

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2011

AUGUST 18, 1960

The Cretaceous Holostean Fish *Macrepistius*

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In 1894 Cope published a brief description of a new and distinctive holostean found by the geologist R. T. Hill in the Glen Rose formation near the town of Glen Rose, Texas. Cope considered this fish, named by him *Macrepistius arenatus*, to be related to *Lepidotus*, although he did point out certain obvious differences from that genus. Woodward (1895) referred *Macrepistius* to the Macrosemiidae on the basis of resemblances with *Ophiopsis*. Further preparation and study of the unique type specimen, consisting of a nearly uncrushed skull and the posterior half of the body, have revealed additional details which indicate that *Macrepistius* is either a specialized caturid or a caturid derivative.

The drawings for this paper were made by Michael Insinna, and the photographs were taken by Chester Tarka.

GEOLOGIC OCCURRENCE

On the basis of certain remarks by Hill (1893) and the map by Scott (*in* Sellards et al., 1932), it is probable that the single known specimen of *Macrepistius* was found in the lower portion of the Glen Rose formation either in the town of Glen Rose or, more likely, in exposures along the Paluxy River about 4.5 miles west of Glen Rose. The present writer prospected in this area in 1954 but found only a few scraps of bone. The other fish remains from the Glen Rose formation include an unidentified clupeoid (not *Diplomystus*) found near the town of Granbury (Eastman, 1917), and an undescribed holostean brain case (U.S.N.M. No. 13628).

Five ammonite zones have been recognized in the Trinity group by

Scott (1939). The Glen Rose formation represents the zone of *Knemiceras roemeri*, which is considered to be middle Albian. The limestones and marls of the Glen Rose in Somervell County are part of the offshore, sublittoral facies of the Trinity group, which were deposited in a northward transgressing sea. The abundance of echinoids, oyster beds, and coral reefs suggests a water depth of less than 20 fathoms over wide areas (Scott, 1940). The presence of mud cracks and dinosaur footprints indicates that the bottom was occasionally exposed to the atmosphere. *Macrepistius* apparently inhabited the shallower waters of the neritic zone, and its dentition suggests a diet of shelled invertebrates.

Fish remains, as well as ammonites, are relatively rare in marine deposits containing a rich benthonic invertebrate fauna. Although the scarcity of ammonites may be related to the shallowness of the water or to variations in temperature and salinity (Scott, 1940), fish were undoubtedly present in abundance as they are today in such environments. The paucity of fish remains must be related mostly to an abundance of benthonic scavengers and to disintegration by bacterial action prior to burial in an aerobic environment (Brongersma-Sanders, 1957). The occurrence of occasional associated fish skeletons in the Glen Rose formation is therefore of particular interest. Conditions favorable for the preservation of these skeletons obviously existed, although probably only locally and for short periods of time.

TAXONOMY AND DIAGNOSIS

ORDER AMIOIDEA

FAMILY CATURIDAE (EUGNATHIDAE)

GENUS *MACREPISTIUS* COPE, 1894

Macrepistius COPE, 1894, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 9, p. 441, pl. 19, fig. 2.

GENOTYPE: *Macrepistius arenatus* Cope.

GENERIC DIAGNOSIS: Fusiform, moderately deep-bodied caturid attaining an estimated length of about 44 cm., and differing from the other members of the family Caturidae by the following combination of characters: Skull depth nearly equal to length. Exposed portions of dermal bones delicately tuberculated. Nasals probably meeting in midline. Antorbitals possibly reaching anterior supraorbitals. Frontals narrow, slightly constricted between orbits, almost five times the length of the nearly square parietals. Supraorbital bones numerous. Infraorbital bones elongated dorsoventrally. Ventral portion of suborbital series apparently represented by four or more small bones. Maxilla extending to posterior border of orbit. Mandible typically caturid,

with well-developed coronoid process. Marginal and palatal teeth closely spaced, low, with rounded, tumid crowns. Vertebral centra hourglass-shaped, well ossified, with precentra and postcentra in caudal region. Dorsal fin elongated, total length unknown but extending into posterior third of body. Caudal fin moderately forked, with dorsal fringing fulcra. Other fins unknown. Scales rhombic, smooth, denticulated in anterior part of body, and with numerous vascular canals penetrating ganoine layer.

Macrepistius arenatus Cope, 1894

TYPE: A.M.N.H. No. 2435, nearly complete skull and posterior half of body.

SPECIFIC DIAGNOSIS: Same as for genus, as above.

HORIZON AND LOCALITY: At present known only from the lower portion of the Glen Rose formation, lower Cretaceous (middle Albian), near the town of Glen Rose, Somervell County, Texas.

DESCRIPTION

BODY FORM: Although the anterior half of the trunk is missing, it has been possible to restore the body length and outline (figs. 1, 4B) with reasonable assurance by an analysis of the squamation pattern remaining behind the skull and on the posterior half of the body. The procedure is based on that of Breder (1947) and has been discussed by Schaeffer (1955). As reconstructed, the maximum body depth is somewhat less than one-quarter of the total body length. In cross section, the trunk was ovoid. The long and presumably low dorsal fin could probably undulate as in *Amia*, and may have been used to propel the body slowly while feeding. There is no indication that the dorsal fin was elongated simply to diminish body roll, as the center of gravity must have been low in relation to the centers of roll and buoyancy.

SKULL: The compact skull of *Macrepistius* (figs. 2, 3, 4A) is unique among known amioids in being nearly as deep as long and in having a rather abruptly sloping preorbital profile superficially resembling that of the doctor fish (*Acanthurus*). The skull profile is also suggestive of that of the pycnodonts, which have a highly developed crushing dentition. The exposed parts of the heavy dermal bones are ornamented with fine tubercles and ridges. The sensory canals are difficult to trace, but the pattern appears to be typically amioid.

The skull roof is broadest behind the orbits, narrowing to about half of that width anteriorly. The triangular suprascapular bones are

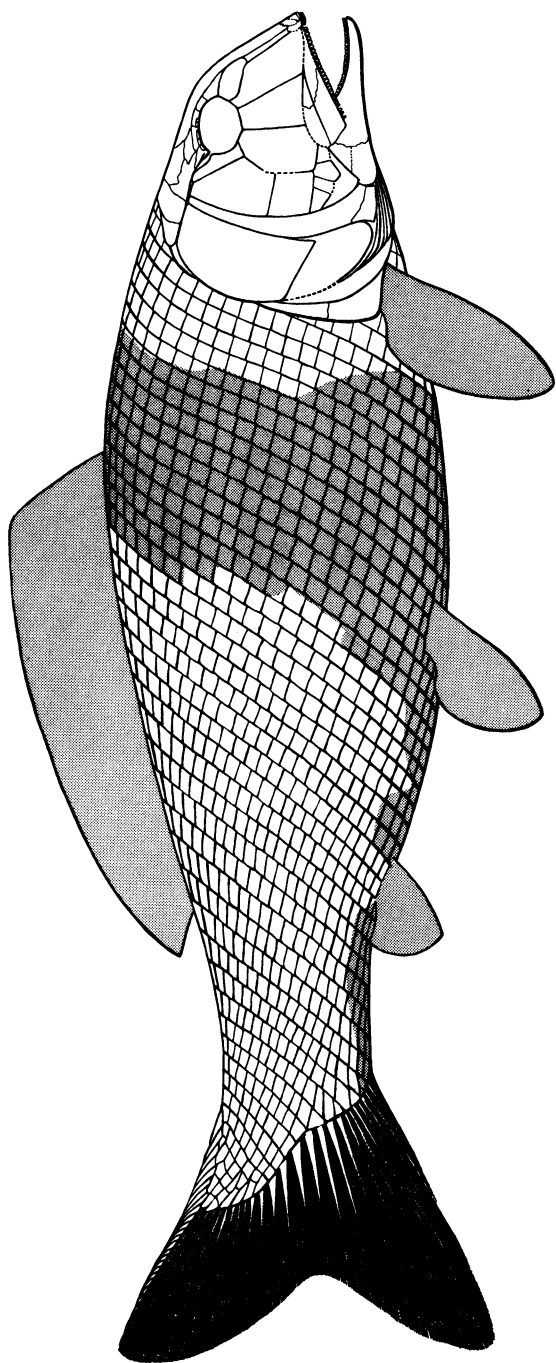


FIG. 1. *Macrepistius arenatus*, reconstruction, stippled areas not preserved. Approximately $\times 2/5$.

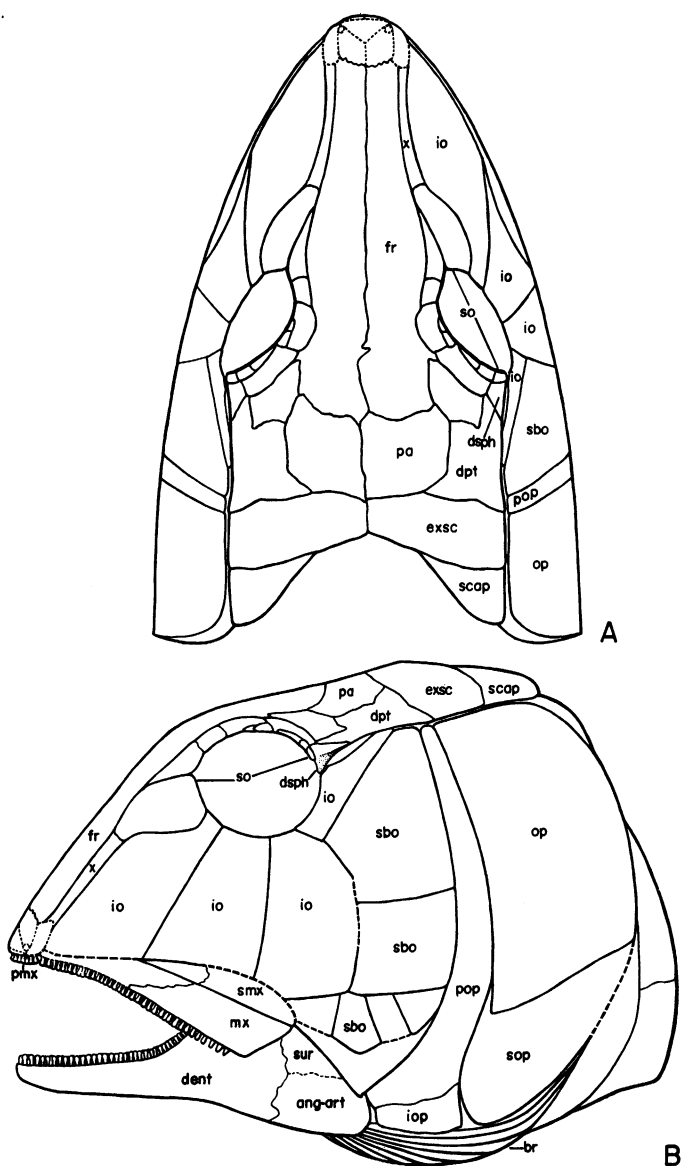


FIG. 2. *Macrepistius arenatus*, reconstruction of skull. A. Dorsal view. B. Lateral view. Abbreviations: ang-art, angulo-articular; br, branchiostegal; dent, dentary; dpt, dermopterotic; dsph, dermosphenotic; exsc, extrascapular; fr, frontal; io, infraorbital; iop, interopercular; mx, maxilla; op, opercular; pa, parietal; pmx, premaxilla; pop, preopercular; sbo, suborbital; scap, suprascapular; smx, supramaxillary; so, supraorbital; sop, subopercular; sur, surangular; x, unidentified element, possibly part of antorbital or exposed portion of autopalatine.

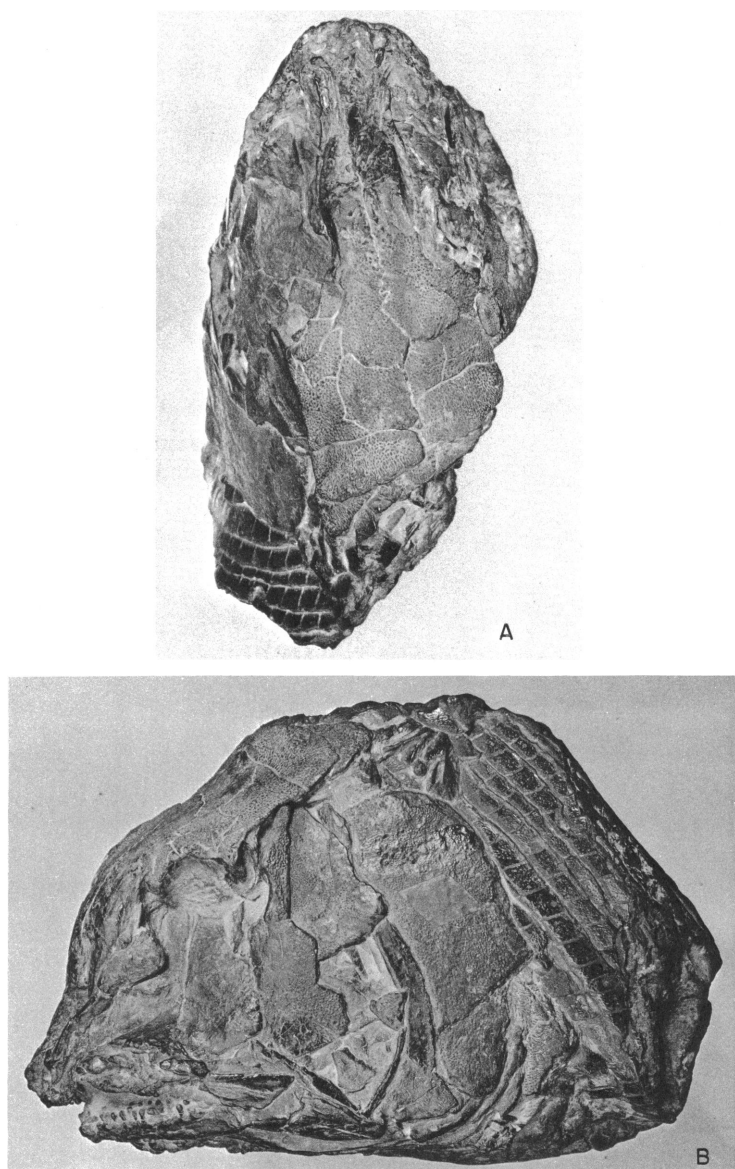


FIG. 3. *Macrepistius arenatus*, A.M.N.H. No. 2435. A. Skull in dorsal view. B. Skull in lateral view. $\times 2/3$.

separated as in *Eugnathus* and *Caturus* rather than meeting behind the extrascapulars as in *Heterolepidotus*. The nearly rectangular extrascapulars meet in the midline as in the caturids, and in contrast to their separation in the macrosemiids. The parietals are nearly square, relatively larger than the dermopterotics, and in contact anterolaterally with an inner supraorbital. The frontals are narrow throughout their length, with only a slight constriction between the orbits and with no appreciable postorbital expansion. The supraorbital bones are numerous, and on the posterior portion of the upper orbital rim they are arranged in several rows. There is a strong resemblance in the pattern of the supraorbital-dermosphenotic series in *Heterolepidotus* and *Macrepistius*. *Caturus* and *Eugnathus* also have numerous supraorbitals, frequently arranged in several rows.

The rostral area is crushed and difficult to interpret. The rostral, nasals, and antorbitals cannot be clearly distinguished, but it is evident that they are disposed much as in *Heterolepidotus*. The posterior half of the maxilla is preserved in place on the left side, along with a fragment of the supramaxilla. The former is typically caturid in form but lacks the definite indentation on the posterior border which appears to be characteristic of this family (Rayner, 1941).

The infraorbitals present a unique appearance among known holosteans. The three elements in this part of the circumorbital series are greatly elongated dorsoventrally. In other holosteans and in teleosts in which the skull is deepened in association with a crushing or grinding dentition (e.g., pycnodonts, sparids), the cheek elements are, by comparison, usually much reduced. The opposite condition in *Macrepistius*, involving enlargement of the infraorbitals, represents a modification of the usual caturid cheek pattern also in connection with a crushing dentition. The posterior circumorbital is more elongated in *Macrepistius* than in the other known caturids and has two embayments along the anterior border. The lower embayment forms the posterior border of the orbit, while the upper is associated with the lateral borders of the dermosphenotic and the dermopterotic. The suborbital series is similar in number and arrangement to that in *Heterolepidotus*, except that the lowest element is apparently subdivided into four or more elements. A narrow bone situated between the frontal and the anterior infraorbital and extending from the anterior supraorbital to the antorbital area may represent an exposed portion of the palate rather than an elongation of the antorbital or the exposed ascending process of the premaxilla (see Discussion).

The opercular elements show some modification related to the deep-

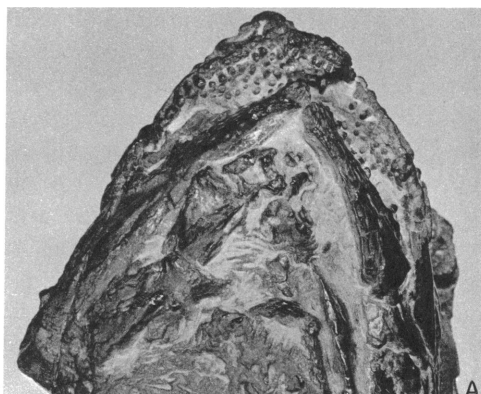


FIG. 4. *Macrepistius arenatus*, A.M.N.H. No. 2435. A. Skull in ventral view. $\times 1$. B. Posterior portion of body. $\times 2/3$.

ening of the skull. The preopercular has a more vertical position than is typical of the caturids. The opercular is nearly twice as deep as wide, and the subopercular is relatively deeper than in the other caturids. The interopercular in form and disposition resembles closely that of *Heterolepidotus*.

Another unusual feature of *Macrepistius* is the combination of a crushing dentition with jaw proportions ordinarily associated with predation. The mandible, as is the maxilla, is characteristically caturid. The highest point on the coronoid process is about halfway between the symphysis and the articulation, which is well behind the orbit. These proportions, plus the over-all length of the jaws, do not provide the most efficient design for powerful adduction. As discussed below,

the powerful adductor mandibulae muscles probably compensated for this seemingly inefficient arrangement.

The maxillary, palatal, and mandibular teeth are identical in form and size. They have rounded, tumid crowns instead of being conical and pointed as in all other known caturids. The implications of this difference in tooth form, along with associated changes in the skull, are also considered in the Discussion.

AXIAL SKELETON: The vertebral centra (fig. 5) of *Macrepistius* are hourglass-shaped and well ossified. The abdominal centra bear separate neural arches and long, ossified, pleural ribs. As in the amiids, the

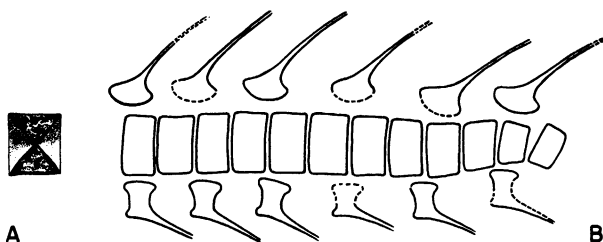


FIG. 5. *Macrepistius arenatus*, A.M.N.H. No. 2435. A. Caudal vertebra in longitudinal section. B. Caudal vertebrae.

caudal centra are divided into precentra and postcentra, with the postcentrum supporting separate neural and haemal arches. In contrast to the situation in the amiids, however, the precentra and postcentra are individually about the same size as the abdominal centra.

APPENDICULAR SKELETON: The shoulder girdle shows no unusual features. The supracleithrum has a tuberculated area along the posterior border near its attachment to the suprascapular. Post-cleithra are present, as in *Heterolepidotus*, but their total number and arrangement cannot be determined. The pectoral fins are missing except for a few radials on the right side. The pelvic fins and the anal fin are also missing. The dorsal fin, represented by the bases of some of the rays, was obviously elongated. Cope's estimate of 32 dorsal rays is reasonable for the total number. The caudal fin is robust and moderately forked. It is composed of about 23 rays. Fulcra are present along the dorsal border.

The scales are smooth and typically caturid. They are nearly equilateral immediately behind the skull but more rhomboid and smaller in the posterior third of the body. In the anterior part of the body, the free margin of the scales is finely denticulated.

Histologically, the scales are of the lepidosteoid type (fig. 6), with the dentinal or cosmine layer reduced or absent. The terminal arborizations of the lepidosteoid tubes are situated just below the ridges of lamellar bone in contact with the ganoine. A few large vertical canals penetrate the entire scale, and their openings are clearly visible on the outer surface of the ganoine layer. In *Lepidosteus*, according to Kerr (1952), these canals contain undifferentiated mesodermal cells and capillaries running from the dermis below the scale to that above. Similar canals are sparsely present in *Heterolepidotus*, but seem to be

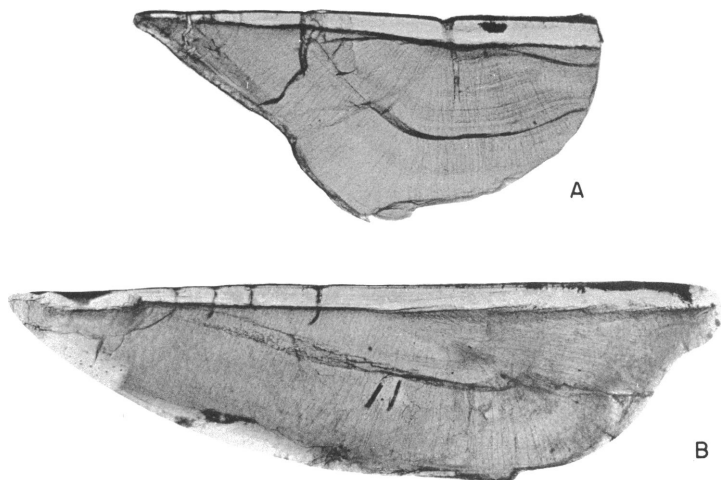


FIG. 6. *Macrepistius arenatus*, A.M.N.H. No. 2435, vertical sections of posterior flank scales. A. Transverse. B. Longitudinal. $\times 18$.

absent in the available specimens of *Caturus* sp. They are probably related to an elaboration of the capillary net in the thin dermal layer covering the upper surface of the scale.

DISCUSSION

The observable characters of *Macrepistius* indicate that it belongs to Group I (Eugnathidae, Amiidae, Macrosemiidae) rather than to Group II (Semionotidae, Lepidosteidae) of Rayner's (1941) classification. Although the dentition is somewhat similar to that of *Lepidotus* among the semionotids, other resemblances to this genus, or to any other semionotid, are outweighed by the differences in the form of the jaws, in the pattern of the cheek and roof elements, and in the structure of the vertebral column.

Assignment of *Macrepistius* to one of the families within the Amioidea (essentially Group I, which excludes the Pachycormidae) is necessarily based mainly on the dermal bone pattern. The Amiidae, including the late Jurassic *Liodesmus*, lack the supraorbitals and suborbitals characteristic of the Caturidae. Both are present in *Macrepistius*. The Macrosemiidae, beginning with *Ophiopsis*, show a clear-cut trend towards reduction in the length of the jaws, relative deepening of the mandible at the level of the coronoid process, and an associated anterior swing of the subopercular, interopercular, and suspensorium. The skull is moderately constricted between the orbits, and the dermethmoid is extensively exposed dorsally. These changes were already characteristic of all the late Jurassic macrosemiids but are less emphasized in *Ophiopsis*. They are not evident in *Macrepistius*.

In most caturids the parietal bones are decidedly shorter than the dermopterotics. In addition, the parietals usually have an irregular shape, with a marked embayment on the anterior border. In *Macrepistius*, however, the nearly square parietals are about the same length as the dermopterotics, and the anterior embayment is slight. Such is also the situation in *Eoeugnathus* (fig. 7A, B), a probable middle Triassic caturid, as well as in the amiids, and it resembles that in the presumably ancestral parasemionotids. It is possible, therefore, that the large, square parietals of *Macrepistius* represent a retention of the primitive condition in which they equal the length of the dermopterotics. It should be noted, however, that the relative proportions of the parietals and dermopterotics may vary within a single caturid genus. In *Eugnathus orthostomus* (Woodward, 1895) they are about the same length (fig. 8), while in *E. praelongus* (Saint-Seine, 1949) the parietals are decidedly shorter. It is therefore difficult to attach any particular significance to the condition in *Macrepistius*, even though the reduced parietals have been cited as an important family character (Rayner, 1941).

Eugnathus is regarded by Saint-Seine (1949, p. 281) as a central type among the eugnathids. As does *Heterolepidotus*, it has an elongated preorbital region, with the nasals meeting in the midline and the antorbitals situated lateral to them. Such an arrangement also appears to be present in *Macrepistius*. In *Caturus*, however, the preorbital area is relatively short (fig. 7C, D). The nasals are separated and reduced in size. Saint-Seine (*ibid.*, p. 283) considers the antorbital to be absent in *C. drieri*, and the "lacrymal" to be in contact with the lateral border of the nasal. Rayner (1948), however, calls this same bone the antorbital in *C. porteri*. The problem here seems to be that the latter species has

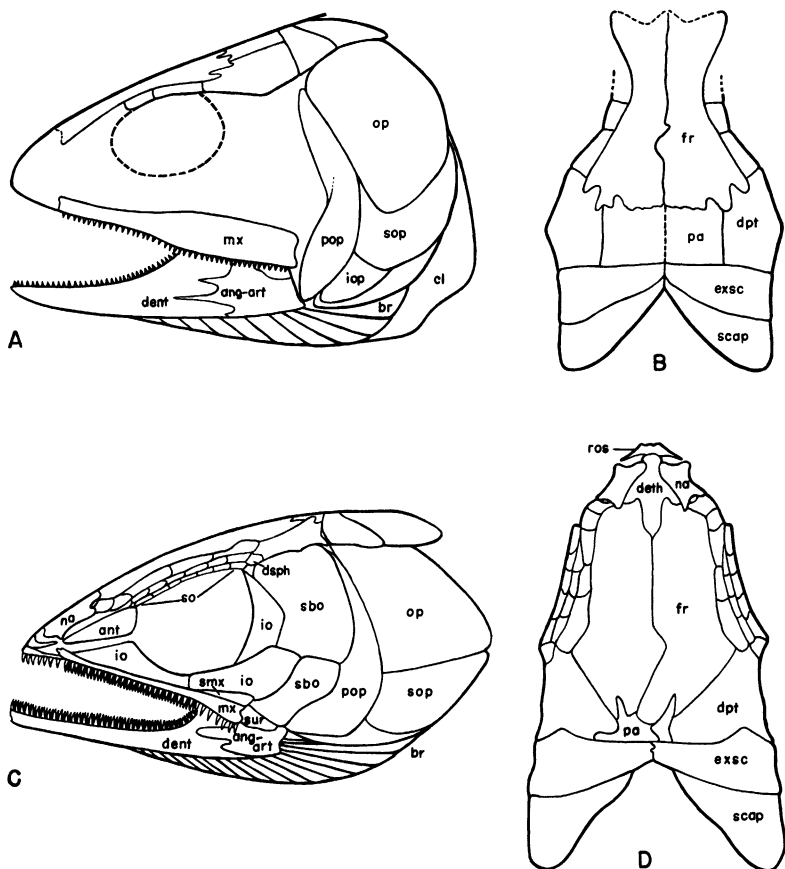


FIG. 7. Skulls. A. *Eoeugnathus megalepis*, lateral view. B. *Eoeugnathus megalepis*, dorsal view. After Brough, 1939. C. *Caturus drieri*, lateral view. D. *Caturus drieri*, dorsal view. After Saint-Seine, 1949. *Abbreviations:* ang-art, angulo-articular; ant, antorbital; br, branchiostegal; cl, cleithrum; dent, dentary; deth, dermethmoid; dpt, dermopterotic; dsph, dermosphenotic; exsc, extrascapular; fr, frontal; io, infraorbital; iop, interopercular; mx, maxilla; na, nasal; op, opercular; pa, parietal; pop, preopercular; ros, rostral; sbo, suborbital; scap, supracapular; smx, supramaxillary; so supraorbital; sop, subopercular; sur, surangular.

the usual three infraorbital bones in addition to the antorbital, while *C. drieri* has only two. In any case, if the anterior element in the infraorbital series is regarded as the antorbital, it extends from an anterior contact with the premaxilla to the orbital border. Such is the condition in the presumably ancestral parasemionotids (Lehman, 1952), and it

may reasonably be regarded as the primitive one. *Caturus*, then, seems to be primitive in having a short preorbital region and an antorbital which forms part of the orbital border. It is advanced in the separation of the nasals and the consequent exposure of the dermethmoid.

With the elongation of the preorbital region, as in *Eugnathus* and *Heterolepidotus*, the antorbital is generally believed to have been lengthened, as were the infraorbitals. Dr. E. I. White and Mr. Brian Gardiner have kindly examined the specimen of *Heterolepidotus* figured by Brough (1939, fig. 36B), and they are of the opinion that the antorbital reaches the orbit. The available skull of *Heterolepidotus*

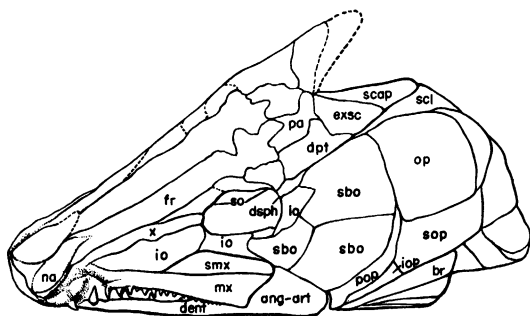


FIG. 8. Skull of *Eugnathus orthostomus* (after Woodward). Abbreviations: ang-art, angulo-articular; br, branchiostegal; dent, dentary; dpt, dermopterotic; dsph, dermosphenotic; exsc, extrascapular; fr, frontal; io, infraorbital; iop, interopercular; mx, maxilla; na, nasal; op, opercular; pa, parietal; pop, preopercular; sbo, suborbital; scap, suprascapular; scl, supracleithrum; smx, supramaxillary; so, supraorbital; sop, subopercular; x, unidentified element, possibly part of antorbital or exposed portion of autopalatine.

(fig. 9) and that of *Macrepistius* suggest, however, that the antorbital may be the same length as the nasal. If this can be verified in other specimens, the bar-like bone behind the antorbital remains to be identified.

Brough, in his figure of the British Museum specimen of *Heterolepidotus* mentioned above, identifies the bone extending from the snout to the orbital border between the frontal and the "lacrymal" as the ascending process of the premaxilla. This element is covered by the frontal and anterior infraorbital in his restoration of the skull (1939, fig. 42). Actually the ascending process of the premaxilla has been described in only a few caturids. There is evidence in *Caturus* (Woodward, 1895; Saint-Seine, 1949) that it was short and narrow rather than elongated. The premaxillae in the dissociated skull of

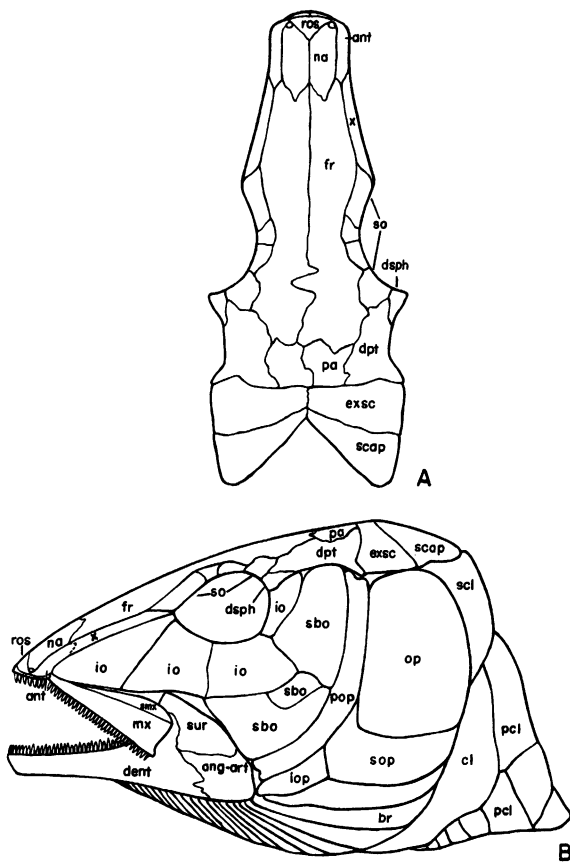


FIG. 9. Skull of *Heterolepidotus latus*, A.M.N.H. No. 4691. A. Dorsal view. B. Lateral view. *Abbreviations:* ang-art, angulo-articular; ant, antorbital; br, branchiostegal; cl, cleithrum; dent, dentary; dpt, dermopterotic; dsph, dermosphenotic; exsc, extrascapular; fr, frontal; io, infraorbital; iop, interopercular; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcl, postcleithrum; pop, preopercular; ros, rostral; sbo, suborbital; scap, suprascapular; scl, supraclathrum; smx, supramaxillary; so, supraorbital; sop, subopercular; sur, surangular; x, unidentified element, possibly part of antorbital or exposed portion of autopalatine.

Heterolepidotus typicus figured by Woodward (*op. cit.*, p. 309) have short, *Amia*-like, ascending processes, and he states (*op. cit.*, p. 313) that these processes are equal in length to the dentigerous portion of the bone.

It seems evident, therefore, that the elongated element cannot be the

ascending process of the premaxilla. Further study may demonstrate that it is simply part of an elongated antorbital. There is, however, another possibility regarding its identity, if the antorbital proves to be the same length as the nasal. In *Lepisosteus*, part of the palatopterygoid is normally exposed in the snout region between the frontal and the anteriorly extended infraorbital series. This articulation between the palate and these roofing bones probably represents a means of providing for increased rigidity in the elongated snout. The same condition, presumably involving the autopalatine, may exist in *Eugnathus* and *Heterolepidotus* and also in *Macrepistius* in which additional rigidity would be provided for the crushing dentition.

JAW MECHANISM: In most actinopterygians having a coronoid process, the mandible may be regarded as a combination of a bent lever and a straight lever. Although it is probably not possible to make a functional separation between these lever systems regardless of whether the subdivisions of the adductor mandibulae contract in unison or in sequence, a distinction is made for purposes of discussion. For both levers, the resistance arm is represented by the long axis of the mandible between the symphysis and the articulation. The effort arm of the bent lever is essentially the coronoid process. The effective length of this effort arm is the perpendicular distance (in relation to the horizontal axis) between the articulation or fulcrum and the point of muscle attachment. This length will differ for each part or subdivision of the adductor mandibulae inserting on the posterior border of the coronoid. The straight-lever analogy applies only to the mandibular ramus, with the effort applied by that portion of the adductor which inserts either in the fossa of the mandible or on its median surface.

In actinopterygians that grind or crush their food, the mandibular ramus (resistance arm) is usually reduced in length, and the coronoid area may be relatively enlarged and deepened. Many genera with short, powerful jaws also have a deepened or vertically extended palate accompanied by an increase in the mass of the adductor mandibulae. *Macrepistius* has the unusual combination of a mandible with typical catrid-amiid proportions and a crushing rather than a predaceous dentition. The vertical expansion of the palate and cheek was undoubtedly associated with an enlarged adductor mandibulae (roughly one-third greater than in *Heterolepidotus*) which inserted, as in *Amia*, both on the coronoid and on the inner side of the mandibular fossa. This larger and more powerful muscle provided functional compensation for the long mandibular ramus plus the crushing dentition. In contrast, the rather similar tritoral dentition of *Lepidotus* is

associated with a relatively short mandibular ramus and a skull that is not deepened as in *Macrepistius*.

The known caturids have styliform teeth which are quite unlike the crushing or grinding teeth of *Macrepistius*. The inclusion of this genus in the Caturidae rather than in a new family appears reasonable, however, on the basis of present evidence. Two other holostean families show a similar diversity in tooth form. *Acentrophorus*, *Semionotus*, *Dapedius*, and certain other genera in the Semionotidae have styliform teeth. In *Lepidotus*, as noted above, the marginal teeth are robustly styliform, but the inner teeth are tritoral. The anterior marginal teeth of *Sargodon* are incisiform, and the inner ones are apparently tritoral. In the Amiidae, *Kindleia* from the Edmonton (Jordan, 1927) and the Lance formations, and *Stylomyledon*¹ from the Paskapoo formation (Russell, 1928, 1929), have tritoral dentitions. *Kindleia*, however, has neither a reduced mandible nor a deepened palate. There is thus evidence that the same general sort of modification occurred independently in the dentitions of the Semionotidae, Eugnathidae, and Amiidae, with predaceous and presumably bottom-feeding forms representing divergent trends in the same family.

In the Holostei, a single, central ossification, with complete or nearly complete restriction of the notochord, evolved independently in three groups: the semionotoids, the amioids, and the pholidophoroids. Alternation in the caudal region, with separate precentra and postcentra, is apparently restricted to the amioids as they are now defined, except for two genera in the pholidopleurid subholosteans in which this subdivision occurs in a limited part of the caudal series. Alternation in the caudal region occurs in most of the caturids, but only as alternating crescents. *Eurycormus*, however, has complete precentral and postcentral cylinders, while *Neorhombolepis* has solid centra, with apparently no caudal alternation (Woodward, 1916). On the basis of the known plasticity in the ossification of the centrum within the Caturidae, it is reasonable to assume that the hourglass centra of *Macrepistius*, as well as the alternation in the caudal region, could have evolved from a caturid ancestor with either crescentic or cylindrical centra.

The recognition of *Stufenreihen*, as opposed to comparative anatomical sequences, has proved to be far more difficult in fishes than in the mammals or even in the lower tetrapods. The problem of the ancestry of *Macrepistius* represents a case in point. This genus is, at present,

¹ In a paper to be published shortly, R. D. Estes will demonstrate that *Stylomyledon* is indistinguishable from *Kindleia* and that the latter is close to *Amia* in the dermal bone pattern of the skull.

isolated in regard to the specialized features of its morphology. There seems to be no reasonable doubt that it was derived from a caturid resembling *Heterolepidotus*. It is conceivable, however, that the evolutionary line represented by *Macrepistius* split off from the typical caturids before there was a trend towards reduction in the relative size of the parietals but after some preorbital elongation had occurred. The snout may well have been lengthened and then "down-warped" as the teeth became more tumid.

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