

5. On the Cranial Osteology of the Clupeoid Fishes. By
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(Text-figures 118-143.)

INTRODUCTION.

In the spring of 1896, Prof. G. B. Howes suggested to me that an investigation on the structure of the skull in the lower Teleostean fishes would be a profitable piece of research, since there was every prospect of the results proving a valuable means of testing the validity of the existing schemes of classification of the fishes in question, and because an accurate knowledge of the structure of the skull in the lower Teleostean fishes was essential to a successful study of the remains of those extremely interesting extinct fishes which lie on the boundary-line between the Teleosteans and the Ganoids.

The investigation has proceeded slowly and intermittently, owing to repeated interruptions and to pressure of other work; but sufficient progress has now been made to allow of the publication of some of the results. Descriptions of the skulls of *Elops*, *Megalops*, and *Albula*, together with some general observations on the Teleostean skull, have already appeared in the 'Proceedings of the Zoological Society,' 1904, ii. pp. 35-81, and observations on the cranial osteology of the Mormyridæ, Notopteridæ, and Hyodontidæ in the Journal of the Linnean Society, xxix. 1904, pp. 188-217. A third paper, on the skull of the Osteoglossidæ, Pantodontidæ, and Phractolæmidæ, has just been completed, and has been offered to the Linnean Society; the present contribution deals with the skull of the Clupeoid fishes.

Eleven genera are considered in this paper, namely:—*Chirocentrus*, *Clupea*, *Pellona*, *Pellonula*, *Pristigaster*, *Hyperlophus*, *Chatoëssus*, *Dussumieria*, *Engraulis*, *Coilia*, and *Chanos*. A "Summary" of the observations and some "Comments" thereon are given on pp. 488-493.

Skulls of *Chirocentrus*, *Clupea*, *Chatoëssus*, *Engraulis*, *Coilia*, and *Chanos* were specially prepared for the purposes of the investigation, and were disarticulated according to the method explained in the 'Proceedings of the Zoological Society,' 1904, ii. p. 36; the other skulls examined are the property of the British Museum, and I take this opportunity of acknowledging my indebtedness to Mr. G. A. Boulenger for offering to me every facility in his power for the examination of the skulls under his charge.

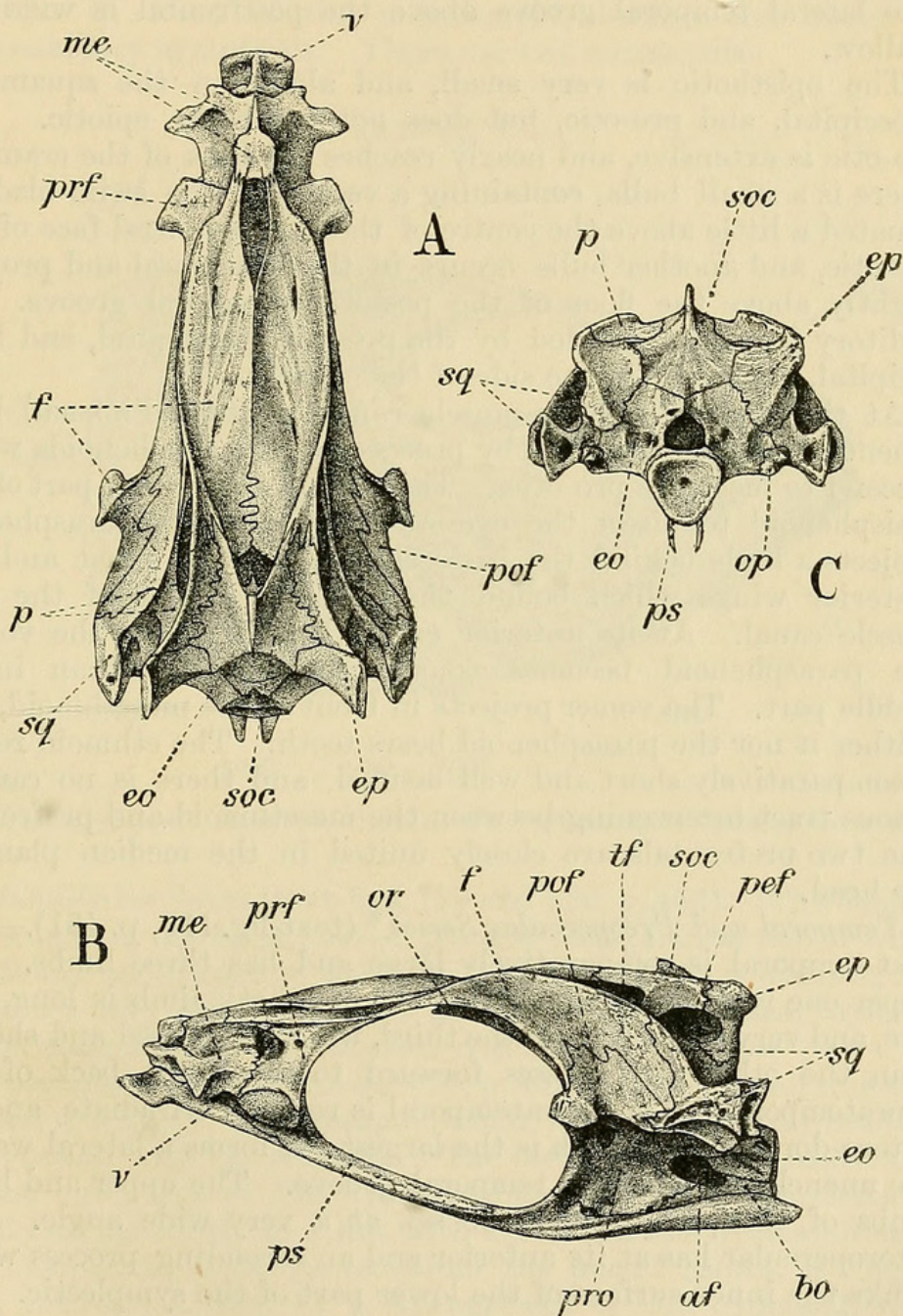
CHIROCENTRUS DORAB.

The only published figure of the skull of *Chirocentrus* that I have been able to discover is a not very serviceable sketch of

the hinder part of the cranium, seen from above, given by Klein (Jahresh. Ver. vaterl. Naturk. Württ. xli. 1885, pl. 3. fig. 82).

Material examined.—In addition to a skull (A) specially prepared for the purposes of this investigation from an alcohol-preserved specimen kindly furnished by Prof. Howes, two skulls were examined, one (B) belonging to a complete skeleton, marked 89.2.1.2059, in the Osteological Collection of the British Museum, and another (C) bearing no distinctive number.

Text-fig. 118.



Cranium of *Chirocentrus dorab*. A, dorsal view; B, left side; C, back view.
For explanation of lettering see p. 493.

Cranium (text-fig. 118).—The parietals are separated by the supraoccipital, and there is a small median fontanelle, divided
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longitudinally by a bar of cartilage, between the supraoccipital and the frontal bones (wanting, however, in specimen B), and another fontanelle between the anterior ends of the frontals. The posterior temporal groove is deep, but is not roofed over. The groove narrows away to a point anteriorly, and situated near its termination is a temporal foramen leading into the upper part of the cranial cavity. Behind the temporal foramen is a deep pre-epiotic fossa, bounded above and in front by the parietal, below by the squamosal, and behind by the epiotic, and terminating blindly against the deeper part of the supraoccipital. The lateral temporal groove above the postfrontal is wide and shallow.

The opisthotic is very small, and abuts on the squamosal, exoccipital, and pro-otic, but does not touch the epiotic. The pro-otic is extensive, and nearly reaches the back of the cranium. There is a small bulla, containing a vesicle of the swim-bladder, situated a little above the centre of the latero-ventral face of the pro-otic, and another bulla occurs in the squamosal and projects slightly above the floor of the posterior temporal groove. An auditory fenestra, bounded by the pro-otic, exoccipital, and basioccipital, is present in the side of the cranium.

At the front of the eye-muscle canal is situated a small basisphenoid, bounded laterally by processes of the alisphenoids which descend to meet the pro-otics. There is no descending part of the basisphenoid to bisect the eye-muscle canal. The parasphenoid projects a little behind the basioccipital, and has right and left posterior wings which bound the posterior outlet of the eye-muscle canal. At its anterior end, where it meets the vomer, the parasphenoid becomes considerably broader than in its middle part. The vomer projects in front of the mesethmoid, and neither it nor the parasphenoid bears teeth. The ethmoid region is comparatively short and well ossified, and there is no cartilaginous tract intervening between the mesethmoid and prefrontal. The two prefrontals are closely united in the median plane of the head.

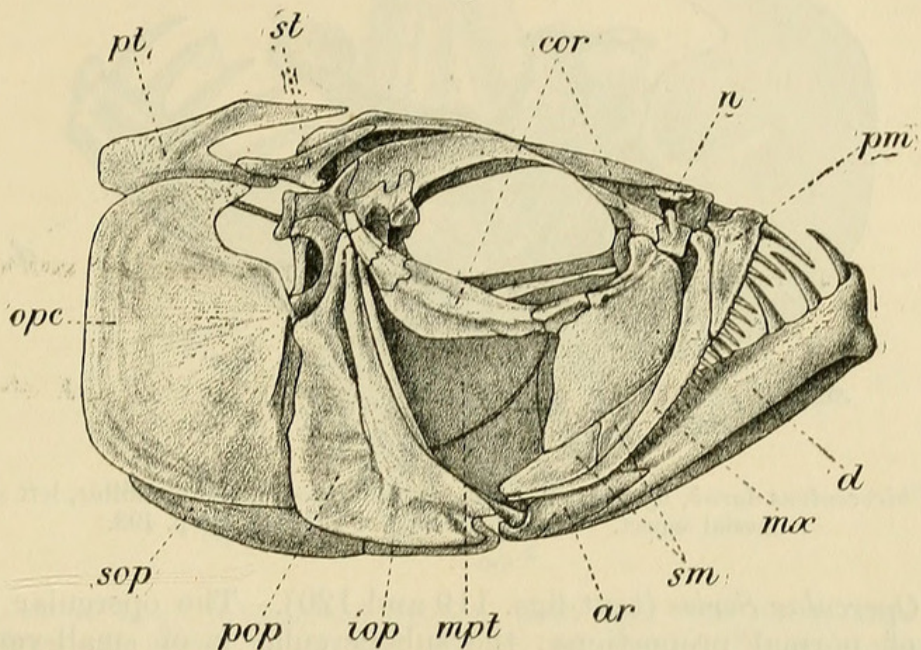
Temporal and Preopercular Series * (text-fig. 119, p. 451).—The post-temporal is comparatively large and has three limbs. The upper one rests over the epiotic; the opisthotic limb is long, rod-like, and very slender; and the third, which is pointed and shorter than the other two, passes forward to touch the back of the supratemporal. The supratemporal is roughly triradiate, and its antero-dorsal ray or limb is the largest; it forms a lateral wall to the unenclosed posterior temporal groove. The upper and lower limbs of the preopercular are set at a very wide angle. The interopercular has at its anterior end an ascending process which flanks the inner surface of the lower part of the symplectic.

* The reasons for including the preopercular and interopercular bones in this series, and for excluding them from the opercular and branchiostegal series, are given in a former paper (Proc. Zool. Soc. 1904, ii. pp. 68 and 75). For reasons given in the same paper, it is considered expedient to regard the post-temporal as a constituent of the skull.

Circumorbital Series (text-fig. 119).—The total number of circumorbital bones on each side is nine; the largest is that which lies antero-ventrally to the eye. The nasal is very small.

Maxillary Series (text-fig. 119).—Both premaxilla and maxilla bound the gape above. They both bear long, pointed teeth, and the anterior tooth of the premaxillary series is much larger than the others. As already noticed by Valenciennes (Hist. Nat. Poiss. xix. 1846, pp. 150, 152, and 154), the premaxilla is firmly attached to the maxilla in *Chirocentrus*, whereas in *Clupea* it is readily movable upon the maxilla. The two maxillæ meet one another in front of the mesethmoid, behind and above the premaxillary symphysis. There are two surmaxillæ.

Text-fig. 119.



Chirocentrus dorab, right side of skull. For explanation of lettering see p. 493.

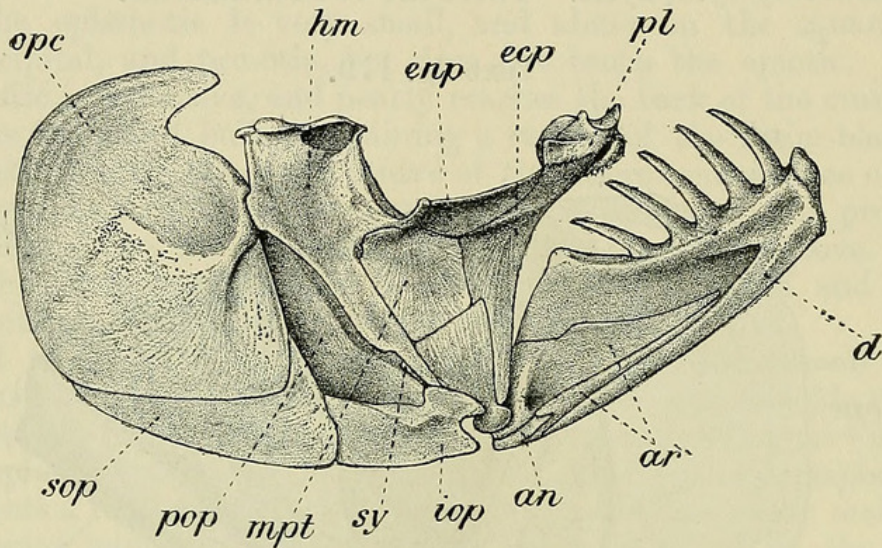
Mandibular Series (text-figs. 119 and 120, p. 452).—The dentary bears eight or ten large, curved, pointed teeth, four or five of which are firmly anchylosed to the bone*. The angular is distinct, and there is a very small sesamoid articular; the endosteal articular is not distinct from the ectosteal articular.

Hyopalatine Series (text-fig. 120, p. 452).—The hyopalatine arch is short and deep. The hyomandibular has a single broad head for articulation with the cranium. The metapterygoid extends high up the outer face of the hyomandibular, and the symplectic is small and lies nearly in a line with the axis of the hyomandibular. The symplectic, when viewed from the buccal aspect, is largely (not entirely) hidden by a downgrowth of the hyomandibular,

* Smith Woodward (Brit. Mus. Cat. Foss. Fishes, iv. p. 88) says of *Chirocentrus*: "Teeth firmly fixed in shallow sockets." He mentions, however, but one extinct species of *Chirocentrus* (*C. polyodon*), and states that it is "doubtfully of this genus."

and in an external view is barely visible between the quadrate and the preopercular. This concealment of the symplectic is utilised as a family character by Boulenger (Ann. Mag. Nat. Hist. (7) xiii. 1904, p. 164). The palatine is short and completely ossified, and has two distinct articular heads, one for the mesethmoid and vomer, and one for the prefrontal; its ventro-external surface enters into extensive synovial articulation with the maxilla. There are four or five minute teeth on the palatine, but none on the pterygoid bones.

Text-fig. 120.



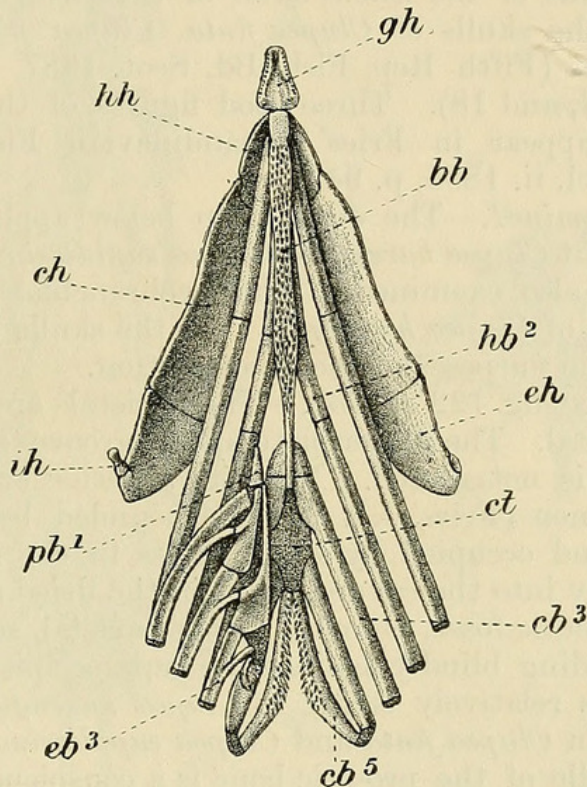
Chirocentrus dorab, hyopalatine arch, opercular bones, and mandible, left side, mesial aspect. For explanation of lettering see p. 493.

Opercular Series (text-figs. 119 and 120).—The opercular bone is of normal proportions; the subopercular is of small vertical extent, and has at its anterior end a strongly developed process rising against the anterior edge of the opercular. The branchiostegal rays are eight in number. The front four are shaped like the blade of a scythe, and there is a fairly regular transition in a backward direction to the larger and lamellate posterior members of the series. The first five are attached to the outer surface of the ceratohyal, and the other three to the outer surface of the epihyal.

Hyobranchial Series (text-fig. 121, p. 453).—The interhyal is ossified. The upper hypohyal is considerably smaller than the lower. The glossohyal is small and bears a few minute teeth on its superolateral edges. The first basibranchial is short, the second and third are exceptionally long. A long dentigerous plate overlaps the three basibranchial bones, and a similar plate, of large size, but readily removable, and not shown in the figure, overlies the common cartilage of the fourth and fifth basibranchials. The dorsal parts of the branchial skeleton appear short in proportion to the ventral, but the disparity is probably to be accounted for

by the abnormal length of the latter. The first pharyngo-branchial is conical, fully ossified, and in a line with the first epibranchial; there is no spicular bone. The second pharyngo-branchial is triangular, and about $2\frac{1}{2}$ or 3 times as long as broad. The third pharyngobranchial is long; its anterior part is slender and rod-like, and runs along the mesial edge of the second pharyngobranchial.

Text-fig. 121.



Chirocentrus dorab, hyobranchial skeleton, dorsal view. The epibranchials and pharyngobranchials of the right side are not shown. For explanation of lettering see p. 493.

CLUPEA FINTA, etc.

In 1820 Weber (De Aure et Auditu Hominis et Animalium, pl. 8. figs. 64–66) gave three views of the cranium of the Herring, and a remarkably accurate description of the osseous bullæ that enclose the dilatations of the anterior end of the swim-bladder. Rosenthal's figures (Ichthyotomische Tafeln, Aufl. 2, Berlin, 1839, pl. 4) are moderately accurate, but of no particular value; and Brühl's figures (Vergl. Anat. aller Thierklassen, Abschn. 1, Skelettehre der Fische, 1847, pl. 5. fig. 32 and pl. 10) are copied from those of Weber and Rosenthal. The figure of the skull of the Herring in the 'Histoire Naturelle des Poissons' of Cuvier and Valenciennes (pl. 593) is hardly worth mentioning. The side view of the complete skeleton of the Alose given by Agassiz in his 'Recherches sur les Poissons Fossiles' (Atlas, v. pl. L) is good, but only the superficial bones are seen, and none of them are named.

Hyrtl, in his paper on the Accessory Branchial Organ of Clupeoid Fishes (Denkschr. Akad. Wiss. Wien, x. 1855, pl. 1. figs. 2 and 3) has published figures of the branchial skeleton of *Clupea thryssa* (*Meletta thryssa*) and *Clupea mallowocca* (*Alausa tyrannus*), but they are of little service in the present connection. Vrolik (Niederl. Arch. Zool. i. 3, 1873, pp. 268–270, and figs. 28 and 29) has given a short description and two figures of the cranium of the Herring; and Matthews has contributed a very complete account of the whole skull of that fish, with observations also on the skulls of *Clupea finta*, *Clupea pilchardus*, and *Clupea sprattus* (Fifth Rep. Fish. Bd. Scot. 1887, pp. 274–292, and figs. 15, 17, and 18). Three good figures of the cranium of the Herring appear in Fries' 'Scandinavian Fishes' (ed. 2, by F. Smitt, vol. ii. 1895, p. 949).

Material examined.—The description below applies mainly to *Clupea finta*, but *Clupea harengus*, *Clupea sapidissima*, and *Clupea sprattus* were also examined. The hyobranchial skeleton described is that of *Clupea harengus*. All the skulls were specially prepared for the purposes of the investigation.

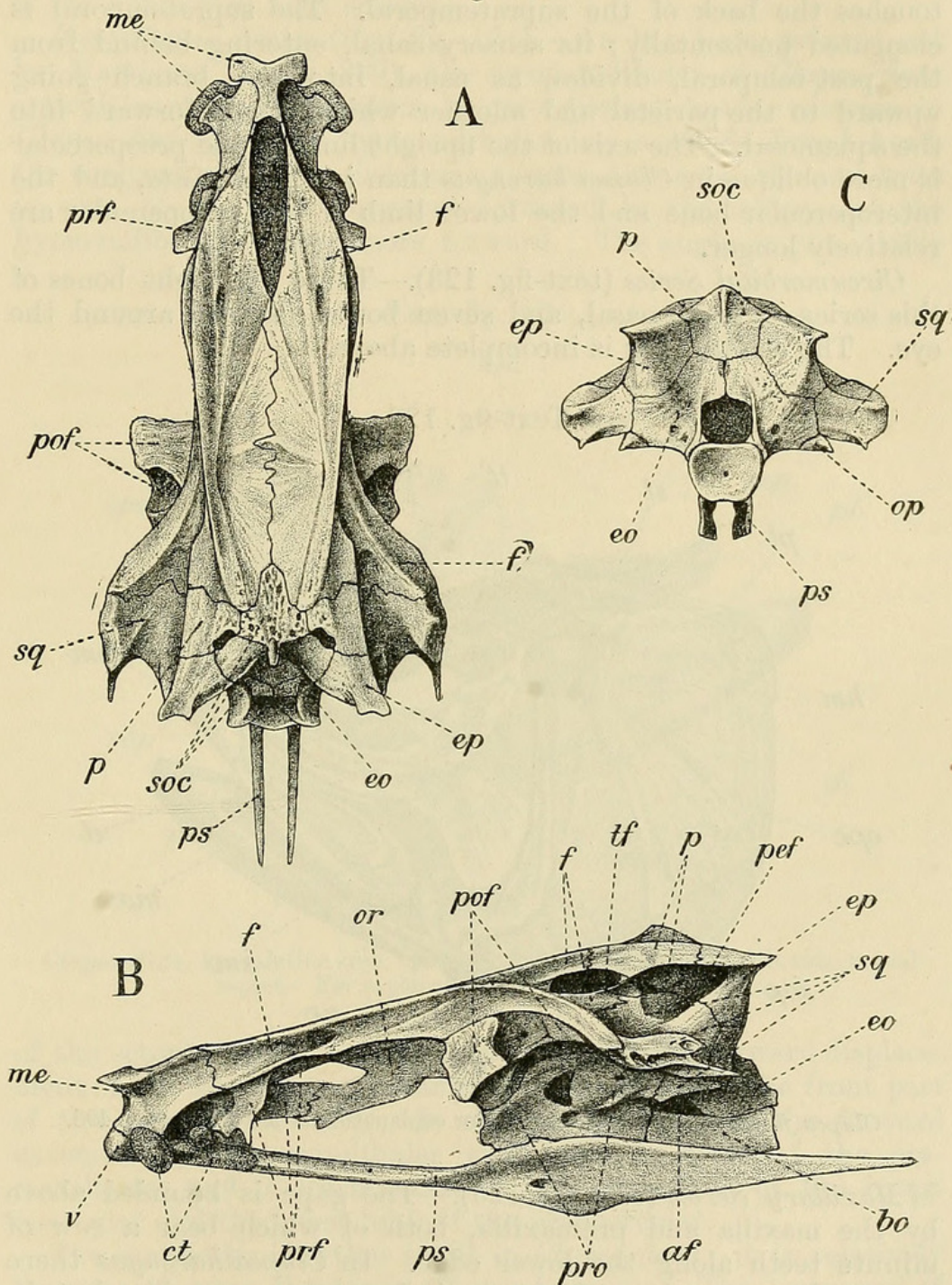
Cranium (text-fig. 122, p. 455).—The parietals are separated by the supraoccipital. The posterior temporal groove (*mastoid groove* of Fries, *l.c.*) is not roofed. Near its anterior end is an oval temporal foramen (Fries, *l.c.* p. 947), bounded by the parietal and frontal, and occupied by a fatty mass in the fresh fish, but leading directly into the cavum cranii in the dried skull; behind it is the pre-epiotic fossa, bounded by the parietal, squamosal, and epiotic, and ending blindly against the supraoccipital. The pre-epiotic fossa is relatively larger in *Clupea harengus* and *Clupea sprattus* than in *Clupea finta* and *Clupea sapidissima*.

In the middle of the pro-otic bone is a conspicuous bulla containing a spherical vesicle of the swim-bladder. A second bulla is present in the squamosal, but this is not visible in *Clupea finta* except by breaking open the bone; in *Clupea harengus* it is just visible on the surface. *Clupea sprattus* has no squamosal bulla (Matthews, *l.c.*, and Ridewood, Journ. Anat. and Phys. xxvi. 1891, p. 36, and fig. E, p. 32). In *Clupea harengus* the duct that leads through the exoccipital bone from the pro-otic and squamosal vesicles to the swim-bladder is dilated and fusiform in shape. The auditory fenestra, in the ventro-lateral aspect of the cranium, has an irregular outline; it is bounded by the pro-otic, exoccipital, and basioccipital, and leads into the perilymphatic cavity of the ear.

The episthotic is moderately small; it touches the pro-otic, squamosal, and exoccipital bones, but not the epiotic. The basisphenoid is small and transversely set, and its descending process is a mere spicule of bone which fails to reach the parasphenoid. The orbitosphenoid sends forward a process which meets a backwardly directed process of the united prefrontals. The parasphenoid is straight, or nearly so, in *Clupea finta*, but the middle part is slightly depressed in the other species examined.

The posterior wings, on the right and left sides of the posterior opening of the eye-muscle canal, are thin and delicate. They become separate from one another beneath the middle part of the pro-otic (they separate in front of the pro-otic in *Clupea harengus*),

Text-fig. 122.



Cranium of *Clupea finta*. A, dorsal view; B, left side; C, back view.
For explanation of lettering see p. 493.

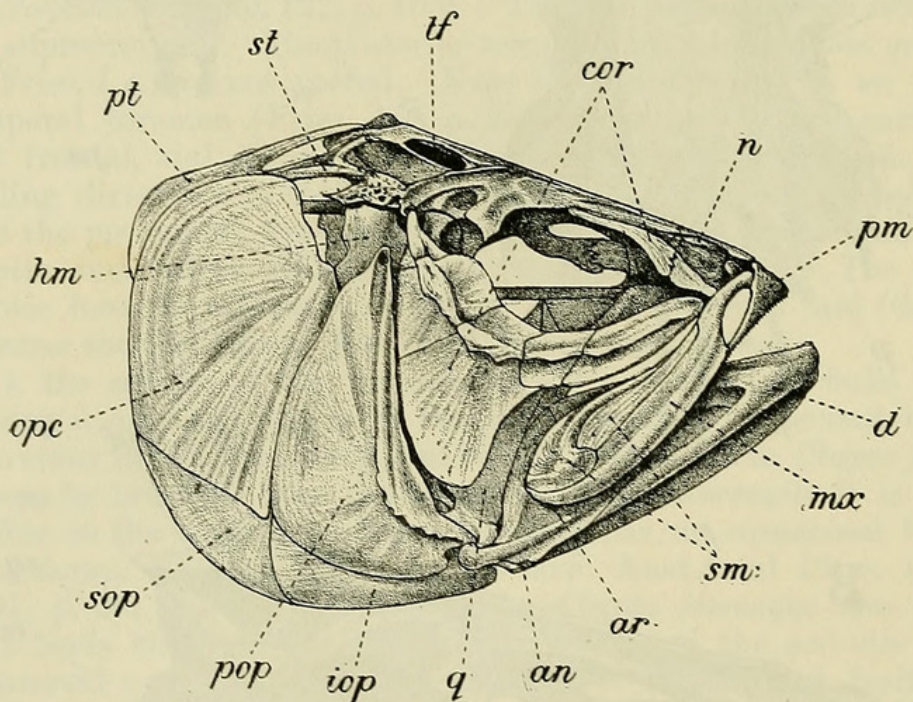
and extend a considerable distance behind the occiput. There are no teeth on the parasphenoid nor on the vomer in *Clupea finta*, but vomerine teeth are present in *Clupea harengus* and

Clupea sprattus. There is a median fontanelle between the mesethmoid and the frontal bones.

Temporal and Preopercular Series (text-fig. 123).—The post-temporal is rather large and slender. It has two long limbs attached to the epiotic and opisthotic respectively; the third limb, that which carries the sensory canal, is very short, and touches the back of the supratemporal. The supratemporal is elongated horizontally; its sensory canal, entering behind from the post-temporal, divides, as usual, into one branch going upward to the parietal and another which passes forward into the squamosal. The axis of the upright limb of the preopercular is more oblique in *Clupea harengus* than in *Clupea finta*, and the interopercular bone and the lower limb of the preopercular are relatively longer.

Circumorbital Series (text-fig. 123).—There are eight bones of this series—a small nasal, and seven bones disposed around the eye. The orbital ring is incomplete above.

Text-fig. 123.



Clupea finta, right side of skull. For explanation of lettering see p. 493.

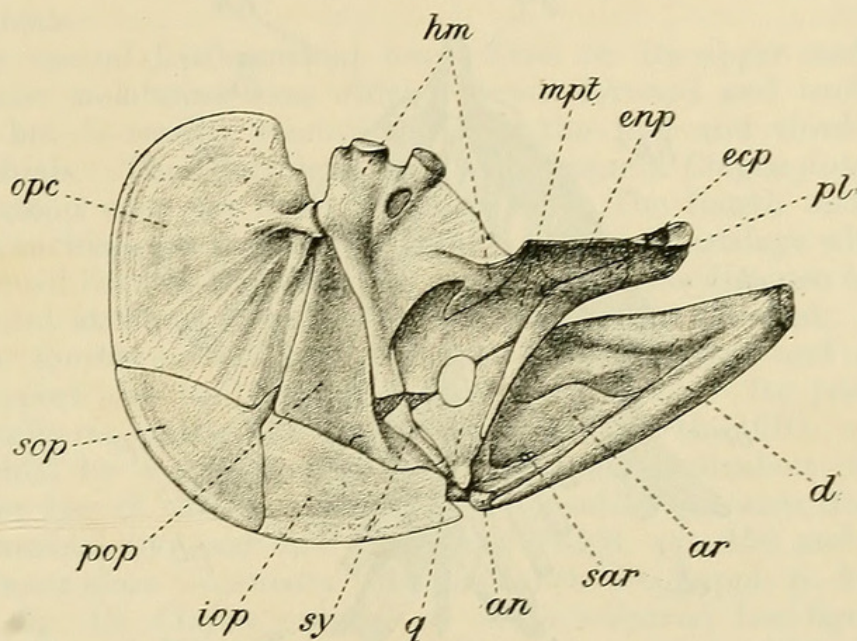
¶ *Maxillary Series* (text-fig. 123).—The gape is bounded above by the maxilla and premaxilla, both of which bear a row of minute teeth along the lower edge. In *Clupea harengus* there are rarely more than three teeth in each premaxilla, but in *Clupea finta* the number is between twenty and thirty. Two surmaxillary bones are present on each side.

Mandibular Series (text-figs. 123 and 124, p. 457).—The mandible is rather high in proportion to its length, particularly so in *Clupea harengus*. In *Clupea finta* the highest point of the mandible lies

over the hinder half of the ramus ; in *Clupea harengus* and *Clupea sprattus* it lies over the front half. The mandibular symphysis is more in advance of the premaxillæ in the two latter species than in the first. The angular bone is distinct. There is a small sesamoid articular in *Clupea finta*, but not in *Clupea harengus*. There are about five teeth situated in a row at the anterior end of the dentary in both species.

Hyopalatine Series (text-fig. 124).—As has been pointed out by Matthews (*l. c.* p. 289), the hyomandibular of *Clupea finta* articulates with the cranium by two distinct heads, whereas in *Clupea harengus* the hyomandibular has a single broad head. On comparing *Clupea finta* and *Clupea harengus*, the quadrate is seen to be more forwardly rotated in the latter, and the hyomandibular to slope more forward. The angle in the middle

Text-fig. 124.



Clupea finta, hyopalatine arch, opercular bones, and mandible, left side, mesial aspect. For explanation of lettering see p. 493.

of the ectopterygoid, also, is smaller, so that the forward displacement of the quadrate-articular joint does not affect the front part of the hyopalatine arch. It results, however, in the forward extension of the mandibular symphysis in front of the premaxillaries, and is accompanied by an elongation of the interopercular and the lower limb of the preopercular.

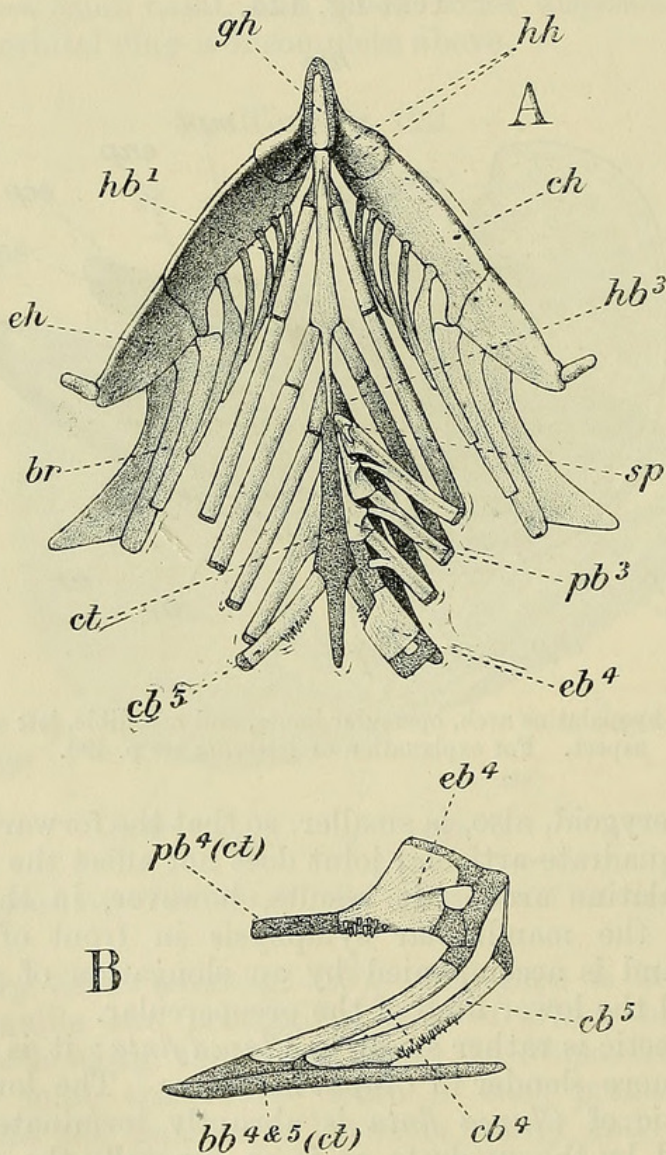
The symplectic is rather small in *Clupea finta*; it is relatively longer and more slender in *Clupea harengus*. The lower end of the symplectic of *Clupea finta* is abruptly terminated, and is not enveloped by the quadrate as is so generally the case. The palatine is shorter and broader in *Clupea finta* than in *Clupea harengus*, and has a distinct cartilaginous head for articulation with the prefrontal, whereas in *Clupea harengus* it is the pre-

frontal which has the boss of cartilage, the palatine merely offering a flat facet for articulation with it.

I fail to comprehend the meaning of Owen's remark (*Anat. Vert. i.* 1866, p. 117) that "in the Shad the palatine articulates with the premaxillary as well as the maxillary." The palatine does not touch the premaxilla in *Clupea finta*.

There are no teeth on the palatine or pterygoid bones in *Clupea finta*, but two or three minute teeth occur on the palatine of *Clupea harengus*, while in *Clupea sprattus* there is a row of minute teeth on the palatine, extending back even on to the entopterygoid. Matthews states (*l. c.* p. 291) that in the Sprat there are a few delicate teeth on the metapterygoid. These I have failed to discern.

Text-fig. 125.



Clupea harengus. A, hyobranchial skeleton, dorsal view. The epibranchials and pharyngobranchials of the left side are not shown. B, fourth and fifth branchial arches of the right side, mesial aspect, more enlarged than fig. 125 A. For explanation of lettering see p. 493.

Opercular Series (text-figs. 123 and 124, pp. 456, 457).—The opercular and subopercular bones are of average proportions; the latter is relatively larger in *Clupea harengus* than in *Clupea finta*. There are seven branchiostegal rays in *Clupea finta*—five rather slender ones borne by the ceratohyal, and two broader ones attached to the outer face of the epihyal. In *Clupea harengus* the numbers are five and three respectively.

Hyobranchial Series (text-fig. 125, p. 458).—The lower hypohyal of *Clupea harengus* is larger than the upper. The urohyal is large and extends back behind the posterior extremity of the third basibranchial. The glossohyal is a conical cartilage, flanked on its upper surface by a thin membrane-bone. This is covered by mucous membrane bearing small teeth; but the teeth, although they may leave scars when removed, are not intimately attached to the bone. The only elements of the hyobranchial skeleton which bear teeth anchylosed with the bone are the fifth ceratobranchials.

The second basibranchial bears fixed on its upper surface a toothless membrane-bone which extends forward and backward over, but is readily removable from, the first and third basibranchials. The equivalent membrane-bone in *Clupea finta* does not extend over the third basibranchial. The fourth and fifth basibranchials are represented by an elongated cartilage which is continued back in the form of a slender rod some distance behind the point at which the fifth ceratobranchials are attached.

The fourth epibranchial is rather large and flat, and serves to support the wall of the epibranchial organ. Its posterior extremity is united with the upper end of the fifth ceratobranchial by a ligament which is the exact equivalent of that slender bar of cartilage which in *Engraulis* represents the fifth epibranchial (*cf.* text-figs. 125 B and 135 B, pp. 458 and 475). In *Clupea alosa* Gegenbaur (*Morph. Jahrb.* iv. Suppl. p. 24 and pl. ii. fig. 13, *Clupea vulgaris* or *Alosa vulgaris*) has figured a fifth epibranchial cartilage. The first pharyngobranchial is small and cartilaginous, but a well-developed spicular bone rises vertically from the upper surface of the anterior extremity of the first epibranchial.

PELLONA MOTIUS.

In *Pellona motius* (Brit. Mus. 1888.11.6.64, E. C. Madras) the top of the cranium is much narrower than in *Clupea*, and the two principal longitudinal ridges on the upper surface are closer together and more nearly parallel. The part of the cranium behind the orbit is greatly reduced in an antero-posterior direction, but not in a vertical direction. The temporal foramen is smaller than in *Clupea* and the pre-epiotic fossa shallower.

The pro-otic, squamosal, and exoccipital appear to be completely hollowed out for the accommodation of the caecal diverticula of the swim-bladder; but the exact relations of the bullæ can only be made out by freely incising the hinder part of the cranium,

which in the circumstances was not permissible. The pro-otic bulla is elongated in a direction transverse to the axis of the skull, and in a posterior view of the cranium a portion of the squamosal bulla is visible on the mesial side of the descending ridge of the epiotic bone. An auditory fenestra is present.

The opisthotic bone is small and flat; the orbitosphenoid does not extend to the prefrontals; and there is no distinct fenestra between the mesethmoid and the frontal bones, although the anterior ends of the right and left frontal bones are separated by a narrow space. The parasphenoid has the same relations as in *Clupea*; there are no teeth on the parasphenoid and vomerine bones.

The post-temporal and supratemporal bones resemble those of *Clupea*, except that both are relatively shorter. There is a small nasal on each side of the head, and seven bones around the eye.

Vestigial teeth occur on the edges of the premaxilla and maxilla. The maxilla and two surmaxillæ are of greater vertical extent and less horizontal extent than in *Clupea*. The mandible is rather short and high, and the highest point is over the middle of the length of the ramus. The angular bone is small and distinct. There are six or eight minute teeth at the front of each dentary bone.

The hyomandibular articulates with the cranium by a single broad head. The ectopterygoid is sharply bent, even more so than in *Clupea harengus*. The buccal surfaces of the entopterygoid, ectopterygoid, and palatine are covered with a kind of shagreen of closely-set, minute denticles.

The bones of the opercular series are much the same as in *Clupea harengus*, but they are relatively smaller. The interhyal is ossified. The urohyal has the form of a thin, triangular plate of considerable vertical extent.

The fourth epibranchial is relatively less expanded than in *Clupea*. The three basibranchial bones, the glossohyal, and the first and second hypobranchials are covered with a shagreen of denticles similar to that found on the entopterygoid.

PELLONULA VORAX.

Pellonula vorax (Brit. Mus. 89.11.20.11, Stanley Falls) has a skull which bears a fairly close resemblance to that of the Herring. The upper surface of the cranium is smoother, and the part of the cranium behind the orbit relatively shorter. The bony bullæ resemble those of *Pellona* rather than those of *Clupea*, and a portion of the squamosal bulla is visible in a posterior view of the cranium on the mesial side of the descending ridge of the epiotic bone. The exoccipitals and basioccipital were not present in the specimen examined, so that the presence of an auditory fenestra could not be determined.

The orbitosphenoid does not extend to the prefrontals. A

median fontanelle occurs between the mesethmoid and the frontal bones. There are no teeth on the parasphenoid and vomer.

The relations of the post-temporal are the same as in *Clupea*, but the bone is shorter; the vertical limb of the supratemporal is longer than the horizontal limb.

Each premaxilla bears about eight fairly large and pointed teeth, but the maxilla is edentulous. The highest point of the mandible is in advance of the middle of the length of the ramus. At the front of the dentary are five or six rather long, pointed teeth, smaller, however, than those of the premaxilla. The angular bone is distinct.

There is a single row, in places a double row, of small teeth running along the middle of the convex surface of the entopterygoid, and a row of about six larger teeth, as large as those of the dentary, set transversely across the front of the palatine.

There are six branchiostegal rays on each side; those which are attached to the ceratohyal resemble in shape the branchiostegal rays of the Anchovy rather than those of the Herring, *i. e.* they are not curved rods, but have the form of plates, each with a conspicuous antero-ventral projection.

PRISTIGASTER TARTOOR.

Pristigaster tartoor (Brit. Mus. 1889.2.1.2026, Malabar, F. Day) has a high, narrow skull, partaking of the general lateral compression of the body. The parietal bones are separated; the temporal grooves are shallow, as in *Clupea*; there is a temporal foramen and an auditory fenestra. In the squamosal bone is a spherical vesicle of the swim-bladder, the bony envelope of which projects into the large shallow pre-epiotic fossa. The vesicle in the pro-otic is much larger than that in the squamosal bone, and its bony envelope bulges upon the ventro-lateral face of the pro-otic, and also projects in two places on the anterior or orbital face of the pro-otic bone.

There is a small opisthotic bone, a small basisphenoid, and an orbitosphenoid; the orbitosphenoid extends forward towards the prefrontals, but fails to reach them. There are right and left posterior wings to the parasphenoid, and the eye-muscle canal opens between them.

The post-temporal has three limbs; the anterior or supratemporal limb is unusually long, the deep or opisthotic limb is long and slender. The supratemporal is triradiate, and the upright ray, passing to the parietal bone, is longer than the other two. The upright limb of the preopercular is about twice as long as the horizontal limb, and makes with it an angle of 130 degrees.

The nasal is a small, tubular bone. Around the orbit are seven bones: two narrow postorbitals, two suborbitals, the second larger than the first, two preorbitals, the lower larger than the

upper, and a long tapering bone lying antero-dorsally to the orbit. The gape is small, and its upper margin is formed almost entirely by the premaxillæ, although these are small bones, while the maxillæ are large. A single row of minute teeth occurs along the edge of the premaxilla, and these are met by a similar row along the sharp front edge of the dentary. The ventral edge of the maxilla is provided with a single row of teeth, but, as in *Clupea*, these do not bite against any mandibular teeth. There are two surmaxillæ above each maxilla.

The angular bone is distinct from the articular. The ventral surfaces of the palatine and entopterygoid bones are extensively covered with minute teeth; there are no teeth on the vomer. The subopercular is reduced in size; the branchiostegal rays are five or six in number on each side. A spicular bone is present, and has the form of an upright rod which broadens out at its lower end.

HYPERLOPHUS COPII.

The genus *Diplomystus* was established by Cope in 1877 (Bull. U.S. Geol. Geog. Surv. Territ. iii. 1877, p. 808) for certain extinct species of fish allied to *Clupea*, but differing in the possession of "a series of dorsal scuta, which extend from the supraoccipital region to the base of the dorsal fin." The genus has since been found to be represented at the present day by species living in the rivers of New South Wales and Chili.

The generic name *Diplomystus* is, I understand from Mr. Boulenger, preoccupied by a Siluroid fish, or, to be more exact, the name of this Siluroid (*Diplomyste*, Duméril; *Diplomystes*, Bleeker; *Diplomystax*, Günther) so closely resembles the name *Diplomystus* as to render the latter invalid. In such case the wisest plan is to apply to "Herrings with occipito-dorsal serrature" the name *Hyperlophus*, as suggested by Ogilby in 1892 (Rec. Austral. Mus. ii. 1892, p. 26).

The specimen examined is one in the British Museum Collection, prepared from a fish about $3\frac{1}{2}$ inches in length, and marked "*Hyperlophus copii*, 97.10.27.38, N. S. Wales, Ogilby."

The parietal bones are separated; the temporal grooves are as in *Clupea*; a temporal foramen is present and an auditory fenestra. The pre-epiotic fossa is present, but with the exception of its upper part it is largely obliterated by the bulging of the squamosal bulla. The vesicle of the swim-bladder in the pro-otic bone is large, and its bony envelope projects upon the ventro-lateral face of the pro-otic. The opisthotic is small; the basisphenoid cannot be recognised in the specimen under consideration; the orbitosphenoid extends forward to meet the prefrontals. There are right and left posterior wings of the parasphenoid, and the eye-muscle canal opens between them.

The post-temporal has an epiotic and an opisthotic limb, but no supratemporal limb. The supratemporal is triradiate, and the ray which passes to the parietal is longer than the other two.

The upright and horizontal limbs of the preopercular are about equal in length, and enclose an angle of 100 degrees. The nasal bone is small and tubular; there is a postorbital bone of moderate size, two suborbitals, two preorbitals, the upper one smaller than the lower, and a narrow bone lying antero-dorsally to the orbit.

The gape is so small that, although the premaxilla is small and the maxilla large, the latter forms only a small portion of the oral border when the mouth is opened to its widest extent. There is but a single surmaxilla*, which from its shape and position is clearly to be identified with the posterior of the two present in *Clupea*. The angular bone is distinct. The mandibular ramus stands high, and the highest point is situated far forwards; the outline of the ramus is intermediate between that of *Clupea harengus* and that of *Chatoëssus* (text-fig. 128, p. 466). There are no teeth on the dentary, and none on the premaxilla, maxilla, palatine, entopterygoid, ectopterygoid, and vomer.

The opercular bones are normal; there are five branchiostegal rays on each side; the interhyal is bony; there are two hypohyals, the lower larger than the upper. The glossohyal is long, narrow, with minute teeth; the urohyal is large and extends backward considerably behind the posterior limit of the epihyal.

CHATOËSSUS EREBI.

Material examined.—In addition to a skull specially prepared for the purposes of this investigation from an alcohol-preserved specimen kindly furnished by Prof. G. B. Howes, two skulls were examined, belonging to complete skeletons in the Osteological Collection of the British Museum (67.5.6.99 and 67.5.6.5, both from Cape York, N. Australia).

Cranium (text-fig. 126, p. 464).—The cranium is stout and rather broad, and is remarkable for the spines that project from the squamosal, postfrontal, and prefrontal bones. The middle part of the parasphenoid is greatly depressed, which gives an appearance of considerable depth to the middle of the cranium.

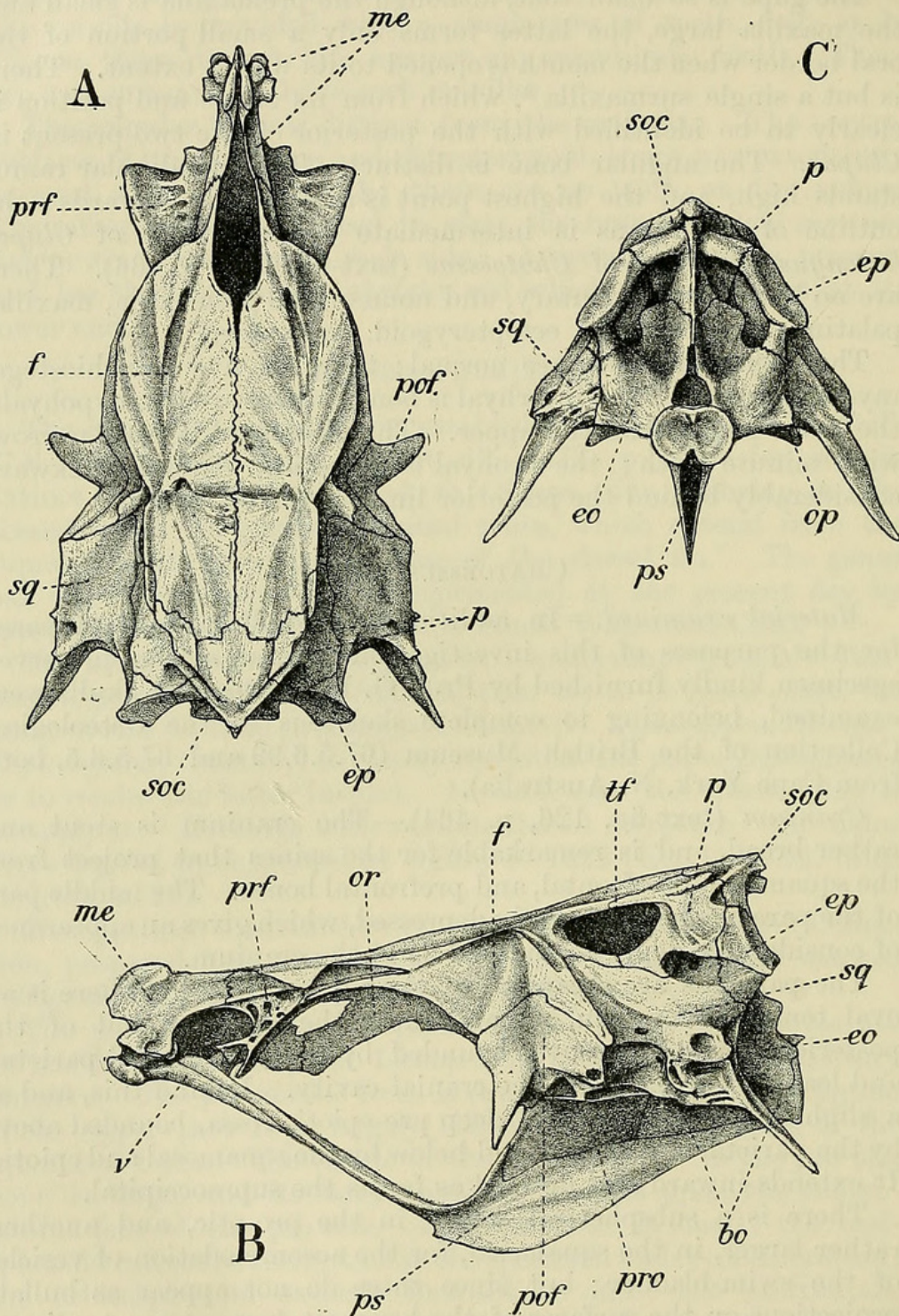
The parietals are separated by the supraoccipital. There is an oval temporal foramen, situated near the anterior end of the posterior temporal groove, bounded by the frontal and parietal, and leading directly into the cranial cavity. Behind this, and at a slightly lower level, is a deep pre-epiotic fossa, bounded above by the parietal and epiotic, and below by the squamosal and epiotic. It extends inward and upward as far as the supraoccipital.

There is a subspherical cavity in the pro-otic, and another, rather larger, in the squamosal, for the accommodation of vesicles of the swim-bladder; but since these do not appear as bullate projections on the surfaces of the bones, it is necessary to dissect

* Smith Woodward (Brit. Mus. Cat. Foss. Fishes, iv. p. 139) records *Diplomystus* as having two surmaxillæ. There is a possibility that one surmaxilla had been lost from each side of the skull examined by me before it came into my hands, but from the appearance of the maxillary series of bones I do not think that this is at all likely.

the skull to determine their presence. The opisthotic is moderately small, and more ventral than posterior in position; it touches the pro-otic, squamosal, and exoccipital, but is remote from the

Text-fig. 126.



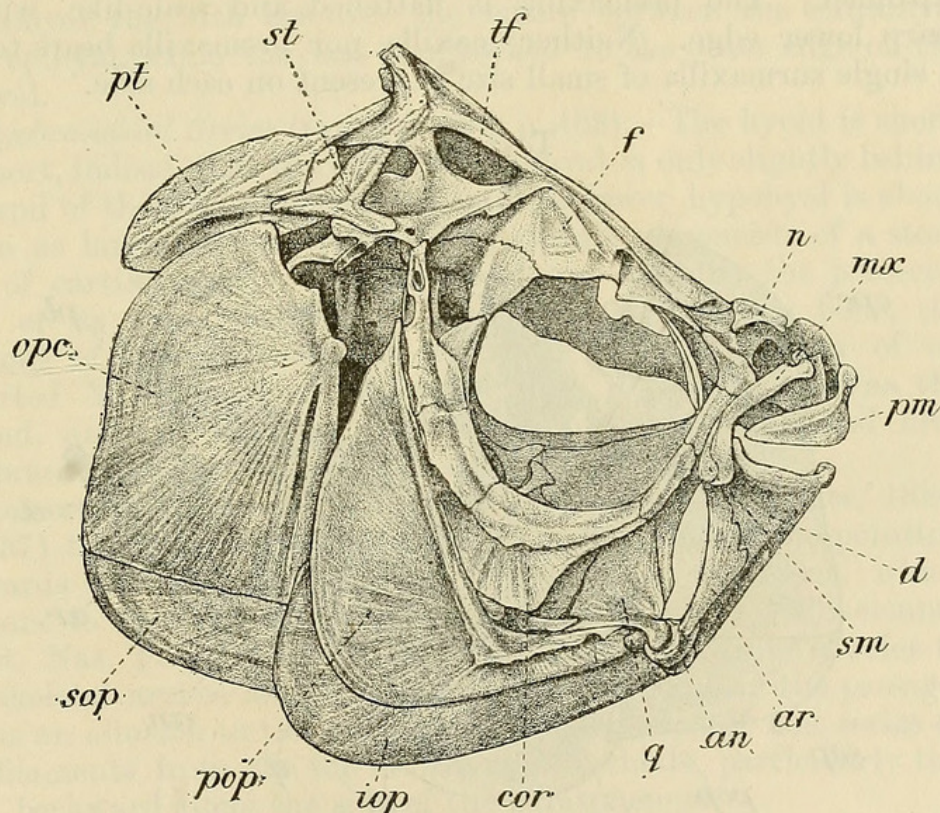
Cranium of *Chatoëssus erebi*.—A, dorsal view; B, left side; C, back view.
For explanation of lettering see p. 493.

epiotic. An auditory fenestra is present, bounded by the pro-otic, exoccipital, and basioccipital. At the back of the cranium are

two depressions, bounded externally by the epiotics. The epiotic has on its postero-superior surface a large, oval, smooth facet for articulation with the post-temporal; and from the apex of the epiotic there projects backward into the muscles of the trunk a separable osseous brush. A similar brush projects back from the apex of the supraoccipital, which has no crest or spine.

The parasphenoid extends very nearly to the posterior end of the basioccipital, and although the right and left sides of the posterior outlet of the eye-muscle canal are formed by vertical laminae of the parasphenoid, there are no projecting posterior wings of this bone. The middle portion of the parasphenoid bears a sharp ventral keel. Neither parasphenoid nor vomer bears teeth. A small basisphenoid is present, but it has no descending portion bisecting the eye-muscle canal. The orbitosphenoid is fairly large, and has a forwardly directed process that meets a backward growth of the combined prefrontals. A fontanelle is present in the roof of the skull between the mesethmoid and the frontals.

Text-fig. 127.



Chatoëssus erebi, right side of skull. For explanation of lettering see p. 493.

Temporal and Preopercular Series (text-fig. 127).—The post-temporal is large, and the attachment of its upper limb to the postero-superior surface of the epiotic is quite intimate, and not by means of a broad loose ligament. The deep limb is rod-like and is attached to the back of the opisthotic. The third limb is

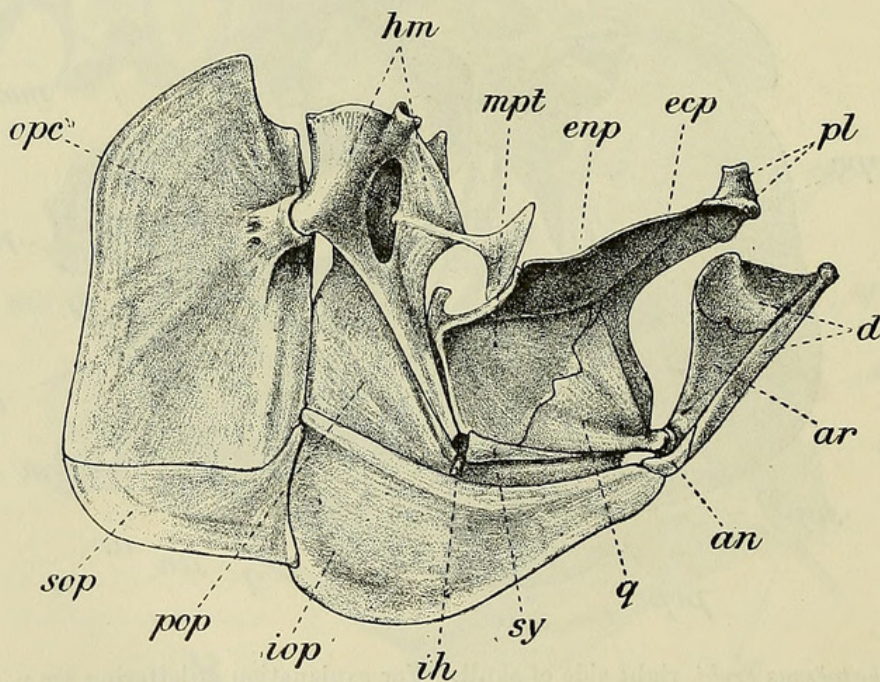
very short and is united with the back of the supratemporal. The supratemporal has the usual triradiate arrangement of the sensory canal.

The horizontal limb of the preopercular is a little more than half as long as the upright limb, and makes with it an angle of about 95 degrees. The interopercular is large, considerably larger than the subopercular, and comes into direct contact with the angular bone, without the intervention of the usual ligament.

Circumorbital Series (text-fig. 127, p. 465).—There are nine bones of this series. The nasal is roughly rectangular in shape, with a narrow tube for the sensory canal passing lengthwise over its surface. The form and relations of the other bones are readily to be comprehended by a glance at text-fig. 127.

Maxillary Series (text-fig. 127, p. 465).—The gape is very small and bounded above by the premaxillæ. The maxilla is only slightly longer than the premaxilla. Fries (Scand. Fishes, ed. 2, ii. 1895, p. 952) states that the premaxilla is longer than the maxilla in the *Chatoëssinæ*, but such is not the case in the specimens now under consideration. The front part of the maxilla is of considerable vertical extent, and the posterior extremity is also expanded. The premaxilla is flattened and scale-like, with a sharp lower edge. Neither maxilla nor premaxilla bears teeth. A single surmaxilla of small size is present on each side.

Text-fig. 128



Chatoëssus erebi, hyopalatine arch, opercular bones, and mandible of left side, mesial aspect. For explanation of lettering see p. 493.

Mandibular Series (text-figs. 127 and 128).—The remarkable shape of the mandible is doubtless due to the reduction of the gape not being accompanied by an adequate forward displacement of the quadrate-articular joint. The coronoid process thus comes

to lie over the anterior half of the ramus; it is formed mainly, but not entirely, by the dentary. The angular is distinct. There are no teeth.

Hyopalatine Series (text-fig. 128, p. 466).—The hyomandibular articulates with the cranium by two heads: a small anterior and a broad posterior one. It is long, and its axis slopes forward and makes an angle of about 110 degrees with the symplectic, which is disposed almost horizontally. The extremity of a triangular process which rises upward and forward from the external face of the hyomandibular lies over the outer surface of the postfrontal spine, and forms with it a kind of sliding joint. The palatine is very short and broad, and has a single head for articulating with the ethmoid region of the cranium. There are no teeth.

Opercular Series (text-figs. 127 and 128, pp. 465, 466).—The opercular and subopercular bones are of average proportions. The branchiostegal rays are six in number; the first three are rather slender and closely set, and situated some distance in advance of the other three, which are greatly expanded and overlap the former three. The first four are attached to the outer edge of the ceratohyal, the fifth lies over the suture between the ceratohyal and epihyal, while the last is attached to the outer edge of the epihyal.

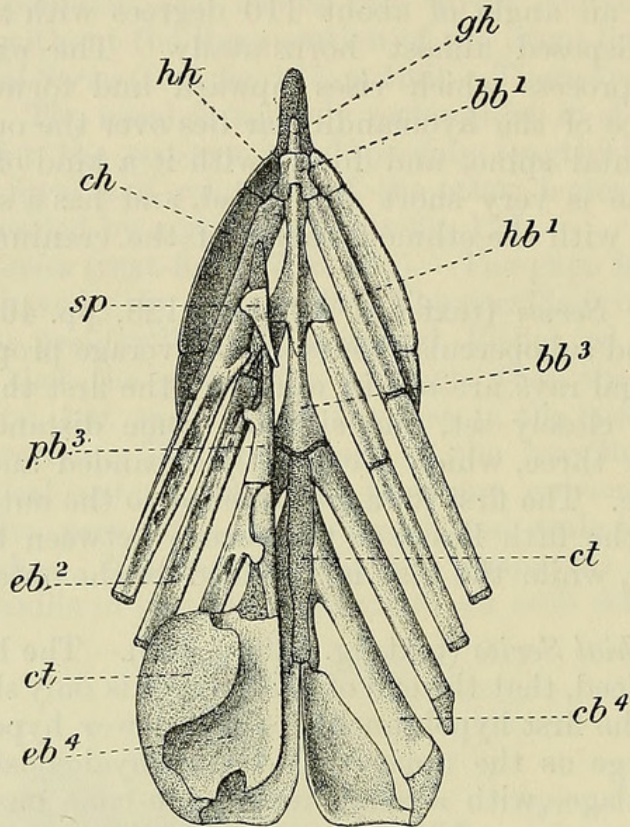
Hyobranchial Series (text-fig. 129, p. 468).—The hyoid is short, so short, indeed, that the end of the epihyal is only slightly behind the end of the first hypobranchial. The lower hypohyal is about twice as large as the upper. The glossohyal consists of a stout rod of cartilage, with a small membrane-bone on the posterior part of its upper surface. The urohyal is a strong bone, the sections of the posterior half of which have the form of an inverted Y. The third basibranchial is nearly as large as the second, and the cartilage that represents the fourth and fifth basibranchials is drawn out to a considerable length.

Concerning *Chatoëssus* Günther states ('Study of Fishes,' 1880, p. 657) that the branchial arches form two angles, one pointing forwards and the other backwards. This statement, which appears to be based upon the description given by Valenciennes (Hist. Nat. Poiss. xxi. 1848, p. 96), does not, I believe, refer to the skeletal arches as one might suppose on reading the passage, but is an allusion to the remarkable continuation of the series of gill-filaments from the top of the epibranchials, particularly the first, backward along the side of the parasphenoid.

The anterior ends of the fourth ceratobranchials are expanded both forwards and backwards, so that while not relinquishing their connection with the anterior ends of the fifth ceratobranchials, they nearly touch the mesial ends of the third ceratobranchials. The fifth ceratobranchials are considerably expanded, as also are the fourth epibranchials. The latter have a curved wall of cartilage extending upward and inward from the outer edge of the bone, in relation with the epibranchial organ.

In the first two branchial arches the epibranchial is longer than the ceratobranchial, but in the third the reverse is the case. The third hypobranchials are small and concealed in a dorsal view by the breadth of the posterior end of the third basibranchial.

Text-fig. 129.



Chatoëssus erebi, hyobranchial skeleton, dorsal view.—The epibranchials and pharyngobranchials of the right side are not shown. For explanation of lettering see p. 493.

Whereas in most forms the fourth pharyngobranchial is represented by a cartilage with a removable dentigerous membrane-bone on its ventral surface, in *Chatoëssus* the membrane-bone (devoid of teeth) flanks the cartilage on three sides, ventral, mesial, and dorsal, and simulates an ossified fourth pharyngobranchial. The first pharyngobranchial is cartilaginous, and a large spicular bone is present. There are no teeth on any part of the hyobranchial skeleton.

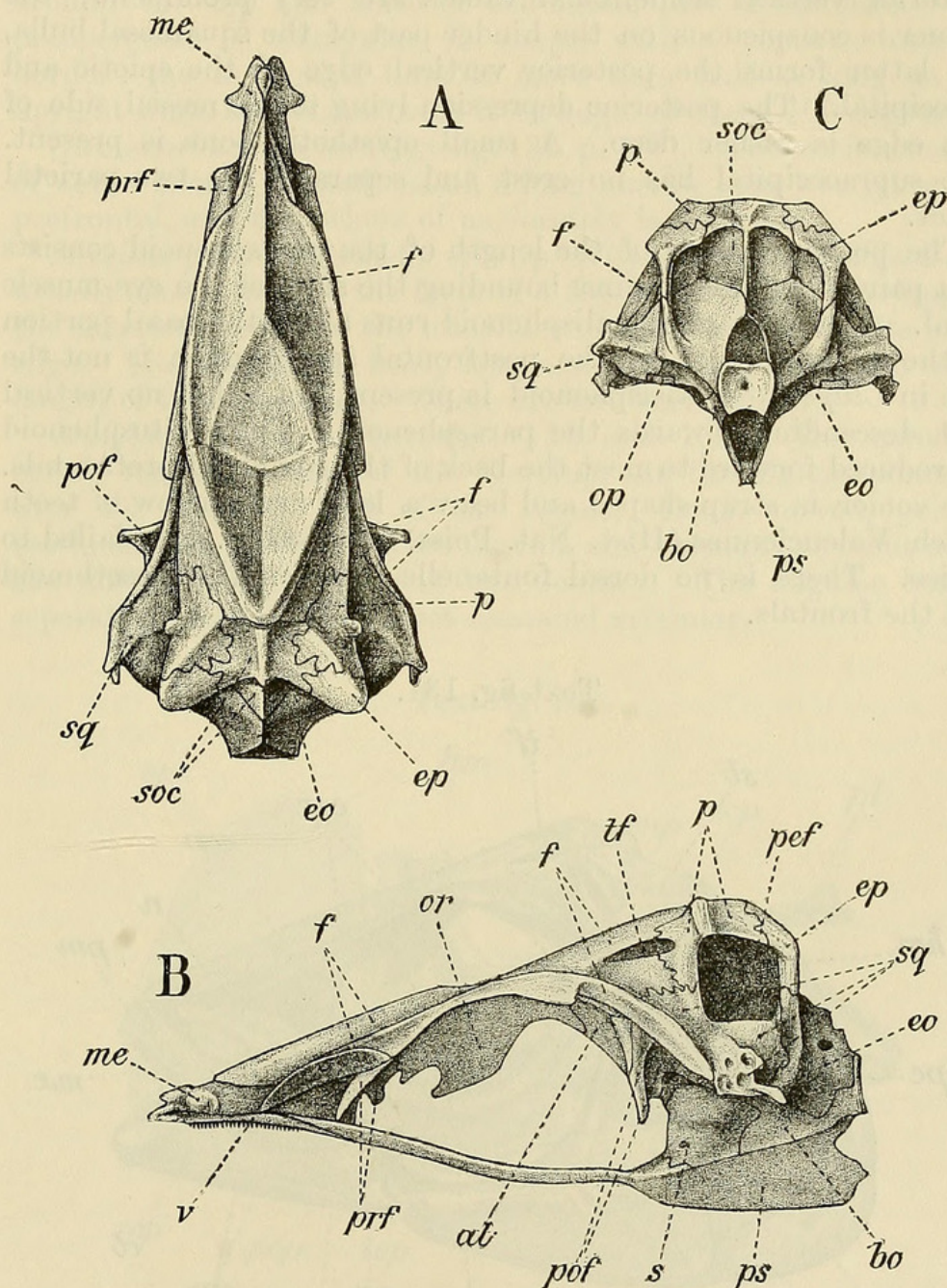
DUSSUMIERIA ACUTA.

Material examined.—In addition to a skull specially prepared for the purposes of this investigation from an alcohol-preserved specimen from Madras kindly furnished by Mr. G. A. Boulenger, another skull was examined, belonging to a complete skeleton in the Osteological Collection of the British Museum (Brit. Mus. 1889.2.1.2038, Bombay).

Cranium (text-fig. 130, p. 469).—The cranium has all the cha-

racteristic features of that of *Clupea*. The posterior temporal groove faces more laterally than in *Clupea* owing to the width of the cranium in the squamosal region being proportionately less. The temporal foramen near the anterior end of the groove is a

Text-fig. 130.



Cranium of *Dussumieria acuta*.—A, dorsal view; B, left side; C, back view.
s, point of attachment of the spicular bone to the pro-otic. For explanation
of other lettering see p. 493.

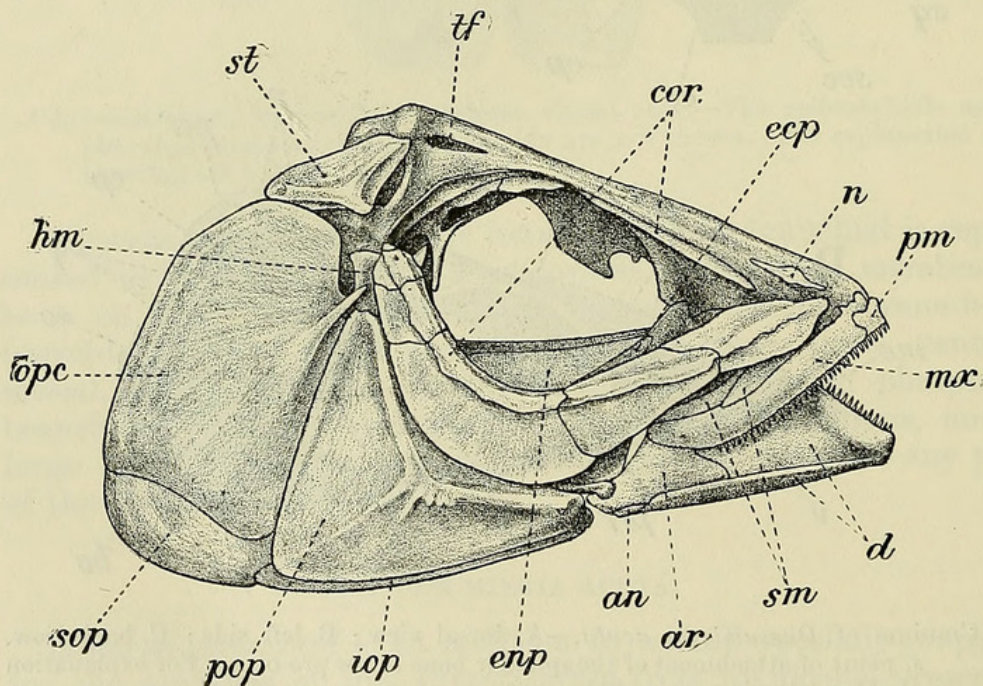
narrow horizontal slit, but the pre-epiotic fossa is large. This fossa is bounded above by the parietal, below by the squamosal, in front by the parietal and squamosal, and behind by the epiotic. It is about half as deep as wide, and the inner wall is mainly

membranous, but partly formed by lamellar extensions of the supraoccipital, epiotic, and squamosal bones.

There is an auditory fenestra between the pro-otic, exoccipital, and basioccipital. A large osseous bulla, enclosing a terminal vesicle of the swim-bladder, occurs in the pro-otic, and another in the squamosal. The bony envelopes of the horizontal and posterior vertical semicircular canals are very prominent; the former is conspicuous on the hinder part of the squamosal bulla, the latter forms the posterior vertical edge of the epiotic and exoccipital. The posterior depression lying to the mesial side of this edge is rather deep. A small opisthotic bone is present. The supraoccipital has no crest and separates the two parietal bones.

The posterior third of the length of the parasphenoid consists of a pair of parallel laminae bounding the sides of the eye-muscle canal. A process of the alisphenoid runs along the basal portion of the anterior edge of the postfrontal spine, which is not the case in *Clupea*. A basisphenoid is present, but it has no vertical part descending towards the parasphenoid. The orbitosphenoid is produced forward to meet the back of the combined prefrontals. The vomer is strap-shaped and bears a long median row of teeth which Valenciennes (Hist. Nat. Poiss. xx. 1847, p. 468) failed to notice. There is no dorsal fontanelle between the mesethmoid and the frontals.

Text-fig. 131.



Dussumieria acuta, right side of skull. For explanation of lettering see p. 493.

Temporal and Preopercular Series (text-fig. 131).—The post-temporal has a long limb resting upon the epiotic prominence, a shorter, rod-like limb attached to the back of the opisthotic, and

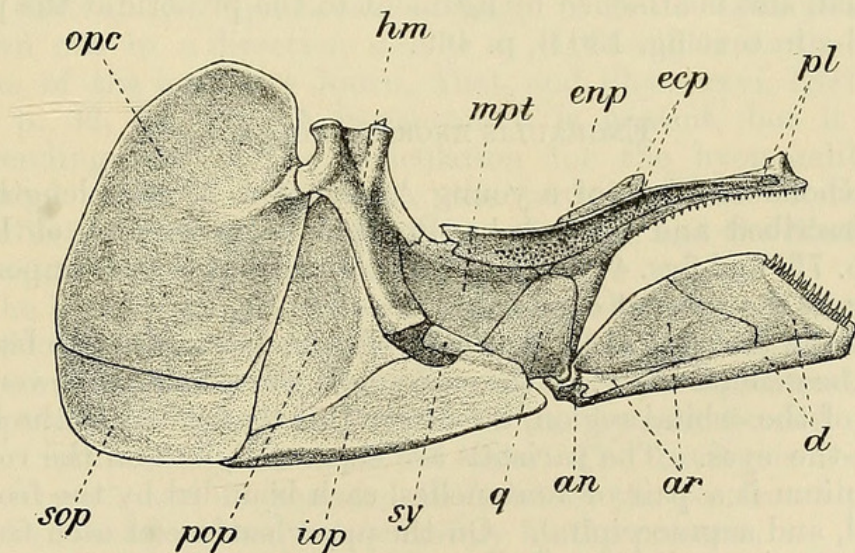
a still shorter lamellar limb overlapped by the back of the supratemporal. The supratemporal forms a kind of outer wall to the large pre-epiotic vacuity. There is also a pair of ordinary body-scales, about as large as the supratemporals, which project back from the transverse ridge of the parietals. These, together with the supratemporals and the preoperculars, form a kind of girdle around the top and sides of the hinder part of the head. The preopercular is triangular in shape, with a concave anterior border; the horizontal limb is more than half as long as the upright limb, and makes with it an angle of about 100 degrees.

Circumorbital Series (text-fig. 131, p. 470).—This series consists of seven bones: a small nasal, a long narrow bone overlying the prefrontal, and five others of moderately large size.

Maxillary Series (text-fig. 131, p. 470).—The premaxilla is unusually short, and has the form of a flat, square scale, overlapping the anterior portion of the maxilla, and with teeth along its lower edge. The maxilla is fairly long and is toothed along the whole length of its lower edge. There are two surmaxillæ.

Mandibular Series (text-figs. 131 and 132).—The mandible closely resembles that of the Herring, and the highest point lies over the anterior half of the ramus. Long, curved, pointed teeth, similar to those of the maxilla and premaxilla, occur along the antero-superior edge of the dentary. The angular bone is separate; there is no distinct sesamoid articular.

Text-fig. 132.



Dussumieria acuta, hyopalatine arch, opercular bones, and mandible of left side, mesial aspect. For explanation of lettering see p. 493.

Hyopalatine Series (text-fig. 132).—The hyomandibular has two distinct heads for articulation with the cranium, the posterior slightly larger than the anterior. The symplectic makes an angle of about 125 degrees with the axis of the hyomandibular; it is flat, and is largely overlapped on its inner surface by the inter-

opercular. The palatine, ectopterygoid, and entopterygoid bear teeth. The ectopterygoid has an outwardly projecting ledge which serves to support the eyeball, and which comes into close relation with the upper edge of the middle of the three large bones of the suborbital series. The ectopterygoid is curved in the middle of its length, but not sharply bent.

Opercular Series (text-figs. 131 and 132, pp. 470, 471).—The gill-cover is large, and the opercular and subopercular bones are of corresponding proportions. The branchiostegal rays are thirteen in number; eight of these are set on the outer side of the lower edge of the ceratohyal, and five on the epihyal. The shape is approximately the same in all, but the hinder ones are larger than those in front. Valenciennes (Hist. Nat. Poiss. xx. 1847, p. 469) and Günther (Brit. Mus. Cat. Fish. vii. 1868, p. 466) put the number of branchiostegal rays as fifteen.

Hyobranchial Series.—The lower hypohyal is slightly larger than the upper. The posterior one-third of the glossohyal cartilage is ossified; a narrow membrane-bone with a row of teeth along the middle covers the whole. The first, second, and third basibranchials are covered by separate membrane-bones, each bearing a narrow central row of teeth, but the investing lamina of the second basibranchial extends forward over the hinder part of the first basibranchial. The urohyal is long and slender. The fourth epibranchial is about as much expanded as in the Herring. The first pharyngobranchial is cartilaginous, and a spicular bone rises from the front end of the first epibranchial, and is attached by ligament to the pro-otic at the point marked *s* in text-fig. 130 B, p. 469.

ENGRAULIS ENCRASICHOLUS.

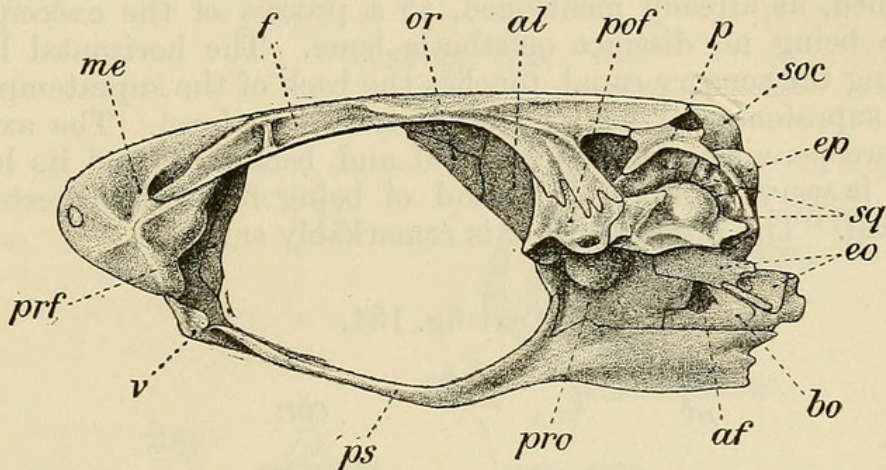
The chondocranium of a young Anchovy of 25 mm. length has been described and figured by Pouchet (Journ. Anat. et Phys. 1878, p. 75, and figs. 49 and 50), but the account has no important bearing in the present connection.

Cranium (text-fig. 133, p. 473).—The most remarkable feature about the general aspect of the cranium is the considerable vertical extent of the orbital region, a feature directly related to the large size of the eyes. The parietals are separated, and on the roof of the cranium is a pair of fontanelles, each bounded by the frontal, parietal, and supraoccipital. On the upper surface of each frontal bone are two cross bars or arches of bone, the anterior one strictly transverse, the second oblique.

A distinct opisthotic is not present; the deep or opisthotic limb of the post-temporal is attached to a process of the exoccipital lying immediately over the foramen for the tenth nerve. The posterior temporal groove is shallow, and the temporal foramen, near its anterior end, is large and bounded by the frontal and parietal, with sometimes also a small portion of the squamosal below. Owing to the large size of the squamosal bulla that

encloses a vesicle of the swim-bladder, the pre-epiotic fossa above it is rendered very shallow as compared with that of *Clupea*. The auditory fenestra, opening into the perilymphatic cavity, is bounded by the pro-otic, exoccipital, and basioccipital, as in *Clupea*.

Text-fig. 133.



Cranium of *Engraulis encrasicolus*, left side. For explanation of lettering see p. 493.

The foramen for the trigeminal nerve is of large size; it faces more anteriorly than usual, and is bounded by the alisphenoid and pro-otic, instead of by the pro-otic alone. The pro-otic bulla, like that of the squamosal, is large; it is not spherical, but is drawn out in a direction nearly at right-angles to the median plane of the head (see Journ. Anat. and Phys. xxvi. 1891, p. 36, and p. 32, fig. D). A basisphenoid is present, but it has no descending limb. The articulation for the hyomandibular is situated rather far forward; the anterior head of the hyomandibular articulates with the postfrontal, and the hinder with the squamosal.

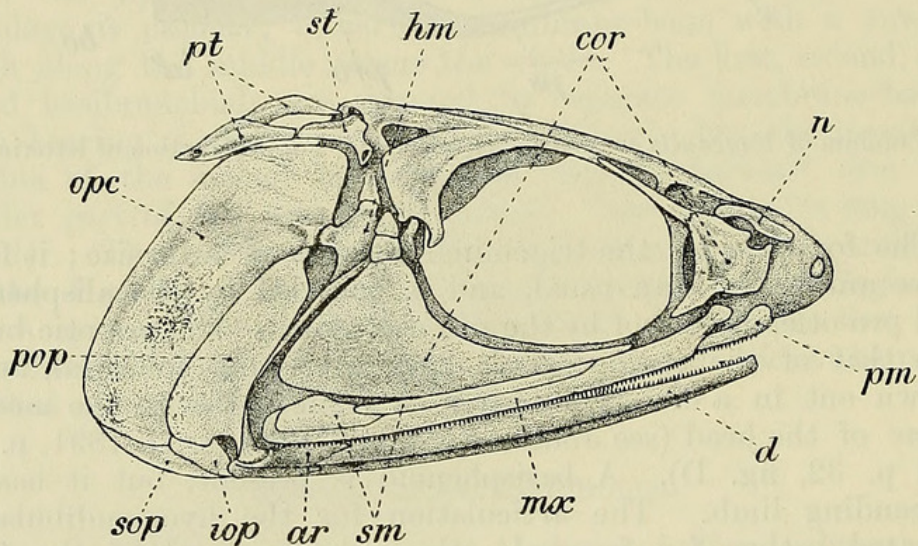
The lateral temporal groove is broad and shallow. Removal of its floor exposes a fairly large cavity opening laterally by two apertures—one over the articular process of the squamosal for the reception of the posterior head of the hyomandibular, and the other immediately in front of this. The cavity is roofed by the frontal, and is bounded in front by the postfrontal, behind by the squamosal, and below mainly by the pro-otic.

The parasphenoid is depressed at about the middle of its length, doubtless in relation with the large size of the eyes. It does not project behind the occipital articulation, but it ends posteriorly in a pair of parallel lamellæ on the right and left sides of the posterior outlet of the eye-muscle canal. Both parasphenoid and vomer are edentulous. The front of the cranium is formed by the mesethmoid, and not by the vomer (cf. *Clupea*). The mesethmoid is large, of considerable vertical extent, but thin; the prefrontals are relatively small. The orbitosphenoid is small, and

makes no attempt to support the great membranous interorbital septum, neither does it send a process forward to meet the prefrontals as it does in *Clupea*.

Temporal and Preopercular Series (text-fig. 134).—The post-temporal has the usual three limbs. The longest is the upper limb, loosely attached by ligament to the upper surface of the epiotic. The opisthotic limb is delicate and rod-like, and is attached, as already mentioned, to a process of the exoccipital, there being no distinct opisthotic bone. The horizontal limb, bearing the sensory canal, touches the back of the supratemporal. The supratemporal has the usual triradiate form. The axis of the preopercular slopes downward and backward, and its lower limb is very short, and instead of being forwardly directed is vertical. The interopercular is remarkably small.

Text-fig. 134.



Engraulis encrasicholus, right side of skull. For explanation of lettering see p. 493.

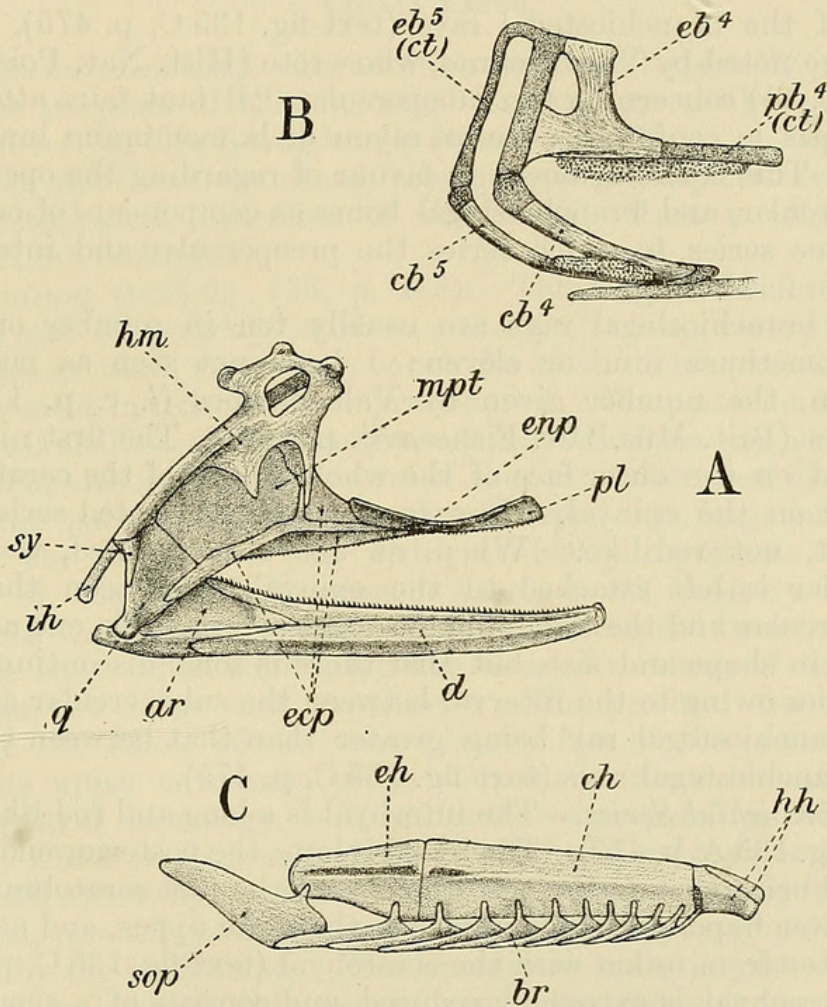
Circumorbital Series (text-fig. 134).—The bones of this series are six in number. The largest lies below and behind the eye, and above this bone are two small postorbitals. Both nasal and preorbital, particularly the latter, are relatively larger than in *Clupea*.

Maxillary Series (text-fig. 134).—The premaxilla is small, and bears teeth on the posterior half of its lower edge. The two premaxillæ extend, without meeting, below the mesethmoid, and not in front of it as in *Clupea*; it is, in fact, the projection of the ethmoid region in advance of the mouth that gives the characteristic appearance to the head of *Engraulis*. The maxilla is long, and is toothed all along its edge except at the anterior end, where it is overlapped by the premaxilla. There are two surmaxillæ, a broad one behind and a long thin one in front. They lie in an extensible membrane which is continuous with the lower edge of

the suborbital plate, and they form a triangle with the posterior half of the maxilla when the mouth is widely opened.

Mandibular Series (text-figs. 134 and 135 A).—The mandible is long, and the dentary bears teeth along the whole of its upper edge. The coronoid process is situated far back, and does not rise high in proportion to the length of the ramus. The angular is not distinct from the articular, and there is no sesamoid articular.

Text-fig. 135.



Engraulis encrasicolus.—A, hyopalatine arch and mandible of left side, mesial aspect; B, fourth and fifth branchial arches of left side, mesial aspect; C, hyoid of right side, with branchiostegal rays and subopercular bone, external view. For explanation of lettering see p. 493.

Hyopalatine Series (text-fig. 135 A).—The most striking features of the hyopalatine arch are related to the backward thrust of the quadrate articulation. The axis of the quadrate slopes backward; the axis of the hyomandibular also slopes backward, but the symplectic is not in the same line with it, as might have been expected. The hyomandibular articulates with the cranium by two distinct heads, and the opercular head is fairly long. The edges of the palatine and ectopterygoid bear microscopic teeth,

and a row of similar teeth occurs on the middle of the palatal surface of the entopterygoid.

Opercular Series (text-figs. 134 and 135 C, pp. 474, 475).—The opercular bone is remarkably large; the subopercular is comparatively small, and extends forward beneath the interopercular, and is bound to the posterior part of the outer face of the epihyal in such a way that it has a tendency, during the process of disarticulation of the skull prior to the maceration of the parts, to leave the opercular bone and to come away with the hyobranchial skeleton. In such cases it is liable to be mistaken for the hindmost of the branchiostegal rays (text-fig. 135 C, p. 475), a fact long ago noted by Valenciennes, who wrote (*Hist. Nat. Poiss.* xxi. 1848, p. 11) concerning the subopercular, “il faut faire attention de ne pas le confondre avec un rayon de la membrane branchiostège.” This is an argument in favour of regarding the opercular, subopercular, and branchiostegal bones as components of one and the same series, to which series the preopercular and interopercular do not belong.

The branchiostegal rays are usually ten in number on each side, sometimes nine or eleven; I have not seen as many as thirteen, the number given by Valenciennes (*l. c.* p. 11) and Günther (*Brit. Mus. Cat. Fishes*, vii. p. 386). The first nine are situated on the outer face of the whole length of the ceratohyal, the last on the epihyal. They form a well-graduated series, and are flat, not rod-like. When, as above mentioned, the subopercular is left attached to the epihyal, it is seen that the subopercular and the last branchiostegal ray resemble one another closely in shape and size, but that there is some discontinuity in the series owing to the interval between the subopercular and the last branchiostegal ray being greater than that between the last two branchiostegal rays (text-fig. 135 C, p. 475).

Hyobranchial Series.—The interhyal is a long and rod-like bone (text-fig. 135 A, p. 475). The hyoid is long, the posterior end of the epihyal being close to the posterior end of the first ceratobranchial. The lower hypohyal is much larger than the upper, and excludes the latter from union with the ceratohyal (text-fig. 135 C, p. 475). The glossohyal is extremely reduced, and consists of a small cone of cartilage, with a small cap of edentulous membrane-bone on its upper surface. The urohyal is long and slender.

A narrow membrane-bone, with crowded small teeth, extends over the whole length of the second basibranchial, and projects forwards over the posterior half or more of the first basibranchial and backwards over the anterior sixth of the third basibranchial. The second basibranchial is remarkably long, a fact which disturbs the parallelism of the first and second ceratobranchials. The first hypobranchials are long, almost as long as the first ceratobranchials; the second, however, are small and triangular, and are fused with the sides of the posterior end of the second basibranchial. The third hypobranchials are normal, and slope obliquely down the sides of the third basibranchial.

The epipharyngeal teeth and the hypopharyngeal teeth on the fifth ceratobranchials are larger and more pointed than the teeth of the basibranchial skeleton. A slender cartilaginous fifth epibranchial is present, confluent at its upper end with the cartilaginous posterior part of the fourth epibranchial (text-fig. 135 B, p. 475). Between the cartilaginous and ossified parts of the fourth epibranchial is a fenestra closed by membrane. The first pharyngobranchial is cartilaginous and small; the spicular bone is remarkably long and slender.

COILIA NASUS.

Material examined.—In addition to a skull specially prepared for the purposes of this investigation from an alcohol-preserved specimen from Kiu Kiang kindly furnished by Mr. G. A. Boulenger, another skull was examined, belonging to a complete skeleton in the Osteological Collection of the British Museum (Brit. Mus. 91.1.31.30, Shanghai).

Cranium (text-fig. 136, p. 478).—The cranium is broad and short, and its posterior surface, instead of rising vertically from the basioccipital, slopes very much forward. The parietal bones nearly meet in front of the supraoccipital. The posterior temporal groove is shallow, and has neither a pre-epiotic fossa nor a temporal foramen, although on the course of the suture between the frontal and the parietal bones is a minute depression, large enough to admit the point of a pin, which evidently represents the last trace of the closed foramen. There is no auditory fenestra between the pro-otic, exoccipital, and basioccipital bones.

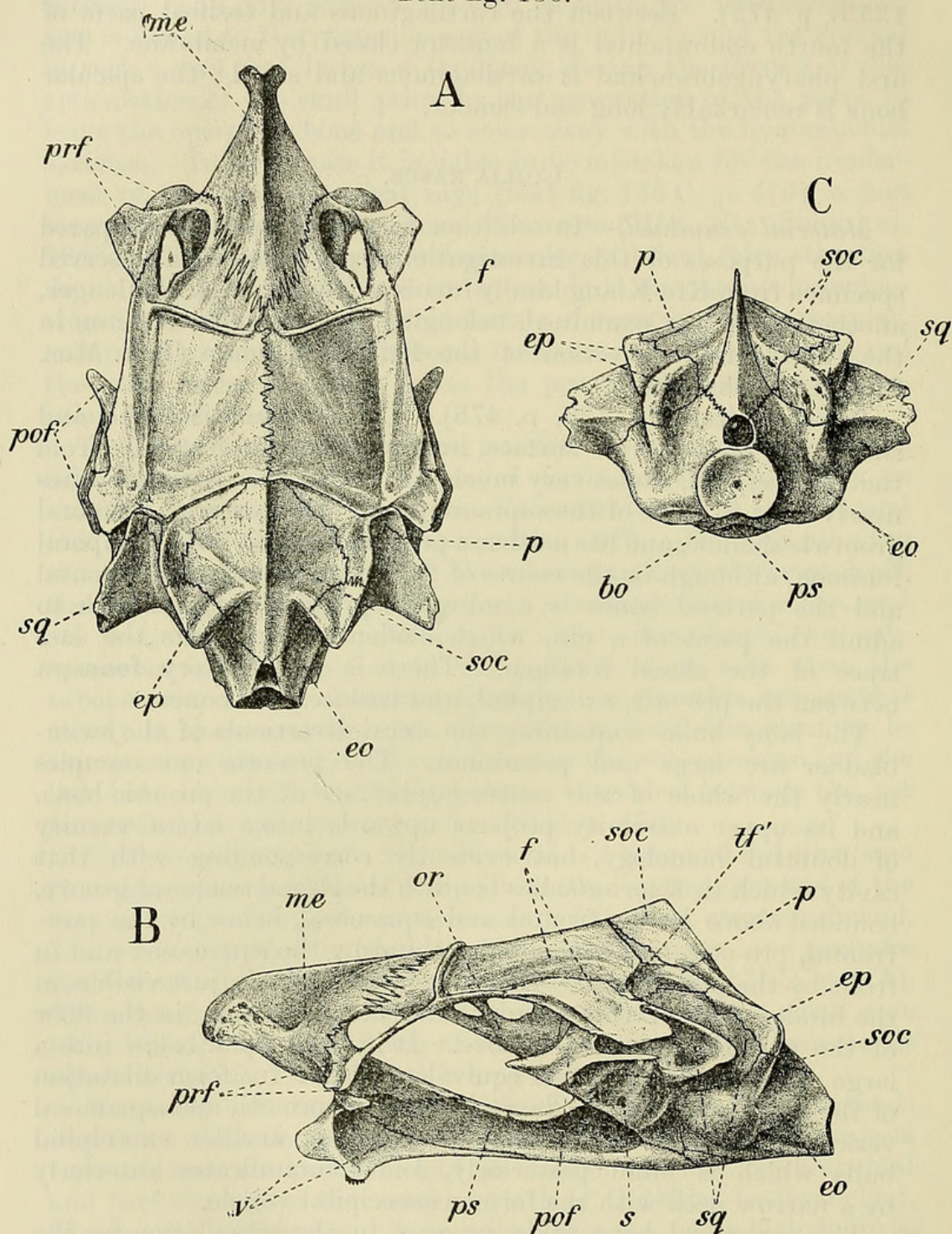
The bony bullæ containing the cæcal diverticula of the swim-bladder are large and prominent. The pro-otic one occupies nearly the whole of the ventro-lateral face of the pro-otic bone, and its upper extremity projects upwards into a lateral vacuity of doubtful homology, but evidently corresponding with that cavity which in *Engraulis* lies beneath the lateral temporal groove, bounded above by the frontal and squamosal, below by the post-frontal, pro-otic, and squamosal, behind by the squamosal, and in front by the postfrontal. The squamosal bulla is just visible in the hinder part of this vacuity, and also above it, in the floor of the posterior temporal groove. It is freely open below into a large exoccipital bulla*, the equivalent of the fusiform dilatation of the air-duct which in *Clupea* leads to the pro-otic and squamosal vesicles. Behind this, however, is another smaller exoccipital bulla which is blind posteriorly, and communicates anteriorly by a narrow neck with the former exoccipital vesicle.

The squamosal bone takes no part in the articulation for the head of the hyomandibular; this is formed mainly by the post-frontal, but partly also by the pro-otic. The appearances are such as strongly to suggest that the posterior head of the hyo-

* These relations can only be made out by making suitable incision into the cranial bones.

mandibular of *Engraulis* and its corresponding articular facet in the squamosal bone have disappeared in the present genus. In text-fig. 138 (p. 481) the part marked *hm'* is the articular head

Text-fig. 136.



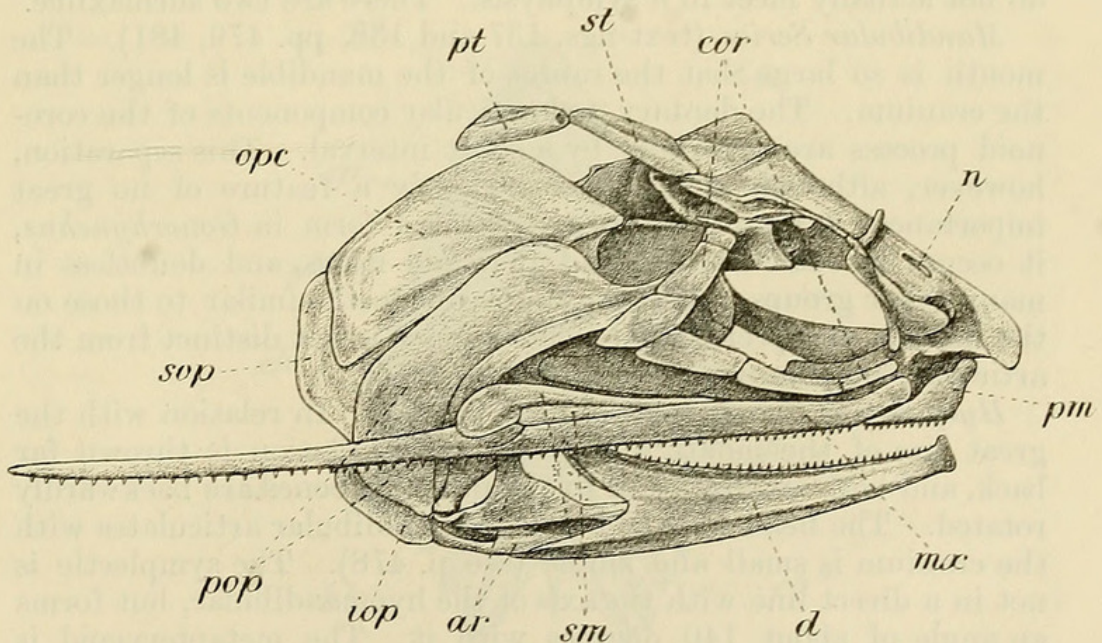
Cranium of *Coilia nasus*.—A, dorsal view; B, left side; C, back view. *s*, point of attachment of the spicular bone to the pro-otic; *tf'*, last trace of temporal foramen. For explanation of other lettering see p. 493.

of the hyomandibular, the part above and behind the fenestra is comparatively remote from the side of the cranium.

The parasphenoid has no ascending processes in the region of the pro-otics, but there is a well-marked process of each pro-otic, directed forward and downward, which is suturally united with the supero-lateral edge of the parasphenoid. The parasphenoid is short, and underlies but a small portion of the basioccipital. It has no posterior wings, and the eye-muscle canal does not open behind, although there is a minute depression at the back of the parasphenoid, in the region where the opening might be expected to occur. The anterior part of the parasphenoid is broad, V-shaped in section, and united by elaborate jagged sutures with the prefrontals and vomer. The vomer has five or six teeth on each side, the two patches being widely separated. The mesethmoid projects considerably in advance of the vomer and has a dorsal crest; yet the ethmoid region as a whole is short.

Running across the roof of each frontal is an arched bar of bone. The alisphenoids face forwards, *i. e.* they lie transversely to the cranial axis instead of sloping forward and inward. The orbitosphenoid is fairly large, and is tubular in its hinder two-thirds. It passes back between and below the alisphenoids, and comes into extensive relation with the pro-otic bones. The tubular part does not lie close up under the median suture of the frontals, but is separated by a vertical fenestrated sheet of the orbitosphenoid bone. The opisthotic is absent, and there seems to be no basisphenoid.

Text-fig. 137.



Coilia nasus, right side of skull. For explanation of lettering see p. 493.

Temporal and Preopercular Series (text-fig. 137).—The post-temporal has but one limb, a long one, the anterior extremity of which rests on the epiotic prominence. This limb is concealed in text-fig. 137 by the supratemporal. The rest of the bone

consists merely of a semi-tubular scale touching the back of the supratemporal. The supratemporal is a tubular scale which does not exhibit the usual triradiate character, since the parietal division of the sensory canal branches in the skin just anterior to the supratemporal bone. The axis of the preopercular slopes strongly backward; the anterior edge of the bone is concave and not angulate, so that the proportions of the upper and lower limbs cannot be determined.

Circumorbital Series (text-fig. 137, p. 479).—The nasal is very small. Beneath the nasal sac are two bones, both rather firmly attached to the prefrontal. There are three postorbitals and three suborbitals, the former series making an acute angle with the latter.

Maxillary Series (text-fig. 137, p. 479).—The extraordinary length of the maxilla is one of the most remarkable features of the fish under consideration; indeed, it is difficult to understand what purpose the teeth on the hinder part of the maxilla can possibly serve. A similar prolongation of the maxilla is met with in some species of *Engraulis*, attaining a maximum in *Engraulis mystax* and *Engraulis setirostris* (Cuvier and Valenciennes, Hist. Nat. Poiss. xxi. 1848). The actual length of the projecting part of the maxilla varies in different specimens of *Coilia*, doubtless owing to fracture during life; but it may be taken as a rule that the toothed part of the maxilla is two-and-a-half times as long as the tooth-bearing part of the dentary. The premaxillæ extend below the mesethmoid, not in front of it; they nearly touch, but do not actually meet in a symphysis. There are two surmaxillæ.

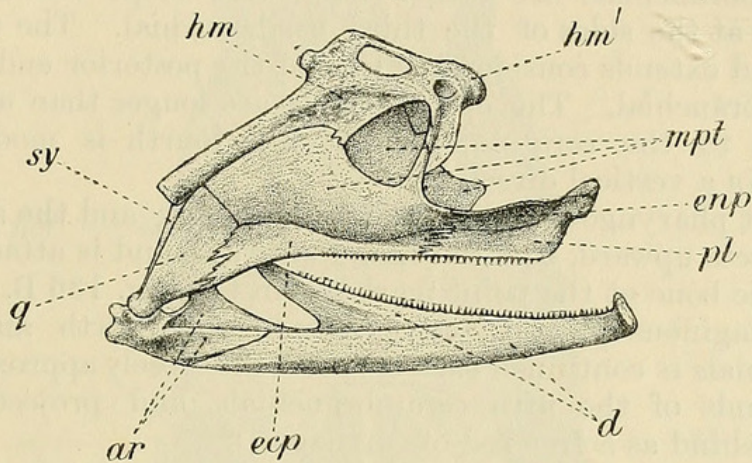
Mandibular Series (text-figs. 137 and 138, pp. 479, 481).—The mouth is so large that the ramus of the mandible is longer than the cranium. The dentary and articular components of the coronoid process are separated by a short interval. This separation, however, although striking, is evidently a feature of no great importance; it occurs in an exaggerated form in *Gonorhynchus*, it occurs in some Percoid and Berycoid fishes, and doubtless in many other groups. The dentary bears teeth similar to those on the maxilla and premaxilla. The angular is not distinct from the articular, and there is no sesamoid articular.

Hyopalatine Series (text-fig. 138, p. 481).—In relation with the great size of the mouth the quadrate articulation is thrown far back, and both quadrate and hyomandibular bones are backwardly rotated. The head by which the hyomandibular articulates with the cranium is small and single (see p. 478). The symplectic is not in a direct line with the axis of the hyomandibular, but forms an angle of about 140 degrees with it. The metapterygoid is large, and the entopterygoid small. The ectopterygoid is nearly straight, and the palatine articulates with the prefrontal by two contiguous heads, which are right and left, not anterior and posterior. Teeth are borne on the edge of the palatine and the anterior part of the edge of the ectopterygoid.

Opercular Series (text-fig. 137, p. 479).—The opercular bone has a

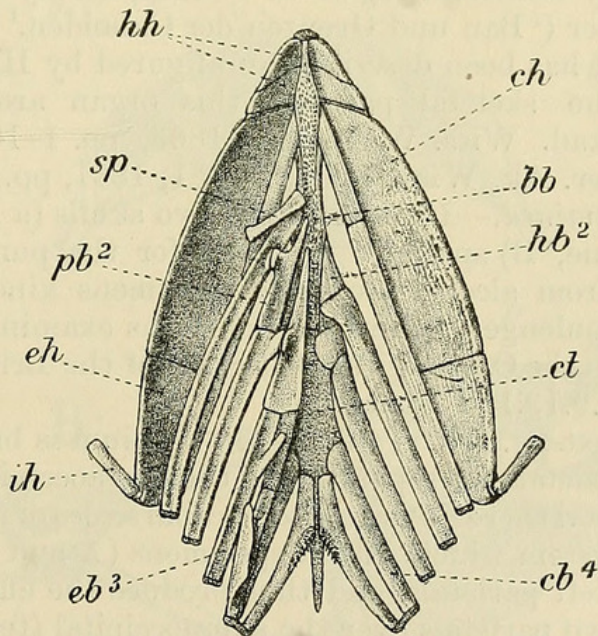
strongly marked backward slope; the opercular and subopercular bones are of average size, and take no share in that enlargement which is so marked in the bones of the mouth. There are eleven branchiostegal rays on each side. The first is attached at the front of the ceratohyal, the ninth at the junction of the ceratohyal and epihyal, and the remaining two on the epihyal. They are all curved rods except the last two, which are somewhat lamellate.

Text-fig. 138.



Coilia nasus, hyopalatine arch and mandible of left side, mesial aspect: *hm'*, head of hyomandibular articulating with the cranium. For explanation of other lettering see p. 493.

Text-fig. 139.



Coilia nasus, hyobranchial skeleton, dorsal view. The epibranchials and pharyngo-branchials of the right side are not shown. For explanation of lettering see p. 493.

Hyobranchial Series (text-fig. 139).—The interhyal is a long, rod-like bone. There are two hypohyals, the upper one small and situated antero-superiorly to the lower, which alone is in

contact with the front of the ceratohyal. The glossohyal is an ill-defined cartilage of small size. The second basibranchial is large in comparison with the first and third, but it is a hollow shell of bone, the interior of which is occupied by a fatty mass. The dentigerous membrane-bone that covers it overlaps the posterior three-fourths of the first basibranchial and the anterior third of the third basibranchial.

The second hypobranchials are fused with the sides of the second basibranchial, but the line of demarcation is obvious. The third hypobranchials are rather long, and slope forward and downward at the sides of the third basibranchial. The urohyal is long, and extends considerably behind the posterior end of the third basibranchial. The epibranchials are longer than usual in proportion to the ceratobranchials; the fourth is moderately expanded in a vertical direction.

The first pharyngobranchial is cartilaginous; and the spicular bone projects upward, backward, and outward, and is attached to the pro-otic bone at the point marked *s* in text-fig. 136 B, p. 478. The cartilaginous plate that represents the fourth and fifth basibranchials is continued back between the closely approximated anterior ends of the fifth ceratobranchials, and projects some distance behind as a free rod of cartilage.

CHANOS SALMONEUS.

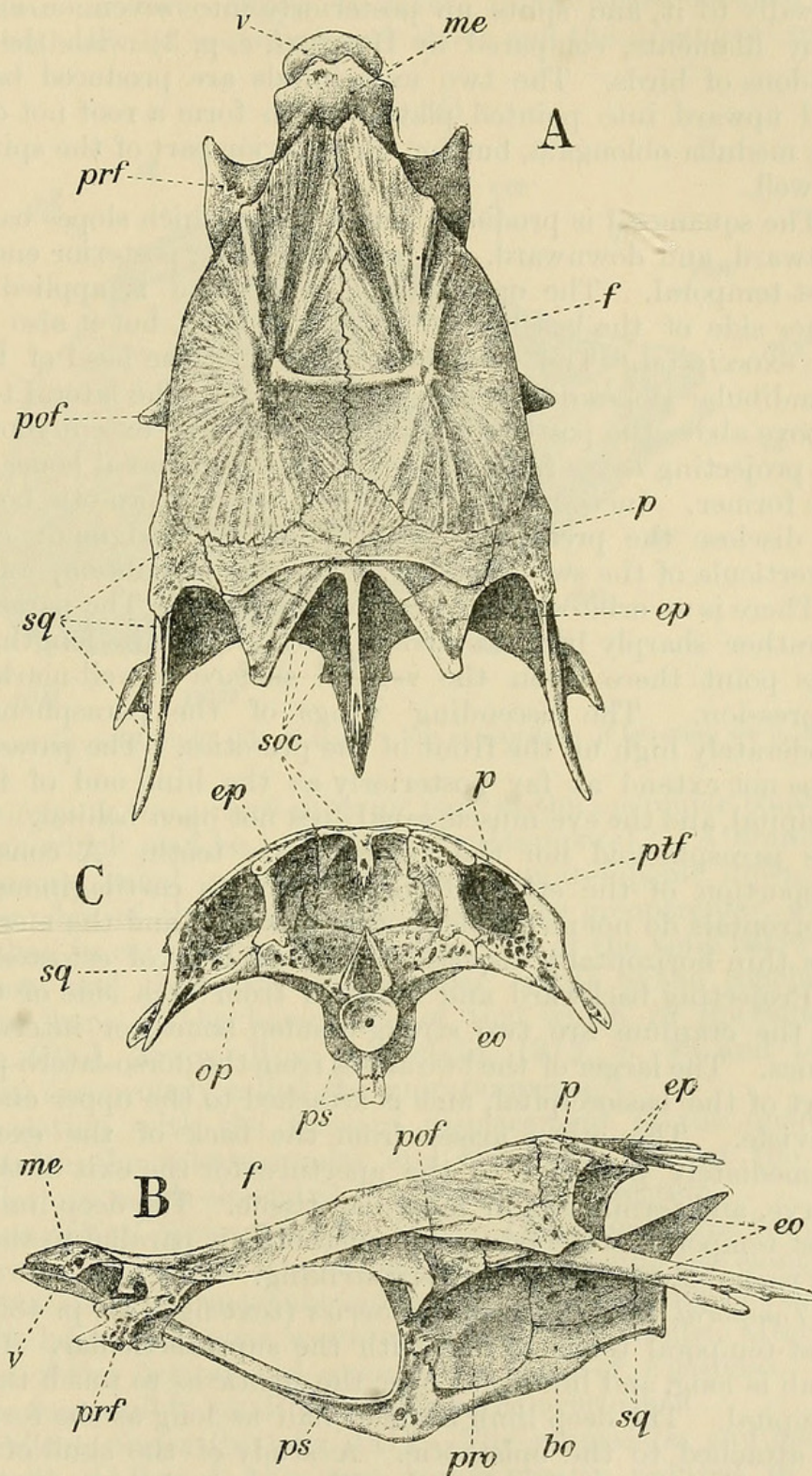
The accessory branchial organ of *Chanos*, briefly alluded to by Johannes Müller ('*Bau und Grenzen der Ganoiden*,' Berlin, 1846, pp. 74 and 75), has been described and figured by Hyrtl, but the relations of the skeletal parts to this organ are not shown (Denkschr. Akad. Wiss. Wien, xxi. 1863, pp. 1-10 and pl. 1; also Sitzungsber. Ak. Wiss. Wien, xliii. 1, 1861, pp. 155 & 156).

Material examined.—In addition to two skulls (a large one, A, and a small one, B) specially prepared for the purposes of this investigation from alcohol-preserved specimens kindly furnished by Mr. G. A. Boulenger, a third skull (C) was examined, belonging to a skeleton in the Osteological Collection of the British Museum (Brit. Mus. 98.9.13.1, Tongatabu).

Cranium (text-fig. 140, p. 483).—The cranium is broad and flattened. The parietals are separated by the supraoccipital, but above the supraoccipital there lie two sensory-canal scales of the transverse commissural system which in old specimens (A and C) fuse with the right and left parietals, and thus produce the effect of a false union of the two parietals over the supraoccipital (text-fig. 140 A, p. 483). The posterior temporal fossa is large and completely roofed in. Its inner wall is formed by the supraoccipital and epiotic, its floor and outer wall by the postfrontal and squamosal, and its roof by the frontal, parietal, squamosal, and epiotic. Its anterior end is blind, and lies over the middle part of the postfrontal bone. Hyrtl (*l. c.* p. 3) has pointed out that the great posterior temporal

vacuity is occupied by the upper longitudinal trunk-muscle, and contains nothing else.

Text-fig. 140.



Cranium of *Chanos salmoneus*.—A, dorsal view; B, left side; C, back view.
For explanation of lettering see p. 493.

Owing to the considerable extent to which the epiotic bones project posteriorly, and to the hollowness of the posterior surface

of the supraoccipital, there is a large depression at the back of the cranium between the two epiotics. This is not subdivided by a median crest of the supraoccipital, but a supraoccipital spine lies dorsally to it, and splits up posteriorly into seven or eight fine bony filaments, compared by Hyrtl (*l. c.* p. 3) with the ossified tendons of birds. The two exoccipitals are produced backward and upward into pointed plates, which form a roof not only for the medulla oblongata, but for the anterior part of the spinal cord as well.

The squamosal is produced into a spine which slopes backward, outward, and downward, and extends to the posterior end of the post-temporal. The opisthotic is small, and is applied to the inner side of the basal portion of this spine, but it also touches the exoccipital. The articular surface for the head of the hyomandibular slopes downward and forward. The lateral temporal groove above the postfrontal spine is to a large extent roofed over by projecting eaves from the frontal and squamosal bones, mainly the former. Incision into the squamosal and pro-otic bones fails to disclose the presence of bullæ for the lodgment of cæcal diverticula of the swim-bladder. There is no subtemporal fossa.

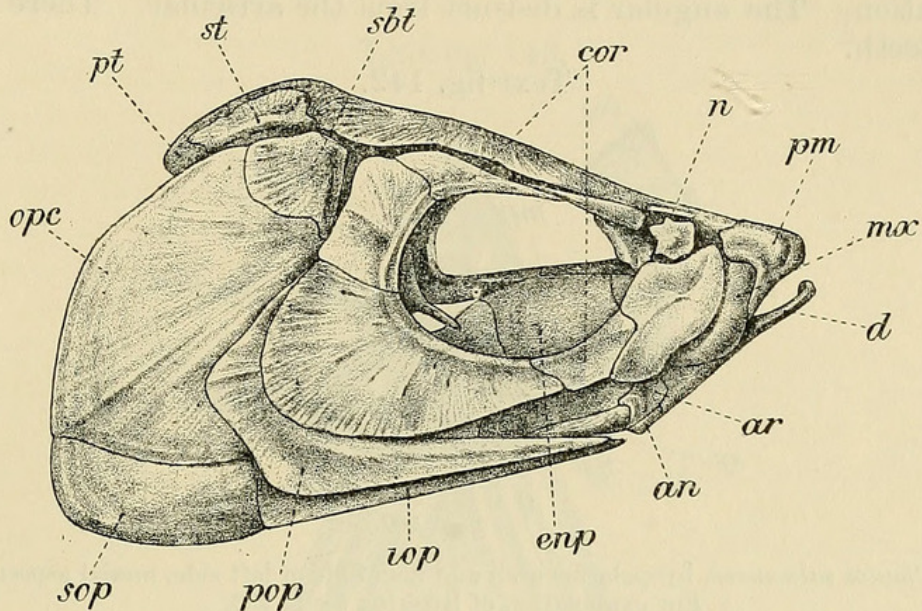
There is no orbitosphenoid nor basisphenoid. The parasphenoid is rather sharply bent at about the middle of its length, and at this point there is on the ventral surface a well-marked oval depression. The ascending wings of the parasphenoid rise moderately high up the front of the pro-otics. The parasphenoid does not extend as far posteriorly as the hind end of the basioccipital, and the eye-muscle canal does not open behind. Neither the parasphenoid nor the vomer bears teeth. A considerable proportion of the ethmoid region remains cartilaginous. The prefrontals do not meet one another mesially, and the mesethmoid is a thin horizontally disposed lamina of bone of ectosteal origin.

Projecting backward and outward from each side of the back of the cranium are two strong tendon-bones, or intermuscular bones. The larger of the two arises from the dorso-latero-posterior part of the basioccipital, and is attached to the upper end of the clavicle. The other arises from the back of the exoccipital, immediately posterior to the aperture for the exit of the vagus nerve, and terminates in muscular tissue. The deep limb of the post-temporal, attached to the opisthotic, is parallel to these, and its resemblance to them is very striking.

Temporal and Preopercular Series (text-fig. 141, p. 485).—The post-temporal tends to fuse with the supraclavicular. Its upper limb is long, and lies so far over the epiotic as to touch the supraoccipital. The deep limb is about half as long as the former and is attached to the opisthotic. A study of the skull of *Chanos* leaves little room for doubting that the opisthotic limb of the post-temporal belonged primarily to the same category as the tendon-bones that project back from the exoccipital, but has now become united by its posterior end with the post-temporal bone (see preceding paragraph).

The third limb of the post-temporal is wanting, since the supratemporal overlaps the body of the post-temporal. The supratemporal is a flat scale of bone, with the usual triradiate sensory canal near its lower edge. It covers in the space between the epiotic limb of the post-temporal above and the squamosal spine below.

Text-fig. 141.



Chanos salmoneus, right side of skull. For explanation of lettering see p. 493.

Overlapping the antero-superior part of the opercular bone is a flat bone which may be termed the "subtemporal." A branch of the sensory canal passes from the supratemporal down the anterior edge of the bone on its way to the preopercular, which fact, taken in conjunction with the position of the bone below the squamosal and above the preopercular, points to the conclusion that the bone is the homologue of that which, in the Salmon, Parker (Phil. Trans. Roy. Soc. clxiii. 1873, p. 99 and pl. 6. fig. 1, *st*) erroneously called the supratemporal.

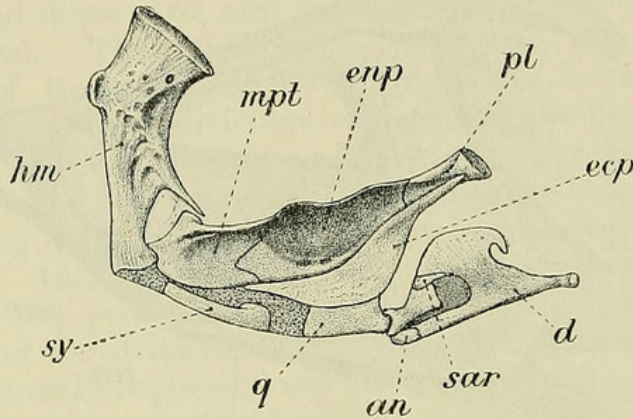
In relation with the forward displacement of the quadrate articulation, the interopercular and the lower limb of the preopercular are much elongated in a horizontal direction.

Circumorbital Series (text-fig. 141).—There are eight bones of this series. The orbital ring is complete, there being two elongated supraorbitals which meet above the eye. The anterior of the two is in the large specimens examined (A and C) swollen after the manner of the frontal and some other bones of *Ephippus*. The nasal is remarkably small and liable to be overlooked.

Maxillary Series (text-fig. 141).—The premaxilla and maxilla are short and broad, the gape being greatly reduced in size. Except when the mouth is opened to an unnaturally wide extent, the premaxilla alone bounds the gape above. Both the premaxilla and maxilla are thin, curved scales with sharp lower edges, devoid of teeth. There is no surmaxilla.

Mandibular Series (text-figs. 141 and 142).—The mandible is of remarkable shape, since the anterior part is quite thin, having the form of a curved rod, whereas the coronoid process is broad and stands high. The coronoid process is formed entirely by the dentary, there being no ascending process of the articular. A sesamoid articular is present; it lies above the anterior part of the endosteal articular, and is slightly movable in a wet preparation. The angular is distinct from the articular. There are no teeth.

Text-fig. 142.



Chanos salmoneus, hyopalatine arch and mandible of left side, mesial aspect.
For explanation of lettering see p. 493.

Hyopalatine Series (text-fig. 142).—The hyomandibular articulates with the cranium by a single broad head, the upper edge of which, instead of being horizontal, slopes downward and forward. In relation with the reduction in the size of the mouth, the quadrate has been drawn so far forward as to have parted from the symplectic and metapterygoid entirely, and it is attached to the ectopterygoid in such a way that a fair proportion of this bone lies behind it. The hyomandibular appears to be but little affected, and its axis is nearly vertical. There is an angle of about 110 degrees between the axes of the symplectic and hyomandibular. No teeth occur on the palatine and pterygoid bones.

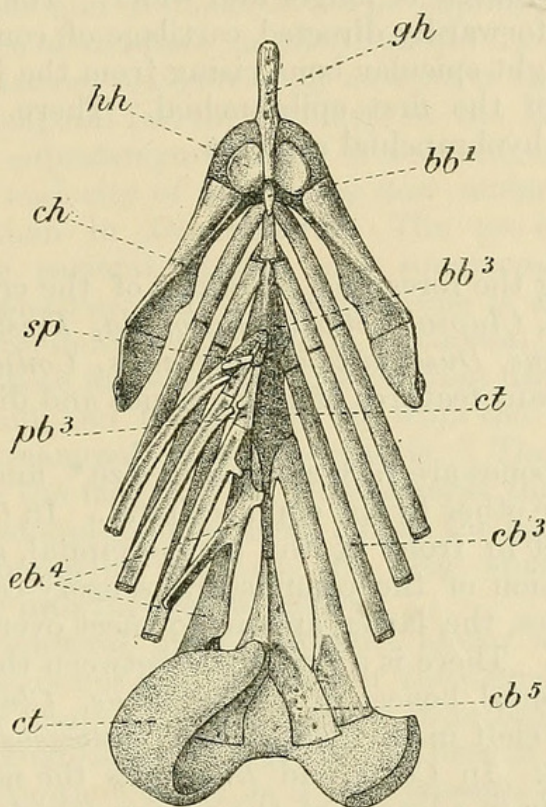
Opercular Series (text-fig. 141, p. 485).—The opercular and subopercular bones are of average proportions; the ascending process of the subopercular which rises along the front edge of the opercular is high and slender. There are only four branchiostegal rays on each side. They are long, and rather broad and lamellate. Two are attached to the outer face of the posterior part of the ceratohyal, and two on the outer face of the epihyal. On examining the skull of *Chanos*, one cannot fail to be impressed by the regular manner in which the branchiostegal rays grade off into the opercular and subopercular bones, whereas the preopercular and interopercular fail to fit into the series.

Hyobranchial Series (text-fig. 143, p. 487).—The most striking features of the hyobranchial skeleton are the smallness of the hyoid,

the great size of the urohyal, and the enlargement of the hinder parts for the support of the wall of the epibranchial organ. The structure of this organ has been described by Hyrtl (*l. c.* p. 4).

The lower hypohyal is considerably larger than the upper. The hind end of the glossohyal overlaps the front of the first basibranchial, and a thin flake of bone projects from the back of the first basibranchial over the front of the second. A similar

Text-fig. 143.



Chanos salmoneus, hyobranchial skeleton, dorsal view. The epibranchials and pharyngobranchials of the right side are not shown. For explanation of lettering see p. 493.

flake extends from the second basibranchial over the front part of the third. The anterior half of the glossohyal is cartilaginous, but is covered by a membrane-bone which is continued back over the endosteal glossohyal. The third basibranchial is larger than the first and second put together—as a rule the second basibranchial is the largest of the three. The third hypobranchials are fused with the sides of the third basibranchial, but the boundary line between them is not obliterated.

There is a symphysis of considerable length between the two fifth ceratobranchials, and from the front of this symphysis there passes forward a bar of cartilage which, in front of the anterior ends of the fourth ceratobranchials, enlarges into a roughly hexagonal plate. The separation of the anterior ends of the fourth and fifth ceratobranchials is noteworthy. Behind the symphysis of the fifth ceratobranchials is a horizontal tract of cartilage,

continuous with the pair of great cartilages which curve upward from the suturally united posterior ends of the fourth and fifth ceratobranchials. The upper ends of these great cartilages meet in the middle line above, but do not fuse; from the anterior edge of each there stretches forward an extensive tract of thin, but tough membrane, which fills in the angle between the body of the fourth epibranchial and the remarkably long process of the same which slopes upward and backward from near its anterior end.

The first three epibranchials are of approximately the same length, but the fourth is longer and wider. The first pharyngo-branchial is a forwardly directed cartilage of conical shape, and there is an upright spicular bone rising from the junction of this with the front of the first epibranchial. There are no teeth on any part of the hyobranchial skeleton.

SUMMARY.

On comparing the foregoing accounts of the cranial osteology of *Chirocentrus*, *Clupea*, *Pellona*, *Pellonula*, *Pristigaster*, *Hyperlophus*, *Chatoëssus*, *Dussumieria*, *Engraulis*, *Coilia*, and *Chanos*, the most important features of resemblance and difference appear to be as follows.

The parietal bones are rather small in size*, and are separated the one from the other by the supraoccipital. In *Coilia*, however, they nearly meet in front of the supraoccipital, and in *Chanos*, owing to the fusion of the commissural sensory-canal bones with the parietal bones, the latter appear to meet over the top of the supraoccipital†. There is a fontanelle between the anterior ends of the two frontal bones in *Chirocentrus*, *Clupea*, *Pellonula*, *Pellona* (a mere cleft in this genus), and *Chatoëssus*, but not in the other six genera. In *Coilia* and *Engraulis* the mesethmoid projects considerably in advance of the vomer, which is not the case in the other genera.

Of the genera under consideration, the only one in which the posterior temporal groove is roofed over is *Chanos*. The temporal foramen appears to be a special feature of the Clupeoid skull. It is an aperture, usually oval in shape, with the long axis horizontal, bounded by the frontal and parietal bones. In no instance have I found the postfrontal bone forming part of the boundary, although Boulenger regards this as the normal condition‡. The only departure from the general rule that has come within my knowledge is in the case of *Engraulis*, in which a small portion of the squamosal may come between the parietal and the frontal in the

* Small is, of course, but a relative term, and opinions may differ as to the employment of the word. "Très petits," the expression used by Boulenger (Poissons du Bassin du Congo, 1901, p. 123), appears to me to convey an exaggerated idea of the smallness of the parietal bones. I leave the figures that illustrate this paper to speak for themselves.

† Cope, it is worth noting, included the Lutodiridæ (*i. e.* Chanidæ) under the heading "Parietals united" (Trans. Amer. Phil. Soc. n. s. xiv. 1871, p. 455).

‡ Poiss. Bass. Congo, 1901, p. 123. "Un grand trou de chaque côté du crâne bordé par le frontal, le postfrontal, et le pariétal."

lower edge of the foramen, but does not invariably do so. The temporal foramen is reduced to a pin-point depression in *Coilia*, and is wanting entirely in *Chanos*.

The pre-epiotic fossa, another Clupeoid feature, is a depression at the side of the cranium, bounded by the epiotic, squamosal, and parietal bones. It is wanting in *Chanos*; in *Coilia* it is entirely obliterated, and in *Pristigaster* and *Hyperlophus* largely filled up by the prominent squamosal bulla. The pre-epiotic fossa is probably homologous with the "lateral cranial foramen" of the Mormyroid fishes and *Notopterus*. The supratemporal bone lies over the aperture of the fossa in the Clupeoid fishes, but being a reduced bone it serves less obviously as a cover for the fossa than does the supratemporal for the foramen in the Mormyridæ. In *Notopterus* the supratemporal bone is reduced in size quite as much as in the majority of the fishes now under consideration, and more so than in *Dussumieria*. The pre-epiotic fossa is bounded by the parietal, epiotic, and squamosal, whereas the foramen of *Notopterus* and the Mormyridæ is set a little lower down, and is surrounded by the epiotic, squamosal, and exoccipital, the parietal in these fishes occupying a position nearer the median plane of the head, and being shut off from the foramen by the union of the squamosal with the epiotic. The suggestion is strengthened by the fact that in *Dussumieria* the bottom of the fossa is unossified and membranous. If in the preparation of the skull the membrane be removed, the fossa appears as a large foramen leading into the cranial cavity.

The lateral temporal groove, situated above and behind the postfrontal bone, is not well marked in the Clupeoid fishes, with the exception of *Chanos*; in most cases it is broad and shallow, and is barely recognisable as a groove. There is no subtemporal fossa. The opisthotic bone is as a rule present, but small; it is wanting in *Engraulis* and *Coilia*.

The bullæ in the pro-otic and squamosal bones for the lodgment of cæcal diverticula of the swim-bladder are remarkably constant. Both, however, are wanting in *Chanos*, and the squamosal bulla is not present in *Clupea sprattus*, although it occurs in the other species of *Clupea* examined. The auditory fenestra, bounded by the pro-otic, exoccipital, and basioccipital bones, is also a distinctive feature of the Clupeoids, although it occurs also in *Hyodon*, in which it is bounded by the same three bones. It is wanting in *Chanos* and *Coilia*. The orbitosphenoid and basisphenoid bones are variable in size; both are wanting in *Chanos*. In *Clupea*, *Hyperlophus*, *Chatoëssus*, and *Dussumieria* the orbitosphenoid meets the prefrontal bones.

The eye-muscle canal opens behind in all but *Chanos* and *Coilia*, and except in these two genera and *Chatoëssus* the parasphenoid is produced into a pair of posteriorly directed vertical laminae of bone. In *Chatoëssus* the vertical laminae are present at the sides of the posterior opening of the eye-muscle canal, but they are not produced backward into freely projecting wings.

Not one of the eleven genera under consideration has parasphenoidal teeth, and only *Coilia*, *Dussumieria*, *Clupea harengus*, and *Clupea sprattus* have teeth on the vomer.

The post-temporal bone has an epiotic limb in all, and a deep or opisthotic limb in all but *Coilia*. In *Chatoëssus* the union between the post-temporal bone and the epiotic is more of the nature of a synovial articulation than a ligamentous connection. The supratemporal bone is of the same character in all, and in all but *Coilia* the sensory canal that it carries is triradiate. A subtemporal or supraopercular bone is present in *Chanos*.

The nasal bone is small and loosely embedded in the skin, and there are from five to eight bones disposed around the eye. In *Chatoëssus* and *Chanos* the premaxilla bounds the upper border of the mouth; in the other nine genera the gape is bounded above by both premaxilla and maxilla, although in *Pristigaster* and *Hyperlophus* the maxilla takes but a small share. In *Chirocentrus*, *Clupea*, *Pellona*, *Pristigaster*, *Dussumieria*, *Engraulis*, and *Coilia* both maxilla and premaxilla bear teeth, although in *Pellona* the teeth are vestigial: in *Pellonula* the premaxilla bears teeth, but not the maxilla; in *Chanos*, *Chatoëssus*, and *Hyperlophus* both premaxilla and maxilla are edentulous. The premaxilla is firmly united to the maxilla by fibrous tissue in *Chirocentrus*. Two surmaxillæ are present on each side of the head in all but *Hyperlophus*, *Chatoëssus*, and *Chanos*; *Hyperlophus* and *Chatoëssus* have one, and *Chanos* none.

The angular is a distinct bone in all but *Engraulis* and *Coilia*. The endosteal part of the articular can be recognised, but in no case is it separate from the ectosteal part. A small sesamoid articular is found in *Chirocentrus*, *Clupea finta*, and *Chanos*.

The hyomandibular articulates with the cranium by two heads in *Clupea finta*, *Hyperlophus*, *Chatoëssus*, *Dussumieria*, and *Engraulis*, and by a single head in *Chirocentrus*, *Clupea harengus*, *Pellona*, *Coilia*, and *Chanos*. In *Coilia* the single head present is probably equivalent to the anterior of the two heads found in *Engraulis*. In *Chanos* alone of the genera under consideration is the quadrate separated from the symplectic and metapterygoid. Teeth are borne by the palatine bone in *Chirocentrus* (4 or 5 minute teeth), *Clupea sprattus* (a row of teeth), *Clupea harengus* (2 or 3 minute teeth), *Pellona*, *Pellonula*, *Pristigaster*, *Dussumieria*, *Engraulis*, and *Coilia*; the palatine is edentulous in *Chanos*, *Chatoëssus*, *Hyperlophus*, and *Clupea finta*. The ectopterygoid is toothed in *Pellona*, *Dussumieria*, *Engraulis*, and *Coilia*, but not in *Chirocentrus*, *Clupea*, *Pellonula*, *Pristigaster*, *Hyperlophus*, *Chatoëssus*, and *Chanos*; the entopterygoid is toothed in *Clupea sprattus* (a few teeth), *Pellona*, *Pellonula*, *Pristigaster*, *Dussumieria*, and *Engraulis*, but not in the other forms examined.

The branchiostegal rays are most numerous in *Dussumieria* (13), *Engraulis* (11), *Coilia* (11), and are fewest in *Chanos* (4). *Chirocentrus* has 8, *Clupea* 7 or 8, *Chatoëssus* 6, *Hyperlophus* 5. The interhyal is bony in all, except, perhaps, in *Chanos*. In all

of the forms studied there are two hypohyals on each side, and the lower of the two is larger than the upper. The first pharyngo-branchial is ossified in *Chirocentrus*, but remains cartilaginous in the other genera; the ossified ligament known as the spicular bone is present in all except *Chirocentrus*. In *Engraulis* and *Coilia* the second hypobranchials are fused with the sides of the second basibranchial, and in *Chanos* the third hypobranchials are fused with the sides of the third basibranchial, but in none of the three cases are the sutures obliterated.

COMMENTS ON THE SKULL OF THE CLUPEOID FISHES.

Of the eleven genera the skulls of which have been described in the previous pages the greatest interest centres around *Chanos* and *Chirocentrus*. As regards the others, the craniological characters are such as would justify the placing of *Engraulis* and *Coilia* in one family, the Engraulidæ, and *Clupea*, *Pellona*, *Pellonula*, *Pristigaster*, *Hyperlophus*, *Chatoëssus*, and *Dussumieria* in another, the Clupeidæ.

Both *Engraulis* and *Coilia* have a large gape, a backwardly thrust quadrate bone, and a large and prominent mesethmoid. The skull of *Coilia* differs from that of *Engraulis* in several respects, but these are all of such a nature as might be explained by high specialisation; such characters, for instance, are the reduction of the temporal foramen, the obliteration of the pre-epiotic fossa, the absence of the auditory fenestra, the absence of paired posterior wings of the parasphenoid and the closure of the eye-muscle canal, the absence of the opisthotic limb of the post-temporal, and the loss of the posterior of the two heads by which the hyomandibular articulates with the cranium. The paradoxical extension of the maxilla behind the mandibular articulation is foreshadowed in some species of *Engraulis*, e. g. *E. mystax* and *E. setirostris*.

The skull of *Chatoëssus* conforms with the Clupeoid type, in spite of certain aberrant features, such as the absence of projecting wings from the back of the parasphenoid, the intimate articulation of the epiotic limb of the post-temporal with the cranium, the small size of the mouth, the bounding of the mouth above by the premaxilla alone, the absence of teeth, and the loss of one of the surmaxillæ. The characters of the skull do not warrant the separation of *Chatoëssus* from the Clupeidæ to constitute a distinct family, although possibly on other grounds the action of Gill (Smithsonian Miscell. Coll. No. 247, 1872, p. 17) and Jordan and Gilbert (Bull. U.S. Nat. Mus. No. 16, 1882, pp. 262-274) may prove to be justifiable.

Chirocentrus agrees so closely in the structure of its skull with the Clupeidæ, that appeal must be made to other organs of the body for evidence to support the views of those who would make of it a distinct family, the Chirocentridæ (e. g., Valenciennes, Hist. Nat. Poiss. xix. 1846, pp. 150-168; Kner, Reise der

Fregatte Novara, Zool. i. 1869, Fische; Cope, Trans. Amer. Phil. Soc. n. s. xiv. 1871, p. 455; Gill, *l. c.* p. 17; Smith Woodward, Brit. Mus. Cat. Foss. Fishes, iv. 1901). Their justification appears to lie mainly in the fact that *Chirocentrus* possesses in its intestine a spiral valve which is not present in *Clupea* and its allies (Valenciennes, *l. c.* p. 160 and pl. 565), in the absence of cæca (*ibid.* p. 162), and in the presence of a pseudobranch in *Chirocentrus* and its absence from most Clupeoids (Müller, Abhandl. Akad. Wiss. Berlin, 1844 (1846), p. 191). The only craniological differences worth mentioning are the considerable depth of the posterior temporal groove of *Chirocentrus*, the small size of the orbitosphenoid, the firm union between the premaxilla and maxilla (Valenciennes, *l. c.* pp. 150, 152, and 154), the more or less complete concealment of the symplectic (Boulenger, Ann. Mag. Nat. Hist. (7) xiii. 1904, p. 164), the bony nature of the first pharyngobranchial, and the absence of a spicular bone. The value of the evidence of the last two items is certainly not great, for except when (as in *Elops*) both ossified first pharyngobranchial and spicular bones are present, it is not possible to deny absolutely that what appears to be the first pharyngobranchial bone is not the spicular bone which has become shortened and thickened and more forwardly directed than usual.

The resemblances existing between the skeleton of *Chirocentrus* and that of such extinct forms as *Portheus*, *Ichthyodectes*, and *Saurodon*, which attained their maximum development in Cretaceous times, suggest that the former genus is a survival of an ancient type (see Smith Woodward, *l. c.* p. vii); but the teeth of the existing *Chirocentrus* are not lodged in distinct sockets as are those of the Saurodontidæ.

As regards *Chanos*, the evidence of the skull favours the view of separating the genus from the Clupeidæ, and of according it a family rank. *Chanos* has experienced a variety of treatment at the hands of taxonomists. It was first regarded as a species of *Mugil* (Forskål, Desc. Anim. 1775, p. 74; Gmelin, Syst. Nat. Linn. i. 3, 1788, p. 1398), and later as a species of *Leuciscus* (Gray and Richardson, Dieffenbach's 'Travels in New Zealand,' 1843, ii. p. 218). Valenciennes (Hist. Nat. Poiss. xix. 1846) placed it with *Gonorhynchus* among the "Malacoptérygiens intermédiaires entre les Brochets et les Clupes." Günther (Brit. Mus. Cat. Fishes, vii. 1868) placed it in a group "Chanina" of the family Clupeidæ, and Kner (Reise der Fregatte Novara, Zool. i. 1869, Fische), Cope (Trans. Amer. Phil. Soc. n. s. xiv. 1871, p. 455), and Gill (Smithson. Miscell. Coll. No. 247, 1872, p. 17) separated it from the Clupeidæ and placed it in a family of its own.

The inclusion of *Chanos* within the family Albulidæ, a step which has commended itself to so experienced an ichthyologist as Smith Woodward (Brit. Mus. Cat. Foss. Fishes, iv. pp. 60 and 64), is justified in so far as the posterior temporal fossæ are roofed over, which is not the case in any other Clupeoid fishes, and in the presence of a well-marked lateral temporal groove, partially roofed

over; also in that the bullæ in the squamosal and pro-otic bones present in other Clupeoid fishes for the lodgment of cæcal diverticula of the swim-bladder are wanting, as also are the auditory fenestra, the pre-epiotic fossa, and the temporal foramen also in the fact that the parasphenoid is not produced into a pair of posteriorly directed wings. On the other hand, such features as the reduction in the size of the mouth are as likely to be due to convergence as to genetic affinity.

The absence from the skull of *Chanos* of the orbitosphenoid and basisphenoid bones is a mark of degradation, and supports neither the hypothesis of a natural affinity between *Chanos* and the Albulidæ, nor that which would associate *Chanos* with the Clupeidæ; and the same may be said of the absence of teeth, the reduction in the number of branchiostegal rays, and the absence of surmaxillæ. The closure of the posterior outlet of the eye-muscle canal is a mark of specialisation, and in this respect also *Chanos* differs from both the Albulidæ and the Clupeidæ (except *Coilia*). The absence of a subtemporal fossa, which is present in the Elopidae and Albulidæ, but absent from the Clupeoid fishes, is an argument against Woodward's view; and again, the parietals meet one another in *Albula*, whereas in *Chanos* they are in reality separated by the supraoccipital, although a secondary union may be brought about by means of the commissural sensory-canal bones which fuse with the parietals.

Abbreviations employed in the Text-figures.

<i>af</i> , auditory fenestra.	<i>mx</i> , maxilla.
<i>al</i> , alisphenoid.	<i>n</i> , nasal.
<i>an</i> , angular.	<i>op</i> , opisthotic.
<i>ar</i> , articular.	<i>opc</i> , opercular.
<i>bb</i> , dentigerous plate covering the basibranchials.	<i>or</i> , orbitosphenoid.
<i>bo</i> , basioccipital.	<i>p</i> , parietal.
<i>br</i> , branchiostegal rays.	<i>pb</i> , pharyngobranchial.
<i>bs</i> , basisphenoid.	<i>pef</i> , pre-epiotic fossa.
<i>cb</i> , ceratobranchial.	<i>pl</i> , palatine.
<i>ch</i> , ceratohyal.	<i>pm</i> , premaxilla.
<i>cor</i> , circumorbital bones.	<i>pof</i> , postfrontal.
<i>ct</i> , cartilage.	<i>pop</i> , preopercular.
<i>d</i> , dentary.	<i>prf</i> , prefrontal.
<i>eb</i> , epibranchial.	<i>pro</i> , pro-otic.
<i>eep</i> , ectopterygoid.	<i>ps</i> , parasphenoid.
<i>eh</i> , epihyal.	<i>pt</i> , post-temporal.
<i>enp</i> , entopterygoid.	<i>ptf</i> , posterior temporal fossa.
<i>eo</i> , exoccipital.	<i>q</i> , quadrate.
<i>ep</i> , epiotic.	<i>sar</i> , sesamoid articular.
<i>f</i> , frontal.	<i>sm</i> , surmaxilla.
<i>gh</i> , glossohyal.	<i>soc</i> , supraoccipital.
<i>hb</i> , hypobranchial.	<i>sop</i> , subopercular.
<i>hh</i> , hypohyal.	<i>sp</i> , spicular bone.
<i>hm</i> , hyomandibular.	<i>sq</i> , squamosal.
<i>ih</i> , interhyal.	<i>st</i> , supratemporal.
<i>iop</i> , interopercular.	<i>sy</i> , symplectic.
<i>me</i> , mesethmoid.	<i>tf</i> , temporal foramen.
<i>mpt</i> , metapterygoid.	<i>v</i> , vomer.



Ridewood, W G. 1904. "On the Cranial Osteology of the Clupeoid Fishes."
Proceedings of the Zoological Society of London 1904, 448–493.
<https://doi.org/10.1111/j.1469-7998.1905.tb08349.x>.

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