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The Braincase of the Holostean Fish *Macrepistius*, with Comments on Neurocranial Ossification in the Actinopterygii

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The uncrushed and nearly complete holostean (caturid) braincase (U.S.N.M. No. 13628) described below was collected in 1934 by Gayle Scott in the Lower Cretaceous (Albian) Glen Rose Formation, 1 mile southeast of Boyd, Wise County, Texas. The narrow ribbon of Glen Rose exposed in this area belongs to the lower part of the formation (Sellards, Adkins, and Plummer, 1932, fig. 18) and probably includes the same horizon from which the type specimen of *Macrepistius arenatus* (A.M.N.H. No. 2435) was obtained (Schaeffer, 1960). The dermal roof of the isolated braincase indicates beyond reasonable doubt that it can be assigned to *M. arenatus*.

I am obliged to Drs. David H. Dunkle and Clayton Ray for permission to describe this specimen, prepared by the acid method, from the U. S. National Museum collection. Additional preparation, particularly of the undamaged left trigeminofacialis chamber, was carried out by Martin Cassidy, who also made a cast of the entire neurocranium. The drawings were executed by Miss Jennifer Perrott and the photographs taken by Chester Tarka.

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Although the primary purpose of the present paper is to supplement our still meager knowledge of the holostean neurocranium, the details of the *Macrepistius* otic region, in particular, have prompted some general remarks about holostean and halecostome braincases in relation to their origin from the palaeonisciform type. Dr. Colin Patterson has generously provided information on an undescribed braincase of *Heterolepidotus* in the British Museum (Natural History), and Professor F. R. Parrington has kindly lent a specimen of *Cosmoptychius* from the Cambridge University Museum of Zoology.

The following abbreviations are used for catalogued specimens:

A.M.N.H., the American Museum of Natural History

U.S.N.M., United States National Museum, Smithsonian Institution

C.U.M.Z., Cambridge University Museum of Zoology

DESCRIPTION OF NEUROCRANIUM

The dermal roof pattern of the isolated neurocranium differs from that of the type specimen (Schaeffer, 1960, fig. 1) in having one of the supraorbital bones (fig. 1), which is situated between the frontal and dermopterotic, excluded from contact with the parietal. This is presumed to represent individual variation rather than a constant specific difference. The roof ornamentation is the same in both specimens and, in both, tubercles are absent on the anterior half of the frontals.

The occipital region of *Macrepistius* (fig. 2) is apparently unique for an amioid in having paired supraoccipitals. These partly fused rectangular elements are separated by distinct sutures from the overlying parietals, the laterally situated epiotics and the ventral exoccipitals. The well-developed posttemporal fossae are typically framed by the epiotic, dermopterotic, and intercalar. The exoccipitals meet above the foramen magnum and are in contact with the incompletely preserved basioccipital along its lateral border. The missing occipital condyle was formed entirely by the basioccipital. Concave attachment areas for the epaxial musculature are prominently developed on the supraoccipitals and exoccipitals.

The intercalar is a large, irregularly shaped bone with a well-defined notch around the vagal foramen (fig. 3). As a dermal element that presumably ossified outside of the perichondrium, it apparently covers adjacent parts of the exoccipital, autopterotic, prootic, and basioccipital. Its superficial enlargement accounts for the frequently serrated and beveled margin. A prominence above the vagal notch is the attachment area for the ligamentous connection with the suprascapular.

The autopterotic (figs. 3, 7) is separated from the overlying dermop-

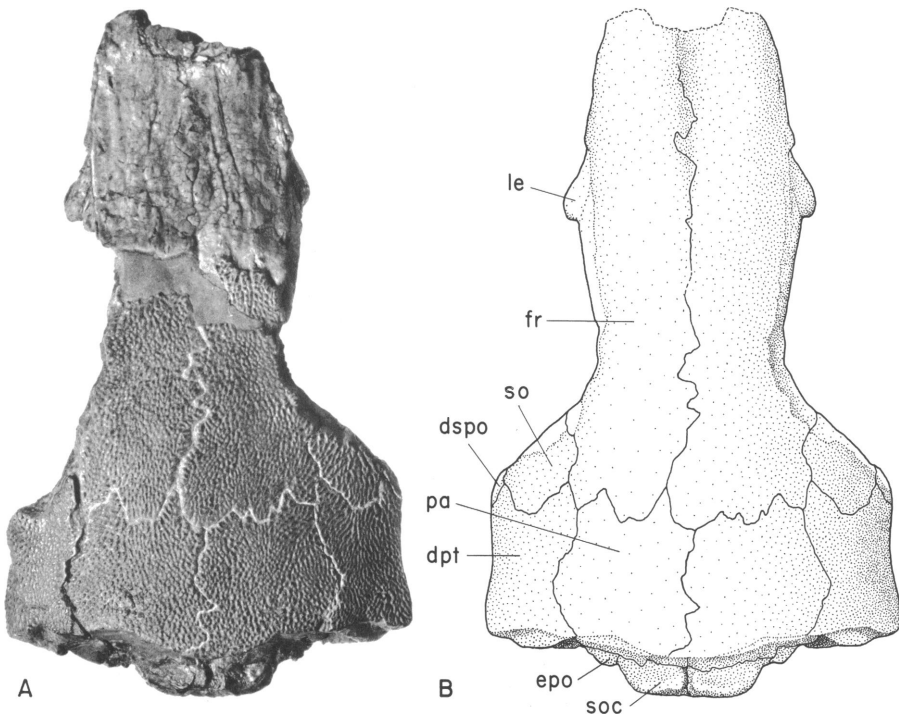


FIG. 1. *Macrepistius arenatus*, U.S.N.M. No. 13628. Dorsal view of neurocranium. A. Photograph, as preserved. B. Reconstruction. Both *ca.* $\times 1.25$.

Abbreviations: dpt, dermopterotic; dspo, dermosphenotic; epo, epiotic; fr, frontal; le, lateral ethmoid; pa, parietal; so, supraorbital; soc, supraoccipital.

terotic. It meets the autosphenotic anteriorly, the intercalar posteriorly and the prootic ventrally. The posteroventral portion of the autopterotic, along with the adjacent part of the exoccipital, is apparently covered by the anterior flange of the intercalar. The dilator fossa is situated on the ventrolateral border of the dermopterotic, and below it is the prominent hyomandibular facet.

Before describing the prootic and the trigeminofacialis chamber, it will be helpful to consider the basisphenoid (fig. 4) and its topographic relationships. The vertical pedicle articulates in the usual manner with the parasphenoid, and the diverging arms above the pedicle articulate with the median wings of the pleurospenoid that together form the upper border of the optic fenestra. A median vertical flange of the basisphenoid extends anteriorly from the pedicle to meet the nearly complete

orbitosphenoid below the anterior border of the small interorbital fenestra. The internal carotid artery passed forward under a bony ridge that connects this flange with the parasphenoid, turned dorsally in a shallow groove on the side of the flange, and passed through a short vertical tunnel in the upper third of the pedicle to reach the cranial cavity.

The prootic (figs. 3, 4) is in contact with the autosphenotic and the autopterotic dorsally, the intercalar and probably the exoccipital posteriorly, the parasphenoid ventrally, and in the postorbital wall with the

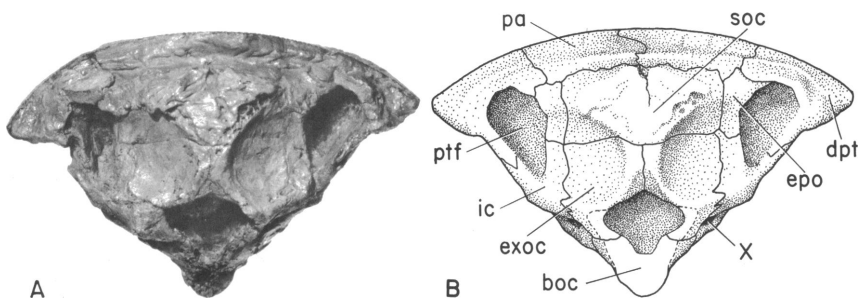


FIG. 2. *Macrepistius arenatus*, U.S.N.M. No. 13628. Neurocranium in posterior view. A. Photograph, as preserved. B. Reconstruction. Both *ca.* $\times 1.25$.

Abbreviations: boc, basioccipital; dpt, dermopterotic; epo, epiotic; exoc, exoccipital; ic, intercalar; pa, parietal; ptf, posttemporal fossa; soc, supraoccipital; X, foramen for vagus nerve.

pleurosphenoid and the basisphenoid. The posterior myodome is contained entirely within the prootic. The inner flange of the prootic (prootic bridge), which forms the roof of the myodome, is joined along its anterior border by a distinct and separate flange of the basisphenoid that projects laterally about where the pedicle is divided into the arms that extend to the pleurosphenoids.

A relatively large irregular opening at the junction of the pleurosphenoid, basisphenoid, and prootic probably served as the exit for the oculomotor nerve (fig. 4). As this opening in the actinopterygians is frequently several times larger than the nerve (Patterson, personal commun.), the nerve may have been supported by connective tissue. The profundus foramen is in the pleurosphenoid between the exits for the oculomotor and the trigeminal nerves. The superficial ophthalmic nerves emerge from a single foramen above the trigeminal foramen.

The trigeminofacialis chamber (figs. 4, 5) is here defined as the cavity between the ascending process of the parasphenoid and the related lateral

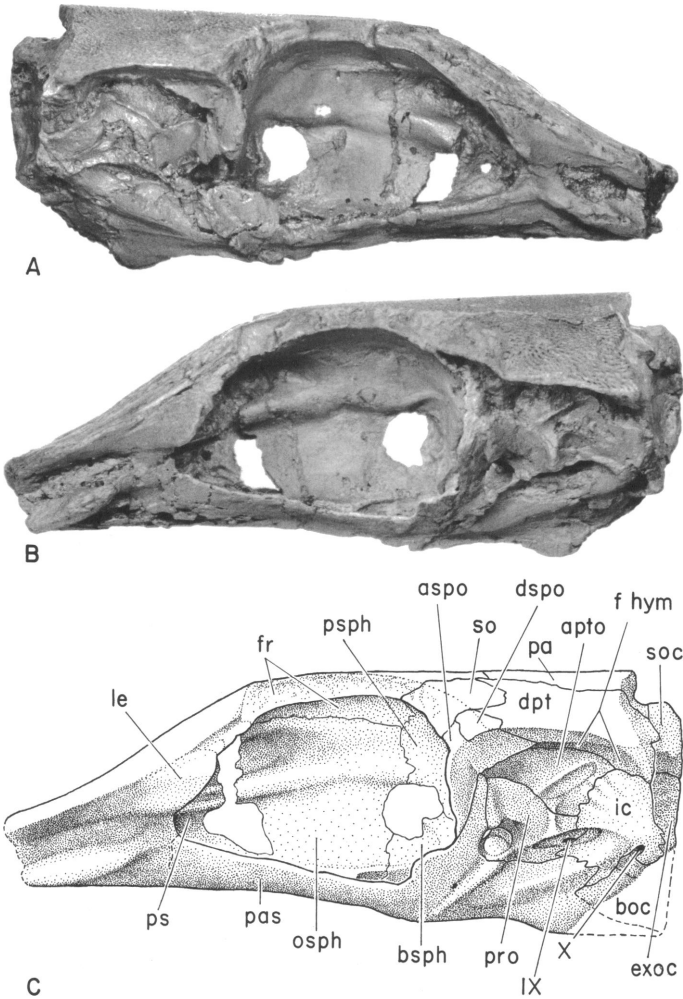


FIG. 3. *Mecrapistius arenatus*, U.S.N.M. No. 13628. Neurocranium in lateral aspect. A. Photograph of right side, as preserved. B. Photograph of left side, as preserved. C. Reconstruction in left lateral view. All *ca.* $\times 1.25$.

Abbreviations: apto, autopterotic; aspo, autosphenotic; bsph, basisphenoid; boc, basioccipital; dpt, dermopterotic; dspo, dermosphenotic; exoc, exoccipital; fr, frontal; ic, intercalar; le, lateral ethmoid; osph, orbitosphenoid; pa, parietal; pas, parasphenoid; pro, prootic; ps, preorbital septum; psph, pleurosphenoid; so, supra-orbital; soc, supraoccipital; IX, foramen for glossopharyngeal nerve; X, foramen for vagus nerve.

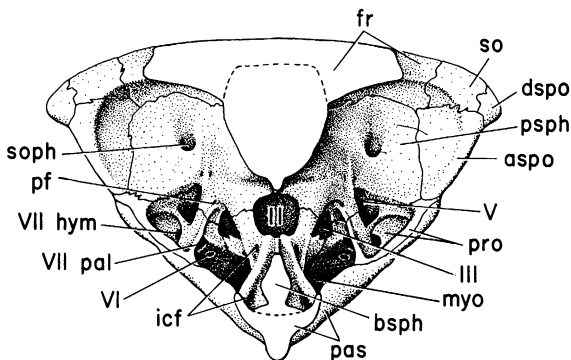


FIG. 4. *Macrepistius arenatus*, U.S.N.M. No. 13628. Reconstructed cross section of neurocranium at level of postorbital wall, viewed from front. *Ca.* $\times 1.5$.

Abbreviations: aspo, autosphenotic; bsph, basisphenoid; dspo, dermosphenotic; fr, frontal; icf, internal carotid foramen; myo, posterior myodome; pas, parasphenoid; pf, foramen for profundus nerve; pro, prootic; psph, pleurosphenoid; so, supra-orbital; II, optic fenestra; III, foramen for oculomotor nerve; V, foramen for mandibular branch of trigeminal nerve; VI, foramen for abducens nerve; soph, foramen for superficial ophthalmic branches of trigeminal and facial nerves; VII hym, foramen for hyomandibular trunk of facial nerve; VII pal, foramen for palatine branch of facial nerve.

commissure, which together form the outer wall of the chamber and the true lateral wall of the braincase above the prootic bridge.¹ This extra-

¹ The distinction between the pars ganglionaris and the pars jugularis of the trigeminofacialis chamber is based on the separation of the trigeminal and facial ganglia from the jugular canal by the lateral wall of the neurocranium. When Allis (1919) first used these terms he had in mind the divided chamber in *Scomber* and in the scorpaenoid teleosts, as opposed to the single chamber in *Amia* and *Lepisosteus*. He was, of course, unaware of the condition in the palaeonisciforms, most fossil holosteans, and the halecostomes.

The primitive lateral wall of the neurocranium in the area of the lateral commissure is composed of the pila antotica (pila prootica) anterior to the trigeminal foramen, the prefacial commissure between the trigeminal and facial foramina, and the anterior basicapsular commissure posterior to the facial foramen. From studies of the neurocranium in the palaeonisciforms (Nielsen, 1942; Rayner, 1951; Schaeffer, 1968), in various groups of fossil holosteans (deBeer, 1937; Rayner, 1951; Beltan, 1957; Gardiner, 1960), and in the halecostomes (Griffith and Patterson, 1963; Patterson, 1967) it is evident that all these embryonic components were present in the lateral cranial wall of these fishes. Patterson's (1964) figures and descriptions of the trigeminofacialis chamber in the elopiforms, ctenothrissiforms, clupeiforms, beryciforms, and perciforms also indicate persistence of the primitive cranial wall in these major groups of teleosts. The prefacial commissure is absent in all forms that have a common foramen or fenestra for the trigeminal and facial nerves and the pila antotica may be replaced by a secondary commissure, as in *Acipenser*, *Amia*, *Lepisosteus*, and *Salmo*.

It is the confluence of the pars ganglionaris and the pars jugularis as seen in *Amia* and

mural chamber is crossed by an oblique strut of the prootic that meets the pleurosphenoid on the medial side of the trigeminal foramen. A large canal medial to the ascending process transmitted the jugular vein. The facial foramen opens into a small, separate recess below the jugular aperture that may have housed the facial ganglion. From this recess the palatine branch of the facial nerve entered the dorsal part of the myodome and the hyomandibular branch passed laterally behind the ascending process.

A conspicuous feature on the lateral surface of the otic region (fig. 5) is a groove that extends in an oblique direction from the anterior part of the intercalar to the internal carotid foramen. The groove is deepest in the

Lepisosteus that Goodrich (1930, p. 277) called the trigeminofacialis chamber. He believed that the chamber is secondarily divided by a bony wall in the Teleostei. The problem of chamber subdivision is further complicated by deBeer's (1937) interpretation of the condition in *Salmo*. Because of the absence of the pila antotica and the prefacial commissure, the trigeminofacialis chamber at the chondrocranial stage is a single space bounded medially by the dura mater and laterally by the lateral commissure. During ossification, the cartilage of the lateral commissure is partly resorbed to form a canal enclosed by inner and outer bony lamellae. As this canal contains the jugular vein and the orbital artery, deBeer identified it as the pars jugularis in spite of its apparent location within the lateral commissure rather than medial to it, as, for example, in *Elops*.

In a real sense the trigeminofacialis chamber has never been "divided." The partition between the pars ganglionaris and the pars jugularis is part of the primordial lateral wall of the neurocranium, which, in terms of embryonic components, is surely as ancient as the earliest gnathostomes. However, in some groups of actinopterygians, with a complete lateral cranial wall the trigeminal and facial ganglia are situated external to their respective foramina. This was apparently the case in the palaeonisciforms, as there is no indication of the trigeminofacialis recess (Stensiö, 1925; Nielsen, 1942). In *Polypterus* (Allis, 1922) these ganglia are also situated in the jugular canal, but the facialis ganglion includes only that part of the ganglionic complex related to the palatine and hyomandibular nerves. The condition in holosteans, including *Macrepistius*, that retain the prefacial commissure, is usually difficult to ascertain; Griffith and Patterson (1963) believed that the ganglia in *Ichthyokentema*, a halecostome, were medial to the cranial wall. The position of the ganglia in teleosts is rarely discussed, although it might provide a character of some taxonomic significance. In any case, the location of the ganglia in the jugular canal in different actinopterygian groups further complicates the definition of the pars ganglionaris and the pars jugularis.

If we restrict the term trigeminofacialis chamber to the extramural cavity between the lateral cranial wall and the lateral commissure, the terms pars ganglionaris and pars jugularis are no longer meaningful. The position of the trigeminal and facial ganglia in relation to the cranial wall may qualify but not alter the definition. Likewise, the loss of the lateral cranial wall in the amiids, lepisosteids, and some teleosts (making the chamber also partly intramural), and the various modifications in the teleost chamber discussed by Patterson (1964) require only modifying or qualifying comments. This structural complex obviously changed in various ways during the actinopterygian radiation, mainly in relation to the courses of the nerves and blood vessels. The composition of the lateral wall was also modified, as was the posterior extent of the lateral commissure (outer wall of the jugular canal).

vicinity of the glossopharyngeal foramen (IX), which is situated at the anterior border of the intercalar. In *Amia* (Allis, 1897, pp. 684–685) the main ganglion of the glossopharyngeal nerve is outside the skull, lying across the glossopharyngeal foramen and medial to the anterior division of the levator arcus branchialis internus. The ramus anterior of the ninth

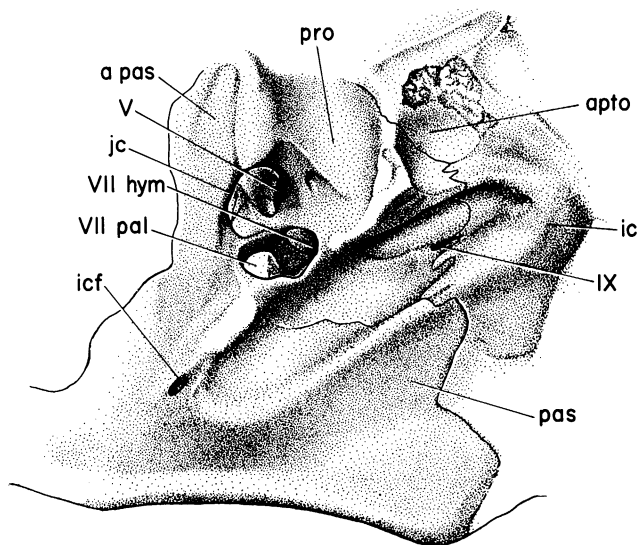


FIG. 5. *Macrepistius arenatus*, U.S.N.M. No. 13628. Detailed view of left otic region.

Abbreviations: apas, ascending process of parasphenoid; apto, autopterotic; ic, intercalar; icf, internal carotid foramen; jc, border of jugular canal; pas, parasphenoid; pro, prootic; V, foramen for mandibular branch of trigeminal nerve; VII hym, foramen for hyomandibular trunk of facial nerve; VII pal, foramen for palatine branch of facial nerve; IX, foramen for glossopharyngeal nerve.

cranial nerve runs forward and downward to the infrapharyngobranchial of the first branchial arch where it divides into the ramus pharyngeus and the ramus pretrematicus. The ramus pharyngeus continues in the same direction and finally enters the palatine canal via the internal carotid foramen. In view of this condition in *Amia*, it may be concluded that the deepest part of the oblique groove in *Macrepistius* contained the glossopharyngeal ganglion and that the ramus anterior and the ramus pharyngeus followed the groove to the internal carotid foramen.

The oblique groove, however, seems too wide and deep to contain only a branch of the glossopharyngeal nerve. It has a nearly constant width throughout its length, with elevated dorsal and ventral edges. Opposite

the jugular canal and the hyomandibular foramen there is a depression in the dorsal rim, suggesting that the jugular vein passed through the posterior part of the groove. A dorsally directed knob or ridge extends from above the deepest part of the oblique groove to another shorter and shallower groove that nearly parallels the larger one, on the autopterotic. A similar knob is present on the prootic and autopterotic of *Caturus* and *Heterolepidotus*. Patterson (personal commun.) suggested that this protuberance is the articulation for the first suprapharyngobranchial. As the first branchial arch is usually attached to the neurocranium a short distance behind the hyomandibular foramen and medial to the hyomandibular bone, this is very probable.

The subtemporal fossa, in which the *M. levators arcuum branchialium* originate, is divided in *Heterolepidotus* by the above-mentioned ridge (Patterson, personal commun.); shallow depressions are present in the same position in *Macrepistius*. These levator muscles may also have arisen from the anterodorsal rim of the oblique groove (in *Amia* they arise from a low, oblique ridge that extends onto the intercalary; there is no subtemporal fossa). A small facet-like depression above the ridge, which is mostly confined to the autopterotic, may be the origination area for the adductor hyomandibularis.

The pleurospenoid (fig. 4) forms the major part of the postorbital wall. It is typically in contact with the frontal dorsally, the autosphenotic dorsally and laterally, the prootic and basipterygoid ventrally, and the orbitosphenoid anteriorly. The pleurospenoid projects anteriorly to the optic fenestra where it meets the orbitosphenoid in a nearly vertical suture. The orbitosphenoid forms an almost complete interorbital septum. The dorsal expansion of the septum to accommodate the olfactory nerves is V-shaped above the optic fenestra but rounds off anteriorly into a tube that continues to the postnasal wall.

A vertical, median partition, the preorbital septum, projects posteriorly from the postnasal wall (fig. 6). It was separated from the orbitosphenoid by a band of cartilage. As this septum incorporates the olfactory nerves, it must represent ossification in the preoptic roots of the orbital cartilages. A similar septum is present in *Pteronisculus* (Nielsen, 1942, fig. 17) and is apparently partly ossified in *Aspidorhynchus* (Rayner, 1948) and in *Ichthyokentema* (Griffith and Patterson, 1963). It remains unossified in *Amia*.

Although the postnasal wall of the *Macrepistius* braincase is fairly well preserved, the foramina and muscle attachment areas on either side of the preoptic septum are difficult to interpret. As this part of the braincase in extinct holosteans and in the halecostomes has received little attention, it has been necessary to base the interpretation on Allis (1897), deBeer

(1937), Jarvik (1942), Daget (1950), and on serial sections of a 28 mm. *Amia*.

In *Polypterus* the superior oblique muscle has its origin in the preorbital canal (orbitonasal foramen), which is dorsally situated in the postnasal wall, and which also transmits the lateral (superficial) opthalmic and profundus nerves along with the opthalmic artery and vein. The inferior oblique muscle is attached to the ventral border of the postnasal wall, near the so-called orbitonasal canal for the nasal vein. The foramen ol-

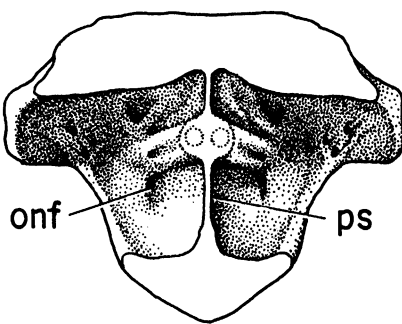


FIG. 6. *Macrepistius arenatus*, U.S.N.M. No. 13628. Reconstructed cross section of neurocranium at level of postnasal wall, viewed from behind. Ca. $\times 2.4$.

Abbreviations: onf, orbitonasal foramen; ps, preorbital septum.

factorium evehens for the olfactory nerve (along with its counterpart of the opposite side) is in a nearly central position. Although the terminology is somewhat confused, it appears that these structures have about the same relationships as they do in *Acipenser* and, in fact, may represent the primitive osteichthyan condition. The origins of the superior and inferior oblique muscles (in the anterior dorsal and ventral myodomes) are similarly separated in *Pteronisculus* and *Boreosomus* (Nielsen, 1942) and in the coelacanth. In *Amia* and *Lepisosteus* the oblique eye muscles converge on and pass anteriorly through the orbitonasal foramen (fenestra) of deBeer (1937, p. 101) after arising from the nasal septum. This "foramen" is ventrolateral to, but almost confluent with, the foramen olfactorium evehens (Allis, 1897, pl. 25, fig. 25). The combined profundus and lateral opthalmic nerves enter the postnasal wall through a notch in its dorsomedian border.

The morphology of the postnasal wall in *Macrepistius* (fig. 6) can be interpreted as essentially a duplication of the *Amia-Lepisosteus* pattern. On either side of the preorbital septum there is a canal that converges

with the olfactory tube as both enter the postnasal wall. Presumably this contained both oblique muscles. There are also foramina on the dorsal portion of the postnasal wall, presumably for branches of the profundus and lateral ophthalmic nerves (Jarvik, 1942).

The ethmoid region is well ossified and complete except for the rostral portion. The lateral ethmoid (fig. 3) is situated mostly above and behind a horizontal groove in the ethmoid proper that may have contained the buccal branch of the facial nerve and the superior maxillary branch of the trigeminal on their way to the snout area. As the snout was apparently broken at the level of the nasal capsules, it is probable that the capsules were situated above or behind the posterior processes of the premaxilla. This means that the olfactory nerves must have passed through the cancellous bone that is visible in the broken end of the snout, even though definite canals cannot be seen.

The ventral surface of the parasphenoid (fig. 7) has a fairly sharp median crest extending almost its entire length. There is no evidence of associated dental plates or of basipterygoid processes. The ventral surface of the ethmoid region to which the missing vomers were attached has paired longitudinal grooves for the anterior palatine rami of the facial nerve. These nerves ran forward between the parasphenoid and the base of the neurocranium after passing through the palatine foramina (Allis, 1897, p. 619). The ascending process, which includes the foramen for the internal carotid, is unusually high for an amioid.

DISCUSSION

The assignment of *Macrepistius* to the Caturidae on the basis of the dermal skull (Schaeffer, 1960) is confirmed in part by the neurocranium. Nevertheless it is difficult to characterize this complex structure in a way that will exclude it from the amiids except on the basis of reduction of ossification in the latter. In regard to the other amiiform families, the macrosemiid neurocranium has not been described and the braincase of the promecosominids, paracentrophorids, and catervariolids (placed in the Amiiformes by Gardiner, 1960 and Andrews et al., 1967) is unknown. The pachycormiforms (Lehman, 1966; Obruchev et al., 1967; Andrews et al., 1967), which were long regarded as specialized amiiforms (Romer, 1966), probably share a common ancestry with the latter, as indicated by the dermal skull. However, the otic and occipital regions are separated by a lateral cranial fissure. This would appear to be a more primitive condition than that in the amiiforms.

Among the caturids, neurocrania have been described for *Caturus* (Rayner, 1948; Gardiner, 1960), *Osteorchachis* (Gardiner, 1960), and

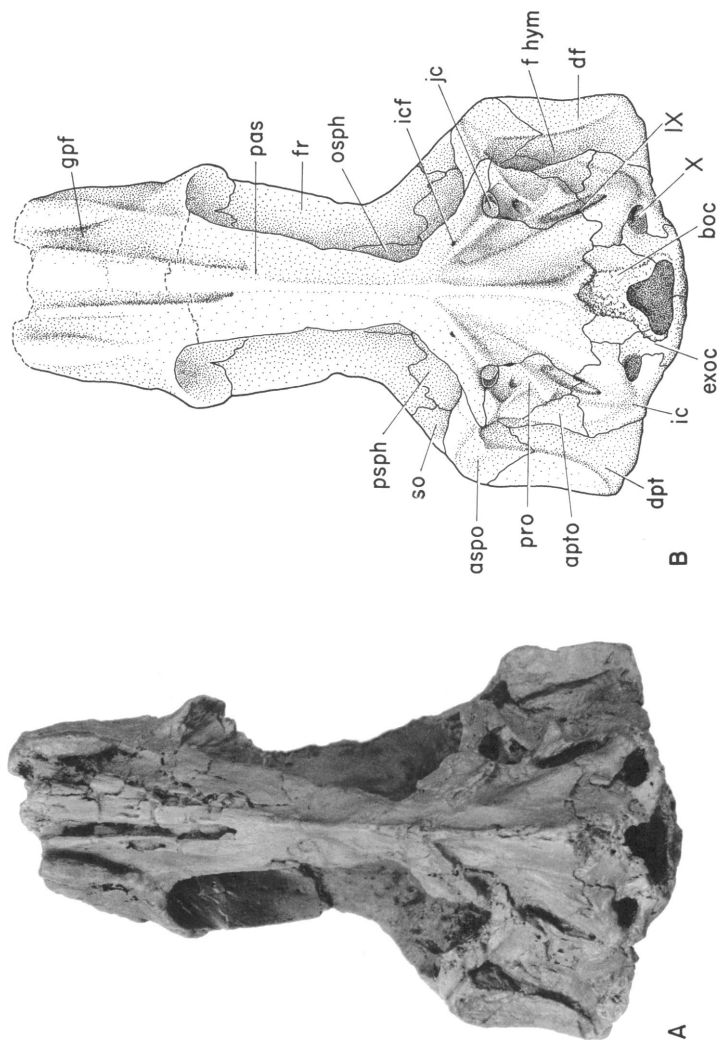


FIG. 7. *Macrepiptius arenatus*, U.S.N.M. No. 13628. Neurocranium in ventral view. A. Photograph, as preserved. B. Reconstruction. Both ca. $\times 1.25$.

Abbreviations: apto, autospherotic; aspo, autospherotic; boc, basioccipital (incomplete); df, dilatator fossa; dpt, dermopterotic; exoc, exoccipital; f hym, facet for articulation of hyomandibular; fr, frontal; gpf, groove for anterior palatine ramus of facial nerve; ic, intercalar; icf, internal carotid foramen; jc, jugular canal; osph, orbitosphenoid; pas, parasphenoid; pro, prootic; psph, pleuro-sphenoid; so, supraorbital; IX, foramen for glossopharyngeal nerve; X, foramen for vagus nerve.

Heterolepidotus (Gardiner, 1960). For the amiids, it is known in *Sinamia* (Stensiö, 1935), in *Enneles* (Silva Santos, 1960), and, of course, in *Amia*. On the basis of this sample, it is evident that *Macrepistius* agrees with the other caturids in having a completely ossified otic region and an orbito-sphenoid that forms a nearly complete interorbital septum. *Sinamia* (Stensiö, 1935) also has a complete orbitosphenoid, but the otic ossification is reduced as in *Amia*.

A separate autopterotic (Gardiner's "opisthotic") has been reported in the above-mentioned caturid genera, and, as noted above, it seems to be present in *Macrepistius*. However, the autopterotic-prootic suture is rarely well defined and further examination of this area in additional caturid skulls is desirable. One other point of interest in regard to the prootic and autopterotic is the ridge that crosses the subtemporal fossa. In addition to its presence in *Heterolepidotus* and *Macrepistius*, there is a suggestion of it in Rayner's (1948) drawing of *Aspidorhynchus*.

All the genera mentioned above have an anterior flange on the intercalar. This extension is also present in the aspidorhynchiforms, which have a similar otic pattern (including the possible presence of an autopterotic), and the same elements surrounding the border of the posttemporal fossa. The meaning of these resemblances in terms of relationship is difficult to assess, particularly as the caudal skeleton suggests affinity with the Leptolepiformes (Patterson, personal commun.).

Although the paired supraoccipitals of *Macrepistius* have not been reported in other caturids (or as paired elements in any other actinopterygian), a single supraoccipital has apparently developed independently in *Dapedium* (Gardiner, 1960), *Aspidorhynchus* (Rayner, 1948), and in the halecostomes. There is no ready explanation for the sporadic appearance of this bone, although its presence may be related to the differential growth phenomenon discussed in the next section. The differences in relative size and position are also of interest in this regard.

On the basis of present knowledge it is difficult to make meaningful comparisons of the trigeminofacialis chamber within the caturids or in the amiiforms generally. This complex area of the neurocranium should provide characters of systematic significance, such as the loss of the pre-facial commissure in the amiids.

The parasphenoid also shows some interesting generic differences, but again, their systematic value is not clear. Among the caturids, *Caturus* (Rayner, 1948, Gardiner, 1960), *Furo* and *Heterolepidotus* (Patterson, personal commun.) have a basipterygoid process. In *Caturus* the parasphenoid seems to be involved in the articular surface, but in *Heterolepidotus* only the prootic component forms this surface. The basipterygoid process

is absent in *Osteorhachis*, *Macrepistius*, and in the amiids. The ascending process of the *Macrepistius* parasphenoid which encloses the internal carotid foramen has a broader base than in other caturids. Parasphenoid teeth are present in *Caturus*, *Heterolepidotus*, and *Neorhombolepis*, but absent in *Osteorhachis* and *Macrepistius*.

THE RELATIONSHIPS OF *MACREPISTIUS*

In order to consider the possible affinities of *Macrepistius* an attempt has been made to define the primitive and advanced states for certain caturid characters (table 1). About half of the caturid genera are poorly known or incompletely described, therefore these decisions must be regarded as tentative. Other amiiforms have also been examined, mainly to support conclusions about the primitive conditions, but no attempt is made to designate a "sister" group for the Caturidae. For illustrations of caturid and other amiiform genera the reader is referred to Gardiner (1960), Schaeffer (1960), and Lehman (1966).

Many of the characters apparently primitive for the caturids may also be primitive for the Amiiformes and possibly for the Holostei. As our primary concern here is with the derived caturid characters, it will be helpful to consider first the derived characters that are presumably unique to *Macrepistius* and therefore of limited value in postulating relationships.

Most or all of the unique *Macrepistius* characters may be related to feeding and locomotion. The unusually deep palate, the presumed enlargement of the adductor mandibulae muscle, the related extreme deepening of the infraorbitals and opercular, and the rounding of the tooth crowns all suggest a mode of feeding different from that of the other caturids. Although the loss of the basipterygoid processes and parasphenoid teeth are shared derived characters, it is probable that these changes are in some way also related to this feeding specialization. The paired and partly fused supraoccipitals may represent a solution to a differential growth "problem" in the occipital region—a problem similar to that which evoked the development of a single supraoccipital in *Daepedium*, *Aspidorhynchus*, and the halecostomes (see below). The role of the epaxial musculature in turning and elevating the head may have been involved in the origin of this novel modification.

The vertebral column of *Macrepistius*, with its abdominal monospondylic and caudal diplospondylic centra and with its reduced notochordal canal, is also different from the column in other caturids. The condition in *Macrepistius* may have arisen from a form with either hemicentra or annular centra (rather than from a form without centra—although this

TABLE 1
PRESUMED PRIMITIVE AND DERIVED CONDITIONS OF SELECTED CHARACTERS IN THE CATURIDAE

Character	Primitive condition	Derived condition
Neurocranium		
Shape in cross section	triangular ^a	depressed
Interorbital septum	almost complete ^a	—
Otic walls	complete, probably separate autopterotic ^a	—
Intercalars	anterior flange present ^a	—
Epiotics	meet in midline	separated by supraoccipitals ^a
Subtemporal fossae	not divided	divided by ridge ^a
Posttemporal fossae	well developed ^a	reduced
Basipterygoid processes	present	absent ^a
Parasphenoid teeth	present	absent ^a
Dermal Skull		
Preorbital length	less than orbital width	greater than orbital width ^a
Nasals	meet behind rostral ^a	separated
Parietals	rectangular	irregular ^a
Supraorbitals	2 to 5 ^a	more than 5
Infraorbitals	narrow	deep ^a
Suborbitals	2 or 3, subequal	variable in size and number ^a
Maxilla	ends in front of suborbitals	ends below suborbitals ^a
Mandible	dentigerous ramus and coronoid of equal length	dentigerous ramus longer than coronoid ^a
Dentition	teeth with pointed crowns	teeth with tumid, rounded crowns ^a
Opercular	depth less than 2 × that of subopercular	depth more than 2 × that of subopercular ^a
Premaxilla	ascending process present ^a	—
Postcranial Skeleton		
Vertebrae	centra absent	centra present ^a
Dorsal fin	short based	long based ^a
Caudal endoskeleton	8 or more hypurals, each supporting 1 principal ray ^a	—
Squamation	scales rhomboidal, lepisosteoid ^a	—

^a Indicates condition in *Macrepistius*.

possibility cannot be categorically eliminated). The change has unknown functional implications, but considered in relation to the elongated dorsal fin, which is another unique character, the locomotor behavior may have been somewhat different from that of other caturids.

With regard to shared derived characters, only a few comparisons are possible. *Osteorhachis* agrees with *Macrepistius* in lacking basipterygoid

processes and parasphenoid teeth, and in having somewhat deepened infraorbitals. *Osteorhachis* is apparently advanced in comparison with *Macrepistius* in possessing a depressed neurocranium, reduced post-temporal fossae, a moderately elongated narrow dentigerous ramus on the mandible with widely spaced pointed teeth, and in having a relatively longer maxilla. *Heterolepidotus* resembles *Macrepistius* in the deepening (although less extreme) of the infraorbitals and opercular and in having the subtemporal fossa divided by a ridge. *Macrepistius* and *Caturus* share an increase in the number of supraorbitals, but their arrangement, shape, and total number are quite different: independent development of this condition is indicated. None of the other caturid genera shares with *Macrepistius* the derived characters in table 1, or is well enough known for adequate comparison.

On the basis of table 1 and the above remarks, I can recognize two ways of viewing the relationships of *Macrepistius*:

1. If particular significance is attached to the absence of basipterygoid processes and parasphenoid teeth (which may be, but are not definitely, present in all other caturid genera), it is possible to regard *Osteorhachis* and *Macrepistius* as "sister" genera. In doing this the significance of the depressed braincase in *Osteorhachis* is de-emphasized. It is then implied that this braincase, which may be unique among the caturids, evolved only in the line leading to *Osteorhachis*.

2. If it is admitted that the basipterygoid processes and parasphenoid teeth can be lost independently in two caturid genera, then it can be postulated that *Heterolepidotus* (which has these structures) and *Macrepistius* are "sister" genera.

Because of insufficient evidence, I see no reason to choose one of these hypotheses over the other. Certain derived characters of *Macrepistius*, including the paired supraoccipitals, the dentition, the form of the centra, and the elongated dorsal fin are unique among the amiiforms. Assigning *Macrepistius* to a new family on the basis of these characters merely side-steps the question of affinity. We may assume that it arose from some caturid that had no supraoccipitals, but that had pointed teeth, semi- or annular centra, and a short dorsal fin. In conclusion I regard "sister" relationships with either *Osteorhachis* or *Heterolepidotus* as expedient and reasonable hypotheses in terms of the operational limitations discussed at the beginning of this section.

REMARKS ON NEUROCRANIAL OSSIFICATION

Wherever ossification of the endoskeleton occurs in fishes it is either restricted to a layer of perichondral bone surrounding the cartilage, or it

includes both perichondral and endochondral bone with partial or complete replacement of the cartilage. Although in all higher vertebrates perichondral and endochondral ossification are interrelated phases of a single morphogenetic process, in some primitive fishes a thin layer of perichondral bone represents the only endoskeletal ossification during the entire life span. If we assume that replacement of embryonic cartilage by bone (endochondral ossification) is as ancient as perichondral ossification, it follows that endochondral ossification was partly or completely inhibited in several groups of early fishes. The alternative, that the replacement mechanism gradually evolved as an elaboration or extension of perichondral ossification, is, at present, equally plausible. It should be noted, however, that recent work on endochondral ossification suggests that replacement is initiated by physiological changes in the chondrocytes. In this case growth of the perichondrium (or periosteum) into areas of hypertrophied cartilage is a response to these changes (McLean and Urist, 1968).

The variable development of the perichondral and endochondral bone in the neurocranium of the major groups of non-actinopterygian fishes can be reviewed briefly. Among the Agnatha, only the osteostracans have the neurocranial and visceral portions of the head skeleton covered or lined with perichondral bone; in a few late genera (e.g., *Boreaspis*, Stensiö, 1927, p. 296) the cartilage existing between the inner and outer layers of the perichondral bone is partly or completely replaced by endochondral bone. The fusion of the basal layer of the exoskeleton with the outer perichondral layer of the endoskeleton presumably means that the intervening perichondrium is resorbed or ossified—a phenomenon that to my knowledge has not been described in any bony fish. Many placoderms have a well-developed perichondral layer, but very few (e.g., the petalichthyids, Ørvig, 1951) are known to have any endochondral ossification. The apparent absence of osteogenic potency in the elasmobranch and holocephalan endoskeleton (as distinguished from the ability to form calcified cartilage) remains unexplained; possibly the ancestors of these groups also lacked this potency. The several parts of the cartilaginous acanthodian neurocranium are usually covered with perichondral bone, but the only evidence of endochondral ossification is in the jaw elements of a few genera.

The neurocranium of the palaeonisciform actinopterygians and of the rhipidistians, among the early osteichthyans, is both perichondrally and endochondrally ossified. The braincase of the Devonian dipnoan *Chirodipterus* (Säve-Söderbergh, 1952) is completely covered with perichondral bone; endochondral bone occurs in the posterior and ventral parts of the

ethmoid region, in the ventral and presumably lateral parts of the otic area and in the entire occipital region. In the living lungfishes only the so-called exoccipitals are ossified. A reduction in neurocranial ossification, although not so extensive, is also evident in the coelacanth. The neurocranium of the Devonian *Nesides* (Stensiö, 1937; Bjerring, 1967) is covered with perichondral bone; endochondral bone occurs in the roof of the notochordal canal, in the vicinity of the basipterygoid and antotic processes, and in the ethmoid region. In *Latimeria* (Millot and Anthony, 1958) the ectethmoid and the basisphenoid of the anterior neurocranial moiety are both perichondrally and endochondrally ossified. In the posterior moiety the large prootics, the supraoccipitals, the exoccipitals, the two components of the basioccipital (one above and one below the notochord), and the so-called preoccipital elements (above and below the notochord anterior to the basioccipitals) appear to be ossified in the same way. Loss of ossification in the post-Devonian coelacanth thus involved mainly a reduction in the perichondral bone that surrounded cartilage.

Although there is no indication of embryonic ossification sites in the typical adult palaeonisciform neurocranium (Nielsen, 1942), a presumed immature braincase of *Cosmoptychius*, C.U.M.Z. No. GN 300 (fig. 8), originally described by Watson (1928), is composed of a separate occipital (posterior) unit, separate paired autosphenotics and otics, and a basicranial ossification (Watson's basisphenoid) on the dorsal surface of the parasphenoid that apparently includes the floor of the hypophyseal recess, a pit representing the hypophyseal passage and the floor of the myodome. A notch on the posterior border of the basicranial ossification indicates the anterior termination of the notochord. The low, displaced position of the otic ossification suggests, as Watson noted, that the area around the foramen magnum was not yet ossified.

In adult specimens of the palaeonisciform *Birgeria* (Nielsen, 1949) there are also separate neurocranial ossifications (fig. 9A), probably the same ones as in *Cosmoptychius*, but more extensively ossified and, in lateral aspect, nearly in contact. The vagus nerve had its exit in the lateral occipital fissure, the glossopharyngeal in the otic ossification, and the branches of the facial and trigeminal from the mostly unossified area (which must have included the trigeminofacialis chamber and the jugular canal) ventral to the autosphenotic. Anterior paired ethmoid ossifications are supported by the parasphenoid. These are less extensive than the fused ethmoid region of, for example, *Pteronisculus* (Nielsen, 1942), and there is no evidence of ossification between them and the sphenoid.

Polypterus (fig. 9B) has about the same ossification pattern as *Birgeria*

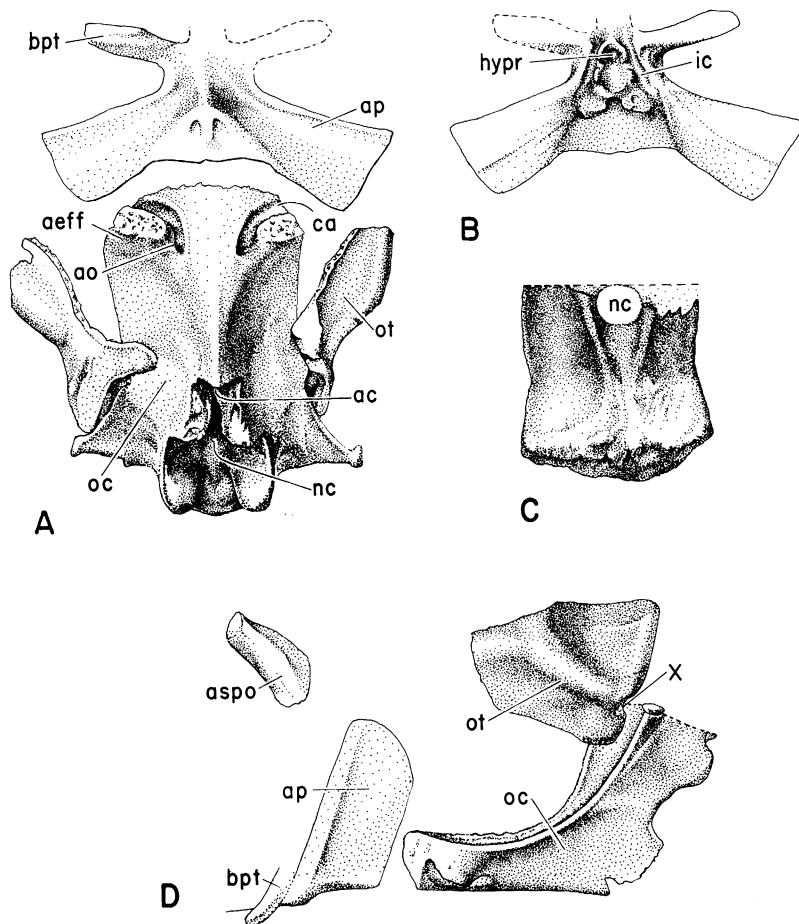


FIG. 8. *Cosmoptychius striatus*, C.U.M.Z. No. GN 300. Immature neurocranial ossifications from cast of natural mold. A. Ventral view. B. Dorsal view of parasphenoid and basicranial ossification. C. Anterodorsal view of incomplete occipital (posterior) ossification. D. Lateral view reconstructed following Watson (1928). All ca. $\times 3$.

Abbreviations: ac, aortic canal; aeff, groove for first efferent artery; ao, groove for lateral aorta; ap, ascending process of parasphenoid; aspo, autosphenotic; bpt, basipterygoid process; ca, groove for common carotid artery; hypr, hypophyseal recess and fenestra; ic, groove for internal carotid artery; nc, notochordal canal, followed by groove in C; oc, occipital (posterior) ossification; ot, otic ossification; X, foramen for vagus nerve.

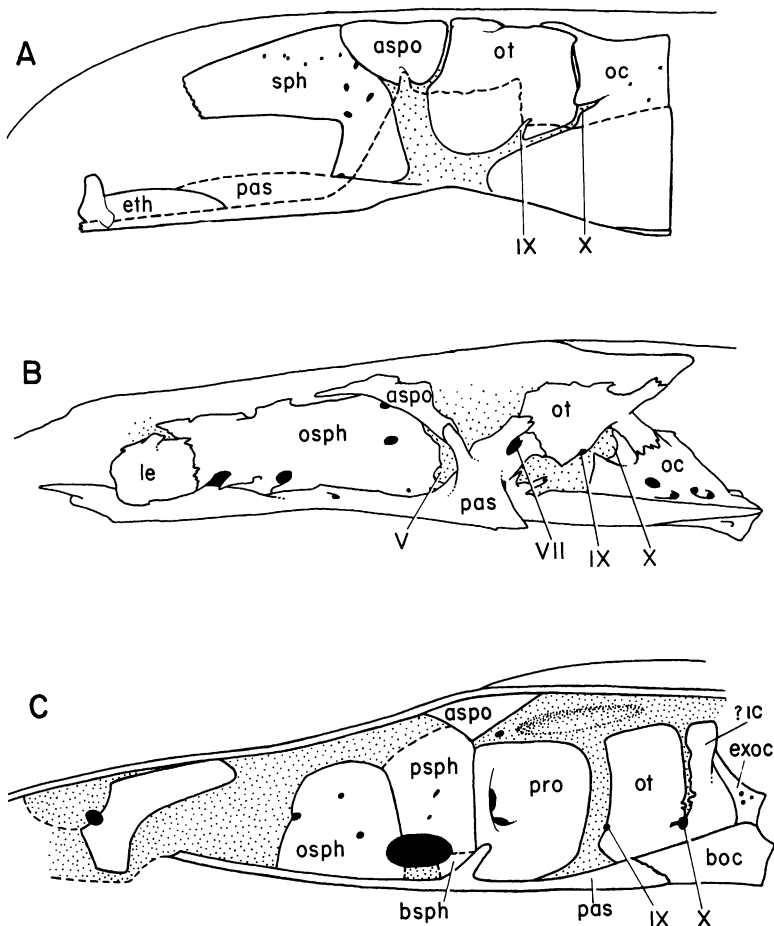


FIG. 9. Chondrostean and holostean neurocrania in lateral aspect. A. *Birgeria groenlandica*, after Nielsen (1949). B. *Polypterus* sp. C. *Pachycormus macropterus*, after Lehman (1949).

Abbreviations: aspo, autosphenotic; boc, basioccipital; bsph, basisphenoid; eth, ethmoid; exoc, exoccipital; ?ic, possible intercalar; le, lateral ethmoid; oc, occipital (undivided); osph, orbitosphenoid; ot, otic; pas, parasphenoid; pro, prootic; psph, pleurosphenoid; sph, sphenoid; V, foramen for trigeminal nerve; VII, foramen for hyomandibular branch of facial nerve; IX, foramen for glossopharyngeal nerve; X, foramen for vagus nerve.

(Stensiö, 1921; Allis, 1922; Daget, 1950). There is an undivided occipital segment without a notochordal, but with a short aortic canal. The lateral occipital fissure is eliminated by the 76 mm. stage; the vagal foramen is

situated between the occipital and otic units. The single otic element (opisthotic of Allis and of Stensiö) ossifies in the posterodorsal part of the otic capsule and is surrounded anteriorly and ventrally by cartilage. The outer and inner dorso-medial laminae of the secondarily elaborated ascending process of the parasphenoid (terminology of Jarvik, 1954) frame the posterior opening of the jugular canal, which is included in the cartilaginous area between these laminae and the autosphenotic. The facial foramen opens into the jugular canal near its posterior end; the trigeminal foramen is immediately anterior to the canal and is partly surrounded by cartilage. According to deBeer (1937), the posterior process of the *Polypterus* otic, which has a ligamentous attachment with the suprascapular, develops intramembraneously—representing an intercalar-like development. Most of the otic bone is thus embedded in the cartilaginous wall that extends from the vagal foramen anteriorly to the trigeminal foramen. The autosphenotic usually fuses with the dermosphenotic but is suturally separated from the sphenoid. In contrast to *Birgeria*, the large sphenoid ossifications of each side are widely separated ventrally. The lateral ethmoids, which vary from one to three on each side, complete the list of cartilage bones.

One possible explanation for the resemblances between the neurocrania of *Birgeria* and *Polypterus* is that both have retained the immature palaeonisciform ossification pattern. Although a braincase of the *Birgeria* type is the exception rather than the rule among the palaeonisciforms, it provides a clue as to how the subdivided adult holostean and halecostome neurocrania may have arisen. If we assume that in the lineages leading from the palaeonisciforms to the various holostean and halecostome groups there was selection for persistence of separate neurocranial ossifications into progressively later stages of the life cycle, we can visualize this shift as a neotenic adaptation for differential growth of the neurocranium beyond the chondrocranial stage. The further subdivision of the occipital, otic, and sphenoid ossifications can be regarded as an extension of the same phenomenon.¹

¹ There is also the possibility that a similar pattern of embryonic ossification sites was present in the first osteichthyans and perhaps in the acanthodians. Support for this hypothesis is found in the endochondral ossifications of the early dipnoans, the coelacanth, the apparent presence of a separate occipital ossification in *Eusthenopteron* (Jarvik, 1954) and in the resemblances between the neurocranial elements of the acanthodians and those of *Cosmoptychius*. These sites and their interaction with each other in producing the components of the adult neurocranium usually involve perichondral, and sometimes but not always endochondral, ossification, as in the acanthodian neurocranium.

During discussion with Dr. Gareth J. Nelson (who kindly commented on the entire manu-

Subdivision of the occipital plate into paired exoccipitals and a median basioccipital in the holosteans and halecostomes is such a constant feature that it may reflect the disposition of embryonic ossification sites in the palaeonisciform occipital moiety. The epiotics, which ossify on the dorsal surface of the auditory capsule, are topographically and functionally part of the occipital surface, usually meeting above the exoccipitals. Their sutural contact with the exoccipitals would cover the dorsal part of the lateral occipital fissure. Reduction of the median part of the epiotics "provided space" for the supraoccipitals, which appeared independently in *Dapedium* (Gardiner, 1960), *Macrepistius*, *Aspidorhynchus* (fig. 11C), and in the halecostomes.

Although the origin of the post-temporal fossa and its possible relationship to the fossa bridgei remain problematical, I am inclined to agree with Griffith and Patterson (1963, pp. 35–36) that the posttemporal fossa is a new structure in the holosteans and halecostomes. It has, in fact, probably developed several times independently as suggested by the shallow depressions on the occipital surface of the parasemionotids (Lehman, 1952, fig. 104) and in *Dapedium* (Gardiner, 1960, fig. 38). Differences in fossa development make this probability even more convincing. This fossa was never fully developed in the semionotiforms. In the early amiiforms and the aspidorhynchiforms it is framed posteriorly by the epiotic, intercalar, and dermopterotic (Rayner, 1948; Gardiner, 1960), and in the halecostomes by the epiotic and the autopterotic (Griffith and Patterson, 1963).

The otic ossification pattern of the holosteans and halecostomes shows little resemblance to that found in *Cosmoptychius*, *Birgeria*, and *Polypterus*. Perhaps a partial clue to the changes in this region is provided by the pachycormiforms. In both *Hypsocormus* and *Pachycormus* (fig. 9C) the lateral occipital fissure (which typically includes the vagal foramen) has persisted ventrally to the basioccipital, which extends anteriorly beneath it. Although Lehman (1949) identified the ossification posterior to the fissure and anterior to the exoccipital as the "postopisthotic" it seems reasonable to assume that all of the elements posterior to the fissure, including the postopisthotic, were derived from the same embryonic

script), he suggested that the palaeonisciform neurocranium might represent a specialized or derived condition. In this case, the palaeonisciforms as well as the holosteans and halecostomes would have evolved separately from ancestors with a subdivided neurocranium as in the holosteans and halecostomes. In my opinion, the main argument against this hypothesis is that all known adult actinopterygian neurocrania prior to the appearance of the holosteans and halecostomes are of the palaeonisciform type, with *Birgeria* alone exhibiting partial subdivision.

components as the occipital ossification of the palaeonisciforms.

Lehman objected to calling his "postopisthotic" the intercalar (the identification of Stensiö, 1935; Rayner, 1948; Gardiner, 1960) on the grounds that the intercalar is a membrane bone. Even though the intercalar of *Amia* (fig. 10B) is entirely membranous (de Beer, 1937), the possibility remains that it was originally a cartilage element situated behind or above the vagal foramen. Beltan (1957) noted that there is an impression for the posterior semicircular canal on the medial surface of the *Caturus* (fig. 10A) intercalar. If this observation can be substantiated, it means that the posterior part of the intercalar above the vagus canal (Rayner, 1937; fig. 9) is a component of the cranial wall. This suggests, but does not necessarily prove, that a portion of the caturid intercalar is of cartilaginous origin. It would be of some interest to check, by sectioning, the relationships and histology of the relatively small intercalar in the semionotids, halecostomes, and aspidorhynchids. There is, however, evidence that the anterior extension of this element in the extinct amiiforms and aspidorhynchiforms is a membranous development. The differences in the position, shape, and size of the intercalar are probably related to modifications in shoulder girdle movements that are, in turn, tied to the expansion and contraction of the orobranchial chamber. These differences range from the prominent expansion over part of the exoccipital and prootic, as in *Caturus* (fig. 10A), to a very small ossification dorsal to the exoccipital in *Lepidotes* (fig. 10C) and *Ichthyokentema* (fig. 11B), and finally to the complete disappearance of the intercalar in *Lepisosteus* (fig. 11A).

The basioccipital and the basal portion of the palaeonisciform occipital ossification develop from the embryonic basal plate that extends anteriorly to the basicranial fenestra. In the Mesozoic holosteans and halecostomes the basioccipital meets the posterior border of the prootic, probably even when covered by the anterior flange of the intercalar. The exoccipital, which remains in its primitive position posterior to the lateral occipital fissure and/or the vagal foramen in the pachycormids and probably in the furids and the aspidorhynchids, "spread" anteriorly in the semionotids beyond the vagal foramen, and in at least some halecostomes, e.g., *Ichthyokentema*, beyond the glossopharyngeal foramen. The apparent anterior expansion of the exoccipital and the intercalar might explain the disappearance of the lateral occipital fissure. The metotic fissure, however, which is the embryonic precursor of the lateral occipital fissure, disappears during the chondrocranial stage in *Acipenser*, *Amia*, *Lepisosteus*, and *Salmo* (deBeer, 1937). This suggests that the factors favoring elimination of the fissure may have been operative in holostean

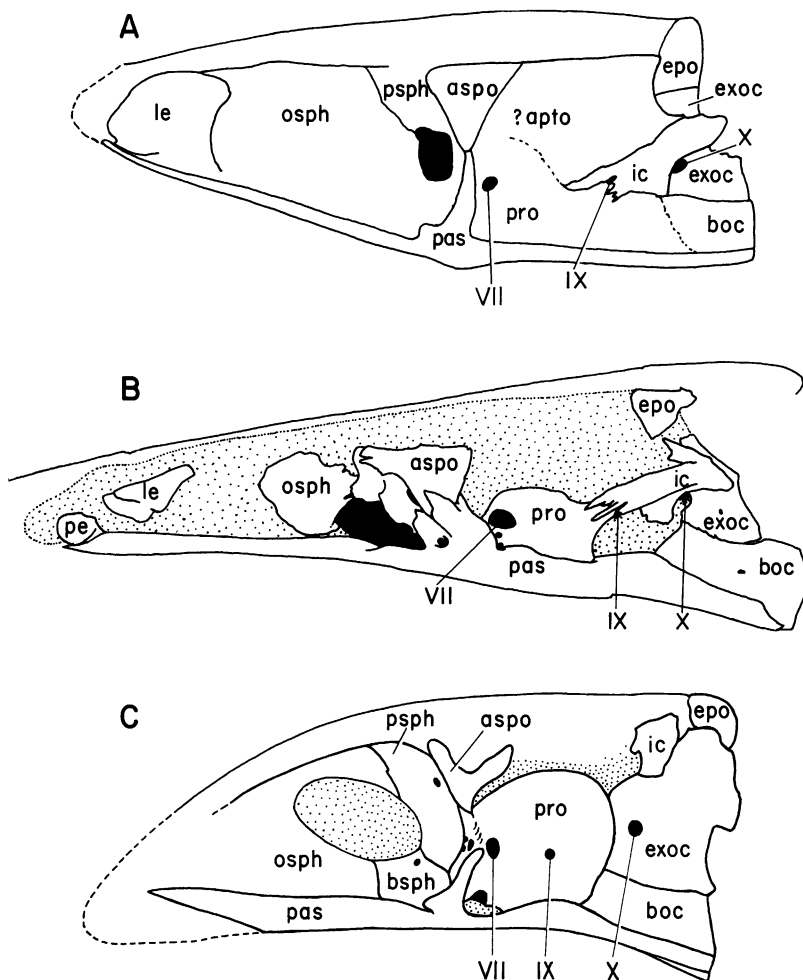


FIG. 10. Holostean neurocrania in lateral aspect. A. *Caturus chirottes*, after Rayner (1948) and Gardiner (1960). B. *Amia calva*. C. *Lepidotes mantelli*, after Gardiner (1960).

Abbreviations: apto, autopterotic; aspo, autosphenotic; boc, basioccipital; bsph, basisphenoid; epo, epiotic; exoc, exoccipital; ic, intercalar; le, lateral ethmoid; osph, orbitosphenoid; pas, parasphenoid; pe, pre-ethmoid; pro, prootic; psph, pleuro-sphenoid; VII, foramen for hyomandibular branch of facial nerve; IX, foramen for glossopharyngeal nerve; X, foramen for vagus nerve.

ontogeny before ossification in the occipital or otic regions. If so, the chondrocranium provided a "pathway" for this anterior expansion.

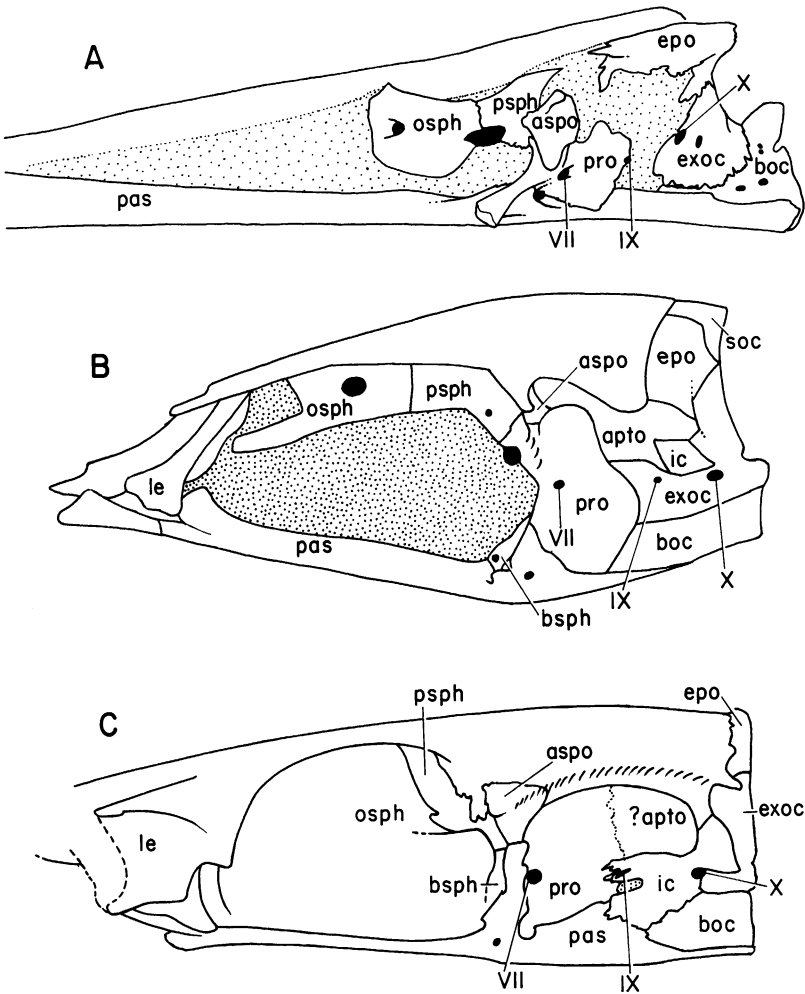


FIG. 11. Holostean and halecostome neurocrania in lateral aspect. A. *Lepisosteus spatula*. B. *Ichthyokentema purbeckensis*, after Griffith and Patterson (1963). C. *Aspidorhynchus* sp., after Rayner (1948) and from B.M.N.H. No. 9843.

Abbreviations: apto, autopterotic; aspo, autosphenotic; boc, basioccipital; bsph, basisphenoid; epo, epiotic; exoc, exoccipital; ic, intercalar; le, lateral ethmoid; osph, orbitosphenoid; pas, parasphenoid; pro, prootic; psph, pleurosphenoid; soc, supraoccipital; VII, foramen for hyomandibular branch of facial nerve; IX, foramen for glossopharyngeal nerve; X, foramen for vagus nerve.

In the pachycormiforms (Lehman, 1949) the single otic ossification site of the palaeonisciforms was apparently divided into an anterior

prootic and a posterior "opisthotic" (ot, fig. 9C). Both are anterior to the lateral occipital fissure, and the "opisthotic" is in articulation ventrally with the basioccipital. The halecostomes *Ichthyokentema* (Griffith and Patterson, 1963) and *Leptolepis* (Patterson, 1967) have an ossification in the same position as the pachycormiform "opisthotic," except that it is separated from the basioccipital by the exoccipital. In the halecostomes this element is called the autopterotic, but it must be homologous, in part, with the pachycormiform "opisthotic." Either name is topographically appropriate, but as "autopterotic" is generally used in the teleosts, it can be employed in the holosteans as well. Although the autopterotic is absent in the semionotiforms, there is a cartilaginous area in *Lepidotes* (Rayner, 1948; Gardiner, 1960) and in *Lepisosteus* dorsal to the prootic and to the anterior part of the exoccipital. If separately ossified, the bone would be identified as the autopterotic. The autopterotic is also absent in *Sinamia* and *Amia* (fig. 10B) among the amiiforms, but there is evidence of its presence in *Caturus* (fig. 10A), *Heterolepidotus*, *Osteorhachis*, and *Macrepistius*.

The remainder of the holostean-halecostome neurocranium is fairly uniform in regard to ossification pattern. The autosphenotic has a well-defined homologue in *Birgeria* and *Polypterus*, and the separate autosphenotic ossification in the immature *Cosmoptychius* is good evidence that it was a primary ossification in the palaeonisciform braincase. The basisphenoids, pleurosphenoids, and orbitosphenoids are also constant enough in their relationships in the holosteans and halecostomes to suggest that the sphenoid ossification of the palaeonisciforms developed from ossification sites that subsequently gave rise to these separate units.

The lateral ethmoids were carried over from the palaeonisciform level and, in fact, the organization of the entire ethmoid region has changed only in details related, in part, to the anterior myodomes and to the loss of ossification.

As discussed above, the persistence of separate ossification units in the adult *Birgeria* may be understood as a neotenic adaptation. The further subdivision of the occipital, otic, and sphenoid ossifications, which is characteristic of all actinopterygians above the palaeonisciform level, is more difficult to explain. Actually we can go little beyond the suggestion that this subdivision reflects primary ossification sites in the palaeonisciform neurocranium and that it provided for further differential expansion in this part of the cranial cavity.

In *Salmo* (deBeer, 1937) ossification of the autosphenotic is initiated by the appearance of perichondral lamellae on both the outer and inner lateral walls of the lateral semicircular canal—which implies two peri-

chondral ossification centers. The basisphenoid forms from three centers: one is situated where the interorbital septum joins the floor of the cranial cavity, the other two are in the dura mater on either side of the cross-piece of the T-shaped basisphenoid rudiment. The basioccipital develops from four perichondral lamellae that form on the dorsal and ventral surface of the basal plate on each side of the notochord. In addition, endochondral ossification centers are involved in replacing the cartilage of the basal plate. By way of comparison, the autosphenotic of *Ictalurus* (*Amiurus* of deBeer, 1937) begins with only an outer perichondral lamella, and the basisphenoid first ossifies in the membrane that extends across the hypophyseal fenestra. The basioccipital of *Ictalurus*, however, ossifies as in *Salmo*.

Although little comparative information is available on the details of early neurocranial ossification in the living actinopterygians, it is evident that the location and number of ossification centers involved in the ontogeny of a particular cartilage bone is related in part to the detailed form of the chondrocranial model. Although the number and disposition of the centers responsible for one bone may differ among the higher taxa, it is probable that these centers are organized in some sort of morphogenetic field. If this is the case, the total functional field and its interaction with adjacent fields becomes more important than individual centers.

During development the chondrocranium is literally surrounded by osteogenic tissue, but complex intercellular epigenetic sequences must be involved before and during the appearance of any part of the osteocranium. These sequences, in turn, must be programmed by control mechanisms that are ultimately based on differential gene action. The conservatism of this epigenetic system is particularly evident in the embryonic chondrocranium, although changes at this developmental level also may occur, as is indicated by the elimination of the occipital fissure.

Most of the modifications in the neurocranial ossification pattern between the palaeonisciforms and the higher actinopterygians may be accounted for by relatively minor alterations in epigenetic sequences related to the ossification stage. Although some differences may occur in the number and location of ossification centers responsible for a particular cartilage bone, it is probable that the pattern in the higher actinopterygians is based on the general disposition of these centers (or fields) in the palaeonisciforms. This hypothesis is in line with the known stability of the epigenotype, and, as noted above, it helps to explain the similarities between the holostean and halecostome neurocrania.

In essence, then, we are concerned with three presumably interrelated problems. One is the sequence of ossification, which may differ in related taxa (Weisel, 1967). The second is the disposition and interrelationship of the ossification sites involved in the formation of a single cartilage bone, which may also differ in related taxa. Finally, there is the problem of differential ossification, which usually has broader phylogenetic implications.

It is well known that in some fishes certain parts of the neurocranium remain cartilaginous, whereas other areas become both perichondrally and endochondrally ossified. Kemp and Hoyt (1969) have provided an interesting discussion of the factors that initiate osteogenesis and regulate its sequence, but they have not speculated about the factors that promote or inhibit ossification in particular parts of the endoskeleton. Although perichondral and endochondral bone may be equally ancient, it will be recalled that among the early fishes a thin layer of perichondral bone surrounding the cartilaginous neurocranium was particularly prevalent. Although this layer may have increased the strength of the neurocranium, there was a marked tendency for perichondral bone covering cartilage to disappear in the post-Devonian coelacanth and dipnoans.

The hypothesis that stress may promote the local disposition of calcium salts in osteogenic tissues has been advanced by Washburn (1947), Schaeffer (1961), and McLean and Urist (1968). It also seems to be supported by the disposition of endochondral bone in the occipital region, around the notochordal canal, and in the otic and ethmoid regions of the coelacanth and the Devonian dipnoans. In addition, the basisphenoid area, including the prootic bridge, is more extensively ossified in the kinetic coelacanth neurocranium than in the akinetic dipnoan one. The complete endochondral ossification of the rhipidistian and most palaeonisciform neurocrania might then be regarded as the ultimate response to forces affecting the braincase during feeding, respiration, and locomotion. Although these forces have not been analyzed, it is evident that they were in part differently distributed in the coelacanth and rhipidistians. It is also evident that the jaw mechanisms in the rhipidistians and palaeonisciforms are more similar to each other than either is to that of the coelacanth. This resemblance presumably reflects the primitive osteichthyan condition in which the adductor mandibulae muscle arose in the maxillary-palatoquadrate chamber (Schaeffer and Rosen, 1961).

It might be argued that the neurocranium of the earliest osteichthyans was completely ossified endochondrally and that the coelacanth and dipnoans subsequently lost this bone except in the areas of greatest stress.

But the alternative, that the ancestral neurocranium had little or no endochondral bone, is equally plausible. This is apparently the situation in the acanthodians, which probably had a kinetic braincase and a jaw mechanism very similar to the palaeonisciform-rhipidistian one. On the basis of either alternative, it might be concluded that the distribution of forces in the palaeonisciform and rhipidistian neurocranium was more general, and in the coelacanth and dipnoans more concentrated in specific areas.

Other factors that may influence the distribution of both perichondral and endochondral bone in the neurocranium and elsewhere in the skeleton are buoyancy, equilibrium, and protection (Schaeffer, 1961). Assuming strong selection for bone reduction in relation to buoyancy and equilibrium adjustment in the coelacanth and dipnoans, it follows that the competence to produce endochondral bone was lost except in areas of greatest stress. This explanation could also account for the differences in neurocranial ossification pattern between (1) the coelacanth and dipnoans, and (2) the palaeonisciforms and rhipidistians. It could also explain the ossified centra in some Devonian lungfishes as well as their absence in all other dipnoans, and it helps to interpret the peculiar combination of a persistent notochord and long ossified ribs in a few dipnoan and coelacanth genera. The different total patterns of endoskeletal ossification in different osteichthyan groups with diverse ways of life indicate that a variety of solutions is possible to provide a viable, functional compromise among all the factors mentioned above.

It is perhaps unnecessary to note that many of the problems discussed in the present paper require experimental investigation before they can be properly elucidated or perhaps even before we can ask the right questions about them. For the fishes there is no direct evidence concerning the morphogenetic factors that determine the location of neurocranial ossification centers or concerning the way in which particular centers cooperate to produce a single neurocranial ossification. On a broader level, we badly need more information on the nature of the interaction among ossification centers in relation to the fusion or subdivision of both membrane and cartilage bones. Can experiments be designed to test the hypothesis that differential or selective ossification of the fish skeleton is, in fact, the result of a compromise among such factors as mechanical stress, buoyancy, equilibrium, and protection? Even the physical properties of cartilage (calcified and uncalcified) and bone (which varies considerably in histology, thickness and flexibility) in living fishes have not been adequately determined and compared.

SUMMARY

The braincase of *Macrepistius arenatus* from the Glen Rose Formation (Lower Cretaceous, Albian) of Texas resembles that of other caturids in the following ways: (1) It has a completely ossified interorbital septum and otic region; (2) It possesses both autopterotic ("opisthotic") and prootic ossifications; and (3) It has an enlarged intercalar that partly surrounds the vagal foramen. It differs from other caturids (and apparently from other actinopterygians) in having paired, partly fused, supra-occipitals that are clearly separated from the epiotics. The parasphenoid is toothless and lacks basiptyergoid processes.

The cranial wall is complete in the area of the trigeminofacialis chamber. The jugular canal is represented by an opening medial to the ascending process of the parasphenoid. A recess below the jugular canal that has separate openings for the palatine and hyomandibular nerves probably contained the facial ganglion. The trigeminofacialis chamber is here defined as the extramural space between the lateral commissure and the primordial lateral wall of the braincase. This chamber has never been secondarily divided into a pars ganglionaris and a pars jugularis in the actinopterygians (as originally claimed by Allis, 1919) although its boundaries and associated foramina have been modified in various ways.

An attempt to work out the relationships of *Macrepistius* on the basis of shared derived characters has resulted in two hypotheses—a "sister" relationship with either *Osteorhachis* or *Heterolepidotus*. Because of insufficient evidence it is not possible to favor either hypothesis. The analysis of caturid and other amiiform character states indicates, however, that the unique specializations of *Macrepistius* evolved from a caturid with pointed teeth, relatively narrow palate and infraorbitals and no supra-occipitals.

Comparison of the neurocranial ossification pattern in *Macrepistius* with that in a variety of other actinopterygians has emphasized the basic uniformity of the pattern throughout the holosteans, halecostomes, and teleosts, as noted by Rayner (1948). This situation presumably reflects the disposition of the embryonic ossification sites in the palaeonisciform neurocranium, which, in the adult, is usually composed of two major ossifications. The persistence of numerous separate neurocranial bones in the higher actinopterygian groups probably represents a neotenic adaptation of prolonged differential growth of the braincase beyond the chondrocranial stage. These conclusions are based, in part, on neurocranial ossification patterns in an immature specimen of the palaeonisciform *Cosmoptychius* and in adult specimens of *Birgeria* and *Polypterus*.

Factors that determine the location and number of neurocranial ossification centers in relation to the chondrocranial model, the organization of the ossification centers in relation to the formation of a particular bone, and finally, the conditions that promote or inhibit perichondral and endochondral ossification in a particular part of the neurocranium (or in the rest of the endoskeleton) are poorly understood. In the absence of pertinent experimental data we can do little more than speculate on these problems. There is, however, circumstantial evidence that the extent of perichondral and endochondral ossification represents a compromise between the ancestral genotype and factors such as stress, buoyancy, equilibrium, and protection.

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