapodous forms (see Cranial nerves).

THE OLFACTORY ORGAN AND ASSOCIATED GLANDS.

The first cavity that we meet with in the anterior region of the olfactory organ is what Wiedersheim (1879) described as the cavum nasale principale. In the case of *I. glutinosus* (Wiedersheim 1879, Waldschmidt 1887, Sarasins 1890), *Geotrypetes* (Norris and Hughes 1918), *Dermophis* (Norris and Hughes 1918, de Jager 1939), *I. monochrous*

and Scolecomorphus uluquruensis, owing to the development of an eminentia olfactoria (processus conchoides, composed of projections from prevomer and sphenethmoid bones), the cavum nasale principale is incompletely divided into a median and a lateral chamber. According to Sarasins (1890), the lateral part is composed not only of a sensory part in which glands of Bowman are present, but also a ciliated respiratory part. Thus it is incorrect to say that the lateral part is purely respiratory, as de Jager (1939) has described. She noted that (p. 194) "The median olfactory part consists of olfactory cells which are absent from the lateral respiratory part with its cubical epithelium and mucous cells (Fig. 1). This typical division of the cavum nasale principale into two parts has been universally stressed" It should be noted here that the typical division of the cavum nasale principale is seen only in cases where an eminentia olfactoria is developed (see text-fig. 4, mcp., lcp.) and in these the lateral portion is composed of not only respiratory but also olfactory epithelium. However, in an account of the olfactory organ of H. rostratus, Laubmann (1927) has not referred to a sensory or respiratory part but simply describes the cavum nasale principale (Hauptnase or chief nose) as formed of a lateral nose and a median one with a sulcus differentiating them. Marcus (1930) has also referred to the "Hauptnase" but does not allude to the physiolo-This condition has also been noticed in C. gracilis, gical separation. U. oxyurus, Chthonerpeton indistinctum, S. annulatus (Wiedersheim 1879) Herpele and Caecilia (Norris and Hughes 1918) and U. narayani (text-figs. 1, 3, 8, 9, mcp., lcp.) and B. boulengeri.

A second cavity which we meet with in the sectional views of the apodan head in the narial region is the "Nebennase" of Wiedersheim (1879) or the organ of Jacobson (Sarasins 1890). Laubmann (1927) described this cavity as "Tastnase" or the organ of touch in the nose of H. rostratus. Marcus (1930) doubted the validity of this interpretation and therefore called this cavity as "Nebennase" (secondary nose), and I have followed the nomenclature employed by Wiedersheim and The "Nebennase" opens into the tentacular sac by two ducts (text-figs. 1, 2, 8, 16, nld.) and internally, it (text-fig. 9, nn.) opens into the mesial or into the lateral part of the cavum nasale principale. As regards the internal opening, it is significantly pointed out by Norris and Hughes (1918) that "The development of a processus conchoides produces other modifications of the nasal topography. Jacobson's organ ["Nebennase"], which in Herpele and Caecilia (figs. 8, 9, 10) connects with the mesial portion of the nasal chamber, in the other type communicates with the lateral portion (figs. 6, 7, 10)"

The two ducts opening into the tentacular sac, called "Tranenröhrchenen" (lacrymal ducts) by Sarasins, were first discovered by Leydig (1868) in S. annulatus and C. gracilis and were called by him "falschen Nasenöffnung" (pseudonasal opening). Wiedersheim (1879) described the two ducts of the "Nebennase" opening into the tentacular sac as tentacle canals for he thought that these emptied the secretion of the glands surrounding the "Nebennase" (which he therefore erroneously called the "tentakeldrüse") into the tentacle sac and Greeff (1884) working on D. thomensis confirmed the observations of Wieder-

sheim. Laubmann (1927) differed from these two authors and called these two ducts as "Tastnasenröhrchen" and ascribed a different function to the "Nebennase" On account of the constant exsertion and withdrawal of the tentacle, a certain amount of air gets into the "Nebennase" through the "Tastnasenröhrchen" and the former is thus enabled to function as an "Organ of touch" and he therefore, called the "Nebennase" as "Tastnase" (the nose where the seat of touch is located). According to this author, then, the air that is taken in through the anterior nares and also through the tentacular nasolacrimal ducts helps the animal in olfaction, in feeling and also in respiration. Marcus cautiously remarks (1930, p. 662):

Ob der Tentakel ein echter 'Tastfühler' sei, also erhebliche Tacktile Reize vermittelt, lasse ich dahin gestellt.

and further notes that during borrowing, the anterior nares close up and air is led into the nose by the tentacular ducts ("Nebennasenröhrchen") for respiration and olfaction and when the latter close up, air enters through the anterior nares. This ingenious explanation will hold good in a form like Hypogeophis where the tentacle is far behind the anterior nares; but in those cases where the tentacle and, therefore, the openings of the nasolacrimal ducts are below the anterior nares as in Uraeotyphlus, air cannot be led in during borrowing (provided these animals lead a subterranean life) for both inlets will be closed. In fact, Ichthyophis is not a borrower at all, for all the specimens collected so far are from under decaying vegetation or wood in moist surroundings. Therefore, these Apoda may be described as "surface cryptic" forms.

In *U. narayani*, the "Nebennase" (text-fig. 16, *nn*.) is elongated longitudinally and its two ducts (nasolacrimal ducts, *see* text-figs. 1, 8, *nld*.) open into the tentacular sac as in other forms. The internal opening into the median part of the cavum nasale principale is situated by the side of the sphenethmoid.

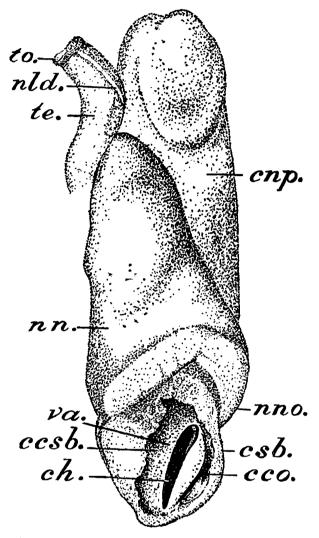
The organ of Jacobson is also described by Laubmann (1927) and Marcus (1930, Fig. 5) in *Hypogeophis*. This is a diverticulum (Laubmann, Figs. 9a, 9b and 9c) of the cavum nasale principale opening into the latter and in the same region the opening of the "Nebennase" can also be seen. According to this author, the Jacobson's organ is developed as a result of the mechanical rotation of the nasal organ. Such a structure is not noticed by me in *U. narayani* and also by other workers in the genera examined by them.

Sarasins (1890) described a third cavity which they called "Choanenschleimbeutel" and Wiedersheim (1879) also described this third cavity in association with "Nebennase" De Jager (1939) mentions that Laubmann (1927) does not refer to a "Choanenshleimbeutel"; however, we read in Laubmann that in the choanal region there is a cavity with a valve opening towards the choana. Marcus (1930) describing the same animal as Laubmann, noted that a posterior portion

¹ Sarasins (1890, p. 199) had already noted that the nasolacrimal duets led air into the nose, but could not ascribe any function to it.

of the olfactory sac could be homologised with Sarasins' "Choanen-shleimbeutel" He says (p. 679).

Durch die eben beschruebene Falte im hinteren Nasengang (Choanenschleimbeutel der Vetter Sarasin) ist ein Mechanismusgegeben, der wie eine Ventilklappe die hauft bei der Ausatmung in jede der beiden Nasenteile dirigieren kann.



Text-fig. 16.—Uraeotyphlus narayani Seshachar.

The olfactory organ from ventral aspect: the wall of the "Choanenschleimbeutel" is cut to show the cavities inside. Only one nasolactimal duct is visible: ×24.

cco., cavity of the "Choanenschleimbeutel" into which choanal glands open; ccsb., cavity of the "Choanenschleimbeutel"; ch., choana; cnp., cavum nasale principale; csb., "Choanenschleimbeutel"; nld., nasolacrimal duct; nn., "Nebennase"; nno., the bend of "Nebennase" before it opens into "Choanenschleimbeutel"; te., tentacle; to., tentacular orifice; va., valve.

The occurrence of this choanal chamber (text-figs. 3, 4, 16. csb.) with a valvular flap (va.) is a common feature among the apodan genera studied by me.

The nasal glands.—In addition to the glands of Bowman in the olfactory epithelium, two more sets of glands can be identified in the nasal region of Apoda generally. These are, (1) Nasal glands (Nasendrüse) situated dorsally or dorsolaterally (Pl. V, fig. 4 and text-figs. 3, 4, 9, ng.) in posterior sectional views to the cavum nasale principale

opening into the latter by ducts. These were first described by Wiedersheim (1879) in S. annulatus, C. gracilis and H. rostratus, U. oxyurus and Chthonerpeton indistinctum. The presence of the same was noticed by Sarasins (1890) in I. glutinosus and they are have been designated as "dorsale Drüse" in H. rostratus by Laubmann (1927). Norris and Hughes (1918) delineate these glands in their fig. 8 and I have also observed them in my preparations. In D. mexicanus, Norris and Hughes represent them in their figs. 5, 6 and 7 and de Jager (1939) also confirms this both in D. mexicanus and D. gregorii; I have observed their presence in the latter species also. In Boulengerula and Scolecomorphus, my sectional views show well developed glands as also in I. monochrous. Obviously, the glands occur uniformly in the Apoda. glands of the "Nebennase" (Nebennasendrüse). Wiedersheim (1879) described the glands opening into the "Nebennase" as the "tentakeldrüse" for, the two ducts of the "Nebennase" were thought to arise from these glands and open into the tentacle sac. Sarasins (1890) described the glands opening into the "Nebennase" as the "Drüse der Jacobson'sche Organ "Norris and Hughes (1918) followed Sarasins's nomenclature. Laubmann (1927) described in H. rostratus "Tastnasendrüse" associated with the "Tastnase" De Jager (1939) noted that these glands open into the choanal chamber in D. mexicanus while in D. gregorii, few glands are embedded in the "ventrolateral wall of the choanenshleimbeutel into which they open", unlike what has been described by Wiedersheim, Sarasins and Laubmann, where the glands open into the secondary nose. In U. narayani, a large number of glands (text-figs. 3, 9, nng.) surround the lateral part of the "Nebennase" and open into it.

THE TENTACLE.

Englehardt (1924) and Laubmann (1927) put forward the view that the tentacle in the Apoda is an organ of touch ("Tast-organ"). But Marcus (1930) pertinently points out that it is a "Klopf-fühler" helping the cryptic animal in respiration and smelling. He says (p. 659).

Dagegen ist es sehr wahrscheinlich, das die Klopf-fühler der unter der Erde bohrenden Blindwühle des Atmen und Reichen durch die Nebennase erlauben, wenn die vorderen Narinen fest verschlossen sind, indem sie freien Atemraum schäffen.

Wiedersheim (1879) gives a dissected horizontal view of the M. retractor tentaculi in C. (Uraeotyphlus) oxyurus, where the tentacle enclosed in the tentacular canal into the tip of which the opening of nasolacrimal ducts, orbital glands and glands of the nasal region are shown. In the case of Ichthyophis (Sarasins 1890, Englehardt 1924), it has been noticed that the tentacular part (stopsel) which projects beyond the skin is covered partially at its base by a fold of the same (tentakelfalte) which extends internally also; this tentacular fold to which the retractor muscle is attached moves up and down in the tentacular sac (tentakelsack). The tentacle is retracted by the M. retractor tentaculi. Sarasins (1890) ascribed the exsertion of this to erection, but Marcus

(1930) in this connexion noted that the M. compressor glandulae oculi functioned not only as a compressor of the gland but also as a protractor of the tentacle

In *Uraeotyphlus*, the external tentacular fold referred to above is absent and the tentacle itself is short and blunt, and I have not been able to detect any sensory innervation.¹

The homology of the retractor muscle which controls the activity of the tentacle has not been definitely settled. Sarasins (1890) was doubtful whether it was a part of the rectus internus or a modification of retractor bulbi. Marcus (1910) also believed in the retractor bulbi modification. Norris and Hughes (1918) described in the case of Herpele and Caecilia that the retractor muscle was a modified rectus Edgeworth (1935) considered it to be a modified externus muscle. retractor oculi. De Jager (1939) referred to the retractor muscle as a modified rectus externus. It is known in all these cases, that the abducens nerve innervates the rectus externus and also the retractor bulbi; it is natural therefore, to expect one of these muscles to be modified into a retractor tentaculi. In all the cases so far examined in Ichthyophis (Sarasins 1890, Norris and Hughes 1918, Englehardt 1924), Dermophis and Geotrypetes the M. rectus externus is present and the retractor bulbi is absent (vide Eye muscles, where I have shown that the retractor bulbi of Norris and Hughes, is a rectus medialis), and it can be surmised that the latter muscle is converted into the retractor tenta-But in those forms where the eye muscles are completely degenerate (Herpele, Caecilia, Scolecomorphus, Boulengerula) one of the two muscles innervated by the abducens may have been transformed. But in Ichthyophis, it has been shown by Englehardt (1924) that the retractor muscle is double, and is separated by a connective tissue layer (see also Norris and Hughes 1918, fig. 19) and therefore, finds comparision with the double retractor bulbi of Triturus. double condition, I have also noticed in Uraeotyphlus, I. monochrous, Scolecomorphus, Dermophis and Boulengerula, suggesting thereby that in forms where the eye muscles are degenerate, the M. retractor tentaculi may be a modified retractor bulbi. As in I. glutinosus, the double nature of the retractor muscle becomes obvious when the rectus internus passes through the former in I. monochrous, Dermophis and Uraeotyphlus. In the latter the muscle ends in the region of the optic foramen as in Dermophis. In Scolecomorphus, a large M. retractor tentaculi (see text-fig. 4, mrt₁) is noticed and in addition to this, there arises one (mrt₂) from the tentacular fold which is separated from the retractor by orbital glands (og.). Postchoanally these two merge into each other and are surrounded by the compressor muscle. tractor muscle is inserted on the os Basale ventrally to the trigeminal In Boulengerula, the retractor insertion into the tentacle is far anterior and in the choanal and postchoanal regions the muscle is noticed in two parts being separated by orbital glands. Posteriorly the double nature is retained and the muscles postoptically are inserted into the os Basale.

¹ I have not used any special stains for detecting sensory innervation,

THE EYE AND ITS MUSCLES.

It is well known that in the Apoda, the eye may be covered over completely or it may be visible externally. Structural degeneration naturally accompanies the condition where the eye is hidden as in *Herpele*, Caecilia, Scolecomorphus, etc.

Wiedersheim (1879) briefly referred to the eye of Siphonops.

While de Jager (1939) remarked that the eye was degenerate in *Dermophis*, I find that the eye is well developed with all its six muscles. Norris and Hughes (1918) clearly demonstrated this and I reproduce a photomicrograph (Pl. VI, fig. 5) to show a well developed eye and the associated structures like eye muscles (em.), orbital glands (og.), M. retractor tentaculi (mrt.) and optic nerve.

In Boulengerula, Nieden (1913) noted that the "Augen unter den Schädelknochen verborgen" and de Villiers (1938) also remarked that in Boulengerula, "The eye is totally degenerate and hidden beneath the paraquadrate as in Scolecomorphus" confirming the observations of Peter (1908, Fig. 8). Nieden made the same remark about Scolecomorphus, and obviously de Villiers follows that author in saying that the 'totally degenerate' eye is hidden below the paraquadrate (squamosal), which however, appears only posteriorly, nor is it hidden for that matter under any bone. The photomicrograph reproduced (Pl. V, fig. 1) shows that it (e.) is directed towards the lower jaw and is devoid of a lens, of eye muscles and nerves including the optic. Towards the maxillopalatine bone, the eye is partially surrounded by the tentacular sac into which the orbital glands (og.) open. After the eye disappears from sections, the M. retractor tentaculi appears attached to the wall of the tentacular sac.

In the case of *Herpele* examined by me, the eye is not only degenerate but is also hidden under the maxillopalatine bone.

In *U. narayani*, the eye is well developed both in the young and the adults examined as in *I. glutinosus* and *I. monochrous*. The photomicrograph (Pl. VI, fig. 6) passes through the optic nerve (on.) region and in the eye, a sclerotic, choroidea (pigment), iris, retina, cornea and lens (not seen in figure) can be clearly made out besides some of the eye muscles.

As early as 1868, Leydig described four eye muscles in Siphonops, but Wiedersheim (1879) does not refer to them. Sarasins (1890) described in I. glutinosus six eye muscles; four rectus and two oblique in association with a retractor tentaculi which probably is a modified M. retractor bulbi. Marcus (1910) found all the eye muscles in Hypogeaphis larva including a levator bulbi muscle (compressor muscle of the orbital gland). He also described a M. retractor tentaculi which he derived from the retractor bulbi (c.f. the tentacle). Norris and Hughes (1918) described in Dermophis six muscles; superior and inferior oblique (dorsal and ventral oblique), superior and inferior rectus (dorsal and ventral rectus), a rectus externus (r. lateralis) and a rudimentary retractor bulbi. A rectus internus (r. medialis) is absent, while a retractor tentaculi is present. According to the same authors in Geotrypetes, all the rectus and oblique muscles except r. internus, and a retractor bulbi and two retractor tentaculi muscles (a M. retractor

tentaculi and a M. retractor of the tentacular sheath,—the latter considered by them to be a modified r. internus) are present. In *Herpele* and *Caecilia* the eye muscles are absent; however, the tentacular muscle is described as a modified M. rectus externus.

Englehardt (1924) in his account of the tentacle and eye of *I. glutinosus*, records six eye muscles. While the obliques superior is lost between the ethmoid cartilage and orbital gland, the inferior oblique is lost between the retractor (R2) and orbital gland ventrally. Of the rectus muscles, the medialis ends in the connective tissue between the retractor and orbital gland; the lateralis in between the orbital gland ducts an retractor; the superior and inferior end between the compressor and orbital gland ducts. According to the same author the oculomotor innervates the rectus and obliques inferior muscles.

Edgeworth (1935) followed the works of Norris and Hughes (1918) and Englehardt (1924) and recorded that the ocular muscles and nerves were present in *Ichthyophis*, *Dermophis* and *Geotrypetes*, while "in *Caecilia* and *Herpele* the eye is partly or fully covered by maxilla and is rudimentary" A retractor tentaculi innervated by abducens nerve and homologised with the retractor bulbi (retractor oculi) of Urodela and Anura is also recorded.

de Jager (1939) reported (erroneously) that all the eye muscles have degenerated in *D. mexicanus* and *D. gregorii* except the r. externus which has become the M. retractor tentaculi.

Both in I. monochrous and U. narayani, all the eve muscles are present,—two oblique and four rectus muscles. Tracing the sections rostrocaudally, in \bar{U} . narayani, it is noticed that the oblique muscles appear arising from the connective tissue covering the maxillopalatine towards the eye. While the insertion of the obliquus superior is noticed on the eye-ball in the anterior sections, that of the inferior appears more posteriorly. Between the o. superior and inferior and enclosed within the orbital glands, the rectus internus is seen. In a region where the rectus internus enters the m. retractor tentaculi, the insertion of the o. superior and inferior and the rectus inferior can be seen. Posteriorly, the r. superior and inferior enclosed within the orbital glands and the rectus externus inserted on the eye-ball can be The rectus internus passes through the M. retractor tentamade out. culi as in I. glutinosus (Englehardt 1924) and along with the rectus superior is lost between the orbital gland, M. retractor tentaculi and the compressor muscle. The rectus externus and inferior become so thinned out in the region between the connective tissue spanning the orbital and trabecular cartilages and the compressor muscle that it is difficult to trace them further. In both Ichthyophis and Uraeotyphlus, a retractor bulbi is absent as such and is modified into the tentacular However, according to Norris and Hughes (1918) in Geotrypetes and Dermophis, a rectus internus is absent and they note that in these two (p. 507) "a delicate muscle slip follows the optic nerve from the retractor tentaculi to the eye-ball, probably a retractor bulbi" Moreover, in the case of Geotrypetes, the retractor of the tentacular sheath is homologised with the rectus internus because of position and innervation. In Ichthyophis, the same authors state that the eye

muscles are as described by Sarasins (1890, Fig. 72, four rectus and 2 oblique). It is clear therefore, that Norris and Hughes have accepted the muscle passing through the retractor tentaculi to the eye-ball as rectus internus in *Ichthyophis* (see their Fig. 19) to which, however, they assign the name of a retractor bulbi in *Dermophis* and *Geotrypetes* and thus deny the presence of a rectus internus. Having examined *Dermophis*, *Ichthyophis* and *Uraeotyphlus*, I am convinced that the muscle designated as retractor bulbi by Norris and Hughes is actually the rectus internus which, as described by Englehardt passes through the retractor muscle and therefore, contrary to the observations of Norris and Hughes and de Jager, all the eye muscles are well developed in *Dermophis*.

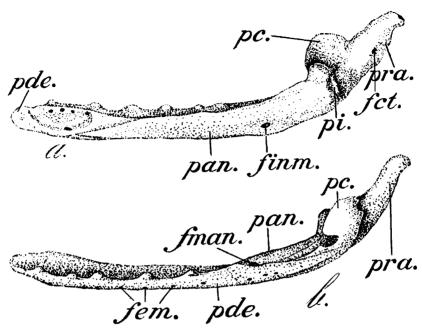
THE LOWER JAW.

Sarasins (1890) did not describe the lower jaw bones in detail but noted that it is composed of a dentary and an articular and that the inner tooth row belongs to the opercular (spleniale). Marcus, Winsauer and Hueber (1933) described in the case of *Hypogeophis*, a posterior gonial and an anterior dentary. The dentary carries the two rows of teeth. The gonial with which the articular fuses to form a gonioarticular, in the region of the suspension gives internally to a process,—the processus internus and laterovertically to a process—the processus condyloides (processus articularis mandibularis, Luther 1914), which articulates with the external aspect of the processus articularis of the quadrate and the jaw proceeds posteriorly as the processus retroarticularis mandibulae (Luther).

According to Eifertinger (1933) each ramus of the jaw consists of two composite bones, formed by the fusion of a number of elements during development. The posterior pseudoangular (gonioarticular) is composed of angular, gonial (prearticular, de Beer 1937), complimentary, and articular while the pseudodentary is formed by mentomandibular (mentomeckelian, de Beer 1937), dentary, splenial, coronoid and supraangular. The anterior portion of the dentary, the articular and the mentomeckelian are cartilage bones and the rest are membrane This nomenclature of the fused bones in the lower jaw was accepted by Marcus (1933), but he pointed out that the pseudodentary is composed of dentary, mentomandibular, splenial and coronoid (no mention is made of supraangular) while the pseudoangular is formed by angular, gonial (complimentary?) and the articular. In his fig. 6c Eifertinger (1933) describes in the posterior part a gonial and angular while in fig. 7a (44 mm. Hypogeophis larva) a gonioangular and extra element 'complimentare' are noted. Marcus (1933) however, while labelling a separate gonial and angular in his fig. 2b described (as gonial in fig. 2c), the region called by Eifertinger as 'complimentare' significantly mentions in this connexion that (pp. 181, 182)

In der Abb. 2c ist durch 4 Punkte, welche die Naht zwischen Dentale und Coronoid caudal fortsetzen angedeutet, dass im Goniale G oft die Spitze des Knochens selbständing verknöchert, und so vielleicht einem Complementare entspricht.

In *U. narayani*, as in *Hypogeophis*, two segments in each ramus of the lower jaw can be made out; a pseudodentary (text-fig. 17a, b, pde.) and pseudoangular (pan.). No exact differentiation into regions



Text-fig. 17.—Uraeotyphlus narayani Seshachar.

a. the lower jaw from within: $\times 9$. b. outer view, slightly inclined: $\times 9$.

fct., foramen for chorda tympani; fem., foramina for the twigs of ramulus mandibularis extermus V; finm., foramen for ramulus intermandibularis; fman., foramen for ramulus mandibularis V; pan., pseudoangular; pc., processus condyloides; pde., pseudodentary; pi., processus internus; pra., processus retroarticularis.

where the original independent bones were present could be made out. A processus condyloides (pc.), a processus internus (pi.) and a posterior processus retroarticularis (pra.) are present. The orifices for the entry of ramus alveolaris VII (chorda tympani) (fct.) and the ramus mandibularis V (fman.) in the pseudoangular can also be seen. Anteriorly the pseudodentary of either side is united at the apex of the jaw into a symphysis by a reminiscent piece of cartilage. Two rows of teeth are borne upon this bone.

While the processus condyloides (see text-fig. 7a, pc.) is prominently developed in *Uraeotyphlus* [compared by Hueber (1933), with the 'Hammer, Haupteil' of the mammalian ear] it is feebly developed in *Herpele* and *Dermophis* and *Scolecomorphus*, and is absent in *Boulengerula*.

THE JAW MUSCLES.

The latest account dealing with the development and disposition of adult arrangement of masticatory muscles is by Edgeworth (1925, 1935) who distinguishes four of them. I have employed the same nomenclature in describing the jaw muscles of adult *Uraeotyphlus* as Edgeworth.

Edgeworth (1925, 1935) considers the two muscles adductor mandibulae externus and adductor mandibulae internus (M. pseudotem-

poralis) of Hueber¹ as a single one since they arise singly in the early stages. He however, adds (Edgeworth 1935, p. 42) that "it separates into medial and lateral parts", and nerves pass through these two. But in [adult] Ichthyophis and Siphonops, according to the same author the muscle "persists as a whole" I have examined adult Ichthyophis, and it shows the separation of the muscle into two, as described by Luther (1914, p. 9, fig. 3) with its origin and insertions as in Uraeotyphlus (see below). Whatever the origin of these two parts of the muscle may be, it will facilitate description if we could give them distinct names and, therefore, I have called the M. pseudotemporalis as M. levator mandibulae internus and the M. adductor mandibulae externus (Hueber) as M. levator mandibulae anterior.

The four masticatory muscles are :-

(1) M. levator mandibulae anterior (Edgeworth 1925, 1935) (Synonyms: M. Adductor mandibulae externus major plus M. pseudotemporalis. Luther 1914, Hueber 1933.

M. temporalis. Norris and Hughes 1918.

M. Masseter 1.

M. temporalis 1. Englehardt 1924.)

M. temporalis 2.

(2) M. levator mandibulae externus (Edgeworth 1925, 1935) (Synonyms: M. Adductor mandibulae externus minor.

Luther 1914.

M. masseter 2. Norris and Hughes 1918.

M. masseter. Englehardt 1924.

M. Adductor mandibulae posterior. Hueber 1933.)

Luther (1914) described no M. adductor mandibulae posterior in Apoda, but Hueber (1933) has since described the same in *Hypogeophis*.

(3) M. levator mandibulae posterior (Edgeworth 1925, 1935) (Synonyms: M. pterygoideus sic. Luther 1914, Norris and Hughes 1918, Hueber 1933.)

According to Edgeworth (1925) this muscle is homologous with the same muscle in Anura and Urodela.

(4) M. levator quadrati (Synonyms: sic Luther 1914, Norris and Hughes 1918, and Hueber 1933. M. pterygoideus Englehardt 1924.)

According to Edgeworth (1925, 1935) the opinion of Hueber that the M. levator quadrati is homologous with the M. constrictor dorsalis of fishes, is incorrect for, the latter did not adduce any embryological evidence in favour of his opinion.

In Uraeotyphlus (text-fig. 10, lma.), the M. levator mandibulae anterior arises from the frontal bone and is inserted on the pseudoangular of the lower jaw. Internally to this muscle, the M. levator mandibulae internus (lmi.) is noticed along with the "Caput preorbitale" (cp.) (see Luther 1914, p. 69) and the origin of the latter is described below. Both these muscles (l. m. internus and the "Caput

¹ See Marcus, Winsauer and Hueber, p. 171, 1933.

preorbitale" portion) are inserted on the pseudoangular by a common tendon while the M. levator mandibulae internus arises from the dorso-lateral aspect of the pleurosphenoid.

The M. levator mandibulae externus (text-figs. 10, 11, lme.) arises principally from the processus ascendens of the quadrate bone and is also inserted into the pseudoangular of the lower jaw.

The M. levator mandibulae posterior (text-figs. 11, 12, lmp.) arises from the ventral aspect of the processus pterygoideus of the quadrate and the insertion is on the retroarticular process of the pseudoangular. In Scolecomorphus (text-figs. 13a, b), it is noticed that the M. levator mandibulae posterior has a separate origin instead of from the ventral aspect of the processus pterygoideus as in other Apoda. This process is very small and the M. l. m. posterior arises from the anterior face of the basipterygoid process where the connective issue strand (cs.) from the processus ascendens (pa.) comes and meets it.

The M. levator quadrati (text-fig. 10, lq.) arises from the lower aspect of the pleurosphenoid bone and is inserted into the processus pterygoideus of the quadrate dorsally.

I describe here the "Caput preorbitale" mentioned above and in this connexion describe the compressor muscle of the orbital glands also. In Uraeotyphlus, the compressor muscle makes its appearance as one attached on the internal aspect of the upper portion of the prefrontal and posterior sections reveal the compressor muscle as an internal (circular) and an outer (obliquely longitudinal) portion. part of this outer portion becomes separated in the region of the optic (plus oculomotor) foramen and runs with the M. l. m. internus into the lower jaw where it is inserted. This is the one described by Luther (1914) as "Caput preorbitale" Such a muscle has been noticed in Ichthyophis (and also in Dermophis according to Norris and Hughes 1918) while in Caecilia (Norris and Hughes 1918), the muscle appears to be inserted on the sheath of the compressor muscle or on the lateral wall of the skull. In my sections of Dermophis gregorii, the condition is as the one described for Caecilia.

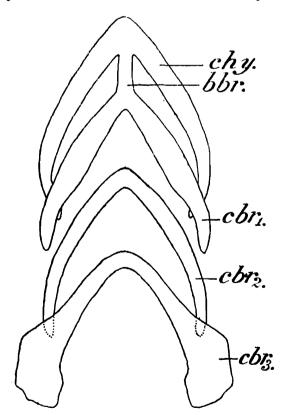
The M. compressor orbitalis has been found in all the Apoda so far studied and the development of the muscle in each case is one of degree; the muscle is extraordinarily well developed in *Herpele*, it is fairly well developed in *Ichthyophis*, *Uraeotyphlus* and *Dermophis* and it is poorly formed in *Scolecomorphus* and *Boulengerula*. The tendon of this muscle arises from the connective tissue covering the optic (*plus* oculomotor) foramen and surrounds the orbital glands. According to Luther (1914) and Edgeworth (1925) the muscle is a modified levator bulbi.

The M. levator mandibulae internus is not noticed uniformly among Apoda. While the muscle is well developed in *Ichthyophis*, *Uraeotyphlus*, *Dermophis*, and *Herpele*, it is absent in *Boulengerula*, *Scolecomorphus* (de Villiers 1938, 1939) and *Geotrypetes* (Norris and Hughes 1918). Consequent on this the path of the maxillary and mandibular branches of the trigeminal also differs. In *Hypogeophis*, *Ichthyophis*, *Uraeotyphlus* and *Herpele*, the maxillary branch runs between the M. l. m. anterior and M. l. m. internus in the region of these muscles, and in *Boulengerula*,

the nerve passes between the M. l. quadrati and the M. l. m. anterior since the M. l. m. internus is absent, while in Scolecomorphus where a M. l. quadrati is also absent the ramus maxillaris passes between the M. compressor orbitalis and the M. l. m. anterior. In Dermophis gregorii, the same nerve runs internally to the M. l. m. internus portion (i.e., between it and the connective tissue covering of the optic (plus oculomotor foramen) which is in close apposition with the M. l. m. anterior and is separated dorsally by a blood vessel. The two muscles cannot be clearly differentiated as in Ichthyophis. Probably on account of this fact de Jager (1939) remarks that a M. pseudotemporalis is absent in D. gregorii while it is prominently present in D. mexicanus.

THE HYOBRANCHIAL SKELETON.

In the adult *Ichthyophis* (Sarasins 1890, M. Fürbringer 1922, de Beer 1937) we notice that in the hyobranchial skeleton, the ceratohyal of either side is fused and is connected with the similarly united ceratobranchial by the first basibranchial, the larval basihyal and second basibranchial having disappeared. [In larval *Ichthyophis* (Sarasinse 1890), C. tentaculata (Henle 1839) and C. hypocyanea (J. Müller 1835), the fourth ceratobranchial arises as an independent arch and then fuses with the third.] Edgeworth (1935) however, mentions a basibranchial in the hyobranchial skeleton of the larvae of Apoda and also notes the absence of a basihyal in Siphonops and Hypogeophis. In Ichthyophis, there are four ceratobranchials in the adult. In Hypogeophis (Gewolf 1923) the ceratohyal of either si deis connected by a U-shaped (Gewolf



Text-fig. 18.—Uraeotyphlus narayani Seshachar.

The hyobranchial skeleton in situ. ventral view: $\times 9$. bbr., basibranchial; cbr_1 , cbr_2 , cbr_3 , ceratobranchials 1, 2, and 3; chy., ceratohyal.

basibranchial which meets and fuses with the first pair of ceratobranchials, [Edgeworth (1935) shows the first pair of ceratobranchials disunited ventrally], and with the third ceratobranchial, the fourth and fifth have fused. In Boulengerula Peter (1908) draws a figure (Fig. 8) in which the united ceratohyal is mesially in contact with the first cera-But my sections show that the ceratohyal and ceratobranchial are united mesially by a basibranchial. In Uraeotyphlus (text-fig. 18), Scolecomorphus, Herpele and Dermophis, as in Boulengerula and Ichthyophis, the ceratohyal (chy.) is connected with the ceratobranchial (cbr_1) by a basibranchial (bbr_1) cartilage and there are only three pairs of ceratobranchials $(cbr_1. cbr_2. cbr_3.)$ in all these examples. in Ichthyophis, the ventral ends are mesially united and the dorsal end of the third shows a thickening which probably represents the fused third and fourth. Whether there are one or two basibranchials (copulae 2 and 3) and a single basihyal (copula 1) during developmental stages of Uraeotyphlus as in Ichthyophis, can only be settled when early developmental stages are procured. The 9 cm. young specimen of Uraeotyphlus discloses all the characters of the adult hypbranchial skeleton.

THE CRANIAL NERVES.

The cranial nerves¹ have been described by various authors in several Apodan genera. I have not had access to Fischer's (1843) paper.

Wedersheim (1879) gave a good account of the nerves of *I. glutinosus* and *S. annulatus*. He recorded the following nerves:—

- (a) Each olfactory nerve is double and comparable with the two roots of a spinal nerve.
- (b) The optic nerves are vestigial.
- (c) No mention is made of eye muscle nerves (III, IV and VI).
- (d) The ophthalmicus profundus V arises independently and an anastomosis between it and ramus maxillaris V is described.
- (e) There is no ramus palatinus VII, probably it is united with trigeminus. An anastomosis between the facial nerve and gasserian ganglion is recorded.
- (f) The auditory nerve is well developed and arises by four roots.

Waldschmidt (1887) disagreed with Wiedersheim (1879) in the spinal nerve homology of the olfactory nerve. In S. annulatus, he described (Figs. 32 and 33) the following:—

- (a) The oculomotor sends a branch to compressor muscle and another to the ramus maxillaris V
- (b) The trochlear and abducens are absent.
- (c) A nerve arising from gasserian ganglion is shown to correspond with the ophthalmicus superficialis VII.
- (d) A nerve considered to be palatinus facialis is described.

Sarasins (1890) mention the double nature of the olfactory nerve and the supply to the organ of Jacobson from the ventral part. The auditory nerve enters the internal ear by five or six orifices.

¹ I am not describing the IX and X nerves for I hope to study these in connexion with the sympathetic system.

Burckhardt (1891) in describing the eye muscles and nerves in *Ich-thyophis* noted the absence of the trochlear and abducens nerves like Waldschmidt and Wiedersheim. The organ of Jacobson is innervated by the ventral olfactory nerve and the VIII, IX and X nerves arise by more than one root.

Marcus (1910) described in *Hypogeophis* the presence of all the three eye muscle nerves. The embryo has a lateral line complement, viz., ophthalmicus superficialis, ramus buccalis and ramus mandibularis externus (?). A recurrens VII joins the sympathetic.

By far the most complete account of cranial, spinal and sympathetic nerves was given by Norris and Hughes (1918), we are concerned here with the Section on the cranial nerves only—

- (a) The olfactory nerves are double; the olfactory glomeruli are arranged in a posterolateral group and an anterior medial and lateral group.
- (b) The oculomotor, trochlear and abducens nerves are present in Dermophis, Geotrypetes, Ichthyophis (the adult Ichthyophis is devoid of a trochlearis). In Herpele and Caecilia, the nerves have completely disappeared.
- (c) Describing the trigeminal nerve of *Herpele*, a separate profundus ganglion is recorded. The ramus mandibularis gives rise to three branches, (1) a ramulus intermandibularis entering the lower jaw through the pseudoangular, (2) a ramus alveolaris (r. mandibularis internus) which unites with a similarly named nerve of VII and innervates the teeth and the lateral epithelium of the floor of the mouth, and (3) a ramus mandibularis externus which running in the lower jaw innervates the skin. Smaller ramuli from the r. mandibularis V enter into the MM. levator mandibulae anterior, l. m. externus, l. m. posterior, and compressor orbitalis.

The ramus maxillaris after passing through the jaw muscles divides into medial and lateral branches. The medial branch sends a commissure to lateral ramus palatinus facialis (temporary union) and also one to medial r. palatinus. While the lateral r. maxillaris supplies the skin at the side of the head, the medial goes to the sheath of the tentacle and the skin of the ventral and ventrolateral surfaces of the snout. In Geotrypetes, the r. maxillaris does not divide into lateral and medial branches but there is a branch given off which unites with palatinus VII.

The ramus ophthalmicus profundus arising from the ophthalmic ganglion runs anteriorly and at the level of the choana, a large branch is given off. This branch (op1) supplies the head and the tentacular sheath. A few fibres of this commingle with those of r. maxillaris. A second branch (op3) possibly supplies the Jacobson's gland and primarily the skin on the head. A third branch (op2v) arises from the ventral side of the ophthalmicus profundus (op2) and supplies the ventral epithelium of the snout after some

anastomoses with the branches of medial maxillary V. The principal nerve (op2) goes to the skin of the ventral side of the tip of the snout.

Besides these, a somatic sensory arising from the gasserian ganglion and another sensory (Vd) called the 'dorsal fifth' are also described.

(d) The geniculate ganglion though connected with the gasserian can be easily differentiated; four groups of fibres arise from The ramus palatinus, after leaving the ganglion and traversing a short distance divides into a medial and lateral branch. The connexions with the r. maxillaris V are de-The hyomandibular nerve gives rise to a scribed above. motor branch which enters the depressor mandibular muscle and a visceral sensory which entering the lower jaw as the r. mandibularis internus VII (chorda tympani) unites with the similar branch of the trigeminal and runs to the symphysial region. The r. jugularis proceeds posteriorly after giving off branches to muscles (viz., interhyoideus, constrictor colli). In Dermophis and Geotrypetes the distribution is the same.

The ramus ophthalmicus superficialis VII arising from the geniculate ganglion courses through the gasserian, anastomosing peripherally with the branches of the r. ophthalmicus profundus and goes to the skin. This is noticed in *Dermophis*, *Herpele* and is absent from *Geotrypetes*.

(e) The auditory nerve arises by five roots, four going to the sacculus and the one dorsal to the macula neglecta.

Kuhlenbeck (1922) described the brain of *Ichthyophis*, *Siphonops* and *Hypogeophis*. A rudimentary oculomotorius and double olfactory were recorded.

Englehardt (1924) gave an account of the distribution of the nerves of *Ichthyophis*, but he does not refer to the papers of Norris and Hughes (1918) and Marcus (1910).

- (a) The trochlear is absent and the rudimentary oculomotor proceeds to rectus and obliquus inferior eye muscles and the abducens to the retractor tentaculi muscle.
- (b) Of the trigeminal, the ramus nasalis (ophthalmicus profundus) innervates the skin and tentacle sac; the ramus maxillaris innervates the compressor muscle, tentacle and upper jaw. A branch also unites with the facial nerve. The r. mandibularis supplies the masseter, the major and minor temporal muscles and the lower jaw.

The hyomandibularis branch of facial proceeds to the depressor muscle and lower jaw muscles; the fate of r. buccalis is not mentioned and from the r. nasalis (palatinus facialis) a twig joins the gasserian ganglion and another unites with r. maxillaris V No mention is made of r. mandibularis internus.

de Villiers (1938) described the trigeminal, facial and abducens nerves in Boulengerula and Scolecomorphus.

- (a) An abducens is absent from Boulengerula but prominently present in Scolecomorphus.
- (b) In Boulengerula, there is a commissure connecting the trigeminal and facial ganglia which is absent from Scolecomorphus; only in Boulengerula, the ophthalmicus profundus ganglion is separated from maxillo-mandibular ganglion.
- (c) The palatinus facialis stops short at the sensory ganglion of trigeminal in Boulengerula and in Scolecomorphus the r. palatinus which runs anteriorly receives a branch from maxillary V; the distribution of hyomandibularis VII is not described and in both genera, a chorda tympani is wanting.

de Jager (1939) did not add anything new to what has already been described by Norris and Hughes (1918) but differed in certain important points. She recorded in *D. mexicanus* the following:—

- (a) The geniculate and gasserian ganglia overlap but do not fuse.
- (b) There are two prootic foramina,—a dorsal for r. maxillo-mandibularis and a ventral for ophthalmic branch. The r. ophthalmicus profundus has its own ganglion.
- (c) A temporary anastomosis of r. palatinus with ophthalmicus profundus in the profundus ganglion is recorded on one side.
- (d) The presence of an anastomosis between maxillary V and palatinus facialis is noted.
- (e) An abducens is absent; no mention is made of oculomotor and trochlear nerves.
- (f) A branch from maxillary V innervates the compressor muscle of the orbital gland.

The olfactory nerve.—The double nature of the nerve has been noticed from a long time. The ventral division is the shorter of the two and we may briefly examine the passage of these nerves in U. narayani. Arising from the olfactory lobe, each pair (right dorsal and ventral, and left dorsal and ventral) traverses independently in a canal in the sphenethmoid bone and soon however, the right ventral gives rise to a ramulus which passes craniad in a separate canal. Anteriorly the larger ventral olfactory nerve emerges from the bony canal (text-fig. 9, von.) and proceeds to innervate the medial and lateral divisions of the "Nebennase" (see Olfactory organ) and also its glands. At the region the innervation of the "Nebennase" is noticed, the median unpaired ramulus (von_b .) of the right olfactory nerve also gains exit and proceeds to the right side to innervate the ventral olfactory epithelium. In all the series of the head of Uraeotyphlus, this feature is noticed.

The dorsal olfactory nerve also gains exit from the sphenethmoidal bony canal and runs in close approximation with the ophthalmicus profundus V (with no anastomoses) and distributes itself over the olfactory epithelium.

In Herpele, my slides show the right and left ventral olfactory before entering the ventral canals in the sphenethmoidal septum, each gives rise to a small and a large ramulus respectively. These also run in independent canals in the septum and emerge in the region of the "Nebennase" to supply the right and left olfactory epithelium. This feature however, is not recorded by Norris and Hughes (1918). In Dermophis the supply of the "Organ of Jacobson" and "olfactory epithelium covering the convexity of the ridge on the floor of the olfactory chamber" by the ventral olfactory nerve as recorded by Norris and Hughes is corroborated by me. The extra branch seen in Uraeotyphlus and Herpele is not present.

The optic and eye muscle nerves.—There is considerable difference of opinion with regard to the optic and eye muscle nerves among Apoda. Norris and Hughes review the previous literature on the subject like that of Waldschmidt (1887) on S. annulatus, Burckhardt (1891) on I. glutinosus and Marcus (1910) on H. rostratus. The observations of Norris and Hughes (1918) may briefly be summarised as follows:—

- (a) An optic nerve is noticed in *Dermophis*, Geotrypetes and in the adult *Ichthyophis*.
- (b) Of the eye muscle nerves, oculomotorius is noticed in Dermophis (vestigial), Geotrypetes and Ichthyophis (very vestigial), a trochlear is present in Dermophis (vestigial), Geotrypetes (vestigial) and absent from Ichthyophis; an abducens is noticed in Dermophis (large), Geotrypetes and Ichthyophis. It innervates the tentacular muscle. In Herpele and Caecilia, these nerves are absent except the abducens which innervates the M. retractor tentaculi.

Englehardt (1924) in describing the tentacle and eye of *I. glutinosus* confirmed the presence of an abducens nerve (going to the tentacle), of an oculomotor (innervating the rectus and obliquus inferior) and the absence of a trochlear.

de Villiers (1938) noted the presence of an abducens in Scolecomorphus while its absence was recorded in Boulengerula.

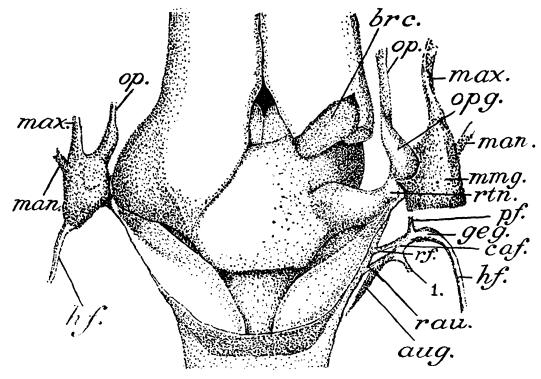
de Jager (1939) working on *D. mexicanus* and *D. gregorii* recorded that "All the eyemuscles and nerves have degenerated, except the M. rectus externus" and that an abducens was not recognizable.

In *U. narayani*, the optic nerve is well developed. The photomicrograph (Pl. VI, fig. 6) shows the optic nerve. Both in the juvenile and in the adult, the oculomotor is so vestigial that it could be found only with difficulty. The trochlear is definitely absent. The abducens is a powerful nerve and innervates the M. retractor tentaculi.

The trigeminal nerve.—As the descriptions of later authors like Englehardt (1924), de Villiers (1938) and de Jager (1939) vary considerably from those of Norris and Hughes (1918), I propose to describe in brief the passage and division of these nerves making relevant references to the above authors where necessary. It will be noticed that the observations of Norris and Hughes are almost completely borne out by my studies.

The gasserian ganglion (text-fig. 19) in *U. narayani* is seen externally to the os Basale (prootic region) and while the posterior part of

the ganglion (mmg.) gives rise to the maxillary (max.) and the mandibular (man.) branches, the anterior portion (opg.) gives rise to the oph-



Text-fig. 19.—Uraeotyphlus narayani Seshachar.

A part of brain showing the origin of trigeminal, facial and auditory nerves. On the right side a portion of the hemisphere is cut and the structures are stretched a little: ×24.

aug., auditory ganglion; brc., brain cut to show the root of trigeminal nerve; caf., commissure between auditory and facial nerves; geg., geniculate ganglion; hf., r. hyomandibularis facialis; man., r. mandibularis V; max., r. maxillaris V; mmg., maxillomandibular part of gasserian ganglion; op., r. ophthalmicus profundus V; opg., ophthalmicus profundus part of gasserian ganglion; pf., r. palatinus facialis; rau., root of auditory nerve; rf., root of facial nerve; rtn., root of trigeminal nerve; 1., utricular nerve.

thalmicus profundus (op.) nerve. The ophthalmicus profundus ganglion is separate from the maxillo-mandibular part though closely apposed to it.

The ramus mandibularis V.—The disposition of the mandibular branch of the trigeminal in Uraeotyphlus follows the description given for the same by Norris and Hughes (1918). Arising from the maxillomandibular part of the gasserian ganglion (text-fig. 19, mmg.) it passes through a notch in the quadrate bone and then internally to M. levator mandibulae externus into the lower jaw through a foramen in the pseudoangular bone. In the jaw, three branches can be followed. A branch, ramulus intermandibularis to supply the intermandibular muscle and the skin, a r. mandibularis internus (alveolaris) which unites with a similarly named nerve of the facial, and a main branch,—r. mandibularis externus (composed of two divisions) which run between the speudoangular and the pseudodentary and then in a canal in the latter to the symphysial region. Further, before proceeding to the lower jaw the r. mandibularis gives off small twigs which innervate the lateral skin passing through squamosal (Pl. V, fig. 5, $v_3 ls.$) and the MM. l. m. anterior, l. m. externus $(v_3me.)$, l. m. posterior and the compressor

orbitalis $(v_3cpc.)$. The united mandibulae internus nerve (mandibulae internus V plus chorda tympani) also runs anteriorly; a ramulus of this is noticed to enter the region near the sublingual glands but not into the tongue as de Jager (1939) records in Dermophis where the nerve leaves the symphysial region to supply the epithelium of the floor of the mouth and the muscles of the tongue as in the higher tetrapodous forms and the latter point is also not recorded by Norris and Hughes (1918). Branches of the external mandibular enter the skin. I have examined the young specimen of Uraeotyphlus also and the above description drawn from this and the adults closely corresponds with that of Norris and Hughes.

In *Ichthyophis* larvae however, as described by Norris and Hughes (1918), the r. mandibularis externus runs externally to the jaw along with the r. mentalis externus VII. Englehardt (1924) recorded that the r. mandibularis innervated the masseter (Vc1), temporalis major (Vc2), temporalis minor and the lower jaw (Vc3). No mention is made of the branches that enter into the lower jaw.

The ramus maxillaris V.—Leaving the maxillomandibular part of the gasserian ganglion (text-fig. 19, mmg.), the nerve is first noticed associated dorsally with a branch (Pl. V, fig. 5, os.) between the MM. l. quadrati and l. m. anterior. More anteriorly the maxillary branch separates itself from this ramulus and runs between the MM. l. m. internus and l. m. anterior. Before running between these two muscles, and while through them, small ramuli are given off, the first of which unites anteriorly below the M. compressor orbitalis with the medial branch of palatinus facialis. This anastomosis is anterior to the temporary one between the lateral palatinus facialis and maxillary V. The principal maxillary branch now divides into two (text-figs. 3, 9, max₁., max_{2b} .) which are enclosed anteriorly in a canal in the maxillopalatine bone (text-fig. 3, map.). Below the tentacular canal, the two branches of the maxillary are still enclosed in the bone but far apart in individual canals. The lateral branch (text-fig. 9, max_{2b} .) distributes itself to the side while the bigger inner branch running anteriorly (text-fig. 8, max_{1b} .) supplies the tentacular region.

In *Ichthyophis*, the maxillary branch has its lateral ramus (max₂) as its main component, while the median (max₁.) unites with the median palatine (pal_1) branch. A lateral palatine branch (pal_2) unites temporarily, a feature also noticed in Herpele (Norris and Hughes 1918). In Dermophis (Norris and Hughes 1918) the arrangement of the maxillary nerve is as in Herpele. In Geotrypetes the maxillary does not divide into medial and lateral branches but a branch from it joins palatinus facialis. A double anastomosis of palatine and maxillary occurs. united branch from maxillary and mandibular passes to the M. compressor orbitalis. Englehardt (1924) noted in Ichthyophis that the maxillary V innervated the compressor muscle (Vb4), skin (Vb1, Vb2), tentacle (Vb6) and upper jaw (Vb6); an anastomosis with r. buccalis facialis (Vb3 plus VIIa2) and a branch (Vb5) to r. nasalis facialis are also recorded. De Jager (1939) described a twig from the maxillary V to the compressor muscle in Dermophis, a point also corroborated by me,

The ramus ophthalmicus profundus V.—Having differentiated (textfigs. 11, 19, rop. op.) from the inner aspect of the profundus ganglion (textfig. 19, opg.), it runs anteriorly surrounded by the ganglion, a few fibres of which enter the r. palatinus facialis. Running by the side of the pleurosphenoid more towards the orbital cartilage, it gives off a branch (op_1) and in the choanal region the main branch (op_1) is enclosed in a canal (see text-fig. 6, sphc.), then in a groove in the sphenethmoid bone while the branch (op_1) occupies a dorsal position. It (op_1) runs anteriorly after giving off a large branch which enclosed in the frontal bone (see text-figs. 3, 9, op_{1b}) supplies the dorsal skin and this does not establish any connexion with ophthalmicus superficialis VII as described by Norris and Hughes (1918); the other is then enclosed in the dorsal part of the tentacular canal in the maxillopalatine bone (text-fig. 9, op_1 .) and supplies the tentacular region. This ramulus (op_1) closely corresponds with (op_1) of Norris and Hughes. A second branch (op₂.) arises from the ophthalmicus profundus during its passage in the canal and the main branch (see text-figs. 3, 9, op.) and the second (see text-figs. 1, 3, 9, op₂.) run below the sphenethmoid roof-like exten-This latter ramulus runs in the roof of the nasal chamber near the "Nebennase" but does not supply any fibres to the glands of the latter (though Norris and Hughes describe so) but proceeds to innervate the side after passing through a foramen (f. epiphaniale?) in the septo-The branch (op_3) of Norris and Hughes's description tallies A third (op_3) and a fourth (op_4) branches are given off with this. from the ophthalmicus profundus. These two branches lie near the Branch (op_3) (see text-fig. 1, op_{3b} .) runs for a dorsal olfactory nerve. short distance below the nasal bone and then passes through it for the The fourth branch (see text-figs. 1, 8, op₄.) passes downwards by the side of the septum nasi and then through the prevomer for the innervation of the floor of the upper jaw and this branch is comparable with (op2v) of Norris and Hughes. The principal branch (op.) runs in a canal in the nasal bone and proceeds after passing through a foramen (f. apicale?) in the premaxilla for the innervation of the snout region giving off during its course a large number of twigs dorsally (see text-fig. 1, ops.).

Englehardt (1924) described the ophthalmicus profundus V in *Ichthyophis* as r. nasalis trigeminus from which branches proceeded to skin (Va1), tentacle sac (Va2) and to the snout (Va3, Va4).

In Urodela, the ophthalmicus profundus divides into a minor, a ventral, a lateral and a median branch and the latter two gain exit through the foramina epiphaniale and apicale respectively for the innervation of the snout region. However, it is difficult to recognise similar branches clearly in Apoda and at any rate, in their figure 7q, Marcus, Stimmelmayr and Porsch (1935) indicate the two foramina apparently believing them to be for the two branches of the profundus nerve. Norris and Hughes (1918) while making no mention of the probable comparison with the Urodelan median (nasalis internus) branch, notes that their (op2v) and (op1 partly) are comparable with the ventral and lateral Urodelan branches respectively. However, it is just possible that the branches $(op_1, partly)$, (op_2, op_2) and (op_4, op_3)

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Uraeotyphlus may find comparison with the ophthalmicus profundus minor, nasalis internus, nasalis externus and ventral branches of Urodela.

The facial nerve.—The facial nerve takes its exit through a separate foramen,—the facial foramen (see text-fig. 6, ff.) in the lateral wall, i.e., the prootic portion of the os Basale. The prootic (prof.) and facial foramina are separated by a bony prefacial commissure (pfc.). The geniculate ganglion (text-fig. 19, geg.) is small and extracranial and is separate from gasserian ganglion in the adult while in the young stage examined, the ganglia are united.

No connexion between the gasserian and geniculate ganglia has been

shown by Englehardt (1924) in Ichthyophis.

The ramus palatinus VII.—The palatine branch arising from the geniculate ganglion enters through the palatine foramen, the palatine canal² (see text-fig. 6, pca.) and then runs in association with the carotid artery in the carotid canal and emerges finally with the carotid artery into the cranioquadrate passage from the carotico-palatine foramen (in fig. 6, the bristle enters through the carotid foramen and comes out through the carotico-palatine foramen). The palatine nerve occupies a position below the profundus ganglion which is situated anteriorly and this is maintained till the ophthalmicus profundus is differentiated when a few fibres from the latter enter into the palatine (Pl. V., fig. 5). This anastomosis is an important feature for in no apodan form studied so far, a nervous connexion between the two is described, though de Jager (1939) makes mention of such an anastomosis in Dermophis on one side only. In Urodela and Anura, this anastomosis commonly occurs. In the region of the tentacular muscle, the ramus palatinus in Uraeotyphlus is separated from the ophthalmic branch by this muscle. The palatine anteriorly divides into a median (see text-fig. 10, pf_1 .) and a lateral branch (pf_2 .). A small twig arising from the maxillary branch of trigeminal meets temporarily the lateral palatine branch; more anteriorly, another division of maxillary fuses with the median palatine. The composite palatine branch (pf_1max_b) runs in the choana region while the lateral palatine (pf_2) runs dorsally and then ventrally to the maxillopalatine (see text-figs. 3, 9, pf_2 .) to the anterior region. The anastomoses between the palatinus facialis and maxillary V are noticed only in Anura. The further distribution of the ramuli of these is as described by Norris and Hughes (1918) i.e., (pf_2) to choanal epithelium and maxillary teeth and $(pf_1 max_b)$ to medial wall of choana, roof of mouth and vomerine teeth.

In Ichthyophis, Scolecomorphus, Boulengerula and Herpele the palatine nerve first runs in the palatine canal of os Basale and then assumes the usual condition. This feature of the passage of the palatine in the os Basale for a short distance is not noticed in other examples viz., Dermophis, Caecilia and Geotrypetes (Norris and Hughes 1918).

A minute ganglion at the junction of the lateral branch of the palatine with the maxillary V is described in *Dermophis*, larva of *Ichthyo*-

¹ This seems to be a variable factor, for in an adult individual while on one side there is a connection between the extracranial facial and gasserian ganglia, no connection is noticed on the other side.

² This may be a canal or a groove in *Uraeotyphlus*; further the palatine branch on one side does not enter the palatine canal in one of the specimens studied.

phis and Herpele. I have not been able to detect a similar ganglion in adult Uraeotyphlus and in Geotrypetes it is apparently absent according to Norris and Hughes (1918). In the young stage of Uraeotyphlus that I have examined, it is noticed that the lateral branch (pf_2) before it receives a branch from the maxillary V (max_b) enlarges into a ganglion,—the palatine ganglion. Obviously this is purely a larval feature for, in both Ichthyophis and Uraeotyphlus larvae the ganglion is noticed while in the adult it has disappeared. The same is probably the case in Geotrypetes where the adult lacks one.

Englehardt (1924) noted that a twig (VIIa1) connected ramus palatinus with gasserian ganglion; the division of the palatine was not noticed. A connexion with maxillary V (Vb3 plus VIIa2) by ramus buccalis facialis and the more anterior union of r. nasalis facialis (palatinus facialis) with a branch of maxillary (Vb5) have also been recorded.

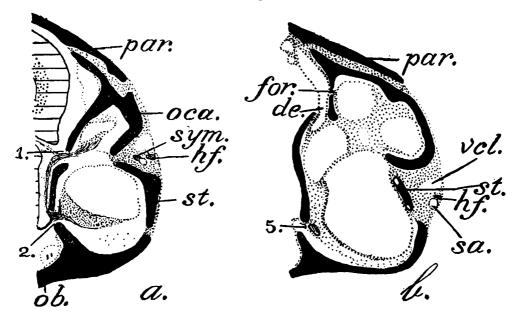
The ramus hyomandibularis VII.—After the separation of the palatine branch, the ramus hyomandibularis (text-fig. 19, hf.) arises from the geniculate ganglion (geg.) and runs posteriorly and dorsally to the stapes (see text-figs. 7a, b, hf.). The first branch given off from the geniculate ganglion uniting with the sympathetic fibres of the gasserian runs posteriorly by the side of the otic capsule in association with the r. hyomandibularis. A slender nerve is now given off from the r. hyomandibularis which running between the MM. depressor mandibulae and l. m. posterior enters a canal in the lower jaw as the ramus alveolaris (chorda tympani) in association with the r. mandibularis internus V. A bigger third proceeds to innervate the M. depressor mandibulae. The main branch,—r. jugularis runs posteriorly supplying the muscles in its course.

In Ichthyophis larva a mentalis externus, a jugularis and a third branch which divides into mentalis internus and an alveolaris are described by Norris and Hughes (1918). In the adult, the r. alveolaris arises independently. The origin therefore, of the chorda tympani from the hyomandibular branch in Uraeotyphlus differs from that in Ichthyophis. In Dermophis and Herpele (Norris and Hughes 1918), a rammus jugularis is described and it innervates the interhyoideus and constrictor colli muscles as in Ichthyophis and Uraeotyphlus. trypetes also there is a jugular branch. However, in the descriptions of the cranial nerves of Dermophis (D. mexicanus and D. gregorii) the fate of the hyomandibular is differently described by de Jager (1939). After giving off the r. alveolaris, the hyomandibular divides into three ramuli; the first innervates the M. depressor mandibulae (M. cephalodorsomaxillaris) while the other two are "ultimately lost amongst the branches of IX and X." No reference is made to the jugularis Englehardt (1924) described three branches (VIIb1, VIIb2, VIIb3) of the hyomandibular but their destination has been incompletely noted as MM. depressor and mylohyoideus.

The ramus ophthalmicus superficialis VII.—At the region of the differentiation of r. mandibularis V, the fibres of the ramus which in its topographical disposition corresponds with what has been described as "ophthalmicus superficialis" by Norris and Hughes (1918) can be made out in the maxillomandibular part of the gasserian ganglion.

Anteriorly, this nerve is disposed dorsally to the maxillary branch (Pl. V, fig. 5, max.) and is located between the MM. l. quadrati and l. m. anterior and more anteriorly between the MM. l. m. internus and l. m. anterior (os.). It divides into two: the dorsal branch ends in the M. l. m. anterior while the ventral passes dorsally to the muscle and supplies the skin. No motor branch is described by Norris and Hughes (1918) and the anastomosis between branch (op_1 .) of ophthalmicus profundus and ophthalmicus superficialis VII is also not seen by me.

The auditory nerve.—In Uraeotyphlus posterior to the prefacial commissure, the auditory nerve is met with, a part of which is in union with the fibres of the seventh nerve (text-fig. 19, caf.). The auditory ganglion (aug.) is rather thin and from it ramuli run into the internal ear through the bony septum. The number of ramuli may vary in the same individual as, e.g., in Ichthyophis and Uraeotyphlus, it may be five or six. In all the Apoda so far examined, the first ramulus supplies the utricular part (text-fig. 19, 1) while the remaining innervate the saccular portion. In Uraeotyphlus, the fourth ramulus enters the saccular part (see text-fig. 7d, 4) in the region of the endolymphatic foramen which is situated dorsally. Figure 7e is posterior to the endolymphatic foramen. Two figures (20a and 20b) are drawn for Dermophis to show two ramuli entering in at the same region to the utri-



Text-fig. 20.—Dermophis gregorii Boulenger.

Two consecutive transverse sections in the auditory region: $\times 33$.

de., ductus endolymphaticus; for., foramen in the bony septum; hf., r. hyomandibularis facialis; ob., os Basale; oca., otic capsule; par., parietal; sa., stapedial artery; st., stapes; sym., sympathetic nerve; vcl., vena capitis lateralis; 1, 2, 5., auditory orifice for the utricular (1) and saccular nerves.

cular and saccular portions (Fig. 20a, 1, 2) respectively and further, foramen 5 (text-fig. 20b, 5) is noticed along with the dorsal endolymphatic foramen. While de Jager (1939) has recorded only four ramuli in *Dermophis*, I notice five, of which four innervate the saccular portion. There is one other interesting point in the endolymphatic region of the ear of *Dermophis*. There is a foramen (text-fig. 20b, for.) in the

septum dorsally to the endolymphatic foramen through which the epithelium of the endolymphatic canal is in contact with the semi-circular canal of the internal ear. I am unable to say at present what exactly is the significance of this. In Scolecomorphus, four or five ramuli are noticed. In Boulengerula, there are again five and the endolymphatic foramen is between the third and fourth. In Siphonops, Wiedersheim (1879) recorded only four foramina.

THE CRANIAL NERVES OF BOULENGERULA AND SCOLECOMORPHUS.

I shall consider the cranial nerves of the two African genera Boulengerula and Scolecomorphus together and remark only on the salient features noticed in them.

The intracranial connexion between the geniculate and the gasserian ganglia and in the latter the separate existence of ophthalmicus profundus and maxillo-mandibular parts are known in *Boulengerula*; in *Scolecomorphus* the two ganglia (trigeminal and facial) are connected extracranially and the gasserian ganglion is a composite one.

In Figs. 6a, 6b and 6c drawn by de Villiers (1938) for Scolecomorphus, the origin of the trigeminal nerve is clearly shown. However, I have not been able to make out a "ganglion palatinum" in my sections of Scolecomorphus.

The first branch to separate itself off from the gasserian ganglion is the ramus mandibularis in *Scolecomorphus* and *Boulengerula*. A ramus mandibularis internus enters the lower jaw and unites with the chorda tympani where a few ganglion cells are noticed (*Boulengerula*). However, de Villiers (1938) denied the existence of a chorda tympani in these two genera. The united branch supplies the skin and tongue muscles in *Boulengerula*. Peculiarly in *Boulengerula* a ramus mandibularis externus is absent, while in *Scolecomorphus* it is prominently present.

There is a ramulus going to the compressor muscle from the ramus maxillaris in both genera; in *Boulengerula*, the r. maxillaris divides into a lateral and a larger medial one and from the latter there is a palatine commissure. In *Scolecomorphus*, the r. maxillaris sends first a palatine commissure and then a small ramulus to innervate the side (comparable with the lateral palatine branch) and the principal branch becomes ventrally disposed to the maxillopalatine and proceeds to the tentacular region.

There are only three branches of the ophthalmicus profundus in Boulengerula. The first, running for a short distance in the frontal bone supplies the dorsal skin; a second branch running lateroventrally and gaining exit through the nasopremaxilla-maxillopalatine supplies the anterior skin. The third or the principal branch is enclosed in the nasal portion and distributes itself to the snout. In Scolecomorphus, the first branch passes through the frontal as in Boulengerula; the second running dorsally to the orbital glands gets exit through the prefrontal; a third innervates the lateral and the tentacular region after passing through the septomaxilla. The fourth running by the side of the septum passes through the prevomer and premaxilla to the snout. The principal branch also innervates the snout.

The facial nerve.—A bony prefacial commissure is present in both The r. palatinus runs for a short distance in the palatine canal in Boulengerula and anteriorly the r. palatinus is situated below the ophthalmicus profundus ganglion as in Fig. 8 drawn by de Villiers (1936, p. 237) though his labellings 'em' and 'bV1' should be read as M. retractor tentaculi (instead of eye muscle) and palatinus facialis (instead of branch of ophthalmicus profundus) respectively. palatine nerve does not divide into lateral and medial branches but however, receives a branch from the r. maxillaris V. De Villiers denied the presence of a palatine branch in Boulengerula and in a later paper also he (1938, p. 19) recorded that "The palatine of VII stops short at the sensory ganglion of V in all the four sides available for comparison", and shew no palatine in Fig. 8 (1936, p. 237) or in Fig. 3 (1938, p. 11) and reaffirmed this on page 24 (1938) by saying that the facial has only one branch and, i.e.,—the hyomandibular. In Scolecomorphus, there is only one maxillo-palatine anastomosis and the undivided r. palatinus proceeds through the prevomer to the snout.

It must be remarked here that no anastomosis between the ophthalmicus profundus V and r. palatinus occurs in *Scolecomorphus*, though the profundus ganglion is not distinct from the gasserian ganglion.

KINETISM.

I only review in brief the problem of kinetism in Apoda here. The autostylic and mostly monimostylic condition of the cranium noticed in Amphibia was considered primary by K. Fürbringer (1904) who derived it from a Dipnoan one. Later Versluys (1912) who discovered the M. levator quadrati in Apoda described the streptostyly noticed among the members of this group as primitive and Luther developed this line. The latter author (1914, p. 12) in homologising the M. l. quadrati with the M. constrictor dorsalis I of fishes came to the same conclusion as Versluys and if however, this condition is derived from the monimostylic Urodela, then the presence of M. l. quadrati becomes questionable.

Edgeworth (1925) after studying a few developmental stages of I. glutinosus and a Siphonops larva added that the processus ascendens of the quadrate is fused with the orbital cartilage in early stages in I. glutinosus and in Siphonops "there is a cartilaginous continuity between the quadrate and the lateral process of the basal plate" besides mentioning other points of contact between the chondrocranium and Thus he comes to the conclusion that (p. 237) "These phequadrate. nomena suggest that the streptostylic condition of adult Gymnophiona is not primary, but secondary to an original monimostylic one. contrary opinion fails to explain the above described structures" has been pointed out by de Beer (1937) in this connexion that the terms streptostylism and monimostylism are applicable to adult and not larval crania. Obviously, Edgeworth does not take into consideration the observation of Peter (1898) where no processus ascendens connection with orbital cartilage is reported.

¹ Edgeworth mentions that his embryo is younger than the one modelled by Peter and therefore if the latter author had studied the same stage as Edgeworth, it may be surmised that the connection might have been discovered.

According to Marcus, the streptostyly of the Apoda is an ancestral acquisition and in this connexion Marcus, Stimmelmayr and Porsch (1935, pp. 418, 419) point out:—

Heute bin ich überzeugt, dass dem Chondrocranium keine ausschlaggebende Bedeutung fur derartig weitgehende Hypothesen zuzusprechen ist, da temporar Verwachsungen vorkommen, die wieder gelöst werden, so dass jeder sich aussuchen kann, was er für seine Hypothese braucht.

Hueber (1933) described the kinetism in the skull of Hypogeophis in detail while pointing out at the same time the primary or secondary nature of the stylism has not engaged his attention. It is recorded that the two segments,—the basal composed of the os Basale and the quadrate comprising the other bones move on each other; the skull is, therefore, amphikinetic. But Luther (1914) and Lakjer (1927) consider the Apodan skull to be mesokinetic. De Beer (1937) while accepting that the skull of Hypogeophis is kinetic in Versluys's sense and is "capable of certain amount of internal movement although the quadrate is fixed to the squamosal" pointed out that the skull must be classified as monimostylic on Stannius's scheme. No doubt the quadrate is firmly bound to the internal aspect of the squamosal, but is certainly capable of some movement and is always separated by a cer-The quadrate is never fused with tain amount of connective tissue. squamosal, contrary to what de Beer (p. 426) mentions in the case of Hypogeophis. In fact, no Apodan example so far studied is typically monimostylic, all of them being strictly streptostylic. Marcus, Stimmelmayr and Porsch (1935) confirm this when they say (p. 417) that in Hypogeophis 'Der Schädel ist hyostyl und streptostyl' (1914) also mentions that the movement of the quadrate is considerably lessened but is not completely lost.

Hueber (1933) while mentioning that the connective tissue between the bones acts as a cushion during burrowing noted however, that since the bones are so closely bound the movement between the bones in a streptostylic sense may not be possible thus implying a functional monimostyly. Stadtmüller (1936) also noted that since the Apodan quadrate was united with squamosal (syndesmotically) or pterygoid, it exhibited De Villiers (1938) also mentioned "sympektische monimostyly" that no movement was possible between quadrate and squamosal and therefore, the quadrate was monimostylic. In all these cases, it is difficult to say if no movement is possible between the quadrate and squamosal; so long as they are not fused, a certain mobility can be expected and as Luther remarks it is only a question of degree. Thus according to me, it is correct to assume that there is not even functional monimostyly and therefore, they are typically streptostylic and kinetic unlike what de Beer (1937) shows in his table on page 426.

According to Hueber (1933) in *Hypogeophis*, the movements of the quadrate and basal segments are possible at these four points:

(1) processus columellaris (processus oticus) of the quadrate and the stapes (columella),

(2) processus cultriformis (rostrum) of the os Basale and the prevomers,

- (3) processus pterygoideus of the quadrate and the basipterygoid process, and
- (4) os Basale and the parietals.

Of the Apodan genera examined by me none possesses all these four kinetic points. In *Ichthyophis* and *Uraeotyphlus*, the processus pterygoideus of the quadrate and the basipterygoid process are syndesmotically united; in *Scolecomorphus*, a stapes is wanting and therefore, a quadratostapedial articulation is lost though there is a processus oticus; in *Dermophis* (de Jager), the processus oticus and stapedial process are united and therefore, the movement is lost. The significance of the loss of kinetism is that the Apodan skull is slowly becoming akinetic.

SUMMARY AND CONCLUSION.

Summary.—The study of cranial morphology of Uraeotyphlus shows certain features in which it differs from its South Indian congener Ichthyophis, thereby amply supporting Peters's treatment of Uraeotyphlus as a separate genus. The anterior disposition of the tentacle, the absence of an external tentacular fold and the zygokrotaphic condition of the cranium have already been noticed by Peters and other workers.

The new facts which the present study reveals are largely a set of negative features by which *Uraeotyphlus* could be differentiated from *Ichthyophis* and they are:

- (1) The absence of an eminentia olfactoria in *Uraeotyphlus* and therefore the opening of the secondary nose ("Nebennase") more towards the nasal septum.
- (2) The absence of a passage in the stapes of *Uraeotyphlus* for the stapedial artery.
- (3) The absence of a buccal branch of facial nerve in *Uraeotyphlus* and in the young stage examined, the r. mentalis externus VII and r. mandibularis externus V do not run outside the jaw. The origin of the chorda tympani (r. alveolaris VII) is different; while it arises independently from the ganglion in *Ichthyophis*, it is a branch from the hyomandibular nerve in *Uraeotyphlus*.
- (4) The uniform occurrence of an anastomosis between the ophthalmicus profundus ganglion and the r. palatinus facialis in *Uraeotyphlus*. This is an important feature for Norris and Hughes describe that in all Caeciliae, on account of the distinctness of the profundus ganglion from the rest of the gasserian, the palatine anastomosis is transferred from the profundus to the maxillary branch. In *Uraeotyphlus*, the profundus is no doubt a distinct ganglion but possesses both palatino-profundus and palatino-maxillary anastomoses.

(5) The highly abbreviated embryonic and larval periods and the appearance of adult characters very early in larval life if not in the embryos of *Uraeotyphlus*.

(6) The shape of the skull; triangular in both *Ichthyophis* and *Uraeotyphlus* but in the latter the apex is more pointed than in *Uraeotyphlus*.

Now, the other important points in the study of the cranial morphology of Scolecomorphus, Boulengerula, Dermophis, Herpele and Uraeotyphlus may be recounted:

- (1) In *Ichthyophis* and *Uraeotyphlus*, there is a syndesmotic connexion between the basipterygoid process and processus pterygoideus of the quadrate. In *Scolecomorphus* anterior to the palatobasal articulation there is a thick connective tissue strand running from the processus ascendens of the quadrate to the cartilaginous facet of the basipterygoid process; from the same certilaginous facet arises the M. levator mandibulae posterior instead of from the ventral aspect of the processus pterygoideus. Thus in *Scolecomorphus*, while one kinetic muscle (l. quadrati) is absent, the other (l. m. posterior) extends between the basipterygoid process and the lower jaw instead of between the processus pterygoideus and the lower jaw.
- (2) In Boulengerula, the stapedial artery passes through a passage in the stapes.
- (3) In Scolecomorphus, there is a well developed eminentia olfactoria and Uraeotyphlus and Boulengerula lack it.
- (4) Ichthyophis skulls exhibit both crescentic and circular postfrontals; while in those with crescentic postfrontal, the prefrontal and septomaxilla may be separated by the approximation of nasal and maxillopalatine, in those with circular postfrontals, the prefrontal and septomaxilla are always apposed. In Uraeotyphlus, the circular postfrontal characterises the adult and the prefrontal and septomaxilla are always separated.
- (5) The number of acustic foramina range from four to six; in Boulengerula, Scolecomorphus and Dermophis, it may be four or five (de Jager describes only four in Dermophis) and in Uraeotyphlus, it may be five or six. While the stapes with its footplate is well developed in Apoda, Scolecomorphus is the only one to lack it. It is thought (Versluys) that the squamoso-quadrate complex transmits vibrations to the internal ear through the stapes, in which case Scolecomorphus even with four or five acustic innervation, is probably deaf.
- (6) The processus condyloides of the lower jaw is well developed in *Ichthyophis* and *Uraeotyphlus*, feeble in *Herpele*, *Dermophis* and *Scolecomorphus* and absent from *Boulengerula*.
- (7) The degenerate eye is hidden under the squamosal in Boulengerula while in Scolecomorphus it is directed towards the lower jaw and is not hidden contrary to the descriptions of Nieden and de Villiers.
- (8) Eye muscles are absent in Boulengerula and Scolecomorphus. In Dermophis, eye muscles and optic nerve are well developed contrary to the observations of de Jager. A M. rectus internus is described in Dermophis which was denied by Norris and Hughes.

- (9) The double appearance of retractor tentaculi muscle is noticed in *I. monochrous*, *Dermophis*, *Uraeotyphlus* and *Boulengerula*. In *Scolecomorphus* anteriorly the retractor is partly inserted into the tentacle and partly into the tentacular fold.
- (10) There is only genioglossus muscle in the tongue of Scolecomorphus, Ichthyophis, Hypogeophis, Uraeotyphlus, Dermophis, Herpele and Boulengerula.
- (11) The intermaxillary glands of Fahrenholz (zwischenkieferdrüse) are present in *Uraeotyphlus* and absent from *Herpele*, *Boulengerula*, *Dermophis*, *Ichthyophis* and *Hypogeophis*. In *Scolecomorphus*, there is a set of postdental glands and dorsally to this, a set of glands resembling very much the dorsal glands is seen. Since topographically this resembles the intermaxillary of *Uraeotyphlus*, this has also been called intermaxillary gland.
- (12) The presence of a Bursa angularis oris in Scolecomorphus and a set of oral glands in Herpele are recorded.
- (13) In Scolecomorphus even though the profundus is not separate from the remaining gasserian ganglion, there is no profundus-palatinus anastomosis contrary to the observations of Norris and Hughes.
- (14) A palatinus facialis is prominently present in Boulengerula contrary to the descriptions of de Villiers.
- (15) The dorsal olfactory nerve runs undivided for a long distance in the bony canal of the sphenethmoid in *Boulengerula*.
- (16) The ramus mandibularis externus V is absent as an independent nerve in Scolecomorphus and Boulengerula.
- (17) The ramus mandibularis internus VII (chorda tympani) is present in *Scolecomorphus* and *Boulengerula* contrary to the findings of de Villiers.
- (18) While Laubmann characterises the tentacle as a "Tastfühler", Marcus regards it as a "Klopffühler" aiding the animal during burrowing in respiration and olfaction. When the anterior nares close up air is led into the olfactory chamber through the nasolacrimal ducts. This explanation is applicable in all those cases where the tentacle is not situated directly below the anterior nares but behind it as in *Ichthyophis* and *Hypogeophis*. In *Uraeotyphlus* the tentacle is below the naris and during the act of burrowing (if the surface cryptic life can be described so) when the anterior nares close up the tentacle also cannot function and therefore, no air can be led into the "Nebennase"

Conclusion.—Whether the Apodan skull is primitive and, therefore, bears close resemblance to stegocephalian ancestors or the compactness of the cranium has been acquired secondarily due to a burrowing mode of life is a difficult question to answer. Stadtmüller (1936) mentions in this connection that the ossification of the skull depends upon the use of the head as a borer, but it has already been pointed out that one of the South Indian members, Ichthyophis, is not a typical bur-

rower, not digging by the head to lead a subterranean life but lives under rotten vegetation where there is sufficient moisture; this has been called a "surface cryptic" life. According to Cope (1871), Sarasins (1890), Gaupp (1895), Peter (1898), Luther (1914), Jaekel (1927), Goodrich (1930), Werner (1930-31), Versluys (1931), Edgeworth (1935) and de Beer (1937) the stegokrotaphy has been acquired secondarily. In discussing this question we have only to look for clues in the morphology of bones and not in the internal organs since it is impossible to know anything about the soft anatomy of Stegocephalia.

Marcus and his students following Broili, have come to the conclusion that the Apoda are the surviving members of Stegocephalia having come down to the present times in the tropics on account of their cryptic habits. Amongst other features of primitiveness, it is suggested that the possession of a periorbital ring of bones and an interparietal in *Hypogeophis* recalls the stegocephalian relationship. But the occurrence of an interparietal foramen and bone (Hueber 1933) is not accepted by other workers (Stadtmüller).

De Beer (1937, p. 192) in discussing the evolution of Apoda, remarks that "On the other hand, it is noticed that the postfrontal and supratemporal are lacking in Gymnophiona; which they would hardly be if these forms were primitive, since these bones are regularly present in reptiles. The complete roofing in Gymnophiona is therefore probably secondarily developed in connexion with the burrowing habit." It is only the supratemporal that is lacking in Apoda and the postfrontal is noticed in the two genera *Ichthyophis* and *Uraeotyphlus*. Probably the supratemporal has been merged in the adjacent bones and such consolidation is not uncommon amongst Apodan examples.

Boas (1914) found fossae in the Apodan skull and compared them with similar ones in Stegocephalia. According to him, the posterior temporal fossa is lost on account of the fusion of the "temporal roof and paroccipital" part while a pteroccipital gap (seen above and below the stapes when viewed from behind) and lower temporal fossa are present. Thus while the presence of a periorbital ring of bones and fossae point towards stegocephalian ancestry, the absence of a separate supratemporal weights against it.

It is interesting to note that the possession of kinetism throws light on the evolution of these forms. De Beer (1937, p. 427) points out that "the very wide distribution among vertebrates of the basipterygoid process as an articulating facet against which the pterygoid bone can move, points towards the kinetic condition as being the primitive one for the bony skull." Thus the Apodan skull being typically kinetic, is necessarily primitive. Further de Beer (1937, p. 198) infers that "The importance of this case of kinetism is that it is associated with a completely roofed skull, thus showing that there is no intrinsic improbability in the view that the Stegocephalia may have been kinetic." The kinetic possibility has already been observed by workers in Stegocephalia (Stadtmüller, 1936, p. 587). With reference to Apoda, this may mean that the roofed skull possesses kinetic points all of which have been acquired from a stegocephalian ancestor or even though the roofing is secondarily developed due to cryptic habits, yet

the kinetism is retained and therefore the similar stegocephalian skull may also have been kinetic, the latter view put forward by the adherents of the secondary consolidation theory. This naturally leads us to conclude that the kinetism is an ancestral acquisition provided it has not arisen de novo in Apoda. Similarly the temporal fossae referred to above.

While the Apoda show these three primitive characters, viz., the possession of periorbital ring of bones, fossae and kinetism, it must also be noted that the cryptic habit is resulting towards greater consolidation of the roofing bones; the formation of a composite naso-premaxilla-maxillopalatine in Boulengerula may be cited as an instance. Further, the gradual loss of kinetism is also attributable to it. In Ichthyophis and Uraeotyphlus, the basipterygoid articulation is lost and is syndesmotic; in Scolecomorphus the quadrato-stapedial articulation is lost since the stapes has disappeared. While one kinetic muscle (l. quadrati) is absent in this, the other (M. l. m. posterior) has changed its point of origin. The quadrate in all these is so firmly bound with the squamosal that the movement between the two is considerably lessened thereby heralding a monimostyly. In other words the primitive Apoda are gradually evolving from a kinetic to an akinetic condition.

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