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The resemblance in origins in these examples might suggest homology with the holocephalan muscles.

On the other hand, the levator maxillae superioris lies, always, caudad or superficial to the R.maxillaris V., whilst these holocephalan muscles lie rostrad and deep to that nerve. The development of the levator maxillae superioris from the upper portion of the mandibular muscle plate appears to render it quite impossible that the muscle should acquire a situation rostrad and deep to this nerve. For the present, the most that can be said is that these muscles are derived from the same part of the muscle plate as the pterygoideus.

The pterygoideus. That this is the homologue of the pterygoideus of the plagiostomes seems to be quite satisfactorily proven by its relation to the mandibular and maxillary rami of the Vth nerve, and by a comparison with the pterygoideus muscle in *Chiloscyllium*.

The quadrato-mandibularis muscle lying behind the pterygoideus, with the nerve between them, is very much reduced and would appear to represent the pars posterior only of the plagiostome muscle.

It will be noted that in these last two muscles the Holocephali again present resemblances rather to the Amphibia and Teleostomi than to the rest of the Elasmobranchii.

From the foregoing review it is apparent that in their epiarcualia obliqui, epibranchial spinal, coraco-branchialis and hypobranchial spinal muscles the Holocephali are essentially elasmobranchial in character. In the form of the branchial levators, the levator operculi and the interhyoideus they resemble the teleosts. In the form of the interbranchial muscles, the adductors of the jaws and the depressor mandibulae they resemble the amphibians.

THE MUSCLES OF THE BONY FISHES.

The whole of the teleostomes are, in their cephalic musculature, essentially similar. There are differences between individual members of the Teleostei as great as those between them, as a group, and *Polypterus* and/or *Lepidopterus* and *Amia* ; nor, with the possible exception of the branchio-mandibularis muscle, are such differences of a more significant character.

TELEOSTOMES.

		Branchial Segments.	Hyoid Segment.	Mandibular Segment.
Superficial constrictors	Dorsal ..	Absent	Lev.operc.hyohyoideus	Absent
	Ventral	Absent	Hyohyoideus Protracto	r hyoidei Submentalis Interm.post.
Deep Constrictors	Dorsal ..	Absent	Absent	Dil.operc.
	Ventral ..	*Subarcualis transv.	Absent	Absent
Levators		Lev.arc.branch	Add.arc.pal., Add.hyom., Add.operc.	Lev.arc.pal.
Epibranchial Spinal Muscles ..		Retr.dors.arc.br.	Absent	Absent
Adductor Muscles	Dorsal ..	Epiarc.obliqui, transversi and recti	Absent	Pterygoideus
	Middle ..	Add.arc.br.	Absent	Temporomassetericus
	Ventral ..	*Subarcualia obl.	Absent	Absent
Ventral Interarcual Muscles ..		*Subarcualia recti	Absent	Absent
Depressors		Claviculo-branch.	Absent	Absent
Hypobranchial Spinal Muscles		Claviculo-hyoideus	Genio-hyoideus	Absent

* These muscles are derivatives of, or substitutions for, the interbranchialis muscles of the Plagiostomes. They develop from the deep portion of the primordial muscle plate.

Material.—One specimen of *Polypterus* (*senegalus* ?).* Several heads of *Amia* and of *Lepidosteus osseus* and *platystomus*. Among modern teleosts I have dissected *Platycephalus fuscus* Cuv. and Val., *Mugil cephalus* Linné, *Girella tricuspidata* Quoy and Gai., and *Anguilla reinhardti* Stdr. Of these four species I have had many specimens, the four fish being very common. In addition I have had one or more specimens of the following, and all have been more or less completely dissected and studied : *Epibulus insidiator* Pallas, *Drepanichthys punctatus* Linné, *Zanclistius elevatus* Ramsay and Ogilby, *Cantherines ayraudi* Q. and G., *Gonorhynchus greyi* Rich., *Fistularia petimba* Lacep., *Hemirhamphus intermedius* Cantor, *Balistapus aculeatus* Linné, *Tandanus tandanus* Mitchell, and *Cnidoglanis megastomus* Rich.

For most of this last group of species my thanks are tendered to the Trustees of the Australian Museum and to Mr. G. P. Whitley.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

There are neither superficial nor deep constrictor muscles present in the branchial segments of any of the teleostomes.

It is very doubtful whether the epibranchial spinal muscles of the elasmobranchs are developed in the bony fishes. Edgeworth (1911, p. 266) discusses the " Muscles Derived from Trunk Myotomes Passing to the Upper Ends of the Branchial Bars ". He confirms Furbringer's observations (1897) as to the origin of these muscles in the Elasmobranchs and their innervation by occipito-spinal nerves, and further asserts that the retractor arcuum branchialium dorsalis of Teleosts has similar origin in *Amia* and in *Lepidosteus*. In view of the fact that, for the purposes of the work quoted from, Edgeworth studied the development of the muscles of those two forms and also of *Salmo*, it would appear that this is the only spinal epibranchial muscle in the teleosts. In *Scyllium* these epibranchial muscles are developed from the first to the fourth spinal myotomes. In *Amia* the muscle is developed from the sixth to the thirteenth, and in *Lepidosteus* from the third to the ninth trunk myotomes (vide Edgeworth), therefore, though of similar origin, it is doubtful whether it is strictly homologous with the spinal epibranchial muscles of the Elasmobranchii.

The branchial arches of the Teleosts are, when compared with those of the Elasmobranchs, crowded together under the cranium and they have become extensively fused dorsally. We have seen this crowding initiated in the Holocephali and have observed it to be accompanied by a suppression of the superficial constrictors, a marked reduction in the size of the deep constrictors, and a reduction in the number of the branchial levators. In the Teleosts the crowding is more pronounced, and is accompanied by a suppression of the deep constrictors as well as of the superficial ; the levators, on the other hand, are not so reduced in number, whilst the other branchial epibranchial muscles present not only greater development, but also an increase in number and in diversity of form.

In the result we have, in addition to the levators, the following dorsal branchial muscles to describe : epiarcualia obliqui, epiarcualia transversi and epiarcualia recti.

Adductores arcuum branchialium are present and are quite similar to those of the Elasmobranchs.

There is also a striking increase in the number and variety of ventral branchial muscles. In addition to the depressors, and the coraco-branchialis, there are also subarcualia obliqui, subarcualia transversi and subarcualia recti.

Edgeworth (1911) reserves the term " hypobranchial cranial " for the coraco-branchialis and its homologue the pharyngo-clavicularis. He states that, in the Teleostomi, in branchial segments where these muscles are not formed there is a downward and inward growth of the ventral ends of the branchial myotomes to form the lower portions of the obliqui ventrales (subarcuales obliqui). He further states that the portions of the branchial myotomes next above the " anlagen " of the coraco-branchialis form the upper portions of the subarcuales obliqui in teleostoman embryos, and that these may or may not unite with the lower portions. In a later work (1928) describing the development of some of the cranial muscles of Ganoid Fishes, including *Acipenser*, he demonstrates that from the ventral end of a branchial muscle plate there may

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*** This was a young specimen 50 mm. in length, which I received from Prof. Graham Kerr, to whom my grateful thanks are tendered. The specimen was divided in halves along the mid-sagittal plane. Both halves were stained with carmine and picric acid ; one was dissected under a Greenough binocular dissecting microscope, the other was cut into serial sections parallel to the plane of division. For the sectioning of the specimen and its mounting I have to thank Prof. C. W. Stump.**

develop any one of the three forms of ventral branchial muscle met with in the Teleosts, and further, that an originally single transversus ventralis (subarcualis transversus) may split, in later embryonic stages, into a subarcualis transversus and subarcualis obliquus, and, finally, that the oblique muscle "may be formed either from a fully developed transversus, i.e., from one which meets its fellow in the midline . . . or from an incomplete one, i.e., from one which passes inwards towards but does not actually join its fellow."

It will be remembered that the deep branchial constrictor (interbranchial muscle) of the Elasmobranchs is developed from that portion of the branchial muscle plate which lies between the "anlage" of the coraco-branchialis below and the adductor arcuum branchialium and epiarcualis obliquus above. In short it is developed from the same portion of the plate as the intrinsic ventral branchial muscles are developed in the Teleosts.

These muscles, therefore, truly replace the interbranchial muscles of the Elasmobranchs, having with them a common origin, and to this extent they may be regarded as homologous.

The following description of the muscles is based largely on the dissections of *Platycephalus, Anguilla* and *Girella* supported by notes and comparisons on other forms where called for.

THE LEVATORES ARCUUM BRANCHIALIUM.

Of these there are, commonly, four developed, but the first two or three may divide longitudinally, giving rise to internal and external portions which, in the adult, are described as separate muscles.

Platycephalus.—There are five branchial levators present. Four of these arise close together, medial to and behind the cranio-hyomandibular articulation, from the ventral surface of the pterotic bone. Of these four, two are internal and two external levators, and corresponding relation one to the other is found at their origin. The two external are in line immediately next the hyomandibular face and the other two in line medial to them. The general direction of the four from their origin is mediad, caudad and slightly ventrad. The first internal levator is inserted onto the anterior margin of the os pharyngeum superior.* The second internal is inserted onto the same bone further back, medial to the articulation of the second infrapharyngobranchial. The first external levator is inserted onto the anterior surface of the first infrapharyngobranchial just above its attachment to the epibranchial. The second external levator is inserted into the tip of the fourth epibranchial and by a small slip of muscle and a fine tendon, forming an anterior head, into the third epibranchial cartilage as well. The fifth levator belongs to the external series. It arises, at some distance from the others, from the extreme postero-lateral corner of the pterotic bone and passes ventrad direct to its insertion onto the tip of the fourth epibranchial cartilage lateral to the insertion of the second levator.

Anguilla.—Here also there are five levatores arcuum branchialium. Of these, four may be described as external and one only as internal. The levator of the first arch arises from the periosteum of the suboperculum. The point of origin is far up near the dorso-posterior tip of the bone on its inner surface. From this origin the muscle passes caudad, and slightly ventrad and laterad, to be inserted on the dorso-medial edge of the first epibranchial just above its joint with the ceratobranchial. The second, third and fourth levators arise close together from the base of the skull medial to and in front of the hyomandibular joint. They are inserted into the second, third and fourth epibranchials, precisely as is the first. The fifth arises medial to and below the other three and passes back nearly parallel to the others but medial and ventral to them, to be inserted onto the capsule of the joint between the epi- and pharyngo-branchials of the third arch. This is apparently the only internal levator of the series.

Mugil, Tandanus and Cnidoglanis.—In these three also I find but five levators, and their origin and insertions are little different from those described in the preceding two genera.

Epibulus.—Here there are six levators inserted in line one behind the other along the outer edge of the dorsum of the branchial basket. Of these the anterior four arise together just behind and medial to the hyomandibular facet. They are inserted into the epibranchials of the first four arches just above the joints with the ceratobranchials. The posterior two external levators arise from the postero-lateral corner of the inferior surface of the skull just medial to the cranial attachment of a very strong cranio-scapular ligament. They pass ventrad and slightly laterad

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* The os pharyngeum superior in *Platycephalus* is formed by the fusion of the pharyngobranchials of the second, third and fourth arches, as far as one may judge by the adult conditions.

to be inserted onto the outer ends of the fourth and fifth epibranchials. The more posterior of these two is carried ventrad behind the fifth epibranchial by a fine tendon which is attached to a posteriorly and ventrally directed spur of the ceratobranchial of the same arch. There are also two internal levators. These arise in company with the anterior external levators and are inserted into the pharyngobranchials of the second and third arches.

Girella.—This genus was found to have the levators arranged exactly as described by Allis (1903) in his account of the anatomy of the head of *Scomber.*

The Ganoids.—The levators of the Ganoids have been described by Allis. Those of *Amia* are essentially similar to those of *Epibulus, Girella* and *Scomber.* The fifth external levator is inserted onto the fourth arch as in *Epibulus* and is also continued ventrad to an insertion onto the fifth ceratobranchial and, finally, as in *Scomber* and *Girella,* is further attached to the clavicle. There is no sixth external levator present. In *Polypterus* there are only five branchial levators. Of these the first is inserted into the junction of the first pharyngo- and epibranchials, the second and third into second and third pharyngobranchials and the fourth into the tip of the fourth ceratobranchial. The fifth is inserted into the clavicle.

Innervation.—These muscles are innervated by branches of the post-trematic rami IXth and Xth nerves.

DISCUSSION.

The levatores arcuum branchialium in the bony fishes are, in the various genera, variable in number, site of origin, and insertion. It may be said of them (1) that they vary in number from five to eight, (2) that they arise from the inferior surface of the skull in the neighbourhood of the hyomandibular facet, medial to the origin of the levator and adductor muscles of the operculum, (3) that commonly several arise close together in this situation, (4) that usually one or more arise further back at a little distance from the anterior group, (5) that the anterior one, two or three pairs are developed from single muscles, (6) that the internal levators are inserted into pharyngobranchials, or pharyngoepibranchial junctions, (7) that the external muscles are inserted into the epibranchials in proximity with the epi-ceratobranchial joint, (8) that the most posterior of these levators may be inserted into the clavicle and not into a branchial element.

Edgeworth (1911, pp. 239, 241, 291) regards this last as a reduced trapezius (see also Straus and Howell, 1936).

THE EPIBRANCHIAL SPINAL MUSCLES (RETRACTORES DORSALES ARCUUM BRANCHIALIUM).

Apparently there is never more than a single pair of these muscles developed in any of the bony fishes. In the great majority the muscles arise from the side of the first one or two vertebrae, in some forms reaching as far back as the third. Normally it is a flat ribbon-like muscle which passes forward from its origin nearly horizontally to an insertion onto the posterior margin of the branchial skeleton in front of the posterior transverse epiarcual muscle. The actual element on which the muscle is inserted is apparently determined to some extent by the degree of divergence of the dorsal branchial members from in front caudad. Where there is a more or less closed posterior angle between the posterior arches dorsally the insertion is onto the fourth or fifth epi- or pharyngobranchial, but where this angle is more open the insertion may be onto the third or even the second pharyngobranchial, in front of the anterior transverse muscle.

The width of the muscle varies greatly, and in some forms, e.g. *Girella,* the muscle is a relatively thin rounded cord-like strand. In most cases there is no fusion with any other muscle, but in *Amia* and in *Platycephalus* the muscle is broad and fuses anteriorly with the anterior transverse muscle and with its own antimere.

Anguilla is quite peculiar ; in this form the muscle is a quadrangular sheet of muscle fibres which arise from the fascia dorsalis immediately under cover of the anterior portion of the origin of the hyo-hyoideus and, curving ventrad in contact with the trunk muscles, is inserted into the tip of the first and along the median edge of the second pharyngobranchial, and by a fine membranous extension onto the third pharyngobranchial. This membranous extension arches over the internal levator and passes laterally to the branches of the vagus nerve and to the anterior tributaries of the dorsal aorta, and then curves slightly mediad below them to the insertion.

THE EPIARCUALIA OBLIQUI (OBLIQUE DORSALES) AND EPIARCUALIA RECTI (INTERARCUALES DORSALES).

Doubtless these are but forms or extensions of the one variety of intrinsic dorsal branchial muscle of the Elasmobranchs. The term " interarcual " has been discarded for the more explicit designations above. The " obliqui " are those muscles whose origin and insertion are both on elements of the same arch, whilst the " recti " are those whose origin on one and insertion on another arch would entitle them to the designation interarcual had not this term already been used to indicate both varieties.

The recti vary in number from one to three. In *Platycephalus* there is but one, which arises from the anterior and medial curved margin of the os pharyngeum superior. At its origin the muscle is relatively thick and flat, but becomes narrowed and nearly cylindrical as it passes caudad and laterad to be inserted into the dorsal end of the fourth ceratobranchial, just where that is attached to the third. In *Anguilla* there are two epiarcualia recti. The first is a very short little muscle which arises from the dorsal end of the fourth epibranchial and is inserted into the third pharyngobranchial. The second is equally small and partly fused with the second obliquus. It arises from the fifth ceratobranchial and is inserted in front of the second obliquus onto the os pharyngeum superior. Allis, who (1903) designates them interarcuales dorsales, describes three in *Scomber*. In *Amia* Allis (1897) describes two obliqui dorsales which pass from an element of one arch to an insertion on another arch, and would therefore fall within the present group.

The epiarcualia obliqui are more variable in number. In *Platycephalus*, as in *Amia*, there are no epibranchial muscles which arise from and are inserted onto elements of the same arch. In *Anguilla* there are two of these muscles. The first arises from the epibranchial and is inserted into the pharyngobranchial of the third arch, the second arises from the epibranchial of the fifth arch and is inserted into the os pharyngeum superior. In *Scomber*, Allis describes three epiarcualia obliqui.

In *Lepidosteus* there are neither epiarcualia obliqui nor recti.

EPIARCUALIA TRANSVERSI.

There are apparently always two of these muscles present in the Teleostome, excepting only *Lepidosteus* in which neither of the two is present.

In *Platycephalus* the anterior transverse epiarcual muscle is a thin sheet of fibres which takes origin on each side from the first and second infrapharyngobranchial and is inserted into a median aponeurosis. The posterior margin of the muscle lies dorsally to the origin of the epiarcual rectus. The posterior transverse arises from the fourth epibranchial and posterior edge of the os pharyngeum superior and, passing horizontally mediad, becomes continuous with its antimere. The retractor dorsalis arcuum branchialium passes forward to its insertion in contact with the ventral surface of this muscle, separating it very completely from the sphincter oesophagi.

In *Anguilla* the anterior transverse muscle lies between the two third arches. The posterior transverse is intimately fused with the sphincter oesophagi.

In *Scomber*, Allis describes both muscles.

In *Amia* both muscles are present.

Unfortunately we have little exact knowledge about the development of the dorsal branchial muscles. The most important contributions known to me are those of Edgeworth. It would appear that they are all developed from that portion of the branchial muscle plate which, in the Elasmobranchs, gives rise to the epiarcualia obliqui only, and that two or more of these teleostoman forms of branchial epibranchial muscles may be developed from a single primordium. Further, it appears that the muscle or muscles developed from this primordium may grow forward or backward to gain attachments to arches in front of or behind that to which the muscle-plate properly belongs.

It follows from the foregoing that we must homologize all these three varieties of dorsal branchial muscle with the single form we are familiar with in the Elasmobranchs. It also follows that the numerical identification of any muscle related to more than one arch, unless it be obviously portion of an oblique muscle, will rest upon its innervation ; and that, if there be a dual innervation, its developmental history alone will decide the question as to whether it be two muscle-plate derivatives fused, or a single derivative which has acquired a secondary motor innervation.

THE ADDUCTORES ARCUUM BRANCHIALIUM.

These do not call for extended description; when present, they are always essentially the same. Each arises from the posterior, and upper, end of a ceratobranchial and is inserted into the epibranchial close to the joint with the former. The muscle is always short and relatively stout and it lies anterior and medial to the joint.

The number of these muscles which may be present varies from five to three, the last two may, as in *Platycephalus*, be more or less completely fused at their origin.

In the Elasmobranchs, Edgeworth does not regard the fifth of this series as being homologous with the others, because, whereas they are developed from the branchial muscle plates, this is developed from the constrictor oesophagi which in turn is developed from the splanchnic mesoblast and is therefore not a branchial muscle.

In the Teleosts, however, a muscle very similar to the constrictor, but developed from the fifth branchial muscle plate, takes its place; this Edgeworth designates the Sphincter oesophagi (1928, pp. 76-77).

In the work just referred to, Edgeworth draws a distinction between the adductores arcuum branchialium of the Elasmobranchs and those of the bony fishes on account of certain features in their development and a difference in the course of the motor nerve to the muscles in the two groups. He would not regard the adductors in the groups as homologous series, and proposes to designate the muscles in the Ganoidei " attractores ". Whilst not even implying any inaccuracy in his observations, it does not appear reasonable to regard these muscle series as other than homologous. That they are developed in slightly different manner in the two groups may well have come about directly, without, as his view implies, the suppression of the primitive adductor and its replacement later by another muscle. This latter would involve us in the further assumption that an adductor was absent from one phylogenetic stage, unless it be assumed that the later muscle dispossessed one already in possession of the site.

The case of the fifth adductor in the Elasmobranchs is different. It is not at all unreasonable to assume that the massive constrictor primordium and, later, the muscle itself, had extended its attachment along the margin of the fifth arch and displaced and finally quite usurped the situation and function of the small branchial derivative. There is no discontinuity involved in the assumption.

VENTRAL BRANCHIAL MUSCLES.

THE SUBARCUALIA OBLIQUI, TRANSVERSI AND RECTI.

That these three forms of intrinsic ventral branchial muscle develop from a common primordium has already been stated. They are numerically as variable as the dorsal branchial muscles. In *Amia* there are four oblique ventral muscles, the fourth being that which Allis designated the obliquus ventralis IV^1, two subarcualia recti, the muscles which Allis designated obliqui ventrales IV^2 and IV^3, and two subarcualia transversi. In *Platycephalus* I find a single obliquus, a single rectus and two transversi. In *Anguilla* there are a single rectus, three obliqui and two transversi. In *Scomber* Allis described no subarcualia recti, two obliqui and two transversi. *Polypterus* is of interest as presenting, in the adult, traces of the origin of the muscles. Edgeworth has studied the development of the muscles in *P. senegalus*. There are two recti and three obliqui. Rectus and obliquus 1 are developed from the first branchial muscle plate. Obliquus 2 almost joins its antimere to form an anterior transversus medially, and laterally it is partially fused with the first rectus. The muscle derived from the third muscle plate remains as a simple obliquus, that from fourth muscle plate becomes a rectus and grows forward to become attached to the second arch. There are only four arches in *Polypterus* and we have here all four muscle plates represented. There is, in addition, a posterior transversus which is developed from the fourth muscle plate.

Edgeworth regards the subarcualis transversus as more primitive than the obliquus; he tabulates the latter as being developed from the former, and we have, in a previous page, quoted his statement to the effect that an obliquus may be developed from a fully formed or from an incomplete transversus.

Since the branchial muscle plates are not primarily joined one to the other ventrally, it would appear more in keeping with their history to regard the oblique as the primitive form and the temporary ventral union, observed in some instances, as an abortive attempt to form a transversus.

THE BRANCHIAL DEPRESSOR MUSCLES.

The muscle which we know as the coraco-branchialis in the Elasmobranchs has been designated the pharyngo-clavicularis by Allis. Edgeworth, however, applies the one name to the muscle in all the fishes.

It would appear that only two portions, at most, of the quinquepartite muscle of the Elasmobranchs are developed in the bony fishes. It is proposed here to recognize the development of the clavicle on the pectoral girdle and to designate the muscles claviculo-branchialis internus and externus, remembering, of course, that each is paired.

The claviculo-branchialis internus in *Platycephalus* is a relatively large spindle-shaped muscle which arises by a fine tendon from the mesial edge of the anterior end of the fifth ceratobranchial, beneath the posterior margin of the anterior subarcual transverse muscle and between the origin of the posterior transverse muscle medially and that of the external claviculo-branchialis laterally. From this origin the muscle passes, horizontally, caudad and slightly laterad, to be inserted by another fine tendon into the lateral edge of the clavicle near its dorsal limit. The tendon of insertion lies against the lateral surface of the anterior pectoral muscle medially and the postero-median wall of the fifth branchial cleft laterally.

The claviculo-branchialis externus is a short quadrilateral sheet of muscle fibres, of no great thickness, which arises from the dorso-lateral edge of the clavicle above the anterior limit of the origin of the anterior pectoral muscles, and passes directly dorsad to be inserted into the inner edge of the ventral surface of the fifth ceratobranchial along the anterior quarter of the length of the bone.

In *Anguilla* there is only the claviculo-branchialis externus. This is a relatively massive muscle which arises from the lateral surface of the clavicle along the greater part of its length. The most anterior fibres of the muscle pass cephalad and slightly dorsad to be inserted into the fifth hypobranchial, the most posterior pass almost directly dorsad to be inserted onto the ventral surface of the fifth ceratobranchial. The intermediate fibres are inserted onto the whole of the length of the interior surface of the cerato- and basi-branchials between the two limits. The posterior limit is about one-third of the length of the bone from its posterior end.

Scomber and *Amia* are intermediate in condition between *Anguilla* and *Platycephalus*, *Amia* approaching the more nearly to the conditions in *Platycephalus*.

In *Polypterus* there is but a single muscle, as in *Anguilla*. Allis finds that it is possible to separate the muscle into anterior and posterior parts at its insertion. The latter is said to be inserted on to that part of the fourth arch which corresponds to the hypobranchial, the other on the portion which corresponds to the ceratobranchial. This separation is most marked in *P. bichir* and least so in *P. ornatipennis* (Allis, 1922, p. 259).

Although reduced in number of component parts, there is no room for doubt that these two muscles are completely homologous with the corresponding components of the elasmobranch coraco-branchialis. That this is so is made abundantly clear by the work of Edgeworth on the development of the muscles in the Ganoids (1928) and Elasmobranchs (1926).

It is not without interest to note that the division of the muscle into partes internus (medialis) and externus (lateralis) is foreshadowed in the batoid Elasmobranchs (see antea, p. **36**).

THE PHARYNGO-HYOIDEUS.

This very misleading name is bestowed by Allis upon a muscle which arises from the bone which he designates " sternum " and Vetter " urohyal ", and which is inserted on to the fifth ceratobranchial. For reasons set forth elsewhere I have designated the bone in question " infrabasibranchial ".

Actually the muscle has neither origin nor insertion on any part of the hyoid arch, and is in all probability one of the subarcualia recti. It is not found in the absence of the infrabasibranchial.

In *Platycephalus* the muscle arises from the anterior third of the dorsal edge of the dorsal ridge of the bone, sharing this portion of the ridge with its antimere. From its origin the muscle passes caudad and slightly dorsad and laterad, to be inserted by a fine tendon onto the inferior surface of the fifth ceratobranchial about one-third of the length of the bone from its posterior end. At its origin the muscle is flat, but it becomes nearly cylindrical just behind the posterior limit of the origin. The fibres are inserted into a tendinous sheath which covers the lateral surface of the muscle; posterior to the insertion of the fasciculi the tendon is continued caudad for a distance equal to half the length of the fleshy part of the muscle.

Innervation.—This is from the post-trematic ramus of the first branch of the vagus.

The muscle in *Scomber* (*fide* Allis) is very similar; it is innervated by a twig from the post-trematic ramus of the second division of the vagus, and perhaps also by a similar twig from the fourth division.

HYPOBRANCHIAL SPINAL MUSCLES.

THE GENIO-HYOIDEUS (S. BRANCHIO-MANDIBULARIS).

This muscle was designated branchio-mandibularis by Allis, who adopted the name from Vetter. Edgeworth has studied its development not only in the bony fishes but also in the Elasmobranchs and in several Amphibians, as well as in the Rabbit. From his work it appears quite clear that the muscle is completely homologous with the genio-hyoideus of the Amphibia and with the anterior portion of the coraco-mandibularis of the Elasmobranchs. I have adopted Edgeworth's designation for the muscle.

The genio-hyoideus is found, amongst the Teleosts, only in *Amia*, *Lepidosteus*, *Polypterus* and, probably, in *Calamichthys*. It is also present in all the Chondrostei.

It is a small muscle which arises from the mandible on either side of the symphysis, and passes caudad to be inserted onto the third ceratobranchial or basibranchial.

Innervation.—This is by a twig from the occipito-spinal ventral trunk.

THE CLAVICULO-HYOIDEUS.

This is a massive muscle, usually more or less completely fused along the mid-line with its antimere, which arises from the greater part of the ventral surface of the clavicle. From this extensive origin the muscle passes cephalad, tapering rapidly, to be inserted onto the hypohyal. When an infrabasibranchial is present the muscle is inserted onto both dorsal and ventral surfaces of that bone, surrounding it almost completely. The attachment to the hypohyal, however, is still provided for by the two very strong ligaments that bind the antero-lateral corners of the infrabasibranchial to the hypohyals.

Not uncommonly this muscle is quite inseparable from the anterior pectoral muscles at its origin.

Innervation.—This is by the occipito-spinal nerves.

This muscle is completely homologous with the coraco-hyoideus of the Elasmobranchs, but it seemed advisable to recognize, in its designation, that the clavicle is present in the place of the coracoid, as was done in the designation of the claviculo-branchialis.

THE CONSTRICTOR MUSCLES OF THE HYOID AND MANDIBULAR SEGMENTS.

We have already noted that the ventral constrictors of these two segments are, in certain Teleosts, so fused as to render a study of their development in every form necessary before it were possible to state where the one begins and the other ends. The dorsal constrictor of the hyoid segment is continuous with the ventral, and it therefore becomes necessary to treat together the derivatives of the elasmobranchian Csv.1, Csv.2, and Csd.2.

THE SUBMENTALIS MUSCLE AND THE INTERMANDIBULARIS POSTERIOR.

These muscles have variously been designated by previous writers. Each is, however, homologous with only portion of the Csv.1 of the Elasmobranchs and to that extent the use of the name intermandibularis for either is misleading. On the other hand one is probably completely homologous with the submentalis of the Amphibia and higher vertebrata.

Platycephalus.—The intermandibularis posterior (Csv.1*a*) is exposed by the removal of the skin. It is composed of two small triangular, thin sheets of muscle, each of which arises from a short line along the inner surface of the dentary. This line commences just a little behind the symphysis. The posterior few bundles of fibres of the two sheets are quite continuous across the mid-line, but in front of these the fibres become successively shorter, the most anterior hardly extending far enough to appear medial to the slight " overhang " of the dentary. In the result there is left between and in front of the two muscle sheets a fine but strong fibrous sheet, which is attached to the dentary bones in continuation of the line of origin of the muscle right forward to the symphysis.

The line of origin of the muscle is not immediately deep to the skin. There intervenes between the skin and the muscle an appreciable interval, filled in front by loose connective tissue, but posteriorly the superficial origin of the protractor hyoidei lies in the space. There is no fusion between this muscle and the protractor hyoidei.

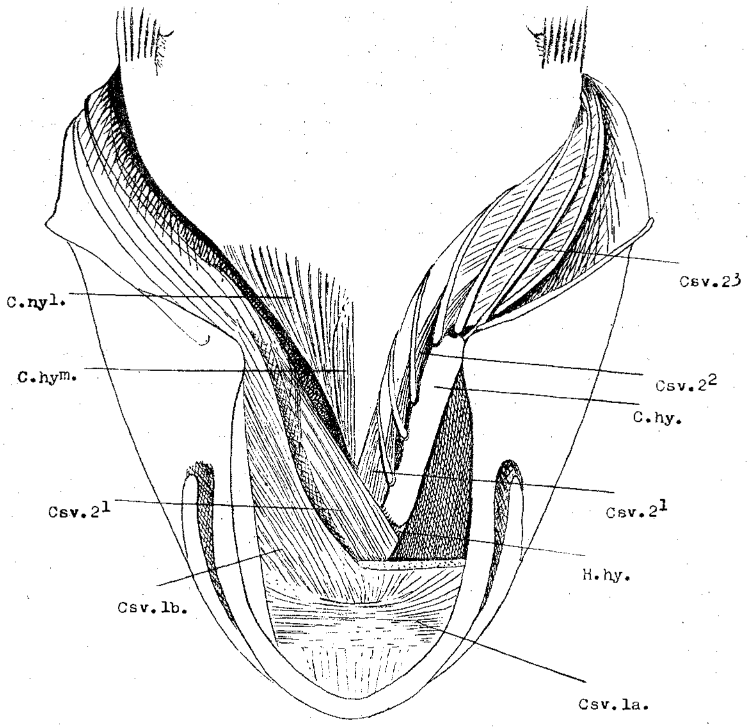

Fig. 22.—*Platycephalus.* Mandibular and hyoid muscles, seen from below, the right side dissected deeper than the left. Csv.1a., M. intermandibularis posterior; Csv.1b., M. protractor hyoidei; C.hy.l. & m., The lateral and medial parts of the M. claviculo-hyoideus; C.hy., The ceratohyoid cartilage; Csv.2, M. hyo-hyoideus; H.hy., The hypohyal cartilage.

Mugil.—In this genus the submentalis is peculiar in being placed dorsally to the protractor hyoidei, immediately beneath the oral mucosa. It is, however, not dorsal to the basihyal (glosso-hyal), which lies in a fold of the oral mucosa which covers it both dorsally and ventrally, so that it projects, as in many other fishes, forward on the floor of the mouth. The submentalis muscle lies beneath the mucosa on which this projecting glosso-hyal lies, with the five dorsal tendons of the protractor hyoidei between them. The muscle arises from a relatively short line along the inner surface of one dentary just below the reflection of the mucosa therefrom. The line commences at the symphysis. All the fibres are quite continuous across the mid-line and are inserted along a precisely similar line of the other dentary.

Amia.—The intermandibularis in this form presents two parts: (*a*) The submentalis (intermandibularis of Allis) which is essentially similar to the submentalis of *Anguilla.* (*b*) The intermandibularis posterior (genio-hyoideus inferior of Allis). This arises on each side from the dentary bone along a line resembling essentially that of the origin of the muscle in *Platycephalus.* The whole of the fibres of both sides reach a median ventral raphe, having a direction slightly caudad to reach their median insertion. There is no attachment of this muscle to the hyoid arch, and, moreover, though inserted into a median raphe common to it and the genio-hyoideus superior (protractor hyoidei of this work), the fibres of the two muscles are at a marked angle to one another and there is fusion of the two muscles.

Anguilla (Fig. 24).—The submentalis in this form is a very small bundle of short muscle fibres which arise from one dentary just beside the symphysis and are inserted into a similar position on the other.

Polypterus.—The intermandibularis posterior is essentially similar to that of *Amia.*

Scomber.—The muscle here is similar to that of *Mugil,* but more extensive, as though it represented that of both *Platycephalus* and *Anguilla* or both anterior and posterior parts of that of *Amia,* but here the two parts are quite continuous and with the posterior rather more reduced than the anterior. It would appear from the description of Allis that the muscle is placed nearly as deeply as is that of *Mugil* (Allis, 1903).

Lepidosteus.—In this form the intermandibularis posterior is an extensive muscle which takes origin from the mandibular ramus along a line which extends from just in front of the joint almost to the symphysis. This line of origin is just beneath the skin. The posterior fibres have a direction caudad and mediad, the fibres in the middle of the antero-posterior length of the muscle pass directly mediad, and those in front of this point incline more and more sharply cephalad. I have been unable, in the small specimens at my disposal, to find any division of the muscle into partes anterior and posterior.

THE PROTRACTOR HYOIDEI.

This muscle was described by Allis under the name of genio-hyoideus superior in *Amia* and genio-hyoideus inferior and superior and hyo-hyoideus superficialis in *Scomber* (1903, 1919), and his first designation for the muscle has been accepted by Herrick (1899) and Norris (1925). Edgeworth (1911) pointed out that the muscle is certainly not the homologue of the genio-hyoideus of higher vertebrates, and to avoid confusion with that muscle he designated this the hyomaxillaris.

Apparently the most extensive study of this muscle yet published is that of Holmqvist (1910, 1911). He bestowed the very apt designation protractor hyoidei upon the muscle. Since this designation has received greater recognition than that of Edgeworth it has been decided to adopt it here. Edgeworth in his later work (1928) rather adds to the confusion by using the designation interhyoideus for the muscle, though he states, " the protractor hyoidei of many teleostei is a compound muscle, being an intermandibularis posterior plus interhyoideus ". If this be so the muscle, in these " many " instances, is not completely homologous with the interhyoideus of the Elasmobranchs, and to that extent the adoption of the name here would introduce confusion.*

The protractor hyoidei is an elongated, flat to oval muscle which arises from the ventral, or, in laterally compressed fishes, lateral, surface of the ceratohyoid anterior to the branchiostegal rays, and passes cephalad and mediad to be inserted into the mandible of its own side just to one side of the symphysis. There is some variation in the muscle in different fishes. The two muscles most commonly fuse anteriorly one with the other along their contiguous mesial margins, and here, as in *Scomber,* there may develop a median, massive, crowding together of muscle fasciculi, giving rise to the appearance of a separate component of the muscle. The insertion onto the ramus of the lower jaw may be placed entirely ventral, entirely dorsal, or partly ventral and partly dorsal to the submentalis muscle. Again, the insertion may be entirely onto the lower jaw or in part into the tough fibrous tissue of the side of the floor of the mouth close to the jaw bones.

In the siluroides *Tandanus* and *Cnidoglanis* (Fig. 23) the condition of the protractor hyoidei is of particular interest. A submentalis similar to that of *Anguilla* is present and is relatively massive. Behind this there is a muscle which resembles an intermandibularis posterior. This

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* Edgeworth also appears to have been confused by Allis's terminology, and thereby has added to the confusion Allis (1903) described in *Scomber* an intermandibularis, a geniohyoideus inferior and superior, and hyohyoideus superior and inferior. In a later contribution (1919) Allis says that portion of his geniohyoideus superior constitutes a hyohyoideus superficialis. Now his geniohyoideus inferior in *Scomber* is very certainly not homologous with the intermandibularis posterior of *Amia*, which also he designated geniohyoideus inferior ; it is only a peculiarly developed portion of the geniohyoideus superior. This, apparently, Edgeworth failed to recognize, and, perhaps also misled by the rather peculiar conditions in the Siluridae which he studied in this connection, he regarded Allis's geniohyoideus as synonymous with his interhyoideus and the protractor hyoidei of Holmqvist. Actually the three muscle portions which, in the two contributions, Allis designates geniohyoideus inferior, geniohyoideus superior, and hyohyoideus superficialis, together form the muscle which Edgeworth names interhyoideus and which in this work is termed the protractor hyoidei. The M.hyo-hyoideus superficialis has no real identity, it is but a variant of the M.genio-hyoideus or of the inferior portion of the M.hyo-hyoideus.

arises from the ramus of the jaw on each side of the submentalis and joins its fellow of the other side behind that muscle. There is no intermingling of the fibres of these two muscles. The second muscle is the pars superficialis of the protractor hyoidei. It is a flat sheet of muscle fibres and is continued back, close to the ramus of the jaw, to be inserted onto the upper end of the ventral surface of the ceratohyal close to the lateral edge of that surface, and just lateral to the attachment of the last five branchiostegal rays. The muscle is relatively broad in front and tapers to a point at its most posterior point of insertion. This superficial portion of the protractor hyoidei completely covers the ventral surface of the deeper portion. The deeper portion of the muscle is divided, incompletely, into medial and lateral parts. The pars medialis has a fleshy and tendinous origin from the ventro-lateral surface of the ceratohyal along a line which commences at the point of attachment of the fifth branchiostegal ray, passes forward along the medial margin of the bone to the third ray, and then crosses to the outer margin. The muscle rapidly swells into a considerable bulk and passes cephalad and slightly mediad to be inserted onto the inner surface of the ramus of the lower jaw along a line at the edge between its inferior and medial surfaces for a short distance on one side of the symphysis. This muscle is not fused with its antimere. The pars lateralis is a smaller muscle than the pars medialis but has a more extensive origin from the ceratohyal. This tendinous and fleshy origin covers all the surface of the bone between the origins of the partes superficialis and medialis. The muscle passes forward between the pars medialis and the ramus of the jaw to be inserted into the tough fibrous investment which covers the mandibular periosteum. The point of insertion is just behind the posterior end of the line of insertion of the pars medialis and ventral to the point of issue of the terminal branch of the mandibular ramus of the Vth nerve from the dentary bone.

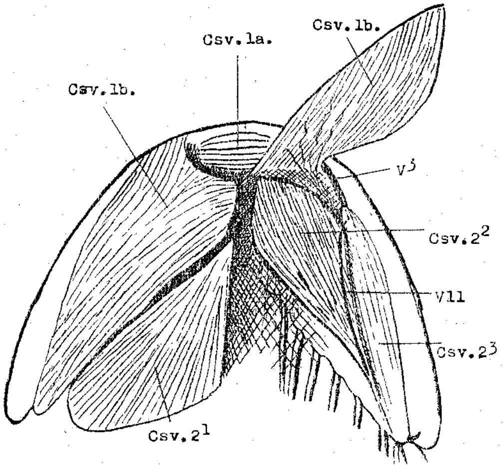


Fig. 23.—***Tandanus.*** **Mandibular and hyoid muscles, seen from below, the left side dissected deeper than the right. Csv.1a., The M. submentalis ; Csv.1b., The M. protractor hyoidei, pars superficialis ; Csv.2^1, The M. hyo-hyoideus ; Csv.2^2 & 2^3, The medial and lateral parts of the M. protractor hyoidei.**

The last two parts are very intimately fused and are inseparable at and near their insertion, but in their anterior two-thirds they separate completely leaving two clean surfaces of contact. There is no fusion between these deeper portions of the muscle and the pars superficialis.

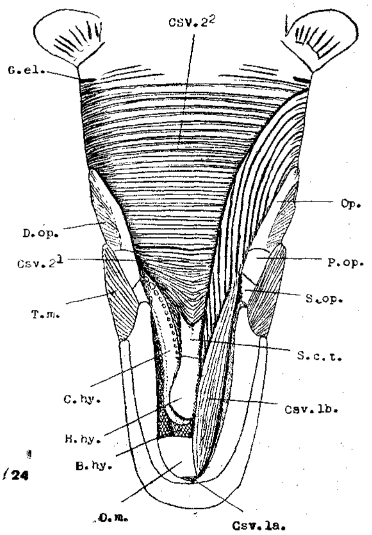
Innervation.—The Vth nerve gives off a brush of fibres as soon as it issues from its foramen, the main trunk continuing forward against the inner surface of the jaw. The brush of fibres are, all but one, distributed over and terminate on the deep surface of the pars superficialis, but confined to the anterior two-thirds of the muscle. The one exception, the largest of the series, turns ventrad and mediad and perforates the anterior tip of the pars lateralis. It was traced caudad between the partes medialis and lateralis and was ultimately lost among the fine tendons of origin of the two parts. No branches were observed to leave this nerve. It is assumed that it is the communicating branch from the VIIth nerve described by Herrick in *Gadus* (1899, p. 157) and in *Amia* by Allis.

In view of the possibility of the exceptional twig being a communicating branch from the VIIth nerve, it is not possible to be quite definite on this question in so far as the pars superficialis is concerned. It is probably innervated by the Vth, but there may also be an innervation by the VIIth. Edgeworth (1928, p. 62) states that in *Silurus* and *Amiurus* this muscle, which he designates intermandibularis posterior, is innervated by the Vth.

The partes medialis and lateralis are innervated by twigs from the hyomandibular branch of the VIIth nerve which come forward beneath the branchiostegal rays.

This is in accord with Edgeworth's statements in connection with the two siluroids he discusses. He designates these two portions of the muscle the interhyoideus, but says of the muscle that it arises from the cerato- and hypohyal or cerato- and epihyal and "passes inwards and forwards to a median aponeurosis separating it from its fellow, in *Silurus* also by a tendon to the hypohyalia of the same and opposite sides". It seems possible that this failure to find the insertion onto the ramus of the lower jaw was due to the immaturity of the specimens he studied; there is also, possibly, some confusion with the hyohoideus, for it seems highly improbable that those two siluroids should have differed so much in the insertion of the protractor hyoidei from the two species I have studied.

In *Anguilla* (Figs. 24, 25) the protractor hyoidei is an elongated, flattened, muscle which arises in front, from the inferior edge of the dentary to one side of the symphysis by a short rounded tendinous and fleshy origin and passes backward close against the ramus of the jaw to be inserted into the lateral edge of the ceratohyal a short distance behind its joint with the hypohyal, and in front of where the first two or three branchiostegal rays are articulated to it. The muscle



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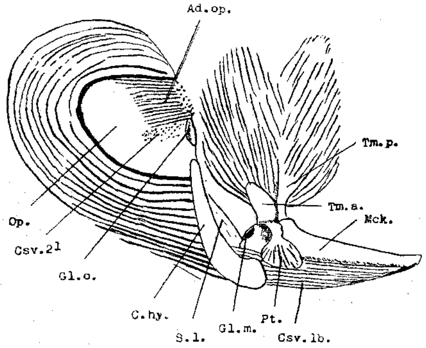

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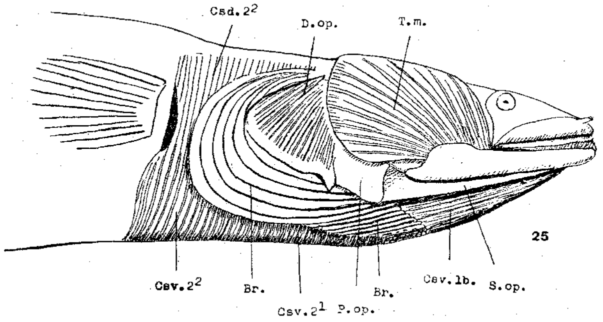

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Fig. 24.—***Anguilla.*** Mandibular and hyoid muscles. B.hy., Basihyal cartilage; C.hy., Ceratohyal cartilage; Csv.1a., The M. submentalis; Csv.1b., M. protractor hyoidei; Csv.2^1 & 2^2, The M. hyo-hyoideus; D.op., The M. dilator operculi; G.cl., Gill cleft; H.hy., The hypo-hyal cartilage; O.m., Oral mucosa; Op., Operculum; P.op., Preoperculum; S-c.t., The sternoclavicular ligament; S.op., Suboperculum; T.m., M. temporo-massetericus.

Fig. 25.—***Anguilla.*** Lateral view of the same muscles as Fig. 24. Br., The branchiostegal rays.

Fig. 26.—***Anguilla.*** The left mandible and ceratohyal cartilage with its branchiostegal rays, with some attached muscles, seen from the medial aspect. Ad.op., The M. adductor operculi; Gl.m. & Gl.o., The articular surfaces of the mandible and of the operculum; Csv.2^1, The area of origin of the anterior portion of the M. hyo-hyoideus; Pt., The tendon of the M. pterygoideus; Tm.a. & p., Anterior and posterior parts of the M. temporo-massetericus; S.l., The subopercular ligament.

is quite definitely superficial to the plane of the branchiostegal rays. The muscles of opposite sides are not fused at any point.

Innervation.—Here again the presence of a ramus communicans from the hyomandibular trunk of the VIIth nerve introduces a doubt. Three small twigs from the mandibular trunk of the Vth were observed to terminate on the ventral, superficial, surface of the anterior portion of the muscle. These twigs leave the terminal branch of the trunk just after it emerges from its foramen in the dentary. The terminal nerve continues forward against the inner surface of the dentary, gives off a tiny twig to the submentalis and then breaks up into a brush of sensory twigs behind and to one side of the symphysis.

The ramus communicans from the hyomandibular VII passes forward beneath the opercular bones and the branchiostegal rays, then reaches the lateral edge of the protractor hyoidei and runs forward to the dentary foramen between the muscle and the ramus of the jaw ; it joins the fifth just after that emerges from the bone.

Platycephalus (Fig. 22).—The protractor hyoidei of this form arises from the inner surface of the dentary by the intermediary of a strong, but thin, fascial sheet which lies dorsal to the intermandibularis posterior muscle. The two protractor hyoidei muscles are intimately fused at the mid-line along the anterior half of their length. The muscle fibres arise from the fascial sheet just under cover of the posterior margin of the submentalis, and all the area in front of this line between the two jaws and in the plane of the muscle is occupied by the fascial sheet, which, most strongly attached on either side of the symphysis, is also bound to the rami of the jaws on each side as far back as it extends. Behind the posterior margin of the submentalis the protractor hyoidei has a short line of fleshy origin from the dentary, and this line extends just a short distance anterior to the posterior margin of the intermandibularis posterior and superficial to that muscle. The most careful dissection of a number of muscles has failed to discover any trace of division into parts, as in the siluroids, or any fusion of this muscle with the intermandibularis posterior.

Besides the origins just stated, the deeper fibres along the medial margin of both muscles arise from a fascial ribbon which in turn is attached to the lateral edge of the glossohyal.

The muscle passes caudad and slightly laterad, tapering somewhat, to a fleshy and tendinous insertion on the posterior one-third of the ventral surface of the ceratohyal.

Innervation.—The related nerves in this genus are essentially as in *Anguilla,* but in addition there are twigs from the nerve to the hyo-hyoideus which run forward and terminate on the ventral surface of the posterior end of the protractor hyoidei.

Mugil.—The two hyoid protractors are very intimately fused for the greater part of their length. They arise on each side of the symphysis by a fleshy origin ventral to the submentalis and by a tendinous origin dorsal to that muscle. The muscles separate anteriorly in their deeper, dorsal portion so that two fine pencils of fibres pass forward above the submentalis and end in the fine, thread-like tendons.

The anterior two-thirds of the muscles are fused along the mid-line, the posterior thirds diverge to be inserted into the cerato- and hypohyals.

The innervation is as in *Platycephalus.*

The protractor hyoidei in *Girella* is so essentially similar in all respects to that of *Mugil* that it calls for no further comment.

Scomber.—Although Allis (1903) describes this muscle in two parts, superior and inferior, there is no doubt that his pars inferior is but a specialized grouping of the fused medial fibres of the muscle. Having thus cleared the ground, it may be stated that *Scomber* differs from *Mugil* and *Girella* only in that the tendinous and fleshy insertions are, as it were, reversed in their relation to the submentalis.

An examination of a number of other forms enables me to say with some confidence that the anatomy of the protractor hyoidei as above described for *Platycephalus, Mugil, Girella* and *Scomber* is characteristic of the Acanthopterygii.

Amia.—The protractor hyoidei here is a quite simple muscle resembling that of *Platycephalus,* but without the short, more superficial, insertion ventral to the posterior margin of the intermandibularis posterior.

Innervation.—It seems only reasonable to believe that the anterior portion of the muscle is innervated mainly, if not entirely, by the mandibular division of the Vth nerve (Allis, 1898, pp. 613, 614). Herrick (1899, p. 159) says that in *Amia* " the genio-hyoideus (protractor hyoidei and intermandibularis posterior of this work) and intermandibularis (submentalis of this work) are clearly supplied from the V ", but on a previous page (p. 157) he remarks that Vetter says of the protractor hyoideus of *Esox* that it is innervated largely by extension of the ramus hyoideus. After stating that this does not hold for *Menidia*, he continues : " . . . this is, however, true in *Gadus*. Or at any rate the r. hyoideus runs forward from the branchiostegal membrane in this species to anastomose with the nerve for the genio-hyoideus within the substance of that muscle. The figure and description by Allis indicate a similar condition in *Amia*."

These statements are somewhat contradictory, but from the evidence before us it would seem safe to conclude that the posterior end of the muscle is, as in many modern Teleosts, probably innervated by the Vth nerve.

Lepidosteus.—The elongation of the rami of the jaws has been accompanied by changes in the related muscles. The protractor hyoidei is quite continuous medially with the hyo-hyoideus and here the fibres arise from a median raphe. The origin from the ramus of the jaw is, however, preserved by the lateral fibres of the muscle. These arise from the inner surface of the ramus at about the middle of its length. The muscle lies dorsal to the extensive intermandibularis posterior muscle.

Innervation.—This is by an anastomosis between branches from the ramus mandibularis V and ramus hyoideus VII (Norris, 1925, p. 364).

Polypterus.—Here, as in *Amia*, Allis designates the intermandibularis posterior " genio-hyoideus inferior ". Having made the necessary correction, it may be stated that the protractor hyoidei in *Polypterus* is essentially similar to that of other bony fishes. For the greater part of its length its medial fibres arise from a median aponeurosis as do those of *Lepidosteus*, this aponeurosis taking the place of the fusion along the mid-line so commonly seen in the modern Teleosts. Posteriorly the muscle is quite continuous with the medial fibres of the hyo-hyoideus as is that of *Lepidosteus*.

Innervation.—Allis (1919, p. 299) is quite emphatic that there is no anastomosis between the contiguous branches of V and VII which may be traced onto this muscle, and that the whole of it is innervated by the Vth only.

Edgeworth (1928) draws what appears to be an arbitrary and unnecessary distinction between those muscles which are completely continuous medially and posteriorly with the hyo-hyoideus and those which are not. Thus the two muscles in *Lepidosteus* are described together as the constrictor hyoideus ventralis, whilst the almost equally fused muscles in *Polypterus* are treated as separate muscles. He draws the same distinction between the homologous muscles in *Polyodon* and *Acipenser*.

Before reviewing these muscles brief reference may be made to the forms described by Holmqvist (1911).

The eel-like *Gymnarchus* is remarkably similar to *Anguilla*. It is probable that in this form, as in the Eels, there is a small submentalis. *Albula* presents an arrangement of the muscles which may well be regarded as an intermediate condition between those of the Eels and the normal Acanthopterygii. *Esox* is very similar to *Platycephalus*, the fibres of the intermandibularis having, however, a diagonal direction in place of one directly transverse. *Salmo, Osteoglossum, Abramis, Raniceps, Perca, Zoarces* and *Callionymus* are but modifications of the normal acanthopterygian type. One questions whether a small submentalis is not present in *Barbus*. In nearly all of these forms the identification which Holmqvist makes of the intermandibularis posterior is quite arbitrary. *Siluris glanis* is essentially similar to *Tandanus* and *Cnidoglanis*.

REVIEW OF THE SUBMENTALIS, INTERMANDIBULARIS POSTERIOR AND PROTRACTOR HYOIDEI.

Holmqvist found, as I have found, that the submentalis, intermandibularis posterior, and anterior portion of the protractor hyoidei in the bony fishes generally are innervated by the Vth nerve, whilst the posterior portion of the last was innervated by the VIIth nerve. Quoting direct from Allis, " Holmqvist (1911) says that the intermandibularis and protractor hyoidei of all the bony fishes are derived, respectively, from the mandibular and hyal portions of the primitive musculus constrictor ventralis. The primitive condition of the intermandibularis (submentalis plus intermandibularis posterior) is said to have been that of a muscle extending transversely from one ramus of the mandible to the other, and this condition is said to be actually found in the Selachii, in *Lepidosteus* and Teleostei, and in *Amia*, the muscle is said to have undergone a vertical cleavage into two parts, one of which is called the intermandibularis I (submentalis) and the other the intermandibularis II (intermandibularis posterior) . . . The protractor hyoidei is said to be . . . derived from that deeper layer of the constrictor ventralis of the Selachii that has its insertion on the cerato-hyal." This, of course, is the interhyoideus of the earlier pages of this work.*

The development of these muscles in the Ganoids and in *Caranx* has been studied by Edgeworth (1928) and his observations appear to confirm the conclusions of Holmqvist.

With these conclusions I am in almost entire accord, but would particularize a little further.

The observations of Edgeworth on *Caranx trachurus* clearly prove that which may well have been anticipated from the innervation and anatomical relations of the muscles. The protractor hyoidei is in most bony fishes, if not in all, a composite muscle derived from the posterior portion of the Csv.1 and from the interhyoideus.

The submentalis is derived from the anterior portion of the Csv.1 and is completely homologous throughout the bony fishes.

The intermandibularis posterior is a derivative of the posterior portion of the Csv.1. It may maintain its identity, as in *Polypterus, Amia* and, perhaps, *Platycephalus*, or it may lose its identity in part, as in the Siluridae, or completely, as in the majority of Teleostoi, by fusion with the anterior end of the protractor hyoidei.

The constant innervation of the anterior end of the protractor hyoidei by the Vth nerve in those forms in which the intermandibularis posterior maintains its identity leads us to believe that this anterior portion of the protractor is derived from a portion of the Csv.1 posterior to that from which the intermandibularis posterior was derived. It is not improbable that this portion of the mandibular muscle plate had become attached to that of the hyoid segment prior to the earliest stages studied by Edgeworth. It is noteworthy that in *Amia* and in *Lepidosteus* the two muscle plates are continuous at the earliest stages he describes, and that his earliest stages of *Polypterus* are a good deal more advanced than are those stages of *Caranx trachurus* in which he demonstrates the fusion of the intermandibularis posterior and the anterior end of the protractor.

The submentalis muscle fibres are quite continuous across the mid-line from one ramus of the jaw to the other; the fibres of the intermandibularis posterior are, with the exception of a few along its posterior margin, inserted into a median tendinous raphe. This leads to the suggestion that the muscle in *Lepidosteus* is, as already indicated above, an intermandibularis posterior, and that no submentalis has been developed, and that the intermandibularis posterior only is present in *Polypterus*, as suggested by Edgeworth (1928, p. 60). Contrariwise, the submentalis only is present in the majority of the Teleostei, the intermandibularis posterior having been completely submerged in the protractor hyoidei.

The condition of these muscles in the siluroid fishes raises another question, which, however, we can do little more than raise in the present state of our knowledge of their development. May it be that in these fishes the pars superficialis of the protractor hyoidei is developed from the anterior portion of Csv.2 and posterior portion of Csv.1, whilst the partes medialis and lateralis are derivatives of the interhyoideus, and, if so, does it follow that the protractor hyoidei of the majority of the Teleostei is compounded of these three derivatives?

Remembering that there is always an overlapping of the innervation of Csv.1 and Csv.2 along their contiguous, and inseparable, margins, this seems not improbable.

THE HYO-HYOIDEUS.

Platycephalus (Fig. 22).—(1) Pars anterior (Csv.2^1) arises from the lateral margin of the hypohyal and passes caudad obliquely across the mid-line to be inserted into the median edges of the first and second branchiostegal rays. The muscle is a triangular sheet having a fleshy origin from the hypohyal, and in its course to its insertion that arising on the right side passes ventral to the hypohyal and also ventral to the hyo-hyoideus arising on the left side. The muscle tapers posteriorly and is inserted by a relatively long tendon. (2) Partes abductores branchiostegalium (Csv.2^2) are four little muscles which are placed in the interspaces between the bases of the first five branchiostegal rays. Each arises from the base of the ray in front, from the capsule of its joint with the ceratohyal, and from the ceratohyal close to that capsule, and is

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* Since the above was written I have been able to consult Holmqvist's two papers, but find no need for addition to or emendation of the foregoing quotation and remarks.

inserted onto the antero-medial edge of the ray behind a short distance from its base. (3) Partes adductores branchiostegalium (Csv.2^3) are three narrow, thin sheets of muscle fibres which fill the interspace between the full length of the last four rays. (4) Pars dorsalis is an extensive, thin sheet of muscle fibres which arises from the lateral edge of the last branchiostegal ray, the seventh, and passes dorsad to be inserted into the dorsal margin of the operculum and into the fascia dorsalis under cover of that bone.

Innervation.—This is by the hyoid branch of the VIIth nerve. The nerve reaches the superficial surface of the muscle under cover of the operculum, and its numerous twigs course mediad and cephalad on the surface of the muscle, but they dip beneath, i.e. dorsal to, the branchiostegal rays as they pass them.

It appears that the pars anterior, acting in conjunction with the branchiostegal abductors, acts to open out the whole branchiostegal membrane, whilst the remainder of the muscle has an opposite action.

The hyo-hyoideus of *Platycephalus* has been selected for detailed description because it is a remarkably complete muscle. This is an exceedingly variable muscle, and in the numerous fishes which have been examined the pars anterior alone is constantly present. The pars dorsalis is, in my experience, the portion of the muscle that is most commonly absent. In some forms either the abductors or the adductors are found definitely deep to the branchiostegal rays, so that in my earlier dissection notes I described them as branchiostegalis profundus and superficialis, but later, discovering that there was no constancy as to which was deep and which superficial, the designations were abandoned in favour of those used above.

In the Apodes the hyo-hyoideus is quite peculiar and very unlike the muscle in the rest of the Teleostei.

Anguilla (Figs. 24, 25).—Pars anterior is a relatively broad ribbon of muscle which arises from the postero-lateral edge of the skull below the sulcus for the head of the hyomandibular and from the deep surface of the operculum just below its joint with the hyomandibular. This line of origin is much shorter than the width of the muscle ventrally, for as the fibres pass toward the ventrum of the fish they diverge, extending cephalad well forward of their origin. The most posterior fibres pass directly ventrad.

Pars posterior is a very broad sheet of muscle fibres which, like the anterior part, lies in contact with the mucosa of the side wall of the mouth and atrio-pharynx. It arises from the fascia dorsalis along a line which commences in front, immediately behind the postero-lateral and dorsal corner of the skull, above the articulation of the operculum to the hyomandibular, and extends back to just above the root of the pectoral fin. From this origin the fibres pass directly ventrad to the mid-line ventrally. A narrow, yet not linear, tendinous interruption intervenes between the dorsal third, and ventral two-thirds of the sheet for a short distance at the level of the dorsal margin of the fin. This interruption commences just in front of, and dorsal to, the gill slit and extends forward a little past the middle of the antero-posterior length of the sheet.

Both parts of this muscle are quite uninterruptedly continuous, across the mid-line ventrally, with the muscle of the other side. There is no trace of any attachment of either part to any element of hyoid or branchial arches.

Both muscles lie deep to the operculum and to the branchiostegal rays. These may be quite readily dissected free from the underlying muscle and that in turn from the structures deep to it. The fibres of the two muscle parts are parallel at their contiguous margins, but it is always possible to separate them along this line, which lies immediately behind the last fasciculus arising from the deep surface of the operculum, between it and the most anterior fasciculus arising from the fascia dorsalis; separation at no other point can be effected without splitting fasciculi.

Innervation.—This is by twigs from the hyoid branch of the VIIth nerve, which are distributed over the surface of the muscle beneath the operculum and branchiostegal rays.

There is little room for doubt that the hyo-hyoideus of the bony fishes is a derivative of the hyoid constrictor sheet of the Elasmobranchs, the Csd.2 and Csv.2.

We have already noted that the anatomy of the protractor hyoidei in the Siluridae suggests the possibility that the most anterior of the Csv.2 fibres enter **into** the formation of the superficial portion of that muscle.

Later, it will be necessary to discuss the possibility that other Teleost muscles are derived from the dorsal part of the Csd.2.

THE HYOID MUSCLES OTHER THAN THE CONSTRICTORS.

There are four of these muscles, the adductor arcus palatini, the adductor hyomandibulae, the adductor operculi and levator operculi.

THE ADDUCTOR ARCUS PALATINI AND THE ADDUCTOR HYOMANDIBULAE.

Platycephalus.—In this fish, as in *Scomber* (*fide* Allis) these two muscles are quite interruptedly continuous. They arise from the lateral edge of the synpterygoid (parasphenoid). The origin extends from a little in front of the middle of the antero-posterior diameter of the orbit back to the myodomial boundary and then dorsad half-way round that boundary, and is also carried back along the same bone to the prootic. The insertion is onto the ventral surface of the palatal arch along a line which commences on the outer edge of the palatine just where that sutures with the maxilla, runs back along the palatine and then along the suture between the palatine and quadrate, next along the mesial, free margin of the metapterygoid, to terminate at the suture between this last and the prootic bone.

The muscle is thickest near its posterior end and becomes quite a thin sheet anteriorly.

Innervation.—The posterior margin of the muscle lies ventral to the fascialis foramen. The hyomandibular trunk of the VIIth nerve passes laterad and slightly caudad from the foramen, and appears behind the middle of the posterior edge of the muscle. Just before it comes into view, the motor nerve to these two muscles is given off. The nerve enters the dorsal surface of the muscle close to the posterior margin and runs forward in the muscle nearer the ventral than the dorsal surface and about the middle of its width ; twigs trending both mediad and laterad are given off at intervals along its length.

In no one of the fishes which I have dissected have I been able to find a clean plane of cleavage between a portion of this muscle, which might be regarded as an adductor of the hyomandibular, and a portion which might be regarded as an adductor of the arch of the palate. It is noteworthy that in the more primitive forms there is developed only so much of the muscles as is inserted into the hyomandibular ; the reference here is, of course, to *Amia* and *Polypterus.*

Apparently in *Menidia* the two portions of the muscle are separated, for Herrick (1899, pp. 137, 138) describes separate motor nerves in that fish to the two muscles.

THE ADDUCTOR OPERCULI.

Platycephalus.—This is a relatively massive muscle which arises from the inferior surface of the pterotic and opisthotic, the origin covering the whole of those surfaces. The general direction of the fibres is laterad and dorsad, parallel to the surface of origin. The fibres converge somewhat to be inserted onto the inner surface of the operculum immediately behind the articular head. For the most part this insertion is onto the base of a strengthening rib, on the inner surface of the bone, which commences at the head and extends to the postero-dorsal corner.

Innervation.—The motor nerve to this muscle leaves the hyomandibular trunk just after that to the last muscle, and plunges into the muscle after crossing the exposed bare surface of the prootic bone which lies between the anterior margins of this muscle and the posterior margin of the adductor arcus palatini in front.

There is some variation in the site of origin and the manner of insertion of this muscle in different fishes, but none of these is of sufficient importance to call for separate description.

THE LEVATOR OPERCULI.

Platycephalus.—The levator operculi appears in this fish as though it were the dorsal continuation of that portion of the pars dorsalis of the hyo-hyoideus which is inserted into the inner surface of the operculum. It arises from the dorso-lateral edge of the skull behind the operculo-hyomandibular joint, and in this origin is continuous with that portion of the hyo-hyoideus which has a similar origin behind it. It is inserted onto the dorsal odge of the operculum. It lies immediately beneath the skin and upon the adductor operculi, where that passes across the narrow interval between the operculum and the skull.

Innervation.—The motor nerve in this muscle is a twig from that branch of the hyomandibular which Herrick (1899) calls the ramus hyoideus and which is essentially the motor nerve to the superficial hyoid muscles, the hyo-hyoideus and posterior end of the protractor hyoidei.

Throughout the bony fishes the levator operculi is essentially as in *Platycephalus.* Its origin appears to be constantly from the postero-lateral corner of the skull. Commonly this origin is more restricted than the insertion, so that the fibres diverge fan-like from the origin. Again it is common for the insertion to extend over more or less of the superficial surface of the operculum. In some fishes the muscle is more or less fused with the adductor operculi, e.g. *Amia* and *Anguilla* (Figs. 25, 26).

Review.

Whilst their development places it beyond doubt that these four muscles, together with the hyo-hyoideus and posterior end of the protractor hyoidei, are all hyoid muscles, their innervation by two widely separated branches of the facial nerve separates them into two groups, superficial and deep.

Of the four which we now discuss, three belong to the latter group and one only to the former; this last is the levator operculi.

This muscle had been homologized in the past with that which it seems so obviously to represent in *Platycephalus*, portion of Csd.2. There appears no reason to doubt that this homology is the correct one.

Turning our attention to the Selachii, it will be remembered that in those fishes the dorsal end of the hyoid muscle plate gave rise, deep to the constrictor sheet, to the levator hyomandibulae, and that in the adult this muscle lies behind the spiracle and the hyomandibular branch of the facial nerve, in contact with the deep surface of the Csd.2. The muscle arose from the skull behind and above the auditory capsule and was inserted onto the superior and anterior surface of the hyomandibular cartilage.

In those fishes in which the adductor hyomandibularis is separated from the adductor arcus palatini, or in which that muscle is not developed, *Amia* and *Polypterus*, this hyoid adductor preserves all the relations of the hyoid levator of the Selachii. It is, moreover, developed from the dorsal portion of the hyoid muscle plate deep to the primordium of the hyo-hyoideus.

Since the adductor arcus palatini and the adductor operculi are also developed from the same primordium, and in some fish never become separated from the hyomandibular adductor, it were unreasonable to refuse to regard all three muscles as being derivatives of the elasmobranch hyoid levator.

MANDIBULAR MUSCLES OTHER THAN THE VENTRAL CONSTRICTORS.

In this group there are the following muscles: the levator arcus palatini, the dilator operculi and the mandibular adductor muscles.

The Levator Arcus Palatini.

Platycephalus (Fig. 27).—The muscle arises from the side wall of the skull behind the orbit and from a cranio-palatal fascial partition between it and the adductor arcus palatini mesial to it. This area of origin extends from the posterior boundary of the orbit caudad to the inferior margin of the dilator fossa above and the suture-line between the prootic and os transversum below. These two boundaries meet at the anterior margin of the hyomandibular facet. The general direction of the fibres is caudad and laterad. The deeper and more anterior fibres are inserted into the flange which stands out from the outer surface of the metapterygoid and into that bone itself above the flange. The more posterior and superficial fibres pass superficial to the postero-medial corner of the origin of the pterygoideus to be inserted into the suture-line between the hyomandibular and the preoperculum.

The postero-medial corner of the origin of the pterygoideus referred to runs upward and backward deep to the insertion of the deeper fibres of the levator arcus palatini, lying in the angle between the flange and the main part of the os transversum.

Innervation.—This is by a branch from the mandibular ramus of the Vth nerve which leaves the main nerve under cover of the muscle and curves round its anterior margin, and then passes caudad over its surface and ends in the dilator operculi. Several twigs are given off to the muscle as it passes over it.

Paradicichthys.—It was not intended to attempt a description of the cranial muscles, nor, indeed, would this have been possible in a satisfactory measure from a single specimen. As the preparation of the skull progressed, however, the arrangement of the muscles was noted, and certain peculiarities of the levator arcus palatini which were observed are deemed worthy of mention. (See p. 105 for description of the skull.)

The muscle is clearly divisible into three divisions. Of these, the first may be termed the abductor hyomandibularis. This is a digastric muscle; the upper belly arises from the outer portion of the floor of the dilatator fossa and the back of the upper post-ocular scute, its fibres gathering into a broad, short tendon which passes down and back through that foramen described as formed between the shelf-like process on the upper outer face of the body of the hyomandibula and the outer corner of the post-orbital lamina of the sphenotic. The foramen in question is to a large extent closed by a strong membrane. The fibres of the lower belly of the muscle are attached to the outer face of the hyomandibula below the " shelf ", and above and in front of the ridge which crosses the body diagonally to the antero-inferior corner of the bone. These fibres arise from the tendon as it spreads out immediately it passes through the foramen.

The second division of the muscle may be termed the abductor arcus palatini. This arises as a strong cord-like tendon from the back of the lower post-ocular scute and from the outer corner of the post-orbital lamina of the sphenotic; the tendon passes directly downward and through the narrow foramen between the two laminae of the hyomandibula and os transversum, then opens out and gives origin to muscle fibres which are attached to the inner surface of the epipterygoid over the area already described.

The third division of the muscle, which may be designated the levator arcus palatini, sensu stricto, is essentially similar to the anterior portion of the muscle in *Scomber*, as described by Allis (1903).

It may be stated that the three divisions of the levator arcus palatini just described can be recognized in the great majority of fish, but it is only in a few that the divisions are as distinctly separable as in the present case.

The above may be accepted as a description of the levator arcus palatini as it is found in the majority of the modern Teleosts.

In the two Siluroid fish I have been able to dissect, the muscle is much reduced. It is a small flat muscle which arises from the dorso-lateral edge of the skull in front of the posterior end of the hyomandibular joint and passes ventrad to be inserted into the dorsal margin of the hyomandibular just below the joint.

Lepidosteus.—In this fish the hyomandibular portion of the muscle is differentiated from the more anterior portion. Allis recognizes levator arcus palatini and retractor hyomandibulae, as well as dilator operculi and the specialized slip of the latter which he terms muscularis spiracularis.

PROTRACTOR MAXILLAE OF THE SILURIDAE AND LEVATOR MAXILLAE SUPERIORIS PART 4 OF AMIA.

The protractor maxillae of the two siluroid fish *Tandanus* and *Cnidoglanis* is a relatively thick muscle which arises from the side of the skull above the anterior attachments of the palatal arch, and passes caudad and laterad to be inserted onto the posterior end of the maxilla, the insertion enswathing the posterior end of the bone on all but its deep surface.

Innervation.—This is by a branch from the Vth nerve which leaves the anterior and inferior surface of the mandibular ramus deep within the orbit.

The little muscle which Allis (1897) described as the fourth part of the levator maxillae superioris in *Amia* appears to be strictly comparable with this protractor muscle.

THE DILATOR OPERCULI.

Platycephalus.—The muscle arises from the dilator fossa and passes caudad and laterad deep to the dorsal tip of the preoperculum and is inserted into the superficial surface of the operculum just beyond the capsule of its joint with the hyomandibular.

Innervation.—This is by the terminal twig of the motor nerve from the mandibular ramus of V to the levator operculi, as described above.

In *Tandanus* and *Cnidoglanis* the dilator operculi is a relatively massive muscle which arises deep to the levator arcus palatini from the side wall of the skull above the anterior end of the long hyomandibular articulation.

EXCEPTIONAL MUSCLES OF THE MANDIBULAR SEGMENT.

In various of the more or less aberrant Teleosts there are found muscles which are without close parallels in the more normal fishes. Their innervation and anterior situation indicate that these are derivatives of the mandibular muscle plate, and probably from the dorsal portion. They are, therefore, probably derived from that portion of the mandibular muscle primordium from which are derived the last two muscles. For this reason they are briefly referred to here.

(1) *The Retractor labii superioris of Drepane.*—This is a fine thread-like strand of muscle fibres which arises from the medial surface of the preorbital bone and passes directly forward along the dorsal edge of the ascending process of the premaxillary labial bone to be inserted into that edge close to the junction of the process and the body of the bone.

Innervation.—This is by a very delicate twig from the mandibular trunk of the Vth nerve which leaves the main nerve deep within the orbit and runs forward below the ophthalmic ramus of the nerve.

(2) *The erector muscles of the barblets in the siluroid fishes.*—In the two which I have dissected the muscle to the median barblet arises from the dense connective tissue over the side of the mesethmoid in front of the prefrontal and slightly behind the base of the barblet. That of the labial barblet arises from the periosteum of the maxillary labial bone. Herrick (1901) writes of a slip of the adductor mandibulae which functions as the adductor of the maxillary barblet in *Ameiurus*. There is no such slip present in either of the fishes I have studied.

The Mandibular Adductor Muscles.

Before describing these muscles it is advisable to present an explanation of the nomenclature adopted. To this end it is necessary to summarize briefly again the findings relative to these muscles in the lower tetrapods.

Reviewing the relation of the components of the masticatory complex and commencing with the muscles of the reptiles, we have:

(1) A superficial sheet of fasciculi, the Retractor anguli oris, which is superficial to all three branches of the Vth nerve;

(2) An almost superficial mass of fibres, the Temporalis, which also is superficial to all the branches of the Vth nerve;

(3) A deeper layer, the Massetericus, which may or may not be inseparably fused with the last and, like it, lies superficial to the branches of the Vth nerve. The origin of this and of the last muscle is from the skull dorsal to and behind the foramen of the Vth nerve;

(4) A deep mass of fibres, the Pterygoideus externus, which may or may not appear in part superficially at their origin, which pass to their insertion anterior to the foramen of the Vth nerve, are crossed superficially by the ramus maxillaris, and are inserted into the lower jaw in front of and/or medial to the ramus mandibularis V just as that enters Meckel's fossa;

(5) A deep mass of fibres, the Pterygoideus medius, which arise from the wall of the skull ventral to, and either in front of and/or behind, the foramen of the Vth nerve. The muscle is crossed superficially by the ramus mandibularis and, it may be, also by the ramus maxillaris; and

(6) Another mass of fibres, the Pterygoideus internus, very deeply placed, which arise from the upper surface of the roof of the palate and from the side wall of the cranium behind the via masticatoria. This lies deep to all the other components and the ramus mandibularis is, of course, superficial to it, with the pterygoideus medius between.

The essential facts are (1) the temporalis and massetericus are superficial to the nerve rami; (2) the pterygoideus externus is crossed between origin and insertion by the R.max. and is either inserted in front of the R.man. or is internal to the nerve at its insertion; (3) the pterygoideus medius and internus lie deep to both rami of the nerve, and for the most part behind them.

In the Amphibians the same relations hold good. The pterygoideus medius is never developed and the pterygoideus internus only in the Coccillians. Here again the relations to the rami mandib. and max. are constant and are just as in the Reptiles.

Turning next to the Dipnoans, it is found that there are but two separate portions of the adductor muscle mass. It is significant that these two portions are separated by the two rami of the Vth nerve. There appears no reason to doubt that the anterior portion may be identified as the pterygoideus externus, whilst the posterior portion must represent either or both the temporalis and masseter.

In an attempt to recognize the forerunners of these muscles amongst the fishes, one may turn to the Holocephali. In these Elasmobranchs there is a small adductor mandibulae which lies entirely behind the rami of the nerve, and anteriorly a massive adductor and a series of smaller ribbon-like muscles which activate the upper lip. These latter all lie deep to the ramus maxillaris. It were little short of unsupported speculation to attempt to homologize the ribbon-like muscles, but the function of the larger adductor muscle and its relation to the two rami of the nerve fully justify its identification as the pterygoideus externus of the Dipnoi and the Tetrapods. The most serious objection to this identification is its origin, in front of the orbit instead of behind it. This, however, will be seen later to be not so serious, as it will be found that other, undoubtedly homologous, muscles are found in bony fishes arising behind or in front of the orbit in different species, and that in the cockatoos the pterygoideus externus arises in front of the orbit.

Comparison of the muscles of the Holocephali with those of *Chiloscyllium* enables one to recognize at once the homologous muscles. The pterygoideus externus is that which lies in front of the two rami of the Vth nerve, and the comparison of the muscles of *Chiloscyllium* with those of the rest of the Plagiostomes leads one to the inevitable conclusion that if the forerunner of the pterygoideus externus is recognizable at all in the Elasmobranchs it can be none other than the muscle which Vetter designated the " Add. β " and Marion, the " Levator labii superioris ".

Apparently the temporalis and the masseter are represented in the complex quadrato-mandibularis of the Elasmobranchs, and it is not improbable that the relatively constant subdivision of that muscle which is described in this work actually foreshadows the subdivision of the muscle into the components found in the Tetrapods.

Turning now to the Bony Fishes, and commencing with *Polypterus*, the mandibular adductors present division into four readily separable parts. Of these, two lie superficially to the rami of the nerve and are inserted onto the mandible superficially to or behind the R.mand. These Allis described as the superficial and deep portions of the adductor mandibulae. It would appear that the superficial portion is the homologue of the temporalis, and that the deeper portion is the homologue of the masseter. There are also two divisions of the adductor muscles lying deep to, and inserted medial to, the rami of the nerve. The more superficial of these was designated the temporalis by Allis. This it cannot well be on the evidence of its relation to the nerves. It appears quite reasonable to identify it as the precursor of the pterygoideus medius, and the other arising further forward as the pterygoideus externus.

In the modern Teleostei the ramus maxillaris of the Vth nerve runs forward dorsally to the origin of all the muscles. There are no muscles lying deep to this ramus, and it fails us as a reference structure.

In *Amia*, however, there are two little muscles arising far forward and crossed superficially by the R.max. and further back the great bulk of the adductor muscles lie deep to the R.mand. Now in this fish the only adductor muscle to be inserted externally to the R.mand. and to lie entirely superficial to the ramus is that which Allis described as the lower portion of the superficial part of the adductor mandibulae. Although Allis stated that the separation of this portion of the muscle was wholly artificial, I find that the cleavage plane occupied by the ramus mandibularis beneath this portion is quite clean and very definite.

If the relation to the ramus mandibularis be a determining factor, then this superficial portion of the adductor mandibulae must be the homologue of the muscles superficial to the ramus in the Tetrapods, that is to say the temporalis and the masseter.

Throughout the rest of the Bony Fishes we find always two main divisions of the adductor muscles ; there is always one portion which is superficial to or arises behind the R.mand. and is inserted onto the mandible lateral to it, and there is the other portion which arises in front of the ramus or deep to it and is inserted onto the mandible medial to it. These vary in their relative and actual size—now one, now the other is the larger.

It is believed that it is correct, or at least reasonable, to regard the former as representing the temporo-masseteric group of the Tetrapoda and the latter as representing the pterygoid group.

In conformity with this belief, and in order to maintain an uninterrupted sequence in the nomenclature, the mandibular adductor muscles of the bony fishes are described in the following pages as temporo-masseteric and pterygoid.

The question arises, however, as to just what is the homology of these two divisions with the adductor muscles in the Elasmobranchs. In these fishes there is by no means such a clear-cut division into two divisions. The homology of the muscle which, in this work, has been designated " M. pterygoideus " throughout the whole of the vertebrata is believed to be sufficiently supported by the available evidence to justify the designation. On the other hand, the quadrato-mandibularis of Elasmobranchs is very generally perforated by the ramus mandibularis of the

Vth nerve, and this suggests that its deeper portion may be homologous with the posterior portion of the pterygoid of the bony fishes and with the Mm. pterygoideus medius and internus of the Amphibians and Reptiles.

This question is returned to in the later sections of the work.

THE TEMPORO-MASSETERIC GROUP OF MUSCLES.

These muscles were described by Vetter as the first and second divisions of the adductor mandibularis, the " A^1 " being that which I describe as the pars anterior, and " A^2 " the pars posterior. Allis describes the pars anterior, in *Amia*, as the first part of the levator maxillae superioris ; the pars posterior he describes as portion of the superficial portion of the adductor mandibulae (A^2). In *Scomber* there is no separate pars anterior, and Allis describes the muscle as the superficial portion of the adductor. In *Polypterus* the pars anterior, particularly well developed, is termed " temporalis " by Allis, whilst the pars posterior he describes as the superficial portion of the adductor.

In discussing *Callorhynchus* (1933) I designated the pars anterior " adductor labii superioris ", and the pars posterior the " retractor anguli oris ".

The muscle presents a wide range of variability and a number of these variations will be described.

Platycephalus (Fig. 27).—(A) *Pars anterior.* This is a relatively stout three-sided bundle of fibres which lies medial and dorsal to the other adductor components and between them and the levator arcus palatini. The fibres for the most part arise from the superficial deep fascia, but a few arise from a very thin superficial tendon which lies upon the posterior half of the superficial surface of the muscle, and is itself attached to the anterior edge of the subdermal ridge of the preoperculum below the point whereunder the dilator operculi passes. The general direction of the fibres is cephalad, with an inclination ventrad and laterad, to an insertion into a strongly developed tendinous strand in the maxillo-labial fascia. This strand is attached behind to the ascending process of the lower jaw ; in front it is attached to the posterior edge of the maxillary labial bone close to the articular head. This ligament is so very constantly present that it is proposed to recognize and establish its identity by the designation mandibulo-labial ligament (ligamentum mandibulo-maxillare posterius of Holmqvist, 1911).

The maxillo-labial fascia is a strong membrane which is attached medially to the lateral edges of the maxilla and palatine bones, posteriorly to the anterior edges of the ectopalatine, inferiorly to the inner surface of the articular and/or posterior end of the dentary below the insertions of the mandibular adductors. In front of this last attachment, the fascia presents a free margin in the fold of the lip at the angle of the mouth and is attached in front of the angle to the internal surface of the full length of the inferior edge of the maxillary labial bone. Between this and the premaxillary labial the fascia is folded with the skin to provide the loose membrane between these two bones which permits of the protrusion of the two labial bones.

This fascia also is of very constant occurrence and in the absence of the mandibulo-labial ligament, which is but a specialized portion of the fascia, provides the retractor ligament of the upper lips and their enclosed bones. The free edge of this fascia in the lips at the angle of the mouth is the ligamentum mandibulo-maxillare anterius of Holmqvist.

(B) *Pars posterior.* This is a very massive muscle which arises from the whole of the lateral surface of the preoperculum, except its subdermal ridge, and from the hyomandibular and the deep surface of the posterior suborbital. The whole of the fibres are inserted into a fan-like tendon which divides the muscle into superficial and deep portions. The fibres arising from the hyomandibular and preoperculum are inserted into the broad, thin posterior edge of this tendon and into its deep surface. Those arising from the subocular bone are inserted onto its superficial surface.

The tendon, contracted to a narrow ribbon, is inserted onto the tip and inner surface of the ascending process of the mandible above Meckel's foramen. Its anterior edge is reflected away from the mandible and is bound to the thickened edge of the maxillo-labial fascia and to the mandibulo-labial ligament.

Anguilla (Figs. 24, 25, 26).—(A) *Pars anterior.*—This arises from (1) a medial dorsal septum from the other side of which its fellow arises, and which commences just behind the orbit and extends back to just beyond the posterior limit of the skull ; (2) a triangular membrane which covers, but is not attached to, the anterior end of the trunk muscles immediately behind the skull and slopes backward over the adductor and levator operculi; (3) the whole of one side of the dorsal surface of the skull behind the level orbit. The ventro-lateral surface of the muscle is clad by an expanded tendinous sheet, and it is into this sheet that the muscle fasciculi are inserted.

(B) *Pars posterior.* This arises from (1) a strong narrow band membrane which lies behind and beneath the posterior boundary of the muscle. This band commences above at the triangular membrane behind the pars anterior and passes laterad attached to the posterior edge of the skull, then ventrad and cephalad over the origins of the adductor and levator operculi and the insertion of the dilator operculi, and below that is attached to the posterior edge of the quadrate; (2) the lateral surface of the hyomandibular below the dilator operculi and the contiguous surface of the quadrate. As in the case of the pars anterior, the deep surface of the muscle is clad by an expanded tendinous sheet into which most of the fasciculi are inserted.

The two deep tendons taper as they proceed ventrad, laterad and cephalad towards the ascending process of the lower jaw. Before this is reached they combine to form one broad thick tendon. This is inserted onto the edge of the ascending process of the dentary and inner surface of the bone above, lateral to, and in front of, Meckel's fossa. The tendon is completely covered by the fasciculi of the two parts of the muscle, which are here completely fused. The fusion extends backward for a little less than one-third of the length of the contiguous surfaces.

Mugil (Fig. 28).—In this form the temporo-massetericus is represented by a single muscle in which no division is present. It arises from the inferior edge of the quadrate and a contiguous narrow area low down on the preoperculum. It is a relatively small flat muscle, broader behind, which tapers as it passes forward. Its fasciculi are inserted into a tendon which lies along its dorsal edge and which takes the place of the mandibulo-labial ligament and is inserted into the mandibular labial at about the junction of its middle and outer thirds.

Girella (Fig. 29).—(A) *Pars anterior.* This is a roughly four-sided muscle which arises from the preoperculum behind the orbit. It runs forward, under cover of the orbital scutes, below the orbit and has an insertion into the middle of the length of the maxillary labial by a tendon so short as to give it the appearance, almost, of having a pointed fleshy insertion. The deeper fasciculi are inserted into a tendon on its deep surface, which is bound to the maxillo-labial fascia.

(B) *Pars posterior.* This arises from the lower half of the edge of the subdermal ridge of the preoperculum. The muscle is inserted into the maxillo-labial fascia just behind the free margin of the fascia at the angle of the mouth. This insertion is as broad as the full width of the muscle, and is continued onto the ascending process of the dentary above Meckel's fossa on the one side, and is closely bound to the inferior edge of the pars anterior above it on the other.

Zanclistius.—In this fish, as in *Mugil*, there is but a single muscle. It arises from the anterior edge of the upper half of the vertical limb of the subdermal ridge of the preoperculum and from a very narrow area of the bone in front of the edge. It passes nearly horizontally forward to be inserted into the free edge of the maxillo-labial fascia and into the proximal end of the mandibulo-labial ligament.

Drepane.—Here also the temporo-massetericus muscle is not divided. It is an extensive sheet, of moderate thickness, which arises from the whole length of the anterior edge of the ridge of the preoperculum. The inferior fibres pass dorsad and cephalad, the superior and anterior pass ventrad and cephalad. The insertion is into the posterior edge of the peculiarly modified mandibular labial, and into a mandibulo-labial ligament, which also is peculiarly modified. The insertion into the bone is confined to a partially separated anterior bundle of fibres. The mandibulo-labial ligament is attached in front to the middle of the length of the maxillary labial as usual, and passes back to the muscle in a normal manner, but at the anterior margin of the muscle it is met by a tendinous band which passes ventrad and slightly caudad to be inserted on the outer surface of the mandible just in front of the Q-M. joint. The greater part of the upper fibres of the muscle are inserted into the normal part of this ligament, the lower fibres being inserted into the peculiar ventral limb.

Epibulus.—Although the single temporo-massetericus is here not a large muscle, it has a relatively more extensive origin from the reduced preoperculum. The muscle passes cephalad and ventrad to be inserted into a mandibulo-labial ligament, short and normal in its upper portion, but with a much elongated ventral limb inserted onto the outer surface of the mandible, as in *Drepane.*

Tandanus and *Cnidoglanis.*—The muscle has a fibro-tendinous origin from the usual edge of the preoperculum and from a similar raised subdermal edge of the hyomandibular above it. The tendinous fibres of origin penetrate the muscle and give origin to the muscle fasciculi, so that, though quite thin at its origin, the muscle rapidly becomes bulky. Contracting rapidly in front by the insertion of its fibres onto a deeply placed tendon, the muscle is inserted onto the internal surface of the articular above and lateral to Meckel's fossa, and onto the dorsal edge and outer surface of the bone above and external to the fossa.

The muscle is not divisible into anterior and posterior portions, but the deep tendon is in two definite strands.

Gadus callaris.—The temporo-massetericus in *Gadus* presents anterior and posterior parts. Holmqvist (1911) describes the pars anterior as the first, and the pars posterior as the fourth portion of the adductor mandibulae. This latter is completely fused, at its origin, with the underlying M. pterygoideus.

Amia.—The M. temporo-massetericus of *Amia* is that muscle which Allis described as the lower part of the superficial portion of the adductor mandibulae (A2′). It arises from the lower part of the subdermal edge of the preoperculum, and passes forward to be inserted, in part, into the ascending process of the lower jaw, but mainly into the mandibulo-labial ligament.

Polypterus.—(A) *Pars superficialis.* Quoting from Allis—" the superficial portion of the adductor mandibulae . . . has its origin in part on a line of tough connective tissue that is attached to the internal surface of the dorsal border of the cheek-plate, in part on the external surface of the dorsal portion of the hyomandibular and in part on the external surface of that part of the palato-quadrate that lies posterior to the ridge that runs upward across the quadrate from the outer end of its articular edge . . . The fibres of the muscle converge towards the ascending process of the splenial running antero-ventrally, anteriorly and antero-dorsally, and the dorsal and larger part of them are inserted on the dorsal edge of that process and along the internal surface of its hind edge, the ventral fibres passing directly into the ramus of the mandible and there being inserted on the internal surface of the dermarticular." This portion of the muscle lies entirely external to the ramus mandibularis trigemini.

(B) *Pars profunda.* The deep portion of the adductor mandibulae of Allis (1911). This arises from the quadrate in front of the origin of the temporo-massetericus pars posterior. Its fasciculi are inserted into a tendon which is inserted onto the dermarticular behind and below the insertion of the last part.

Innervation.—The ramus mandibularis of the Vth nerve maintains the constant relation to the muscle that we have observed in all the other bony fishes. It passes to Meckel's fossa between the temporo-massetericus superficial to it and the M. pterygoideus deep to it.

THE PTERYGOIDEUS MUSCLE.

Platycephalus (Fig. 27).—The muscle takes origin from the lateral surface of quadrate and os transversum, its postero-dorsal corner extending dorsad and caudad dorsal to the flange on the surface of the latter bone and, in this position, under cover of the levator arcus palatini. The muscle is relatively bulky and it is penetrated by a bipartite tendon into which its fasciculi are inserted, and which, in turn, is inserted onto the inner surface of the articular behind and below the insertion of the pars posterior of the M. temporo-massetericus.

Innervation.—This is by the mandibular ramus of the Vth nerve which comes into view from under the anterior margin of the levator palatini. Its direction is laterad and cephalad along the outer surface of the anterior edge of the os transversum. It passes superficial to the anterior end of the quadrato-mandibularis and enters Meckel's fossa between the tendons of this muscle and of the temporo-massetericus.

Anguilla (Fig. 26).—The muscle arises from the edge of the skull and from the anterior curved surface of the post-orbital bone. It is a relatively small, oblong, flattened muscle which passes from its origin ventrad with an inclination cephalad and laterad to be inserted into the articular below the fossa and internal to the insertion of the pterygoideus.

Innervation.—This is by the mandibular ramus of the Vth nerve. The nerve issues from its foramen in the cranial wall beneath this muscle and runs forward and laterad to appear in front of it just at the outer edge of the palato-pterygoid bone. It passes from sight by burrowing into the pars dorsalis of the temporo-massetericus just anterior to its tendon. It then turns ventrad and comes to lie posterior to the tendon and, running parallel therewith, it finally enters Meckel's fossa below the insertion of the temporo-massetericus tendons.

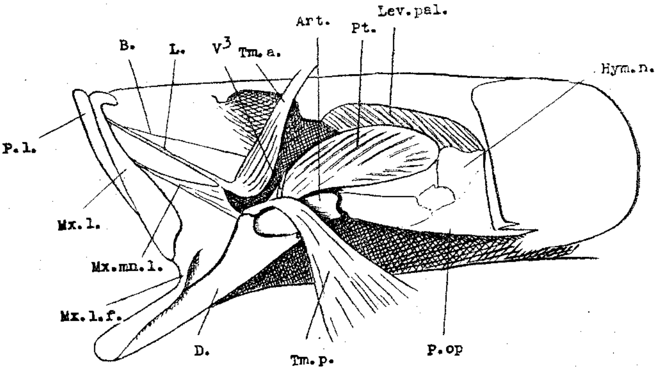
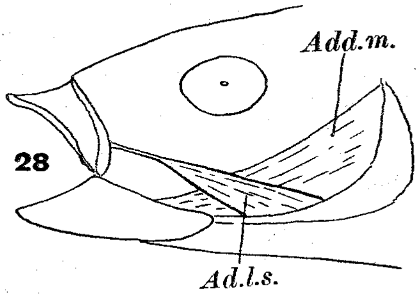


Fig. 27.—*Platycephalus.* The mandibular adductor muscles. Art., The articular bone; B., The line of attachment of the maxillo-labial fascia to the cranial base; D., The dentary bone; L., A separate slip of the maxillo-mandibular ligament; Hym.n., The hyomandibular bone; Lev.pal., The M. levator arcus palatini; Mx.l., The maxillary labial bone; Mx.l.f., The maxillo-labial fascia; Mx.mn.l., The maxillo-mandibular ligament; P.l., The premaxillary labial bone; P.op., The preoperculum.

Mugil (Fig. 28).—The pterygoideus is relatively a very massive muscle in this genus. It arises from the whole of the lateral surfaces of the quadrate, os transversum, and hyomandibular, and from a narrow submerged area of the preoperculum. The fasciculi are inserted into the strands of a brush-like tendon which penetrates the muscle. The point of the tendon " brush " is inserted into the articular behind Meckel's fossa.



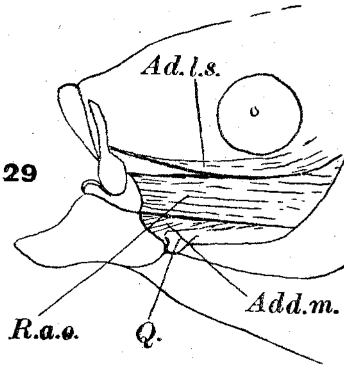


Fig. 28.—*Mugil.* Mandibular adductor muscles.
Fig. 29.—*Girella.* Mandibular adductor muscles.

Innervation.—From the mandibular ramus of the Vth nerve. This may be observed passing across the posterior wall of the orbit from its point of issue from the cranium, laterad and ventrad, and then laterad and cephalad. It crosses the superior surface of the butt of the pterygoid just at the boundary of the muscular portion and commencement of the bare portion of the short tendon of insertion, it then passes deep to the temporo-massetericus muscle and turns forward into Meckel's canal under cover of temporo-massetericus and upon the tendon of the pterygoideus.

Girella (Fig. 29).—The muscle in this genus is smaller than in the preceding, and is largely covered by the two portions of the temporo-massetericus. The origin is from the outer surfaces of the quadrate, hyomandibular and os transversum. The insertion of the fasciculi is into a tendon which is placed deeply and dorsal to most of them, and which, contracting to a relatively broad ribbon, becomes bound to the inferior edge of the tendon of the pars anterior of the temporo-masseetericus and then is inserted along the inferior margin of Meckel's fossa.

Innervation.—Here the mandibular ramus of the Vth nerve issues from beneath the anterior margin of the levator palatini muscle and, turning ventrad, passes superficial to the tendon of the pterygoideus just behind the point of binding to that of the temporo-massetericus pars anterior. It then runs forward, deep to the tendons of the last muscle, parallel with and on the surface of that of the pterygoideus and enters Meckel's fossa.

Zanclistius.—The muscle here appears peculiar because the marked forward inclination of the suspensorium of the lower jaw has thrown the posterior limit of the muscles of mastication beneath the centre of the orbit instead of, as in the majority of the bony fishes, behind the orbit. The origin is from the outer surfaces of the quadrate, hyomandibular preoperculum, and os transversum. The muscle tapers as it passes cephalad and ventrad to its insertion onto the articular behind and above Meckel's fossa. There are three readily separable parts of this muscle. A superficial, which arises from the preoperculum, a deep, which arises from the hyomandibular and quadrate, and a ventral portion, which arises from a very short line at the extreme inferior and anterior end of the subdermal ridge of the preoperculum. The two former portions are flat and placed one beneath the other ; each has a deep tendon into which its fasciculi are inserted. The two tendons are intimately bound together in front of the fasciculi and are also bound to the tendon of the temporo-massetericus. The little ventral portion has an insertion free from the other parts below and behind them.

Innervation.—The mandibular ramus of the Vth nerve runs forward across the floor of the orbit and then cephalad and laterad on the surface of the levator palatini muscle along the dorsal edge of the pterygoideus for half the length of the muscle. It then crosses this last muscle under cover of the temporo-massetericus and turns mediad behind and below the inferior margin of that muscle at its insertion and, reaching the inner surface of the dorsal edge of the articular, passes down and forward to enter Meckel's canal.

Drepane.—The pterygoideus is here an extensive thin, flat muscle which arises from the bones of the suspensorium along their line of suture with the preoperculum. The anterior fibres pass almost directly ventrally, the posterior, or inferior, fibres pass cephalo-dorsally. They all converge to be inserted along the lower margin of Meckel's fossa.

Innervation.—The mandibular ramus of the Vth nerve passes downward and forward across the outer surface of the pterygoideus and under cover of the co-extensive temporo-massetericus to enter Meckel's fossa between the insertions of the two muscles.

Epibulus.—In this rather bizarre fish the pterygoideus is a relatively small muscle which arises from the hyomandibular and os transversum high up and deeply under cover of the levator palatini. The muscle is irregularly quadrilateral in section. It passes cephalad and slightly lateral and ventral, lying immediately below the orbit in front of the levator of the palatal arch, to the transverse level of the front of the orbit. At this point it terminates abruptly in a fine tendon which, bound to the maxillo-labial fascia, turns sharply ventrad and caudad to be inserted into the dentary just in front of the Q-M. joint.

Innervation.—Immediately after it passes laterad from the floor of the orbit the mandibular ramus of the Vth nerve passes over the pterygoideus and below deep to the temporo-massetericus and then runs downward and backward parallel to and between the tendons of the two muscles.

Tandanus and *Cnidoglanis.*—The pterygoideus in these two fishes is a solid muscle which arises from the hyomandibular and metapterygoid. It is clad on its anterior and superficial edge by a tendon into which its fasciculi are inserted. This tendon is inserted into the inferior and posterior margin of Meckel's fossa. An interesting little bundle of fibres arises from the free surface of the tendon close to the insertion and is inserted directly into the articular in front of the insertion of the tendon.

Innervation.—The mandibular ramus of the Vth nerve is here like all other nerves in these fishes, of a truly remarkable size. It passes down and forward under cover of the temporo-massetericus along the upper edge of the pterygoideus, crosses this last just before its insertion, and enters Meckel's fossa between the two tendons.

Amia.—I include as parts of the M. pterygoideus, the first, second and third parts of the levator maxillae superioris of Allis, the major portion of that which he designates the superficial part of the adductor mandibulae and his deeper portion of the same muscle.

(A) *Pars anterior.*—This is that which Allis describes as the third part of the levator maxillae superioris. It arises from the lower part of the edge of the prefrontal and contiguous part of the maxilla close to its posterior edge. The muscle is relatively short and flat, and ends abruptly in a slender tendon which is inserted above Meckel's fossa onto the ramus of the lower jaw.

(B) *Pars medialis* (Lms.^{1}, Lms^2 of Allis). This muscle arises in a situation closely similar to the single part of the pterygoideus in *Epibulus* and, in general, corresponds to that portion of the muscle which, in many of the bony fishes, arises under cover of the levator palatini from the upper end of the hyomandibular. The forward extension of the levator of the palate in *Amia* gives this part of the pterygoideus an unique appearance, which is, however, not in any sense truly peculiar.

(C) *Pars posterior* (Add$_2''$ and Add$_2'''$ of Allis). This arises from the outer face of the preoperculum dorsal to the origin of the pars posterior of the temporo-massetericus, and from the lateral surface of the skull behind the orbit.

(D) *Pars profunda* (A$_3$ of Allis). This arises from the outer surface of the hyomandibular, below the levator palatini, and the outer surfaces of the quadrate and metapterygoid. These two parts of the muscle are strictly comparable with the two major portions of the muscle in *Zanclistius*.

Insertion.—The fasciculi of all three parts are inserted into tendons which arise in brush-like fashion within each part. These tendons are bound together close to the ramus of the jaw and are attached to the ascending process and to Meckel's cartilage around, but mostly dorsal to and in front of, the entrance to Meckel's canal.

Innervation.—In *Amia*, as in the more modern Teleosts, the muscle is innervated by the ramus mandibularis of the Vth nerve. The exit of the nerve from the orbit is somewhat peculiar in that it passes out just under the roof of the orbit, instead of across the floor or around the posterior wall and then along the floor diagonally laterad and cephalad as in all the other fishes I have described. In passing from the orbit the nerve comes to lie on the anterior end of the pars anterior and crosses that to pass superficial to the pars medialis. At the upper edge of the temporo-massetericus it dips under that muscle and runs ventrad between it and the pterygoideus pars medialis and profunda, finally entering Meckel's canal between the tendons of the pterygoideus, on the inner side, and the temporo-massetericus above and lateral to it.

Polypterus.—Two portions of the muscle are recognizable.

(A) *Pars anterior* (musculus pterygoideus of Allis). This arises from the side wall of the skull ventral to and also in front of the main trunk of the Vth nerve. From this origin it passes laterad, ventrad, and slightly cephalad, to be inserted into the internal surface of the dermarticular, its tendon being bound not only to that of the temporo-massetericus pars anterior above and in front of it, but also to that of the pars profunda of the pterygoideus below and behind it.

(B) *Pars posterior.* This is the "temporalis" muscle of Pollard (1892) and Allis (1922). Quoting from the latter (p. 253), "The musculus temporalis has its origin from the ventral surface of the posteronotosphenotic, from the supraorbital band of cartilage, and from that part of the ventral surface of the frontal that roofs the supraorbital fontanelle, the surface of origin of the muscle extending forward to the transverse plane of the foramen opticum. From this long surface of origin, the fibres of the muscle run postero-ventrally, ventrally and antero-ventrally, and passing external to the rami ophthalmicus profundus and ophthalmicus superficialis trigemini, and internal to the rami maxillaris and buccalis trigemini, are all inserted on the external surface of a tendinous band which lies between it and the musculus pterygoideus and which gives insertion, on its internal surface, to the fibres of the latter muscle. This tendinous band passes internal to the ramus mandibularis trigemini, and, diminishing in width, is inserted on the internal surface of the dermarticular."

Review.

There are a few mandibular muscles, such as the protractor mandibulae and muscles of the barblets in the Siluridae, which are present in only a few fishes and which appear to throw no light on problems of general morphology. If we omit these peculiar or, it may be, simply aberrant, muscles there remain for review and comparison four mandibular muscles only : the levator arcus palatini, the dilator operculi, the pterygoideus, and the quadratomandibularis.

The primordium of the mandibular muscles, the mandibular muscle plate, divides, in both Elasmobranchs and bony fishes, into an upper and a lower portion (Edgeworth, 1911). In the Elasmobranchs the upper portion gives rise to the levator maxillae superioris and the constrictor.

In the bony fishes the upper portion gives rise to the levator arcus palatini and the dilator operculi. From the lower portion, in both groups, the adductor muscles of the jaws are developed, as well as the ventral constrictors; these last we have already dealt with.

There are, in the bony fishes, no other derivatives of the upper portion of the mandibular muscle plate than the two just mentioned. We are, however, not able to state with confidence that the two are completely homologous with those derived from the same portion of the plate in the Elasmobranchs. Although the relation of the dilator operculi and its specialized slip, the spiracularis muscle, in *Polypterus* to the spiracle lends support to the idea that this is the homologue of the elasmobranch mandibular constrictor, it is not quite convincing. We may safely only conclude that either these are homologous with those or that the levator arcus palatini is homologous with the levator maxillae superioris, and the dilator operculi is a new muscle derived from it.

Edgeworth (1911) tells us that, in *Scyllium*, after the separation of the mandibular muscle plate into upper and lower portions, the lower portion forms the adductor mandibulae, and later gains, anteriorly, an additional origin from the suborbital cartilage, and further, that this anterior portion of the adductor separates later, forming the levator labii superioris or adductor β of Vetter, the pterygoideus of this work.

He says of the development of the adductor mandibulae in the bony fishes, that . . . " at first passing from the palatoquadrate to Meckel's cartilage, it undergoes various changes in the specimens examined . . . In *Lepidosteus*, *Amia* and, probably, *Polypterus*, the adductor divides into internal and external portions . . . In *Amia* the internal portion sends forwards a projection from its upper end which forms the muscle connected with the olfactory chamber, the levator maxillae superioris portion 4 of Allis ". Still later " the remainder of the internal portion extends upwards above the level of the palatoquadrate and divides into three parts ". These are the remaining portions of the levator maxillae superioris of Allis.

If, as Edgeworth suggests, the adductor muscle primordium in *Polypterus* divides into internal and external portions, then it would appear that the pterygoideus of Edgeworth, Allis and Pollard, and the temporalis of the same authors, must be derivatives of the internal portion, and those muscles will be homologous with the derivatives of the same portion in *Amia*. I have designated these muscles the partes anterior and posterior of the pterygoideus respectively.

Now it is clear from Edgeworth's account that the pterygoideus of the Elasmobranchs and the pars anterior of the pterygoideus in these two bony fishes are developed in a very similar manner from similar portions of the adductor muscle primordium, although it also appears from the same account that the pars anterior anlage of the pterygoideus does not grow forward as in the Elasmobranchs, but is developed a little later from the deeper layer of the general primordium and extends upward.

Reviewing briefly the adductor muscles of the bony fishes: The temporo-massetericus may be present in one or in two portions which may be quite separate or may be fused to very varied degrees. Of these parts the anterior may arise from the skull in front of the orbit (*Amia* and *Polypterus*) from the skull behind the orbit (*Anguilla*) and/or from the bones of the suspensorium (the majority of the bony fishes). The posterior part arises from the bones of the suspensorium.

The pterygoideus may be present as a single more or less massive muscle, or may be more or less completely divided into two, three, or more portions which are more or less fused, one with the other. Of these various portions, one arises from the hyomandibular under cover of the levator arcus palatini, a second arises deeply from the bones of the suspensorium, whilst a third, more or less co-extensive with the last, arises from the same series of bones behind it and passes forward superficial to it.

The relation of the mandibular ramus of the Vth nerve, carrying the sensory fibres for the skin area immediately behind the symphysis of the lower jaw, to these two muscles is absolutely constant; it is always superficial to the pterygoideus and deep to or posterior to the temporo-massetericus. In other words the former muscle is always crossed by or lies behind the sensory nerve in question whilst the latter passes superficial to or lies in front of the nerve.

This relation of the nerve to the muscles is the same as that which we observed in the Elasmobranchs, and, so far as the pars anterior in *Amia* and, presumably, *Polypterus*, their development is the same.

We may say with a great deal of confidence that the pars anterior of the pterygoideus muscle in *Amia* and *Polypterus* is homologous with part, at least, of the pterygoid muscle of the Elasmobranchs.

The situation of the pars posterior of the pterygoid in *Polypterus* (temporalis muscle of Allis), deep to and crossed by the maxillary and ophthalmic rami of the fifth nerve, may appear to be evidence against the statement in the preceding paragraph. I would remind readers that such a relation to those nerves is presented by the pterygoideus muscle in *Pristiophorus*.

As noted by Edgeworth, Pollard (1892) regarded the pars anterior of the pterygoideus (pterygoideus of Pollard) as well as the pars posterior of the pterygoideus of the Elasmobranchs. Edgeworth says that neither of them can possibly be homologous with that.

It probably needs no argument to establish the complete homology of the pars posterior of the temporo-massetericus throughout the bony fishes, but it is not so obvious that the pars anterior of the modern Teleosts is homologous with that of *Amia* and *Polypterus*.

The evidence in favour of this is, admittedly, not entirely convincing. It is, however, believed that the constant relation to the nerves and constancy of function as the retractor of the upper lip are important pieces of evidence in support.

The dissection of the many forms I have been fortunate enough to obtain has convinced me that the two portions of the muscle throughout the bony fishes are truly pterygoid muscles, and the following is advanced in support, and also as explaining how the conviction has arisen.

It is believed that there is no room for doubt that the pterygoideus muscle in *Rana* and *Amblystoma*, or indeed the Amphibia generally,is completely homologous with that of the Dipnoi. Again there is little reason to doubt that the muscle in, e.g. *Ceratodus*, is homologous with that of the Holocephali. That the muscle in *Callorhynchus* or *Chimaera* is homologous with that of the Selachii seems amply and convincingly proven by comparison with that of such forms as *Chiloscyllium*, *Pristiophorus*, and *Mustelus*.

Here is proof that, in the Amphibia, the muscle has acquired an origin behind the orbit, and in acquiring that origin it has maintained the relation to the submental terminal branch of the sensory components of the mandibular ramus of the Vth nerve.

It is its origin behind the orbit that alone raises doubts as to its homology with the pterygoideus muscle in the Elasmobranchs.

The doubts which arise from this factor are, however, to a large extent dispelled by consideration of the varying position of their origins relative to the orbit which the adductor muscles exhibit amongst the Teleostei.

In *Balistapus* (Fig. 29*a*) and its allies not only the temporo-massetericus, but also a part of the pterygoideus, arises anterior to the orbit. In *Gonorhynchus* (Fig. 29*b*) and a number of other fishes the origin is from the inferior margin of the orbit, from one of the suborbital scutes. In *Girella* and very many other typical acanthopterygian genera the origin of the muscles is from the cranium behind the orbit (Fig. 29*c*). Finally, in a very large number of the Teleosts, the origin of the temporo-massetericus is from the hyomandibular, quadrate or preoperculum. *Mugil* may be accepted as exemplary of this last group (Fig. 29*d*).

In view of the fact that the temporo-massetericus muscle has, very definitely, its origin anterior to the orbit in some Teleosts and, just as definitely, behind it in others, it seems that one may, quite reasonably, accept the view that in similar manner the pterygoideus has acquired an origin behind the orbit in the tetrapods.

In conclusion it may be stated that in the Cockatoos the pterygoideus has its origin in front of the orbit.

THE INNERVATION OF THE EYE MUSCLES.

After discussing the serial homologies of the muscles of the hyoid and mandibular arches it is desirable to endeavour to understand the fate of the dorsal portion of the mandibular and hyoid muscle-plates. These, in certain of the vertebrates, are intimately related to the development of the rectus externus and oblique superior eye muscles.

v. Wijhe (1882), and later Neal (1914), regarded the eye-muscles as remnants of the trunk myotomes of the premandibular, mandibular hyoid segments, or at least of the myotomes anterior to the auditory.

Whilst agreeing with this interpretation I find myself unable to accept v. Wijhe's interpretation of the IV, V, VI and VII nerves. Edgeworth also has offered an interpretation of these nerve muscle associations, and this too I find unsatisfying.

I have tabulated below the history of the development of the eye-muscles in the different vertebrate groups. Their innervation needs no tabulation.

Following that tabulation I offer still another interpretation of the facts.*

The eye muscles are developed from :

the first three myotomes in	the first two in	the first only in
	Teleostomi	Dipnoi
Plagiostomi		Urodeles
	Sphenodon	Anura
	Lacertilia	
	Ophidia	
	Chelonia	
		Monotremata
		Marsupialia
		Mammalia

These facts may be presented with more detail as follows :

	Superior, inferior and external and inferior oblique recti. are developed from the :	Superior oblique.	Internal rectus.
Plagiostomi	P	M	H
Acipenser	P	M	M
Amia	P	M	M
Lepidosteus	P	M	M
Dipnoi	P	P	P
Urodeles	P	P	P
Anura	P	P	P
Sphenodon	P	M	M
Lacertilia	P	M	M
Ophidia	P	M	M
Chelonia	P	M	M
Monotremata	P	P	P
Marsupialia	P	P	P
Mammalia	P	P	P

P = premandibular somite. M = mandibular somite. H = hyoid somite.

The interpretation I would offer of these facts is as follows :

Primitively the eye-muscles were but four in number, all developed from the premandibular somite, and innervated by the third nerve, which was the proper motor nerve of the segment. Later, as a result of the extreme flexion of the head, brought about by the unequal growth of the brain segments, this first myotome was brought close to the second and third myotomes dorsally. They were in this situation crowded together and two extra eye-muscles were developed from the contactual apices of these other two myotomes and they were innervated by branches of the third and fourth segmental motor nerves, namely the V and VII.

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* In approaching this question I am quite unable to accept Edgeworth's dictum—"that no theory (explaining the development of the eye muscles) will be found satisfactory which does not also take into account the phenomena in Dipnoi, Urodela and Ganoids and this without any underlying supposition that the conditions in Selachii are necessarily the most primitive, and others found are modifications of them".

Professor Edgeworth has, like myself, devoted many years to the intensive study of the anatomy and development of the vertebrate head, and our writings indicate that we are neither of us prepared to be bound by accepted opinion, but are distinctly radicals in the field we have chosen. It is, therefore, interesting to observe that very similar lines of study should have led us to adopt such different attitudes on this fundamental question. It serves to illustrate very forcibly how important a factor is the personal in any equation which attempts to set forth evolutionary values.

Confining myself to the field in which I have toiled most assiduously, I would point to the very generalized condition of the wholly cartilaginous skull, the simplicity of the nasal and auditory capsules, the simplicity of the brain itself, and especially of the prosencephalon, and finally to the generalized form of the branchial and masticatory frameworks and their musculature. When to these there be added the geological antiquity of the Elasmobranchs, undoubtedly greater than that of any other vertebrates, it seems to me that it were little short of unreasonable not to regard them as more primitive, more nearly reflecting the anatomy and development of the common ancestor of all vertebrates, than any other form available for study today.

One looks forward with interest to reading a detailed exposition of the factors of anatomy and embryology that led Professor Edgeworth to adopt the view he does.

When, later in development, the head was straightened out, the main body of the mandibular and hyoid muscle-plates became completely divorced from the small apical portion. Whilst the main mass resumed its original position, the apical portions retained the new. At the same time there was a relative backward movement of the motor nerve nuclei within the brain. In the result there has been in each generation a relative pull forward on the motor twigs of V and VII, supplying these new eye muscles, which pull is assumed to have brought about the relative forward movement of the nuclei of those twigs, producing nerves IV and VI.

The development of the eye-muscles in the Plagiostomi completely explains the presence of three motor nerves. Though there is lost to us the stage in which the two newer muscles are related to the other muscle-plates in the higher vertebrata, the three nerves clearly indicate the plurality of origin and prove that the embryonic plate in these forms is a composite one.

The conditions in the Teleostomi and the Reptilia present an intermediate stage in which the apex of the hyoid myotome has been, as it were, transferred to the mandibular before tissue differentiation permits of its detection. The fusion of the apical portion of the mandibular and premandibular myotome is the only trace left of the transference of the two dorsal buds together in the development of the muscles in the Amphibia.

The developmental history of the eye-muscles in the Plagiostomes *per se* does not explain the extra motor nerves in certain of the brain segments in front of the auditory vesicle. That explanation is offered by my proposed interpretation of the facts, and it simplifies the problem of the reconciliation of brain and head segments. There would be, according to this interpretation of mine, only three segmental motor nerves in the three segments of the brain in front of the eighth : the premandibular (III), the mandibular (V), and the hyoid (VII).

Both V and VII are to be regarded as having each a branch which has a course entirely independent of the rest of the nerve, namely the IV and VI nerves.

Here, is neither time nor place to enter on an extended discussion on the segmentation of the head and brain, but it is permissable to point out that there are unique features in the generally accepted interpretation of just these neuromeres and their related somites. According to that interpretation these somites differ from all the other somites in the body in that they possess completely independent somatic and visceral motor nerves. Here, are two somites provided with four motor nerves and for two of these nerves, IV and VI, there are no corresponding sensory nerves. Moreover, it is not possible to regard the motor components of V and VII as entirely visceral, for they innervate some muscles which are neither anatomically nor developmentally visceral. This introduces the further anomaly that though one of the motor nerves to each somite is a mixed visceral and somatic nerve, there is yet another somatic motor nerve to each of the somites.

These conclusions may be presented in tabular form :

Neuromere ..	I	II	III	IV	V	VI	VII
Somite ..	?	?	?	?	Pre-mandibular	Mandibular	Hyoid
Motor nerve					III	V+IV	VII+VI
Sensory nerve					Ophth. prof.	V	VII

THE SKULL IN THE ELASMOBRANCHS.

In the head skeleton or skull several distinct entities are more or less closely knit together. They are : 1, the brain capsule, or cavum cranii,* 2, 3 and 4, more or less complete capsules for the lodgement of the three paired organs of the special senses of sight, hearing and balance and of smell, 5, a series of paired and unpaired fused and/or articulated elements related to the jaws

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* The term cranium has been used generally to designate the brain and auditory capsules ; it is impossible, owing to their intimate fusion, to describe either of these separarely in the great majority of instances, because the inner wall of the one is so commonly the outer wall of the other. It is in this sense that the term will be used throughout this work. On the other hand the designations chondrocranium and primordial cranium are usually used to include all the components of the embryonic cartilaginous head skeleton, and with that general application the terms will be used in this work. In some instances, more particularly primitive forms, the description and/or illustration of a cranium will of necessity also include the nasal capsules. The term cavum cranii is used to indicate the brain case only.

and palate and serving the function of mastication, and 6, a series of paired jointed rods which together constitute a set of branchial or visceral arches related, primarily, to branchial respiration.

Of these various entities the auditory or otic capsule, which lodges the organ of hearing and balance, is always attached to and incorporated with the side wall of the cavum cranii towards its hinder end. The nasal capsules, situated in front, are also always attached to the cranium, and with it form part of a cartilaginous or bony continuum. The attachment is more direct and intimate, in the cartilaginous skull, in the more primitive forms. Whilst these two capsules more or less completely enclose their respective organs, the optic capsule is relatively incomplete. In cartilaginous skulls it is commonly but a bay or recess between the other two capsules in front and behind and the cranial wall medially. To these, more or less adventitious walls, there are added more or fewer flanges or processes, which more or less completely enclose the organ, except, of course, on its outer aspect. The optic capsule or orbital socket is, generally speaking, more complete in the bony than it is in the cartilaginous skulls.

In addition to the above six entities there are in many primitive skulls certain paired labial skeletal elements related to the outer aspect of the anterior masticatory components and nasal capsules. Further there are incorporated with the hinder end of the cranium more or fewer vertebrae. In some cases this incorporation is of such a kind that the vertebral origin and nature of the incorporated portion is quite obvious ; in others the original character of the vertebrae is entirely lost, and the evidence of the incorporation has to be sought, not in cranial morphology, but in the relation of certain nerve roots to the cranial wall.

It is desirable that a discussion on the form of the adult cartilaginous skull should open with a description of the most generalized type available. Such a form is presented by almost any typical Selachian. Our illustrations are based on the skull of a five foot specimen of *Carcharias arenarius* Ogilby (Figs. 30, 31, 32 and 33).

The cranium of this Selachian is a continuous cartilaginous structure, in which one recognizes at once the large auditory capsules incorporated into the side wall posteriorly and the outstanding nasal capsules in front. Between these two the orbital recess is very imperfectly converted into an optic capsule by a laterally projecting horizontally flattened ant-orbital process, a rod-like, downwardly projecting post-orbital process which terminates below in a bifurcation, and a more or less incomplete floor, the suborbital process.

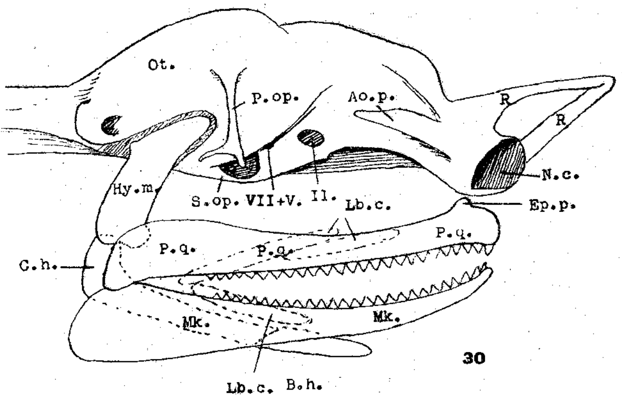
The brain capsule itself presents no division into parts or regions, but is a continuous cavity of varying size. Narrow behind, where it communicates with the vertebral canal, it becomes enlarged as it extends forward, and is widely open in front. Just in front of this wide anterior opening of the cranial cavity, there are, on each side, the medial apertures of the nasal capsules. These last are relatively simple, somewhat barrel-like structures having an opening medially towards the cranial cavity, and another, at the other end of the barrel, which is directed forward and down. A rostral process, developed to a variable extent in all Elasmobranch skulls, is represented in our example by one ventral median and a pair of dorsal processes which are all three united together anteriorly.

Although the cranium is not divided into regions, there are certain perforations in its side wall and a fossa on its floor to which we must pay particular attention, because they are important landmarks. These perforations are the foramina of exit of the cranial nerves, and of ingress of the main cerebral artery. The fossa is the sella turcica or pituitary fossa and lodges the hypophysis cerebri. These foramina and this fossa and the structures which they lodge or transmit bear very constant relations throughout the whole vertebrate series to both brain and skull areas and components. They are therefore trustworthy and reliable features on which to base identifications of these skull areas and components.

By the pituitary fossa the cranial cavity is clearly marked off into " prechordal " and " chordal " or " parachordal " areas, the former lying in front of the anterior end of the notochord, the latter behind that point. These, it will be found, are exceedingly important divisions of the cranium.

On either side of the pituitary fossa in, or close to, the floor of the cranium will be found the two carotid foramina. These admit to the cavity the terminal cerebral branch of the internal carotid artery. Their position is remarkably constant throughout the whole of the vertebrates, and they are of prime importance as assisting us to recognize the homologies of certain related structures.

Of the nerve foramina present in our example, the more important are those for the second, fourth, fifth and seventh together, eighth, ninth and tenth. The smaller apertures for the third and sixth nerves are not of comparative craniological importance in the more primitive skulls.



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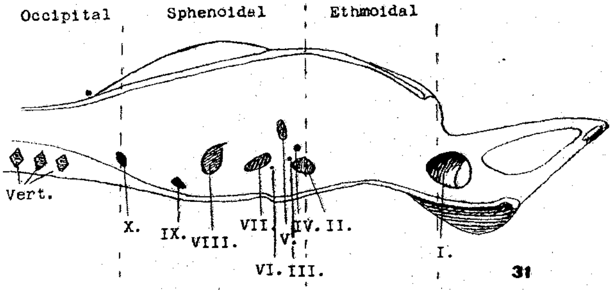

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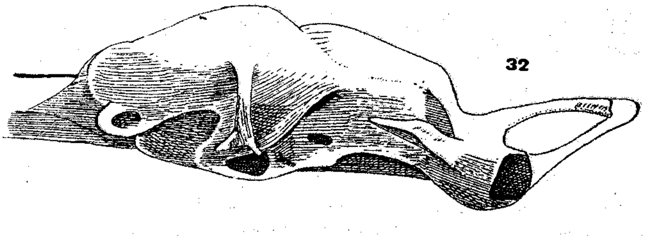

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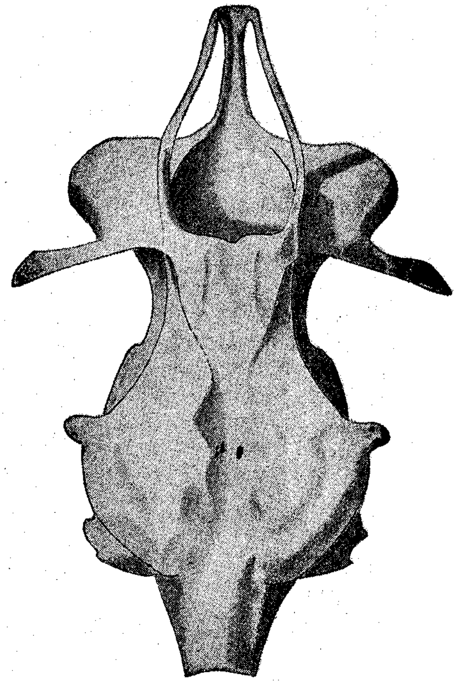


33

Figs. 30, 31, 32, 33.—*Carcharias*. Ao.p., Antorbital process; B.h., Basihyal; C.h., Ceratohyal; Ep.p., Ethmoid process; Hy.m., Hyomandibular cartilage; Lb.c., The labial cartilages, indicated by dotted lines; Mk., Meckel's cartilage; N.c., Nasal capsule; Ot., Otocrane; P.op., Postorbital process; P.q., Palatoquadrate; R., Rostrum; S.op., Suborbital process; Vert., Intervertebral discs; I-X, The foramina for the cranial nerves.

The external apertures of the second, third, fourth, fifth, sixth and seventh nerve foramina will be found on the inner wall of the orbital recess, that for the fifth and seventh being the most posterior and situated just in front of the otic capsule. The foramen for the eighth, the auditory, nerve perforates the inner wall of the otic capsule. That for the ninth emerges just behind that capsule and the tenth is placed still further back. In addition to the above foramina there is present a special foramen for the transmission of the superficial ophthalmic branches of the fifth and seventh nerves. This is situated above and in front of the other foramen for those nerves.

When the otic capsule is entered, it is found to be incompletely divided into compartments which lodge the three semi-circular canals, the sacculus and the utriculus, portions of the auditory organ.

The anterior aperture of the cranial cavity is known as the anterior cranial fontanelle ; it is present in the majority of elasmobranch crania. In the flesh it is closed by a tough membrane which is attached to the side walls and floor in front of the internal apertures of the nasal capsules, which are designated the olfactory foramina.

The nerve foramina are designated for the most part by the nerves they transmit. Thus the second nerve leaves the cranium through the optic foramen, the fourth through the oculomotor foramen, and so on. The foramen for the exit of the main branches of the fifth and seventh nerves is an exception to this rule. There is a good deal of variation in the composition of the nerve trunks which, in the different classes, pass through it, and, moreover, its position immediately in front of the otic capsule is one of such constancy and importance to the student of homologies that it has been designated the *foramen prooticum.* It will be found that in certain forms the prootic foramen is converted into a prootic notch, *incisura prootica,* by the absence of a complete front wall, and cranial roof above it.

For descriptive purposes the cranium may be divided into three regions known respectively as the occipital behind the vagus or tenth nerve foramen, the sphenoid between the vagus and optic foramina, and the ethmoid in front of that last foramen. These names have been derived from certain bones which are constantly related, in bony crania, to the respective areas, and although the bones in question are, some of them, variable in their extent, and indeed at times invade regions both behind and in front of their own proper spheres, still the designations have for the student of comparative craniology very definite applications and are as useful as definite.

The skeletal structures of the skull related to the function of mastication and those related to the branchial basket together constitute the seven visceral arches.

The first visceral arch is the mandibular, or more correctly the maxillo-mandibular. It presents on each side dorsal and ventral halves. The dorsal is variously designated the palato-pterygo-quadrate, the palato-quadrate, and the sub-ocular arch. The ventral half is the mandibular arch, using that term in its restricted sense, or Meckel's cartilage.

The second is known as the hyoid arch, also divided on each side into dorsal and ventral halves ; the upper half is the hyomandibular and the lower commonly designated the hyoid bar, but which commonly is divided into upper, ceratohyal, and lower, hypohyal, portions. The hypohyal elements of the two sides are united to a median ventral basi-hyal or hyoid copula.

The remaining five arches are the branchial arches, each divided on both sides into four segments ; from above down these are pharyngo-, epi-, cerato-, and hypo-branchial cartilages. As in the case of the hyoid arch, so in each of the branchial arches, the ventral segments of the two sides are united to a median ventral basibranchial. More or fewer of the basibranchials may be united into a continuous basibranchial plate. The posterior basibranchial is commonly prolonged posteriorly and has been designated the cardio-branchial, in recognition of its relation to the heart.

The branchial arches are loosely slung to the skull, for the most part by muscular attachments only. The hyomandibular cartilage is, on the other hand, firmly, though movably, articulated to the inferior surface of the otic capsule. Its inferior end is similarly bound to the posterior end of the palato-quadrate cartilage, either directly or, in the Chondrostei, by the intermediation of a little symplectic cartilage ; it is also bound to the upper end of the ceratohyal cartilage.

The palato-quadrate cartilage is firmly bound by a stout fibrous ligament, but without a true joint such as is present between the hyomandibular and the otic capsule, to the cranium behind and below the nasal capsules. This is known as the ethmo-palatine ligament, and may be attached to a similarly named process on the upper aspect of the palato-quadrate cartilage. The palato-quadrate is articulated posteriorly to the hinder end of Meckel's cartilage. The two cartilages together form the upper and lower jaws on each side. The jaw cartilages of the two sides are very firmly united in a median symphysis in front.

The labial cartilages are one, two, or three in number on each side, two enclosed in the upper lip and one in the lower. The anterior upper cartilage is commonly attached to the posterior, and this in turn may be attached by its posterior end to the posterior end of the lower labial cartilage.

In addition to the branchial elements mentioned above, there are commonly present a variable number of extra-branchial cartilages attached in varying modes to the separate arches. These extra-branchials are of taxonomic value, but are for the most part devoid of any significance to the student of the wider problems of homologies and of evolution.

Having described the skull of *Carcharias* in rather general terms we may describe that of one of the Rays, *Urolophus,* with more specific intent. It will serve as a second example of the " Selachian " type.

The cranium has a definitely dorso-ventrally compressed appearance. The three struts of the rostral process may be described as having been united by membranous sheets of cartilage so as to produce a trough-like rostral process, V-shaped in both cross and horizontal sections, and widely open above. The nasal capsules are very similar to those of the preceding form, but the ventral, external, aperture is so extensive that there is no floor. A curved flange of cartilage is attached along the inner half of the upper and posterior edge of the nasal capsule. This flange is nearly vertical but, with a slight backward lean, it swings round onto and then along the outer edge of the cranium above the orbit, it gradually inclines more into the horizontal plane and is continued right back along the outer edge of the otocrane, or otic capsule. There is a narrow suborbital flange attached to the lateral edge of the cranium inferiorly. This merges into a stouter lateral occipital process posteriorly. This last is surmounted by a little arch which springs from its outer edge and bends inward to be attached to the side wall of the cranium behind the otocrane.

The cavum cranii is not divided into regions, except in so far as such are indicated by the nerve foramina. The foramen prooticum is large, and in some of the Rays is divided into two. The internal auditory meatus, foramen for the eighth nerve, is placed low down, almost right in the angle between floor and wall.

The otocrane is small and compact. The nasal capsule is large.

There are no periorbital processes other than the flanges already described.

The visceral arches conform absolutely to the selachian type, but the ethmo-palatine ligament and process are not present. In the result the jaws have a greater mobility than have those of the Sharks. Certain of the muscles of mastication are especially modified to give purposive direction to this increased mobility, and the two jaws together with the lips are, by these muscles, capable of being bodily protruded. The Chondrostei closely resemble the Rays in these features.

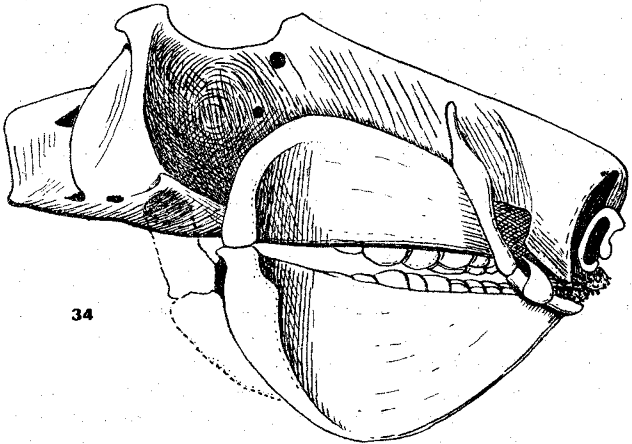
Heterodontus.

(Figs. 34, 35.)

The skull of *Heterodontus portus-jacksoni* with the palato-quadrate in position presents a peculiar resemblance to the skull of the Holocephali. This resemblance is largely destroyed by the discovery that the upper jaw is not continuous with the cranium but only attached by an ethmo-palatine ligament more extensive than usual. Even so, there still remain marked resemblances. The orbit is placed relatively far back, as in the Holocephali, and masks the otocrane behind it, and further, as in these forms, the orbit is tolerably complete and well defined, with all the nerve foramina from the second to the seventh on its inner wall. There are two complete canals for the superficial ophthalmic branches of the seventh nerve in precisely the position of those canals in *Chimaera* and *Callorhynchus.* There is, however, no median dorsal crest to this skull, and the absence of the crest leaves the canals open dorsally.

The anterior cranial fontanelle lies in the horizontal plane ; this is because the skull roof is carried forward on either side and forms an incomplete roof for the sphenoidal cavity in front of the cavum cranii proper. In front of the sphenoidal cavity the skull presents a peculiar resemblance to that of *Neoceratodus.* The roof of the nasal capsules is laterally expanded in the same plane as the roof of the sphenoidal cavity. The two together have the same triangular outline, as viewed from above, as the two nasal roofs in the Dipnoan, and they are similarly thin and fenestrated, the fenestrations being confined to near the front margin. A central furrow separates the nasal roofs of the two sides, and below this furrow there is placed the internasal septum. The furrow is continued right forward to the tip and then passes down and onto the inferior surface of the septum. The septum is as deep in front as it is at its origin behind. Inferiorly it bears, on either side, along its length, a narrow horizontal process which forms a very incomplete median nasal floor (solum nasi). The lateral margin of the nasal roof is turned down and forms a postero-lateral wall, of full depth, to the capsule. Anteriorly the ventral margin of this wall turns medially into the horizontal plane, resulting in the formation of an incomplete lateral area of nasal floor.

Each nasal cavity is, then, triangular as viewed from above or below. Two sides of the two triangles lie parallel, along the mid-line, the nasal septum. The bases of the triangles are forward and slightly outward. The angle which each forms with the mid-line is approximately 80°. The angle which the postero-lateral side forms is approximately 40°. Dorsal and ventral sides are nearly flat and in parallel planes. There is little of the anterior wall and very little floor; the other walls are complete. The vertical walls become concave towards the depth of the cavities, so that looking into the apex of the triangular cavity one observes a circular olfactory passage which opens directly into the sphenoidal cavity.



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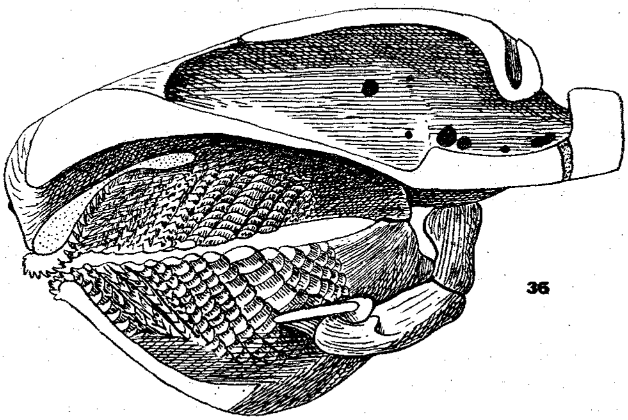


35

Figs. 34 and 35.—*Heterodontus*.

In *Gyropleurodus galeatus* Gill, the dorso-lateral margin of the sphenoidal and cranial cavities carries, on each side, a vertical ridge. Low in front, where it commences immediately above the olfactory passage, this becomes more elevated as it passes back. The two ridges incline towards one another as they pass the middle of the length of the sphenoidal cavity, and then diverge again as the brain cavity widens just in front of the orbit. Here the ridges incline outward and backward, forming the anterior boundary and roof of the orbit. They now approach one another rapidly and decrease in height. Then, bending abruptly outward, they merge with a similar flange which rises in the transverse axis of the skull from the antero-dorsal margin of the otocrane and incline forward over the back of the orbit.

The incomplete canals for the superficial ophthalmic branches of the seventh nerves lie on the roof of the sphenoidal cavity against the inner side of these ridges. The nerves in question enter the orbit relatively high up behind and, after passing forward against the inner wall, perforate the anterior wall to reach the canals exactly as they do in the Holocephali.

In *Heterodontus* the dorsum of the skull is much more simple. Commencing anteriorly, the broad triangular roof of the nasal capsule narrows behind and merges into a narrow horizontal shelf which contributes to the incomplete roof of the sphenoidal cavity. Behind that cavity the shelf widens both mediad and laterad, joining its fellow of the other side behind the anterior cranial fontanelle to form the complete roof of the cranial cavity proper and overhanging the orbit laterally. There is a narrowing again at the posterior boundary of the orbit, which is also the anterior boundary of the auditory capsule. Behind this point there is a marked widening of the dorsum, above the two auditory capsules. At the posterior limit of this capsule the dorsum gives place abruptly to the posterior (almost) vertical wall. The posterior slope is broken across the mid-line by a narrow pit into the depth of which there opens on each side the ductus endolymphaticus.

The side wall of the cranial cavity is very complete, the inner wall of the orbit is almost entirely cartilaginous, and there is a narrow membranous margin to the optic foramen, in place of the relatively extensive deficiency usually found in this region in elasmobranchian skulls. The pituitary fossa and post-clinoid eminences are obvious features on the floor of the cranium. The latter is, as it were, swung onto the side wall, and the rounded eminence that results forms the anterior boundary of the foramen prooticum. At the side of the floor of the pituitary fossa is the foramen oculo-motorius, and above and in front of this the optic foramen. Below and behind the foramen prooticum is a veritable meatus acusticus internus, with its internal facial foramen in front and the auditory foramen behind at its base. Behind this again is the relatively small glossopharyngeal foramen with the larger vagus foramen behind it.

On the lateral external surface of the skull, the last two passages lead out into relatively large glossopharyngeal and vagal fossae, which are situated on the infero-lateral and anterior corner of the capsule. At the infero-lateral and anterior corner of the capsule there is the large triangular joint buttress to which the head of the hyomandibular cartilage fits. Immediately above this, and formed by the strengthening flange of its upper margin, there is a broad shallow groove across the lateral and anterior edge of the capsule. This is the incisura venae capitis lateralis which is quoted in the text as the defined point in the description of the origin of certain of the hyoid and mandibular muscles. The orbit has very incomplete floor and roof, no anterior wall, but a complete posterior wall formed by the otic capsule. An antero-lateral wall is formed by the upper part of the palato-quadrate. The foramen prooticum externum is placed about the middle of the height of the orbital recess immediately in front of the antero-medial edge of the auditory capsule. Just below it is the external aperture of the facial canal. Just in front of it is the external aperture of the canal for the internal cerebral artery. This runs transversely beneath the investment of the front of the post-clinoid eminence and joins its fellow of the other side. Each gives off two branches : one as soon as the canal has penetrated the cranial wall—this is very short and opens at once through the fibrous investment ; the other, just to one side of the centre line, runs ventrad against the clinoid wall under the fibrous investment and divides. One branch opens at once at the side of the pituitary body, the other passes through the pituitary fenestra. The external oculomotorius foramen is in front of the arterial foramen. Quite a large foramen in the floor of the orbit, in front of the external facial and below the oculomotorius, transmits the ramus ophthalmicus profundus VII.

Posteriorly the lateral edge of the floor of the orbit is a ridge ; when this ridge, inclining medially, meets the side wall of the skull at the front of the orbit, it becomes converted into the lower wall of a groove which runs forward and mediad under the floor of the sphenoidal cavity to terminate beneath the posterior end of the olfactory canal. This groove is fitted by nearly the middle one-third of the upper edge of the palato-quadrate.

The nasal capsules have little anterior wall formed directly from the primordial cranium, but they have an adventitial anterior nasal cartilage which strengthens the anterior wall very efficiently. The nasal septum may be said to be split into two vertical halves just as the anterior end ; these halves diverge and curve laterad, extending further inferiorly, then superiorly. The roof bends ventrad anteriorly, terminating in a narrow vertical fringe. As viewed from in front, the free edges of the nasal walls present a superior margin which slopes from the centre laterad and ventrad, and ends by curving mediad. The median margin is nearly vertical but with a slight inclination laterad. Inferiorly the margins do not meet. The peculiarly shaped adventitious nasal cartilage fits the outer curve of the edges and extends mediad in contact with the superior margin. About the centre of that margin it abruptly bends ventrad and mediad, leaving an unfilled triangular gap medially. The arm of the cartilage which bends mediad and ventrad is bifurcated; the larger arm is that which gives direction to the cartilage, and it is attached to the inferior and lateral corner of the out-turned anterior end of the nasal septum. The smaller arm curves around in the vertical transverse plane so as to complete half a circle and ends freely, turning back to the outer piece of the cartilage, which fits the outer curve of the capsular margin. This is also bifurcated, but in this instance the two arms are placed one behind the other. The posterior arm fits against the free ventral and median margin of the incomplete lateral nasal floor. The other, and lesser arm, projects forward somewhat close to, but free from, the laterally projecting small median arm. The cartilage as a whole then may be described as an incomplete hoop whose ends are bifurcated. This hoop surrounds the nasal aperture.

Callorhynchus antarcticus.

The skull of *Callorhynchus* has already been fully described and illustrated (Kesteven, 1933).

The Skull of the Chondrostei.

The development and adult form of the skull of the Sturgeon was described by Parker (1882). Bridge described the skull of *Polyodon* (1879). *Scaphyrhynchus* is essentially similar to *Acipenser*, and *Psephurus* as closely resembles *Polyodon*.

There are, then, two distinct types of recent chondrostean fishes' skulls and these, whilst fundamentally similar, present marked differences.

Gregory (1933) agrees with the view of Watson and Stensio, that the " partly cartilaginous condition is due to retrogressive development (perhaps to the retention of early larval conditions in the adult)". This last suggestion is, of course, quite contrary to the evidence. The early larval chondrocranium is a very incomplete, fenestrated structure, and it is only in late larval and early adult stages that the chondrocranium is completed. It is pointed out later that the complete cartilaginous skull is not a primitive character, but is the peculiar feature of the Elasmobranchii.

Probably the most important feature wherein these chondrocrania differ from those of the Selachii is the wide lateral cranial fenestra. In this they resemble the Holocephali and the bony fishes.

The nasal capsules, though much reduced in size, are essentially elasmobranchiate in character. They are not, as in the bony fishes, simple depressions on the dorsum of the ethmoidal cartilage but have the typical three complete walls of the sharks and rays and, in addition, a complete floor.

The rostrum is very similar to that of the rays and of such sharks as *Pristiophorus*. This is particularly so in *Polyodon* and *Psephurus*. In these two fishes the root of the rostrum is formed by two sloping narrow plates of cartilage. Each commences above and behind at the antero-lateral corner of the nasal capsule, just as in the plagiostomes, and meets its fellow at the mid-ventral line, forming, as in the Rays, an open V-shaped trough. This trough becomes shallower as it reaches forward, and as the superior edges draw toward the mid-line anteriorly its walls become thicker and, expanding laterally, form the long spathulate anterior portion of the rostrum.

There are, of course, no endochondral bones developed in the skull of either of the Polyodontidae, and the covering bones are, for the most part, of a very indeterminate character. The synpterygoid is the only bone whose identification is completely beyond question. It resembles that of the Dipnoi in that it extends posteriad well beyond the limit of the cavum cranii. Bridge described in *Polyodon*, and figured, a " vomer " suturing with the anterior end of the synpterygoid; there is no trace of this bone in my young specimens of *Psephurus*, nor do I find there any trace of the post-temporal of Bridge's description of the adult *Polyodon*. The lateral wing of the synpterygoid (" basi-temporal ala " of Bridge) is much larger in *Psephurus* than in *Polyodon*; it is not only wider antero-posteriorly, but extends higher on the lateral wall of the otocrane. The bone on the side wall of the cranium which Bridge termed post-temporal has been identified as the prootic by Gregory; this is obviously an incorrect identification. It cannot even be identified as a dermo-opisthotic, for it is placed entirely behind the otocrane.

The roof pattern.—In *Psephurus* there is a median splint which commences above the hinder limit of the cavum cranii and ends anteriorly a little in front of the transverse level of the anterior limit of the otocrane. Very narrow behind, the bone becomes wider in front and is bifurcated.

Between its bifid anterior end and overlapping it another splint is placed. This is almost as wide as the posterior splint where the two overlap between the two auditory capsules, but tapers to a very fine and long filament which runs forward well in front of the orbits.

Over the auditory capsules, on each side, there is a very thin scale resembling that which, in *Polyodon*, Bridge termed dermosphenotic, but differing in that its anterior and posterior lateral splint-like elongations are relatively much longer than in *Polyodon*. This bone is narrow over the capsule, but has quite a long suture with both the median bones per medium of anterior and posterior median splints similar to the lateral but not nearly so long.

The roof pattern of *Polyodon* differs markedly from that of *Psephurus* as I have just described it ; whether this is due to the juvenility of my material I am not in a position to say. In *Polyodon* Bridge described a median posterior bone which he termed parietal, suturing in front with paired frontals, and between these a single bone which he called the dermo-ethmoid ; lateral to the parietal and suturing with it a dermo-sphenotic ; behind this a dorsal splint from the post-temporal, and, suturing with it in front, a splint which he terms nasal or dermo-prefrontal (Fig. 36).

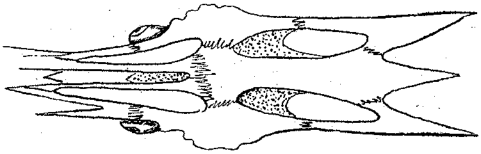
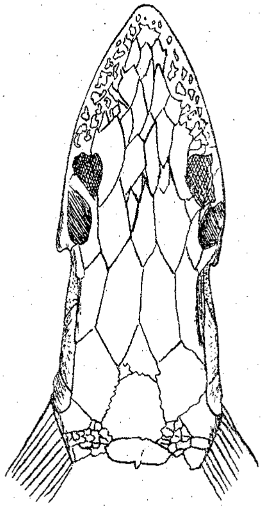


Fig. 36.—*Polyodon*. The dermal roofing bones (from Bridge, 1878).

The basal ossifications on the skull of *Acipenser* are similar to those of *Polyodon*. The synpterygoid is broader. There is a gap between the fore end of this bone and the posterior end of the flat " vomer " in front of it. This last is not continuous to the end of the snout but anteriorly is broken up into a closely fitting series of pairs of scutes. The roof pattern of *Acipenser* is so similar to that of *Scaphyrhynchus* that one illustration would serve for both. These two genera are as bewildering in the plurality of the dorsal scutes as *Polyodon* and *Psephurus* are in their paucity.

Gregory's interpretation of these bones is provisionally accepted and his illustration of *Scaphyrhynchus* is reproduced (Fig. 37).



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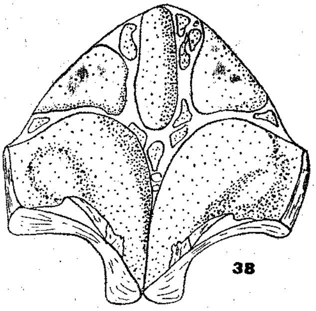

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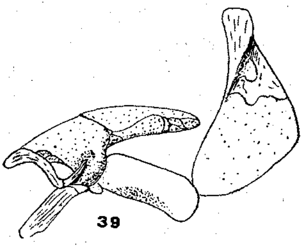

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Fig. 37.—*Scaphyrhynchus*. The dermal roofing bones (from Gregory, 1933).
Fig. 38.—*Acipenser*. The palate (from Parker, 1882).
Fig. 39.—*Acipenser*. The jaws and the suspensorium (from Parker, 1882).

There appears to be no way, as yet, to determine the actual homologies of the numerous scutes on the dorsum of this skull, and, indeed, it is even questionable whether they should not be regarded as evidence that the primitive bony fishes had no settled plan of fragmentation of the bony shield, or was it want of plan in the integration of numerous tiny ossicles? This latter is probably the most likely explanation.

The interpretation of the illustration, then, is accepted, provided the nomenclature is regarded as being purely topographical and not implying homologies.

The palate of the Sturgeons (Fig. 38) is an altogether curious structure. The palato-quadrate cartilages appear as though curved the wrong way, the concavity of the curve being outward instead of, as in all other elasmobranchs and bony fishes, on the inner side. The result is that the anterior ends do not meet in the usual symphysial union, but project forward side by side, and the medial edges of the two cartilages are in contact for a short distance, and then diverge caudad. So broad are the cartilages that they form a nearly complete cartilaginous palate behind the jaw and, swelling posteriorly, extend slightly behind the transverse level of the two Q-M. joints. Behind the "palato-quadrate palate" the roof of the mouth is added to by three large plates and a collection of small pellets of cartilage.

The actual margin of the jaws is supplied by a membrane bone developed independently of the palato-quadrate and by a lesser on each side, laterally, immediately in front of the jaw joint. Although the former touches and is applied to the anterior end and lateral edge posteriorly, Parker was probably correct in regarding these as not ectochondral in origin in either instance, but fairly certainly was he correct in the case of the anterior bone, which he designated the maxilla. Between the maxilla and the cartilage two, probably, ectochondral ossifications are found. These are both small and placed on the lateral surface, and encroach but slightly on to the dorsal surface. The more anterior of these was identified by Parker as the mesopterygoid (metapterygoid of this work), the other he termed the palatine (maxilla). The ventral, that is, the oral, surface of the palato-quadrate is largely covered by an ectochondral plate of bone which Parker identified as the pterygoid (palatine).

In *Polyodon* and *Psephurus* the palato-quadrate is essentially similar to that of the Selachii or Batoidei, and there is developed on its opposing and outer surface a single bone which has been designated the maxilla, and on its inner surface a bone which Traquair identified as the palatine. There is no trace of the curious palate of the Sturgeon.

The collection of palatal cartilages behind the palato-quadrate of the Sturgeon may be dismissed as being *sui generis* and without parallel elsewhere.

The maxilla in both chondrostean types may be regarded as the precursor of, and as completely homologous with, the maxilla in the tetrapods and the bony fishes, that is, with the bone which has, in the past, been so universally designated palatine in the latter fishes.

It is possible that in the Sturgeon we are permitted to observe this bone in the making, as it were. That which Parker designated the maxilla being only the dermal alveolar, tooth-bearing component, whilst the three ectochondral ossifications are the palatine lamina. Prior to the appearance of Landacre's confirmation of the work of Platt and Stone, one would have advanced in support of this suggestion the fact that the teeth are certainly ectodermal structures whilst the ectochondral bone is mesodermal. Even so, although we now know that the cartilage is certainly ectodermal, and its osteogenetic tissue possibly so, it is still possible to recognize in the tooth formation a later ectodermal invasion of the deeper tissues than that from the neural crest which gave rise to the cartilages, so that thus modified the argument still holds.

The lower jaw and its suspension in the Chondrostei (Figs. 39, 40) is essentially similar to that of the Plagiostome, resembling more particularly that of the batoid rather than the selachian forms.

The segmentation of the lower end of the hyomandibular cartilage to form a symplectic has been remarked upon as evidence of teleostean affinities. I know of no teleostean in which the hyomandibular cartilage is segmented. It is highly doubtful whether the so-called symplectic bone of the teleosts is comparable at all with the cartilage of the Chondrostei. The *cartilage* intervenes between the hyomandibular and the quadrate, completely separating the two, and it is formed by segmentation from the lower end of the former. The *bone* is developed in the lower end of the hyomandibular cartilage and here the resemblance ends. It lies behind the quadrate, and does not intervene between that and the hyomandibular.

On the other hand, there is no slightest trace, within the suspensorium of the Chondrostei, of that separation of the quadrate from the rest of the palato-quadrate bar, or of the presence of the metapterygoid process from which the shaft of the quadrate and the epipterygoid are developed. These are two absolutely constant features of the mandibular suspension in the Teleostei and, moreover, essentially characteristic of the whole of the bony fishes. These and the attachment of the palatal arch to the skull, anteriorly separating the two cartilages, are the outstanding features of the teleostean suspensorium and palatal arch.

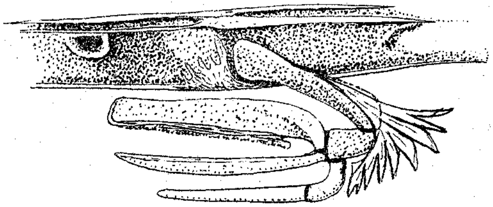


Fig. 40.—*Psephurus.*

Notwithstanding the absence of these essential features, Gregory writes (1933, p. 120), " the entire suspensorium (of the Chondrostei) is *evidently* a modified actinopteran type, differing from the elasmobranch(ian) especially in the presence of a large symplectic and of an ' opercular ' plate " (the italics are mine).

It were foolish to deny Professor Gregory the use of the personal factor in evaluating these features, but one may be permitted to comment that, at least, the evidence is not obvious. It seems that it would be a good deal nearer the truth to say that it is " evidently a slightly modified elasmobranchian suspension ".

It may be said of the skull of the Chondrostei, (1) that whilst it possesses outstanding elasmobranchian features it does not possess one single teleostean feature that is not also possessed by the Holocephali, except the ectochondral bones, and (2) that it differs from the skull of every known bony fish in the complete absence of endochondral ossifications.

Gregory's view of the Chrondostei is that they owe their characteristics to " degenerative specialisations from an actinopteran starting point " (1933, p. 120). This view, however, is based entirely on his interpretation of the special features of the group and is not supported by the citation of any definitely actinopteran characters. He asserts that the " shoulder girdle (of *Polyodon*) is that of an actinopteran, not that of a progressive shark ".

After dissecting that of *Acipenser* and comparing it with that of several selachian and batoid forms I am able to agree with this dictum. Stripped of its derm bones the cartilaginous girdle is most emphatically essentially similar to that of the Elasmobranchs and unlike that of the Actinopterans.

I do not suggest that the Chondrostei should be regarded as progressive sharks. To me they appear to be descendants of a primitive elasmobranchian branch which had been " cut off " with a very small share of that osteogenetic potential which was in fuller measure the heritage of those other branches which yielded the whole of the bony fishes and animals.

Gregory's suggestion that they are derived from an actinopteran starting-point implies an almost complete reversal of evolutionary forces and a return to primitive elasmobranchian conditions.

One striking difference there is between the cartilaginous structures of the chondrostean skull and that of the elasmobranchian fishes. This is that in the Elasmobranchii all the cartilage is either covered or permeated by exceedingly tough fibrous tissue, whilst there is no such covering or permeation in the chondrostean skull. Herein the Chondrostei resemble not only the Teleostei, but also those primitive amphibia, the Dipnoi.

It would almost seem that the acquisition of osteogenetic power was at the expense of this tough perichondrium.

This suggests the following further speculation. The Chondrostei, deficient in osteogenetic power, were unable to develop solid endochondral replacements, or ectochondral covering plates, in or on the cranial walls, and had also lost the power to encase the skull in that tough fibrous investment which not only strengthened them but also made of them fit " fixed " and rigid points for the origin of muscles.

With more or less futility, an attempt was made to compensate for the absence of rigidity by the utilization of the dermal tubercles. These were aggregated into scutes of varying sizes and articulated together in the production of a complete cephalic shield and dorsal and lateral body series.

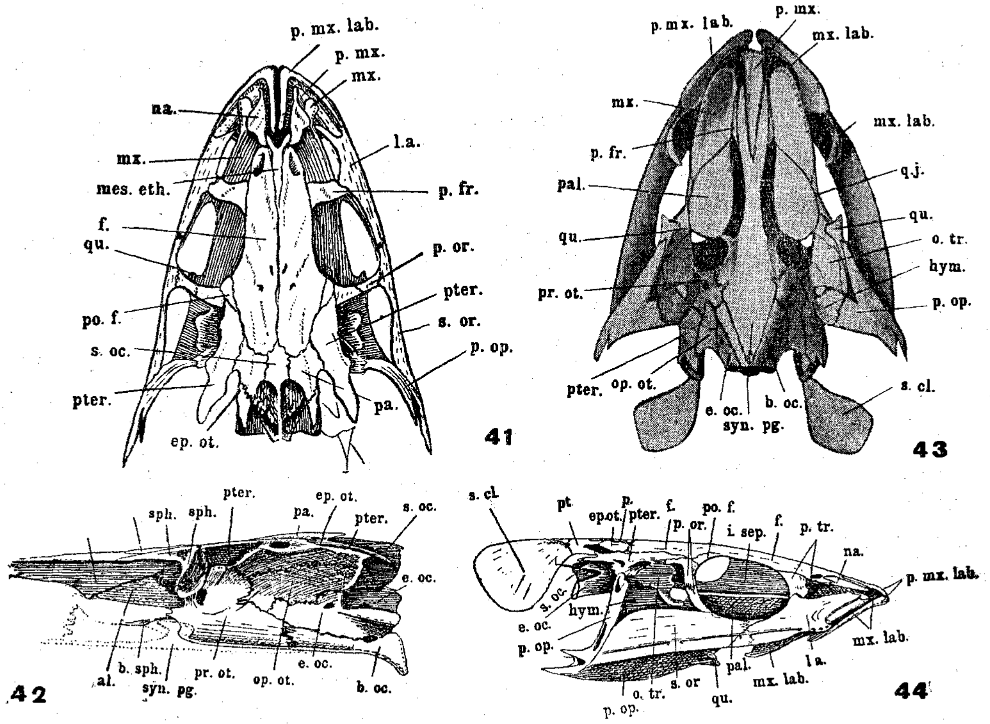
This is, of course, pure speculation and is only intended to point out that the Sturgeons may be regarded as illustrating one of nature's failures—an ineffectual attempt to obtain that cephalic and bodily rigidity with flexibility which was essential to the development of a mechanism capable of directionally purposive rapid movement, and to obtain it without the solid, and yet flexible, endoskeleton.

The " operculum " of *Psephurus* is fitted very neatly to the lower half of the hyomandibular ; in the Sturgeon it is fitted to the hyomandibular for a greater length.

This relation suggests that it is really a preoperculum. Gregory states (p. 426) that it " has no contact with the hyomandibular " and regards it as a suboperculum. This observation and identification probably results from the study of mounted or disarticulated material and the neglect of the material in the flesh and of dissecting instruments.

THE SKULLS OF THE BONY FISHES.

In this, as in other sections describing the skulls, no claim is made to have dealt with the subject exhaustively. The aim has been to describe one or two skulls which may be regarded as typical of each group, with a view to providing a standard of reference for subsequent discussion.



Figs. 41-44.—*Platycephalus.*

The examples chosen here are *Platycephalus* and *Paradicichthys*. Of the former I give only the illustrations which accompanied my detailed description published in 1926. Throughout the description of *Paradicichthys* free use has been made of the terminology which I proposed (1926), in an attempt to provide a standardized nomenclature for ichthyo-craniological descriptions, and in the discussion on the maxillo-ethmoid articulation in the skulls of bony fishes, which appeared at the same time.

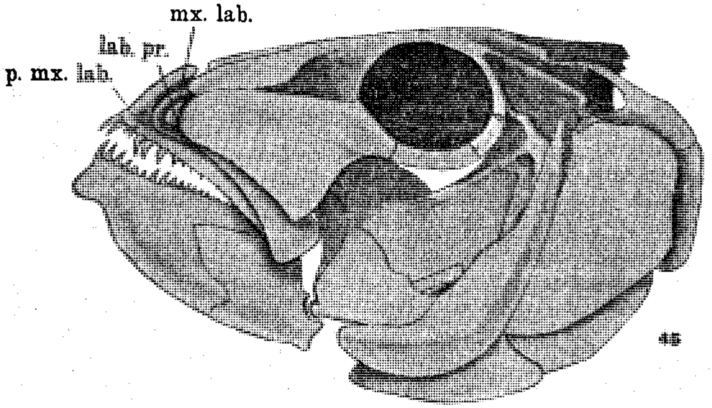
Paradicichthys venenatus Whitley.

(Figs. 45-56.)

The general contours of the skull and its regions will be readily gathered from the drawings.

The dilator fossa is exceptionally large, and extends medially under a large portion of the floor of the temporal fossa. The anterior and upper part of this fossa lies between two laminae of the frontal bone. The lower of the laminae in question sutures with the upper margin of the sphenotic, the upper lamina with the upper margin of the pterotic bone, which latter is thrown right across the sphenotic bone to reach the lamina of the frontal. The floor of the fossa is formed, for the most part, by the outer portion of the upper surface of the body of the sphenotic bone and to a lesser extent by an undercurved part of the pterotic bone which sutures with the sphenotic as it crosses it. This suture is interrupted on both sides of the skull by a foramen, but the foramen on the right side is much larger than that on the left. The foramina probably transmit blood vessels. The roof slopes from the floor upward and forward to the top of the anterior wall; for the most part it is formed by the pterotic bone.

The temporal fossa is also larger than is usual; it is devoid of a roof but, for the rest, well defined. The median wall, slightly overhanging, is formed by the epiotic process behind and an



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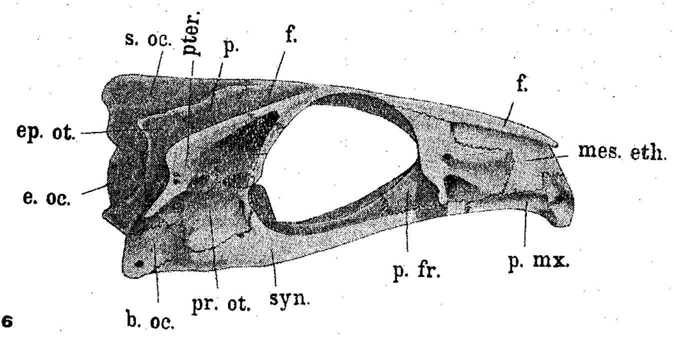

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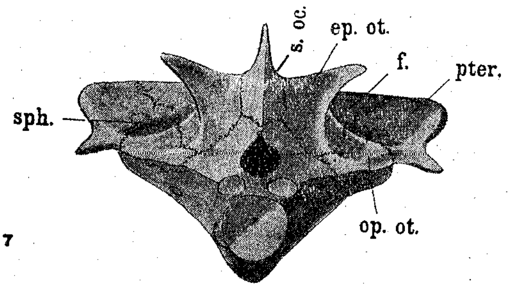

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Figs. 45-47.—*Paradicichthys.*

upstanding flange of the parietal and frontal in front. Posteriorly the floor is defined from the sloping outer wall by a very definite sulcus where the pterotic turns under to suture with the sphenotic bone, and behind this sulcus by an angle along which runs the suture between pterotic and opisthotic bones. In front of the sulcus the fossa is much shallower, and the sloping outer wall meets the bottom of the inner wall at a wide angle, and has become the floor. In front of the pterotic process the outer boundary of the fossa is clearly indicated by the change in the character of the surface of the frontal bone ; beyond the fossa this bone is subdermal and presents the usual roughened surface of subdermal bones. Medial to the pterotic process, the floor of the fossa is formed by the sphenotic and opisthotic bones. The posterior margin of the fossa is a curved ridge which begins above to the inner side as the posterior margin of the epiotic process, prominent and outstanding ; this merges below into a ridge of low relief which turns ourward and then slightly upward again, to reach the posterior end of the outer wall at the root of the pterotic spur. Above this curved margin the fossa is crossed from within out by a prominent rounded ridge which throws the floor behind it almost into the vertical plane. This ridge commences below the epiotic process just in front of its hinder margin and, crossing the body of the epiotic and opisthotic bone, terminates at the root of the pterotic spur. The posterior semicircular canal lies immediately beneath the upper end of the ridge, and was doubtless responsible for its formation.

The occipital fossa is bounded laterally by the inner wall of the temporal fossa. The anterior portion of the floor is nearly in the horizontal plane, whilst the posterior portion is nearly in the vertical ; the angle between these two portions is a ridge which runs across the floor from the epiotic process. The median wall is, of course, the occipital crest and its forward continuation. This wall stands out behind the vertical portion of the floor and is supplemented below by the sloping superior vertical lamina of the exoccipital bone. The floor of the occipital fossa is carried out laterally below the inferior limit of the temporal fossa, and is itself limited below by the buttress of the exoccipital bone.

The large size of the hollow ethmoid bones gives to the preorbital region a deceptive appearance of solidity. The single facet for the maxilla is placed far forward on the anterior end of the prefrontal below and lateral to the nasal cavity. The frontal bones overlie the greater part of the mesethmoid ; only a small vertical portion of that bone is to be seen in front of them. The large nasal bones are firmly bound to the lateral edges of the frontal bones in front of the prefrontals, and also to the upper edges of the first subocular bones, to enclose the greater part of the nasal capsules in bony walls. The nasal apertures lie close together behind the posterior margin of the nasal bone and in front of the prefrontal. In this region the outer wall of the capsule is membranous, filling in a triangular gap between the two bones mentioned and the hinder half of the upper border of the first subocular ; for the rest, the whole of the capsules are enclosed by bony walls.

The trigemino-facialis chamber has the incomplete outer wall formed by a bridge of bone developed from the prootic ; a little square of the same bone thrown up from below forms an incomplete front wall to the chamber.

BONES OF THE CRANIUM.

The *basioccipital* bone presents all the usual parts but it is modified in such a way as to disguise that fact to some extent. The myodomial recess is very large and is completely roofed. The saccular recesses are placed at and above the level of the myodomial roof (" hypomyodomial skull "). Between these two recesses there is a solid, roughly cubical shaped, mass of bone, which, besides forming the inner walls of the saccular recesses, also forms the roof of the myodome and the occipital segment of the cranial floor. The cube is excavated behind by the large azygos sinus, which extends right across the width of the floor. Behind the azygos sinus the basioccipital bone is covered by the two exoccipital bones. This suture between basi- and exoccipital bones swings forward, round the edge of the sinus and along the sides of the occipital segment of the cranial floor, and at the same time along the middle of the length of the roof of the saccular fossa of each side. The basioccipital element in this suture is a narrow flange which stands out from the side of the top of the cubical mass described above. These little flanges, together with the flat top of the cubical mass, replace the horizontal laminae of the exoccipital bones which, in many fish skulls, form the occipital segment of the cranial floor in front of the sinus ; and it may be said that the flanges suture with the exoccipital bones along the line of origin of the replaced laminae. The basal lamina of the basioccipital is very thick and somewhat narrow ; it is incised along the centre of its width toward the hinder end by a deep narrow groove which perforates the entire thickness of the bone just in front of the condylar edge. Only portion of this perforation of the myodomial floor is closed by the hinder end of the synpterygoid bone. Though the saccular recesses are placed at a higher level than the myodome, they do not bulge beyond it laterally, so that there is no trace of a saccular bulla, and the vertical lamina of the bone is without prominences above the myodomial swelling. The fore end of the cubical mass sutures with the hinder ends of the horizontal laminae of the prootic bones. Immediately to the outer side of this contact there is, in the dried specimen, an oval foramen of some size which leads from the saccular cavities on each side to the myodome ; below this foramen the vertical lamina of the basioccipital bone sutures with the myodomial lamina of the prootic ; above and to the outer side of the foramen the suture between the basioccipital and prootic bones crosses the floor of the saccular recess. At the outer end of this last suture the vertical lamina of the basioccipital sutures with the inferior margin of the inferior vertical lamina of the exoccipital bone. There is an oval foramen on both sides of the azygos sinus which leads into the hinder end of the saccular cavity of its side (*vide* Figs. 51A, B).

The *exoccipital* is a much more normal bone than the basioccipital. No part of the superior vertical lamina is actually in the vertical plane, but each slopes towards its fellow, to meet above the foramen magnum. The buttress is well developed, and is continued out by a ridge, developed behind the posterior end of the horizontal semi-circular canal, to meet the prominent posterior edge of the opisthotic bone. The inferior vertical lamina is a little less extensive than usual. The external aperture of the occipito-spinalis foramen is found above, and that of the vago-glossopharyngeal canal below, the buttress. The horizontal lamina is confined to the region of the cranial floor behind the azygos sinus. The internal aperture of the occipito-spinalis canal is situated just above the azygos sinus, and that of the vago-glossopharyngeal canal at the extreme anterior edge of the postotic cranial wall, where it overhangs the posterior ampullary cavity. As is usual the otic mass of the bone lodges the posterior ampullary cavity with the contiguous portions of the posterior and horizontal canals ; it also forms the roof and side wall of the saccular cavity, and this also is usual.

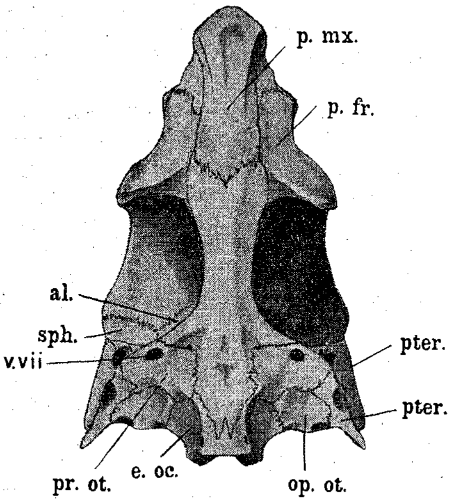
The *supraoccipital* bone presents little of special interest ; the vertical lamina is much reduced, the crest well developed, but not large.

The general shape of the *epiotic* bone will be gathered from the drawings ; the bone forms the postero-superior corner of the otocrane and lodges the greater part of the posterior semi-circular canal. The surface of articulation of the upper arm of the post-temporal, on the dorsum of the epiotic process, is large and smooth.

The *pterotic* bone takes no part in bounding any of the otocranial recesses or canals ; it is a flattened bone which is sutured by its inferior margin to the juxtaposed edges of the opisthotic and prootic bones and to the dorsum of the sphenotic, crossing this last bone to be sutured to the upper of the two lamina into which the hinder end of the frontal splits. Posteriorly this flattened bone stands nearly vertically ; where its anterior margin sutures with the frontal the bone is oriented more nearly in the horizontal plane. The postero-inferior corner of the bone, just above the suture with the opisthotic, is produced into a well developed " spur ". The posterior hyomandibular articular facet is borne on the under side of the bone immediately in front of the root of the spur. The postero-superior corner of the bone is slightly swollen and gives attachment to a band of fibrous tissue which replaces the supratemporal bone.

The irregularly shaped *opisthotic* is wedged in between the pterotic and prootic in front and to the outer side, the epiotic and exoccipital behind and to the inner side, and the sphenotic in front. The bone lodges portion of the horizontal semi-circular canal and at its postero-lateral corner bears the facet for the articulation of the inferior arm of the post-temporal.

The body of the *prootic* bone is relatively small, the myodomial lamina relatively extensive. The former is oriented mainly in the horizontal plane, the latter mainly in the vertical, so that a proper idea of its conformation can only be gathered by the study of both Figures 47 and 49. The extent of the body of the bone showing on the posterior orbital wall is rather greater than is usual ; the angle between these two faces of the body is accentuated by the bridge of bone which forms the outer wall of the trigemino-facialis chamber. The bone takes a lesser share than is common in the formation of the anterior hyomandibular facet. Little of the myodomial lamina is covered by the synpterygoid. The horizontal lamina is sharply differentiated into cranial-floor and saccular-floor components. That portion of the lamina which forms the prootic segment of the cranial floor is triangular in outline, the base of the triangle being at the mid-line, the apex at the trigemino-facialis fossa. At the hinder margin of this segment the lamina dips vertically a little way and then slopes down, back and laterally, forming the oblique anterior wall and part of the floor of the saccular cavity. The lamina between the lower part of the arcuate and the trigemino-facialis fossae is well developed, and the large anterior aperture of the horizontal bony canal is placed immediately to the outer side of, and behind, the former fossa. The carotid canal interrupts the suture between the prootic and the latter bone.



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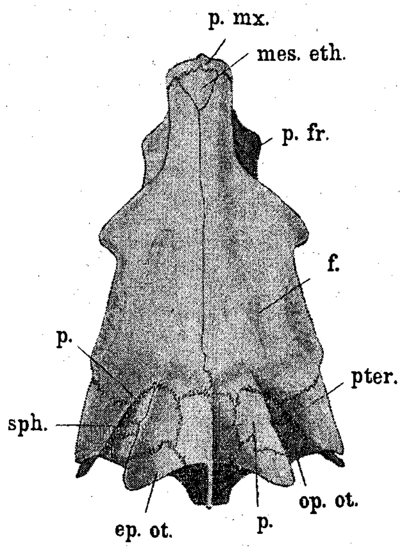

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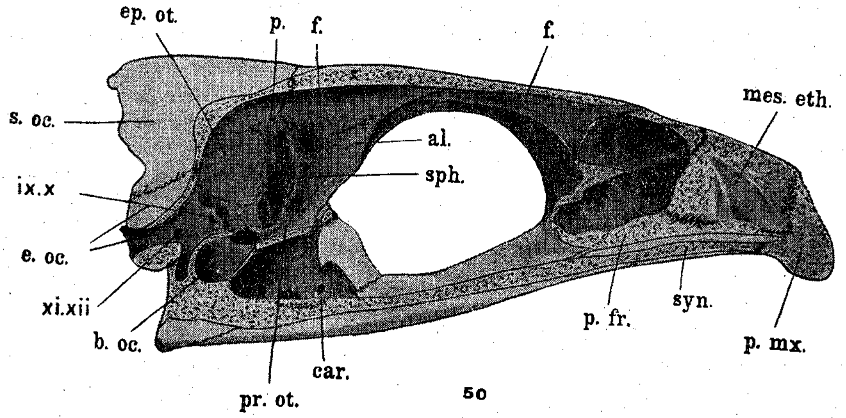

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Figs. 48, 49.—*Paradicichthys.*
Fig. 50.—*Paradicichthys.* **Median section of the neurocranium.**

The *sphenotic* bone bears a rather larger post-orbital lamina than is usual, and at the inferior margin of this lamina the bone bears the greater part of the anterior hyomandibular articular facet. The body is of quite irregular shape ; it appears in the inside of the skull, where it constitutes the upper half of the arcuate fossa and the intracranial temporal fossa.

The *alisphenoid* is a flexed lamina of bone which sutures with the alisphenoid process of the frontal, the sphenotic, prootic, and basisphenoid bones. There is no pterygoid process and no contact with the synpterygoid.

The transverse arm of the basisphenoid is almost in the vertical plane; it sutures with the alisphenoid and with the prootic to the inner side of the trigemino-facialis fossa. The vertical arm is broader and thinner above than it is below where it sutures with synpterygoid.

The *parietal* bone presents a small oval area in the roof of the cranial cavity; externally, it is much more extensive. Of irregular outline, it is placed between the supraoccipital, epiotic, sphenotic, and frontal bones. It is crossed by a prominent ridge which is thin and plate-like in front, where it sutures with a similar process of the frontal, but behind it becomes much stouter and forms a very strong buttress to the epiotic process.

The shape of the *frontal* bone will be gathered from the drawings. Posteriorly the bone is bilaminate on both sides of the little upstanding plate which sutures with the parietal ridge. To the inner side of this line the upper lamina is the cranial roof, the lower lamina, the alisphenoid process; to the outer side of the line the upper lamina is the roof of the dilator fossa, the lower (much shorter) sutures with the superior margin of the postorbital plate of the sphenotic.

The *synpterygoid* is rather broader than in other comparable skulls; it is continued back along the basioccipital almost to the condylar edge, leaving a basi-myodomial foramen between its bifurcated posterior end. There is no alisphenoidal process.

The drawings must again be consulted to gain an idea of the shape of the *prefrontal* bone. The preorbital process is massive and bears no facet for the articulation of the maxilla. There is a knob on the infero-lateral corner, to which the first subocular is firmly bound but not articulated. The situation of the preethmoid maxillary articular facet is quite peculiar. In the great majority of the acanthopterygian fishes this facet is found on the under side of the preorbital process just where it joins the body of the bone. In this form it is divorced from the preorbital process altogether; the body is inordinately prolonged forward and the facet is placed on the extreme anterior edge thereof. The postero-ventral process is a massive corner which sutures with a process of the synpterygoid developed to accommodate it. The postero-dorsal process is poorly developed.

The *mesethmoid* is a larger bone than usual; for the most part covered by the frontal bones, it shows a small subdermal area between their divergent forward ends. The median ridge so characteristic of the bone is present, but is very short and is very nearly vertical.

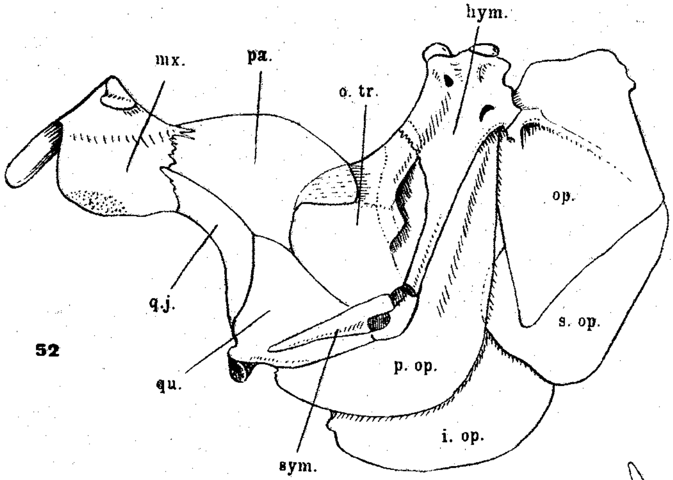
Both these two last bones are constructed of very open-meshed cancellous bone and are further excavated by large cavities filled with loose fatty tissue. No definite cartilage was found between them.

The steep ascending process of the *premaxilla* is flush with the forward end of the mesethmoid. There are two or three rows of small teeth similar to those on the premaxillary labial on the alveolar border. The comparatively broad palatine plate is rather abruptly truncated posteriorly.

BONES OF THE UPPER JAW AND PALATE.

(Figs. 52-56.)

The *hyomandibular* bone may be described as presenting a body and an elongated ventral process. The body is roughly square in outline, the lower side being produced out into the process. The bone is binarticulate; the anterior condyle stands up and forward from the antero-superior corner of the body, the posterior condyle is placed on the dorsal edge of the bone, nearer the posterior than the anterior corner. The upper opening of the canal for the hyomandibular branch of the facial nerve is just behind and below the anterior articular facet, the lower opening is on the posterior edge of the process about the centre of its length. The former is, of course, on the inside of the bone, the latter is outside the strong fibrous tissue that binds the process to the preoperculum. The well developed facet for articulation with the operculum is on the posterior edge of the bone a little below the centre of the body. A stout ridge crosses the body of the bone on the outside from the anterior articular facet to the base of the opercular facet. In front, this ridge takes the form of a rounded buttress to the articular head, further back it becomes higher and sharper, and the free anterior edge of this higher part stands forward over the buttress-like portion. *In situ*, this projecting point nearly touches, and is bound to, the outer corner of the post-orbital plate of the sphenotic. At its hinder end the ridge becomes merged with the prominent upper end of the inferior process of the bone. From the angle where these meet, there arises a low ridge which extends diagonally down and forward across the body of the bone to the antero-inferior corner of the body; just before the inferior margin of the body is reached, this low ridge is undercut so that the extreme corner of the body is bilaminate. The



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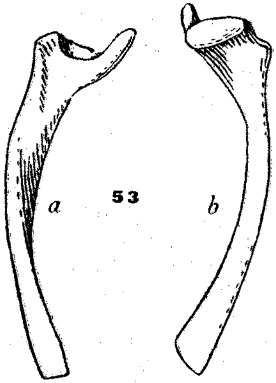

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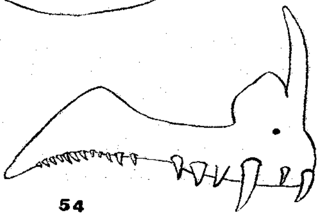

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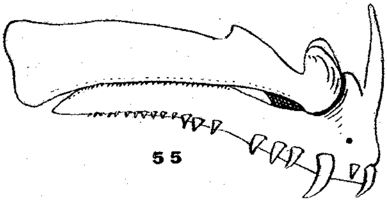

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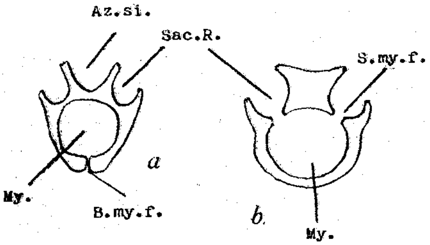

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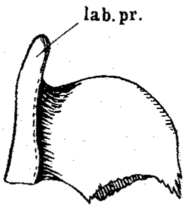

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Fig. 51.—*Paradicichthys.* Transverse sections through the basioccipital bone. A. is the more posterior of the two. Az.si., Azygos sinus; B.my.f., Basimyodomial fenestra My., Myodome; Sac.r., Saccular recess; S.my.f., Sacculomyodomial foramen.

Fig. 52.—*Paradicichthys.* The palatal arch and the suspensorium.

Fig. 53.—*Paradicichthys.* The maxillary labial bone.

Fig. 54.—*Paradicichthys.* The premaxillary labial bone.

Fig. 55.—*Paradicichthys.* The two labial bones.

Fig. 56.—*Paradicichthys.* The maxilla.

outer lamina is thin and sutures with the outer lamina of the top corner of the metapterygoid; the inner lamina, much thicker, sutures with the stout inner lamina of the same bone. Between the two bones there is a narrow passage, and through the passage there passes, in the flesh, a strong tendon of the levator arcus palatini muscle which will be referred to again later. When the bones are in place it is found that the upper surface of transverse ridge is in the plane of, and continues backward and down, the floor of the dilatator fossa, and that this floor is complete but for an oval foramen just behind the orbit. The boundaries of this foramen are: the outer corner of the postorbital plate of the sphenotic in front, the buttress of the anterior articular head of the hyomandibular to the inner side, the shelf-like process of the same bone behind, and the anteriorly projecting point of that process on the outer side. Another tendon of the levator arcus palatini muscle passes through this foramen, and it also will be referred to again later.

The shape of the metapterygoid will be gathered from the drawings (Fig. 52, *o.tr.*); except at the dorsal corner it is a thin lamina of bone; at that corner it is bilaminate and the inner lamina is thickened. The extent of this bilamination has been indicated on the drawing by dotted lines; the whole of the inner surface of the outer lamina covered by the inner, and between it and the inferior, process of the hyomandibular, and also a small triangular area below the inner lamina and in front of the same process, gives attachment to those fibres of the levator palatini muscle which insert on the tendon that has been described as passing down between the two laminae of the bones.

The *symplectic, quadrate, ectopterygoid* and *palatine* bones need no description; their shape is sufficiently shown in the drawings.

The *maxilla* is acrartete. The body of the bone is a plate which is much thickened towards the medial border. The outer thinner portion of the bone sutures flush with both sides of the fore end of the ectopterygoid; the thickened medial portion sutures along its posterior edge flush with the under surface of the fore end of the palatine, but presents a rough surface above the level of the upper surface of that bone, this roughened surface being attached by tough fibrous tissue to the under surface of the preorbital process of the prefrontal bone. The dorso-median and anterior border bears a solid bar of bone which is continued forward as the labial process and carries the articular facet on its truncated posterior end. There is a limited tooth-bearing area on the outer margin of the thinner portion of the bone. The teeth are little pegs, similar to those on the premaxilla, but smaller.

The form of the opercular bones is sufficiently shown in the drawings.

THE PERIOCULAR BONES.

There are four of these bones present. The outline of the first is clearly shown in the drawing; where it is attached to the prefrontal bone it is thickened and bears an articular facet. The second extends the full length of the under side of the orbit; it is attached to the inner side of the first almost as far forward as the attachment of that to the prefrontal. This second subocular bears a subocular shelf along its full length. There are two short postoculars, the upper of which is attached to the frontal just where that bone becomes bilaminate, behind and above the orbit.

THE CRANIAL BOUNDARIES, THE OTOCRANE AND THE MYODOME.

The occipital segment of the cranial floor is formed by the horizontal laminae of the exoccipital bones behind the azygos sinus, and by the basioccipital in front of that sinus. The azygos sinus is particularly large; it extends across the full width, and along nearly half the length of the occipital segment of the floor. A large foramen on both sides places it in communication with the two saccular cavities. In the mesotic region there is a deficiency on each side in the roof of the saccular cavities, but since the lateral cranial obturator membrane rises vertically medial to these deficiencies, there is no basicranial obturator membrane; the fore end of the upper surface of the basioccipital bone sutures with the hinder ends of the horizontal laminae of the prootic bones. Immediately forward of this suture the mesotic section of the floor widens rapidly. The pituitary fenestra is a narrow transverse slit, and is followed by a narrow prepituitary bridge which is tilted almost into the vertical plane.

The lateral cranial obturator membrane is attached above in front to the top of the lamina which separates arcuate from temporal fossa; from here the line of attachment is continued down the free border of that lamina and along the hinder edge of the mesotic section of the floor. It now turns back along the inner (median) side of the gap in the roof of the saccular cavity, then laterally along the hinder margin of that gap. In this situation it is attached to the free anterior margin of the flange developed along the side of the cubical mass of the basioccipital bone. Leaving this structure, it reaches the free anterior margin of the postotic section of the cranial wall. This free margin terminates just above the posterior ampullary cavity, and from this point the line of attachment turns medially and up and becomes lost in the mass of loose connective tissue which fills the top of the cranial cavity above the level of the exoccipito-supraoccipital suture. Thick behind, this mass thins as it reaches forward, leaving the roof of the temporal fossa free of aught but a layer of fibrous tissue.

The lateral cranial obturator membrane is quite well defined as usual, in close proximity to the various bony laminae to which it is attached, but, removed from those laminae, it is even more indefinite than usual, and it is almost impossible to delimit the fatty tissue filling the temporal fossa and that, less fatty, tissue in which the membranous labyrinth is packed.

The temporal fossa is large and the extensive alisphenoid bone makes a more complete front wall than is usual. The spheno-obturator membrane is narrow, but broadens below just above the prepituitary bridge.

There are three perforations in the depth of the well-formed trigemino-facialis fossa; of these the two lower ones open directly into the little trigemino-facialis chamber, and the third just to the inner side thereof. The oculo-motorius foramen is placed to the inner side of the fossa, almost within it, and opens directly forward. The foramen of the sixth nerve perforates the mesotic floor directly in front of the saccular cavity and transmits the nerve to the myodome. No foramen for nerve IV is discoverable; it probably leaves the cranial cavity through the spheno-obturator membrane beside the optic nerve. It may be that that which is described above as the oculo-motorius foramen transmits a branch of the trigemino-facialis complex, in which case the third nerve must leave the cavity through the sphenotic fissure (Kesteven, 1918).

The myodome is particularly large, and its roof more complete than usual. There is no median deficiency, but two large oval foramina near the middle of the length of the roof lead into the saccular cavities. There is a median basimyodomial foramen at the extreme posterior end of the floor, and a rather large carotid foramen perforates the side wall far forward and low down, interrupting the suture between the ascending process of the synpterygoid and the myodomial lamina of the prootic.

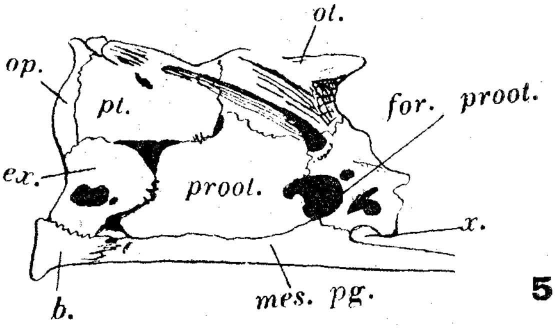
Paradicichthys and *Platycephalus* are two fairly typical examples of the modern teleosts and they may be accepted as fairly exemplary of the Acanthopterygii. Within this large group of the fishes there are many variations in skull form, but such variations affect the relative development of the component bones, so that they may be regarded as alterations of degree rather than of kind. In others of the many groups of the modern bony fishes the variations may be said to be of kind as well as of degree. W. K. Gregory (1933) has recently presented us with brief disjointed descriptions but excellent illustrations of a very large number of these variations in the arrangement and relative development of the bones. Numerous and extensive though these variations be, it is still, in the Teleostei, possible in all instances to regard every skull examined as presenting a variation of the central acanthopterygian type described above, rather than a new type. It were impossible to review all these variations and would serve no good purpose here, but a few of the more important may briefly be referred to.

In general, the median edge of the palatal arch is free from the base of the skull, and the arch of the palate between the two is completed by the "palatine fascia". In certain forms, e.g. *Arapaina, Notopterus, Gymnarchus, Mormyrops* and *Gnathonemus*, on the other hand, the median edges of the palatal arch bones are firmly ankylosed to the synpterygoid along the base of the skull.

The number of otic bones is variable; the full complement of five is present in both the examples described: the opisthotic and sphenotic are the two most commonly absent. The basisphenoid is another bone which may not be present. The myodomial chamber is not developed in quite a number of fishes, e.g. *Tandanus* (Fig. 57). The labial bones are subject to wide variation in size and shape, and in some fishes are absent altogether, e.g. the Eels (Fig. 58). These last two also exemplify two of the many variations in the shape of the maxilla.

The development of some of the bones in the fish skull will be discussed later; at this juncture it may be mentioned that the amount of the chondrocranium remaining, encased in the bones in the adult cranium, is subject to variation. In general it may be stated that those fish among the Teleostei which, by common consent, are regarded as the most primitive, retain more cartilage than do the more modern forms. In this respect the Malacopterygii closely resemble *Amia*, the most modern, in form, of the Ganoids, and present various stages between the almost entirely bony cranium of the Acanthopterygii and this largely cartilaginous cranium.

The recent ganoid skulls must be described.



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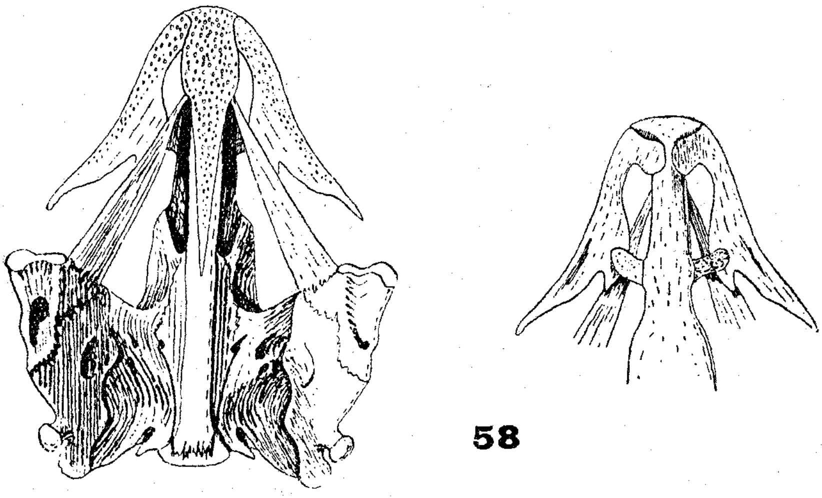

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Fig. 57.—*Tandanus.*
Fig. 58.—*Anguilla.*

Amia.

(Figs. 59, 60D, 61, 62.)

The nearly complete cartilaginous cranium recalls that of the Elasmobranchs, but differs in important respects. The cavum cranii is not continued from end to end at the same level. At the anterior boundary of the otocrane the cranial floor is lifted dorsad away from the base-line of the skull. There is a very large lateral cranial fontanelle exposing much of the structure of the otocrane. Except in the Holocephali, this is a feature not found in elasmobranchian crania. A large myodomial chamber is present below the anterior end of the cavum cranii; it is the presence of this cavity, never found in elasmobranchian skulls, which lifts the cranial floor away from the base-line. In front of the myodome, at the orbit, the cranium is laterally compressed as it is in the Teleostei. Beyond this the sphenoidal cavity is continued forward dorsally to a short distance anterior to the orbit. The two olfactory passages open from its anterior end, separated by a relatively thick cartilaginous partition. There are no olfactory capsules, in the elasmobranch sense; the passages open into comparatively small pits situated on either side of the base of a solid short rostral anterior end of the cranium. Behind the base of this rostrum and in front of the orbit, the cartilaginous axis of the cranium is laterally expanded, and the olfactory pits lie on the upper surface of this expansion near its anterior edge. There is here another point of difference from the elasmobranchian condition. In those skulls, excepting the Holocephali and Chondrostei, the nasal capsules are formed by relatively thin expansions of the anterior end of the cranium which form well nigh complete roof, and medial and lateral walls,

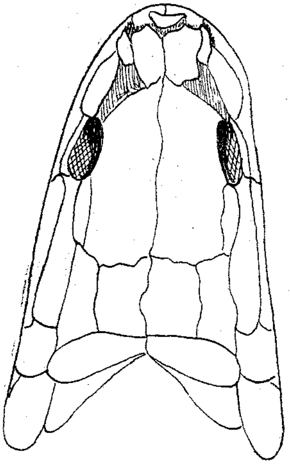


Fig. 59.—*Amia* (from Gregory, 1933).

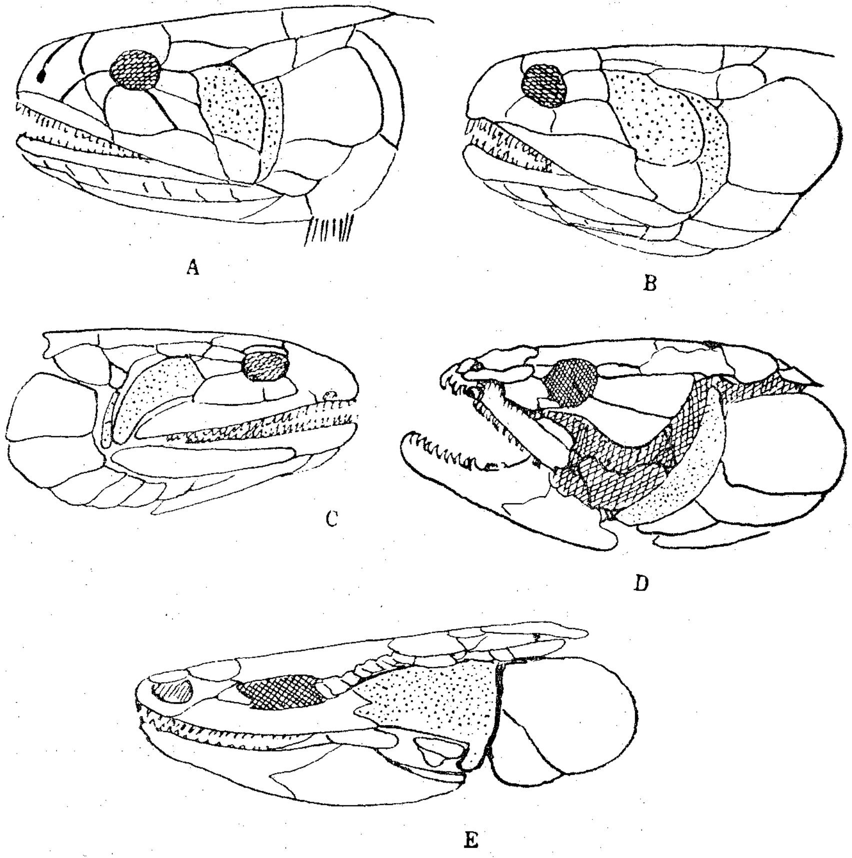


Fig. 60.—Primitive fish skulls.

floor and anterior wall being but poorly developed. Here we have a massive continuation of the cranial axis which provides a very complete floor and leaves all the other boundaries incomplete.

Of otic bones, three only have been recognized in the past; that which Allis designates the petrosal is, without doubt, the prootic; opisthotic and epiotic are also present. The number, size, shape, and relations of the other endochondral bones can be gathered from the figures.

In addition to the usual dorsal roofing bones, *Amia* possesses (1) a pair of scutes covering the epiotic, which have been named " tabulars " and " extrascapulars "; (2) a pair of " post temporal " scutes behind these and a relatively large pair of scutes between the post-frontals and the tabulars and lateral to the parietals—these have been designated squamosals by most writers in the past; Gregory terms them " pterotis " bones. This identification may be provisionally accepted.

The maxillo-palatine arch contains the usual number of bones found in the Teleostei, maxilla, palatine, ectopalatine, metapterygoid, symplectic, hyomandibular and quadrate.

There are three pairs of ossifications related to the anterior end of the ethmoid cartilage. One of these is a pair of small bones definitely developed on the cartilage on either side of the base of the short rostrum. These, Allis terms septomaxillaries. It is extremely doubtful whether they are really homologous with the similarly-named bone in the Amphibian skull, and the question appears not to be subject to satisfactory proof either for or against the identification.

The second pair is developed on the under side of the cartilage; they suture with the anterior end of the synpterygoid on either side of the mid-line and project slightly beyond the cartilage in the adult. Comparison with the prevomer in any or all lower Tetrapoda reveals no feature wherein they differ to an extent which would indicate that they are not homologous.

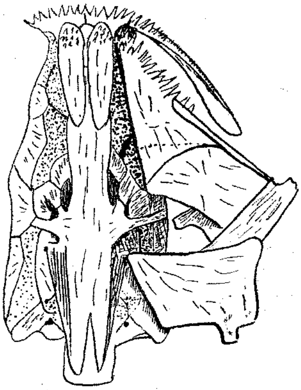


Fig. 61.—*Amia* (modified from Sagemehl.)

The third pair is developed on the upper surface of the cartilage, extending back behind the olfactory pit but having a deficiency over the pit. This pair also project forward, extending beyond the prevomers and also being broader than them. Like those bones they bear teeth. These are the premaxillae.

Both these pairs of bones might appear to be claimants for recognition as the homologue of the premaxillae of the higher vertebrata.

To my mind the evidence against the claim for the first pair is strong in the presence of the second.

Those which we have identified as the prevomers are developed below the cartilaginous solum nasi and they suture with the anterior end of the synpterygoid (parasphenoid), just as do the prevomers in the Tetrapods.

The other pair lie in essentially the position of the premaxillary bones of the Tetrapods, that is, above and in front of the ethmoid cartilage, the portion above being the ascending process. The relation of the ascending process to the nasal bone and the nasal organ is fairly well maintained. Among higher vertebrata the premaxilla may develop either a processus praenasalis or a process extranasalis, the one being medial, the other lateral to the external nares, and both being ascending processes. These processes, however, are never covered by the nasal bones; they are in the same plane as them and make sutural contact with their edges, and are placed anterior to or above the nasal organ. The two processes are present in *Amia*, but have not contributed to the side wall of the nasal organ.

I would particularly draw attention to the fact that in this, as in all other similar comparisons throughout the work, I have invoked the characteristics of whole classes in evidence, and in no case do I base any conclusion on the evidence of the anatomy of a single animal or fish.

The maxillary labials are not supported by a process of the premaxilla as in the Teleostei, but are "pegged in" as it were between the premaxillary and the prevomer. The pit into which its little peg fits is placed immediately behind the tooth-bearing area of the premaxilla and above the antero-lateral corner of the prevomer.

Lepidosteus.

The chondrocranium of this fish is, in the adult, very difficult to harmonize with that of other bony fishes. A reference to its form in early developmental stages, however, discloses close similarity to the chondrocrania of more normal adult types at similar developmental stages. From such comparison one learns that the striking peculiarities of the adult form must all be regarded as late ontogenetic and not phylogenetic features. In other words, this is an individual specialization, comparable to many that might be cited amongst the modern Teleosts.

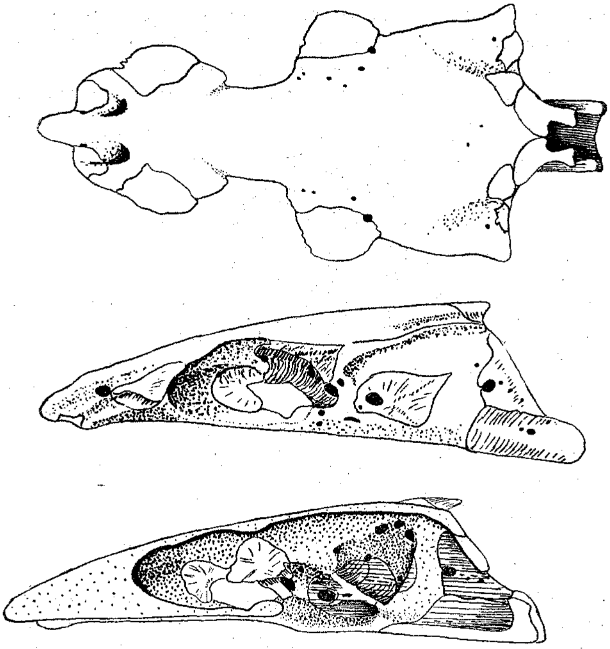


Fig. 62.—*Amia* (after Allis, 1897).

The peculiarities of the bony skull are more apparent than real. The so-called basipterygoid process is not, in the reptilian sense, a basipterygoid process at all. It is a process of the parasphenoid and prootic bones and is closely, if not absolutely, paralleled in certain of the more primitive of the Teleostei, e.g. *Heterotis*, *Osteoglossum* and *Arapaina* (Ridewood, 1904).

The maxillo-palatine arch is fundamentally similar to that of *Amia*, but with the individual bones altered in length by the elongation of the skull in front of the cavum cranii. The relation of the bones in the suspensorium, one to another, is quite typical. Tate Regan (1923) follows W. K. Parker (1882) in identifying the quite normal preoperculum as the interoperculum. This error was corrected by Goodrich (1909).

It is possibly only a coincidence that the three fishes quoted above as having a pseudobasipterygoid process also resemble *Lepidosteus* in the absence of an ectopalatine.

The premaxilla is apparently devoid of ascending processes, but this also is only a matter of appearance. The reduced ascending processes lie behind the nasal capsules. It differs from the ascending process of the premaxilla of *Amia* in that the median process stops short of the anterior aperture of the olfactory canal, but the lateral arm ascends to meet the nasal. The maxillary labial differs from all the other bones of this region in that, in place of being elongated to produce a single more or less splint-like bone, it has been fragmented in the process of extension. It is also different from the bone in *Amia* and the Teleosts generally, in that it is closely applied to the lateral edge of the maxilla.

There is no question that the composite bone is homologous with the single maxillary labial in the fishes generally, so that the condition is particularly interesting as providing one of the stages connecting the conditions presented in many of the Crossopterygians with those so familiar in the modern Teleosts.

The roof pattern is essentially the same as that of *Amia*. Gregory has recently identified the nasals as the ascending processes of the premaxilla. This identification leads him into the further error of identifying a little pair of dermal scales, which lie in front of the nasal capsules and between the two apertures of each, as the nasals. A small pair lying behind and lateral to these he designates adnasals, and suggests that they may be antorbitals. In this situation they differ markedly from the nasal and adnasal of *Amia*, which are said to correspond with the antorbital of palaeoniscids, which last also lies behind the nasal capsule. Inasmuch as that the nasal bone throughout the whole of the rest of the vertebrata lies above and behind the premaxilla, between it and the frontal behind it, the identification of the little scute at the anterior end of the snout of *Lepidosteus* as the nasal is surely at fault.

Gregory suggests that the tiny little dermal scale which lies between the anterior pair of prenasal scales is the mesethmoid of the Teleosts. Since it lies in front of the premaxilla and the ethmoid lies behind those bones, this suggestion is quite unacceptable.

The frontal does not, as in *Amia*, overhang the boundary of the orbit. There intervenes a series of periocular scutes which are continued right round the orbit. Behind these, and completely covering the pterygoideus and quadratomandibularis muscles and filling all the area between the orbital scutes in front, the preoperculum behind, the frontal and pterotic above and the lower arm of the preoperculum below, there is an area of irregular, small dermal scutes.

The periocular scutes are regarded by Gregory as evidence that *Lepidosteus* stands close to the Semionotids, and he says of *Amia*, that it probably stands much nearer to the base of the Teleosts than it does to *Lepidosteus*. The general implication of his remarks on *Amia* is to the effect that it stands nearer to the Teleosts than, in the past, has been admitted. Herein I am in agreement with him, but I cannot agree that the above features indicate that *Lepidosteus* is not closely related to it and that they are not rightly placed together.

Amia certainly lacks the dorsal periocular scutes, but it has the same number of post-orbitals, three, certainly much enlarged, the same number of infra-orbitals, two, and only one additional infra-preorbital. There is here no character on which to separate the two forms. The third post-orbital is attached to the dorsal edge of the maxillary labial and is termed " jugal " by Allis.

Gregory also quotes the forward inclination of the suspensorium as a character of importance indicating semionotid relationship in *Lepidosteus*. This forward inclination is far in excess of anything found in the group he refers to and is, perhaps, not of importance, the intermediate stages in forward inclination being readily obtainable amongst modern Teleosts.

The pseudobasipterygoid articulation of the metapterygoid is, on the other hand, a very striking feature. If it be also a phylogenetically important feature, then it will be necessary to transport *Lepidosteus* on this account alone, and it will be necessary to consider the claims of several of the forms allocated to the Osteoglossoidea and Mormyroidea to close relationship with *Lepidosteus*. They have not only this feature in common, but also they lack the ectopalatine as an independent ossification, and have the median edge of the maxillo-palatine arch firmly sutured to the parasphenoid.

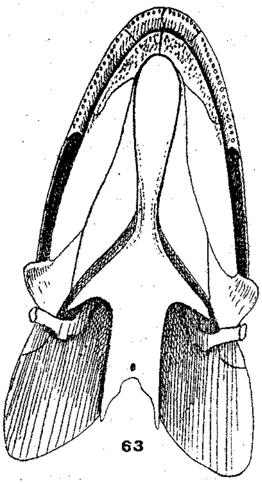
It may also be noted that *Lepidosteus* possesses a very complete primordial chondrocranium, the walls between the cavum cranii and the nasal capsules being especially well developed, almost completely enclosing the sphenoidal cavity. In this respect, again, there is a resemblance to *Gymnarchus*, the only member of the above two groups whose development has been worked out, so far as I can ascertain.

The adult chondrocranium of *Amia* so closely resembles that of *Salmo* that it is probable that its primordial chondrocranium was similarly fenestrated.

Polypterus.

(Figs. 63, 64, 65.)

The chondrocranium of the adult *Polypterus* displays a closer approach to the condition of the primordial chondrocranium of the modern Teleosts than does that of *Lepidosteus.* That this is not a late modification is clearly indicated in the larval stages. In these early stages the nasal capsule is connected to the cavum cranii by simple cartilaginous rods, trabeculae cranii and supraorbital bars (Budgett, 1907, p. 160). In the adult no trace remains of the trabeculae, and only the anterior portion of the supraorbital bars is found. In the otic and ethmonasal regions complete cartilaginous girdles are present. The former includes the otic capsule, the major portion of which persists in cartilage, the latter lodges the olfactory canals.



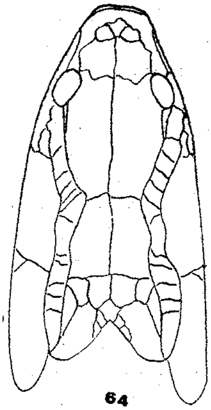


Fig. 63.—*Polypterus.*
Fig. 64.—*Polypterus* (after Gregory, 1933).

This persistence of the wide fenestration of the sphenethmoid region, so characteristic of the primordial chondrocranium, not only of the bony fishes but also of the Tetrapoda generally, might be interpreted as indicating a closer relationship to those forms than to *Lepidosteus* and other forms in which the fenestration is not so marked.

Such a view, however, would overlook the fact that this wide fenestration of the primordial chondrocranium is an early and fundamental condition of every chondrocranium.*

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* The work of Platt, Stone, Landacre, and de Beer, demonstrating that the trabecular derivatives of the cranium are of ectodermal origin, whilst the parachordal are of mesodermal origin, completely explains the why, and largely the how, of this fenestration.

It follows that the complete chondrocranium of the Elasmobranchs, or wherever else found, is to be regarded, not as the persistence of a primitive early embryonic condition, but as the persistence of a late embryonic and adult condition.

In short, the complete is a specialized development from the fenestrated chondrocranium, is characteristic of the Elasmobranchs, and is probably an inherited character from some ancestor common to all those fishes which possess the feature.

It is realized fully that this is an almost fundamental change in our view, which has regarded the complete as the primitive chondrocranium, but it seems to follow necessarily from the facts recorded in the works quoted

It should, perhaps, be pointed out that we may not conclude from the failure to develop a complete chondrocranium in any of its stages of development, that the fish or animal being studied did not come of ancestral stock common to itself and the Elasmobranchii. The most that one is justified in concluding is that, if from elasmobranchian stock, the characteristic chondrocranial stage of that ancestral stock has been dropped from the ontogeny of the example.

The different origin of the two regions of the chondrocranium predetermines fenestration in the sphenethmoid region, so that no matter how accelerated the cranio-visceral development may be, this fundamental stage must appear if any primordial chondrocranial elements at all are developed. On the other hand, since the relatively complete chondrocranium is not primitive and fundamental, but a characteristic of the elasmobranchian stock, it gains in value as a phylogenetic feature.

Professor Gregory, whose view is largely limited by the twin hedges of the bone-paved lane the palaeontologist is constrained to travel, says (1933, p. 123), " I fail to see in the embryo Sturgeon any specially elasmobranchian characters not shown in other fish embryos . . .". Surely the early development of a very complete chondrocranium cannot be interpreted in any other way than as indicating a close alliance with the Elasmobranchii.

The osseus palate and suspensorium are essentially similar to that of *Amia*. The premaxilla is a longer and narrow bone than in that fish and only meets its fellow along a short edge anteriorly. The wide expansion of the synpterygoid at its anterior end occupies the situation of the palatine lamina of these bones in *Amia*. The premaxillary bone is very similar to that of *Lepidosteus*. The median arm of the ascending process, present in *Amia*, is missing in this, as in *Lepidosteus*. The lateral arm is larger than in either of the other fish, and is sutured to the lachrymal (the only infra-preorbital scute present) along its inferior edge, and to the lateral edge of the nasal along its superior margin. The maxillary labial extends back beneath the orbit as in *Amia* and the Teleosts generally. Here, however, it has insinuated itself between the post-orbital scutes, so that the third lies below it, and the two upper scutes above it are much reduced. Not only is this so, but it sutures, between the scutes, with the anterior edge of the " cheek plate ", a bone which has taken the place of the shield of small irregular scutes which cover the muscles of mastication behind the post-orbitals in *Lepidosteus*.

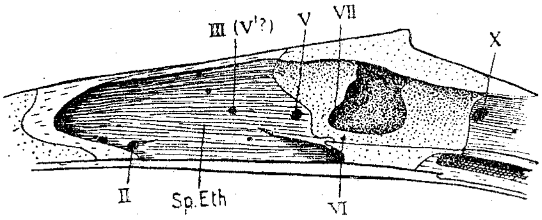


Fig. 65.—*Polypterus* (from Kesteven, 1926*b*, from Allis).

The resemblance which this labial bone in *Amia* and *Polypterus* bears to the maxillary arcade of the Tetrapods is truly extraordinary, so that the long-standing error in their identification was only natural in the absence of embryological evidence.

It must, however, be remembered that (like the labial bones of *Lepidosteus*, *Amia* and the Teleosts generally, with which they are undoubtedly homologous) they are developed quite independently of the palato-quadrate or the horizontal lamina of the ethmoid region of the chondrocranium.

The wide subotic processes of the synpterygoid present a superficial resemblance to the basipterygoid processes of the Tetrapoda and a real resemblance to the condition in *Lepidosteus*. Though the synpterygoid here makes contact with the metapterygoid and the palatine, there is neither sutural union, as in the Mormyroidea and their congeners and *Ophiocephalus*, nor an articulation as in *Lepidosteus*.

If, for the moment, we omit from the comparison the series of spiracular ossicles, the roof pattern of *Polypterus* differs from that of *Amia* in the following minor details only. The adnasals are situated in front of the nasals in place of beside them, and each tabular has been divided nearly in halves.

The spiracular ossicles, which are without close parallel in any of the known recent or fossil fishes, and the division of the tabular give to this roof a primitive appearance decidedly suggestive of close alliance with the crossopterygian fishes rather than with the actinopterygian. This resemblance is heightened by the presence of the large cheek plate and the two gular plates, and is still further increased by the sutural union of the maxillary labial with the infra-post-orbital dermal bone, the cheek plate.

Unfortunately our knowledge of the fossil Crossopterygii is largely confined to the external features of the skulls, and these are so exceedingly variable that it would appear that every new form described provides another pattern in the number and arrangement of the dermal scutes. Amongst this maze of dermal scutes and varying relation with the labial bones it has proven difficult to seize on anything of demonstrably valuable phylogenetic significance.

In only a very few instances have we any thoroughly reliable information as to the structure of the palate and the bones of the cavum cranii, and the relation of the latter to the former.

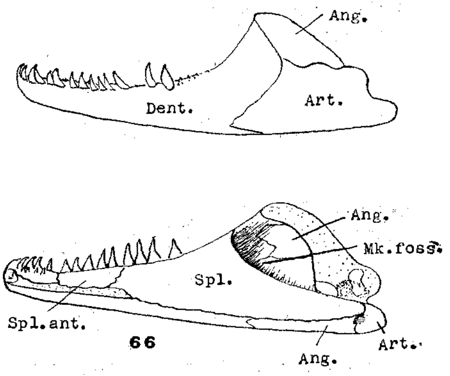
If the most recent interpretations of these few examples are correct and truly representative of the Crossopterygian fishes as a whole, then very assuredly *Polypterus* is infinitely more closely related to the Actinopterygii than to them. Compare in this respect especially the recent interpretation of the palate of *Eusthenopteron* by Watson and by Bryant.

Quite apart, however, from the resemblance, fancied or otherwise, to the crossopterygian fossils, the essential similarity of the cranial structures of *Polypterus* to those of *Amia* and *Lepidosteus* must surely be accepted as indicating a closer relationship between the three forms than has been admitted in the past.

Appendix A.

THE ELEMENTS OF THE LOWER JAW IN THE BONY FISHES.*

The lower jaw of *Scomber*, as figured by Allis (Fig. 66), may be accepted as representing quite typically the normal for the Teleostei. There is a good deal of variation in the relative size of the two larger components, though in the great majority of instances the dentary is the



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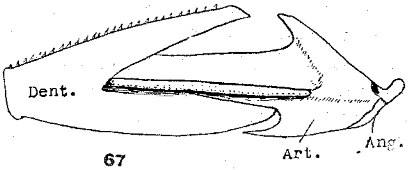

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Fig. 66.—*Scomber* (after Allis).
Fig. 67.—*Amia* (after Allis, 1897).

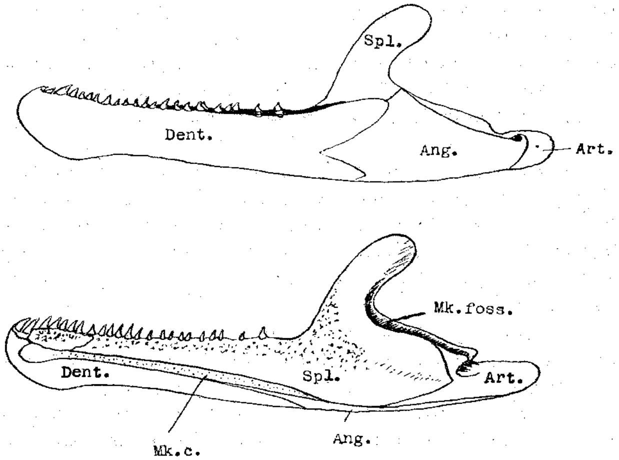

Fig. 68.—*Polypterus* (after Allis, 1922).

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* I have examined the branchial skeleton of a number of fishes, both elasmobranchian and bony, and have been unable to seize upon any features of general morphological interest; they are therefore not reviewed in this work. I would not be understood to assert that these structures are not capable of yielding evidence of general interest, but simply that I have failed to find such evidence. Whether that failure is due to want of interest or fuller knowledge or is really not available I leave the future to decide.

larger. It is common for the dentary to be extended back along the inner side of the articular so as to convert the sulcus along which Meckel's cartilage lies into a canal. This, in the section dealing with the muscles, has been termed Meckel's canal and the posterior opening has been termed Meckel's fossa. The fossa is more or less completely closed, in the flesh, by the tendinous insertions of the pterygoideus and quadrato-mandibularis muscles. When, as in *Scomber*, the canal is widely open for the greater part of its length, it is usually filled by the quadrato-mandibularis inferior. The coronoid, or ascending process of the lower jaw, may be formed by the articular or by the dentary, or by both.

It is of particular interest that all the more primitive fishes have a more complex ossification of the lower jaw than have the Teleostei.

Amia and *Polypterus* (Figs. 67, 68).—My drawings are reproduced from the work of Allis. It is believed that these are sufficiently explanatory to need no further comment. The lower jaw of *Lepidosteus* is essentially similar to that of *Amia*. The bone which Parker (1882, p. 479) terms the coronary is that which Allis identifies as the largest piece of the splenial.

The complex structure of the lower jaw of *Eusthenopteron* was described by Bryant (1919). I reproduce his illustrations. Here again further comment appears uncalled for (Fig. 69A, B).

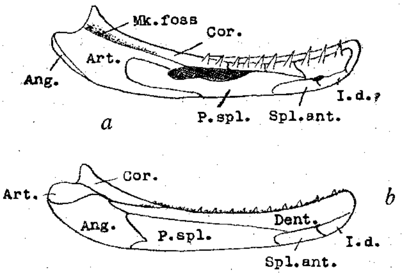


Fig. 69.—*Eusthenopteron* (after Bryant, 1919).

Appendix B.

THE TEETH OF THE FISHES.

It is not proposed in this section to describe any of the very many forms of teeth and their various relations to the bones of the palate, upper and lower jaws, and labial bones. Their variety is so extensive that it were a lengthy work to review even the commonest of them.

The palaeontologist, perhaps to some extent obsessed by the importance of tooth form in the higher vertebrates, has in several instances sought to support arguments as to the phylotic relations of the lower vertebrata, one to another and to the higher vertebrata by citation of similarities in tooth form and relation to the bone.

It were a foolishness to deny the importance of the form of the teeth in the determination of phylogenetic questions as between the members of the higher Tetrapoda, but it is quite certain that these characters become successively less reliable as we descend the scale, and he were a brave man who would attempt to determine the relation of the Crossopterygii to the Tetrapoda or the Dipnoi to the Amphibia on the form of the teeth, their mode of implantation on the bone or cartilage, or their presence or absence on specified bones.

On such evidence as this we should divorce some of the larval siluroids from the adult, the one has sharp spiny teeth lightly set in cup-like depressions, the other short blunt grinding teeth deeply set in sockets. Some of the recent Acanthopterygii have sharp tearing teeth along the outer edge of the labial and dentary bones and grinding plates on the maxilla. The majority of these fish have the teeth set in sockets of varying depth. In the great majority the socket is cup-like, and the teeth are shed and replaced, but in some it is of such depth that there is little room for doubt that the tooth is never shed, but grows continuously through the life of the fish. In the Plectognathi the teeth are developed quite superficially on the outer surface of the labial bones, a method of development entirely different from that of the Teleostei generally.

As an instance of wide variation in dental characters in closely allied fishes one may quote the members of the Blennioidei (Gregory, 1933, pp. 374-37).

Finally, the extreme variability of dental characters among closely allied fish may be illustrated by citation of the many forms of teeth present in the different batoid Selachians, and of the variety of teeth which gave their name to the "heterodont" Selachians.

THE HOMOLOGIES OF CERTAIN OF THE BONES IN THE SKULL OF THE BONY FISHES.

In the foregoing pages a nomenclature for the bones in the palate and for some of those in the skull has been employed which is quite at variance with the commonly accepted nomenclature and its implied interpretation of the homologies of the bones concerned. This nomenclature is the outcome of studies whose results I have published in various papers during the last twenty odd years. There follows here a review of the facts of development, and adult anatomy, both of the recent and fossil forms, which, in my opinion, support the conclusions I have arrived at.

THE EVOLUTION OF THE SUPERIOR MAXILLARY BONES.

The key to the understanding of the evolution of the two superior maxillary bones is to be found amongst the Elasmobranchii. The Plagiostomes probably present the primitive condition. In these fish the mouth is formed directly around the epi- and cerato-mandibular cartilages, the quadrato-mandibular and Meckel's cartilage. The vestigial, extra-, pharyngo- and hypo-mandibular cartilages simply lie amongst the tissues of the cheek and take no part in the formation of the mouth (Figs. 30, 34).

The Chondrostei present a further stage, the end stage along this line of evolution. In them, it will be remembered, the labial cartilages have been lost entirely.

It is a peculiar fact, however, that, although not ancestral to either the Crossopterygians or the Tetrapods, the Acipenserids have developed a true maxilla upon the quadrato-mandibular arch. This bone has always been designated " maxilla ", but there can be no doubt that it is not homologous with the maxilla of the modern bony fishes.

The inception of the maxilla and premaxilla of these latter is to be seen in the Holocephali. Here we see the labial cartilages impressed into the formation of an added fore part of the mouth, in front of the jaws. This added portion is, of course, the mobile upper lip, prehensile in these cartilaginous fishes as in the Teleostei. It is of particular interest to observe that the movements of this lip are brought about by specially modified portions of the superficial, temporo-masseteric, division of the masticatory muscles (Fig. 20).

Turning next to the Teleostei, it is found that the labial cartilages have but a transient embryonic independence, and early become incorporated into the premaxillae and maxillae which are otherwise largely developed as membrane bones (Norman, 1926). Again we observe that these labial bones are moved by specially modified portions of the temporo-masseteric muscle (Figs. 27, 28, 29).

Apparently these labial bones were developed in the ancestors of the Amphibians, for we, undoubtedly, are able to observe their elimination from the armamentarium of the Anura during the later stages of the metamorphosis of the tadpole. The labial cartilages are present, armed with teeth, working against the Meckelian lower jaw and activated by the same portion of the temporo-masseteric group of muscles in the fully developed tadpoles of all Anura (Figs. 75, 76). During the late stages of the metamorphosis the cartilages are absorbed, and their muscle gains a new insertion into the lower jaw.

This, apparently, is the history of the evolution and abolition of the labial bones which have, in the past, been regarded as the maxillae and premaxillae of the Teleostei.

We turn next to the evolution of the true superior maxillary bones.

The discovery of *Latimeria*, a more primitive crossopterygian than *Polypterus*, provides the earliest stage in the evolution of these bones amongst the living vertebrates. Here we find that there are two aggregations of tooth-bearing ossicles related to the anterior end of the palato-quadrate arch anteriorly.

In *Polypterus* (Fig. 63) and early, Triassic, crossopterygians such as *Eusthenopteron*, and *Osteolepis* these aggregations have taken on the form of the tetrapod maxilla and premaxilla.

Amia, *Polypterus*, and some of the Actinopterygians present a combination of the two forms of jaw-bones, and it is just the existence of these intermediate forms which has been responsible for the past misunderstanding of the bones. These fish have retained the labial maxilla and have anchored its anterior end between the true premaxilla in front and dermal bones behind it (Fig. 61). The extraordinary resemblance of the resulting combination to both the labial type of jaw on the one hand and the true jaw on the other has been the cause of the misunderstanding.

Up to this point the embryological evidence has not been stressed because it was felt that the question was one which was likely to interest the palaeontologists, and that, therefore, the case for this interpretation of the bones should be presented, as far as possible, on the evidence of adult form, for that, unavoidably and very naturally, is the form of evidence which our palaeontological colleagues best understand. There is, however, no little embryological evidence in favour of the above interpretation.

Basically, there can be no doubt that the manner of development of bones is not a haphazard process, but is one which has been inherited in perfectly orderly fashion along with other features and functions. Therefore, if we can show that the labial bones develop in a manner and in a location quite different from that of the jaw bones of the Tetrapods, this must be accepted as evidence that the bones are not homologous.

There is little reason to doubt that the pair of upper labial cartilages so commonly present in the Teleostei are completely homologous with those of the Selachii.

Now it has been demonstrated that the premaxilla of the Teleostei develops in relation to the anterior of these cartilages, but that the bone develops largely as a membrane bone (Swinnerton, 1902; Gaupp, 1906; Norman, 1926). The cartilage itself is designated "premaxillary" by de Beer (1937). The posterior cartilage was designated the "maxillary" cartilage by Sagemehl when he found that the maxilla was developed in relation to it (Sagemehl, 1885, 1891).

In the Ganoid fishes these cartilages have not been detected, and it might, therefore, appear that here is evidence that the bone which has been identified as the maxilla cannot be the homologue of the maxilla of the Teleostei. This does not follow because, in quite a number of the modern Teleosts, neither of the labial cartilages appears to have been developed, yet there can be no question as to the homology of the labial bones in all of them.

Perhaps a moment's consideration of the phenomena of the early differentiation of the osteogenetic tissue will help to clear the position.

Dantschakoff (1909) demonstrated that osteogenetic tissues were precisely similar, whether differentiated in relation to cartilage or not. Stump (1925) stated that the evidence of histology very definitely indicated that the cartilage related to developing bone took no part or share in the actual bone formation, that it was simply replaced by the bone. Its only function was to provide a model, as it were, on which the future bone was to be formed. Kesteven, from an extensive survey of the process of ossification of the Saurian basis cranii (1940) and more particularly from a survey of the ossification of the Avian chondrocranium (1941) arrived at the same conclusion.

It appears that when once the site of the differentiation of osteogenetic tissue has been determined, this ontogenetic habit at once becomes more or less fixed.

We may, however, go further. In view of the fact that the cartilage takes no part in the formation of the bone which develops in relation to it, it is quite reasonable to believe that, once the site of the differentiation of the osteogenetic tissue has been determined, the loss of the cartilage to which it was originally related need not have caused any appreciable change in the development and form of the bone itself. Amongst the fishes themselves the fact that, even in the presence of the cartilage, the bones are developed largely as membrane bones, is evidence of a certain established degree of independence of the cartilage in the osteogenesis; so that the development of the bones in the absence of the cartilage is quite understandable.

What appears to be another illustration of the same thing is the regular development of the supraoccipital bone, whether a precursory tectum synoticum was developed or not.

It follows from what has gone before that there is complete justification for accepting as homologous the maxillae of Ganoids such as *Polypterus* and *Amia*, and those of the generality of the Teleostei.

It would seem, also, to follow that the premaxillae in these Ganoids were homologous with those of the Teleostei, differing only in that they are developed in the absence of the cartilage. Undeniably this line of reasoning is open to us, but it is believed that other evidence is stronger and leads to its rejection. But, before proceeding to that other evidence, it is as well to follow the above line of reasoning to its logical conclusion.

If it be assumed that the maxillae and premaxillae of such forms as *Amia* and *Polypterus* are homologous with the labial bones of the Teleostei, it will be assumed that the process of their evolution has been as follows. The labial cartilages have been lost and the labial bones formed entirely in membrane. The premaxillae have then come to acquire a new relation to the anterior end of the ethmoidal cartilage and the maxillae to the lateral margin thereof. Finally, in this new situation, they have attained to the position of the tetrapod bones of the same name.

Though, apparently, this line of reasoning has not, heretofore, been clearly stated, it is, in fact, the line of reasoning which underlies the commonly accepted homologization of the bones in question. The only alternative is an assumption that the labial bones of the Teleostei have been evolved in the directly contrary way, by some process of liberation from the true arch of the jaw, and for this assumption there is not one scintilla of evidence.

The above statement of the argument in support of the accepted interpretation of the bones is entirely reasonable and tempting, but it is open to weighty objections.

The most important of these is the history of the ontogeny of the maxilla and premaxilla in the Anura. There is no room for doubt that these bones in the Anura are completely homologous with those of the rest of the Tetrapoda.

The condition in the early tadpole is myologically almost as primitive as that of the Holocephali. There are present, in front of the ethmoid cartilage, two superior labial cartilages hinged to one another and to the ethmoid cartilage essentially similarly to the labial bones in the Teleostei. These two cartilages constitute, and function as, a prehensile, biting upper jaw. They are activated by a completely separate portion of the temporo-masseteric masticatory musculature, just as are the labial cartilages in the living Holocephali but, in these last, it is a part of the pterygoid muscle which acts upon the labial cartilages. During metamorphosis, for a fleeting period, the myological conditions reproduce with *complete faithfulness* those of the Teleostei. The retractor labii superioris gains a new insertion into the lower jaw. This is the condition found in every one of the fishes which possesses the mobile labial bones. The superficial portion of the temporo-masseteric muscle is inserted into the lower jaw at the coronary process and has also a strong tendinous insertion onto the maxilla, acting as a retractor labii superioris. Following this stage, the superior labial cartilages are completely absorbed, the muscle retains only its insertion into the lower jaw, and the maxilla and premaxilla are developed, as in all other Tetrapoda, in close relation to the ethmoidal cartilage and/or its processes, and the anterior attachment of the palato-quadrate.

There appears to be only one interpretation of this history. It is that the superior labial cartilages and their muscles have been inherited directly from some piscine ancestor. The cartilages are, therefore, almost without doubt, completely homologous with those of the fishes. If this be the fact, then it is out of accord, in important respects, with the history of the evolution of the tetrapod maxilla and premaxilla, as outlined above, in conformity with the generally accepted interpretation of the bones.

In the Anura, not only is there no trace whatsoever of bone development in relation to the cartilages (which, had it been there, might later become related to the ethmoid cartilage), but actually the osteogenetic stroma of the future maxillae and premaxillae is clearly recognizable in close association with the ethmoidal cartilage, whilst yet the labial cartilages are functioning as the jaws.

Since the cartilages are homologous with those of the fishes, they must also be homologous with the bones which are developed in relation to them.

Here, it seems, is the complete evidence that in the Anura, at least, the maxillae and premaxillae are not homologous with the bones so named in the Teleostei.

It is doubtful if anyone will deny the homology of the Anuran bones with those of the rest of the Tetrapoda. It follows, unavoidably, that the maxillae and premaxillae of the Tetrapods are not homologous with the bones so named in the Teleostei.

It is probable that the premaxillae of Ganoids such as *Amia* and *Polypterus* have been developed in the same manner as in the Tetrapods, from a beginning such as is seen in *Latimeria*, and the form of the lip folds in *Latimeria* suggests that some trace, perhaps in cartilage only, will be found of the labial skeleton, when more and better preserved material is examined.

Turning again to the Teleostei, there is related to the anterior end of the ethmoid cartilage a bone which has been termed the vomer. Although, apparently, this designation has never been challenged, it has for many years now been used merely as a convenience. In our almost universal acceptance of Sutton's interpretation of the origin of the vomer, we have all tacitly admitted that this piscine vomer could not have been homologous with the bone so named in all other vertebrates. Westoll and Parrington (1940) have recently advanced very strong evidence that we have all been in error in our acceptance of Sutton's equation, and Kesteven's (1941) demonstration that the so-called rostrum basisphenoidei of the Saurians is a presphenoidal ossification and not parasphenoidal, is strong confirmation of their conclusions.

It will, probably, be agreed that if there were no labial bones in front of this " vomer " in the fishes, it would be identified unhesitatingly as the premaxilla, and there would not be one single feature in its development and adult location out of congruence with such an identification.

This " vomer " has, in recent years, been designated " prevomer " by some writers, but this is an unsatisfactory identification. The prevomers of the Tetrapoda are situated further back, and never extend onto the dorsum of the ethmoid cartilage as this bone so commonly does.

Having taken cognizance of this bone, and recognizing that it is always present in the osseous cranium of the fishes, we have now to add another clause to the line of reasoning which equates the labial bones of the fishes with the maxillary bones of the Tetrapoda. This new clause runs as follows : As the premaxillary labial bone came to gain its new relation to the anterior end of the ethmoid cartilage, it displaced backwards the bone which previously occupied its new position. This clause is necessary in any case, but more so if the " vomer " of the fishes is to be equated with prevomer of the Tetrapods.

This is an unfortunate addition to the argument, for it overloads it. It is hard to understand why, if the cranium was already strongly supported by a well-established bone, another should have taken its place and caused it to migrate backwards.

The weight of the evidence points to the probability that the " vomer " of the Teleostei is in reality the tetrapod premaxilla.

THE MAXILLA.

It has just been demonstrated that there is every probability that the labial bone which has been regarded as the maxilla in the bony fishes is in reality the homologue of one of the superior labial cartilages of the Amphibia. It remains to inquire for, and, if possible to identify, the maxilla of the Tetrapods in the fishes.

The maxilla in the Amphibia and Reptilia is developed in relation to the lateral and ventral walls of the nasal capsule and also in relation to a backwardly projecting " posterior maxillary process " (Gaupp, Fig. 383) of the capsule in the reptiles.

Swinnerton, describing the development of the palatine bone in *Gasterosteus* (1902, p. 545), says : " The (cartilaginous palatine) process is, relatively, much slenderer than at any previous stage, and its extremity, owing to continued growth of the maxillary process, is expanded. Behind this the cartilage is not merely in contact, but in actual continuity with that of the pre-ethmoid cornu. The palatine bone surrounds this point, and extends back almost to the level of the parethmoid." It is, then, around the anterior end of the palato-quadrate arch that the palatine, so-called, in the fishes is developed.

The union of the fore end of the palato-quadrate with the ethmoid cornu appears to be a very primitive feature. I have previously noted that " It is of constant occurrence throughout the Anura, very generally present in larval stages of Urodela, and in those urodeles in which the continuity is broken there is, as also in the gymnophiones, evidence that such continuity has been but recently lost from the ontogeny. The anterior structural continuity of the palato-pterygoid and the ethmoid plate has been recorded in several Teleostei, as a temporary condition in embryonic life, and among the elasmobranchs it is found in the adult Holocephali, and it is not improbable that the anterior articulation of various Selachians will be found to have been preceded by cartilaginous or procartilaginous continuity, as demonstrated for *Acanthias* by Sewertzoff (1899). Among surviving ganoids, *Lepidosteus* is apparently alone in presenting the continuity here under review " (Kesteven, 1931*a*).

In the Anura the fore end of the palato-quadrate cartilage is pinched off and remains as a posterior maxillary process attached to the postero-lateral corner of the solum nasi. This is apparently quite constant among the anurous amphibians. Parker describes and depicts it clearly in Rana (1871), and I have been able to study the development of *Lymnodynastes, Hyla, Crinia* and *Myxophyes*, and find the same thing in all four. Gaupp designates the cartilaginous piece in question, processus maxillaris anterior and posterior of the planum antorbitale (Handbuch, p. 735).

There is little reason to doubt that the processus maxillaris posterior of the reptilian chondrocranium is completely homologous with that of the amphibian, and this, at times, if not always, is demonstrably derived from the fore end of the palato-quadrate cartilage.

Since it is in relation to the two processi maxillares that the maxilla is developed in the lower Tetrapods, and since these are probably homologous with the fore end of the palatoquadrate, around which the so-called palatine of the fishes is developed, it would appear only reasonable to conclude that this bone is homologous with the maxilla of the Tetrapods and should be designated in accord with its homology.

It may be remarked, before leaving this subject, that the position in which this bone is developed is emphatically not one that would justify its identification as the palatine, as in the past.

THE PALATINE.

That which is here identified as the palatine bone in the fishes is the bone that has heretofore been designated meso- or entopterygoid.

The palatine bone in the Tetrapods is a membrane bone situated rather far back in the palate. Of this bone in the reptiles, Williston (1925, p. 20) wrote: "Primitively forming the posterior boundary of the internal nares, articulating with prevomers and pterygoids on their inner sides, the maxillae on their outer, and with the descending process of the prefrontal above".

In the Amphibia there is a relatively wide range of variation in the situation and relation of the bones which have been designated palatine. In the Anura the bone is constantly a narrow splint which develops along the infero-posterior and medial concave edge of the posterior maxillary process, and in the adult is found lying along the anterior margin of the suborbital vacuity as a bony margin to the postero-lateral edge of the palate. In this situation its development resembles closely that of the "mesopterygoid" of the fishes.

In the Urodela the palatine develops further forward, on the inferior surface of the solum nasi. In some instances, e.g. *Sieboldia maxima* and *Menopoma alleghaniensis* (Parker, 1882), it is placed medial to and in front of the internal nares, in the adult of *Triton* and *Amblystoma* it is fused with the prevomers, but in larval stages it is found as a separate ossification, behind the prevomer and medial to the internal nares, developing in the situation of the inner end of the bone in the Anura.

In the Coecillians the palatine is placed lateral to and behind the internal nares, has a long suture with the maxilla, and may suture with the prevomer both in front of and behind the choanae (Wiedersheim, 1879). In these Amphibia, as in the reptiles, the bone apparently develops independently of a cartilaginous basis.

In the embolomerous Amphibia the palatine lies behind the prevomer between the pterygoid and the maxilla. Apparently in some forms it supplied the posterior boundary to the choanae, in others that boundary was supplied by the prevomer, *Pteroplax* (Watson, 1912).

In the reptiles the palatine is always a membrane bone, developed without any relation whatsoever to any chondrocranial structures. As stated by Williston, it commonly, and probably primitively, bounds the choanae posteriorly, but in some forms, e.g. crocodiles, it lies below and in front of them.

Although thus completely divorced from any cartilaginous basis, there is little reason for believing that the palatines of the reptiles are not homologous with those of the amphibians.

It must be admitted that, except for the position of the developing bone in the Anura, there is little in this review of the palatine bone in the reptiles and amphibians to support the identification which heads this section. On the other hand, there is nothing in the history of the development of the bone in those two tetrapod groups, or in its relation to other bones and skull areas in the adult, to indicate that the identification is in error.

Since the developmental evidence is not convincingly strong either to prove or disprove the identification, one is constrained to examine the adult relations of the bone. Though this kind of evidence is not so convincing as positive embryonic evidence can be, it is the only method available to the palaeontologist in identifying the bones in the fossils, and it has not often misled him.

We may define the palatine bone as a component of the palate in its posterior part, developed either quite independently as a membrane bone or in relation to the fore end of the palatoquadrate cartilage and/or the posterior margin of the solum nasi, or to the ventral surface of the solum nasi at varying distances from its posterior margin. In the adult it sutures with the palatine plate of the maxilla and usually lies posterior or posterior and lateral to the prevomers when they are developed. Exceptionally the palatine bones lie ventral to the prevomers. When, as in some reptiles and higher vertebrates, the bone extends posteriorly to the nasal chamber, it may or may not suture with the prefrontal, and in the absence of the prevomers the bones meet in a common suture along the mid-line and suture with the ventral edge of the vomer.

There is no nasal capsule, in any way comparable with the complex capsule of the amphibians and reptiles, developed in the fishes, and, probably correlated with that absence of complexity, there are no prevomers developed in the fishes' skull.

We have, therefore, left us, as landmarks for the identification of the palatine, only the maxilla and general location in the palate.

These are such that the so-called mesopterygoid is the only bone in the fish palate which can be considered. When to this, admittedly unsatisfactory, evidence we add the meagre support of the situation of the developing bone in the Anura, it would appear that we must conclude, either the mesopterygoid is the homologue of the palatine of the Tetrapods or this latter bone is not present in the palate of the fishes, and the mesopterygoid is without an homologue in the palates of the higher vertebrata.

THE ECTOPTERYGOID.

This is the bone which has been designated pterygoid and ectopterygoid.

In the original presentation of my ideas on the homology of the several bones of the fishes' palate, I identified this as the quadrato-jugal of the Tetrapods (Kesteven, 1922, p. 321). Later (1926, p. 217) I wrote: "It is now realized that this identification is incorrect; its position medial to the muscles of mastication is alone sufficient proof that the bone cannot be the quadrato-jugal."

A wider experience and more intimate knowledge of the related structures and their development gained by the study of much of the material that forms the basis of this work now leaves me once more undecided on this question.

Were Allis correct in his identification of the maxilla of *Lepidosteus* as the true homologue of that of the Tetrapods (Allis, 1900, 1919), then were it easy to satisfy ourselves that the jugal and quadrato-jugal of the Tetrapods are derived from certain of the cheek plates.

Not having had the opportunity of studying any stages in the development of *Polypterus* I accepted Allis's interpretations, and, as a further result of those uncritical readings, also accepted (Kesteven, 1931) Gregory's identification of the cheek plates (Gregory, 1915, 1920), one of which he identified as the jugal.

Since, however, the maxilla of *Polypterus*, and the Chondrostei generally, is not the homologue of that of the Tetrapods the question is not so easy of solution. The anterior attachment of these scutes to the labial bone, so-called maxilla, now becomes a reason why we should hesitate to accept their identification as jugal. On the other hand, the suture with the lacrhymal, assuming that is correctly identified, in front and with the squamosal, preoperculum, behind, are relationships which support the identification.

There is another aspect of the question that should not be lost sight of. It would appear that with the labial bones functioning as the upper jaws there is correlated, in the bony fishes, a narrowing of the maxillo-palatine arch behind and between them; this narrowing is not observable in any other forms, except as individual specializations. The true premaxillae and maxillae have persisted as the lateral and anterior limiting bones of the arch. In the great majority of the higher vertebrates there has been, on the other hand, a constriction of the arch posteriorly, to accommodate the muscles of mastication, to obviate their bulging beyond the general contours of the skull, and to permit of their direct action between fixed and moving points. In the result, the posterior end of the maxilla projects more or less outside the lateral margin of the muscles.

It is not inconceivable that the so-called ectopterygoid of the fishes retained its anterior relation to the maxilla and palatine, and came to project backwards laterally to the muscles, just as the maxilla itself has done. If so, it should be identified as the quadrato-jugal.

I know of no evidence which will satisfactorily decide the question between these two claimants for recognition as the quadrato-jugal, and, inclining to accept Gregory's identification, and because of that inclination, I have retained the designation ectopterygoid, believing that the resemblance to the os transversum of the lower Tetrapoda justifies the designation in the present state of our knowledge.

THE PHYLOGENY OF THE FISHES.

The two groups of outstanding interest in a phylogenetic review of the fishes are the Holocephali and the Chondrostei. They are of interest as much, if not more, for the light they throw on the origin of the Elasmobranchs as for the light they throw on the evolution of the bony fishes.

Taking the Holocephali first, we may tabulate their elasmobranch and teleostome features.

Elasmobranchian Characters.

Complete cartilaginous cavum cranii.

Entire absence of ossification of the skull.

The possession of a sphenoidal extension of the cavum cranii.

The possession of a relatively complete cartilaginous nasal capsule.

The form and attachments of the following muscles: epiarcualia obliqui, epibranchial spinal, coraco-mandibularis, and hypobranchial spinal.

Teleostome Characters.

The widely open lateral cranial fenestra displaying much of the structure of the otic labyrinth.

The branchial arches, gathered together beneath the skull and under an "opercular" fold.

The pharyngobranchial cartilages, fused to form a dorsal pharyngeal cartilage essentially similar to the bone of that name.

There is no spiracle.

The form and attachments of the following muscles: levatores arcuum branchialium, the levator operculi, the protractor hyoidei, and the sphincter oesophagi.

It is of interest to note that there is also this duality of characteristics in features beyond the head, the one set indicating close phylogenetic relation to the rest of the Elasmobranchs, the other indicating relationship with the Teleostomi (Bridge, 1904, p. 467; Kesteven, 1933, pp. 443-474).

Turning next to the Chondrostei, we tabulate their conflicting characteristics in like manner.

Elasmobranchian Characters.

Complete cartilaginous cavum cranii.

The form of the suspensorium.

Primitive palato-quadrate upper jaw.

The possession of a typical levator hyomandibularis muscle.

The possession of a branchio-mandibularis muscle.

The form of the protractor hyomandibularis, unquestionably a modified levator maxillae superioris of typical elasmobranch pattern.

The form of the pterygoideus muscle.

The features of the origin and distribution of the cranial nerves (Norris, 1925).

Teleostome Characters.

The presence of true ossification in membrane related to certain skull areas and visceral elements.

The widely open lateral cranial fenestra.

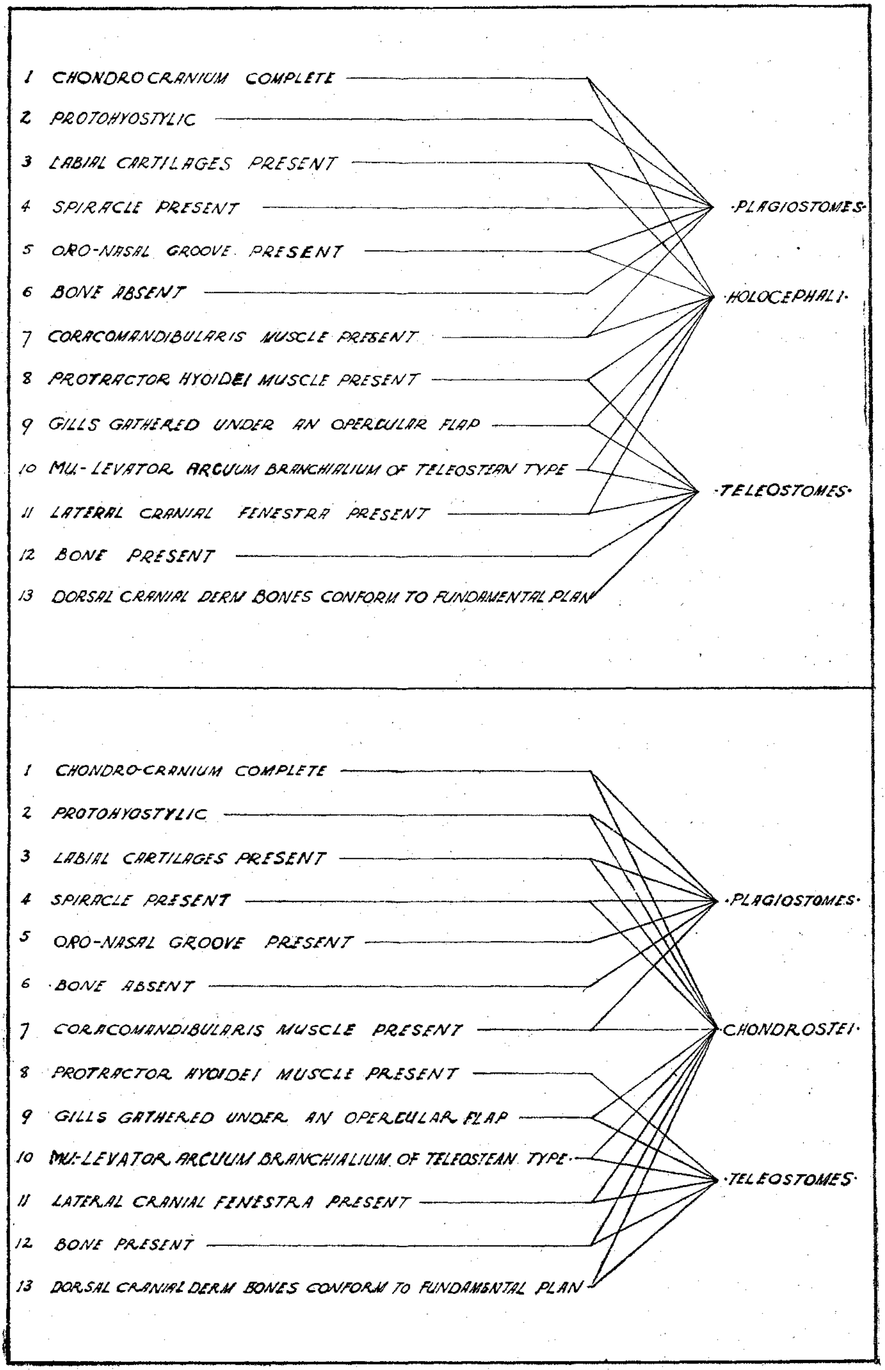
The form of the levatores arcuum branchialium muscles.

The absence of intrabranchial muscles and the presence of a ventral transverse branchial muscle, and of three subarcualia obliqui.

The peculiar dermal scales, with their basal layer of true bone, which are present as covering bones for the head and are also present along the side and dorsum of the body of the Sturgeons, may be regarded as teleostome or elasmobranchian features, according as we stress their superficial or deep layer.

It will appear later that the Holocephali also present features which are very strongly suggestive of close phyletic relation to the Dipnoi.

When thus reviewed, at close quarters as it were, the fishes appear to divide themselves into two great divisions, the Elasmobranchii on the one hand, and the Teleostomi on the other, with two smaller intermediate groups between their extremes.


1 CHONDROCRANIUM COMPLETE
2 PROTOHYOSTYLIC
3 LABIAL CARTILAGES PRESENT
4 SPIRACLE PRESENT
5 ORO-NASAL GROOVE PRESENT
6 BONE ABSENT
7 CORACOMANDIBULARIS MUSCLE PRESENT
8 PROTRACTOR HYOIDEI MUSCLE PRESENT
9 GILLS GATHERED UNDER AN OPERCULAR FLAP
10 MU.-LEVATOR ARCUUM BRANCHIALIUM OF TELEOSTEAN TYPE
11 LATERAL CRANIAL FENESTRA PRESENT
12 BONE PRESENT
13 DORSAL CRANIAL DERM BONES CONFORM TO FUNDAMENTAL PLAN
·PLAGIOSTOMES·
·HOLOCEPHALI·
·TELEOSTOMES·
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·CHONDROSTEI·
·TELEOSTOMES·

Diagram I.

This view of the fishes is, it is submitted, largely caused by the marked numerical superiority of the two extreme groups. Their bulk has dwarfed, and to some extent distorted, the other two. If, for the moment, we wash from our memory all but a selection of Elasmobranchs and Teleostomes, numerically no greater than the Holocephali or Chondrostei, the four groups appear in different perspective. They now present themselves as four equally important, equally divergent, groups of fishes. It at once becomes increasingly apparent that each group is monomorphic, each is a phyletic entity.

We are now able to stand afar off, on the ancestral side of all four, and to regard them as independent, separated, groups of descendants from some one common ancestor, realizing that in the course of their evolution, whilst all have carried forward certain established features in common, each has acquired new characters peculiar to its own group.

Coming closer to the individual groups again we recognize indubitable elasmobranchian characters in three of them, and on that account I have, in the past, been inclined to group these together as being more closely related one to another than to the fourth.

Systematists, generally, have agreed that the Holocephali should be regarded as a section of the Elasmobranchs, and the Chondrostei as a section of the Teleostomi. Phylogenetically, both attitudes are probably incorrect.

I would especially point out that up to a certain point it is possible to regard the Holocephali as boneless teleostomes, and in similar fashion to regard the Chondrostei as bony elasmobranchs. Again, if we change the perspective once more and, going round them, as it were, view these fish groups from the "tetrapod" standpoint, that is, look back on them as possible ancestors, we shall at once find the Holocephali to be a long way the closest to us, at least in many of their cranial and cephalic musculatural features.

In these particular features they appear as though they had been hastening along the "amphibian" road whilst still they were elasmobranchs.

To my mind the overlapping of the distinguishing characteristics of the Elasmobranchs and of the Teleostomi in the Holocephali and Chondrostei points to the following conclusions.

The primitive gnathostome was a very generalized fish, perhaps very similar to *Cladoselache*. This fish had already acquired the ability to submerge its primitive skeletogenous ectoderm and to develop from it the cartilaginous visceral skeleton and the trabecular components of the skull. This primitive gnathostome would have been provided with a fairly complete cavum cranii, contributed to largely by the otic capsules. It also, probably, had relatively complete nasal capsules, and fairly certainly a fenestrated sphenoidal region between the two pairs of capsules. It was also endowed with the power to build dermal scales and scutes.

This implies that its varying descendants should all have been able to form a bony exoskeleton. Some, however, did not do so; these constituted the Plagiostomi, and it is highly probable that the recent plagiostomes more nearly resemble this common ancestor than any of the other fishes.

Amongst the descendants which retained and improved on the power to form an exoskeleton the Teleostomi are the most outstanding. They early developed this exoskeleton on the head and it soon became attached to the cartilaginous skull. They also developed scutes along the edges of the lips and these became attached to the labial cartilages to form the labial bones. Those cartilages being to a large extent anchored by their muscular and fibrous attachments were, at first, also anchored to the dermal scutes of the side of the cheek, and only later gained mobility as we observe them in the modern Teleostei.

Whilst sharing with the teleosts the improved ability to form an exoskeleton and later cranial endoskeleton of membranous origin, the Chondrostei retained more of the original parental characters and failed to perfect the utilization of the skeleton-forming power.

If, as appears probable, the Holocephali are closely allied to the group from which the Tetrapods have been derived, it must be assumed that the recent Holocephali are to the parent stock much as the Polyodontidae are to the Acipenseridae, that is to say, they are degenerate in that they have lost the power to develop the exoskeleton which preceded the endoskeleton, which power was possessed by some of the Carboniferous members of the group. It may be that some such form as *Menaspis* is really nearer the stem of the Tetrapods than are the rest of the Holocephali.

Consideration of the geological antiquity of three of the four groups, and of the variety of the selachians in early Mesozoic and late Palaeozoic times, supports the view here taken that the details of the ancestry of the fishes are still wrapped in the mysterious depths of the late Palaeozoic rocks.

One alone of the four groups is so recent as to make its first appearance in later Mesozoic times, the Chondrostei.

From what little we know of them, it is probable that Pleuropterygii present the nearest approach to the primitive gnathostome at present available to us and, it may be remarked, it was undoubtedly an Elasmobranch. It further appears probable that not only the four recent groups, but also the Acanthodei and the Ichthytomi, should be regarded as illustrating different lines of variation among the descendants.

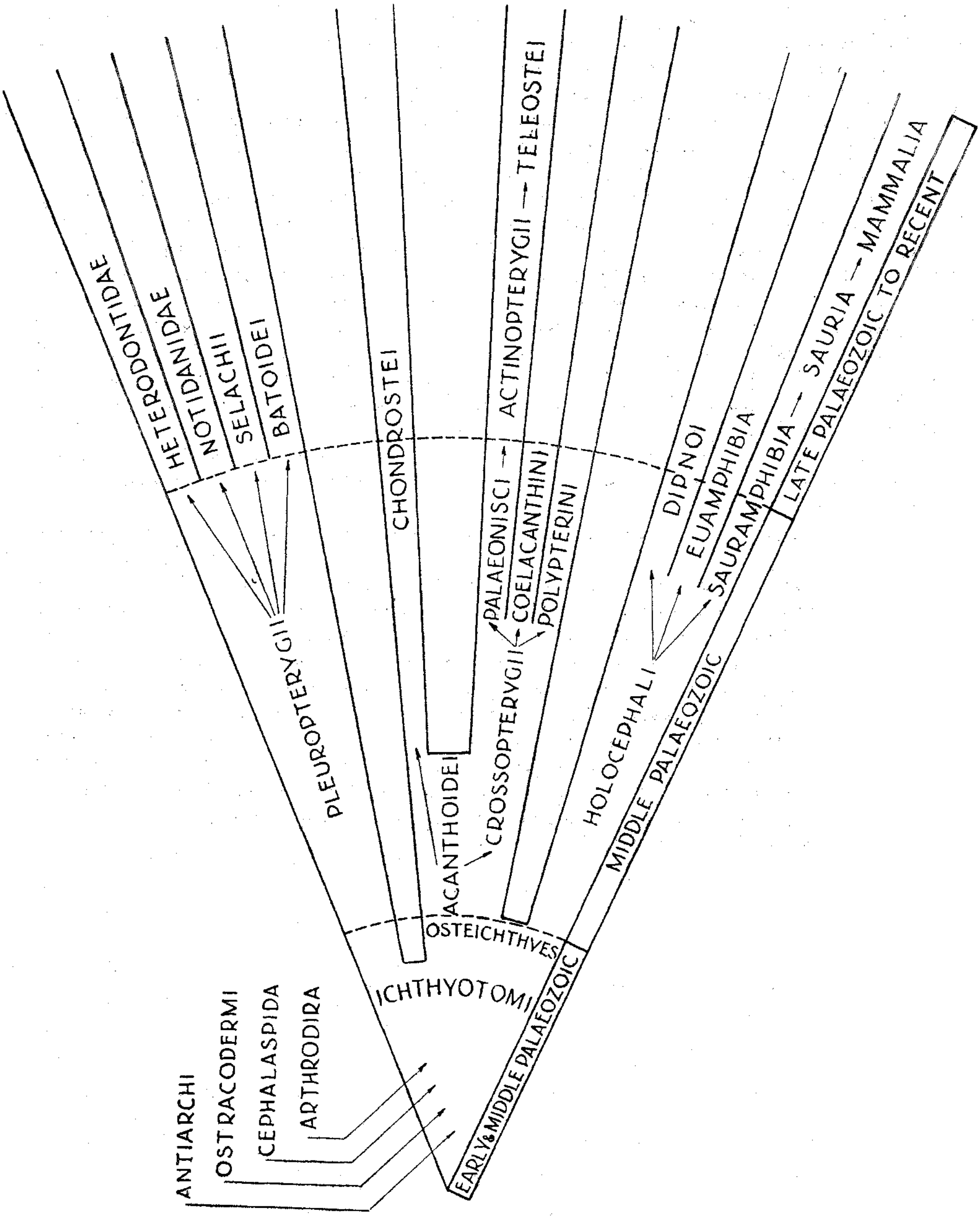

Diagram II.

It is not improbable that, with increased knowledge of the Acanthodei, we shall find them to lie in the direct ancestry of the Chondrostei.

Watson (1925, p. 831), after offering a new reconstruction of *Chondrosteus*, wrote : " Thus such new information as I can add only emphasizes that resemblance between Chondrosteus and the Palaeoniscids which Traquair long ago pointed out, and shows how untenable is the view of Bridge, adopted by Swertzoff, that the Acipenseroides are the most primitive of the bony fishes and owe many of their peculiarities to a persistence of Elasmobranch structures." Even if Watson's belief that the post-orbital and maxilla in *Chondrosteus* " were immovably connected together " should prove correct, the most this would justify us in concluding would be that *Chondrosteus* is probably not an acipenserid. Clearly Watson is in error in concluding that evidence which indicates that *Chondrosteus* is dissimilar to the acipenserids is to be regarded as having any bearing on the origin of the latter forms.

Of the several groups, the Acanthodei, Chondrostei, Teleostomi, and probably the earlier Holocephali, all possessed pericranial ossifications and dermal scales and scutes, and there is in the arrangement of these ossifications a basic pattern which is reproduced in every group, or in forms which may be regarded as probably descended from the group.

The whole of the fishes and the amphibians possess in common a large synpterygoid covering, the basis cranii, excepting only *Eusthenopteron* and the embolomerous amphibians. Further, throughout the whole of these two classes we find the same pattern in the covering bones on the dorsum of the skull, namely, paired parietals, frontals, nasals, and premaxillae. This pattern, though departed from in individual instances, is so constant in occurrence as to indicate assuredly that it must be regarded as a common inheritance (Goodrich, 1930, pp. 285 *et seq.*).

These last considerations might be interpreted as indicating for the bone-forming fishes an ancestry different from that of the Plagiostomi, but it is impossible to disregard the undoubted elasmobranch characters of the Chondrostei and Acanthodei, or the teleostean and amphibian characters of the Holocephali.

The explanation of the conflicting evidence appears to be that all evolved from a common ancestral stock which possessed in varying degrees the inherited potential to develop bones and to develop them in accord with an already established basic plan.

I have attempted to convey these ideas on the evolution of the fishes in diagrammatic form.

It may be remarked that the above diagrammatic presentation (Diagram II) differs from that of 1931, wherein I represented the Dipnoi and Crossopterygii as being derived from a common stock which itself had been evolved from a preceding " Ganoid Stock ".

This changed attitude appears to me called for by the structure of the Holocephali, or by so much of the cephalic anatomy of these fishes as indicates a tendency towards the evolution of the amphibians. Regarding these features as the expression of an hereditary potential which culminated in the development of these Tetrapods, as I do, I am naturally led to conclude that the Amphibia have been evolved without any teleostome phase in their ancestry. Another fact that contributes towards the attitude taken is the discovery that the maxillae of *Polypterus* and its congeners are labial bones, and not, as I then believed, following Allis, truly homologous with the bones of the upper jaw of the Tetrapods.

The following are the dates of publication of the four numbers of this MEMOIR:

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Number 2, pages 63–132: 30 June, 1943.
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CORRIGENDA.

Page 36, line 3. For *Taeniura lymna* read *Taeniura lymma*.
Page 82, line 10 from bottom. For Coccillans read Coecilians.
Page 187, lines 10 and 15. For Caecilians read Coecilians.
Page 100, line 15. For Bridge . . . (1879) read Bridge . . . 1878.
Page 200, line 26. For Bridge in 1893 read Bridge in 1898.
Page 253, line 4. For Lightoller (1935) read Lightoller (1939).
Page 267, line 18. For spheno-pterygoideus anterior read pterygoideus anterior.