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## Notes on the Structure and Relationships of Certain Cretaceous and Eocene Teleostean Fishes

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### ABSTRACT

Advanced characters of the lower jaw suggest that the Eocene †*Phareodus* is an osteoglossine, the Cretaceous †Ichthyodectiformes (†Ichthyodectidae and †Saurodontidae) are taeniopaedians, the Cretaceous †Pachyrhizodontidae are clupeomorphs or euteleosteans, the Cretaceous †Bananogmiidae are taeniopaedians, and the Cretaceous and Eocene †*Diplomystus* agree with Recent Clupeidae and Chirocentridae. It is suggested that †*Phareodus* (as †Phareodontini) be included in the Osteoglossinae, and that the †Ichthyodectiformes, †Pachyrhizodontidae, and †Bananogmiidae be classed as Teleostei, *taxa incertae sedis*. Advanced characters of the caudal skeleton of †*Pachyrhizodus* and †*Bananogmius* may prove useful in recognizing related forms.

### INTRODUCTION

Among Recent teleostean fishes, different patterns of bone fusion are apparent in the lower jaw. To some extent the patterns suggest relationships among and within the main groups of teleosts: Osteoglossomorpha, Taeniopaedia,<sup>2</sup> Clupeomorpha, and Euteleostei (Nelson, In Press). With

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<sup>2</sup> The Taeniopaedia are herein considered a cohort, subdivided into the superorders Elopomorpha (*Elops*, *Megalops*) and Anguillomorpha, with the Anguillomorpha subdivided into the orders Albuliformes (*Albula*, *Notacanthus*, etc.) and Anguilliformes (Nelson, In Press).

this comparative study of Recent material as a basis for interpretation, investigation was extended to fossils. The results so far obtained demonstrate that the same fusion patterns were present already in the Cretaceous.

### MATERIAL AND METHODS

The present study is based on fossil and Recent material in the collections of the Field Museum of Natural History (FMNH), the National Museum of Natural History, Smithsonian Institution, and the American Museum of Natural History (AMNH). I am grateful to Drs. R. Zangerl, S. H. Weitzman, and B. Schaeffer for access to these collections. The specimens illustrated, both fossil and Recent (with the exception of that shown in fig. 7), were treated with ammonium chloride. Conventionally, all specimens are shown as if from the left side; some illustrations, based on actual right-side material, are photographic reversals (right-to-left), as indicated by "(R)" after their catalogue numbers. The photographs are unretouched. Fossils were prepared with the help of Mr. Walter Sorensen, Department of Vertebrate Paleontology, the American Museum of Natural History. I am indebted also to Dr. S. P. Applegate, Los Angeles County Museum; Dr. D. Bardack, University of Illinois; Dr. P. Forey, University of Alberta; Dr. C. Patterson and Dr. P. H. Greenwood, British Museum (Natural History); Dr. A. S. Romer, Harvard University; and Dr. D. E. Rosen, the American Museum of Natural History, for furnishing helpful information, discussion, or for reading and commenting on an early draft of the manuscript. This study was supported in part by Grant GB 8589 from the National Science Foundation.

### ANATOMICAL ABBREVIATIONS

- A, angular bone
- AAR, anguloarticular bone
- AR, articular bone
- ART, anguloretroarticular bone
- BHP, basihyal plate
- BP1-3, basibranchial plate 1-3
- CO, coronomeckelian bone
- D, dentary bone
- F, posterior opening of mandibular sensory canal
- FA, articulation facet of angular bone, possibly (FA') of retroarticular bone
- FAAR, articulation facet of anguloretroarticular bone
- FAR, articulation facet(s) of articular bone, possibly (FAR') of angular bone
- FR, articulation facet of retroarticular bone, possibly (FR') of angular bone
- G, groove for mandibular sensory canal
- H, hypural bones
- M, maxillary bone
- P, postarticular process of angular bone

PA, parasphenoid bone  
 PU1, preural centrum 1  
 R, retroarticular bone  
 S, openings for mandibular sensory-canal tubes and pores  
 SM, supramaxillary  
 U1, ural centrum 1  
 U2, ural centrum 2  
 UR, uroneurals

## RESULTS AND DISCUSSION

### LOWER JAW STRUCTURE

Postarticular process of the angular. One prominent feature of the teleostean lower jaw, especially well developed in the Cretaceous forms discussed here, is the postarticular process of the angular bone—that part of the angular bone extending posterodorsally, lateral to the articular and retroarticular bones, and tending to shield from lateral view the articulation facet for the quadrate. The postarticular process has sometimes been called a “retroarticular process” (e.g., Goody, 1969, p. 7), a term that implies, misleadingly, an involvement of the retroarticular bone (cf. the “retroarticular process” of Haines, 1937, p. 8). The postarticular process seems to be known only in teleosts and may be a character primitive for that group (it is absent, however, in “pholidophorids” such as †*Ichthyokentema*: Griffith and Patterson, 1963). A postarticular process of varying size occurs in many Recent teleosts, and may have been retained as a character primitive for each major group (Osteoglossomorpha, Taenio-paedia, Clupeomorpha, Euteleostei); if so, there has been a repeated tendency to reduce it in part or completely. Among osteoglossomorphs, it seems somewhat reduced in †*Phareodus* (fig. 2A) and *Scleropages* (fig. 2B); it is about as well developed in *Heterotis* [fig. 4A] and *Arapaima* [Nelson, In Press, fig. 2C, D]), but it is absent in all others except *Hiodon* (fig. 4C; and †*Lycoptera*: Gaudant, 1968, fig. 8; Greenwood, 1970, fig. 1). Among taeniopaedians the process is developed in *Megalops* (fig. 3D) and *Elops* (Nelson, In Press, fig. 3J, K), but reduced or absent in all others, e.g., *Albula* (fig. 4B). Among clupeomorphs the process is recognizable in most forms, but it does not conceal the articulation facet for the quadrate (fig. 9A, B); in *Chirocentrus* the process is reduced (fig. 9C, D). Among euteleosteans the process is variably developed (e.g., Nelson, In Press).

Articulation facet for the quadrate. Among teleosts there is variation in the structure of the articulation facet for the quadrate. The facet may be on one (articular; e.g., †*Phareodus* [fig. 2A]) or two (articular and retroarticular; e.g., *Heterotis* [fig. 4A]) cartilage bones; on one cartilage bone (articular) and one dermal bone (angular; e.g., †*Ichthyodectiformes* [figs.

3A–C, 6A]); on one of two possible compound (dermal and cartilage) bones (anguloarticular and anguloarticuloretroarticular; e.g., Clupeidae and Chirocentridae [fig. 9] and e.g., Siluriformes [Nelson, In Press], respectively); or on one cartilage bone (articular) and one compound bone (anguloarticuloretroarticular; e.g., *Hiodon* [fig. 4C]). Because the articular and retroarticular are primitively separate bones in teleosts (Nelson, In Press), it is here assumed that the quadrate articulation primitive for teleosts involved these two cartilage bones, as exemplified by *Heterotis* (fig. 4A). Here, the articulation facet is in two parts, aligned one directly behind the other and separated by a transverse fissure, which in life is filled with cartilage. The surface of the articular (anterior) part of the facet is more or less vertically oriented, and the surface of the retroarticular (posterior) part is horizontally oriented. Together the two parts form a semicircular, concave articulation facet, or socket, of nearly uniform width.

In the major teleostean groups (Osteoglossomorpha, Taeniopaedia, Clupeomorpha, Euteleostei), the articulation facet has been variously modified from its primitive condition. Among osteoglossomorphs, *Hiodon* (fig. 4C) has apparently retained the primitive, two-part articulation facet, but fused the angular and retroarticular bones; †*Phareodus* (fig. 2A) and *Scleropages* (fig. 2B) seem to have lost the retroarticular part of the facet (the retroarticular and articular bones are still aligned one behind the other, separated by a transverse fissure). Among taeniopaedians, there are forms having the articulation facet in two parts: in *Megalops* (fig. 3D) and *Elops*, the posterior part, behind and lateral to the articular (anterior) part is similar in position to the angular part (see below) of the articulation facet of ichthyodectiforms (the posterior part in *Megalops* and *Elops* is separated from the articular part partly by a cartilage-filled transverse fissure and partly by the separation between the angular component and the articular bone); the posterior part of the facet of *Albula* (fig. 4B) also may represent the angular part of ichthyodectiforms, but the posterior part in *Albula* lies directly behind the articular (anterior) part, separated from it by a transverse fissure of a primitive aspect. All known clupeomorphs and euteleosteans have the articulation facet in only one part, primitively on the fused anguloarticular, although the retroarticular may also fuse secondarily.

The condition of the articulation facet of ichthyodectiforms (see below) adds a complicating factor (the angular part of the facet) to the interpretation of jaw structure in teleosts generally: do some of them have a similar angular part, perhaps secondarily modified through fusion of the angular bone with the articular or retroarticular bone? Only in osteoglossomorphs is this question easily answered (in the negative), because of

the unfused condition of the angular bone in *Heterotis* (fig. 4A) and *Arapaima* (no other Recent teleosts are known to have the angular bone unfused), which lack an angular part to the articulation facet. Because of the close similarity of the two-part articulation facets of *Heterotis* (fig. 4A) and *Hiodon* (fig. 4C), there is every reason to assume them homologous, and to reject the possibility that an angular part is represented in *Hiodon*. †*Phareodus* (fig. 2A), also, has an unfused angular bone without a part of the articulation facet. Because of the close similarity in the structure of the facets of †*Phareodus* (fig. 2A) and *Scleropages* (fig. 2B), there is every reason to assume them homologous, and to reject the possibility that an angular part is represented in *Scleropages*. The condition of other osteoglossomorphs is either similar to, or apparently has been derived from, either the *Hiodon* or *Scleropages* type (Nelson, In Press). In the taenio-paedians *Megalops* (fig. 3D) and *Elops*, however, part of the articulation facet lies laterally on what appears to be the angular component of a compound anguloretroarticular bone (the angular component seems recognizable partly because it stains less intensely with alizarin, and partly because of its position relative to the sensory-canal opening). Among clupeomorphs and euteleosteans, it is possible that much or all of the articulation facet lies on the angular component of a compound angulo-articular (Haines, 1937, and Lekander, 1949, pp. 82–83, argued that there is no true articular bone in these groups, and that the angular bone invaded the cartilage; cf. van Wijhe, 1882, pp. 306–307, who argued in favor of fusion). One may, therefore, consider the possibility that the ichthyodectiform condition, with an unfused angular participating in the formation of the articulation facet, is primitive relative to the taenio-paedian condition (anguloretroarticular) on the one hand, and the clupeomorph-euteleostean condition (anguloarticular) on the other; and that the articulation facet of all three “derived” groups contains a secondarily modified angular part. The aspect of lower jaw structure inconsistent with this possibility is the position of the opening for the mandibular sensory canal (medial in ichthyodectiforms, bananogmiids, and elopomorph taenio-paedians, lateral or posterior in other actinopterygians, perhaps indicating a close relationship among those forms with it). Thus, there is yet no compelling reason to conclude that an angular part is present, primitively, except in the taenio-paedian lineage; even there it may be restricted to ichthyodectiforms.

Sensory-canal opening. So far as is known, *Megalops* (fig. 3D) and *Elops* are unique among Recent actinopterygians in having the posterior opening of the mandibular sensory canal on the medial side of a well-developed postarticular process of the angular bone (or angular component). Among

fossil forms, the sensory-canal opening has this position in at least one species of †*Anaethalion* (personal observ.), presumed on other evidence to be closely related to *Megalops* and *Elops* (Forey, In Press). The sensory-canal opening has this position also in ichthyodectiforms and bananogmiids (and, perhaps, even in pachyrhizodontids), suggesting the possibility that they are all interrelated. If so, other lower jaw evidence (fused angulo-retroarticular) indicates that the relationship is between ichthyodectiforms and a group including Recent taeniopaedians and bananogmiids. Accordingly, the lower jaw of other taeniopaedians (e.g., *Albula*) should show a similar medial position for the sensory-canal opening (and, perhaps, an angular part to the articulation facet). Study of the lower jaw of *Albula* (and other non-elopoid taeniopaedians) has thus far been inconclusive, because of secondary modifications obscuring the primitive jaw structure in them (in *Albula*, e.g., the postarticular process is reduced, and the sensory canal much enlarged; the opening of the sensory canal is, nevertheless, visible in medial view [fig. 4B], but so is it, presumably secondarily, also in *Chirocentrus* [fig. 9D], also with a reduced postarticular process).

#### OSTEOGLOSSIDAE

The lower jaw of †*Phareodus* (figs. 1, 2A; material from the North American Eocene) includes distinct dentary, angular, articular, retroarticular, and coronomeckelian bones. The posterior part of the jaw is very similar to that of the Recent Australian and east Asian *Scleropages* (fig. 2B). The only differences are (1) in †*Phareodus* the angular and articular are distinct bones, whereas in *Scleropages* they are fused, and (2) in †*Phareodus* the articular facet is single, not partly subdivided into lateral and medial condyles as in *Scleropages* (also *Osteoglossum* and *Pantodon*; personal observ.).

†*Phareodus* has been most recently investigated by Roellig (1967), who

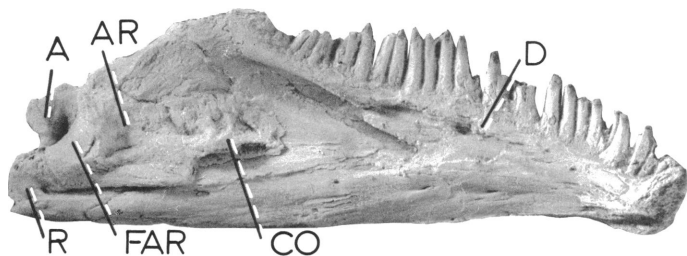


FIG. 1. †*Phareodus testis* (Cope, 1877 [a]), AMNH 2472(R). Left lower jaw, medial view,  $\times 1.3$ .

concluded that the Australian †*Phareodus* is ancestral to *Scleropages*, and that the North American †*Phareodus* represents, by way of secondary migration into North America, the ancestors of *Osteoglossum* of the Amazon Basin of South America. Roellig did not demonstrate any advanced characters to support that scheme of relationships. But there are some advanced characters (15 branched caudal rays, reticulate scales) that indicate that †*Phareodus* belongs to the group (Osteoglossoidea) including *Scleropages*, *Osteoglossum*, *Pantodon*, *Heterotis*, and *Arapaima* (Cavender, 1966a, p. 319; Greenwood et al., 1966; Greenwood and Patterson, 1967, p. 220; Nelson, 1969b, In Press). The lower jaw evidence tends to confirm this concept, and permits a more precise statement, because there is one advanced character (articulation facet confined to the articular bone) that indicates that †*Phareodus* belongs to the group (Osteoglossinae) including *Scleropages*, *Osteoglossum*, and *Pantodon*. The lower jaw of †*Phareodus*, with the angular and articular bones unfused and the articulation facet not in a two-condyle configuration, is more primitive than that of the Recent genera of the Osteoglossinae. †*Phareodus* may, therefore, be placed in its own tribe (†Phareodontini Jordan, 1925, [p. 232], and the Recent genera in two tribes of their own, Osteoglossini (including *Scleropages* and *Osteoglossum*) and Pantodontini (including *Pantodon*). There admittedly is not much evidence presently available to justify a tribal division for the Recent genera of Osteoglossinae. But *Scleropages* and *Osteoglossum* share some characters that could be advanced (e.g., oral brooding: Lake and Midgley, 1970; Schaller and Dorn, 1971) and that might be used to justify such a division.

Based primarily on the interrelationships and distribution of the Recent osteoglossomorphs, Nelson (1969b) considered their historical biogeography and proposed that it involved certain Gondwanian origins and dispersals. Since then, Greenwood (1970) suggested that the east Asian †*Lycoptera* is an early representative of the *Hiodon* lineage (cf. Patterson, ms); Nelson (In Press) found additional evidence to support the suggestion of Greenwood and Thomson (1960) that *Pantodon* is an osteoglossine (most closely related to *Scleropages* and *Osteoglossum*); and the above consideration of †*Phareodus* indicates that it, too, is an osteoglossine (related more closely to the group including *Scleropages*, *Osteoglossum*, and *Pantodon* than to any other fishes). These new concepts of relationships are consistent with the proposed Gondwanian origin and dispersal of the main groups of Osteoglossomorpha (Nelson, 1969b, figs. 21–22). An assumed relationship between †*Lycoptera* and *Hiodon* would only again imply (Greenwood, 1970, p. 283) a secondary distribution of the *Hiodon* lineage in North America (the nearest related groups, the Notopteridae or,

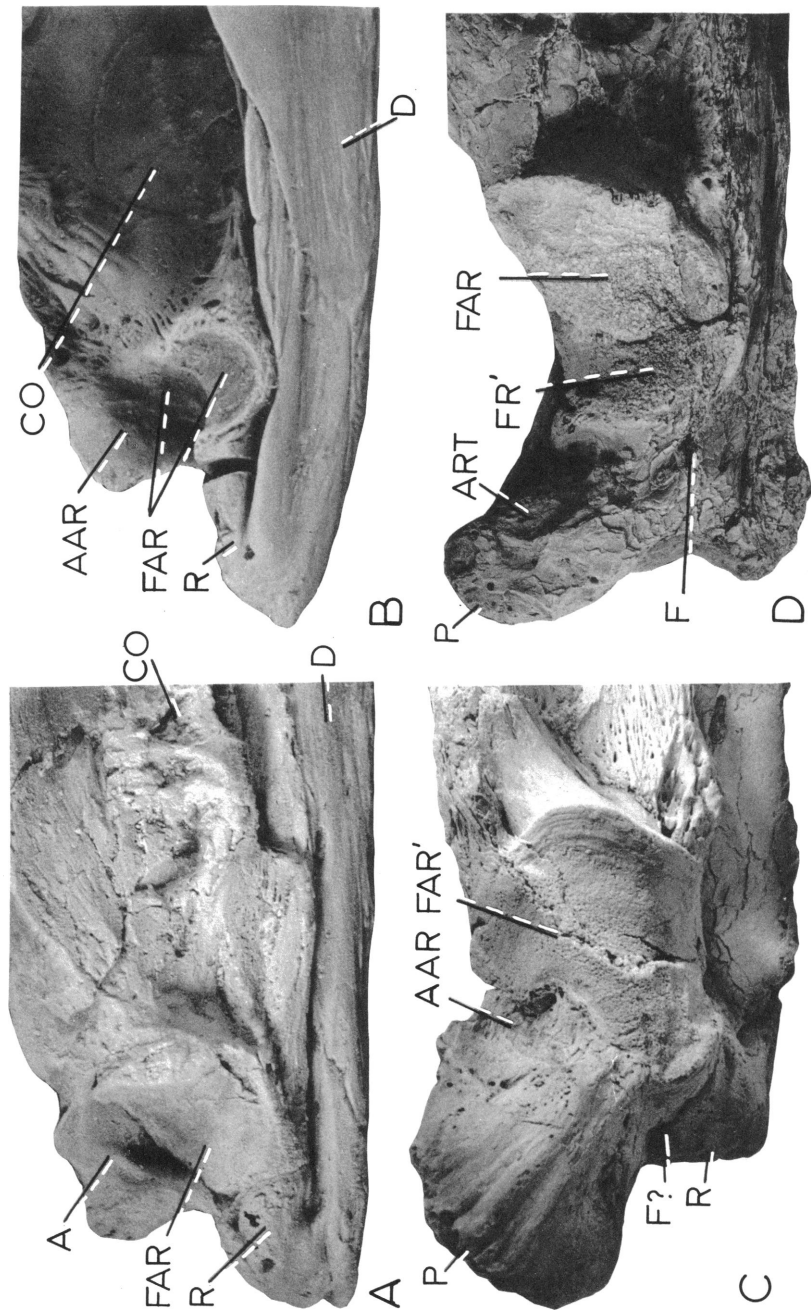


FIG. 2. Left lower jaw, dorsomedial view of posterior part. A. †*Phareodus testis*, AMNH 2472(R), X3.6. B. *Sclerobages leichardti* Günther, 1864, AMNH 29419(R), X3.6. C. †*Pachyrhizodus caninus* Cope, 1872, AMNH 1662(R), X1.6. D. †*Bananogminius evolutus* (Cope, 1877 [b]), AMNH 2101, X1.7.



perhaps, the Mormyridae, being Afroasian in distribution). An assumed relationship between †*Phareodus* and recent osteoglossines would, likewise, imply a secondary distribution of †*Phareodus* in North America (the nearest related groups, possibly the Australian †*Phareodus*, or the Sumatran †*Musperia*, and the recent Heterotinae [South America-Africa], occurring elsewhere). An assumed relationship between *Pantodon*, on the one hand, and *Scleropages* and *Osteoglossum* (Osteoglossini), on the other, raises a question regarding the nature of their disjunction, and the "track" connecting their distributions; assuming that *Scleropages* and *Osteoglossum* (as Osteoglossini) are more closely related among themselves than to *Pantodon* (Pantodontini), one may ask if the osteoglossin-pantodontin relationship extends from Africa through South America to Australia or, alternatively, from Africa through Australia to South America. The nearest relatives are †*Phareodus* (presumably both North American and Australian forms, although the relationship of the Australian form is unclear), with an Australian-North American distribution; turning to them, one finds that Australia is implicated as an area that might have been occupied early by the osteoglossine lineage. One may hypothesize, therefore, an originally African-Australian distribution for the group (Osteoglossinae), which subsequently persisted in Africa (*Pantodon*) and Australia (*Scleropages*), with secondary (and independent) distributions in North America (†*Phareodus*) and South America (*Osteoglossum*). The remaining osteoglossomorphs (Heterotinae, Mormyridae, Notopteridae), however, point toward an earlier origin for the group as a whole (Osteoglossidae and, indeed, Osteoglossomorpha) in a Gondwanian Africa of Afroasia (Nelson, 1969b).

Patterson (ms) has recently considered the problem of the historical geography of the osteoglossomorphs. Assuming that the marine †*Brychaetus* is an osteoglossoid (an assumption reasonable on the evidence provided by Patterson), he concludes that "The addition of *Brychaetus* . . . alters the picture considerably, for it adds a new hypothesis for the place of origin of the osteoglossoids, suggesting . . . that they may have achieved their cosmopolitan distribution by means of seaways." †*Brychaetus*, of course, adds a marine element to the history of the Osteoglossomorpha. But †*Brychaetus* is not only the sole osteoglossoid, but the sole osteoglossomorph known to be marine (see also Bonde, 1966); hence the totality of evidence concerning the relationships and distribution of osteoglossomorphs, both fossil and Recent, indicates that †*Brychaetus* is secondarily marine. In order to justify any other conclusion, additional forms, related most closely to osteoglossomorphs other than †*Brychaetus*, would have to be discovered, and their significance for marine origins determined by a comparative procedure. The †Ichthyodectiformes and †Bananogmiidae, marine groups of

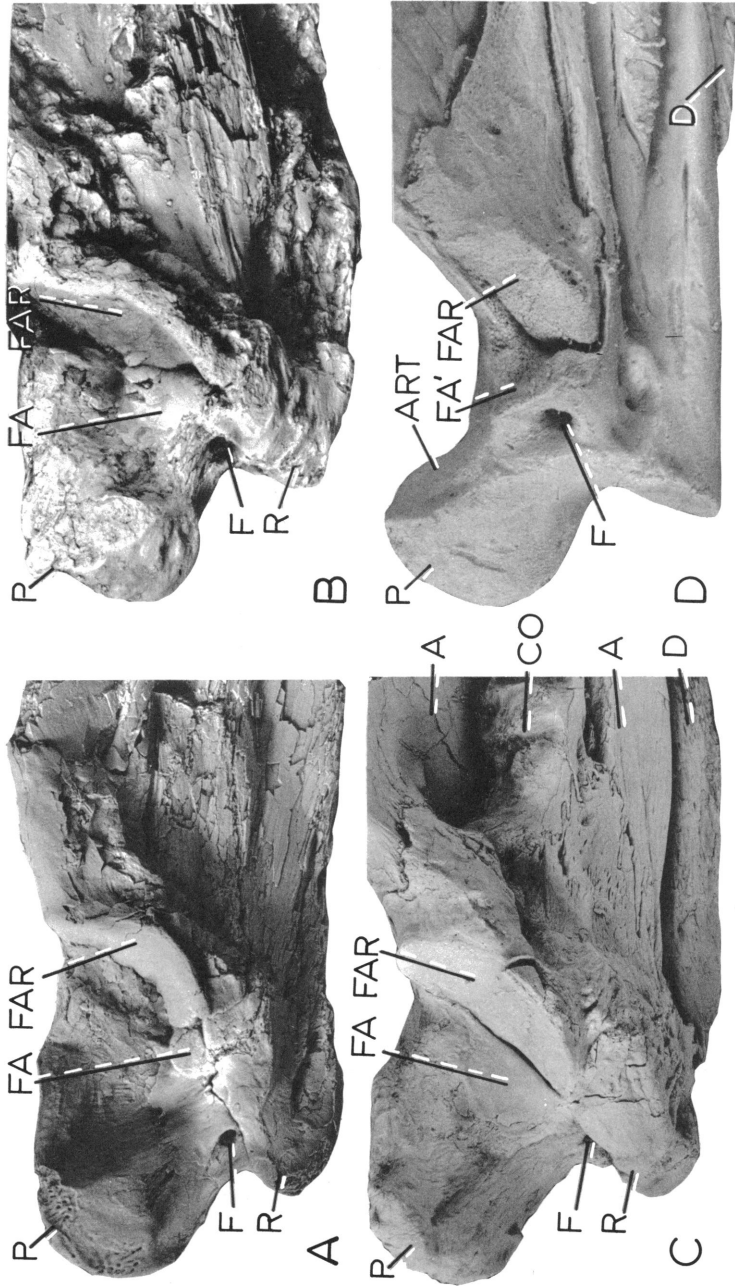


FIG. 3. Left lower jaw, dorsomedial view of posterior part. A. †*Saurodon leanus* Hays, 1830, AMNH 1614, X2.0. B. †*Ichthyodectes etenodon* Cope, 1871, AMNH 1939(R), X1.6. C. †*Xiphactinus audax* Leidy, 1870, AMNH 2373, X1.0. D. *Megalops atlantica* Valenciennes, 1846 (in Cuvier and Valenciennes), AMNH uncat., X3.4.

the Cretaceous, have been considered osteoglossomorphs (Greenwood et al., 1966; Patterson, 1967b; Andrews et al., 1967, p. 657), but the evidence in favor of such relationships seems inconclusive, for other interpretations are possible and, perhaps, equally justifiable (see below).

#### †ICHTHYODECTIFORMES

The lower jaws of †*Saurodon* (fig. 3A), †*Ichthyodectes* (fig. 3B; also Cope, 1875, pl. 45, fig. 1), †*Xiphactinus* (fig. 3C), and †*Gillicus* (fig. 6A; material from the North American Cretaceous) are similar in having distinct angular, articular, and retroarticular bones<sup>1</sup>; the opening for the mandibular sensory canal on the medial, rather than the lateral, surface of the angular; and the articulation facet for the quadrate on two bones, the angular and articular (also Cope, 1875, p. 194; Hay, 1898a, fig. 5; Stewart, 1898b, p. 184, pl. 16, fig. 1; 1899, p. 109; cf. Bardack, 1965b, p. 66). With respect to the unfused condition of the angular bone, †*Saurodon*, †*Ichthyodectes*, and †*Xiphactinus* (and †*Gillicus*?) resemble only *Heterotis* (fig. 4A) and *Arapaima* (Nelson, In Press, fig. 2C, D) among Recent teleosts<sup>2</sup>; with respect to the position of the sensory-canal opening, they resemble only *Megalops* (fig. 3D) and *Elops* (Nelson, In Press, fig. 3J, K) among Recent teleosts; with respect to the angular part of the articulation facet they are unique for no other fishes having the angular and articular bones unfused are known to have an angular part to the articulation facet. In *Megalops* and *Elops* in which the angular and retroarticular bones appear to be fused, the articulation facet is also on two bones; the anterior bone is the articular, and the posterior bone the fused anguloretroarticular. The part of the articulation facet on the anguloretroarticular may be homologous to the angular part of the facet in †*Saurodon*, †*Ichthyodectes*, †*Xiphactinus*, and †*Gillicus*.

<sup>1</sup> Hay (1898a, p. 37, fig. 5; see also 1898b, p. 231; Stovall, 1932, p. 89) stated that the angular ("dermartericular") and retroarticular ("true angular") are fused ("consolidated"), but Crook (1892, p. 116, pl. 15, fig. 1), Stewart (1898a, pls. 7-10; 1900, pl. 37), McClung (1908, p. 236, fig. 1) and Bardack (1965b, pp. 28, 46, 57, fig. 10) show them separate, as they are, clearly, in the present material of †*Ichthyodectes* and †*Xiphactinus* and, less distinctly, in †*Saurodon* and †*Gillicus* where some degree of fusion between angular and retroarticular bones may, indeed, occur (e.g., fig. 3A; also Stewart, 1898b; Loomis, 1900, pl. 24; cf. Bardack, 1965b, p. 66, fig. 20; Bardack and Sprinkle, 1969, fig. 6).

<sup>2</sup> Greenwood (1970, p. 273, figs. 1-2), partly on the basis of alizarin specimens, figured a distinct retroarticular ("angular") for *Hiodon* (and †*Lycoptera*; see also Guadant, 1968, p. 19, fig. 9, pl. 6, fig. 2). In *Hiodon* the retroarticular and angular components stain differentially with alizarin (the retroarticular darker), but they are, nevertheless, fused in the alizarin preparations examined (AMNH 21982 and 23754, *Hiodon tergisus* and *H. alosoides*, respectively).

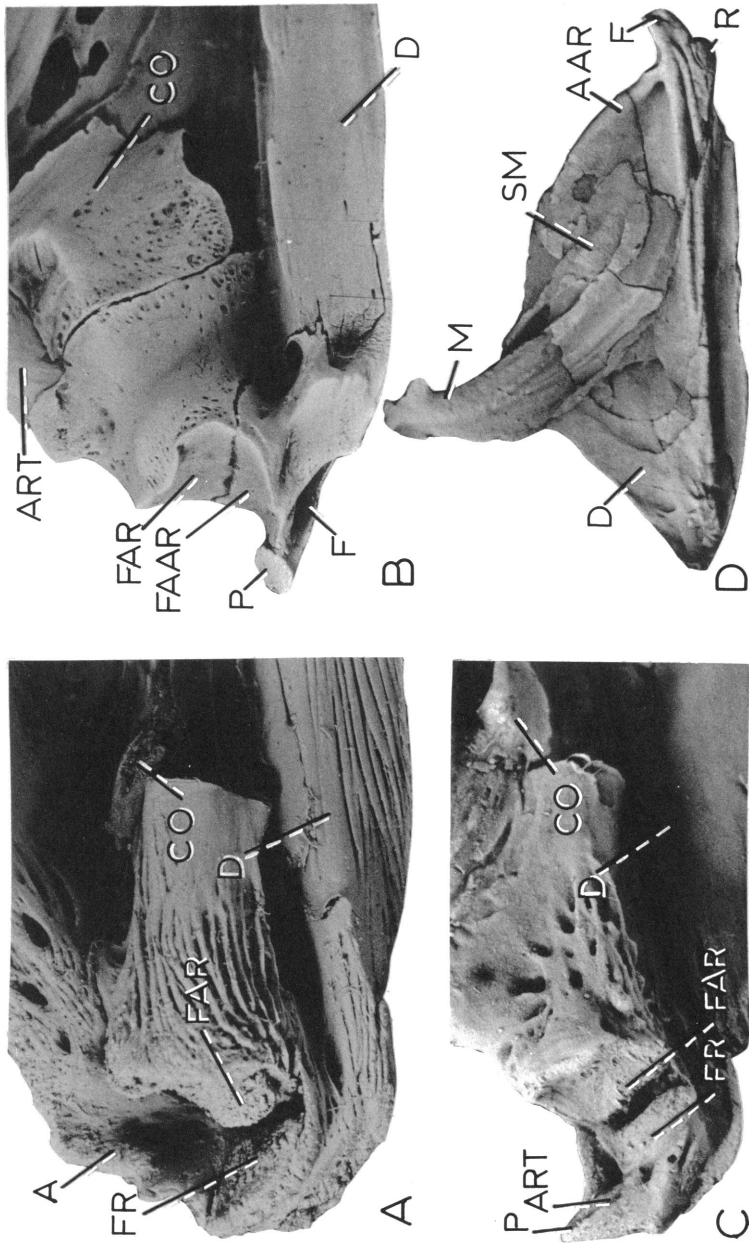


FIG. 4. A. *Heterotis niloticus* Hemprich and Erhenberg, 1828 (in Roellig, 1967, 1969; cf. Aubenton and Daget, 1967; Géry, 1968; Garrick, 1970), AMNH 9816, left lower jaw, dorsomedial view of posterior part,  $\times 6.5$ . B. *Albula vulpes* Linnaeus, 1758, AMNH 21516, left lower jaw, posteroventral view of posterior part,  $\times 4.3$ . C. *Hodon atosoides* (Rafinesque, 1819), AMNH 23755(R), left lower jaw, dorsomedial view of posterior part,  $\times 7.5$ . D. †*Diplomystus* sp., (Green River Shales), AMNH 4300, left lower and upper jaws, lateral view,  $\times 4.7$ .

The †Saurodontidae Cope, 1871,<sup>1</sup> have been most recently dealt with by Bardack and Sprinkle (1969) who, following Stewart (1899), recognized two genera, †*Saurocephalus* and †*Saurodon*. The advanced characters of the group as given by Stewart (1899, p. 110) are (1) "the presence of a pre-dental bone," (2) "the . . . form [lateral compression] of the teeth," and (3) "the . . . foramina or deep notches below the internal alveolar border in both jaws." Other characters, most of which are primitive for teleosts and some of uncertain status, are listed by Bardack and Sprinkle (1969, p. 299).

The †Ichthyodectidae Crook, 1892, have been most recently dealt with by Bardack (1965b), who recognized seven genera; †*Chirocentrites*, †*Cladocyclus*, †*Gillicus*, †*Ichthyodectes*, †*Prymnetes*, †*Spathodactylus*, and †*Xiphactinus* (also Bardack and Sprinkle, 1969, p. 332). Bardack (1965b, p. 17) proposed several "advanced" characters as a basis for this group: (1) "body generally above 1 m. in length" (2) "supraoccipital crest enlarged" (3) "intercalar enlarged" (4) "mouth cleft angled sharply upward from horizontal axis" (5) "premaxillary without ventroposterior process" (6) "dentition enlarged and of uniform or irregular size" (7) "coronoid process short, low, and dorsal profile of mandible dropping sharply toward quadrate-mandibular joint" (8) "longitudinal, lateral ridge of centra enlarged" (9) "anal fin of less than 20 rays" (10) "enlarged scales with radii and punctae." Some (1, 2, 4, 6, 10) of these characters were assumed to be advanced, because they differ from characters of †*Allothrissops*, †*Thrissops*, and †*Mesoclupea*—the presumed ancestors of ichthyodectids. Other characters (3, 5) were assumed to be advanced because they differ from the condition generally present in teleosts. One character (7) was assumed to be advanced because it differs from the character of pholidophorids and leptolepids—the presumed ancestors of teleosts. Still other characters (8, 9) were assumed to be advanced, without comment. The different criteria used to determine the advanced state of these characters make their evaluation difficult and their status seem uncertain. According to Bardack (1965b), †*Spathodactylus* is known to have characters (1), (6), (7), and (8); †*Prymnetes* character (9); †*Cladocyclus* characters (1), (6), and (7), according to Woodward (1901, pp. 107–108), (4) and (10), and, according to Santos (1950, p. 128), (2); and †*Chirocentrites* characters (4) and (6); the characters are said (Bardack, 1965b, pp. 20–21) to occur

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<sup>1</sup> The name Saurodontidae has been in general use (for a review see Stewart, 1899, pp. 109–110), but Bardack and Sprinkle (1969, p. 298) stated that "because the generic name *Saurocephalus* has priority, the family should be called Saurocephalidae" (cf. Stoll, 1961, p. 61, art. 64).

generally in †*Ichthyodectes*, †*Xiphactinus*, and †*Gillicus* (which, however, lacks characters 6 and 7).

Based on study of the genera †*Ichthyodectes*, †*Xiphactinus*, and †*Gillicus*, Cavender (1966b, p. 7) proposed that certain caudal skeleton characters might be advanced: "(1) the distinctive shape of hypural 1, with its rounded anterior process and spine-like posterior projection; (2) ural centrum 1 possesses on its ventral surface a deep facet for receiving the condylar process of hypural 1; (3) the long, well-developed urodermals [uroneurals] are arranged in parallel and form a compact structural unit; and (4) the massive haemal arch of preural 1." Some of the characters (at least 1, 3, and 4) seem to occur also in saurodontids (Bardack and Sprinkle, 1969, fig. 322). Thus, the basis for the family †*Ichthyodectidae* may be approximately the same as that for the order †*Ichthyodectiformes* (see below). In any case, the basis mainly rests on characters known to be shared by †*Ichthyodectes*, †*Xiphactinus*, and †*Gillicus*; few if any of these characters that could be considered advanced are known to occur in †*Spathodactylus*, †*Prymnetes*, †*Cladocycclus*, and †*Chirocentrites*, and it seems reasonable, therefore, to class them as Teleostei, genera *incertae sedis*, until such time as they are known to possess the advanced characters of some teleostean subdivision.

The relationships of ichthyodectids and saurodontids have been most recently dealt with by Bardack (1965b; also Bardack and Sprinkle, 1969), who first placed both groups in, or associated them with, the Chirocentridae (also Applegate, 1967, 1970; cf. Cavender, 1966b; Greenwood et al., 1966; Patterson, 1967a), and then placed them in an order by themselves (†*Ichthyodectiformes*). As listed by Bardack and Sprinkle (1969, p. 332), the basis for the order †*Ichthyodectiformes* is "characters common to saurocephalids [saurodontids] and ichthyodectids": (1) "General shape of bones and positions of sutures" (2) "Large supraoccipital crest" (3) "Parietoepiotic ridge" (4) "Hyomandibular fossa extending posteriorly onto large intercalar" (5) "Post-temporal fossa" (6) "Subtemporal fossa" (7) "Lateral temporal fossa" (8) "General arrangement and size of foramina on postorbital wall" (9) "Canal for lateral head vein formed within exoccipital" (10) "Palatine enlarged anteriorly forming a malleolar process for articulation between maxillary and parathmoid" (11) "Shape, position and relative sizes of mandibular elements" (12) "Vertebrae with single mid-lateral longitudinal ridge between two longitudinal grooves" (13) "Form of caudal skeleton including two ural centra and five urodermals [uroneurals]" (14) "Pectoral fin with broad, blade-like first ray." Of these characters, some (1, 8, 11) seem too imprecisely defined to be recognizable, some (5, 6, 13) are probably primitive for teleosts, and the

remainder seem to be of generally uncertain status. However, some of Cavender's caudal skeleton characters (see 1, 3, 4 above) seem to occur also in saurodontids (Bardack and Sprinkle, 1969, fig. 322) and, if so, might be advanced characters of ichthyodectiforms. Another possibly advanced character is the angular part of the lower jaw articulation facet, known so far in †*Saurodon*, †*Ichthyodectes*, †*Xiphactinus*, and †*Gillicus*. There is, therefore, some basis for the order †Ichthyodectiformes Bardack and Sprinkle, 1969, but little if any for the family †Ichthyodectidae itself. The genera †*Ichthyodectes*, †*Xiphactinus*, and †*Gillicus* may, therefore, be classed as †Ichthyodectiformes, genera *incertae sedis*.

Greenwood et al. (1966) and Patterson (1967b) considered the possibility that ichthyodectiforms are osteoglossomorphs (also Romer, 1966, 1968; Andrews et al., 1967). But Roellig (1967) and Bardack and Sprinkle (1969) pointed out that most of the characters known to be shared by ichthyodectiforms and osteoglossomorphs, including those discussed by Greenwood et al. (1966), are primitive for teleosts. Of the lower jaw characters of ichthyodectiforms, there are two that may be advanced and shared: (1) the medial position of the sensory-canal opening, and (2) the angular part of the articulation facet for the quadrate. Both characters may be shared with taeniopaedians (but see above for a consideration of a possible angular part to the articulation facet of clupeomorphs and euteleosteans).

That the sensory-canal character is advanced is indicated by its distribution among Recent actinopterygians; in forms other than *Megalops* and *Elops* the canal, if present, opens by way of a foramen on the posterolateral surface, or the posterior margin, of the angular (or anguloarticular, or anguloretroarticular; Nelson, In Press). The medial position of the sensory-canal opening in ichthyodectiforms and elopoids may be used as a point of reference for interpreting adjacent structures. In ichthyodectiforms the angular part of the articulation facet for the quadrate lies anterodorsal to the opening, in the same relative position as the posterior part of the articulation facet in elopoids. If the opening in elopoids marks the approximate boundary of a fused angular component, as it does in ichthyodectiforms where the angular and retroarticular bones are unfused, then much or all the posterior part of the articulation facet is on an angular component in elopoids. If so, the angular part of the articulation facet of ichthyodectiforms may be homologous to the posterior part in elopoids. This interpretation of the lower jaw structure suggests a relationship between ichthyodectiforms and elopomorphs, but it is not recommended here that they, therefore, be classified together (in e.g., the Taeniopaedia of Greenwood et al., 1967). Relative to that of taeniopaedians the lower

jaw structure of ichthyodectiforms seems primitive (unfused angular bone, no complex angulodentary overlap [Nelson, In Press]); possibly it is primitive for a division of the teleosts more inclusive than the Taenio-paedia (see above). Because the relationship of ichthyodectiforms remains unclear, they may be classed *incertae sedis* in a teleostean order of their own, the †Ichthyodectiformes Bardack and Sprinkle, 1969.

#### †PACHYRHIZODONTIDAE

The lower jaw of †*Pachyrhizodus* (fig. 2C; also Hay, 1903, fig. 44; material from the North American Cretaceous) has the angular and articular bones fused, but the retroarticular is a distinct bone. The articulation facet for the quadrate is single and large, with a complex contour. No sensory-canal opening could be observed on several acid-prepared specimens (but it possibly is situated medially). With respect to the fused anguloarticular bone, †*Pachyrhizodus* resembles the following groups of teleosts: (1) Osteoglossomorpha (Notopteridae and Osteoglossinae, only), (2) Clupeomorpha, (3) Euteleostei. †*Pachyrhizodus* seems not to be a notopterid or osteoglossine, but it may be a clupeomorph or euteleostean, or have its relationships elsewhere. Other than the lower jaw evidence (fused angular and articular bones), no advanced characters are presently known to suggest one relationship rather than another.

†*Pachyrhizodus* and its presumed relatives are usually classed with *Megalops* and *Elops* (Woodward, 1901; Berg, 1940; Applegate, 1970), but no pachyrhizodontids are known to share any advanced characters only with taenio-paediids. The lower jaw structure of †*Pachyrhizodus* is unlike that of all Recent taenio-paediids (in having the angular and retroarticular bones unfused, and the angular and articular bones fused). †*Pachyrhizodus* may, therefore, be classed *incertae sedis* as a teleostean genus, or if in a monotypic family of its own, the †Pachyrhizodontidae Cope, 1872.

According to Applegate (1970), the †Pachyrhizodontidae include the genera †*Pachyrhizodus*, †*Thrissopater*, †*Elopopsis*, and †*Rhacolepis* (fossil "Elopoidei" without a gular plate), but few if any advanced characters are known to indicate a relationship among these forms. Perhaps the only advanced character indicative of relationships in Applegate's diagnosis (p. 406) is "a large prominent scale bone above the operculum," which he briefly describes for †*Pachyrhizodus* but not for the other genera he attributes to that family (cf. Bartholomai, 1969, fig. 46). The basis for the collective group †Pachyrhizodontidae, therefore, is not established, and the genera †*Thrissopater*, †*Elopopsis*, and †*Rhacolepis* should be classed as Teleostei, genera *incertae sedis*. The caudal skeleton of †*Pachyrhizodus* may



be helpful in recognizing any related forms, for it is peculiar in having some of lower hypurals fused with one or more caudal centra (fig. 8).<sup>1</sup>

#### †BANANOGLIIDAE

The structure of the lower jaw in †*Bananogmius*<sup>2</sup> (figs., 2D, 5B [also Hay, 1903, fig. 37], 5C, D, 6B) and †*Moorevillia* (fig. 5A; also Applegate, 1970, fig. 197G; material from the North American Cretaceous), could be studied in four specimens. In all four there is evidence that the articular bone is distinct, and that the angular and retroarticular bones are fused. Three specimens (figs. 2D, 5A, B, 6B) show a division between the articular and angular bones; from the fourth specimen (fig. 5C, D) the articular bone is missing altogether, apparently having fallen away. Three specimens are relatively complete posteroventrally (figs. 2D, 5C, D, 6B), in the region of the retroarticular, and there is no indication in them of a separate retroarticular bone (cf. Bardack, 1965a, p. 4, fig. 2, who shows a distinct retroarticular in †*Enischnorhynchus*). Two specimens (figs. 2D, 5B, 6B) show the complete articulation facet, divided into two parts, anterior and posterior; another specimen (fig. 5A) is fractured through the midpart of the facet; the fourth specimen (fig. 5D) has only some of the posterior part of the facet. Two specimens (figs. 5D, 6B) have a large medial opening for the mandibular sensory canal; another specimen (fig. 2D) has an indication of it; the fourth specimen is incompletely preserved in that region. As here interpreted, the lower jaw of †*Bananogmius* (and, perhaps, †*Moorevillia* as well) has the angular and retroarticular bones fused, a two-part articulation facet (anterior and posterior), and a medial sensory-canal opening. With respect to the fused angular and retroarticular bones, †*Bananogmius* resembles the following groups of teleosts: (1) Osteoglossomorpha (Hiodontidae and Gymnarchinae only), (2) Taeniopaedia (Elopiformes and some Albuliformes only). With respect to the medial sensory-canal opening, †*Bananogmius* resembles only Elopiformes. †*Bananogmius* seems not to be a hiodontid or gymnarchine, but it may be a taeniopaedian.

<sup>1</sup> This specimen, figured previously by Hay (1903, pl. 3, fig. 1), has since been "prepared" to reveal the hypural bones. Hay's photograph shows two uroneurals, which have been removed from the specimen (only the anterior uroneural can now be found). Hay did not state his reasons for identifying this specimen of an incomplete caudal fin as †*Pachyrhizodus caninus*, but he (p. 61) did have an opportunity to study a complete specimen, and his identification is provisionally accepted here.

<sup>2</sup> †*Bananogmius* Whitley, 1940 (May) has priority over †*Ananogmius* White and Moy-Thomas, 1940 (June). Whitley's (1940, p. 242) reference to "the *Nomenclator Zoologicus*" seems to satisfy "Opinion 138" (Hemming, 1942), concerning availability.

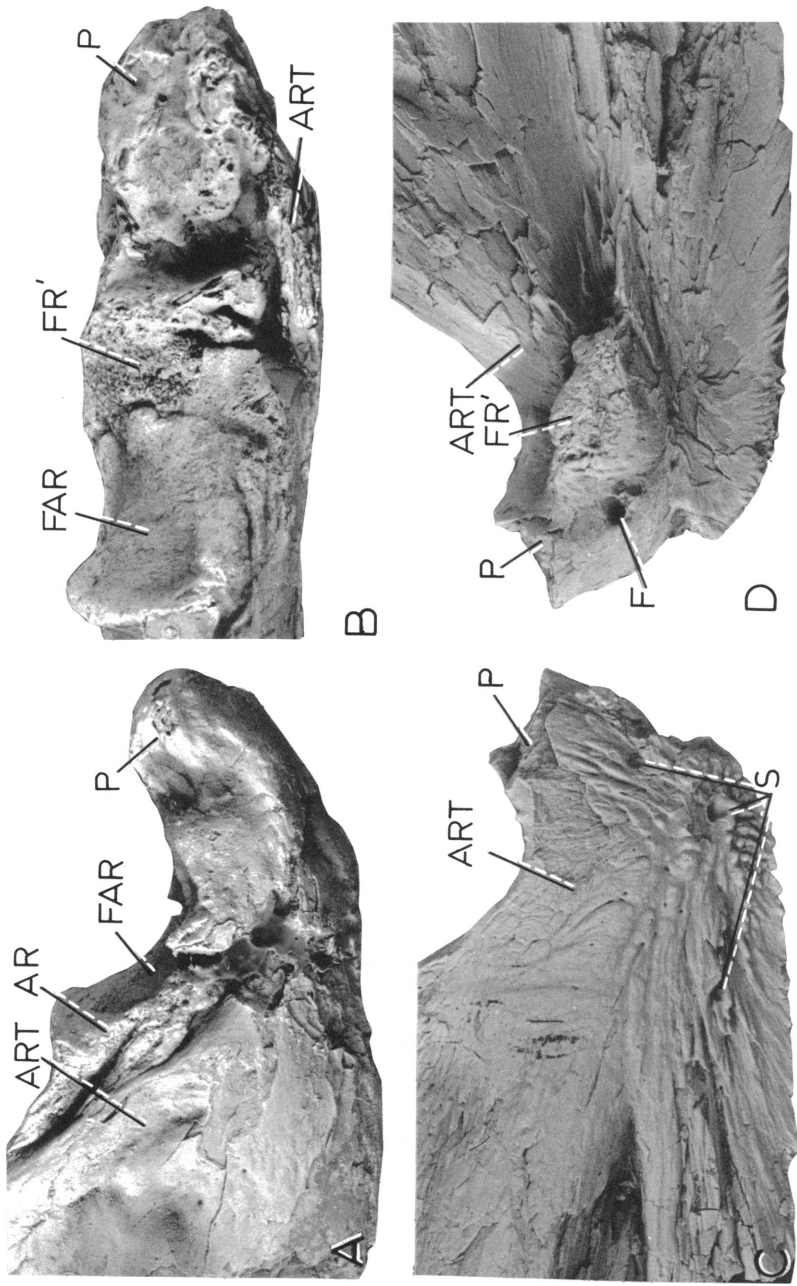


FIG. 5. Left lower jaw, posterior part, all  $\times 2.7$ . A. †*Moorevillia hardi* Applegate, 1970, FMNH PF 3567, lateral view. B. †*Bananogmus evolutus*, AMNH 2101, dorsal view. C, D. †*Bananogmus* sp., AMNH 3074, lateral view (C), dorsomedial view (D).

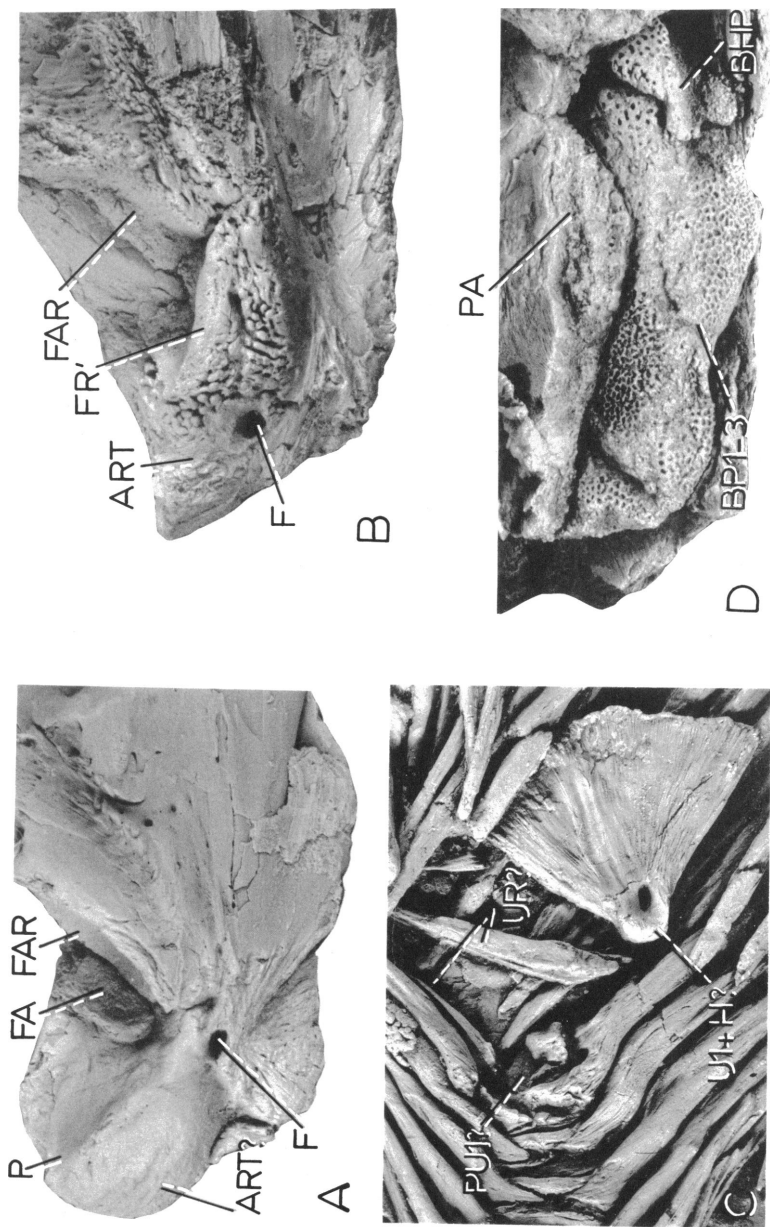


FIG. 6. A. †*Gillicus arcuatus* (Cope, 1875), AMNH 8563, left lower jaw, dorsomedial view of posterior part, X2.0. B. †*Bananogomius* sp., AMNH 3073(R), left lower jaw, dorsomedial view of posterior part, X3.0. C. †*Bananogomius* sp., AMNH 3072, caudal skeleton, lateral view of left side, X1.0. D. †*Bananogomius favirostris* (Cope, 1877 [b]), AMNH 2109, part of head, dorsolateral view of right side, X2.0.

The relationships of the †Bananogmiidae (and the possibly related †Plethodidae, †Protobramidae, and †Tselfatiidae) have been most recently discussed by Patterson (1967b), who considered them osteoglossomorphs (“*incertae ordinis*”) on the basis of the following characters (see also Woodward, 1901; Berg, 1940): (1) no lower intermuscular bones, (2) fused premaxillaries (among plethodids, only in †*Plethodus* and, possibly, †*Martinichthys*; among osteoglossomorphs, only in mormyrids and *Pantodon* [Greenwood et. al., 1966, p. 361]), (3) no uroneurals (“urodermals” of Patterson, 1967b; among osteoglossomorphs there is at least one pair of uroneurals in all forms except notopterids [Nelson, 1969b]), (4) fusion between hypurals and the second ural centrum (among bananogmiids, or forms presumed to be related, known in †*Protobrama* and, according to Patterson, †*Bananogmius* (but see below); among osteoglossomorphs, in all except †*Lycoptera*, *Hiodon*, †*Singida*, and †*Phareodus*). Of the above characters, (1) may be primitive for teleosts (Greenwood, 1970, p. 280). The others, probably advanced, may be shared by some, but not all members of each group (†Bananogmiidae and possibly related forms, on the one hand, and Osteoglossomorpha, on the other). For each such character (2–4), some members of each group seem to retain the primitive condition; if so, the shared advanced characters have developed in parallel, if not convergently (according to Monod, 1968, characters 3 and 4 occur in anguilliforms, and, according to Rosen and Patterson, 1969, also in some gadiforms). The resemblance in lower jaw structure (fused anguloretroarticular) between bananogmiids and some osteoglossomorphs, *Hiodon* (fig. 4C) and *Gymnarchus* (Nelson, In Press, fig. 3E, F), could be one additional parallelism; but, as indicated by the medial sensory-canal opening an assumed homology with the fused anguloretroarticular of taeniopaedians would not involve independent development of the fused condition in the †Bananogmiidae, on the one hand, and the †Taenio-paedia, on the other.

Thus, the proposed bananogmiid-osteoglossomorph relationship (Patterson, 1967b) is not supported by lower jaw structure, which suggests, in contrast, a bananogmiid-taeniopaedian relationship. †*Bananogmius* should, therefore, be somehow classed *incertae sedis* among the Teleostei (see below).

Exactly what fossil forms should be classed with †*Bananogmius* is unclear, partly because the nature (primitive or advanced) of the characters shared by †*Bananogmius* and other forms has not been specified. For example, Applegate (1970, p. 413) grouped †*Bananogmius*, †*Paranogmius*, and †*Moorevillia* in a new family (†Bananogmiidae) with the following diagnosis: “No mucous canals are known on the frontals. The mandible is deepest at its center. The basibranchial bears only one crushing tooth

plate. The preoperculum is L-shaped, with the vertical limb narrow and the anterior limb expanded." The distribution of these characters within the Actinopterygii is not given, none of them are known to occur in †*Paranogmius* (Weiler, 1935), and at least one ("the basibranchial bears only one tooth plate") does not apply to †*Bananogmius*, in which there are two basibranchial tooth plates (fig. 6D; also Hay, 1903, figs. 21, 25; Nelson, 1969a, p. 495). The basis for the collective group †Bananogmiidae, therefore, is not established, and the genera †*Paranogmius* and †*Moorevillia* should be classed as Teleostei, genera *incertae sedis*.

†*Bananogmius* has long been thought to be related to †*Plethodus* (e.g., Hay, 1903, p. 28) because both forms have crushing tooth plates, that have sometimes (e.g., Patterson, 1967b, p. 233) been presumed to have a similar histology, although it has never been described. Other possibly advanced characters, listed by Patterson (1967b, p. 231) in his diagnosis (see also Bardack, 1965a, p. 7; Applegate, 1970, p. 413) of the family †Plethodidae include the following: "dorsal fin arises close to or above the head" and "upper and lower hypurals often fused into a symmetrical, fan shaped plate"; and in his diagnosis (p. 215) of the suborder †Tselfatioidei (to which Patterson attributes the †Plethodidae): "pectorals inserted very high on the flank, . . . most of the fin rays unsegmented . . . urodermals [uroneurals] absent or fused to upper hypurals [but see below]." It is difficult to decide if such characters justify classing †*Bananogmius* with †*Plethodus*, for the existence of most or all of these characters in †*Plethodus* is not determinable from published descriptions. The basis of the collective group †Plethodontoidea Loomis, 1900 (cf. Applegate, 1970, p. 413), therefore, is not established, and the families †Bananogmiidae Applegate, 1970 (monotypic) and †Plethodidae Loomis, 1900 (Anon., 1970) should, if recognized, be classed as Teleostei, families *incertae sedis*.

†*Bananogmius* has been thought to be related, also, to †*Protobrama* and †*Tselfatia*. Patterson (1964, p. 428) listed many characters shared by †*Protobrama* and †*Tselfatia*, but did not indicate which, if any, might be advanced and indicative of a relationship between them. In his later (1967b) diagnosis of the †Tselfatioidei (see above) he listed some characters known for both forms (the condition of the uroneurals of †*Tselfatia* has not been described [Patterson, 1967b, pp. 232–233]), that might be considered advanced, indicative of a relationship, and that could serve as a basis for a group including not only †*Protobrama* and †*Tselfatia* but also †*Bananogmius* and other forms as well ("pectorals inserted very high on flank" and "most of fin rays unsegmented"). But it is difficult to evaluate such characters in the absence of a published analysis of their distribution within the Actinopterygii. It is reasonable, therefore, to suggest

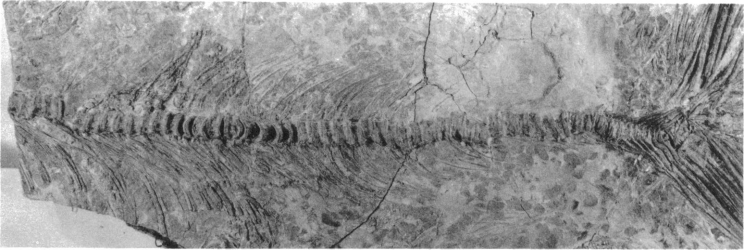


FIG. 7. †*Bananogmius* sp., AMNH 3072, part of axial skeleton showing pleural ribs, lateral view of left side,  $\times 0.2$ .

that a firm basis for the collective group †Tselfatioidei has not yet been established, and that the families †Protobramidae Le Danois and Le Danois, 1964 and †Tselfatiidae Bertin and Arambourg, 1958, if recognized at all (both are monotypic), should be classed as Teleostei, families *incertae sedis*.

The caudal skeleton of †*Bananogmius* (figs. 6C, 8B, C)<sup>1</sup> may be helpful in recognizing related forms, for it exhibits considerable hypural fusion, and a small centrum lacking a well-developed haemal arch, parhypural, or hypural. Of the primitive division between hypurals 1 and 2, there is some indication in the small hole anteriorly located in the hypural plate (the “*foramen hypurale*” of Monod, 1968, pp. 33, 143). Of the primitive division between lower and upper hypurals, there is some indication in the notch in the posterior border of the hypural plate, and the groove extending anteriorly from it. The illustrated material suggests that the lower hypurals (1, 2) and one (3) or more of the upper hypurals are fused. It is difficult to determine if the hypurals are fused with a centrum; but comparison with the caudal skeleton of †*Pachyrhizodus* (fig. 8A) suggests that fusion in †*Bananogmius*, also, may involve hypurals 1–3 and ural centrum 1. Anterior to and articulating with the hypural plate is a small centrum, apparently with a neural arch and spine, or perhaps one pair of uroneurals: in two specimens (figs. 6C, 8B) it seems to be associated with a process arising from the most posterior haemal arch, but this small process is lacking in the other specimen available (fig. 8C). This “haemal” process suggests, nevertheless, that the small centrum primitively was associated with a haemal arch, presumably the parhypural. If so, the

<sup>1</sup> Hay (1903, fig. 15, pl. 2; also Woodward, 1907, fig. 33; Patterson, 1967b, fig. 8) figured these specimens of tail and caudal skeleton (fig. 8B, C) upside down, as is evident by comparison of his figures with 8B, C, with reference to the orientation of 6C and 7.

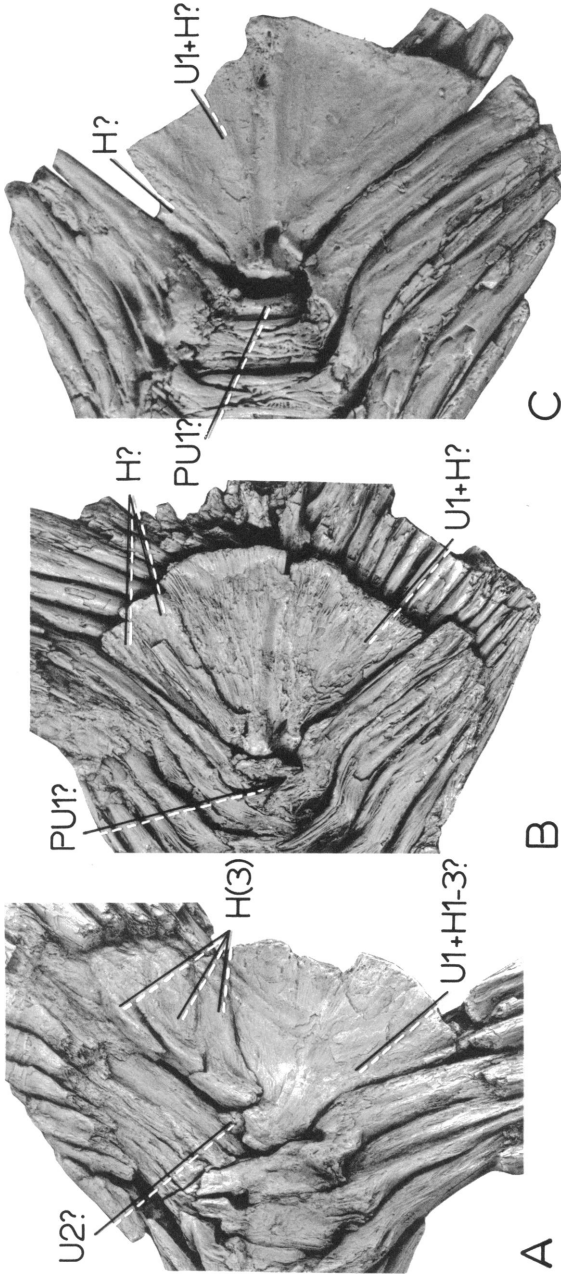


FIG. 8. Caudal skeleton, lateral view of left side. A. †*Pachyphizodus caninus*, AMNH 1900(R),  $\times 0.5$ . B. †*Bananognomius aratus* (Cope, 1877 [c]), AMNH 2403,  $\times 0.9$ . C. †*Bananognomius* sp., AMNH 1977,  $\times 1.9$ .

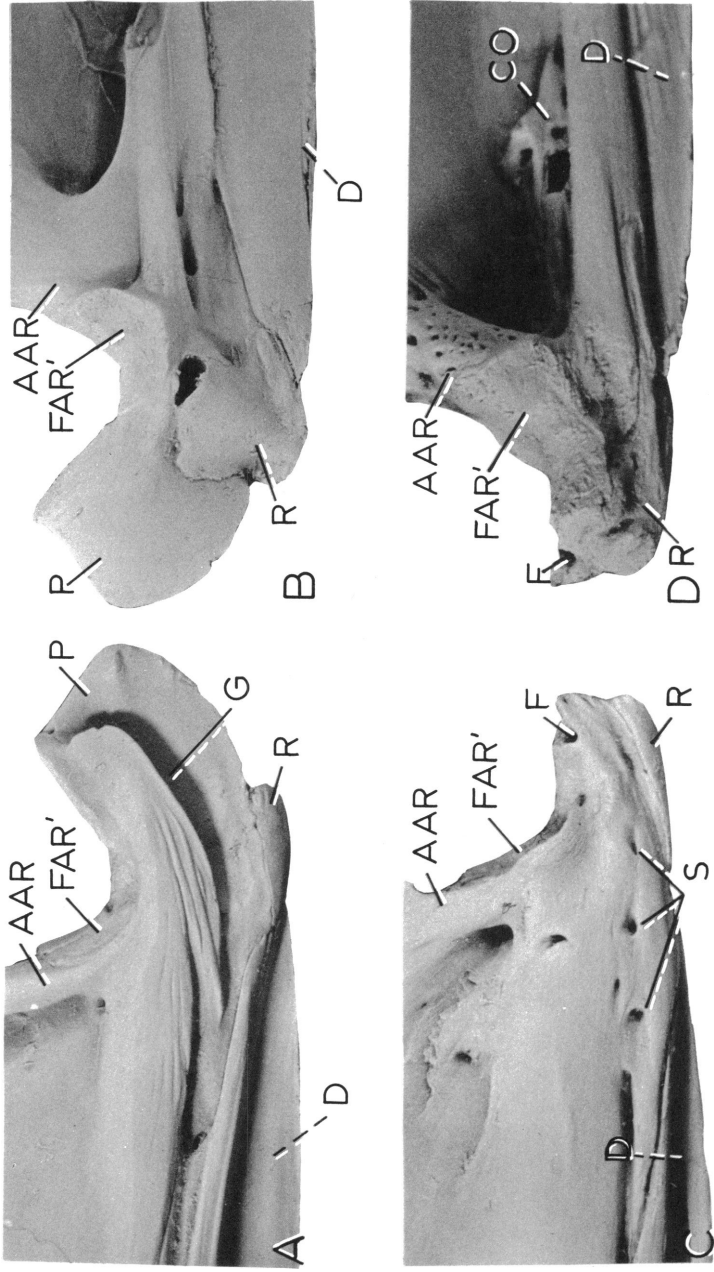


FIG. 9. Left lower jaw, posterior part. A, B. *Ilisha* sp., AMNH uncat. (R), X5.3, lateral view (A), medial view (B). C, D. *Chirocentrus* sp., AMNH uncat. (R), X6.4, lateral view (C), medial view (D).



parhypural was either reduced and lost, or became fused with the next anterior haemal arch and spine. An alternative interpretation is that the small centrum is ural centrum 1 (Patterson, 1967b, p. 233), but the evidence in support of that interpretation has not so far been published (but cf., e.g., *Albula* in Monod, 1968, fig. 96).<sup>1</sup>

#### CLUPEIDAE

The structure of the lower jaw of †*Diplomystus* (fig. 4D; material from the North American Eocene) could be made out only in lateral view. The articulation facet for the quadrate seems to be on a single bone, the anguloarticular. The retroarticular is a distinct bone. The sensory canal opens on the posterolateral surface of the anguloarticular. The overall structure seems duplicated in Cretaceous †*Diplomystus* (Patterson, 1967a), as it is, also, in recent clupeomorphs (Nelson, In Press). The problematical relationships of †*Diplomystus* and other "double-armored" fossil clupeomorphs have been most recently mentioned by Nelson (1970).

#### CLASSIFICATION OF FOSSIL GROUPS

In the above account various fossil forms and groups were considered and recommendations were made that they be ranked in classification as teleostean taxa *incertae sedis*. But why should such fossils be considered *incertae sedis* when they have seldom been so considered before (cf. Patterson, 1967b)? The reasons are: (1) each fossil form or group can be identified as teleostean fishes, as indicated by shared advanced characters<sup>2</sup>; (2) none of the fossils can be identified with reasonable certainty (as reasonable as their identification as teleosts) as members of any of the four cohorts currently defined (Osteoglossomorpha, Taeniopaedia, Clupeomorpha, Euteleostei), because they are not known to share with them patterns of advanced characters<sup>3</sup> (the fossils, therefore, cannot be placed in one or more of these four cohorts, but must be considered to form one or more

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<sup>1</sup> Further information recently sent me by Dr. Patterson shows that his interpretation is correct.

<sup>2</sup> For example, two hypurals on one ural centrum and elongate uroneurals (Patterson, 1967a, p. 98); median basihyal and basibranchial toothplates (Nelson, 1969a, p. 528).

<sup>3</sup> For example, 16 or fewer branched caudal rays, and other osteoglossomorph characters (as summarized by Greenwood et al., 1966; Nelson, 1969b, 1972a; Greenwood, In Press); prootic bullae with intracranial swimbladder diverticula, and other clupeomorph characters (Greenwood et al., 1966; Patterson, 1970; Nelson, In Press); leptocephalus larva, and other taeniopaedian characters (Greenwood et al., 1966; Forey, In Press; Nelson, In Press); and the presently elusive ("undefinable"?; Hubbs, 1966) advanced characters that might define the Euteleostei ("Division III" of Greenwood et al., 1966, p. 251).

taxa of their own); (3) the fossil forms and groups do not share among themselves consistent patterns of advanced characters suggesting that two or more of them are more closely related to each other than to other teleosts (they cannot, therefore, be grouped together in collective taxa of their own); (4) the exact relationships of each fossil form or group are unclear, and future work may reveal advanced characters shared by each fossil form or group and one of the four cohorts, so that each fossil form or group may ultimately be attributed to the Osteoglossomorpha, Taenio-*paedia*, Clupeomorpha, or Euteleostei, or to some still to be defined group of two or more of them (the fossil groups rest, therefore, *incertae sedis*). Some general characteristics of this type of classification have been considered elsewhere (Nelson, 1972b).

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