

On the Cranial Osteology of the Fishes of the Families *Mormyridæ*, *Notopteridæ* and *Hyodontidæ*. By W. G. RIDEWOOD, D.Sc., F.L.S., Lecturer on Biology at St. Mary's Hospital Medical School, London.

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(PLATES 22-25.)

THE Mormyroid fishes have always been an interesting family, and have, on the whole, probably attracted more attention than any similarly circumscribed and terminal group. Owing to their freshwater habit and geographical limitations generally, their evolution has been constrained, and limited in the main to certain parts of their organization, with the result that they exhibit a most curious medley of primitive characters coupled with highly specialized and even degenerate characters. The large size of the brain, the presence of an electric organ in the tail, and the extraordinary shape of the snout in several of the forms are indications of a high degree of specialization, yet many of the other organs of the body show a retention of a primitive condition. There seems to be good reason to believe that the family branched off early from the lower Malacopterygian fishes, and became a terminal group. Their nearest relatives have generally been taken to be the Notopteridæ, with the Hyodontidæ somewhat more remotely allied. The study of the skull in the three families Mormyridæ, Notopteridæ, and Hyodontidæ forms the subject of the present communication.

Renewed interest in the Mormyridæ has recently been evoked by the discovery of a great many new forms in the Congo, described by Boulenger in the following three works:—Proc. Zool. Soc. 1898, pp. 775-821; Ann. Mus. Congo, Zool. i., Bruxelles, 1898-1900; Les Poissons du Bassin du Congo, 1901, Bruxelles, 8vo. It is to him that I am indebted for the material examined during the course of the present investigation, and to him I beg to offer my sincere thanks.

#### MORMYRIDÆ.

The literature on the skull of Mormyroid fishes is not very extensive. *Gymnarchus* has been fully treated of by Erdl (Abhandl. Bayer. Akad. Wiss., v. 1. 1847), and Hyrtl (Denkschr. Akad. Wiss. Wien, xii. 1. 1856). As regards the



other Mormyroids, Heusinger gives a couple of figures, rather crude, of the skull of *Mormyrus cyprinoides* in his paper on the auditory mechanism of certain fishes (Arch. f. Anat. u. Phys., 1826, pl. iv. figs. 8 & 9), but the standard work of reference is, of course, Marcusen's monograph (Mém. Acad. Sci. St. Pétersb., sér. 7, vii. 4. 1864). Marcusen did not include observations on *Gymnarchus* in this work.

#### MORMYROPS DELICIOSUS.

*Cranium* (Pl. 22. figs. 2 and 3).—The cranium is long, and tapers uniformly in an anterior direction almost to a point. The mesethmoid is low, and slightly bifid at the end. The vomer is small and edentulous, and is fused at its sides with the inner faces of the two palatine bones. Beneath the orbital region the parasphenoid has a slightly concave under surface, with vestiges of teeth close to the middle line. It is exceptionally broad just in front of the pro-otic bones, but narrows rapidly behind this, and terminates in a pair of narrow splinters of bone closely applied to the ventral surface of the basioccipital. The eye-muscle canal does not open posteriorly.

There is no opisthotic. The supraoccipital has a well-developed crest. The two parietals are fairly large, and meet in the median line by an extensive suture; the frontals are much elongated. Lying below the epiotic ridge and above the squamosal ridge is a large lateral foramen, occupied in nature by a thick-walled spherical vesicle, but opening in the dried skull directly into the cavum cranii. The foramen is bounded by the squamosal, epiotic, and exoccipital bones\*.

The two alisphenoids are widely separated throughout, and are much drawn out in an antero-posterior direction. Lying in front of the alisphenoid, and touching it above the horizontally elongated optic foramen, is a bone which can only be identified with the orbitosphenoid. It is in extensive union with the parasphenoid below and the frontal above, and its transverse width is greater than its height. The cranial cavity extends into it, and the bone would be separated into a right and a left half were it not that the two parts are connected by a thin

\* Boulenger's description of the lateral foramen of the Mormyroid skull (Les Poissons du Bassin du Congo, 1901, p. 49) as between the parietal and opisthotic is incorrect, for the opisthotic is wanting in all Mormyroids, and the parietal is in all cases separated from the foramen by the squamosal.



flooring which lies immediately above the parasphenoid. There is no basisphenoid, and there are no separate prefrontals.

*Temporal and Preopercular\* Series* (Pl. 22. fig. 1).—There are but two limbs to the post-temporal. The epiotic limb is the longer of the two; it is curved and slender. The other limb is broad and short, and extends forward towards the postero-ventral angle of the supratemporal. There is no deep or opisthotic limb. The supratemporal is a broad thin scale of bone, convex externally, which covers the supero-lateral parts of the squamosal and epiotic, and affords a lateral protection to the fibrous vesicle which lies in the lateral cranial foramen.

The interopercular is a comparatively thick bone behind, but it thins off in front into a long, thin ossified ligament, which lies in the groove that faces downward from the ventral edge of the preopercular and quadrate. The vertical and horizontal limbs of the preopercular are not clearly distinguishable, since the bone has a uniform curve, with the concavity directed forwards and upwards. A fair amount of the inner surface of the preopercular shows between the hyomandibular, interopercular, and opercular (fig. 4).

*Circumorbital Series* (fig. 1).—The nasal is fairly large, and has the form of a long semi-tubular bone which runs horizontally over the nasal sac, and takes a sharp curve downward at its anterior end, and terminates against the upper surface of the premaxilla. The other bones of the series are four in number on each side; they are rather narrow, and in proportion to the size of the skull are feebly developed.

*Maxillary Series* (fig. 1).—The gape is premaxillary, and the two premaxillæ are fused in the median plane, the suture being obliterated. Each premaxilla bears about thirteen teeth, slightly curved, and bluntly pointed. The maxillæ have no teeth, and their anterior ends are separated by the mesethmoid. The anterior portion of each is narrow, the postero-ventral portion is expanded into a racquet-shaped plate. There is no surmaxilla.

*Mandibular Series* (figs. 1 and 4).—The two dentary bones

\* The reasons for including the preopercular and interopercular bones in this series, and excluding them from the opercular and branchiostegal series, are given in a paper on the skull of the Elopidae, &c., shortly to be published by the Zoological Society. For reasons given in the same paper it is considered expedient to regard the post-temporal as a constituent of the skull.



are fused at the symphysis, and the suture is obliterated. Each bears thirteen or fourteen teeth, stout, bluntly pointed and slightly curved. The sesamoid articular is distinct, and is set rather higher up the articular than is usually the case. There is no separate angular bone.

*Hyopalatine Series* (figs. 1 and 4).—The opercular head of the hyomandibular is extremely short. The hyomandibular, strictly speaking, articulates with the cranium by two heads, the posterior about four times as broad (antero-posteriorly) as the anterior; but in the dried skull, in which the synovial cartilage has shrunk up, the distinction is no longer visible, the upper edge is nearly straight, and does not stand at a higher level than that of the metapterygoid, which is in fibrous union with the lateral edge of the parasphenoid. Indeed, the hyopalatine arch is united with the cranium by the whole of its upper edge, and is separable from it with difficulty. In relation, doubtless, with the length of the head, the axis of the hyomandibular slopes well forward, the metapterygoid is about twice as long as high, and the quadrate is drawn out to a considerable length in an antero-posterior direction. There is no separate symplectic, and no separate entopterygoid; the palatine is small and fused on to the side of the vomer. There are no teeth on the palatine or pterygoid bones.

*Opercular Series* (figs. 1 and 4).—The opercular bone is nearly rhombic in shape; the subopercular is small and triangular, and concealed in an external view by the lower part of the opercular bone.

The branchiostegal rays are seven in number on each side; the first four are slender, curved rods, but the fifth and sixth are slightly expanded at their posterior ends. The first two are attached to the hinder part of the ceratohyal, and the next three to the lower edge of the epihyal, although, on account of a process of the ceratohyal which projects backwards on the outer face of the epihyal, they appear to arise from the ceratohyal when examined in an external view. The last two, which are shorter than the fifth, are free from the epihyal, but lie close alongside the ventral edge of the opercular bone.

*Hyobranchial Series*.—The interhyal is cartilaginous. The anterior part of the hyobranchial skeleton is very aberrant. There is no separate hypohyal; but firmly fixed in between the urohyal below and the dentigerous membrane-bone above is a



cartilage-bone of considerable size which may be taken to include the glossohyal (endosteal part) and the first basibranchial. The ceratohyal fits on to the side of this compound bone. The urohyal is a large vertically disposed plate of bone, having a thin posterior edge. It is immovably fixed, and is united not only with the bone just mentioned, but also with the under surface of the anterior two-thirds of the second basibranchial. The usual paired ligament so characteristic of the urohyal is not recognizable. The dentigerous membrane-bone is narrow, bears some forty, more or less vestigial teeth, and extends back over nearly the whole of the second basibranchial. The third basibranchial is a small flat plate of bone.

The first hypobranchials are not rods of bone projecting freely backward and outward from the junction of the first and second basibranchials, and setting the anterior ends of the first ceratobranchials at some distance from the mesial structures, but they are quite short bones, closely applied to the sides of the second basibranchial in such a way that the antero-internal point of the first ceratobranchial nearly touches the side of the second basibranchial. In a somewhat similar way the anterior ends of the second ceratobranchials come close to the mesial series of bones; but in this case the hypobranchials project downward from the sides of the posterior end of the second basibranchial, and are fused with a pair of tendon-bones similar to those of *Notopterus* (see page 206). (It must be borne in mind, however, that the first, second, and third hypobranchials of *Notopterus* are quite normal, and that the paired tendon-bones are readily separable from the antero-inferior ends of the second hypobranchials and the postero-inferior surface of the second basibranchial.) The reasons for not considering the whole bone as the equivalent of the tendon-bone of *Notopterus*, and regarding the second hypobranchial as wanting, is that the upper part of the bone has the appearance of a cartilage-bone, which is not the case in *Notopterus*; that the third hypobranchials are, though small, downwardly directed; and that it strikes one as improbable that the second hypobranchials should disappear absolutely while the first and third remain.

The first pharyngobranchial is present, and has the form of a small triangular plate of bone, horizontally placed, and in contact with the antero-internal edge of the first epibranchial and the anterior edge of the second pharyngobranchial. There



is no spicular bone. The third pharyngobranchial is not longer than the second, and overlaps it only to a very slight extent. The four epibranchials are approximately equal in length, and the fourth is not expanded.

#### PETROCEPHALUS BANE.

*Cranium* (Pl. 23. figs. 6, 7, and 8).—Probably the most remarkable feature about the cranium of *Petrocephalus* is the unusual height of the mesethmoid region. The mesethmoid lies below the frontal bones, the anterior wings of which extend to the extreme front of the cranium, and its lower part is set well in advance of the vomer. The latter bone is small and edentulous, and is fused at its sides with the mesial faces of the two palatine bones. The parasphenoid is of considerable vertical height in its anterior part; it carries on its ventral surface a lanceolate patch of some thirty teeth, which are single-pointed, and thus differ from those of the jaws. The parasphenoid extends as far backward as the middle of the under surface of the basioccipital; there is no posterior opening to the eye-muscle canal.

The articular groove for the reception of the hyomandibular is set low down the side of the cranium, and the pro-otic is four-sided and faces downward, instead of downward and outward. Between the epiotic ridge and the squamosal ridge is a large aperture leading into the *cavum cranii* in the dried skull, but in nature lodging a nearly spherical thick-walled vesicle. The aperture is bounded by the exoccipital, epiotic and squamosal. There is no opisthotic. The supraoccipital has a strongly developed median crest; the two parietals meet in the middle line, and at their junction form a low crest, continuous with that of the supraoccipital.

The frontal bones are rather small, and each has a slender bar of bone arching obliquely over it. The prefrontals are small but distinct; they do not touch one another in the median plane. A basisphenoid is present, and is united above with the orbitosphenoid and alisphenoid, and below with the parasphenoid. The orbitosphenoid is larger than the alisphenoid, and extends from the frontal above to the parasphenoid below.

*Temporal and Preopercular Series* (figs. 5 and 9).—The post-temporal resembles that of *Mormyrops*. The supratemporal



is remarkably large, and has the form of a thin convex plate of bone covering the dorsal part of the squamosal and the lateral parts of the parietal and epiotic bones. It forms a protective covering for the lateral cranial foramen. The preopercular is narrow, and its forwardly directed ventral limb is short; the interopercular is small and is concealed in an external view by the preopercular.

*Circumorbital Series* (fig. 5).—The nasal is a large curved bone. On its dorsal surface is a broad groove which narrows along its anterior surface, and terminates in a point at the ventral end of the bone. The circumorbital bones proper are six in number on each side. The preorbital is of moderate size, the two suborbitals are comparatively large, and the three post-orbitals are narrow incomplete tubes.

*Maxillary Series* (fig. 5).—The gape is premaxillary; the two premaxillæ are fused in the median plane, and the suture is obliterated. They are comparatively short and stout, and each bears about eight teeth, slender, and bifid at the tip. The maxillæ are curved, toothless bones of fair size, which touch one another in the median plane immediately in front of the vomer and behind the mesethmoid. Each has a dorsal process which projects horizontally backward, and is lodged beneath the first suborbital bone. There is no surmaxilla.

*Mandibular Series* (figs. 5 and 9).—The two dentaries are fused in the median plane, but the suture remains visible. Each carries about eleven teeth, slender, and bifid at the tip. There is no clear distinction between the ectosteal, endosteal, and sesamoid constituents of the articular; neither is the angular a distinct bone.

*Hyopalatine Series* (fig. 9).—The union between the upper edge of the hyopalatine arch and the cranium is of a very intimate character; in fact, the palatine has its mesial face so closely united with the vomer, parasphenoid, and prefrontal that to separate it without breaking its substance is impossible. The palatine is a rectangular plate of spongy bone standing vertically against the side of the front of the parasphenoid; the usual articular heads cannot be recognized. There is no separate entopterygoid, and the ectopterygoid, like the palatine, is edentulous. The lower edge of the ectopterygoid has a uniform curve; there is no sharp angulation. The hyomandibular is broad, and articulates with the cranium by what



at first appears to be one long continuous head, although strictly the anterior extremity, immediately over the foramen, is a small separate head. The axis of the hyomandibular is inclined in a forward direction, and, in the absence of a distinct symplectic, is attached to the postero-superior edge of the quadrate.

*Opercular Series* (figs. 5 and 9).—The subopercular is small, and is concealed in a lateral view by the lower part of the opercular bone. The branchiostegal rays are eight in number on each side, and, with the exception of the last but one, all are slender and of uniform width. The first four are attached to the outer face of the ceratohyal, the next two to the epihyal, while the last two are free from the epihyal, but lie close under the ventral edge of the opercular bone.

*Hyobranchial Series*.—The first, second, and third basibranchials are ossified, the first being the largest and the third the smallest. There is no glossohyal. There is a dentigerous membrane-bone, nearly circular in outline, overlying the middle part of the first basibranchial, and immediately behind it is another dentigerous membrane-bone, longer and narrower than the former, and covering the hinder part of the first basibranchial and the anterior half of the second. The teeth upon these bones have single points like those of the parasphenoid. The third basibranchial has the form of a rod curved into the fourth part of a circle, so that, while its anterior part is horizontal, its posterior part projects down vertically between the downwardly directed third hypobranchials. The relations of the hypobranchials and the pair of tendon-bones are exactly as in *Mormyrops*.

The urohyal is short, and consists mainly of a vertical sheet of bone less than twice as long as high; it articulates with the ventro-internal surfaces of the anterior ends of the ceratohyals, and also by an extensive articular surface with the under parts of the posterior three-fourths of the first basibranchial and the anterior one-fourth of the second basibranchial.

The ceratohyals are short and wide. There is but a single hypohyal to each, the upper of the two normally present in Teleosteans. It is small in size, and is wedged closely beneath the anterior of the two dentigerous bones.

There is no first pharyngobranchial, nor a spicular bone; the second pharyngobranchial is a horizontally disposed plate of



bone, roughly square in outline; the third is a slightly curved, forwardly directed rod, which is attached to the posterior end of the second pharyngobranchial, and not, as is more usual, to the mesial edge of its anterior end.

#### Other MORMYRIDÆ.

The skulls of *Mormyrops* and *Petrocephalus* just described were specially prepared for the purposes of this investigation from alcohol-preserved material kindly furnished by Mr. G. A. Boulenger; but for comparison with them I have been glad to avail myself of ready-prepared skulls of five other genera of Mormyroid fishes from the Osteological Collection of the British Museum.

Two species of *Mormyrus* were examined, *Mormyrus caschive* (a complete specimen, Brit. Mus. No. 1441, Nile; and a large fragmentary skeleton, also from the Nile), and *Mormyrus hasselquisti* (Brit. Mus. No. 879, Fashoda). The general aspect of the skull is the same as that of *Mormyrops*, but parasphenoidal teeth are well developed, and there are distinct prefrontal bones; the orbitosphenoid has the appearance of being completely divided into a right and a left part, but without cutting the skull I am unable to make a definite statement on this point. The dentition of the premaxilla and dentary is more feeble\*, and the teeth are bifid at the tip, like those of *Petrocephalus*. The maxilla is of remarkable shape (Pl. 23. fig. 10) in consequence of the exceptional size of the horizontal, posteriorly directed process *a*. The mandibular rami are much longer and narrower than in *Mormyrops* and *Petrocephalus*.

The relations of the hyopalatine arch are similar to those of *Mormyrops*, but in *Mormyrus caschive* there arises from the postero-dorsal part of the pterygoid (probably the ectopterygoid, but as there is no recognizable entopterygoid it is difficult to say for certain) a process of bone which is united by a jagged suture with the antero-ventral part of the orbitosphenoid. In *Mormyrus hasselquisti* there is but the feeblest suggestion of such a connection.

The horizontal limb of the preopercular is approximately as long as the upright limb, the two being set at an angle of about

\* Boulenger (Proc. Zool. Soc. 1898, p. 780) employs this as a distinctive character, *Mormyrops* and *Petrocephalus* having 12 or more teeth in each jaw (upper and lower), whereas all the other genera (except *Gymnarchus*) have not more than 10 teeth in each jaw.



105 degrees; and about one-half of the interopercular is visible in an external view of the skull below the lower edge of the preopercular. The ceratohyal is relatively shorter and stouter than in *Mormyrops*, and the dentigerous membrane-bone longer and more strongly toothed; but the essential features of the hyobranchial skeleton are the same in both.

Prepared skulls of *Marcusenius isidori* (Brit. Mus. No. 796, Nile), and *Gnathostomus cyprinoides* (Brit. Mus. No. 1210, Nile) were also examined, but no new features of interest were discovered.

*Hyperopisus bebe* (Brit. Mus. *Mormyrus dorsalis*, 62.1.17.76, Khartoum) is remarkable for the great development of the parasphenoid and hyobranchial dentition. The teeth are flat-topped, and are closely set in the form of a pavement. Both upper and lower patches of teeth are of considerable breadth, and form a very efficient crushing apparatus.

Two skulls of *Gymnarchus niloticus*\* were examined, one about 10 inches long, and the other (Brit. Mus. 91.4.2.26, Lagos) about  $4\frac{1}{2}$  inches. The skull of *Gymnarchus* has been so well figured by Erdl (Abhandl. Bayer. Akad. Wiss. v. 1. 1847, pl. 5) and Hyrtl (Denkschr. Akad. Wiss. Wien, xii. 1. 1856, pls. 1 & 2), that a bare description will here suffice. Unfortunately the figures of Hyrtl are not lettered, but the numbers attached to the parts in Erdl's figure will serve in the subjoined remarks for the recognition of bones, although the names which he gives to the bones are now obsolete. Marcusen did not include observations on *Gymnarchus* in his monograph on the Mormyridæ.

The cranium is long, and the mesethmoid low. There is no supraoccipital crest; the parietals meet; there is no opisthotic. The lateral cranial foramen of *Gymnarchus* should rather be described as a hemispherical depression, from the depths of which three apertures lead into the cranial cavity. Its margin is formed by the exoccipital, epiotic, and squamosal as in other

\* Although the skull, and particularly the branchial skeleton, of *Gymnarchus* possesses some very remarkable features, I am disposed to follow Günther (Study of Fishes, 1880, p. 626) and Boulenger ("Revision of the Mormyridæ," Proc. Zool. Soc. 1898) in retaining the genus in the family Mormyridæ, rather than to accept the earlier view of Günther (Brit. Mus. Cat. Fishes, vi. 1866, p. 225), and of Cope (Trans. Amer. Phil. Soc., n. s. xiv. 1871, p. 454), that it should constitute a separate family, the Gymnarchidæ.



Mormyroids, and it is covered by a thin scale-like supratemporal (No. 12 of Erdl's figure). The postfrontal is small, and is wedged in between the front part of the squamosal and the upper edge (there is no proper articular facet) of the hyomandibular.

The interorbital septum is thin and bony. At the back of the orbit is the alisphenoid (No. 17 of Erdl), in front of this the orbitosphenoid (No. 18), and below and partially between them is a fair-sized basisphenoid (No. 16*a*). In front of the orbitosphenoid is a curious bone (No. 6) which forms the most anterior part of the interorbital septum, and is united laterally by jagged sutures with the upper edge of the ectopterygoid and the postero-superior edge of the palatine. There seems to be no alternative but to regard this bone as the two prefrontals fused in the median plane. The cranial cavity is continued into the upper part of this bone, and divides anteriorly into two passages transmitting the stalks of the right and left olfactory lobes of the brain.

The connection between the hyopalatine arch and the cranium is of a far more intimate and rigid nature than in any other of the Mormyridæ examined: there can be no possibility of movement of the hyopalatine arch. The axis of the hyomandibular is drawn forward until it is nearly horizontal. The parasphenoid is short, broad, and nearly flat (No. 16 in Erdl's lower figures), and its anterior part is underlaid by the broad thin end of the bone No. 5, which I take to include the vomer, the endosteal mesethmoid †, the two palatines, and the two entopterygoids, fused together. This bone has no teeth; neither has the parasphenoid. The metapterygoid (No. 22) lies nearly horizontal in the floor of the orbit, above the lateral expansion of the parasphenoid. There is no recognizable symplectic.

The posterior extremity of the epiotic ridge (No. 10) is in intimate ligamentous relation with the stout upper end of the supraclavicle (No. 36). The post-temporal (No. 36\*) is quite a small bone, of which none of the three usual limbs (epiotic, opisthotic, and supratemporal) can be recognized. It lies immediately external to the junction of the supraclavicle with the epiotic.

† The ectosteal mesethmoid (No. 7) is readily separable from this. The closer union of the endosteal mesethmoid with the vomer than with the ectosteal mesethmoid is paralleled in *Megalops*.



The nasal (No. 3) is narrow and hook-shaped, and semitubular, The suborbital series is constituted by a chain of 9 to 12 bones, which run nearly in a straight line from the back of the premaxilla to the front of the squamosal. The first of these is an oval plate of bone, the size and shape of which are better represented in Hyrtl's figure than in Erdl's; but the others are merely tubes of bone conveying the cutaneous sensory organ.

The two premaxillæ are rigidly united by an interlocking suture. Each has about seven teeth. The maxillæ (No. 2) are curved rods of bone, without teeth; they are widely separated one from the other, they are attached by fibrous tissue to the posterior ends of the premaxillæ, and are not connected with the cranium in any way.

The two dentaries are not fused at the symphysis; each bears 13 or 14 teeth (see fig. 11), those at the front square-ended\*, like the premaxillary teeth, those behind bluntly pointed. The teeth are minutely serrated along the edges. The articular facet for the reception of the head of the quadrate is formed by two bones. The upper one (No. 26 of Erdl's lower figures) is obviously the endosteal articular, while the bone (No. 25) that forms the other half of the facet represents the angular bone fused with the ectosteal articular. There is a well-developed sesamoid articular (No. 27), suturally united with the antero-superior edge of the endosteal articular (see fig. 11).

The subopercular (No. 30) is relatively small, but it is not entirely concealed by the opercular bone; it agrees with that of other Mormyroids, however, in terminating in a point posteriorly. The interopercular is large and long, and is concealed by the preopercular. The horizontal limb of the preopercular is nearly twice as long as the upright limb: it is represented as too short by Erdl (No. 28, lower figures).

Only four branchiostegal rays are present on each side. Of these, the first is attached to the ceratohyal, the next two to the epihyal, and the last, which is the shortest, lies along the ventral edge of the interopercular, to which its anterior portion is attached by fibrous tissue. Hyrtl (*l. c.* p. 16) states that his specimen had seven branchiostegal rays on the right side and six on the left; but Erdl (*l. c.* p. 229), Duvernoy (*Ann. Sci. Nat.*

\* The curious chisel-edge of these teeth is not the effect of wear, for the reserve teeth, yet uncut, present the same feature.



(3) xx. 1853, p. 160), and Boulenger (Poissons du Bassin du Congo, 1901, p. 50, footnote) all record the number as four.

The epihyal is relatively longer and larger than in other Mormyroids; there are no hypohyals. The urohyal is fused with that bone which in *Mormyrops* (p. 191) was taken to represent the first basibranchial and the endosteal glossohyal combined. This compound bone is the No. 33 of Erdl (bottom of plate, left-hand side); its front part is marked *a*, and its hinder part *b* in Hyrtl's figure 2 of plate 1. The great pair of tendon-bones (*g* of Hyrtl's figure) show less evidence of containing a hypobranchial element than in other Mormyroids; they are strongly curved, and extend horizontally outward and then backward. Their antero-internal extremities are closely bound by ligament in the median plane, but partially between them, and projecting a little in front of them, is a small rod of bone, the reduced second basibranchial. In Hyrtl's figure the letter *h*, although not on the bone, but to the right side of it, is evidently intended to apply to it, for he describes *h* as "der mediane Knochenkern in der Symphyse der mit *g* bezeichnete Knochen." There is no third basibranchial.

Touching one another above the glossohyal is a pair of small bones, apparently representing the dentigerous membrane-bone, although they are toothless. They are not shown in Hyrtl's figure, but one of them is shown in Erdl's lower figures; it is marked No. 35, and is called (p. 228) "kleines Zungenbeinhorn, ein länglicher, ziemlich cylindrischer Knochen. Beide kleine Hörner stossen mit ihrem vorderen Theile an einander, nach hinten divergiren sie." In a footnote on the succeeding page, Erdl compares these small bones with the unpaired dentigerous membrane-bone that lies over the endosteal glossohyal of *Mormyrus*.

The first hypobranchial\* is a small rod-like bone, lying across the anterior extremity of the first ceratobranchial; it fails by a good deal to reach the median line. The second hypobranchial may be fused with the paired tendon-bone, but the third hypobranchial is wanting. The reduction of the hypobranchials, however, does not bring the anterior ends of the ceratobranchials closer to the median line. The ceratobranchials of the right and left sides remain, in fact, widely separated.

The four epibranchials are short and subequal. There is no

\* This and the pharyngobranchials are not shown in Hyrtl's figure.



first pharyngobranchial; the second and third are quite short, the second being triangular and the third square in general outline. The pharyngobranchials of the right and left sides are rather widely separated, and there intervenes a considerable expanse of pharyngeal mucous membrane unsupported by skeletal parts.

*Distinctive Features of the Mormyroid Skull.*

The following features, present in the seven genera *Mormyrops*, *Petrocephalus*, *Marcusenius*, *Gnathostomus*, *Hyperopisus*, *Mormyrus*, and *Gymnarchus*, will doubtless prove to be common throughout the family Mormyridæ.

The parietal bones meet in a median suture, and are not separated by the supraoccipital; an orbitosphenoid is present, but no opisthotic; there is a large lateral cranial foramen, bounded by the squamosal, epiotic, and exoccipital, and loosely overlaid by a thin, scale-like supratemporal\*; there is no posterior opening to the eye-muscle canal. There are no teeth on the maxillary, vomerine, palatine, and pterygoid bones. There is a very extensive attachment of the whole of the upper edge of the hyopalatine arch with the cranium; there is no separate symplectic, and no separate entopterygoid. The palatine is fused with the side of the vomer; the right and left premaxillæ are fused together, although the suture may remain visible, as in *Gymnarchus*; there is no surmaxilla. The subopercular terminates in a point posteriorly, and, except in *Gymnarchus*, is entirely concealed by the opercular. The hypobranchials are greatly reduced, and a pair of large tendon-bones project downward and outward (horizontally outward and backward in *Gymnarchus*) from the hypobranchial region. There is no separate glossohyal; it is either wanting (*Petrocephalus*), or is fused with the first basibranchial. The urohyal is without the usual paired ligament in front; it is rigidly fixed, or even fused (*Gymnarchus*), beneath the anterior part of the copular skeleton.

\* The extensive overlapping of the parietal by the supratemporal, given by Boulenger (Ann. Mag. Nat. Hist. [7] xiii. 1904, p. 164) as a family character, is fallacious. In the Mormyridæ the supratemporal covers very little of the parietal bone; in some species, e. g. *Mormyrops deliciosus* and *Gymnarchus niloticus*, it does not even reach the parietal.



## NOTOPTERIDÆ.

## NOTOPTERUS KAPIRAT.

The hinder part of the cranium of *Notopterus* has been described and figured by Bridge in his paper on the Air-bladder and Auditory Organ of *Notopterus borneensis* (Journ. Linn. Soc., Zool. xxvii. 1900).

*Cranium* (Pl. 24. figs. 13, 14, and 15).—The appearance of the cranium is remarkable on account of the five sharp ridges, two paired and one median, which run lengthwise along it. The median one is formed by the frontals and supraoccipital, the upper lateral by the frontal, parietal, and epiotic, and the lower lateral by the frontal and squamosal. Between the hind ends of the two lateral ridges is a large foramen—the “lateral cranial foramen”—leading, in the dried skull, directly into the cranial cavity. It is bounded in front by the squamosal, behind by the exoccipital, and above by the squamosal and epiotic\*.

The supraoccipital crest is of considerable size, and in front of it the two parietals meet in the middle line of the head. The anterior half of each is superficial, and is covered by skin only, the posterior half is situated at a somewhat deeper level, and is covered by muscle as well as skin. The squamosal extends remarkably far forward, running completely over the postfrontal, and resting its anterior end above the alisphenoid. The epiotic is of small vertical extent. At the back of the cranium, between the supraoccipital crest and the epiotic prominence, is a depression occupied by trunk muscles, and into the constitution of which the exoccipital enters largely. The opisthotic is of moderate size; it is set rather low down, and lies beneath the squamosal and exoccipital, and touches the pro-otic in front.

The postfrontal is small and does not enter into the hyomandibular-cranial articulation. The articular surface for the head of the hyomandibular is formed by the pro-otic and squamosal in front, and by the exoccipital behind, a small portion of the latter bone presenting itself between the squamosal above and the opisthotic below and behind. The exoccipitals just succeed in meeting above the foramen magnum, but do not form any extensive suture. The base of the skull is

\* It is not surrounded by the squamosal (pterotic) as stated by Cope (Tr. Amer. Phil. Soc., n. s. xiv. 1871, p. 454); neither is it bounded by the postfrontal and squamosal as Boulenger states (Poissons du Bassin du Congo, 1901, p. 115, and Ann. & Mag. Nat. Hist. [7] xiii. 1904, p. 164).



inflated, the bulla being formed by the pro-otic and basioccipital at the side, and by the posterior end of the parasphenoid below. Behind the bony swelling is a ventro-lateral vacuity bounded above by the opisthotic and pro-otic, and internally by the basioccipital. This vacuity lodges the inner and upper portion of a rather large air-vesicle, the outer and lower walls of which are fibrous, and are consequently wanting in a macerated skull. The anatomy of this diverticulum of the swim-bladder has been minutely described by Bridge (*l. c.*), who terms it the "auditory cæcum."

The basisphenoid is of fair size. It is nearly horizontally disposed, has no descending limb, and is slightly convex on its lower surface. At its sides it touches both alisphenoid and pro-otic. The foramen between the alisphenoid and the pro-otic is situated unusually high up the back of the orbit. The two alisphenoids meet one another behind the orbitosphenoid, which is rather exceptional; and the olfactory lobes run the whole of their course within the orbitosphenoid and prefrontal bones.

The parasphenoid is broadened out into a rhombus in its hinder portion, and its posterior extremity lies beneath the middle of the length of the basioccipital, or even a little in advance of this. The eye-muscle canal is short and blind. The parasphenoid bears an elongated patch of teeth, and its lateral wings extend a fair distance up the front of the pro-otic bones. The vomer bears a small patch of teeth near its anterior end. It extends rather more anteriorly than the mesethmoid, which fits closely on the front of the prefrontals, the ethmoid region of the cranium being short. There is an extensive union of the right and left prefrontals in the median plane of the head.

*Temporal and Preopercular Series* (fig. 12).—The post-temporal has the form of a tube, elliptical in section, and opening obliquely at both ends on its cutaneous aspect. The anterior end is attached by fibrous tissue to the back of the exoccipital and to the upper part of the opisthotic. The lower edge of this bone must thus be regarded as the opisthotic limb. The epiotic limb is wanting. In *Notopterus afer* (Brit. Mus. 95.7.18.49, Old Calabar) there is a separate opisthotic limb, a long, slender, delicate rod.

The supratemporal is an elliptical scale of bone, which does not carry the sensory tube, but lies at a slightly higher level.



The branch of the sensory tube which forms the parietal commissure arises anteriorly to the supratemporal. The supratemporal lies on the external, *i. e.*, lateral side of the opiotic, and touches the posterior part of the parietal. On account of its small size it fails to act as a cover to the large lateral foramen of the cranium.

There is a more than usually intimate connection between the preopercular and postero-superior extremity of the quadrate. On the lower part of the preopercular are two sharp serrated ridges, which form a posterior continuation of the two serrated ridges of the mandible; and in the middle of the outer face of the preopercular is a circular depression with an incomplete posterior border, by which the sensory canal comes to the surface of the head. In the undissected head this hole is seen to be closed by a delicate, scaleless membrane, similar to that which covers the posterior end of the post-temporal. The upper end of the preopercular fits closely into the lateral notch that occurs near the posterior end of the squamosal (fig. 13). The interopercular lies some considerable distance up the inner face of the preopercular.

*Circumorbital Series* (fig. 12).—The bones of this series are seven in number. The nasal is large, and forms the anterior as well as the dorsal border of the nasal aperture. The two nasal bones touch one another above the mesethmoid, and form a sharp median crest. The first two of the three suborbital bones are moderately large, and have a serrated lower margin. The anterior of the three gives off from its front end a process which passes inward and upward, and enters into a definite articulation with the under side of the prefrontal. A somewhat similar process passes inwards from the posterior end of the second suborbital, accompanied by a similar process from the anterior end of the third. These processes are attached by ligament to the outer surface of the ectopterygoid and entopterygoid. The uppermost postorbital has the form of a tube, through which passes the sensory tube on its way from the dorsal surface of the squamosal and frontal (fig. 13, *sc.*) to the groove in the orbital edge of the postorbital and suborbital bones.

*Maxillary Series* (fig. 12).—Both maxilla and premaxilla bear moderately long, pointed teeth on the external edge of their lower border, and smaller teeth on the buccal side of these. The anterior end of the maxilla lies above the premaxilla, and



articulates with the side of the vomer. There is no sur-maxilla.

*Mandibular Series* (figs. 12 and 16).—The angular is distinct, and of large size. The dentary bears a row of pointed teeth on its outer edge, and crowded small teeth on its supero-internal surface. There are two lines of serrations in each ramus of the mandible, one along the ventral edge of the dentary and angular, and another on the outer face of the dentary. A sesamoid articular of moderate size is present; the endosteal articular is not distinct from the ectosteal articular.

*Hyopalatine Series* (fig. 16).—The hyomandibular articulates with the cranium by a single broad head. The symplectic is much expanded, and unites suturally with the lingual faces of the preopercular, the metapterygoid, and the quadrate. Teeth are borne by the palatine, ectopterygoid, and entopterygoid. The palatine articulates with the ethmoid region by a single head. The ectopterygoid is fused with the palatine, and its lower edge is nearly straight, and has no angulation in the middle of its length.

*Opercular Series* (fig. 12).—The opercular bone is comparatively small in size, and is marked by shallow radiating ridges. The size of the gill-cover is considerably larger than that of the opercular bone would lead one to suppose; there is a broad posterior margin not supported by bone. There is no sub-opercular bone.

The branchiostegal rays are eight in number; they are all curved rods, and the posterior ones show very little tendency towards flattening. The first two lie free in the branchiostegal membrane, the third is attached to the edge of the ceratohyal, and the remaining five to the outer face of this bone, the last, which is the largest, overlapping much more of the bone than the others. None are attached to the epihyal.

*Hyobranchial Series* (fig. 17).—There are twelve long and rather stout gill-rakers on the first branchial arch, but those on the other branchial arches are short and blunt. They are all readily removable from the underlying bone. The interhyal is cartilaginous, or is very slightly ossified.

The epihyal is small as compared with the ceratohyal, and the hypohyal is small, and single on each side. It is probably the lower of the two hypohyals which is wanting, or unossified, since the anterior ligaments of the urohyal, usually connected



with the lower hypohyals, are attached in *Notopterus* to cartilage below the level of the single hypohyal bones. The glossohyal is large and well ossified on the surface, although cartilage persists in the interior, there being no endosteal glossohyal; it bears large, strongly curved teeth around its edge. The first basibranchial is unossified. Above the first, second, and third basibranchials is a membrane-bone which bears small crowded teeth over nearly the whole of its upper surface. Small teeth also occur on the fifth ceratobranchials. The first pharyngo-branchial is small and cartilaginous, and there is no spicular bone.

The urohyal is rather short and broad, and a pair of ossified tendons, similar in structure and function to the urohyal, and together nearly equalling the urohyal in size, project downward, outward, and backward from the lower surface of the posterior end of the second basibranchial.

#### HYODONTIDÆ.

##### HYODON ALOSOIDES.

*Cranium* (Pl. 25. figs. 19, 20, and 21).—The characteristic appearance of the cranium is due to the low position of the anterior three-fourths of the parasphenoid. This part is curved and strongly toothed, and makes a distinct angle with the posterior part. The parasphenoid underlies but a small portion of the basioccipital, and the eye-muscle canal opens at its posterior end by an oval foramen. The vomer is small and edentulous.

The ethmoid region is short. The frontals also are rather short, and the parietals are consequently more anteriorly placed than usual. The two parietals meet in the middle line, but only for a short distance. The supraoccipital separates the hinder parts of the parietals, and possesses a crest which is T-shaped in transverse section. Each of the exoccipitals has a vertical wing situated at the side of the foramen magnum. The opisthotic is rather large, and forms the greater part of what at first glance appears to be the squamosal spine. The opisthotic forms part of the articular cavity for the posterior head of the hyomandibular, which fact is exceptional.

A side view of the cranium shows an oval tract of cartilage bounded by the epiotic, parietal, and squamosal. This is not to be confounded with the lateral foramen of *Notopterus* and the



Mormyridæ, bounded by the squamosal, epiotic, and exoccipital, although there is probably some degree of morphological relationship existing between the two. It finds its nearer equivalent in the lateral depression (pre-epiotic fossa), which in *Osmerus*, *Clupea*, &c. is situated immediately in front of the vertical posterior edge of the epiotic bone.

At the side of the base of the cranium, and below the level of the squamoso-opisthotic ridge, is a great vesicle of the swim-bladder. Its outer wall is composed of fibrous tissue, which is attached to the cranium along the line marked with dots in fig. 20. Its inner wall is formed by the exoccipital and basioccipital, and its anterior wall by a vertical lamina of the pro-otic. Between the exoccipital, basioccipital, and pro-otic is a fairly large auditory fenestra \*, opening into the perilymphatic cavity, and traversed vertically by the pro-otic lamina just mentioned. The foramen for the vagus, situated dorso-posteriorly to the vesicle of the swim-bladder, is of large size.

On separating the cranium from the vertebral column, the basioccipital and the exoccipitals part readily from the half-centrum, and are left exhibiting a rough surface with the usual triradiate suture. The vertebral body † is not shorter antero-posteriorly than the centra that follow, and it is provided with a complete neural arch, the paired spinous processes of which are but little smaller than those of the succeeding vertebræ. *Hyodon* must thus be regarded as one of the instances in which the tendency for the appropriation of the first centrum by the basicranial axis is of the slightest character.

The basisphenoid is situated farther forward than usual, and has no vertically descending process. It extends so far forward beneath the alisphenoids as to touch the orbitosphenoid, and it forms the superior edge of the optic foramen. The orbitosphenoid is U-shaped in section, and, at least in the dried skull, the cranial cavity continues through it to the ethmoid region. The orbitosphenoid nearly touches the prefrontals, but is separated from them by a narrow tract of cartilage. The interorbital septum below the orbitosphenoid and basisphenoid is membranous.

\* The auditory fenestra is a Clupeoid feature, and its occurrence in *Hyodon* is of some interest.

† It is not shown in figures 19, 20, and 21.



*Temporal and Preopercular Series* (figs. 18 and 22).—The post-temporal consists practically of its two limbs, there being no body to speak of. The upper limb is long, and its extremity is loosely attached to the upper surface of the epiotic; the lower is short, and is attached about halfway along the upper surface of the opisthotic. Although the superficial portion of the lower limb carries a sensory tube, the deeper portion of it must obviously, from its relation to the opisthotic bone, be regarded as the opisthotic limb. There may, in fact, be detected an indication of a separation into a more superficial and a deeper part at the posterior end of the limb. The supratemporal is remarkably large. It is a triangular curved lamina of bone which conceals the whole of the parietal, and parts of the frontal, squamosal, epiotic, and supraoccipital. The two supratemporals meet, or nearly meet, in the dorsal median line. The lower portion of the preopercular is large, and extends much lower than the subopercular. The interopercular is long and narrow, stretching from the front of the subopercular to the back of the mandible, so that it is considerably above the level of the lower edge of the preopercular.

*Circumorbital Series* (fig. 18).—There are nine bones of this series. The nasal is small and narrow, and the two postorbitals are large, and overlap the upper part of the preopercular.

*Maxillary Series* (fig. 18).—The gape is bounded above by both maxilla and premaxilla, and the premaxilla is exceptionally long. In a roughly prepared skull the maxilla appears to follow on immediately behind the posterior end of the premaxilla, but it really extends some distance forward along the inner surface of the premaxilla, and is thus overlapped by the premaxilla as it is in so many Malacopterygian fishes. Both premaxilla and maxilla carry a single row of teeth, those of the premaxilla being larger than those of the maxilla. There are no heads, either of the premaxilla or the maxilla, for articulation with the ethmoid region of the cranium, and the articulation with the palatine is of the feeblest character. There is no surmaxilla.

*Mandibular Series* (figs. 18 and 22).—The mandibular ramus is long and narrow, and the coronoid process low. The articular is small as compared with the dentary; its ectosteal and endosteal constituents are clearly distinct, and a suture between the two appears on the external face of the ramus, which is very unusual (fig. 18). The sesamoid articular is comparatively



large. There is no distinct angular bone. The dentary is well toothed, the larger teeth being situated on the labial and lingual edges, the smaller teeth occupying the space between these two rows.

*Hyopalatine Series* (fig. 22).—The hyomandibular articulates with the cranium by two distinct heads; its opercular head is long, and its axis slopes downward and backward. The angle between the symplectic and the axis of the hyomandibular is a little over a right angle. Teeth of fair size occur on the palatine and ectopterygoid, and small teeth on the middle part of the entopterygoid. The ectopterygoid is slightly curved, but has no distinct angulation.

*Opercular Series* (figs. 18 and 22).—The opercular and subopercular bones are rather small as compared with the size of the skull. The branchiostegal rays are nine in number on each side. Six are attached to the ventro-external edge of the ceratohyal, one at the junction of the ceratohyal with the epihyal, and two on the epihyal. They form an evenly graduated series.

*Hyobranchial Series*.—The sides and upper surface of the remarkably large glossohyal consist of ectosteal bone. Examined from below, the anterior three-fourths of the interior are seen to be composed of cartilage, the posterior fourth of cartilage-bone. The latter is situated at a higher level than the first basibranchial, and overlaps the anterior two-thirds of that bone. The glossohyal bears the largest teeth in the head; the large teeth occupy the edges of the upper surface, and the intervening space is occupied by small teeth. The parasphenoid teeth fit very neatly between the large glossohyal teeth, and form a prehensile apparatus from which there can be little escape.

A dentigerous membrane-bone covers the whole of the second basibranchial, the posterior third of the first basibranchial, and the anterior three-fourths of the third basibranchial. It forms a direct continuation of the dentigerous part of the glossohyal. The upper and lower hypohyals are approximately equal in size and are rather large. The urohyal, on the other hand, is small and short.

The third epibranchial has an ascending process, but the first and second have not; the second and third pharyngobranchials,



however, instead of running horizontally, have an upward tilt, and are directed towards the summit of the first pharyngo-branchial, a long, nearly vertical, rod-like bone, which here simulates a spicular bone and is attached to the side of the pro-otic. The fourth epibranchial is an expanded plate of bone, roughly triangular in shape.

*Summary of the Characters of the Skull in the Families  
Mormyridæ, Notopteridæ, and Hyodontidæ.*

The foregoing observations may be summarized as follows:—In *Notopterus*, *Hyodon*, and the Mormyridæ the parietals meet in the median line; teeth occur on the parasphenoid (although they are rudimentary in *Mormyrops* and absent in *Gymnarchus*); an orbitosphenoid is present, and the *cavum cranii* of the dried skull is continued through this bone to the ethmoid region. An opisthotic is present in *Notopterus*; it is exceptionally large in *Hyodon*; it is absent in the Mormyridæ. A basisphenoid is present in *Notopterus* and *Hyodon*, and in *Petrocephalus* and *Gymnarchus*, but not in the other Mormyridæ examined. The eye-muscle canal opens posteriorly by an oval foramen in *Hyodon*, but is blind posteriorly in *Notopterus* and the Mormyridæ.

The postfrontal is small in *Notopterus*, and does not form part of the articular facet for the head of the hyomandibular, whereas in *Hyodon* and the Mormyridæ it is larger and has the more normal relation; it is small, however, in *Gymnarchus*. A pair of diverticula of the swim-bladder, of fair size, occur on the sides of the basioccipital in *Notopterus* and *Hyodon*; their ventral and external walls are of strong fibrous tissue, but cranial bones form the dorsal and internal walls. In the Mormyridæ the basicranial bones are normal.

In *Notopterus* and the Mormyridæ there is a large lateral cranial foramen bounded by the epiotic, squamosal, and ex-occipital. This, in the Mormyridæ, is loosely covered over by the large, thin, scale-like supratemporal, but in *Notopterus* the supratemporal is so small that it fails to form a cover for the foramen. The lateral foramen is not present in *Hyodon*, but there is a cartilaginous tract, bounded by the parietal, epiotic, and squamosal. The supratemporal of *Hyodon* is large and scale-like, but it is firmer than that of the Mormyridæ; the



right and left supratemporals, also, nearly touch one another above the cranium, which is not the case in the Mormyridæ. There is a long, slender epiotic limb to the post-temporal in *Hyodon* and the Mormyridæ (except *Gymnarchus*), but this is wanting in *Notopterus*.

The nasal is a strong, curved, grooved bone in *Notopterus* and *Petrocephalus*, but in *Mormyrops*, *Mormyrus*, and *Gymnarchus* it is more slender, though still conspicuously grooved, while in *Hyodon* it is a delicate tubular bone of small size. The circumorbital bones are, on the whole, much reduced in the Mormyridæ. In *Notopterus* the suborbitals are rather strongly developed; in *Hyodon* it is the postorbitals which have attained the greater development. The inwardly directed processes of the suborbital bones of *Notopterus* for articulation with the prefrontal and the ectopterygoid respectively are not represented in *Hyodon* and the Mormyridæ.

The surmaxilla is wanting in all. The gape is premaxillamaxillary in *Notopterus* and *Hyodon*, the maxilla being well toothed up to near its posterior extremity, but in the Mormyridæ the gape is small and bounded above by the premaxillæ only, and the maxillæ are edentulous. The right and left premaxillæ are fused in the Mormyridæ (the fusion is not complete in *Gymnarchus*), which is not the case in *Notopterus* and *Hyodon*. The angular bone is distinct and of large size in *Notopterus*; in *Hyodon* and the Mormyridæ there is no separate angular.

The hyomandibular articulates with the cranium by a single broad head in *Notopterus*, and by two distinct heads in *Hyodon*; in the Mormyridæ the whole of the upper edge of the hyopalatine arch is in close relation with the cranium, and the cranial head of the hyomandibular projects very slightly, if at all, above the upper edge of the metapterygoid. A separate symplectic bone and a separate entopterygoid are recognizable in *Notopterus* and *Hyodon*, but not in the Mormyridæ. The palatine is fused with the ectopterygoid in *Notopterus*, but not in *Hyodon*, nor in the Mormyridæ. The palatine is fused with the side of the vomer in the Mormyridæ, but it is movably articulated, by a single head, in *Notopterus* and *Hyodon*.

In *Hyodon* the relations of the subopercular are normal, but the bone is rather small in size; in the Mormyridæ the sub-



opercular is also small, tapers to a point posteriorly, and, except in *Gymnarchus*, is concealed by the opercular; in *Notopterus* the subopercular is wanting.

Considerable differences are to be noticed in the hyobranchial skeleton. A single small hypohyal, probably the upper of the two normally present, is to be found in *Notopterus*, and the same holds true for *Petrocephalus*, but in the other Mormyridæ examined there is no trace of a hypohyal. In *Hyodon* the upper and lower hypohyals are both present; they are large and approximately of the same size.

In *Notopterus* the first basibranchial is unossified, which is not the case in *Hyodon* and the Mormyridæ. In the Mormyridæ there is a large bone which either represents the first basibranchial alone or the first basibranchial and the endosteal glossohyal combined; beneath this the urohyal is immovably fixed or is fused. The urohyal in *Notopterus* and *Hyodon*, however, is freely movable, and has the usual paired ligament in front; in *Hyodon* the bone is quite small.

In *Hyodon* the hypobranchials are normal; in *Notopterus*, also, they are normal, but there are in addition a pair of tendon-bones projecting downward and outward from the posterior end of the second basibranchial; in the Mormyridæ the first hypobranchials are extremely short, and the second hypobranchials small and confluent with the equivalents of the paired tendon-bones of *Notopterus*. These tendon-bones are not represented in *Hyodon*.

The first pharyngobranchial of *Notopterus* is cartilaginous; it is also unossified in *Petrocephalus* and *Gymnarchus*, but in *Mormyrus* and *Mormyrops* it is ossified, though small; in *Hyodon* it has the form of a long, upright rod of bone, simulating a spicular bone.

#### *Comments on the Skull of the Mormyridæ, Notopteridæ, and Hyodontidæ.*

On the whole, the study of the craniological characters impels one to the conclusion that the families Mormyridæ, Notopteridæ, and Hyodontidæ, though more closely related *inter se* than is either family with any other family of Malacopterygian fishes, are not more intimately related with one another than was previously assumed to be the case. As has been seen from the summary immediately preceding, the cranial characters of the



families are so conflicting, that any phylogenetic arrangement based upon them is out of the question. The three families must remain, as hitherto, the terminals of a radiating system.

As Boulenger points out (Proc. Zool. Soc. 1898, p. 778), the Mormyridæ cannot rightly be grouped with the Ostariophysi of Sagemehl as Jordan and Evermann (Fish. N. Amer. i. 1896, p. 114) have done, since they possess no Weberian ossicles nor other modification of the anterior vertebræ. The absence of a separate symplectic in both Mormyroids and Siluroids is evidently nothing more than a matter of convergence: the symplectic is absent also in the Eels. The study of the skull of the Mormyroids shows also that they can have no close affinity with the Esocidæ, with which family Johannes Müller associated them. According to Boulenger the nearest allies of the Mormyroids are to be found in the Albulidæ, as suggested by Valenciennes in 1846 (Hist. Nat. Poiss. xix. p. 225 and p. 324).

I regret that the study of the skull brings forward no evidence in favour of this contention. While the Mormyridæ are highly specialized in certain respects, it must be admitted that they retain some primitive features. Of these, the presence of an orbitosphenoid and the meeting of the parietals in the median line are two, but they do not point to any closer resemblance between the Mormyridæ and the Albulidæ than with any other primitive family.

The presence of parasphenoidal teeth in most Mormyroids, in which respect the family agrees with the Albulidæ, may be regarded as another primitive feature retained by both families from the ancestral Teleosteans, a feature which might well be retained by two even strongly diverging families. Although in *Albula* there is no limitation of the freedom of lateral movement of the hyopalatine arch, the arch is certainly in fairly close contact with the cranium along the whole of its upper edge, and in this respect exhibits some resemblance to the condition found in the Mormyridæ; but the feature is an adaptive one, not uncommon in fishes that have a parasphenoidal and lingual dentition well developed, or that can bring the floor of the mouth forcibly against the palate.

The bounding of the upper border of the mouth by the premaxillæ alone and the absence of teeth on the maxillæ are specialized characters affected by numerous families of Tele-



osteans not genetically related, whenever, for some reason or other, a reduction in the size of the mouth takes place.

Of the other characters mentioned in the summary on p. 201 as distinctive of the Mormyroid skull, these are all characters of specialization, and throw no light on the question of affinity with the Albulidæ. The presence of a distinct symplectic in *Albula*, and a distinct entopterygoid, the presence of teeth on the vomerine, palatine, and pterygoid bones, the freedom from fusion of the palatine with the vomer, and of the right with the left premaxilla, the presence of a surmaxilla, the absence of reduction of the subopercular and of the hypobranchial skeleton, the possession of as many as 15 branchiostegal rays instead of 4-8, the existence of a separate glossohyal, the normal character of the urohyal, and the possession by the post-temporal of an opisthotic limb attached to a distinct opisthotic bone, all these are characters that one would naturally expect to see in any Malacopterygian fish of more archaic constitution than a Mormyroid.

On the other hand, the large lateral cranial foramen, covered by a thin scale-like supratemporal, so constant in the Mormyridæ, and the large paired tendon-bones that project down from the side of the second basibranchial are not represented in the Albulidæ; while the roofing of the posterior temporal fossæ and the presence of subtemporal fossæ (lying ventral to the posterior part of the facet for the head of the hyomandibular), characters which *Albula* possesses in common with the Elopidae and Cyprinidæ, are not to be found in the Mormyridæ. The inflation of the hinder part of the base of the cranium of *Albula* is also not recognizable in the Mormyridæ, although, curiously enough, it occurs in *Notopterus*.

Concerning the genera *Notopterus* and *Hyodon* there is but little to be said, except that the latter possesses a greater proportion of primitive characters. Of the forms described in the present paper, there can be little doubt that the Mormyridæ are the most specialized, and *Hyodon* the least specialized; but the close study of the skulls of these fishes does not lend support to a view of relationship recently expressed by Boulenger. On p. 116 of his book 'Les Poissons du Bassin du Congo,' 1901, he writes:—"Les Notoptérides me semblent occuper vis-à-vis des Hyodontides une position analogue à celle qu'occupent les



Mormyrides vis-à-vis des Albulides, c'est à dire qu'ils peuvent en être considérés comme modification excentrique." In considering the possibility of evolution of the Notopteridæ from the ancestral *Hyodon*, one must not lose sight of the fact that *Notopterus*—in the presence of the large lateral cranial foramen bounded by the squamosal, epiotic, and exoccipital, in the attempt (a futile one, it is true) of the thin scale-like supratemporal to cover it, and in the presence of a paired tendon-bone of considerable size projecting down from the side of the second basibranchial—exhibits characters strikingly constant in the Mormyridæ, but not possessed by *Hyodon*.

Although in both *Notopterus* and *Hyodon* there are vesicles of the swim-bladder on the lateral face of the otic region of the cranium, it does not necessarily follow that these structures have had a common origin. The connection between the swim-bladder and the ear must not be relied upon too implicitly as indicating close relationship between such fishes as possess it. That it has arisen independently in different groups is evident from the remarkable difference between the methods by which the result is arrived at. Compare, for instance, *Clupea* on the one hand and the Ostariophysi on the other. Stannius (Handb. d. Anat. d. Wirbelth. i. p. 2) mentions that there is a connection between the swim-bladder and the ear in the Macruridæ among the Anacanthini, and in the Berycidæ and Gerriidæ among the Acanthopteri; while Sagemehl (Morph. Jahrb. x. 1885, p. 51, footnote) observes that it occurs in the Gadidoids *Physiculus* and *Uraleptus*, and in the Scleroderm *Balistes*.

In conclusion, I wish to point out with some emphasis that the remarks in this paper apply to the skull only. I have purposely avoided all reference to other parts of the skeleton and to the soft structures of the body, since these were foreign to the investigation undertaken. The above deductions as to inter-relationships, therefore, cannot in any sense be regarded as final. It is hoped, nevertheless, that they may prove valuable as a contribution to a discussion of the affinities of the families concerned.



## EXPLANATION OF THE PLATES.

## PLATE 22.

- Fig. 1. *Mormyrops deliciosus*. Right side of skull (slightly enlarged).  
 2. " " Cranium, dorsal view (slightly enlarged).  
 3. " " Cranium, left side (slightly enlarged).  
 4. " " Hyopalatine arch of left side, with opercular bones and mandible, mesial aspect (slightly enlarged).

## PLATE 23.

- Fig. 5. *Petrocephalus bane*. Right side of skull ( $\times 2$ ).  
 6. " " Cranium, dorsal view ( $\times 2$ ).  
 7. " " Cranium, left side ( $\times 2$ ).  
 8. " " Cranium, back view ( $\times 2$ ).  
 9. " " Hyopalatine arch of left side, with opercular bones and mandible, mesial aspect ( $\times 2$ ).  
 10. *Mormyrus caschive*. Right maxilla ( $\times 2$ ). *a*, horizontal, posteriorly directed process; *b*, process lying immediately over the posterior part of the premaxilla; *c*, antero-ventral edge, namely, that along which teeth might be expected to occur.  
 11. *Gymnarchus niloticus*. Right ramus of mandible, mesial aspect ( $\times \frac{2}{3}$ ).

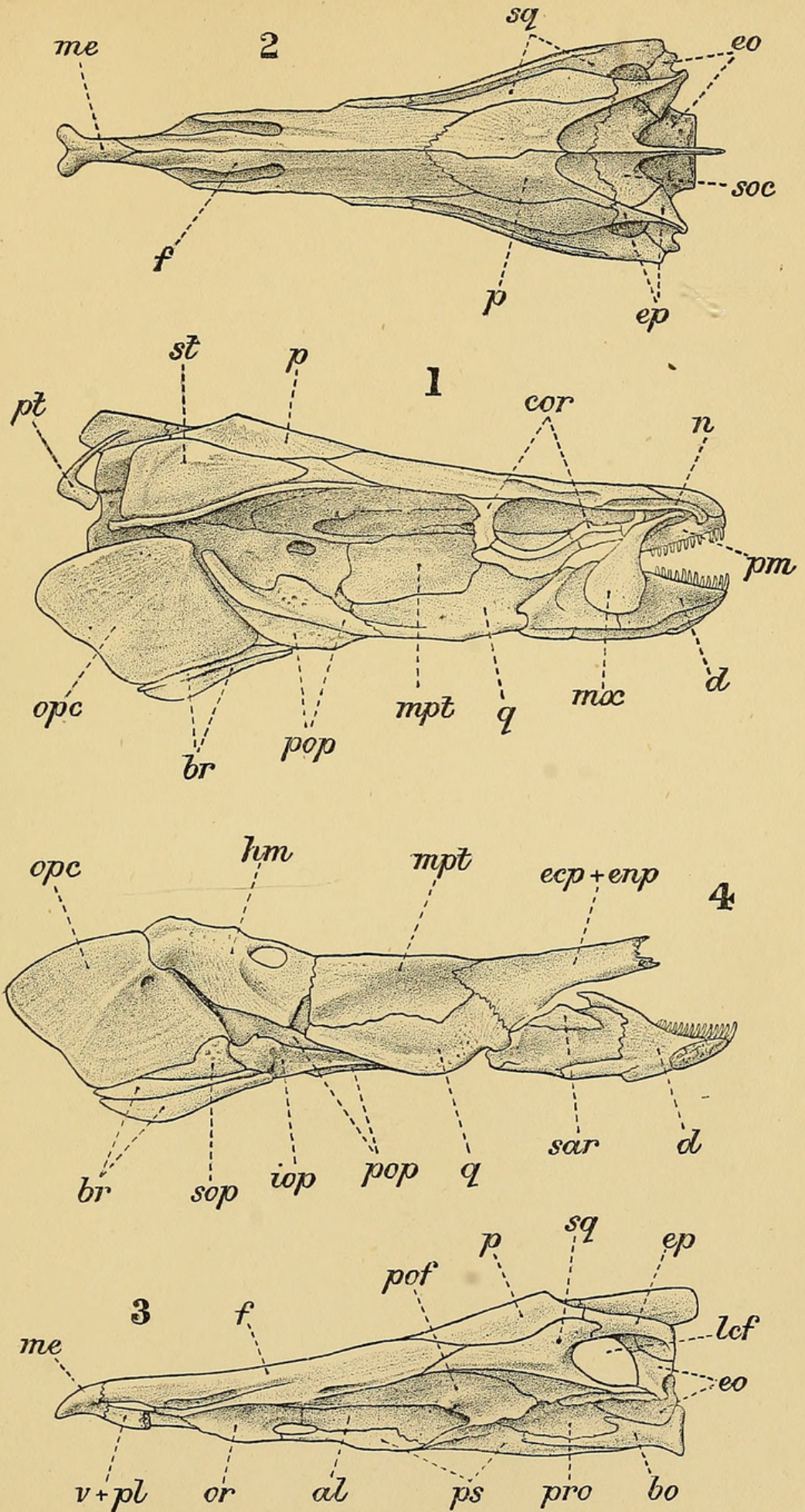
## PLATE 24.

- Fig. 12. *Notopterus kapirot*. Right side of skull (nat. size).  
 13. " " Cranium, dorsal view (slightly enlarged).  
 14. " " Cranium, left side (slightly enlarged).  
 15. " " Cranium, back view (slightly enlarged).  
 16. " " Hyopalatine arch of left side, with mandible, mesial aspect (nat. size).  
 17. " " Hyobranchial skeleton, dorsal view. The epi-branchials and pharyngobranchials of the right side are not shown (nat. size).

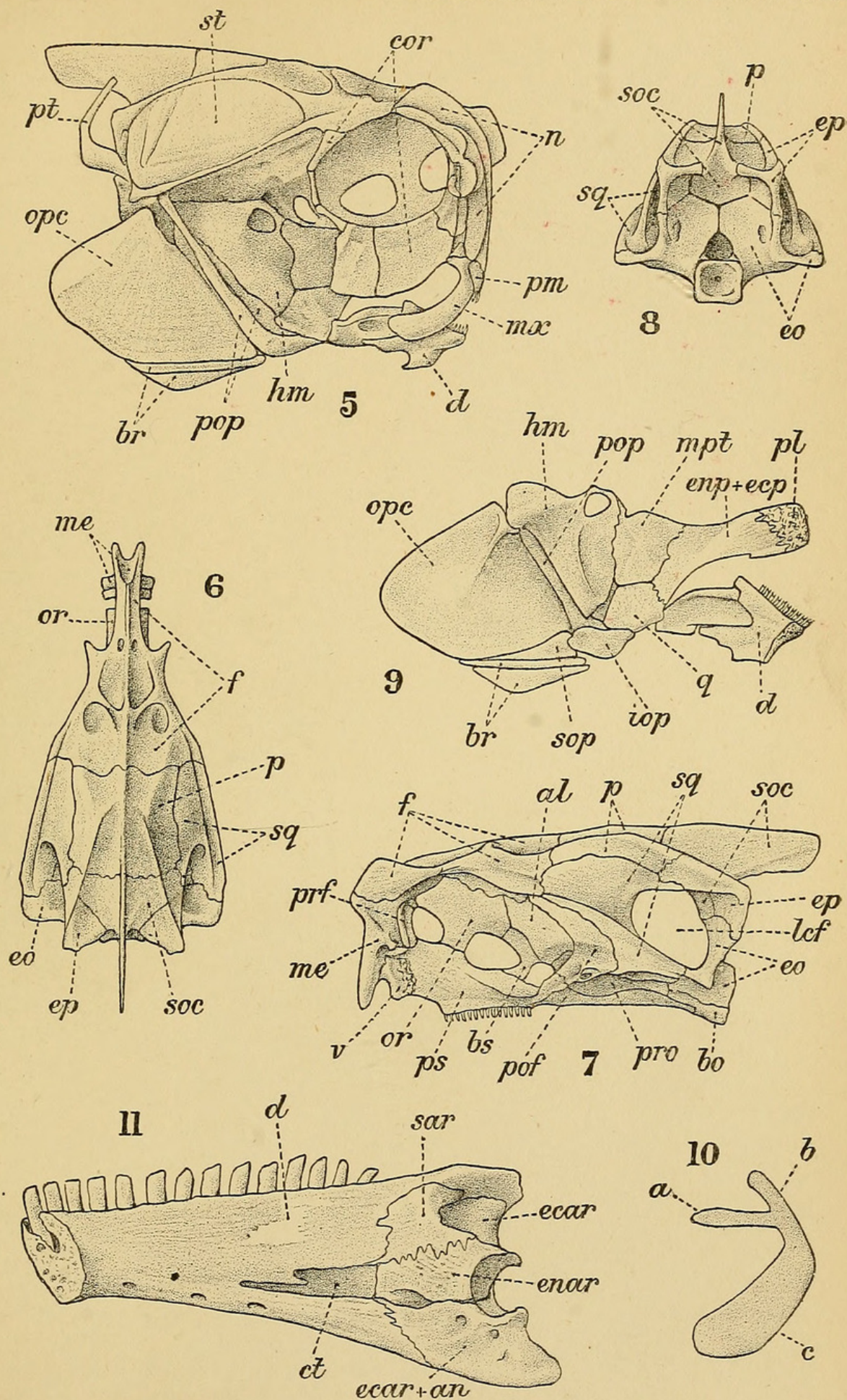
## PLATE 25.

- Fig. 18. *Hyodon alosoides*. Right side of skull (nat. size).  
 19. " " Cranium, dorsal view (slightly enlarged).  
 20. " " Cranium, left side (slightly enlarged).  
 21. " " Cranium, back view (slightly enlarged).  
 22. " " Hyopalatine arch of left side, with opercular bones and mandible, mesial aspect (nat. size).







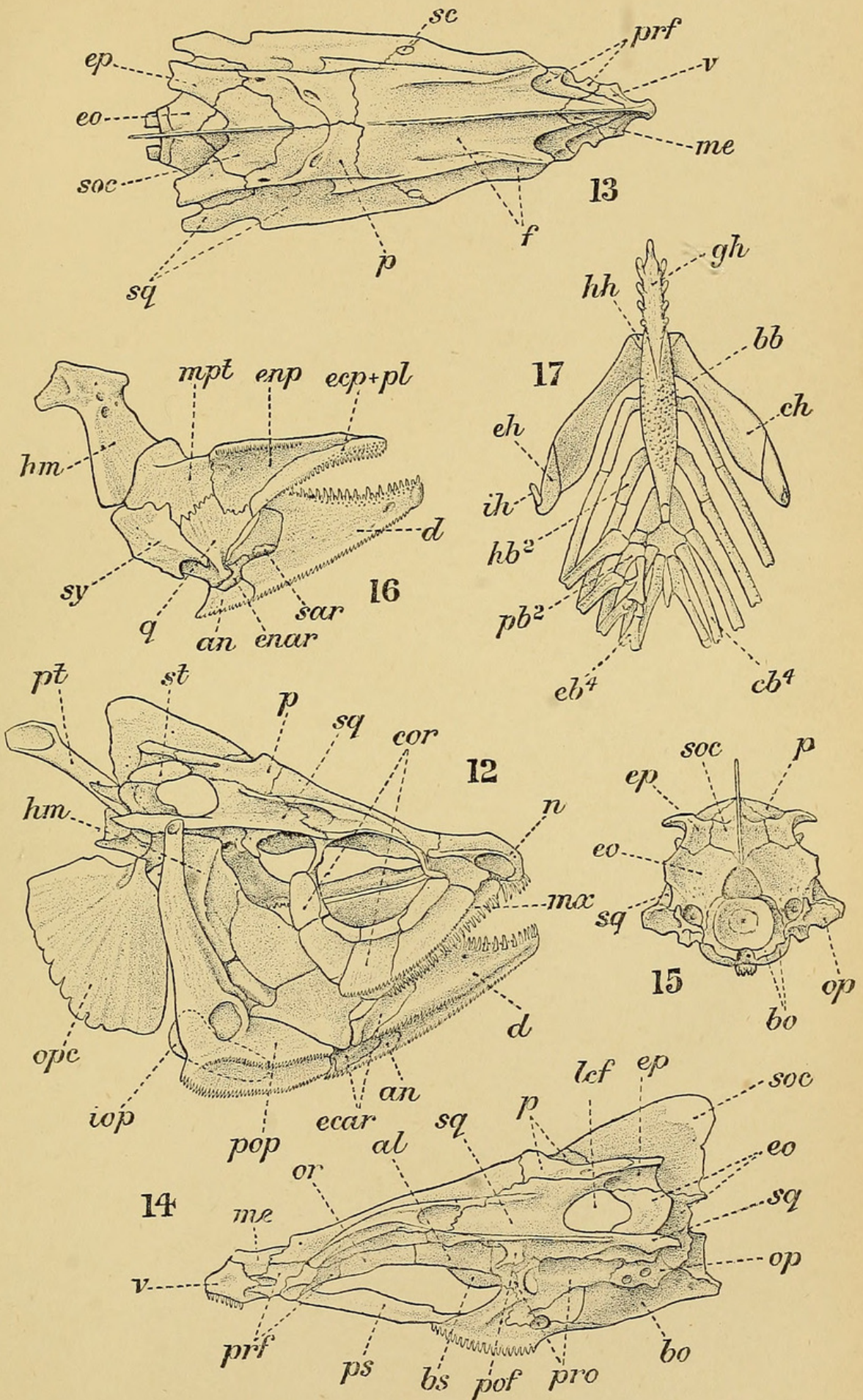


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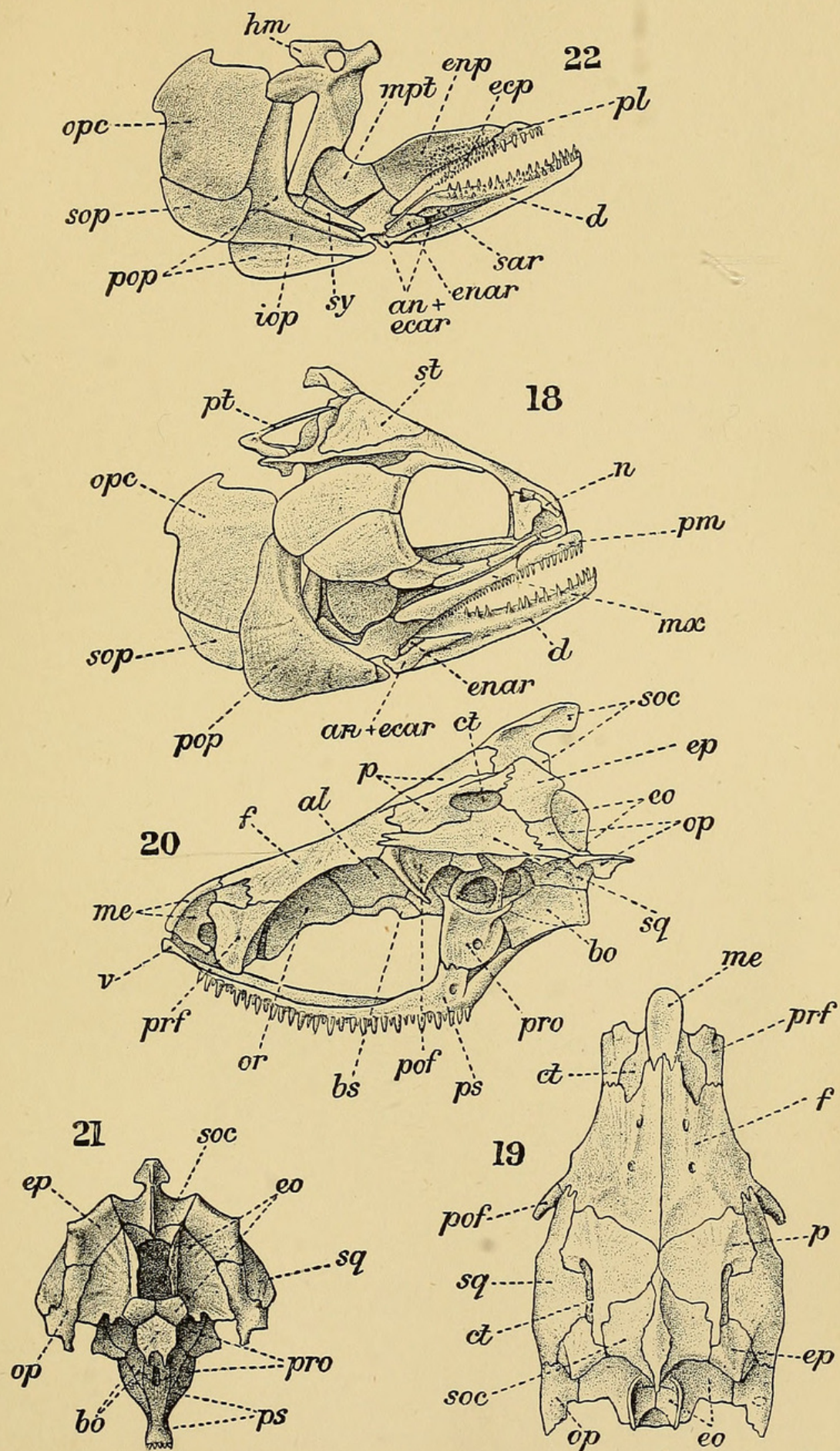
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Figs. 5-9, PETROCEPHALUS; Fig. 10. MORMYRUS;  
Fig. 11. GYMNARCHUS.









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SKULL OF HYODON.



*Abbreviations employed in the Figures.*

<i>a, b, c</i> ... (see explanation of fig. 10).	<i>lef</i> ... lateral cranial foramen.
<i>al</i> ... alisphenoid.	<i>me</i> ... mesethmoid.
<i>an</i> ... angular.	<i>mpt</i> ... metapterygoid.
<i>bb</i> ... dentigerous plate covering the basibranchials.	<i>mx</i> ... maxilla.
<i>bo</i> ... basioccipital.	<i>n</i> ... nasal.
<i>br</i> ... branchiostegal rays.	<i>op</i> ... opisthotic.
<i>bs</i> ... basisphenoid.	<i>opc</i> ... opercular.
<i>cb</i> ... ceratobranchial.	<i>or</i> ... orbitosphenoid.
<i>ch</i> ... ceratohyal.	<i>p</i> ... parietal.
<i>cor</i> ... circumorbital bones.	<i>pb</i> ... pharyngobranchial.
<i>ct</i> ... cartilage.	<i>pl</i> ... palatine.
<i>d</i> ... dentary.	<i>pm</i> ... premaxilla.
<i>eb</i> ... epibranchial.	<i>pod</i> ... postfrontal.
<i>ecar</i> ... ectosteal articular.	<i>pop</i> ... preopercular.
<i>ecp</i> ... ectopterygoid.	<i>prf</i> ... prefrontal.
<i>eh</i> ... epihyal.	<i>pro</i> ... pro-otic.
<i>enar</i> ... endosteal articular.	<i>ps</i> ... parasphenoid.
<i>enp</i> ... entopterygoid.	<i>pt</i> ... post-temporal.
<i>eo</i> ... exoccipital.	<i>q</i> ... quadrate.
<i>ep</i> ... epiotic.	<i>sar</i> ... sesamoid articular.
<i>f</i> ... frontal.	<i>sc</i> ... foramen traversed by sensory canal.
<i>gh</i> ... glossohyal.	<i>soc</i> ... supraoccipital.
<i>hb</i> ... hypobranchial.	<i>sop</i> ... subopercular.
<i>hh</i> ... hypohyal.	<i>sq</i> ... squamosal.
<i>hm</i> ... hyomandibular.	<i>st</i> ... supratemporal.
<i>ih</i> ... interhyal.	<i>sy</i> ... symplectic.
<i>iop</i> ... interopercular.	<i>v</i> ... vomer.





Ridewood, W G. 1904. "On the Cranial Osteology of the Fishes of the Families Mormyridae, Notopteridae and Hyodontidae." *The Journal of the Linnean Society of London. Zoology* 29(190), 188–217.

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