5. The Postorbital Articulation of the Palatoquadrate with
the Neurocranium in the Coelacanthid Fishes. By
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In a recent work (Allis, 1922), I came to the conclusion that
the postorbital articulation of the palatoquadrate with the neuro-
cranium in Wimania and Areleia, two of the Coelacanthidæ, was
homologous with that in the recent Hexanchus and Heptanchus,
and not with that in Lepidosteus. This conclusion was based
largely on my assumption that the vena jugularis of these fishes
ran posteriorly between the articular process of the palatoquadrate
and the cranial wall, instead of accompanying the ramus
ophthalmicus lateralis, as suggested by Stensiö (1921), and
traversing, with that nerve, a foramen that lay between the
alisphenoid and basisphenoid bones of the latter author's
descriptions. Further consideration of the subject, in connection
with a later work by Stensiö (1922), has led me to conclude that
the vein did not have the course ascribed to it by either Stensiö
or myself, but, accompanying the ramus ophthalmicus profundus,
traversed a foramen that lay anterior, instead of posterior, to the
alisphenoid, and so entered a trigemino-facialis chamber in the
cranial wall. This conclusion modifies radically my conception
of the conditions in these fossil fishes, but I, nevertheless, still
think that the articulation of the metapterygoid with the cranium
was of the type found in the recent Hexanchus and Heptanchus,
and not of that in Lepidosteus.

There are, in recent fishes, two processes of the palatoquadrate
that are here concerned, as well as two processes of the neuro-
cranium. One of the processes of the palatoquadrate is the
processus basalis, or pedicle, and the other the processus
metapterygoidææ, and both of them are found in typical condition
in the adult Amia. The processus basalis of this fish forms the
dorso-anterior corner of the metapterygoid, and lies in the plane
of the body of the palatoquadrate. It is directed toward the
lateral edge of the basis cranii, in the region of the orbital
opening of the myodome, and is there connected with it by a band
of connective tissue. The floor of the orbital opening of the
myodome is the homologue of the processus basipterygoideus of
the Sauria (Allis, 1913), and it is lined ventrally, and supported,
by the anterior portion of the ascending process of the
parasphenoid. The processus metapterygoidææ projects dorso-
mesially from the external surface of the metapterygoid, is
directed toward the projecting dorso-lateral corner of the
postorbital process of the neurocranium, and connected with that
process by a membrane that covers the external surface of the
musculus levator arcus palatini (Allis, 1897). It lies between the musculi levator arcus palatini and adductor mandibulae, giving insertion, on its internal surface, to certain fibres of the former muscle and origin, on its external surface, to certain fibres of the adductor. It forms the lateral boundary of the surface of insertion of the levator on the palatoquadrate, the mesial boundary of that surface being formed by the processus basalis together with that portion of the dorso-mesial edge of the metapterygoid that lies between that process and the processus metapterygoideus. That branch of the nervus trigeminus that innervates the levator arcus palatini turns posteriorly around the anterior edge of that muscle, and runs posteriorly on its external surface, thus lying, morphologically, between the processus basalis and the processus metapterygoideus, dorsal to the one and ventro-mesial to the other. That branch of the external carotid that becomes the secondary afferent pseudobranchial artery (Allis, 1912) has similar relations to these two processes, as has also the vena jugularis. The efferent pseudobranchial artery runs upward and forward ventro-mesial to the processus metapterygoideus, but its relations to the processus basalis are not positively evident. It lies external to the ascending process of the parasphenoid, and hence would seem to lie morphologically ventral to the processus basipterygoideus.

In embryos of this fish up to 19.5 mm. in length, the two processes here under consideration are shown by Pehrson (1922, figs. 3–12) apparently both lying on the dorso-mesial edge of the palatoquadrate, the metapterygoid process lying posterior to the basal process and extending farther dorsally in all stages excepting the very earliest. In a 56 mm. specimen, the metapterygoid process has apparently begun to assume its adult position, and the metapterygoid bone has begun to ossify, and it is to be noted that Pehrson shows (l. c. fig. 14) the unossified portion of the pterygoquadrate cartilage forming a V-shaped mass, the basalis and metapterygoideus processes forming the two arms of the V, and the metapterygoid bone lying between them, in the hollow of the V, and not extending upward into either process. The otic process of this fish, and that of the Teleostei as well, is represented in the lateral wall of the trigemino-facialis chamber (Allis, 1914).

The characteristic features of these two processes of this fish thus are: that one of them lies postero-lateral to the other; that the antero-mesial one is directed toward the lateral edge of the floor of the cranium, where the palatoquadrate articulates with it in Lepidosteus; that the postero-lateral one is directed toward the lateral edge of the roof of the cranium, where the palatoquadrate articulates with it in Hexanchus and Hexanchus; that the musculus levator arcus palatini has its insertion on the palatoquadrate between the two processes; that the musculus adductor mandibulae lies external to the processus metapterygoideus and is cut off, by it, from any origin or insertion on the
processus basalis; and that the nerve that innervates the levator, the secondary afferent pseudobranchial artery, and the vena jugularis all lie actually, or morphologically, between the two processes.

In Scomber (Allis, 1903) and the mail-cheeked fishes (Allis, 1909) these two processes (or flanges developed in relation to them) have acquired contact with the hyomandibula and become firmly attached to it, the processus basalis with its internal surface and the processus metapterygoideus with its external surface. But, notwithstanding this marked difference in the direction of the two processes, and also in their relations to the cranium and the hyomandibula, the levator arcus palatini, the nerve that innervates it, and an artery that corresponds to the secondary afferent pseudobranchial artery of Amia, still all lie actually, or morphologically (Cottus), between them, and the adductor mandibulae has its origin on the external surface of the processus metapterygoideus and not at all on the processus basalis. The vena jugularis, also, still lies morphologically between the two processes, for the dorso-mesial edge of the processus basalis is connected, by tissue, with the lateral edge of the basis cranii.

In Amiurus the conditions appear, at first sight, markedly different from those in the fishes above referred to, but they are, nevertheless, quite certainly strictly homologous. In a 32 mm. specimen of this fish, Kindred (1919) shows the pterygoquadrate and hyomandibular cartilages completely fused with each other and forming a V-shaped mass with the point of the V directed ventrally. The hyomandibula has begun to ossify on the posterior limb of the V, the metapterygoid on the anterior limb, and the quadrate on the ventrally directed point. Nothing whatever is shown in the hollow of the V, but it must certainly be spanned by membrane, for it is in exactly this place that the metapterygoid bone first appears in Amia, as above stated, and in the adult Amiurus the corresponding place is occupied by an anteriorly projecting flange of the hyomandibula which sutures anteriorly with the hind edge of the metapterygoid and ventrally with the dorsal edge of the quadrate. Along the dorsal edge of this flange, and of corresponding length, there is a horizontal ridge on the hyomandibula, and the levator arcus palatini is inserted in part on the anterior end of the ridge and in part along the full length of its dorsal surface (McMurrich, 1884). Certain of the deeper fibres of the musculus adductor mandibulae have their origins on the latero-ventral surface of this ridge, the superficial portion of the muscle extending upward external to the ridge. The anteriorly projecting flange of the hyomandibula of this fish thus corresponds both topographically and functionally to the posteriorly projecting flange on the hind edge of the metapterygoid process of the fishes just above considered, and is quite certainly the homologue of that flange; and that it has become a flange on the anterior edge of the hyomandibula, instead of on
the hind edge of the metapterygoid, is no more extraordinary than the incorporation, in this fish, of the dorsal portion of the preoperculum in the hind edge of the hyomandibula (Kindred, 1919). The metapterygoid, the projecting dorso-mesial portion of which forms the processus basalis, is said to be attached to the lateral surface of the cranium by a sheet of muscular and ligamentous tissue. It is not said at what point on the lateral wall of the cranium this sheet of tissue has its attachment, but two sectional views given through the postorbital region would seem to show that the attachment is either to the trabecula or to the lateral edge of the parasphenoid.

In all of the above-mentioned fishes the palatoquadrate has no direct articular contact with the neurocranium, this articulation being acquired through the intermediation of the hyomandibula, to which the palatoquadrate is firmly fixed. In Lepidosteus, Osteoglossum, Hexanchus, and Hemianchus this articulation with the cranium through the intermediation of a hyomandibula still occurs, but in each of them there is, in addition, direct articular contact with the postorbital portion of the cranium; and these are the only recent fishes I know of in which the latter articulation is found, for the palatobasal articulation, found in many of the Selachii, is orbital in position and not postorbital. Gaupp says (1905, p. 707) that an articulation of the palatoquadrate with a processus basipterygoideus is found in many fishes, but, as he does not mention the particular ones, I have not been able to control the statement. Luther (1913) describes the articulation in Lepidosteus, and then says that it is also found in Osteoglossum but in no other teleost. It apparently occurs in certain fossil fishes, as in Boreosomus, one of the Palaeoniscidae described by Stensiö (1921).

In the adult Lepidosteus, Parker (1882) describes two processes related to the metapterygoid, one of which he calls the pedicle and the other the otic process. The pedicle is the larger of the two, and is shown forming the dorso-postero-mesial corner of the metapterygoid, the so-called otic process projecting ventro-posteriorly from the ventral edge of the base of the pedicle. The hind end of the pedicle articulates with the anterior edge of a processus basipterygoideus which projects antero-laterally from the lateral wall of the cranium near its ventral edge, the so-called otic process projecting posteriorly ventral to the processus basipterygoideus. In a 20.5 mm. embryo of this fish, these two processes of the metapterygoid form (Veit, 1911, fig. 17, pl. C.) the dorsal and ventral corners of the actual hind edge of the palatoquadrate, but as this edge of the palatoquadrate of this fish corresponds to the metapterygoid portion of the dorso-mesial edge of the palatoquadrate of Amia, the two processes lie, morphologically, one posterior to the other on the posterior portion of the dorso-mesial edge of the palatoquadrate. They accordingly agree exactly, in this, with the basalis and metapterygoid processes of Amia, and I shall hereafter so refer to them.
The musculus levator arcus palatini of the adult *Lepidosteus* is said by Luther (1913) to have its origin on the sphenotic, and to run from there antero-mesially to have its insertion on the metapterygoid bone and adjacent portions of the palatoquadrate cartilage. Luther says (I.e. p. 13) that: “Dabei umgreift der Muskel das Metapterygoid vor dem Basipterygoid-Gelenk und reicht auch an der Medialseite bis zu etwa 2/3 der Breite des Knochens hinauf.” This would seem to mean that the muscle had its insertion in considerable part on the internal surface of the processus basalis, which would be so unusual for a levator muscle that I have looked it up in transverse sections of an 80 mm. specimen of this fish. In this specimen the muscle, as it approaches the hind end of the palatoquadrate is wrapped around (“umgreift”) the lateral edge of the processus basipterygoideus, and when it reaches the hind end of the processus basalis, that part of the muscle that lies ventral to the processus basipterygoideus is inserted on the lateral surface of the processus basalis, this surface of the latter process being presented ventro-laterally. The processus metapterygoides lies against the ventral surface of this part of the muscle, partly imbedded in it, and apparently gives insertion to some of its fibres, but the larger part of the fibres of the muscle continue onward and are inserted on the external surface of the palatoquadrate anterior to the bases of the two processes, none of them being inserted on its internal surface. That part of the adductor muscle that Luther calls the musculus adductor mandibule postorbitalis lies ventral, and hence external, to the processus metapterygoides, and certain of its fibres have their origins on that process. The action of the levator muscle is said by Luther (I.e. p. 61) to be to pull the palatoquadrate almost directly laterally, the motion at the basipterygoid joint accordingly being a sliding one, in a latero-mesial direction, and this is in accord with the position of the long axis of this joint, which is practically at right angles to that of the long axis of the hyomandibulo-cranial articular joint. The nerve that innervates the levator muscle penetrates it from its external surface, and hence lies morphologically between the metapterygoid and basal processes, as it does in the fishes above considered.

The processus basipterygoideus of *Lepidosteus* is said by Parker (1882, pp. 453 & 461) to be developed in part from the trabecula and in part from the parachordal. Veit first (1907) concluded that it is developed from the hind end of the trabecula and corresponds to a part of the floor of the orbit of the Selachii, but he later (1911) says that it arises in connection with the trabecula and the floor of the trigemino-facialis chamber. I first concluded (Allis, 1909) that it is of trabecular origin and, later (1913), that it is the homologue of the floor of the orbital opening of the myodome of *Amia*; but it is to be particularly noted that there is, in *Lepidosteus*, no parasphenoidal leg of the alisphenoid related to the process, as there is in *Amia*, and that there is no membrane that I can recognize replacing it. Veit says that the process
develops late in *Lepidosteus*, and he considers its articulation with the metapterygoid to be a secondary acquisition, and Luther holds the same opinion. The ventral surface of the process, its anterior edge, and the adjacent portions of its dorsal surface are covered and supported by a process of the parasphenoid which would seem to correspond to an anterior portion of the ascending process of the parasphenoid of *Amia*, and it is apparently this process of the bone that alone gives articulation to the metapterygoid in *Osteoglossum*, as explained below. The process of *Lepidosteus* lies ventral to the ramus ophthalmicus profundus and the vena jugularis, and if it be the homologue of the floor of the orbital opening of the myodome of *Amia*, as I concluded, it would seem as if it must lie, morphologically, between the profundus and trigeminus nerves, for its homologue in *Amia* supports the parasphenoidal leg of the alisphenoid, which actually lies between those two nerves. In its relations to these nerves this process thus differs radically from the postorbital process, which always lies, so far as I know, posterior to all branches of the nervus trigeminus, and usually between the foramen for that nerve and the secondary, or definitive, foramen for the nervus facialis. The processus metapterygoideus also lies morphologically between the trigeminus and facialis nerves, while the processus basalis, which articulates with the processus basipterygoideus, should have, morphologically, the same relations to those nerves that the processus basipterygoideus has.

In *Osteoglossum* a laterally projecting process of the parasphenoid articulates with a semicylindrical groove on the dorsal edge of an antero-dorsally projecting portion of the metapterygoid (Bridge, 1895), which, as it has exactly the position of the processus basalis of *Amia*, is evidently that process, and when the palatoquadrate swings outward and upward, under the action of the levator arcus palatini, the groove on the metapterygoid has a sliding motion on the process. Posterior to this process, there is a short dorsally projecting process of the metapterygoid which lies against the external surface of the hyomandibula, and hence evidently represents the processus metapterygoideus. The laterally projecting process of the parasphenoid has its origin from the base of a pretrigeminus portion of the ascending process of that bone and corresponds to that part of the ascending process of *Lepidosteus* that underlies and supports the basipterygoid process of that fish, and hence is, functionally, a processus basipterygoideus. It corresponds also to that anterior portion of the ascending process of the parasphenoid of *Amia* that underlies the floor of the orbital opening of the myodome of the latter fish, and the pretrigeminus portion of the ascending process of the parasphenoid of *Osteoglossum* corresponds to one of the two legs of the alisphenoid bone of *Amia*, but which one is uncertain, for the relations of the nerves and the vena jugularis to it are not given.

The conditions in *Heptanchus* and *Hexanchus* I have not
personally examined, but they must be similar to those in *Chlamydoselachus*. In the latter fish the most dorsal portion of the dorso-mesial edge of the palatoquadrate forms the processus metapterygoideus, a low ridge on the internal surface of this edge of the apparatus forming the processus basalis (Allis, 1913). In the groove between these two ridge-like processes, the musculus levator maxillae superioris, which is the homologue of the levator arcus palatini of the Teleostei and Ganoidei, has its insertion, the outer edge of the processus metapterygoideus lying between the surface of insertion of the levator muscle and the surface of origin of the adductor mandibulae. That branch of the nervus trigeminus that innervates the muscle runs posteriorly along its external surface, and hence lies morphologically between the two ridge-like processes. In *Heptanchus* and *Hexanchus* the conditions unquestionably here differ only in that the processus metapterygoideus has acquired articular contact with the laterally projecting dorsal portion of the postorbital process, and that, in consequence, the anterior portion of the levator maxillae superioris runs antero-ventrally beneath the overhanging portion of the postorbital process, and hence internal to the processus metapterygoideus. The nerve that innervates this muscle also runs posteriorly internal to the latter process. The levator muscle of these three fishes, and particularly that of *Heptanchus* and *Hexanchus*, can accordingly have but little effect in swinging the palatoquadrate outward and upward, and Luther (1909) says that this motion is impressed upon it by the musculus preorbitalis of his descriptions, which is Vetter's (1874) muscle Add β. This action of this muscle is said to also throw the anterior end of the palatoquadrate downward, the palatobasal (orbital) process sliding downward along its articular contact with the orbital wall. The levator muscle then pulls the palatoquadrate back into place, its action thus being largely, if not entirely, to pull the palatoquadrate dorso-mesially in the plane of the apparatus. The articular attachment of the processus metapterygoideus to the postorbital process, in *Heptanchus* and *Hexanchus*, would evidently have to be somewhat loose to permit of this motion, and Luther (1909) assumes that there is here a certain dorso-ventral sliding motion, and, also, that the levator muscle must act in part as an adductor palatoquadraoti. Furthermore, the attachment of the palatoquadrate to the hyomandibula must be such as to allow a certain amount of motion between them.

In certain others of the Plagiostomi this metapterygoid ridge of the Notidanidae has become a pronounced process, and both Gegenbaur (1872) and Luther (1909) have called it a muscle process. It apparently lies directly upon the dorso-mesial edge of the palatoquadrate, thus having in the adults of these fishes the position that it has in larvae of *Amia*. Where present it has the same relations to the levator and adductor muscles that the ridge-like process of the Notidanidae has, and because of its articular relations to the cranial wall, in the latter fishes, it has
been quite generally considered to be an otic process; but if, as I have endeavoured to show, it is the homologue of the processus metapterygoideus of the Teleostomi, this cannot be. Goodrich considers it to be an otic process and says (1909, p. 98) that it "appears to have been established very early, since there is reason to believe that it existed not only in the Jurassic Cetracotidae (Hybodus), but also in the Cladooselachii, Acanthodii, and Pleurocanthodii."

In certain of the higher vertebrates a pterygo-cranial articulation is found between processes which are apparently the strict homologues either of the processus basalis and basisipterygoideus of Lepidosteus, or of investing bones related to those processes, the motion between the two processes, however, being a dorso-ventral swinging one instead of a latero-mesial sliding one.

In recent Amphibia a cartilaginous processus basisipterygoideus seems not to be found (Gaupp, 1900, p. 537), but it is found in certain of the Stegocephali, as explained immediately below. The palatoquadrate of the Amphibia is said by Gaupp to present four typical processes: a processus oticus, processus ascendens, processus pterygoideus, and processus palatobasalis, the latter process being also called by him (1905, p. 736) simply the processus basalis. In the Urodela, the latter process is said to lie, at first, in contact with the ventral surface of the auditory capsule, at the point where the capsule is connected with the basal plate of the skull, and to later there fuse with it. The process is said to seem to correspond to the palatobasal process of the Selachii, but this seems improbable, for the processus basalis of the Amphibia arises from the pterygoquadrate portion of the palatoquadrate, is directed mesially, and lies against the ventral surface of the floor of the auditory capsule, while the processus palatobasalis of the Selachii arises from the palatine portion of the palatoquadrate, is directed dorsally, and lies against the orbital wall, which forms part of the lateral surface of the cranium.

In Rana, of the Anura, the processus basalis is said by Gaupp (1893, p. 349) to first appear in his fourth stage (young frog about 2 cm. long), there arising from the pars metapterygoidea of the quadrate, close above the root of the processus pterygoideus. It is directed toward the ventral surface of the anterior portion of the auditory capsule, and an articular joint is later formed, this being considered by Gaupp (1905, p. 737) to be a more primitive condition than the fusion of the process with the auditory capsule in the Urodela. In earlier stages of Rana there is a processus muscularis rising from the upper edge of the palatoquadrate, strongly developed in the earliest stage described, but gradually diminishing in importance until its complete disappearance during the metamorphosis. This process lies, in larvae (Gaupp, 1893, p. 292), external to the musculi temporalis and pterygoideus, and gives origin, on its mesial surface, to the masseter, and, on its lateral surface, to the depressor cartilaginis hyoideae and the depressor mandibulae. The relations of the
process to the adductor muscles of the mandible are thus not the same as in fishes, but this is probably not important, for the superior and inferior branches of the nervus trigeminus both run forward dorsal or mesial to the process and then turn outward anterior to it. The process lies between the pars articularis quadrati and the processus basalis, in the same relation to those two processes that the processus metapterygoideus of fishes has, and hence is quite certainly the homologue of the latter process. In the Apoda there is said to be no processus basalis (Gaupp, 1905, p. 753).

In the Stegocephali, the palatoquadrate is said to be movable in certain forms, but fixed in by far the larger number. In Eryops there is, according to Von Huene (1912), a basipterygoid process which is apparently a definite process of the basisphenoid bone, but as there is no suture separating the basisphenoid and parasphenoid, the latter bone may also enter into the process. The pterygoid is said to be attached (befestigt sich) to the process by a broad articular surface, the palatoquadrate thus apparently being movable. In Archeosaurus, the parasphenoid has, according to Watson (1919), a narrow, outstanding basipterygoid process on either side, and the pterygoid articulates with it by a freely movable joint; and similar basipterygoid processes are apparently found in several others of the Rachitomi (l. c. p. 55). In Laccocephalus the mesial process of the pterygoid suturates with the lateral edge of the parasphenoid in a region that corresponds to that from which the ascending process of the bone of fishes has its origin, and cartilaginous extensions of the basisphenoid are said (l. c. p. 54) to "seem to have passed outward above the flat parasphenoid expansions to the epipterygoid and pterygoid." At the hind end of the suture between the pterygoid and parasphenoid there is a foramen which leads into a canal in the parasphenoid and transmits the internal carotid artery. In Capitosaurus the mesial process of the pterygoid suturates both with the parasphenoid and the exoccipital, and there is no basipterygoid process. The quadrate ramus of the pterygoid is said (Watson, 1919, p. 27) to form "a thin plate, rising nearly vertically, to have a long and close connection with the supratemporal and squamosal. Its upper inner corner has a sutural union with the prootic, with which bone and the supratemporal it forms a large foramen leading forwards over the prootic and epipterygoid to the anterior part of the skull. This opening must transmit the vena capitis dorsalis and a lymphatic duct. Just above its articulation with the parasphenoid and below the prootic the inner margin of the quadrate ramus of the pterygoid is notched for the passage of the vena capitis lateralis and the seventh nerve." This part of the pterygoid of this amphibian thus has to this part of the skull the topographical relations that the ascending process of the parasphenoid of fishes has, or that the piscine processus metapterygoideus would have if it were to persist and acquire contact with the cranium after the
disappearance of a musculus levator arcus palatini. The processus oticus is part of the epipterygoid bone and lies anterior and internal to this process of the pterygoid.

In the Sauria the processus basalis of fishes must certainly be represented in the meniscus pterygoideus, but whether the processus basalis of recent Amphibia is represented in the meniscus alone, or in that structure together with the processus basipterygoideus, would seem to be an open question. Regarding the development of these structures in the Sauria, Gaupp says (1905, p. 762) that they are both represented, in young embryos of Lacerta, by a mass of dense tissue which lies between the foot of the processus ascends and the root of the trabecula, and is more closely connected with the former than with the latter. When chondrification takes place, this mass separates into two parts, the mesial one chondrifying as a laterally directed process of the trabecula (the processus basipterygoideus) and the lateral one becoming the meniscus. This manner of development of these two structures in this reptile, and their relations to the ascending process of the palatoquadrate, led me to suggest, in an earlier work, that the mass of tissue referred to might represent the pharyngeal element of the mandibular arch.

In the adult Lacerta, the meniscus lies on the mesial aspect of the Os pterygoideum (Gaupp, 1905, p. 767), and between it and the processus basipterygoideus an articular joint is formed, the palatoquadrate being movable. In Sphenodon, the meniscus and the processus basipterygoideus are also both found (Howes and Swinnerton, 1901), and there is an articular joint between them, as in Lacerta, but whether the palatoquadrate of this reptile is movable, or not, I do not find definitely stated. A mesial process of the Os pterygoideum is shown by Fuchs (1901), in an embryo of this reptile, projecting mesially along the ventral surface of the processus basipterygoideus, and it would seem as if it must interfere with any movement, if it does not actually prevent it. Broom (1922) says that Parker described a meniscus, in 1878, in a fairly advanced specimen of Zootoca, and he himself describes it in a larval Agama hispida, where it lies, as in Lacerta, between a cartilaginous processus basipterygoideus and a dermal pterygoid bone. The articular joint is between the meniscus and the processus basipterygoideus, and Broom considers the meniscus to be the homologue of the mesopterygoid of fishes, basing this conclusion on the conditions found in Eusthenopteron, a fossil Rhipidistid described by Bryant (1919). The so-called mesopterygoid of the latter fish, as shown in the figure reproduced by Broom, is, however, called by Bryant a metapterygoidei, and that part of the bone that has the marked upward extension shown in the latter author's text-fig. 6 would seem to be a processus metapterygoidei metapterygoidei.

From the above references to the conditions in certain of the Amphibia and Reptilia it is seen that, in these animals, the existing postorbital articulation of the palatoquadrate with the
cramium was primarily, in all probability, that of a processus basalis metapterygoidei with the lateral edge of the basis crani at or near the hind end of the trabecula. The processus basalis has, in certain of them, later there fused with the basis crani, while still retaining its connection with the palatoquadrate. In others it has apparently lost its connection with the palatoquadrate but retained that with the neurocranium and then separated into two parts, thus giving rise to a meniscus metapterygoideus and a processus basipterygoideus. The metapterygoid cartilage is always here lined ventrally, and supported by a dermal pterygoid bone, the processus basipterygoideus being similarly lined and supported by a lateral process of the dermal parasphenoid, and in those animals in which the metapterygoid and basipterygoid cartilages are resorbed, or fail to be developed, the two dermal bones replace them and acquire sutural connection with each other.

The conditions in the three Ocelacanthidae so fully and so well described by Stensiö (1921, 1922) may now be considered, and the question is: Is the postorbital articulation of the palatoquadrate of these fishes with the cranium the homologue of that in Heptanchus and Hexanchus, or of that in Lepidosteus, Osteoglossum, and higher vertebrates?

The metapterygoid of these fishes is a substituent bone, as it is in most recent fishes, and at either end of its dorsal edge there is a pointed process. Between these two processes the dorsal edge of the bone is concave, and articulates with a process of the neurocranium that Stensiö considers to be a processus basipterygoideus and which he refers to as the process e. In both Winania and Axelia this latter process is a process of what Stensiö considers to be a median basi-sphenoid bone. It is directed dorso-antero-laterally, and in Winania extends so far dorsally that its dorso-anterior corner is shown in contact with the dermal bones of the roof of the skull. In Axelia it is shorter, but still extends above the middle line of the lateral surface of the cranium. In Diplocercides it is still shorter, and is a process of a median sphenoid bone and not of a basisphenoid. The metapterygoid would seem, from the figures given, to have articulated either with the lateral surface of the process e immediately beneath its laterally projecting dorsal edge, or with that edge itself, and as the dorsal edge of the metapterygoid is longer than the process e is wide, the dorso-anterior end of the metapterygoid would seem to have projected anteriorly somewhat beyond the process e.

The metapterygoid has an even outer surface, without process of any kind, and there is no posteriorly directed process, or other feature, either on this bone or at any place along the hind edge of the palatoquadrate that would indicate a rigid attachment to the hyomandibula. This latter attachment was therefore probably by ligament only, and in this, as also in the general configuration of this part of the palatoquadrate, there is
marked resemblance to the conditions in the Selachii. Stensiö says (1921, p. 73) that there was a large mandibula in *Wimania* (and hence probably in the other two fishes also), and that this presupposes a powerful adductor muscle. Comparison with recent fishes would then indicate that the surface of origin of this muscle on the palatoquadrate must have extended upward at least to the dorsal edge of the metapterygoid, and Stensiö considers it probable that the muscle extended beyond that edge and had its origin in part on the lateral surface of the neurocranium. The levator arcus palatini, if present, would then necessarily have had its insertion, as in *Heptanchus* and *Hexanchus*, either along the dorsal edge of the metapterygoid or partly on that edge and partly on its mesial surface.

On the internal surface of the palatoquadrate there is a large dermal pterygoid bone, and a process of this bone extends to, or nearly to, the point of the dorso-anterior process of the metapterygoid, thus supporting that process. The dorso-posterior process of the metapterygoid, on the contrary, extends considerably beyond the dorsal edge of the pterygoid, this leaving a considerable portion of the internal surface of the metapterygoid exposed beyond the pterygoid. On the lateral surface of the pterygoid there is a strongly pronounced and rounded ridge which extends upward to the point of the dorso-anterior process of the metapterygoid, and strongly suggests that that point represents the dorsal end of some element of the mandibular arch.

The relations of the two processes on the dorsal edge of the metapterygoid to each other, to the palatoquadrate, to the pterygoid, and to the muscles of the arch, thus all strongly suggest that the posterior one is a processus metapterygoideus, and the anterior one either the entire processus basalis or the anterior end of a ridge-like process similar to that in the Selachii, the posterior portion of the ridge lying along the internal surface of the palatoquadrate. There was quite probably a spiracular canal in these fishes, as there is in the recent *Polypterus*, and not simply a diverticulum of that canal, such as is found in the recent Holostei and Teleostei; and, where this canal is present, there is, in recent fishes, no articulation of the processus basalis with the neurocranium.

There is thus strong presumptive evidence that, in these fishes, it is a processus metapterygoideus that articulates with the cranium, and, in recent fishes, this process never articulates with, or even approaches, a processus basipterygoideus. This is evidently in favour of the assumption that the process is a processus postorbitalis, and the relations to it of the cranial nerves is also in favour of this interpretation.

There is, in *Wimania* and *Axelia*, a median bone which, as already stated, Stensiö considers to be a basisphenoid, and it is said by him to consist of a body (corpus), and three processes on either side, one of these processes being dorsal, one anterior, and
The body of the bone is said to be triangular in shape, with the point below, and from there to extend dorso-posteriorly to its thickened base, which is said to lie strikingly high, leaving only a narrow space between it and the roof of the cranium. The bone, as shown in the figures given, has a shape and position which show that it must have occupied, and have completely filled, the hollow of a large cephalic flexure of the brain, both its anterior and its posterior surfaces sloping anteroven- trally. The dorso-posterior edge of the bone is concave, with a short process on either side, and looks like the dorsum sellae of the skulls of certain vertebrates turned upward and backward. The dorsal process of either side projects dorso-antero-laterally from the corpus, and, in Wimania, is, as already stated, so tall that its dorso-anterior corner may be in contact with the postero-lateral corner of the dermosphenotic portion of the fronto-dermosphenotic. The dorsal end of the process thus lies at or near the level of the roof of the cranial cavity, and it is apparently with the ventral surface of the outer end of the process that the metapterygoid articulates. The anterior process of the bone is lamellar in form with its basal portion extending upward along the internal surface of the dorsal process, and it gives support on the dorso-anterior edge of its basal portion to the alisphenoid of Stensiö’s descriptions. Dorsal to these two processes the lateral wall of the cranium must have been of cartilage, and this cartilage and the dorsal process must together have formed a laterally projecting dorsal portion of the posterior wall of the orbital fossa, and hence have formed a postorbital process in the sense in which that term is here employed. Stensiö says there is no postorbital process in these fishes, but it is possible that he employs the term in a somewhat different sense. The basisphenoid is traversed, on either side, by but a single canal, which traverses the anterior process and will be later considered.

In Diplocercides the anterior portion of the basisphenoid of Wimania and Axelia is replaced by a sphenoid bone, which extends forward through the orbit to the ethmoidal region and is everywhere in contact, dorsally, with the ventral surface of the dermal bone, or bones, that here form the roof of the cranium. The process e of Wimania and Axelia is, in this fish, apparently simply a protuberance on the lateral surface of the hind edge of the sphenoid, at about the middle of its height. From it a ridge runs upward along the hind edge of the lateral surface of the dorsal half of the sphenoid, and, as it is considered to be the homologue of the alisphenoid bone of Wimania and Axelia, it is called the alisphenoid wulst. The postclinoid wall of this fish does not project dorsally above the level of the floor of the posterior portion of the cranial cavity, as it does in Wimania and Axelia.

The truncus maxillo-mandibularis trigemini is considered by Stensiö to have issued from the cranium, in each of the three fishes here under consideration, posterior to the alisphenoid, and
in "Wimania" posterior also to the dorsal process of the basisphenoid. The ramus ophthalmicus profundus of "Axelia" is said to run forward internal to the base of the alisphenoid, and to issue from the cranium anterior to that bone, and in "Diplocercides" it has similar relations to the alisphenoid wulst. In "Wimania" it is said to probably have issued through that small canal, above referred to, that traverses the anterior process of the basisphenoid, but, as will later appear, it is much more probable that this canal was traversed by the efferent pseudobranchial artery. The ramus ophthalmicus lateralis trigemini is said to run forward, in "Wimania", over the dorsal process of the basisphenoid, close to the lateral wall of the brain-case, thus evidently issuing from the cranium between the dorsal process and the alisphenoid, and then running forward lateral to the latter bone. In "Axelia" this nerve lies in a groove that crosses the external surface of the alisphenoid, and in "Diplocercides" in a canal that traverses the alisphenoid wulst and is continued onward, a certain distance beyond that wulst, in the body of the sphenoid bone. The vena jugularis is said to have had, in "Wimania", a course similar to that of the ramus ophthalmicus lateralis trigemini. In "Axelia" and "Diplocercides" its course is not given.

The profundus and trigeminus nerves of "Axelia" thus have, in the courses ascribed to them by Stensiö, exactly the relations to the alisphenoid bone of that fish that the corresponding nerves have, in recent fishes, to the parasphenoidal leg (pedicle) of the alisphenoid, the trigeminus nerves all issuing posterior to that leg and the profundus nerve anterior to it; and as the vena jugularis of recent fishes always accompanies the profundus nerve in this part of its course, it seems exceedingly probable that it accompanied that nerve also in "Axelia", and hence passed, as in recent fishes, antero-mesial to the alisphenoid. In "Diplocercides" the conditions differ from those in "Axelia" only in that the ramus ophthalmicus lateralis trigemini traverses a canal in the alisphenoid part of the sphenoid bone, instead of passing lateral to it; but even in recent fishes, as in "Amia", this nerve may traverse a foramen that perforates the parasphenoidal leg of the alisphenoid.

In "Wimania" the conditions, as described by Stensiö, differ from those in "Axelia" and "Diplocercides" in that the ramus ophthalmicus profundus is said to have probably traversed the canal in the anterior process of the basisphenoid, that the truncus maxillomandibularis trigemini presumably ran outward in a notch at the base of the hind edge of the dorsal process of that bone, and that the vena jugularis accompanied the ramus ophthalmicus lateralis trigemini, and hence passed postero-lateral instead of antero-mesial, to the alisphenoid bone. This course for the latter vein would be most exceptional in fishes, and it seems much more probable that both it and the ramus ophthalmicus profundus passed internal to the alisphenoid, as they both apparently did in
Axelia and Diplocercides. The vena jugularis would then con-
tinue posteriorly and, having joined the nervus facialis, issue
with it through the facialis foramen at the hind edge of the
basisphenoid. In this part of its course it must have lain in a
canal in the cranial wall, for that it perforated the dura mater and
entered the central cranial cavity seems wholly improbable. This
canal would thus, in this, exactly resemble the trigemino-facialis
chamber of recent fishes, and it seems wholly impossible that the
truncus maxillo-mandibularis trigemini did not run forward in
it, and issue from it between the process e and the alisphenoid.
If the truncus issued posterior to the process e, as suggested by
Stensiö, it would be separated from its ophthalmicus lateralis
branch by the entire width of that process, which would be
wholly exceptional, as compared with recent fishes, whether the
process be a postorbital one or a basipterygoideus. The notch
at the base of the hind edge of the process e would then probably
transmit the ramus palatinus facialis, which is not otherwise
accounted for.

If the trigeminus and profundus nerves of Wimania and Axelia
had the courses that I have above ascribed to them, they must have
first run upward along the posterior surface of the basisphenoid,
then have passed, on either side, lateral to that posteriorly project-
ing dorsal end of the basisphenoid that resembles a dorsum sellæ,
and then have run forward along the dorsal surface of the body of
the basisphenoid, there either lying free in the cranial cavity or,
much more probably, being enclosed in the canal traversed by
the vena jugularis. In recent fishes these nerves run forward
across the ventral end of the hollow of the cephalic flexure, instead
of upward and forward over it. That part of the basisphenoid
bone of Wimania and Axelia that occupies the hollow of this
flexure could not then have arisen from the conditions found in
recent fishes by the simple chondrification or ossification of tissues
that filled the hollow of the flexure, for the nerves would then
have been enclosed, in situ, in the cartilage or bone so formed
and have traversed canals or foramina in it. And it seems equally
improbable that the bone could have grown upward in the hollow
of the flexure, pushing the nerves before it. It must then be
that, at a certain stage in the development of embryos of
Wimania and Axelia, the anterior end of the notochord was
bent upward and slightly backward, as it is in 33 mm. embryos
of the recent Acanthias (Goodrich, 1918, fig. 14, pl. 2), and
that, in the former fishes, this curvature was not later reduced.
The cartilago acrochordalis, which, in recent fishes, develops in
tissues related to the anterior end of the notochord, was there-
fore, in Wimania and Axelia, directed dorso-posteriorly, and its
morphologically ventral surface, presented dorso-anteriorly, lay
directly beneath the membrane that, in recent fishes, extends
from the anterior edge of the cartilago acrochordalis to the top
of the preclinoid wall. The hind ends of the trabeculae, and the
bases of the alisphenoid cartilages, would accordingly be carried
upward to the positions the corresponding bones of the adult actually occupy, and that part of each anterior process of the median basisphenoid on which the base of the related alisphenoid rests would correspond to the outer end of the processus basipterygoideus of *Amia* and *Lacerta*, the remainder of the anterior process apparently corresponding to that little lamellar process that, in *Amia*, forms the lateral wall of the basal portion of the orbital opening of the myodome and is traversed by the foramen for the efferent pseudobranchial artery. There would have been, internal to the alisphenoid, a space traversed by the *vena jugularis* and *ramus ophthalmicus profundus*, the mesial boundary of this space being formed by cartilage that represents the basisphenoidal leg of the alisphenoid. This leg of the alisphenoid would have been continuous, posteriorly, with the mesial wall of a trigeminofacialis chamber; that wall being either of cartilage or of membrane, and the base of the leg of one side of the head would have been connected with that of its fellow of the opposite side by the preclinoid wall. The optic chiasma must have lain upon the dorsal surface of the latter wall, and the *lobi inferiores* in a depression posterior to it, on the dorsal surface of the membrane (more or less ossified) that covers the dorso-anteriorly presented ventral surface of the cartilago *acrochordalis*. A median opening in this membrane would lead into a large pituitary sac, which would extend ventrally into the space enclosed between the ventral processes of the basisphenoid, these latter processes thus corresponding to those antero-ventral processes of the parachordals of recent fishes that bound laterally the pituitary fossa. The basisphenoid of these fishes would thus apparently correspond to a bone formed by the fused prootics of recent fishes.

There are thus several features in the cranial anatomy of these fishes that indicate that the so-called dorsal process of the basisphenoid corresponds to some part of the postorbital process of recent fishes, and not to the basipterygoid process, the most important being that the process gives articulation to a processus metaapterygoides metaapterygoides and not to a processus basalis, that it has no supporting relations to the alisphenoid, and that the truncus maxillo-mandibularis trigemini quite certainly ran outward anterior to it, between it and the alisphenoid. The basisphenoid of these fishes is such a peculiar bone that all comparisons with recent fishes are more or less tentative, and there is one further feature in their cranial anatomy that seems equally peculiar. In all recent bony fishes (*Crossopterygia, Holostei, Teleostei*) it is, so far as I know, an invariant rule that the dorsal section of the hyomandibular latero-sensory canal runs upward toward, or actually to, a postotic portion of the main infraorbital latero-sensory canal, while in the Plagiostomi this canal turns forward and falls into the infraorbital portion of the main infraorbital canal at the ventro-posterior corner of the orbit. Now, whether correlated to the course of this canal or not, it is a fact that, in all the former fishes the hyomandibula articulates with
the neurocranium dorsal to the vena jugularis, is either traversed by the truncus hyomandibularis facialis or lies anterior to that nerve (Polypterus), and is, if I am correct in my conclusions (Allis, 1918), developed from the branchial rays of the hyal arch, while, in the Plagiostomi, the hyomandibula articulates with the neurocranium ventral to the vena jugularis, and is developed either from the pharyngeal or the epal element of the hyal arch (Allis, 1915). In Polyodon, where the hyomandibula articulates with the neurocranium dorsal to the vena jugularis, and is of the teleostome type, it nevertheless differs from that in the bony fishes in that it lies posterior to the nervus facialis, and in this fish the hyomandibular canal has a position intermediate between the two above referred to. There may be no morphological significance in this, for there is in certain of the Plagiostomi a line of surface pit-organs that has a position similar to that of the preopercular canal of the bony fishes, and in certain of the latter fishes there are surface lines of pit-organs that correspond in position to that of the hyomandibular canal of the Plagiostomi; but it is to be noted that in the Célaganthidae, where a hyomandibula, although presumably present, has not yet been found, the hyomandibular canal has the position of that in the Plagiostomi, while in the Paleoniscideæ, where the hyomandibula was well developed and of the teleostome type, the canal has the position of that in the bony fishes. In the Stegocephali, the canal on the cheek would seem to be formed by the horizontal portion of the canal of the Plagiostomi together with the dorsal portion of the preopercular canal of the bony fishes.

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ARTICULATION OF PALATOQUADRATE IN CCELACANTHIDS.


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