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A Revision of the Fossil Genus †*Diplomystus*, With Comments on the Interrelationships of Clupeomorph Fishes

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ABSTRACT

Several primitive fossil clupeomorphs are described, and a hypothesis of clupeomorph interrelationships is proposed. The genus †*Diplomystus* is revised and the type species for the genus, †*D. dentatus* Cope, 1877, is redescribed. †*Diplomystus dentatus* is closely related to †*D. birdi* Woodward, 1895, and †*D. dubertreti* Signeux, 1951, and all three species form the sister group to †*Ellimmichthys longicostatus* (Cope, 1886). Because the dorsal scutes of †*E. longicostatus* lack the pectinate posterior border diagnostic of †*Diplomystus*, Jordan's (1910 and 1919 [*in* Jordan and Gilbert, 1919]) removal of this species from †*Diplomystus* is considered valid. Both †*Diplomystus* and †*Ellimmichthys* are placed in †*Ellimmichthyidae*, new family (†*Diplomystidae* is preoccupied by a family of South American catfishes). The †*Ellimmichthyidae*, new family, is the sister group to the Clupeiformes. †*Armigatus*,

new genus, is proposed for †*Clupea brevissimus* Blainville, 1818. The relationship of †*Armigatus brevissimus*, new genus, to other clupeomorphs is not clear, and it forms an unresolved trichotomy with †*ellimmichthyids* and clupeiforms.

Many other species erroneously assigned to the genus †*Diplomystus* are removed to make the genus monophyletic and thus useful in systematic and comparative anatomical studies.

The comparative morphology of clupeomorph dorsal scutes is discussed. It is found that "double armor" in clupeiforms is not restricted to a small specialized group, but rather is a widespread character, occurring in clupeids, engraulids, †*ellimmichthyids*, and †*Armigatus*. Detailed morphological study of the dorsal scute in clupeomorphs shows a complex of several characters, some of which can be used to define monophyletic groups within the Clupeomorpha.

INTRODUCTION

The fossil herring-like fish †*Diplomystus* is one of the most widely cited fossil teleosts in the literature. It has been cited or used for

anatomical comparisons with other teleosts by at least 40 different authors and in more than 75 different papers. Yet, as currently

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defined this is a non-monophyletic group and therefore of questionable value in systematic studies.

The genus has largely been a repository for most any articulated clupeomorph fossil with dorsal scutes, since its description by Cope in 1877. Even Cope included a modern type of clupeoid (today called †*Knightia*) in the same genus with †*Diplomystus*. And since Cope about 15 additional taxa have been erroneously placed into the genus. This has caused serious problems in papers using †*Diplomystus* for anatomical and/or out-group comparisons.

The genus †*Diplomystus* was described by Cope (1877) as a clupeid genus including several fossil species from the Green River Formation. He divided the genus into two "sections." In section 1 he included †*D. dentatus* Cope, 1877, †*D. analis* Cope, 1877, and †*D. pectorosus* Cope, 1877; and he included †*D. "humilis"* (Leidy, 1856)² and †*D. altus* (Leidy, 1873) in section 2. He placed a sixth species from the Green River Formation, †*D. theta* (Cope, 1874), as "intermediate between . . . the two sections" (Cope, 1877, p. 811). Section 2 was removed from the genus †*Diplomystus* by Jordan (1907) and placed in a new genus †*Knightia* Jordan, 1907. The genus †*Knightia* is revised elsewhere (Grande, in press). All of Cope's †*Diplomystus* species from the Green River Formation except for †*D. theta* were found to be junior synonyms of †*D. dentatus* Cope, 1877, by Grande (1980). It is not possible to comment on the position of †*D. theta* because there is no known holotype for the species, and its description is insufficient.

More than 15 species have been assigned to the genus †*Diplomystus* in addition to Cope's species, but reasons for most of these assignments are erroneous or tenuous. All species known to the author were reviewed during this project.

² Because †*Clupea humilis* Leidy, 1856 was a homonym of †*C. humilis* von Meyer, 1848, Leidy's name is unavailable. Cope's (1870) †*Clupea pusilla* is unavailable for a replacement because that name is preoccupied by *C. pusilla* Mitchell, 1814. Therefore, the valid name for this taxon is †*Knightia eocaena* Jordan, 1907 (and not †*K. humilis* Leidy as given in Grande, 1980).

The morphology of most of the species (including the type, †*D. dentatus*) is poorly known. "†*Diplomystus*" *brevissimus* (Blainville, 1818) is the only species described in much detail, mainly by Patterson (1967); but no evidence has ever been presented that would indicate that "†*D.*" *brevissimus* and †*D. dentatus* are closely related. Patterson (1967) showed that although "†*D.*" *brevissimus* is a clupeomorph, it is not a clupeoid as had been previously thought.

Several authors (Woodward, 1892, p. 413; Schaeffer, 1947, p. 24; Greenwood, 1968, p. 265 and others) have proposed that "double-armored" clupeiforms (those clupeiforms with both dorsal and ventral scutes) constitute a monophyletic group. Nelson (1970b) challenged this concept by pointing out that *Clupanodon thrissa* (a gizzard shad) and *Ethmidium* (Chilean shad), which are both double-armored, are not closely related to other double-armored clupeids. Nelson (personal commun.) also drew my attention to the fact that many engraulids are also double-armored (although they are peculiar in having only one or two dorsal scutes). A pristigasterin (*Pristigaster cayana*) was also found to have dorsal scutes (see below).

The main objectives of the present work are: to provide a detailed description of †*Diplomystus dentatus* (the type species of the genus); to find derived characters uniting the type with other species, thus defining the genus more rigorously; and to examine the relationship of †*Diplomystus* to †*Knightia* and other groups within the Clupeomorpha. A comparative morphological study of the dorsal scutes in clupeomorphs is also included as an appendix.

ACKNOWLEDGMENTS

I thank Mr. Guido Dingerkus, Drs. Donn E. Rosen, Gareth Nelson, Colin Patterson, and C. Lavett Smith for reading and commenting on various drafts of this manuscript. Dr. Gareth Nelson also assisted in translating some type descriptions from French to English, and by sharing his discovery that many anchovies have dorsal scutes. Mr. Guido Dingerkus aided with some of the photographic work.

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MATERIALS AND METHODS

Fossils used here are deposited in the following institutions: Department of Vertebrate Paleontology, American Museum of Natural History, New York (AMNH); Department of Paleontology, Science Museum of Minnesota, St. Paul (SMMP); British Museum (Natural History), London (BMNH); Muséum national d'Histoire naturelle, Paris (MNHN); University of Michigan, Museum of Paleontology (UMMP); and Department of Paleontology, California Academy of Sciences (CAS). Recent material examined is in the Department of Ichthyology, of the American Museum of Natural History, and the Australian Museum, Sydney, New South Wales (AM). Some uncatalogued specimens from the Smithsonian Oceanographic Sorting Center, Washington, D.C. (SOSC) were also examined and accession numbers for these are given in the text.

†*Diplomystus*, like most clupeomorphs, has two vertebrae in advance of those bearing full length ribs. These are often not visible in fossils because they are normally covered by the superficial bones of the skull. Therefore the number of anterior vertebrae in all fossils was determined by counting the pairs of ribs and then adding two. Only preural centra are included in the vertebral counts. Standard length was measured from the anterior tip of the snout to the posterior end of the third hypural plate. Principal ray counts of the dorsal and anal fins (=“major fin rays” of Grande, 1980) include those rays which extend all the way to the outer fin margin. The term predorsal bones is used in the same sense as in Smith and Bailey (1961).

All other counts and measurements follow Grande (1980) and Hubbs and Lagler (1949).

Fossils were prepared using needles under a dissecting microscope. Dorsal scutes and skeletons of recent teleosts were cleared and stained following Taylor (1967). All original drawings were made using a Leitz camera lucida on a Bausch and Lomb stereomicroscope. All illustrated specimens of †*Diplomystus dentatus* are from locality F-1 of Grande (1980) except for the F-2 specimen in figure 1B. The names of all fossil taxa mentioned in the text are preceded by a dagger (†).

Drawings of dorsal scutes are of the dorsal surface unless otherwise stated. Explanation of morphological terminology used here for dorsal scutes is given in figure 38. In all drawings, the anterior margin faces left (drawings of some fossils have been reversed).

The taxonomic subdivisions (subfamilies) of clupeids and engraulids used in the Appendix follow Whitehead (1968).

ABBREVIATIONS USED IN FIGURES

- Aa, angulo-articular
- Bt p, basipterygoid process of parasphenoid
- C, circulus (or ridge)
- Ch, anterior ceratohyal (=ceratohyal of McAllister, 1968)
- De, dentary
- Dsp, dermosphenotic
- Eh, posterior ceratohyal (=epihyal of McAllister, 1968)
- Enpt t, endopterygoid teeth
- Ep, epural
- Fr, frontal
- HS, haemal spine
- Hy, hypural
- Io, infraorbital
- Iop, interopercle
- Mx, maxilla
- N, nucleus (or focus)
- NS, neural spine
- Op, opercle
- Pa, parietal
- PH, parhypural
- Pop, preopercle
- Pmx, premaxilla
- Ps, parasphenoid
- Ps t, parasphenoid teeth
- Pt, post-temporal

Pto, pterotic
 Pu, preural centrum
 R, retroarticular
 Smx, supramaxillary bone
 Sop, subopercle
 U, ural centrum
 Un, uroneural

TAXONOMIC PLACEMENT OF "†*DIPLOMYSTUS*" *BREVISSIMUS*

†*Clupea brevissimus* Blainville, 1818, was placed in †*Diplomystus* by Woodward in 1888 (see below). Since then this species has been studied in more detail (primarily by Patterson, 1967) than any other species in this genus. It is removed from †*Diplomystus* here for reasons discussed below, and placed into †*Armigatus*, new genus.

†*ARMIGATUS*, NEW GENUS

TYPE SPECIES: †*Clupea brevissimus* Blainville, 1818.

GENERIC DIAGNOSIS: Clupeomorph fishes that differ from all others in the following combination of characters. Unlike Clupeiformes, †*Armigatus* has (1) an osteoglossid-like tooth patch on the parasphenoid; (2) parietals which are in contact between the supraoccipital and frontals, and (3) a large foramen in the anterior ceratohyal. Unlike †ellimmichthyids and †*Ornategulum*, †*Armigatus* has a series of subtriangular dorsal scutes, which extends only two-thirds the distance from the anterior end of the dorsal fin to the posterior end of the dorsocranium.

ETYMOLOGY: *armigatus*, bearer of armor (from Latin); gender masculine.

DISCUSSION: Patterson (1967), after study of "†*Diplomystus*" *brevissimus* Blainville, 1818, determined that "†*Diplomystus*" was not a clupeoid. This observation was not based on the type species, but rather on a primitive clupeomorph which is probably only distantly related to †*Diplomystus*. It is removed from the genus here (see below) and placed in †*Armigatus*, new genus, because it does not form a monophyletic group with †*Diplomystus* (†*D. dentatus*, †*D. dubertreti*, and †*D. birdi*; see fig. 20).

RELATIONSHIP OF †*DIPLOMYSTUS* TO †*KNIGHTIA* AND OTHER CLUPEIFORMS

Much of the confusion that surrounds †*Diplomystus* stems from two misconceptions: (1) that †*Diplomystus* and †*Knightia* are closely related; and (2) that †*Diplomystus* is a clupeoid. One or both of these ideas have been implied or stated by Cope (1877, *et seq.*), Jordan (1907), Thorpe (1938), Schaeffer (1947), Cavender (1966), Greenwood (1968), Nelson (1970a), Taverne (1976), Uyeno (1979), Grande (1980), and others. It is found here that †*Diplomystus* is not a clupeoid (or even a clupeiform), although †*Knightia* is (see fig. 19 for explanation of taxonomic groups as used here).

†*Diplomystus dentatus* is examined here and has [unlike Clupeiformes; and like all †ellimmichthyids (see below), †*Armigatus brevissimus*, new combination (see above), and †*Ornategulum sardinioides* (Pictet) (see Forey, 1973)] (1) no recessus lateralis (fig. 7); (2) the parietals in contact between the supraoccipital and the frontals; (3) an *Osteoglossum*-like tooth patch on the parasphenoid and a basiptyergoid process (fig. 6) (although no parasphenoid tooth patch is known in †*Ornategulum*), and (4) a large foramen in the anterior ceratohyal (fig. 8A) (=the "Beryciform foramen" of McAllister, 1968, p. 6). †*Diplomystus*, unlike clupeoids, has no uroneural fused to the first preural centrum, and has the parhypural fused to the first preural centrum (see figs. 10, 12, and 17). These are all primitive clupeomorph characters. The recessus lateralis, separation of the parietals by the supraoccipital, reduction of size and number of endopterygoid teeth, loss of *Osteoglossum*-like parasphenoid tooth patch, and loss of the "beryciform foramen" are considered to be derived characters of the Clupeiformes (Patterson, 1967, and others). Fusion of the first uroneural to the first preural centrum and separation of the parhypural from the first preural centrum (fig. 19) are considered here to be derived characters of clupeoids. It is evident that †*Diplomystus* is not a clupeiform (as this group is used here—see fig. 20).

†*Knightia*, on the other hand, is a clupeoid. It was found (Taverne, 1975; Grande, in press) to have a recessus lateralis; parietals separated by the supraoccipital; no basipterygoid process or parasphenoid teeth; and no "beryciform foramen" (all clupeiform characters). Also unlike †*Diplomystus*, †*Knightia* has the following clupeoid characters: reduction in relative size of ural centrum 1, uroneural 1 fused with the preural centrum 1, and the parhypural is not fused to the preural centrum 1 (compare fig. 19 to figs. 10, 12, and 17), and no lateral line scales. †*Knightia* also has only one supramaxillary bone (†*Diplomystus* has two), and it has a lower number of branchiostegals and dorsal scutes (Grande, in press), and a different type of dorsal scute, than †*Diplomystus*. †*Knightia* is examined in detail elsewhere (Grande, in press).

Another point of confusion seems to be which species are in the †*Diplomystus* group, and which are in the †*Knightia* group. Forey (1973, pp. 1309, 1314), for example, compares †*Ornategulum* to "†*Diplomystus humilis*," which in fact is not †*Diplomystus* but rather the type species of †*Knightia*.³ Also, Nelson's (1973, pp. 12, 25) "†*Diplomystus*" sp. (AMNH 4300) is actually a specimen of †*Knightia eocaena*. Uyeno (1979) seemed to use the generic names †*Knightia* and †*Diplomystus* interchangeably, when he (p. 22) suggested *Hyperlophus* "[is] the closest relative of †*Diplomystus*" [probably meaning †*Knightia*] and described two new clupeomorph species as †*Diplomystus* spp. He gave information that would not warrant their placement in †*Diplomystus* but that might place them in †*Knightia*.

SYSTEMATICS AND PHYLOGENY OF THE †ELLIMMICHTHYIDAE, NEW FAMILY; REDESCRIPTION OF †*DIPLOMYSTUS DENTATUS* COPE

†ELLIMMICHTHYIDAE, NEW FAMILY

DIAGNOSIS: Clupeomorphs that differ from all others in having subrectangular dorsal

scutes, elongated laterally (figs. 9, 13, 18, and Appendix).

DISCUSSION: These are primitive clupeomorph fishes that lack a recessus lateralis and several other clupeiform characters (see fig. 20). The †*Ellimmichthyidae* contains †*Diplomystus dentatus* Cope, 1877, †*D. birdi* Woodward, 1895, †*D. dubertreti* Signeux, 1951, and †*Ellimmichthys longicostatus* (Cope, 1886). The family name "†*Diplomystidae*" (as used by Patterson, 1970, and Patterson and Rosen, 1977⁴) is preoccupied by a South American catfish family (type genus *Diplomystes*—first pointed out by Nelson, 1976, p. 75). Because †*Ellimmichthys*, Jordan, and †*Diplomystus* Cope (see below) are sister taxa (see fig. 20), we can use the genus †*Ellimmichthys* to form a family name (†*Ellimmichthyidae*) which includes both of the genera. By using †*Ellimmichthys* rather than †*Diplomystus* an unoccupied family name can be constructed.

Because the †*Ellimmichthyidae* is the sister group to the Clupeiformes, and because additional species have been found (work in progress) that may be closely related to †*ellimmichthyids*, it seems advisable to place this family in its own order, the †*Ellimmichthyiformes*, new order. The diagnosis for this order is the same as for the †*Ellimmichthyidae* (because it presently contains only that family) until further revision of the group is made.

Some morphological features of †*ellimmichthyids* include: usually seven predorsal bones with thin laminar expansions (see figs. 1 and 5); pelvic fins in advance of dorsal fin (except in †*D. dubertreti* where position of the pelvic fin is unknown); and ventral scutes numerous (about 24 to 34), running along ventral midline, from isthmus back to anus; two supramaxillary bones present; parhypural fused to vertebral column; and lateral line scales present. These characters (other than those in the diagnosis) are not unique

³ The valid name for this species is †*Knightia eocaena* Jordan, 1907 (see fn. 2).

⁴ Although Whitehead (1967, p. 87), Greenwood (1968, p. 265) and others have suggested that †*Diplomystus* be given familial rank, Patterson (1970, p. 179) was the first to use formally the name "†*Diplomystidae*" to include "†*Diplomystus*."

to the †*Ellimmichthyidae* and are discussed elsewhere in this paper. The extreme development of the laminar expansions of the predorsal bones in adult †*ellimmichthyids* and †*Armigatus* may be a shared derived character uniting the two taxa; but in my opinion, not enough is known about laminar expansions in clupeiforms (pellonulins and other groups) to warrant such grouping at this time. The problem is currently under study.

†*DIPLOMYSTUS* COPE, 1877

†*Copeichthys* Dollo, 1904, an objective junior synonym (Jordan, 1907, p. 137).

TYPE SPECIES: †*Diplomystus dentatus* Cope, 1877 (by original designation).

REVISED GENERIC DIAGNOSIS: †*Ellimmichthyids* that differ from all others in having dorsal scutes with a pectinate posterior border (figs. 9 and 13) along the dorsal midline from the posterior edge of the skull to insertion of the dorsal fin; and having a higher number of dorsal scutes (usually 22–36) than any other †*ellimmichthyid*. The supraoccipital crest is very well developed in †*Diplomystus* (see fig. 1, for example).

The diagnostic information above was also used by Cope (1877) in his original diagnosis for "section 1" of †*Diplomystus* [his "section 2" is what Jordan (1907) renamed as †*Knightia*]. Cope (1877, *et seq.*) placed †*Diplomystus* in the Clupeidae. It is concluded here that although †*Knightia* is a true clupeoid (Grande, in press), †*Diplomystus* is not even a clupeiform (see above and below).

ETYMOLOGY: (not given by Cope) *diplo*, double (from Greek); *mystus*, hidden? or possibly from the word *myst* meaning a mystic (from Greek); gender masculine.

†*Diplomystus dentatus* Cope, 1877

Figures 1–10

†*Diplomystus analis*, Cope, 1877, and †*D. pectorosus* Cope, 1877, and probably †*D. theta* (Cope, 1874); the first two, and probably the third are subjective junior synonyms (see Grande, 1980, pp. 90–91).

TYPE: AMNH 2477, illustrated in Cope, 1884, plate 10, figure 1.

REFERENCE SPECIMENS USED HERE: AMNH 2477 (the type), 763, 2480, 2883, 2979, 8109, 8168, 10465, 10466, 10469–10471, 10473–10476.

HORIZON AND LOCALITY FOR HOLOTYPE: The late Early Eocene Fossil Butte Member of the Green River Formation, near the town of Fossil, Wyoming (=locality F-1 of Grande, 1980). A freshwater limestone deposit.

KNOWN GEOGRAPHIC AND STRATIGRAPHIC RANGE: Known from Early to Middle Eocene Green River Formation sediments in Wyoming and possibly Utah. Most common at localities F-1 and F-2 of Grande, 1980.

REVISED DIAGNOSIS: A large species of †*Diplomystus* (reaching a total length of about 65 cm.) with more anal fin rays (usually 38 to 40), anal pterygiophores (usually 38–41), ribs (17–18) and vertebrae (41–43) than any other species of †*Diplomystus* (or any other †*ellimmichthyid*); more dorsal scutes (about 33 to 36) than any other known species of †*Diplomystus* (or any other clupeomorph); greater number of spines along posterior border of the dorsal scutes (in adults) than any other †*Diplomystus* species (see fig. 9); elongate fusiform in shape, less deep bodied than any other †*Diplomystus* species (compare fig. 1 with figs. 11 and 14), correlated with increased number of caudal vertebrae and associated elements.

ETYMOLOGY: *dentatus*, toothed (from Latin); gender masculine.

DESCRIPTION AND DISCUSSION

GENERAL FEATURES: A laterally compressed clupeomorph with a long anal fin and which has a known maximum total length of about 65 cm. The description below compares †*D. dentatus* to †*Ornategulum*, †*Armigatus*, new genus, other †*ellimmichthyids*, and clupeiforms. This species is the only known freshwater †*Diplomystus*.

ROOFING BONES AND FONTANELLES: Because of lateral compression and lack of dorsoventrally oriented specimens, little can be said about the skull roof. AMNH 10467

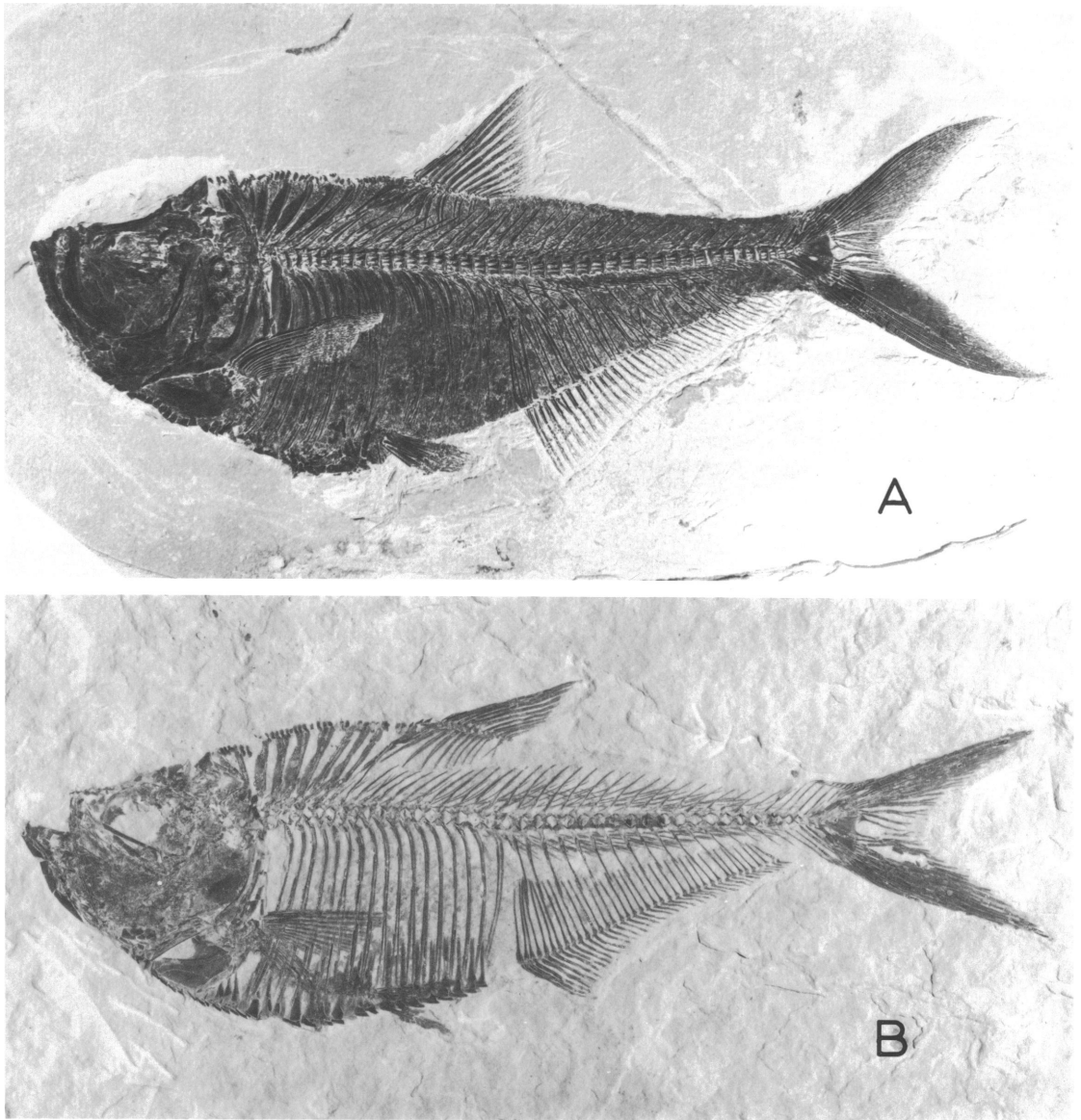


FIG. 1. †*Diplomystus dentatus* Cope, 1877. A, large specimen with fin margins preserved, total length 48 cm. (from Grande, 1980); B, specimen missing the scales and showing the post cranial skeleton (SMMP 78.9.14), total length 8.5 cm.; negative reversed. From the Eocene Green River Formation.

shows that the parietals are in advance of the supraoccipital, and appear to meet at the dorsal midline of the skull as in †*Ornategulum*, †*Armigatus*, and all †ellimmichthyids (and unlike clupeiforms which have the parietals completely separated by the supra-

occipital). The sensory canal branches on the parietal (visible on AMNH 10465). At least some of the canals of the skull roof appear to be contained in "crests" as described for †*Armigatus brevissimus* by Patterson (1967, p. 104). The supraoccipital crest (well pre-

served on AMNH 10467) is relatively large and well developed.

ORBITAL REGION: AMNH 763 (fig. 7) shows the dermosphenotic and the last three infraorbitals with the tube for the sensory canal preserved intact. The infraorbital canal was clearly branched in the dermosphenotic, and did not merge with the preopercular canal as it does in clupeiforms thus indicating the absence of a recessus lateralis. The sensory canal also branches in the lowermost preserved infraorbital bone (io 3?). A complete count of the infraorbital bones was not possible, but there were at least six infraorbitals, counting the dermosphenotic (Forey, 1973, counted six in †*Ornategulum*; Patterson, 1967, counted seven in †*Armigatus*).

PARASPHENOID AND ENDOPTERYGOID: †*Diplomystus dentatus*, like other †ellimmichthyids and †*Armigatus*, and unlike clupeiforms and †*Ornategulum*, has a patch of conical teeth on the posterior end of the parasphenoid (fig. 6) which looks very much like the parasphenoid tooth patch in *Osteoglossum*. †*Diplomystus dentatus* has strong endopterygoid teeth, much like those of *Osteoglossum*. †*Ornategulum*, †*Armigatus*,

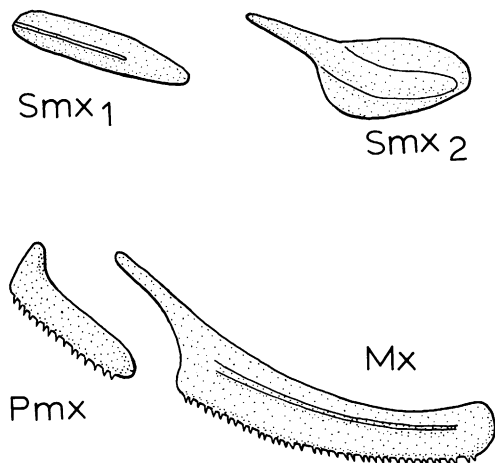


FIG. 2. †*Diplomystus dentatus* Cope, 1877. External dermal bones of the upper jaw. Mx, Smx₁ and Smx₂ all drawn from AMNH 8168 (s.l. 57 mm.). Pmx drawn from AMNH 10465 (s.l. 118 mm.) and drawn smaller to approximately match the Mx in proportionate size. Reversed.

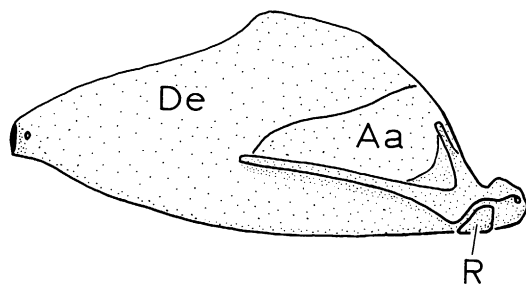


FIG. 3. †*Diplomystus dentatus* Cope, 1877. The lower jaw, medial view, drawn from AMNH 10468 (s.l. 147 mm.), teeth missing. Reversed.

and all †ellimmichthyids have strong endopterygoid teeth. Like †*Armigatus*, *Osteoglossum*, and various other teleosts and unlike clupeiforms, †*D. dentatus* has a basiptyergoid process (fig. 7 in Patterson, 1967, for †*Armigatus*, fig. 6, here, for †*D. dentatus*). The full size of this process could not be established, because it was broken in all specimens of †*Diplomystus* where this feature was visible.

JAWS: The dentary, maxilla, and premaxilla of †*Diplomystus* bear a single row of small, numerous conical teeth (usually not visible on very small specimens). There are two supramaxillary bones. Unlike †*Ornategulum*, but like most higher clupeomorphs, there is no sculpturing on the supramaxillary bones. The dentary, maxilla, premaxilla, and supramaxillary bones are illustrated in figures 2 and 3.

OPERCULAR SERIES AND HYPOBRANCHIAL APPARATUS: The opercular bones are smooth without noticeable sculpturing. The preopercular canal has four branches in the lower arm and about three in the upper arm (†*Armigatus brevissimus* has about 21 branches total, †*Ornategulum* has at least seven, and the condition is not well known in other clupeomorphs). The vertical arm of the preopercle is considerably longer than the lower arm. The bones of the opercular series are illustrated in figure 4.

Branchiostegal rays number about 12; curved and rodlike anteriorly, becoming more spatulate posteriorly. The anterior cer-

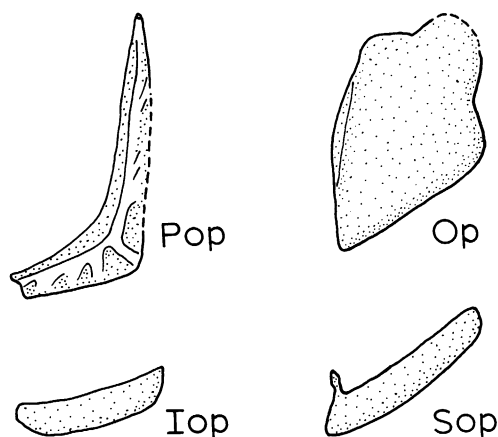


FIG. 4. †*Diplomystus dentatus* Cope, 1877. Bones of the opercular series, drawn from AMNH 8168 (s.l. 57 mm.). Drawing of OP reversed so that anterior for all bones to the left. Dashed lines indicate margin preserved by impression only.

atohyal has a large foramen just above the midsection of the center (=the "Beryciform foramen" of McAllister, 1968, p. 6, fig. 8A).

VERTEBRAL COLUMN, DORSAL, AND ANAL FINS: The specimens examined here had 41–43 vertebrae ($n = 6$), usually 41 or 42, excluding the two ural centra. The third vertebra through the twentieth or twenty-first bear ribs. The "antero-posterior laminar ex-

pansions [of the] anterior neural spines" that Cope (1884, p. 77) described are actually laminar expansions of the predorsal bones (figs. 5 and 1). This is apparent in young individuals that are not fully developed (e.g., AMNH 10470). Similar laminar expansions can also be found in †*Armigatus*, all †ellimichthyids and some clupeoids (e.g., *Potamalos*).

The dorsal fin has 11 or 12 principal rays, the first of which is unbranched, and is the longest ray. The principal dorsal rays are preceded by one or two accessory rays.⁵ The

⁵ For definition of "accessory rays" see Grande, 1980.

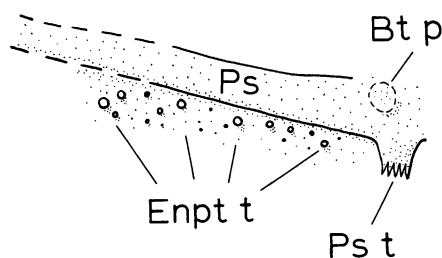


FIG. 6. †*Diplomystus dentatus* Cope, 1877. Endopterygoid teeth and part of parasphenoid showing the *Osteoglossum*-like tooth patch and part of the basitriangular process. Drawn from AMNH 10468 (s.l. 143 mm.). Reversed.

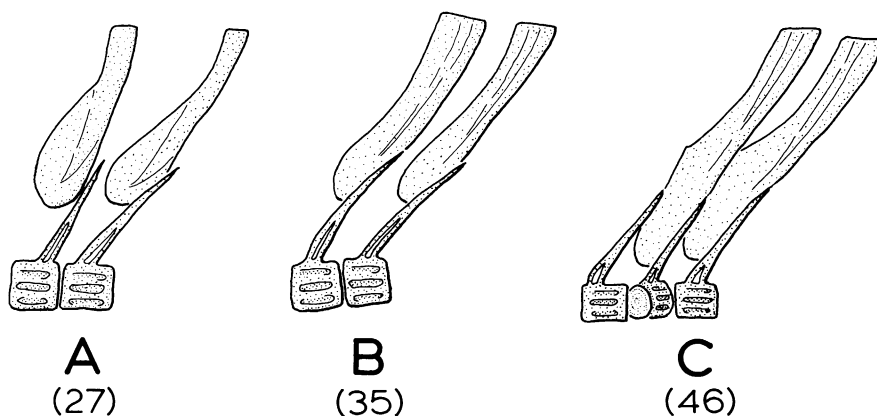


FIG. 5. †*Diplomystus dentatus* Cope, 1877. Growth series showing the development of predorsal bones 4 and 5. Number in parentheses refers to s.l. of each fish in millimeters. A through C were drawn from the following specimens: A, AMNH 10470; B, AMNH 10471; and C, AMNH 10469. C is reversed.

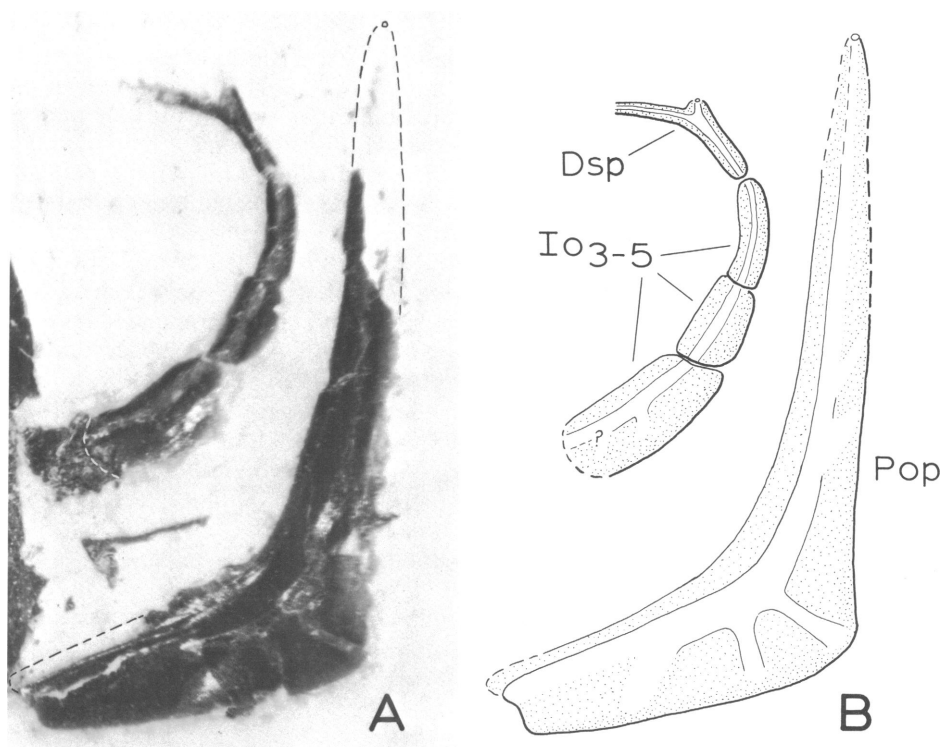


FIG. 7. †*Diplomystus dentatus* Cope, 1877. Preopercle and infraorbitals, with canal system preserved: A, AMNH 763 (s.l. 82 mm.); B, drawing of same specimen. The preopercular canal and the infraorbital canal clearly do not merge, indicating the absence of a recessus lateralis. Black dashed line indicates areas preserved by impression in matrix only. Reversed.

dorsal fin is supported by usually 11 or 12 pterygiophores. The dorsal fin margin is not curved.

The anal fin usually has 39 or 40 principal rays, but the possible range is somewhat larger (Grande, 1980, found 36 to 42 rays in specimens examined there). The first principal anal ray is unbranched, is the longest ray, and is preceded by one or two accessory rays, the first of which is usually unsegmented. The anal fin is supported usually by 39 or 40 pterygiophores, but the range can be from 35 to 42 (Grande, 1980). The anal fin margin is very slightly falcate anteriorly.

PREDORSAL BONES AND SCUTES: There are seven or eight (usually seven) predorsal bones with thin anteroposterior laminar expansions (explained above). These laminar expansions are best developed in adult specimens (figs. 5 and 1).

The predorsal scutes of †*Diplomystus dentatus* continued to develop throughout life (fig. 9). The subrectangular scute with the pectinate posterior border is thought to be a derived character of †*D. dentatus*, †*D. birdi*, and †*D. dubertreti*, because no other known animal has this type of dorsal scute⁶ (see Appendix). The dorsal scutes in †*Diplomys-*

⁶ The predorsal scales of *Brevoortia tyrannus* superficially resemble the dorsal scutes of †*Diplomystus*, but close examination reveals that the condition in *Brevoortia* is merely a series of pairs of medially overlapping scales (Monod, 1961; for example, fig. 6). Dorsal scutes, on the other hand, are unpaired, median elements which are more heavily ossified than the scales and which lie under the skin (usually themselves covered with scales). *Brevoortia* has no dorsal scutes. There is no evidence to indicate that dorsal scutes are derived from scales.

tus usually number between 33 and 36 and run from the posterior edge of the supraoccipital to the dorsal fin, along the dorsal midline.

The abdominal scutes are similar to those found in other †tellimichthyids, †*Armigatus*, and many clupeiforms. They run from the isthmus back to the anus, along the ventral midline (fig. 1). The most anterior abdominal scutes are small; they increase in size posteriorly to near the insertion of the pectoral fin after which they are all approximately the same size. They usually number 32 to 34.

PAIRED FINS: The pectoral fin usually has 14 or 15 rays, although some of the smaller rays are frequently missing (possibly due to lack of preservation) resulting in counts as low as 12 (Grande, 1980).

The pelvic fin inserts slightly anterior to the dorsal fin (fig. 1) and has usually seven (rarely six) rays, the first of which is unbranched. The pelvic fin supports (visible on AMNH 10469) are long and thin and contact each other posteriorly, but are free anteriorly.

CAUDAL SKELETON AND FIN: Cavender (1966) described the caudal skeleton of †*Diplomystus dentatus* (=his “†*Diplomystus* sp.”) in detail, and the specimens examined here agree with his description (fig. 10). There are six hypurals; the first articulates with, but is not fused to, the first ural centrum (as in †*Ornategulum*, †*Armigatus*, and all †tellimichthyids). In most clupeiforms, the first hypural does not articulate with the vertebral column (fig. 19). As in all clupeomorphs, the second hypural is fused to the first ural centrum. The parhypural is fused to the first preural centrum (as in all other †tellimichthyids, †*Ornategulum*, †*Armigatus*, and denticipitoids; and unlike clupeoids). The ural centra are relatively large and well developed as in †*Ornategulum*, †*Armigatus*, and all †tellimichthyids. There are three epurals. Of the three uroneurals, none is fused to the vertebral column. In clupeoids, the first uroneural fuses anteriorly with the first preural centrum. The caudal fin is sharply forked, and the lower lobe is slightly longer than the upper (fig. 1A). It contains 19

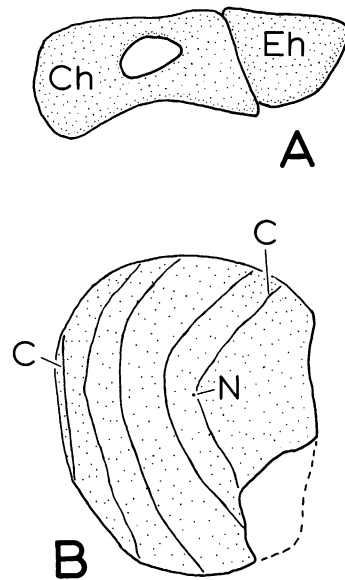


FIG. 8. †*Diplomystus dentatus* Cope, 1877. A) The branchiostegal support apparatus showing the “Beryciform foramen” of McAllister (see text for explanation). Drawn from AMNH 10468 (s.l. 147 mm.). Reversed. B) Isolated scale, drawn from holotype AMNH 2477 showing the curved, vertically arranged circuli. (Growth lines not shown here, but illustrated in Grande, 1980, fig. II.49b.) Many circuli between the five drawn are omitted. Reversed.

principal rays, one unbranched and nine branched in the upper lobe, and eight branched and one unbranched in the lower lobe.

SCALES: Scales small; circuli (surface) semicircular to almost vertical across the scale (see fig. 8B) as in most clupeiforms (not concentrically arranged around the nucleus as stated in Forey, 1973, p. 1314). The circuli are well preserved on the holotype (AMNH 2477) and the pattern appears to be the same in USNM 4005 (holotype of †*D. analis*—synonym of †*D. dentatus*). There are growth rings which are arranged concentrically around the nucleus (fig. II 49b in Grande, 1980). In all known clupeomorphs, the circuli (in the sense of Lagler, 1947, p. 150) are not coincident with the growth rings of the scale. Although growth rings (when visible) are arranged concentrically around the nucleus,

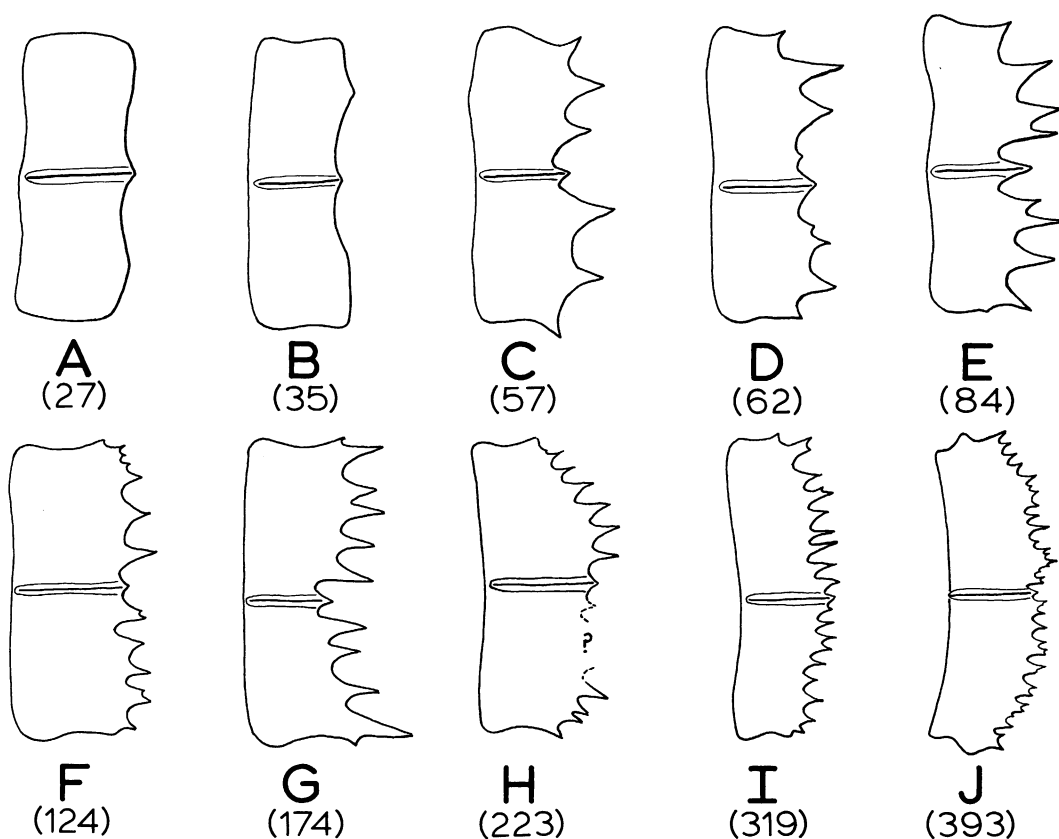


FIG. 9. †*Diplomystus dentatus* Cope, 1877. Ontogenetic series showing the development of the dorsal scute. Number in parentheses refers to s.l. of each fish in millimeters. Drawings A through J were made from the following specimens: A, AMNH 10470; B, AMNH 10471; C, AMNH 2883; D, AMNH 10473; E, AMNH 10474; F, AMNH 10475; G, AMNH 2979; H, AMNH 2480; I, AMNH 8109; and J, AMNH 10476. Scutes oriented so that anterior to the left (as are all illustrations in this paper).

the fine surface ridges (circuli) are either semicircular [as in †*Diplomystus* (fig. 8B), *Potamalosa* and many other clupeiforms] or nearly vertical (as in *Chirocentrus* and some other clupeoid species). Bardack's (1965, p. 51, fig. F or G?) drawing of a scale from *Chirocentrus dorab* does not show the pattern of circuli (the concentric lines drawn are possibly the growth lines).

There are approximately 82–90 scales along the lateral line, 18 scale rows above the vertebral column and 27 scale rows below. Lateral line scales are present (unlike clupeoids) and are well preserved on AMNH

10465. The lateral line runs all the way back to the caudal region. Radii or "grooves" absent.

†*Diplomystus birdi* Woodward, 1895
Figures 11–13

TYPE: BMNH P 96, illustrated in Woodward, 1895, plate I, figure 3.

REFERENCE SPECIMENS USED HERE: AMNH 5745, 5798, 6113, 10188, 10189, and 11106.

HORIZON AND LOCALITY FOR HOLOTYPE:

The Upper Cretaceous marine limestone deposits at Hakel, Mount Lebanon, Lebanon.

LOCALITIES FOR REFERENCE SPECIMENS: Reference specimens from Hajula, another Upper Cretaceous marine limestone deposit in Lebanon and Hakel.

REVISED DIAGNOSIS: A small, fairly deep-bodied fish that differs from all other †tellimichthyids in having about 17 principal dorsal fin rays (16–18); usually 16 dorsal pterygiophores (15–17); and about 30 preural vertebrae.

ETYMOLOGY: *birdi*—named for Rev. William Bird, a noted student of Syrian geology.

DESCRIPTION AND DISCUSSION: †*Diplomystus birdi* is the smallest known species of †*Diplomystus* (the largest specimen known to the author has a total length slightly more than 11 cm.). Like †*D. dentatus* and †*D. dubertreti*, the dorsal scutes are pectinate along the posterior border and the number of scute spines increases with the age of the fish (see fig. 13).

The body depth and shape are variable,

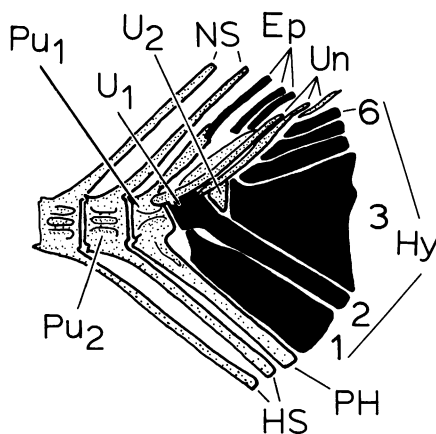


FIG. 10. †*Diplomystus dentatus* Cope, 1877. Caudal skeleton, after a drawing by Cavender (1966) of UMMP 52891 (s.l. 84 mm.). Hypurals, epurals and first ural centrum colored black.

because the limestone containing these fossils is often quite strained. Normally the body shape resembles that shown in figure 11 and in Woodward (1895, figs. 3 and 4).

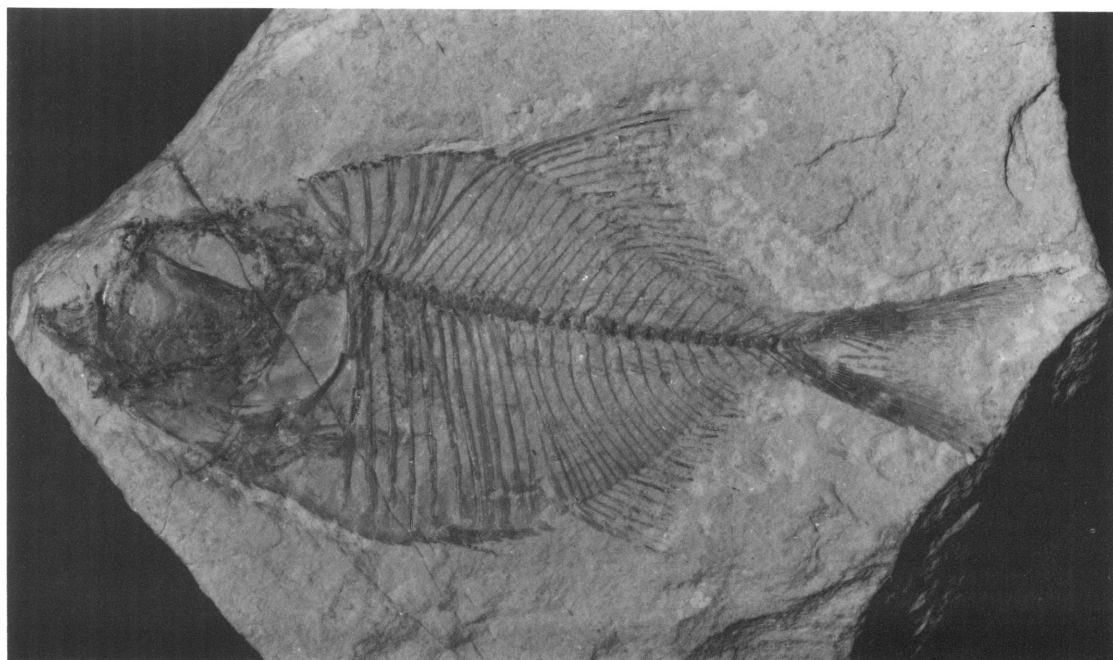


FIG. 11. †*Diplomystus birdi* Woodward, 1895. Nearly complete specimen, AMNH 10188 (s.l. 62 mm.). From the Upper Cretaceous of Hakel, Lebanon.

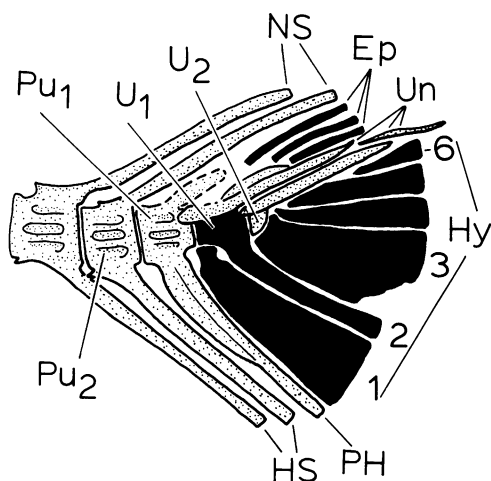


FIG. 12. †*Diplomystus birdi* Woodward, 1895, caudal skeleton, drawn from AMNH 10188 (s.l. 65 mm.), hypurals, epurals, and first ural centrum colored black.

Dorsal scutes number about 23 and there are seven predorsal bones. The dorsal fin has about 17 principal rays plus two accessory rays; and there are about 16 or 17 dorsal pterygiophores. The anal fin has about 23 principal rays preceded by one or two accessory rays. There are about 24 anal pterygiophores (23–25, usually 24). The small pelvic fin is slightly anterior to the dorsal fin. There are about 30 preural vertebrae, and 11 or 12 pairs of ribs. Abdominal scutes number about 24; branchiostegals about 12. For further description see Woodward, 1895, and figures 11–13 here.

†*Diplomystus dubertreti* Signeux, 1951

Figure 14

TYPE: MNHN 1946-18-17, figure 14.

REFERENCE SPECIMENS: MNHN 1946-18-248 (fig. 1, Signeux, 1951).

HORIZON AND LOCALITY FOR HOLOTYPE: The Upper Cretaceous marine chalk deposits at Sahel Alma, Lebanon. This species has not been reported elsewhere.

REVISED DIAGNOSIS: A deep-bodied fish that differs from all other †ellimmichthyids in having about 21 to 23 principal dorsal fin

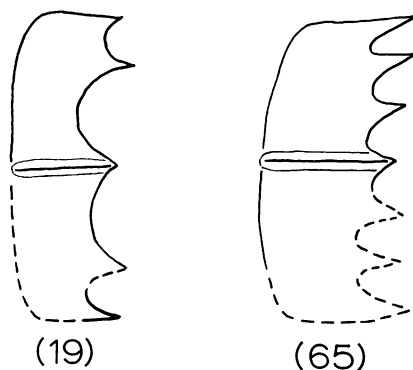


FIG. 13. †*Diplomystus birdi* Woodward, 1895, dorsal scutes; number in parentheses refers to s.l. of the fish in millimeters; juvenile scute from AMNH 10189 and adult from AMNH 11106 (the adult specimen is broken so s.l. is an estimate). Dashed lines represent restoration.

rays. †*Diplomystus dubertreti* is also a larger species than its closest relative, †*D. birdi*; it reaches a total length of at least 16.5 cm. (Diagnosis after Signeux, 1951.)

DESCRIPTION AND DISCUSSION: This species is quite rare and is known by only a few specimens. The body appears to have been extremely deep (fig. 14 here and fig. 1 in Signeux), but this is based on only two specimens, and the rock from Sahel Alma (the only known locality for this species) is often quite strained.

This species has dorsal scutes very similar to those of †*D. birdi* (with pectinate borders bearing fewer spines than †*D. dentatus*). Dorsal scutes number about 20, and there are seven predorsal bones. The dorsal fin has about 21 to 23 principal rays preceded by two small accessory rays. The anal fin has 27 principal rays (supported by 27 pterygiophores). There are about 33 or 34 preural vertebrae and 12 or 13 pairs of ribs. For further description see Signeux (1951).

†*ELLIMMICHTHYS* JORDAN, 1919

TYPE SPECIES: †*Diplomystus longicostatus* Cope, 1886. Designated by Jordan 1919 [in Jordan and Gilbert, 1919, p. 27].

GENERIC DIAGNOSIS: Clupeomorph fishes

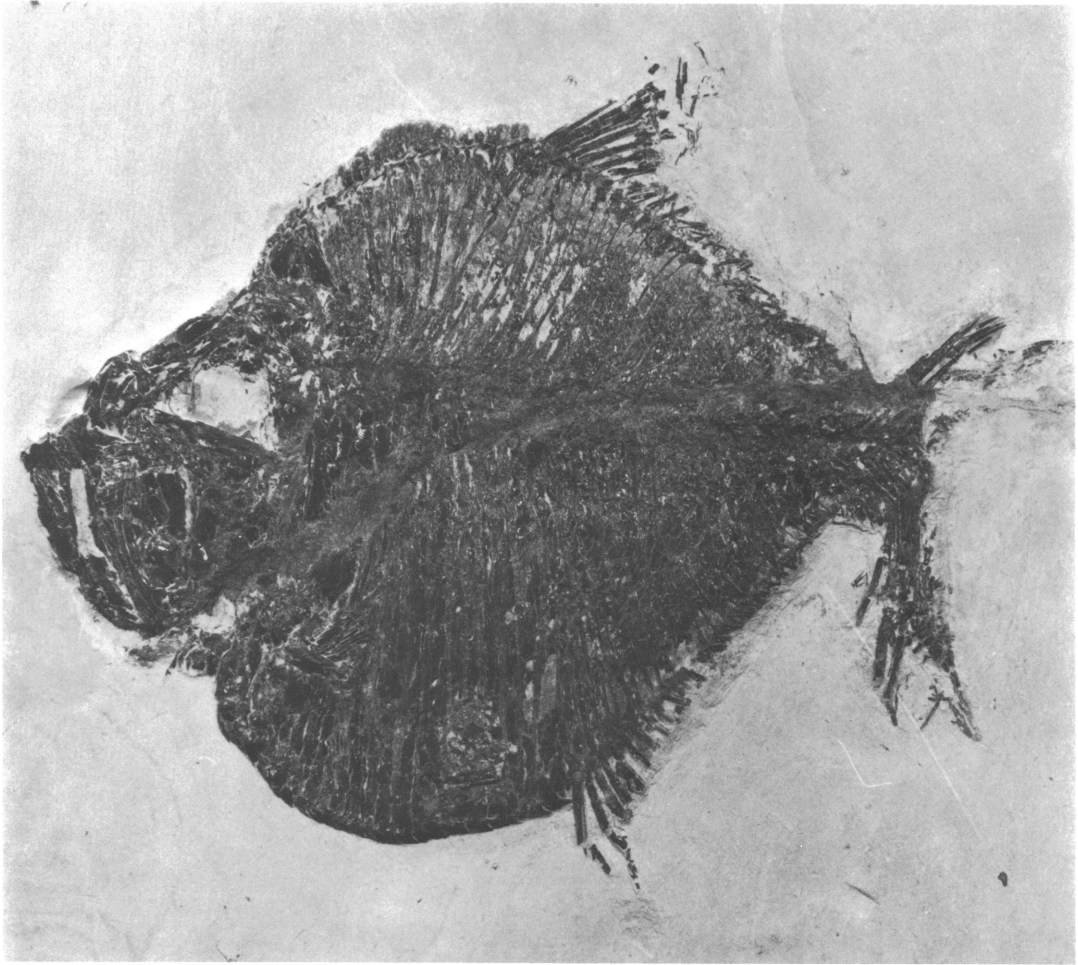


FIG. 14. †*Diplomystus dubertreti* Signeux, 1951; holotype (MNHN 1946-18-17) (s.l. 13 cm.). From the Upper Cretaceous of Sahel Alma, Lebanon.

closely related to †*Diplomystus*, sharing a subrectangular dorsal scute shape, and differing from that genus in lacking the pectinate scute border. The middle posterior border of the scute is recessed (fig. 18).

ETYMOLOGY: *ellim*—from †*Ellimma* Jordan (1913); *Ellimma*—etymology not specified by Jordan; *ichthys*—a Greek word for fish; gender masculine.

DISCUSSION: Because the dorsal scutes of “†*D.*” *longicostatus* lack the pectinate posterior border diagnostic of †*Diplomystus* (see Jordan, 1907, p. 136; and above and below), Jordan’s removal of this species from †*Dip-*

lomystus is quite justifiable. Its placement into †*Ellimmichthys* also permits construction of an unoccupied family name for the †*Diplomystus*-†*Ellimmichthys* group (see above).

†*Ellimmichthys longicostatus*
(Cope, 1886)
Figures 15–18

†*Diplomystus longicostatus* Cope, 1886;
and †*Ellipes longicostatus* Jordan, 1910.
First name changed here for reasons explained above in discussion of †*Ellimmich-*



FIG. 15. †*Elimmichthys longicostatus* (Cope, 1886); slab with two nearly complete specimens (AMNH 734). Upper specimen (dotted in outline) is designated as neotype. Scale = 5 cm.; specimen coated with ammonium chloride. From the Lower Cretaceous of Bahía, Brazil.

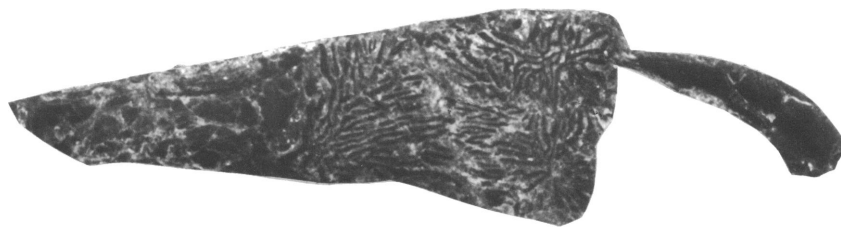


FIG. 16. †*Ellimmichthys longicostatus* (Cope, 1886); closeup of the left side of the skull roof from the neotype (from fig. 15) which shows sculpturing diagnostic of this species.

thyidae, new family; †*Ellipes* is preoccupied by *Ellipes* Scudder, 1902, a genus of crickets.

TYPE: Lost (first reported lost by Schaeffer, 1947); should be in Department of Vertebrate Paleontology, AMNH, but still cannot be located.

REFERENCE SPECIMEN AND NEOTYPE: AMNH 734, a slab with two nearly complete fish, illustrated in figure 15. The upper, more complete specimen is here designated as the neotype.

HORIZON AND LOCALITY FOR REFERENCE SPECIMEN, NEOTYPE, AND LOST TYPE: From Lower Cretaceous deposits along the coast near Itacaranha, Province of Bahia, Brazil. Preserved in a black sandstone (considered to be marine by Cope, 1886, p. 4, and others).

REVISED DIAGNOSIS: An extremely deep-bodied fish (greatest body depth about 63 percent of standard length) that differs from all other †ellimmichthyids in having strongly sculptured skull roofing bones; only 10 principal anal fin rays and about nine anal pterygiophores; and 22 or 23 pairs of ribs.

ETYMOLOGY: *longicostatus*, having long ribs (from Latin); gender feminine.

DESCRIPTION AND DISCUSSION: The dorsal scutes are well preserved on AMNH 734 and one scute is illustrated in figure 17. Although the posterior border is interrupted near the center ("emarginate" of Cope, 1886, p. 3) the overall shape is still subrectangular. The dorsal scutes are definitely wider than long

(although Cope, 1886, p. 3, states that they are longer than wide). There is ornamentation on the dorsal surface of the scute. Although the dorsal surface of the scutes are embedded in the rock, the dorsal ornamentation is visible due to the translucency of the scutes.

There are seven predorsal bones, and the dorsal scutes number about 12.

The body depth is extremely deep (as in †*D. dubertreti*) being about 63 percent of the standard length.

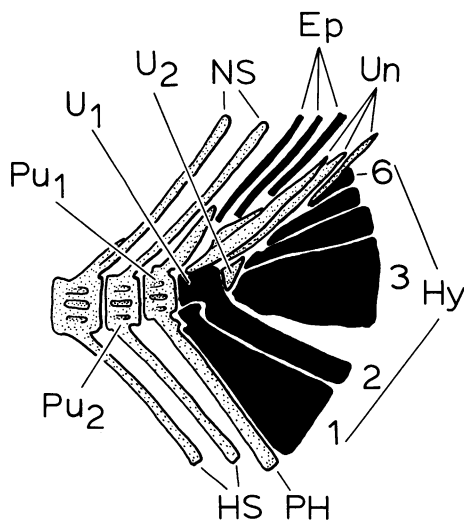


FIG. 17. †*Ellimmichthys longicostatus* (Cope, 1886); caudal skeleton, after Patterson and Rosen (1977) (from BMNH P.7109); hypurals, epurals, and first urocentrum colored black.

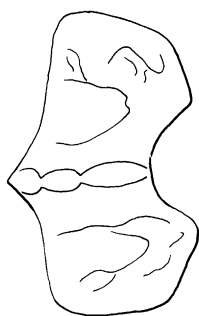


FIG. 18. †*Ellimmichthys longicostatus* (Cope, 1886) new combination; dorsal scute drawn from AMNH 734 (neotype; s.l. 87 mm.). Anterior to left.

The anal fin has 10 principal rays preceded by an accessory ray; and there are nine anal pterygiophores. The dorsal fin has 10 or 11 principal rays and two accessory rays; there are about 12 dorsal pterygiophores. The pelvic fin, although broken, appears to be very small (lower specimen in fig. 15) in AMNH 734 and is in advance of the dorsal fin.

There are 36 or 37 preural vertebrae (with only about 10 caudal vertebrae); and 22 or 23 pairs of ribs. The abdominal scutes extend backward from the isthmus to the anus, and number about 28.

TAXA REMOVED FROM THE GENUS †*DIPLOMYSTUS*

Nearly all types of dorsal scutes found in teleosts are examined here (see Appendix and figs. 9, 13, and 18). On the basis of this information, †*Diplomystus dentatus* Cope, 1877, †*D. birdi* Woodward, 1895, and †*D. dubertreti* Signeux, 1951, are more closely related to each other than to any other known species; and “†*D.*” *longicostatus* Cope, 1886, is proposed as the sister group to these three species (explained below) and is placed in †*Ellimmichthys* Jordan for reasons explained above (fig. 20).

No shared derived characters were found to indicate that “†*Diplomystus*” *brevissimus* (Blainville, 1818) (originally described as †*Clupea brevissimus* Blainville, 1818) is an †ellimmichthyid. Woodward (1888, p. 134) placed this species in the genus †*Diplomys-*

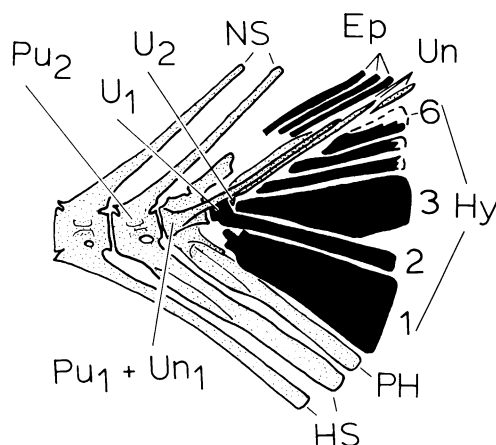


FIG. 19. †*Knightia eocaena* Jordan, 1907, showing the typical clupeoid caudal skeleton (note fusion of Un_1 to Pu_2); drawn from AMNH 10461 (s.l. 104 mm.); hypurals, epurals, and first ural centrum colored black.

tus on the basis of its dorsal scutes, and “all the typical characters of †*Diplomystus*” (characters which he does not specify and which are evidently plesiomorphous). This taxon cannot be placed in †*Diplomystus* because it would make that genus paraphyletic. It also cannot be retained in the genus *Clupea* for the same reasons (it is not even a clupeiform as shown by Patterson, 1967). The species is here placed in †*Armigatus*, new genus (see above).

“†*Diplomystus*” *primotinus* Uyeno, 1979, and “†*D.*” *kokuraensis* Uyeno, 1979, both from Early Cretaceous rocks of Japan, are removed from †*Diplomystus* here because no character information was given to warrant placement in that genus. On the basis of the scute drawings given by Uyeno (1979, fig. 1A–D) and Uyeno and Yabumoto (1980, figs. 2 and 3), and a reduced centrum U_1 (illustrated in Uyeno and Yabumoto, 1980, fig. 1), these appear to be clupeoids. Better preserved skull, dorsal scute, and caudal skeleton material is needed to further classify these fossils.

Schaeffer (1947, p. 22) put †*Ellimma elmodenae* Jordan and Gilbert, 1919 (from the Miocene Monterey Formation of southern

California) into †*Diplomystus*, without explaining why (although he refers it to †*Knightia* elsewhere in that paper). The type (CAS 55404) was examined and found to be a clupeoid, rather than a species of †*Diplomystus*.

“†*Diplomystus*” *tenuissimus* de Stefano, 1918, was found by Arambourg (1927, p. 42) to be a myctophid.

†*Clupea vectensis* Newton, 1889 (from the Oligocene of the Isle of Wight) was placed into †*Diplomystus* by Woodward (1889), but this was because of similarities to †*Knightia* (“†*D. humilis*” at that time). Examination of the dorsal scutes and other skeletal elements suggest placement in †*Knightia* or in a group closely related to †*Knightia*.

“†*Diplomystus*” *marmorensis* Woodward (in Newton, 1904) (from the Miocene of Turkey) was originally placed in the †*Knightia* group by Woodward, and was found here to be a clupeoid. No dorsal scutes were observed on the holotype (BMNH P 10015).

“†*Diplomystus*” *dartevellei* Casier, 1965 (from Lower Cretaceous deposits of the African Congo) was placed in †*Diplomystus* on the basis of its deep body, prepelvic scutes and other primitive characters, not diagnostic of †*Diplomystus*, but of a larger group including †ellimmichthyids, clupeiforms and †*Armigatus*. It is therefore removed from †*Diplomystus* and placed as Clupeomorpha, *incertae sedis* until it can be classified.

“†*Diplomystus*” *goodi* Eastman, 1912 (from Cretaceous deposits of West Africa) was examined (AMNH 6146, 6151, 6162, 6166, and 6168), and none of the specimens observed were well enough preserved to classify accurately. Eastman's description has no character information to justify placement in †*Diplomystus*. Taverne (1975) described “†*D.*” *goodi* as having a well-developed first ural centrum, parasphenoid teeth, basiptyergoid process, parietals in contact on skull, and a free first uroneural; but these are all primitive clupeomorph characters and do not indicate that the taxon belongs in †*Diplomystus*. Therefore, “†*D.*” *goodi* is removed from †*Diplomystus* and placed in Clupeomorpha, *incertae sedis*.

“†*Diplomystus*” *solignaci* Gaudant and

Gaudant, 1971 (from the Upper Cretaceous of Tunisia) was placed in †*Diplomystus* on the basis of primitive characters common to most major clupeomorph groups and of its subtriangular dorsal scutes (p. 158). The subtriangular dorsal scute is thought here to be the primitive type of dorsal scute because it occurs in primitive clupeomorphs (†*Armigatus*), clupeids (*Ethmidium*), and several engraulids (see Appendix). “†*D.*” *solignaci* is removed from †*Diplomystus* and classified as Clupeomorpha, *incertae sedis*.

†*Histiurus elatus* Costa, 1850 (see Costa, 1864), †*H. serioloides* Costa, 1864, and †*H. ventricosus* Costa, 1865 (all from Upper Cretaceous rocks of Italy) were placed in †*Diplomystus* by Woodward (1901, p. 146). He gave no reason for doing so, and the original descriptions and illustrations do not indicate an assignment in †*Diplomystus*. They are therefore regarded as Clupeomorpha, *incertae sedis*.

†*Diplomystus coverhamensis* from Upper Cretaceous deposits of New Zealand was described (Chapman, 1918, p. 26) as resembling [†*Armigatus*] *brevissimus* Blainville. There are no characters to warrant its placement into †*Diplomystus* as used here. It is removed from †*Diplomystus* and placed in Clupeomorpha, *incertae sedis*.

One extant taxon from Australia, *Hyperlophus sprattelides* Ogilby, 1892 [a junior synonym of *H. vittatus* (Castelnau, 1875)] was placed in †*Diplomystus* by Woodward (1892, p. 413). *Hyperlophus* is a clupeoid. There are no known extant †ellimmichthyids.

INTERRELATIONSHIPS OF CLUPEOMORPHS

†*Ornategulum sardinioides* (Pictet) is described in detail by Forey (1973) and †*Armigatus brevissimus* (Blainville) by Patterson (1967). A hypothesis of interrelationships for clupeomorphs is given by the cladogram in figure 20. The numbers in the cladogram refer to shared derived characters listed in the classification below. The classification is arranged so that each taxon is followed by the members it includes (given in brackets), and the synapomorphies for the group (de-

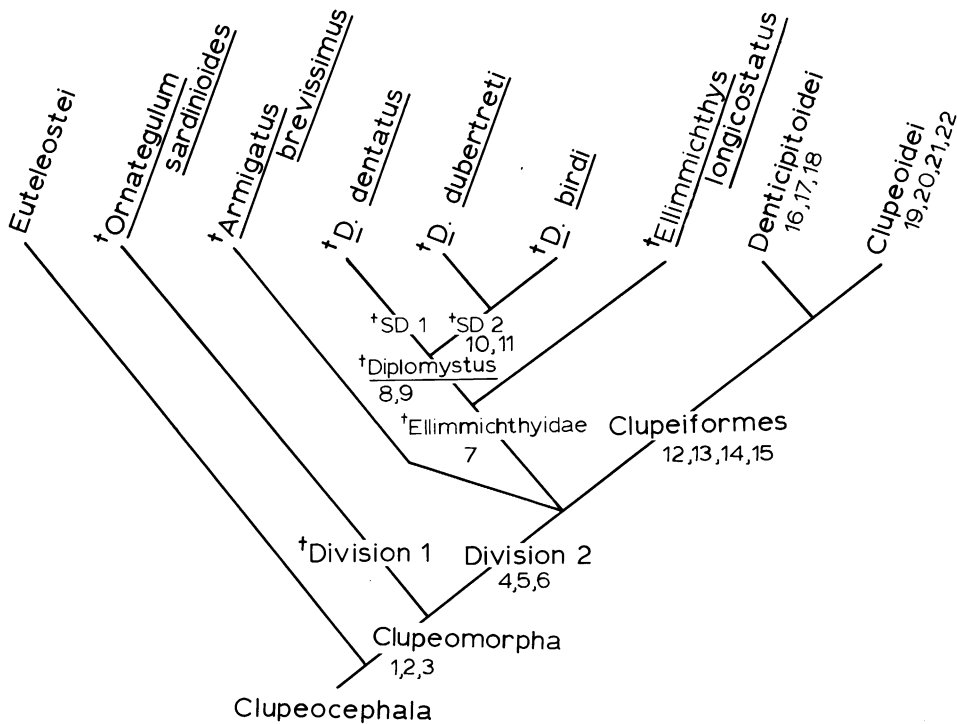


FIG. 20. A cladogram of proposed interrelationships of †ellimmichthyids with other clupeomorph fishes. The numbers on the cladogram refer to synapomorphic characters listed in the text. The †Ellimmichthyidae is contained in the order, †Ellimmichthyiformes (not shown). SD = subdivision. For definition of Clupecocephala and Euteleostei see Patterson and Rosen (1977).

rived characters shared by all the members of the group). For example, the Clupeiformes contains the Denticipitoidei and the Clupeoidei which share derived characters 12, 13, 14, and 15. Because monotypic taxa have no synapomorphies, no characters are listed for them; instead, there is a reference to a specific diagnosis which contains the autapomorphies which define these species. Some taxonomic groups remain unnamed here (Division one and two of the Clupeomorpha, for example) until a study of the interrelationships of fossil and recent clupeoids (in progress) can be completed. A biogeographic cladogram of the groups shown in figure 20 is given in figure 21.

The proposed theory of interrelationships in figures 20 and 21 indicates several things. First of all, the †Ellimmichthyidae (a group

containing †*Diplomystus* as revised here, and the genus †*Ellimmichthys*) is not in Clupeiformes. Therefore †*Knightia* and several other clupeoid species placed in †*Diplomystus* by various authors (discussed above) must be removed from †*Diplomystus*. Consequently, anatomical comparisons by Nelson, Forey, and others using the so-called “†*D. humilis*” as representative of †*Diplomystus* must be re-evaluated because “†*D. humilis*” is, in fact, the type species of the clupeoid †*Knightia* (see fn. 2).

Also, no character information could be discovered to resolve a trichotomy involving †*Armigatus*, †ellimmichthyids and Clupeiformes; but all three groups make up the sister group to †*Ornategulum*. Based on material observed here, the North American †ellimmichthyiform, †*D. dentatus*, is more

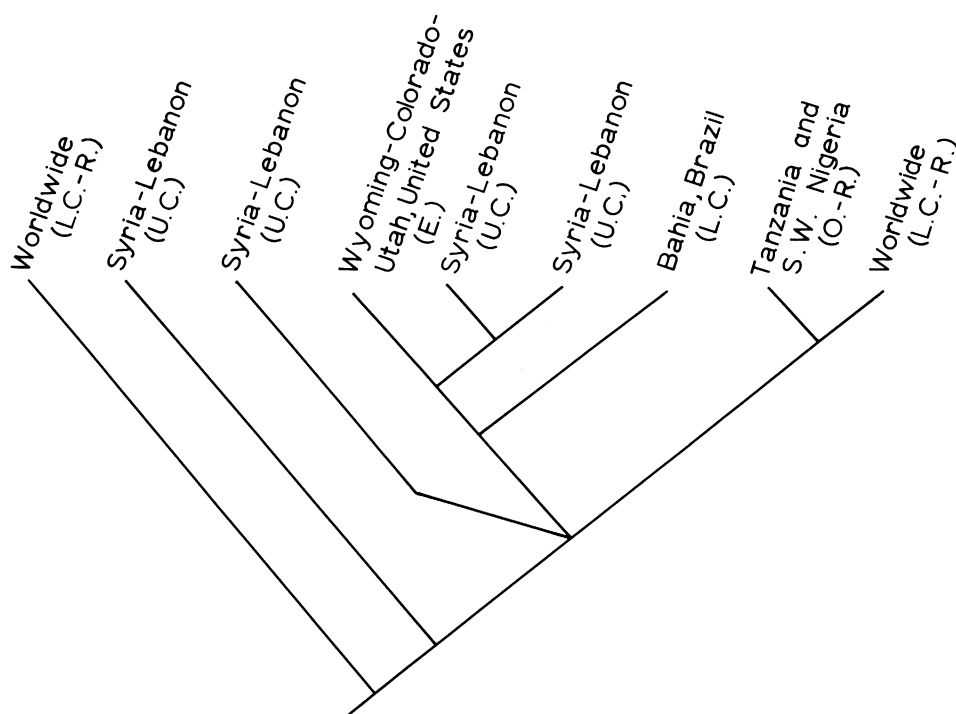


FIG. 21. The geographic localities and known ages of the groups shown in figure 20. L.C. = Lower Cretaceous, U.C. = Upper Cretaceous, E. = Eocene, O. = Oligocene and R. = Recent.

closely related to an unnamed group from Syria and Lebanon (containing †*D. birdi* and †*D. dubertreti*) than to any other known taxon.

If †ellimmichthyiforms and clupeiforms exclusively shared a common ancestor, then divergence from that common ancestor took place at least as early as Lower Cretaceous. This would be indicated by the fact that both †ellimmichthyiforms and clupeiforms are known as Lower Cretaceous fossils (†ellimmichthyiforms by the Lower Cretaceous †*Ellimmichthys* discussed here, and clupeiforms by “*Clupavus* sp.,” illustrated in figs. 10 and 11 of Taverne, 1977). †*Diplomystus dentatus* is the most recent species of †ellimmichthyid known, and it is known only from the Early and Middle Eocene of North America. †*Diplomystus dentatus* is similar to several other fish species of the Eocene Green River Formation (such as †*Notogo-*

neus—a gonorynchid; and †*Phareodus*—an osteoglossoid) in that it has no close relatives in the Recent North American fish fauna.

Clupeomorpha [contains divisions 1 and 2 as used here]. (1) Hypural 2 fused with the first ural centrum at all stages of development (and hypural 1 free from first ural centrum). (2) Supratemporal commissural sensory canal primitively passing through parietals and supraoccipital (see Patterson and Rosen, 1977). (3) Otophysic connection involving a diverticulum of the swim-bladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase (Patterson and Rosen, 1977).

Division 1 [monotypic, contains †*Ornategulum sardinioides* (Pictet)—see Forey, 1973].

Division 2 [contains †*Armigatus brevissimus* (Blainville), new genus, †*Ellimmichthyiformes*, new order, and *Clupeiformes*]. (4) The development of dorsal scutes with a median keel primitively subtriangular in shape (see Appendix). (5) The development of pre-

pelvic and postpelvic abdominal scutes, with median spines. (6) The presence of a well-defined pre-epiotic fossa (assumed to be secondarily lost in *Denticeps*, possibly obliterated by expansion of pterotic bulla—see Greenwood, 1968, p. 232) (Forey, 1973).

†*Armigatus brevissimus* [see Patterson, 1967, for description].

†*Ellimmichthyiformes*, new order [contains one family (†*Ellimmichthyidae*) with three species of †*Diplomystus* and one species of †*Ellimmichthys*. (7) Lateral expansion of dorsal scute “wings” which give scute a subrectangular shape (see text).

†*Ellimmichthys* [monotypic, contains †*E. longicostatus* (Cope) new combination—see text].

†*Diplomystus* [contains †*D. dentatus*, †*D. birdi* and †*D. dubertreti*—see above]. (8) Spines on edge of posterior dorsal scutes (see text). (9) Increase in number of dorsal scutes (to 22 to 36) and reduction or loss of median recess in the posterior edge of the scute.

Subdivision 1 [contains †*D. dentatus* only—see text].

Subdivision 2 [contains †*D. birdi* and †*D. dubertreti*]. (10) Increase in number of dorsal fin rays (to about 17 or more) and dorsal pterygiophores (to about 16 or more). (11) Decrease in number of preural vertebrae (to 34 or less).

Clupeiformes [contains Denticipitoidei and Clupeoidei]. (12) The presence of a recessus lateralis (infraorbital canal merges with preopercular canal rather than passing up into a long dermosphenotic stretching well forward above orbit as in lower clupeomorphs). (13) Supraoccipital completely

separates parietals (vs. parietals meeting in middle of skull in lower clupeomorphs). (14) Reduction in size and/or number of teeth on the endopterygoid (vs. strong numerous teeth). (15) Loss of so-called “Beryciform foramen” (see McAllister, 1968) of the anterior ceratohyal.

Denticipitoidei [contains the monotypic genera *Denticeps* and †*Paleodenticeps*].

(16) The presence of odontodes (denticles) covering the dermal bones of the skull (Greenwood, 1968). (17) Reduction in number of uroneurals to 1 (vs. 2 or 3 in other clupeomorphs). (18) The presence of a pelvic plate (Greenwood, 1968, p. 269); several other characters given in Greenwood (1968).

Clupeoidei [contains *Dussumieriidae*, *Clupeidae*, *Engraulidae* and *Chirocentridae*; and includes about 310 Recent and about 90 fossil species]. (19) Reduction in relative size of the first ural centrum. (20) Fusion of the first uroneural with the first preural centrum. (21) Loss of lateral line scales. (22) Separation of the parhypural from the first ural centrum (within clupeoids, the parhypural is known to be fused to the centrum only in *Dussumieria acuta*—Gosline, 1960, fig. 7).

Following Whitehead (1968) and others, the Clupeidae includes five subfamilies: Clupeinae, Pellonulinae, Alosinae, Dorosomatinae, and Pristigasterinae; and the Engraulidae includes two subfamilies: Engraulinae and Coilinae.

Clupeoidei also contains the fossil family †*Clupavidae* if Taverne's (1977) restorations are accurate.

APPENDIX

DORSAL SCUTES IN CLUPEOMORPH FISHES: THE “DOUBLE-ARMORED HERRINGS”

SYSTEMATIC LIST OF CLUPEOMORPH DORSAL SCUTES ILLUSTRATED HERE

Clupeomorpha—Division 2

†*Armigatus brevissimus* (Blainville, 1818) [fig. 22]

†*Ellimmichthyiformes* (includes †*Ellimmichthyidae* only)

†*Ellimmichthys*

†*E. longicostatus* (Cope, 1886) [fig. 18]

†*Diplomystus*

†*D. dentatus* Cope, 1877 [fig. 9]

†*D. birdi* Woodward, 1895 [fig. 13]

Clupeiformes

Clupeidae

Clupeinae

†*Ellimma*

†*E. branneri* (Jordan, 1910) [fig. 23]

Pellonulinae

†*Knightsia*

†*K. eocaena* Jordan, 1907 [fig. 26A]

†*K. alta* (Leidy, 1873) [fig. 26B]

†*K. new species A* (Grande, in press) [fig. 26C]

- Potamalosa*
P. richmondia (Macleay, 1879) [fig. 24]
Hyperlophus
H. vittatus (Castelnau, 1875) [fig. 25A]
H. translucentus McCulloch, 1917 [fig. 25B]
incertae sedis
 "†*Clupea*" *vectensis* Newton, 1889 [fig. 28]
 †New genus and species B (Grande, in press) [fig. 27]
Alosinae
Ethmidium
E. maculatum (Valenciennes, 1847) [fig. 29]
Dorosomatinae
Clupanodon
C. thrissa (Linnaeus, 1758) [fig. 30]
Pristigasterinae
Pristigaster
P. cayana Cuvier, 1829 [fig. 31]
Engraulidae (nomenclature follows Wongratana, 1980)
Engraulinae
Stolephorus
S. macrops Hardenburg, 1933 [fig. 32A]
S. tri (Bleeker, 1852) [fig. 32B]
Thrissina
T. baelama (Forskål, 1775) [fig. 33]
Thryssa
T. breviceps Roberts, 1978 [fig. 34A]
T. dussumieri (Valenciennes, 1848) [fig. 34B]
T. hamiltoni (Gray, 1835) [fig. 34C]
T. kammalensis (Bleeker, 1849) [fig. 34D]
T. mystax (Schneider, 1801) [fig. 34E]
T. purava (Hamilton-Buchanan, 1822) [fig. 34F]
T. setirostris (Broussonet, 1782) [fig. 34G]
T. vitrirostris (Gilchrist and Thompson, 1908) [fig. 34H]
Setipinna
S. breviceps (Cantor, 1850) [fig. 35A]
S. melanochir (Bleeker, 1849) [fig. 35B]
S. papuensis Munro, 1964 [fig. 35C]
S. gilberti Jordan and Starks, 1905 [fig. 35D]
S. phasa (Hamilton-Buchanan, 1822) [fig. 35E]
S. godavari Babu Rao, 1961 [fig. 35F]
S. taty (Valenciennes, 1848) [fig. 35G]
Coilinae
Coilia

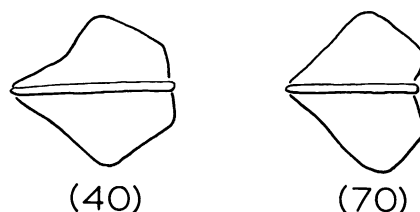


FIG. 22. †*Armigatus brevissimus* (Blainville, 1818). The dorsal scutes in two specimens. The specimen on the left was drawn from AMNH 5373 and the specimen on the right was drawn from AMNH 5354. Numbers in parentheses refer to s.l. of fish in millimeters.

- C. dussumieri* Valenciennes, 1848 [fig. 36A]
C. mystus (Linnaeus, 1758) [fig. 36B]
C. nasus Günther, 1868 [fig. 36C]
C. neglecta Whitehead, 1968 [fig. 36D]

Most dorsal scutes are relatively delicate structures and are often not preserved or are poorly preserved in fossil species. Therefore, the dorsal scute counts given below for fossil species are estimates based on observations of many specimens.

†*Armigatus*: The only known species, †*A. brevissimus*, has a subtriangular scute (fig. 22). There are 11 or 12 scutes which extend from the anterior end of the dorsal fin forward, about two-thirds of the way to the skull (dorsal scutes appear to extend all the way to the skull in all other dorsal-scuted clupeomorphs discussed here, except for engraulids and *Pristigaster*).⁷ The length of each scute is slightly shorter than that of a preural centrum.

†*Ellimmichthyidae*: †*Ellimmichthyids* all have the lateral wings of the dorsal scute elongated and blunted at the lateral edges, giving the scute a subrectangular outline. †*Ellimmichthys longicostatus* (fig. 18) has a complex pattern of sculpture on the dorsal surface. The length of each scute is about equal to the length of one preural centrum (although the width is much greater than the length as in all †*ellimmichthyids*); and they number about 12.

†*Diplomystus* is highly derived in having

⁷ See addendum.

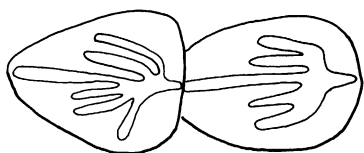


FIG. 23. †*Ellimma branneri* (Jordan, 1910). Drawing of two anterior dorsal scutes from AMNH 10040 (s.l. 93 mm.).

the posterior border of the scute pectinate; pectination increases with increase in body size (figs. 9 and 13). †*Diplomystus birdi* (fig. 13) has about 23 dorsal scutes, and each scute is slightly shorter in length than the length of a centrum. †*Diplomystus dentatus* is further specialized in having a higher number of dorsal scutes than any other known clupeomorph (33 to 36), and a higher number of scute "spines" (fig. 9) in the adult stage, than any other species of †*Diplomystus*. The length of the scute in †*D. dentatus* is less than that of a preural centrum.

Clupeinae: †*Ellimma branneri* (Jordan, 1910) was the only⁷ clupeine species found to have dorsal scutes. [This species is not in the genus †*Knightsia*, as placed by Schaeffer (1947) and others, because, among other things, it has two supramaxillary bones

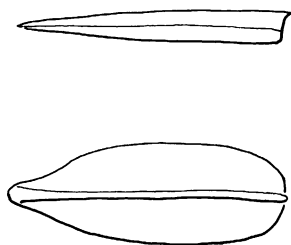


FIG. 24. *Potamalosa richmondia* (Macleay, 1879). Dorsal scute drawn from AMNH 28513 (s.l. 156 mm.). Above, lateral view showing median crest running from anterior edge to beyond posterior edge. The median crest runs the entire length of the scute, along the dorsal surface in most clupeomorphs (except for *Clupanodon thrissa*, *Pristigaster cayana*, and engraulids). Below, dorsal view.



A



B

FIG. 25. *Hyperlophus* dorsal scutes. A, *H. vittatus* (Castelnau, 1875) drawn from AMNH 3050 (s.l. 60 mm.); B, *H. translucidus* McCulloch 1917, drawn from AM I.18464-001 (paratype) (s.l. 48 mm.).

(Grande, in press).] †*Ellimma branneri* has a complex pattern of sculpture on the dorsal

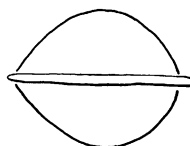


(29)

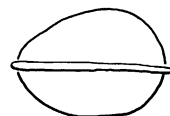


(63)

A



B



C

FIG. 26. †*Knightsia* dorsal scutes. A, †*K. eocaena* Jordan, 1907, young individual and an adult. Numbers in parentheses refer to s.l. in millimeters. Young individual is AMNH 10420, adult is AMNH 2499; B, †*K. alta* (Leidy, 1873), drawn from AMNH 10433 (s.l. 86 mm.); C, †*K.*, new species A (description, Grande, in press) from the late Middle Paleocene Tongue River Formation, Powder River Co., Montana. Drawn from AMNH 10404 (s.l. 70 mm.).

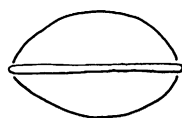


FIG. 27. †New genus and species of clupeid from the early Middle Eocene Laney Member of the Green River Formation, Wyoming. Drawn from AMNH 10458 (s.l. 28 mm.).

surface (fig. 23) of the scutes. The scutes number 11 or 12, and the length of each scute is about equal to the length of a preural centrum.

Pellonulinae: †*Knightia*, *Potamalosa*, *Hyperlophus*, and possibly “†*Clupea*” *vectensis* and the undescribed species in figure 26 are the only known pellonulines with dorsal scutes. Their scutes are distinctive in having a symmetrical oval to circular shape,⁸ with a median crest that extends over both the anterior and the posterior edge of the scute. Although this scute type occurs in all of the “Hyperlophini” (a group name used by Whitehead, 1973, p. 13, to include pellonulines with dorsal scutes), it also occurs in a probable clupein fossil (fig. 27), in some clupeoid fossils whose relationships are unknown, and in some Recent clupeins which bear only a single scute—see addendum.

All species of †*Knightia* (fig. 26) have about 12 to 14 dorsal scutes, which are each about the length of one preural centrum. The scutes often are difficult to see on specimens because of incomplete preservation, or a covering of the thick scales characteristic of this group. “†*Clupea*” *vectensis* (fig. 28) has a dorsal scute morphology similar to †*Knightia* and has about 13 scutes, each about as long as a centrum. The undescribed clupeid (description, Grande, in press) whose scute is illustrated in figure 27, has about 12 or 13 scutes, each about as long as a centrum.

Hyperlophus has a scute morphology very similar to that of †*Knightia*. *Hyperlophus vittatus* (fig. 25A) usually has 29 dorsal scutes

⁸ The shape is sometimes variable (from oval to circular) even within a single individual. The normal scute types were used here for illustrations.

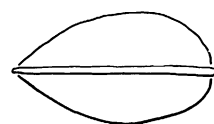


FIG. 28. “†*Clupea*” *vectensis* Newton, 1889, dorsal scute drawn from BMNH P.6854 (s.l. 27 mm.).

and each is slightly shorter than the length of a preural centrum. *Hyperlophus translucidus* (fig. 25B) has about 17 or 18 dorsal scutes and each is about the same length as a preural centrum.

Potamalosa has a somewhat elongate dorsal scute (about 1.5 centra in length) which narrows anteriorly (fig. 24). Dorsal scutes in *P. richmondia* (the only valid species—Grande, in prep.) usually number 14.

Alosinae: *Ethmidium maculatum* has about 24 dorsal scutes, and all are subtriangular in shape except the most anterior scute (as in fig. 29) and slightly less in length than a preural centrum. The first (most anterior) dorsal scute is more rounded and about 50 percent larger than the rest.

Dorosomatinae: The dorsal scutes of *Clupanodon thrissa* have an asymmetrical shape, and the median crest on the dorsal surface does not reach its anterior or posterior edge (fig. 30). They number about 20 and are slightly shorter in length than a preural centrum.

Pristigasterinae: *Pristigaster cayana* (AMNH 10186 SW, two specimens 95 and 84 mm. s.l.) has two asymmetrical scutes (fig. 36) between the supraoccipital crest and the first predorsal bone. The scutes have no median crest and have a slightly concave dorsal surface. The second scute shows a very

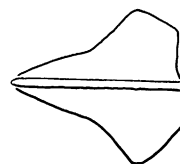


FIG. 29. *Ethmidium maculatum* (Valenciennes, 1847), dorsal scute drawn from AMNH 7738 (s.l. 165 mm.).

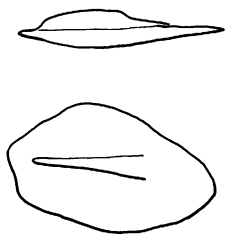


FIG. 30. *Clupanodon thrissa* (Linnaeus, 1758). Dorsal scute drawn from AMNH 17738 (s.l. 165 mm.). Above, lateral view showing median crest present only on part of the dorsal surface of the scale, and reaching neither the anterior nor the posterior edge; Below, dorsal view.

small posterior spine. The anterior (and largest) scute is slightly less than one PUC in length (PUC = preural centrum).

There has been some confusion in the literature concerning the occurrence of dorsal scutes in *Pristigaster*. Valenciennes (1847a, p. 335) gives the first indication of them when he states:

“Les interépineux dorsaux font une petite saillie au-dessus des muscles, transversent la peau et sortent par deux petites pointes qui rendent cette partie du corps dentellée.” [The predorsal bones make small bumps above the muscles, penetrating the skin and projecting by two small points which make this part of the body denticulated.]

Bertin and Arambourg (1958, p. 2227) also cite *Pristigaster* as having predorsal scutes, but Whitehead (1967, p. 101) suggests that the scutes were identified “possibly through a misinterpretation of the pre-dorsal bones.”

In the two specimens examined here it was



FIG. 31. Dorsal scutes in *Pristigaster cayana* Cuvier, 1829. Drawn from AMNH 10186 sw (s.l. 95 mm.).

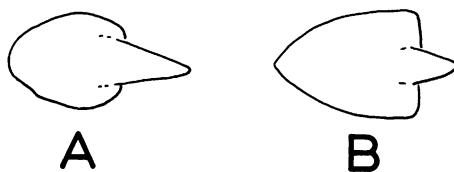


FIG. 32. *Stolephorus* dorsal scutes. A, *S. macrocephalus* Hardenburg, 1933, drawn from CAS 46939 (s.l. 50 mm.); B, *S. tri* (Bleeker, 1852), drawn from USNM 204235 (s.l. 62 mm.).

found that *Pristigaster* does indeed have dorsal scutes. They are not merely the tops of predorsal bones, and are in advance of the 5 predorsal bones found in this species. The scutes were observed in both specimens (listed above) and were removed from the larger specimen to make the drawing in figure 36.

The position of the dorsal scutes in *Pristigaster* is unusual. All other dorsal-scuted clupeomorphs that lack a complete series of scutes from the head back to the dorsal fin (such as †*Armigatus* and engraulids) lack anterior scutes (those just behind the head). *Pristigaster* is unique⁷ in lacking posterior scutes (those just anterior to the dorsal fin).

Signeux (1964) describes a fossil pristigasterine, †*Gasteroclupea branisai* from the Upper Cretaceous El Molino Fm. of central Bolivia (also illustrated in Schaeffer, 1963, fig. 6). It appears to have about 25 dorsal scutes, but they were badly crushed on the specimen observed here. Unlike *Pristigaster*, and like most clupeomorphs with dorsal scutes, the scutes are arranged in a series along the dorsal midline, running from just behind the head back to the dorsal fin origin.

Engraulidae: Dorsal-scuted engraulids are peculiar in having reduced the number of



FIG. 33. *Thrissina baelama* (Forskål, 1775), dorsal scute drawn from CAS 29385 (s.l. 110 mm.). The scute spine on this species is very poorly developed.

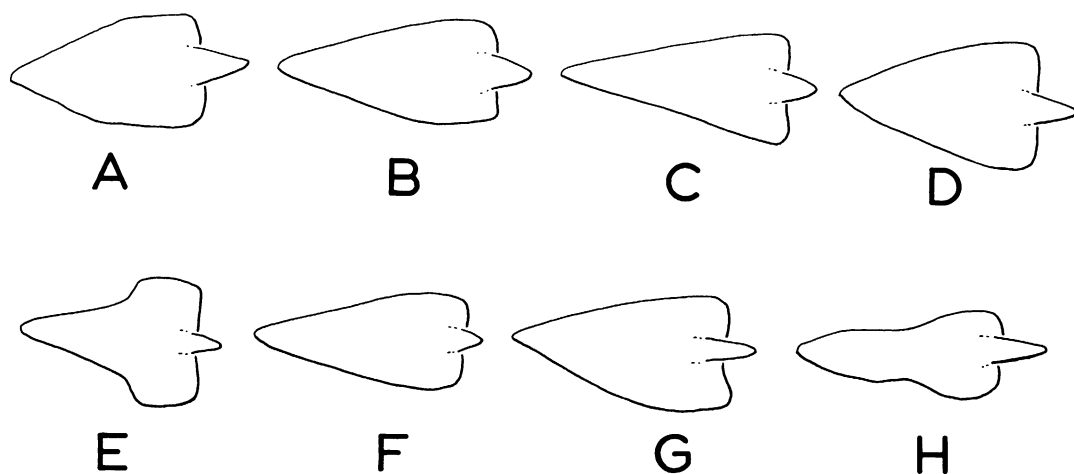


FIG. 34. *Thyssa* dorsal scutes. A, *T. brevicauda* Roberts, 1978, drawn from AMNH 38190 (s.l. 39 mm.); B, *T. dussumieri* (Valenciennes, 1848), drawn from AMNH 38191 (s.l. 103 mm.); C, *T. hamiltoni* (Gray, 1835), drawn from AMNH 38188 (s.l. 90 mm.); D, *T. kammalensis* (Bleeker, 1849), drawn from AMNH 38189 (s.l. 66 mm.); E, *T. mystax* (Schneider, 1801), drawn from AMNH 18295 (s.l. 72 mm.); F, *T. purava* (Hamilton-Buchanan, 1822), drawn from CAS 47099 (s.l. 113 mm.); G, *T. setirostris* (Broussonet, 1782), drawn from AMNH 38192 (s.l. 88 mm.); H, *T. vitrirostris* (Gilchrist and Thompson, 1908), drawn from CAS 33932 (s.l. 102 mm.).

dorsal scutes to 1 or 2.⁹ They also have a dorsoposteriorly pointing spine near the anterior end of the scute (fig. 37). There is no median crest on engraulid scutes (also a derived feature). Among engraulids, only the genera *Thrissina*, *Thyssa*, *Setipinna*, *Coilia* and some of the *Stolephorus* species appear to have a dorsal scute.¹⁰ *Papuengraulis* (with one species, *P. micropinna* Munro, 1964) was not available for study, but the illustration given in Munro (1967) indicates that it

⁹ Although the author has not observed any engraulids with two dorsal scutes, G. Nelson (person commun.) has observed two on rare occasions.

¹⁰ The dorsal scute should not be confused with the anterior lateral expansion of the first pterygiophore which is sometimes spatulate enough to resemble a scute, often bears a small paired ray, and is present in both scuted and unscuted engraulids. In dorsal-scuted engraulids, this pterygiophore expansion underlies the posterior edge of the scute making it difficult to see the posterior border of the scute (unless the specimen is cleared and stained). Engraulid dorsal scutes, unlike the pterygiophore expansions, are unpaired structures which are not part of any other osteological element, and bear no paired rays.

does have a dorsal scute. It is interesting to note that only the Indo-Pacific engraulids have a dorsal scute; and that all Indo-Pacific engraulids, except for *Lycothrissa* and some *Stolephorus* species, have a dorsal scute.

The dorsal scutes of *Setipinna* (fig. 35) are more elongate than those of any other known clupeomorph (about equal in length to $1\frac{3}{4}$ to $5\frac{1}{2}$ preural centra). Scute length (measured from the anterior edge of the scute to the posterior tip of the spine) for each species, given in preural centra lengths (PUCs) are approximately as follows: *S. breviceps* ($5\frac{1}{2}$ PUCs); *S. melanochir* (3 PUCs); *S. papuensis* ($3\frac{1}{2}$ PUCs); *S. gilberti* (2 PUCs); *S. phasa* ($2\frac{1}{2}$ PUCs); *S. godavari* (2 PUCs); and *S. taty* ($1\frac{3}{4}$ PUCs). Except for the species with the most elongated scutes, the scute in the genus *Setipinna* is subtriangular in outline.

The dorsal scutes of *Thyssa* (fig. 34) are all basically subtriangular in outline, and range in length from about 1 to $1\frac{1}{2}$ PUCs, except for *T. purava* which is about 2 PUCs in length. In addition to the species listed in figure 32, *T. rastrorsa* Roberts, 1978 (CAS

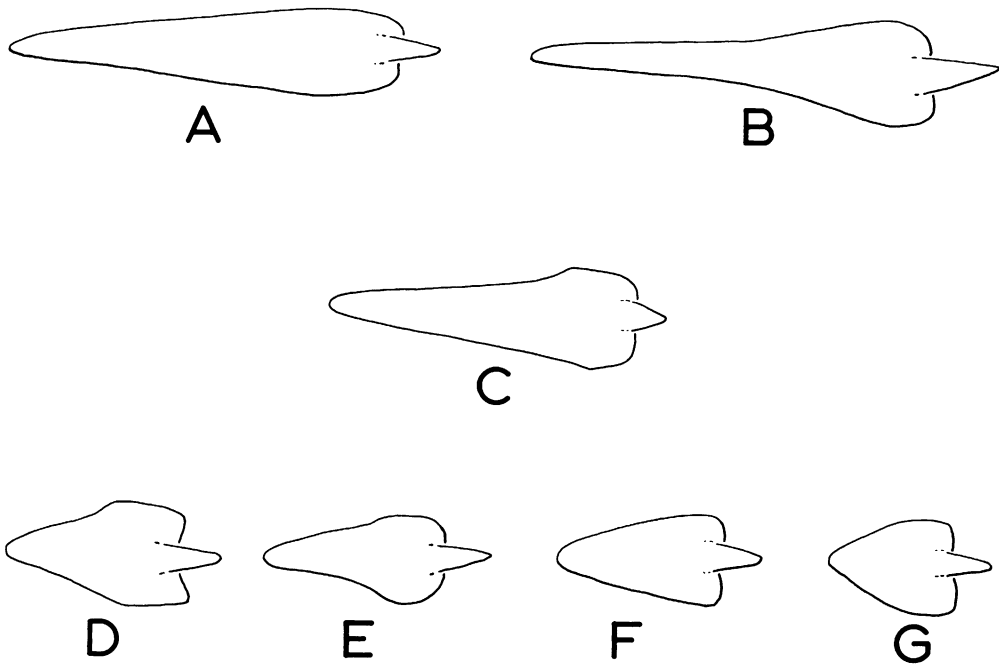


FIG. 35. *Setipinna* dorsal scutes. A, *S. breviceps* (Cantor, 1850), drawn from AMNH 17703 (s.l. 134 mm.); B, *S. melanochir* (Bleeker, 1849), drawn from AMNH 9525 (s.l. 220 mm.); C, *S. papuensis* Munro, 1964, drawn from AMNH 17551 (s.l. 87 mm.); D, *S. gilberti* Jordan and Starks, 1905, drawn from CAS 47091 (s.l. 142 mm.); E, *S. phasa* (Hamilton-Buchanan, 1822) CAS (SU) 25624 (s.l. 155 mm.); F, *S. godavari* Babu Rao, 1961, drawn from SOSC 4 (s.l. 78 mm.); G, *S. taty* (Valenciennes, 1848), drawn from SOSC 4 (s.l. 98 mm.).

[SU] 41548); *T. scratchleyi* (Ramsay and Ogilby, 1887) (USNM 217035); and *T. malabarica* (Bloch, 1795) (USNM 217040) were also examined and were found to have dorsal scutes 1 to 1½ PUCs in length and of the same general morphology as illustrated here for the other species of *Thryssa*.

The dorsal scutes of *Coilia* are all nearly identical in the four species studied (fig. 36). They are all subtriangular and fairly small (about 1 PUC).

Within the genus *Stolephorus*, only some of the species have dorsal scutes. Those observed here were in *S. macrops* and *S. tri* (fig. 32). *Stolephorus tri* shows a typical subtriangular shape, and *S. macrops* has a very rounded subtriangular shape, with a very large spine. The scutes of both species are about 1 PUC.

Stolephorus heterolobus (Rüppell, 1837)

(CAS [SU] 25161); *S. buccaneeri* Strasburg, 1960 (CAS 30100); *S. indicus* (van Hasselt, 1823) (AMNH 18291); *S. bataviensis* Hardenberg, 1933 (AMNH 27550); *S. andhraensis* Babu Rao, 1966 (USNM 204230); *S. holodon* (Boulenger, 1902) (CAS [SU] 31337); and *S. commersonii* Lacépède, 1803 (CAS [SU] 38399) were also examined, and none had dorsal scutes.

The dorsal scute of *Thrissina* is quite distinctive (fig. 33). *Thrissina baelama* (Forskål, 1775) and *T. encrasicholoides* (Bleeker, 1852) both have the same general scute shape. The spine is quite reduced in these species and the posterior edge of the scute, unlike that of any other known engraulid, is convexly rounded in outline. The length of the scute is about 1 PUC.

OTHER ACTINOPTERYGIANS WITH DORSAL SCUTES: Some euteleosts (e.g., the alepisau-

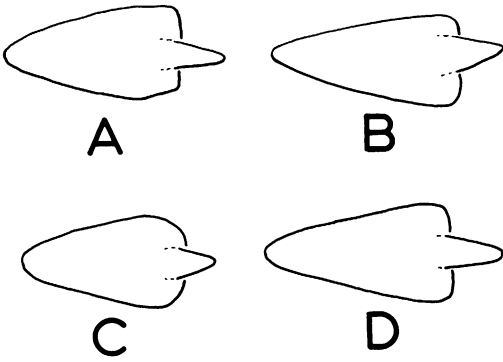


FIG. 36. *Coilia* dorsal scutes. A, *C. dussumieri* Valenciennes, 1848, drawn from CAS (SU) 68196 (s.l. 108 mm.); B, *C. mystus* (Linnaeus, 1758), drawn from AMNH 10322 (s.l. 210 mm.); C, *C. nasus* Günther, 1868, drawn from AMNH 10321 (s.l. 125 mm.); D, *C. neglecta* Whitehead, 1968, drawn from CAS 33904 (s.l. 134 mm.).

roids, †*Eurypholis* illustrated in Piveteau, 1966, p. 204, †*Enchodus* illustrated in Goody, 1969, p. 92, and †*Saurorhamphus* illustrated in Goody, 1969, p. 124), acipenserids, and †pseudodontiforms (e.g., †*Macromesodon*, †*Microdon*, and †*Coelodus*, illustrated in Piveteau, 1966, pp. 176, 178, and 179) have dorsal scutes, but these are morphologically distinct from clupeomorph dorsal scutes. Euteleosts primitively do not have dorsal scutes, and it is proposed that

the clupeomorph dorsal scute (primitively subtriangular with a median crest extending over the entire length of the dorsal surface) was independently derived for Division 2 of the Clupeomorpha (fig. 20).

DISCUSSION: All known clupeomorphs with dorsal scutes also have ventral scutes and therefore, all clupeomorphs with dorsal scutes are "double-armored." The presence

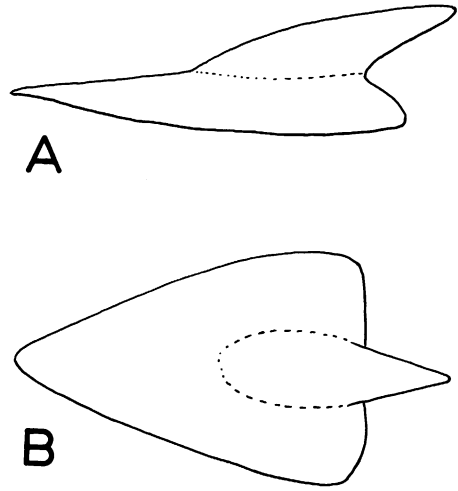


FIG. 37. Typical engraulid dorsal scute (*Thryssa kammalensis*, drawn from AMNH 38189) showing the peculiar "spine." A, lateral view; B, dorsal view.

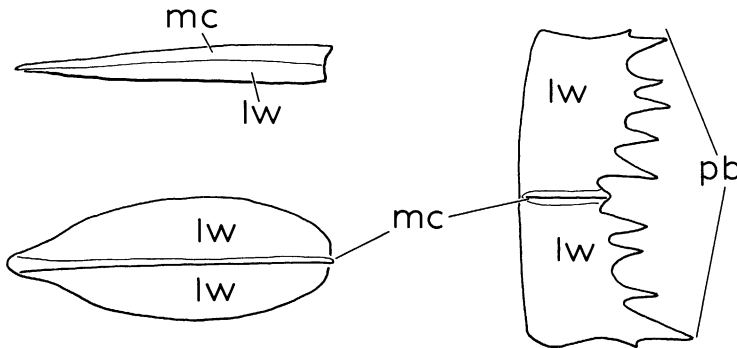


FIG. 38. Explanation of morphological terminology used for dorsal scutes. Anterior faces left. A, *Potamalosa* scute (upper = lateral view; lower = dorsal view); B, †*Diplomystus* scute (dorsal view). lw = lateral wing; mc = median crest; pb = pectinate border.

of "double armor" is found, at least primitively, in most major clupeomorph groups (Clupeidae, Engraulidae, †*Ellimmichthyidae*, and †*Armigatus*). Therefore, the presence of double armor (or dorsal scutes) is not synapomorphic for any group more specific than Division 2 of the Clupeomorpha as shown in figure 20 (which includes all known clupeomorphs except †*Ornategulum sardinioides*). Therefore, I agree with Nelson (1970b) that the "double-armored herring" group proposed by Schaeffer (1947, p. 24) and implied by Woodward (1892), Eastman (1912), and others is an unnatural (non-monophyletic) group. It is proposed here to be non-monophyletic unless it includes all members of Clupeomorpha Division 2.

We find when looking at the detailed morphology of dorsal scutes in clupeomorphs, that they are complex, and that certain morphological types are indicative of smaller (less general) clupeomorph groups (described above). A subtriangular scute with a median crest on the dorsal surface is proposed as the primitive scute type for Clupeomorpha, Division 2 because it is found in †*Armigatus*, clupeids, and engraulids. I disagree with Uyeno's (1979, p. 22) statement that "the predorsal scutes [which are] round at both ends . . . appear to be the most primitive form, since the predorsal scutes must have originated from cycloid scales covering the mid-dorsal line of the predorsal region." The dorsal scutes in most clupeomorphs are embedded in the skin, which is itself covered with scales. There is no evidence, developmental or otherwise, to indicate that the scutes originated from cycloid scales along the midline; and the most parsimonious interpretation of dorsal scute morphological characters in combination with other types of clupeomorph characters, suggests that the subtriangular scute with a median dorsal crest is the primitive type of dorsal scute for clupeomorphs.

A subrectangular shape due to lateral expansion is seen as a derived character of †ellimmichthyids; the appearance of a pectinate posterior border is a derived character of †*Diplomystus*. Engraulid dorsal scutes are specialized in that they are greatly reduced

in number (to one or rarely two), have lost the median crest on the dorsal surface, and have acquired a prominent spine. Some species of *Setipinna* are further specialized in having a greatly elongated dorsal scute (see above). Clupeids have several scute types, including a primitive subtriangular type in *Ethmidium*, and several types proposed here as more specialized (less general in occurrence) such as the symmetrical circular-to-oval shape in hyperlophins and some clupeins, the asymmetrical scute with an incomplete median crest in *Clupanodon thrissa* and the slightly concave, asymmetrical scute in *Pristigaster* which lacks any median crest. Complex sculpturing of the dorsal scute surface appears to have developed independently in †ellimmichthyids (†*Ellimmichthys longicostatus*) and clupeids (†*Ellimma branneri*). The pattern of sculpturing is quite different between the two groups.

ADDENDUM

After this paper went to press, Gareth Nelson and I found that several clupeins and at least one alosin (at least some species of *Herklotsichthys*, *Opisthonema*, *Sardinella*, and *Alosa*) have a single dorsal scute just behind the skull and before the first predorsal bone (similar in position to the two dorsal scutes of *Pristigaster*). The clupein scute is similar in morphology to the "hyperlophin" type of scute (see figs. 24–28); oval in shape (longest diameter in the anterior-posterior direction) with a median crest and no sculpture on the lateral wings. The occurrence of this scute within clupeids is currently being studied.

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