

RECENT AND FOSSIL  
CLUPEOMORPH FISHES WITH  
MATERIALS FOR REVISION OF  
THE SUBGROUPS OF CLUPEOIDS

LANCE GRANDE

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## ABSTRACT

The Clupeomorpha are a diverse, widespread group of fishes containing (as defined here) about 317 Recent and over 150 known fossil species. They are known as far back as the Early Cretaceous, and today are worldwide in distribution. Surprisingly little is known about this group phylogenetically. This study briefly reviews past work on clupeomorph interrelationships and examines the skeletal morphology of clupeomorphs to produce materials for a revision of the subgroups of clupeiform fishes. By concentrating on clupeomorph osteology, fossils can be added to the resulting classification.

Comparative osteological data, based on examination of over 750 skeletal preparations, are summarized by 20 tables and several cladograms. The osteology of a pellonuline (*Odaxothrissa vitata*) and dorosomatine (*Dorosoma cepedianum*) is descriptively illustrated in detail. Also, a list of all nominal fossil species known to the author which appear to belong in Clupeomorpha as defined here, is provided (based on examination of either illustrations or specimens of over 150 fossil species), and the species in this list are briefly discussed.

It was found that several skeletal characters define groups such as Clupeomorpha, Clupeomorpha Division 2, Clupeiformes, Clupeoidei, and

some clupeoid subgroups. Based on osteological characters, the family Pristigasteridae should be excluded from the superfamily Clupeoidea (which includes Chirocentridae and Clupeidae); and the groups Pristigasteroidea, Engrauloidea, Clupeoidea, Clupeidae, Pellonulinae, and Dussumieriinae were each found to be monophyletic. Several fossil groups are removed from Clupeomorpha (*†Ornategulum*, *†Clupavidae*, *†Engraulis evolans*, and others). Cladograms for Pristigasteroidea, Dussumieriinae, and Pellonulinae are given based on osteological characters.

No osteological characters were discovered to indicate that Dorosomatinae, Alosinae, Clupeinae, or these three groups together, are monophyletic. The biggest remaining problem in clupeomorph systematics is seen as discovering the interrelationships of the members of these three subfamilial "groups of convenience" among Clupeoidei.

It is hoped that this work will serve as a base for future phylogenetic studies on clupeomorph fishes by paleoichthyologists and neoichthyologists interested in clupeomorph osteology. The interrelationships of clupeid fishes and the placement of many fossil species within Clupeomorpha are still under study.

## INTRODUCTION

The Clupeomorpha, commonly known as the herring and herringlike fishes, are a diverse widespread group containing (as used here) about 317 Recent species and over 150 known nominal fossil species. They inhabit freshwater, marine, or brackish environments, and some species inhabit two or all of these environments during their lifetime. Clupeomorphs are known as fossils as far back as Early Cretaceous (see discussion of fossil clupeomorphs below). This is one of the most abundant fish groups on earth (about one-third of the world's total commercial fishing catch according to Blaxter and Hunter, 1982, p. 3), yet surprisingly little is known about their interrelationships and evolutionary history. In the past, reviews and descriptions of this group have been largely confined to external morphology. Whitehead, for example

(in various works from 1962 to present), has published over 1000 pages on clupeomorph fishes; while his work contains highly useful keys for identification of species (based mainly on external morphology) and solves many nomenclatorial problems in the clupeomorph literature, it has not really addressed the problem of how clupeomorph groups are related to each other.

There are also very few detailed phylogenetic studies on fossil clupeomorphs. Most contemporary descriptions of fossil clupeomorphs (Bardack, 1965a; Gaudant and Gaudant, 1971; Schaeffer, 1949; Uyeno, 1979; and others) do not have enough morphological information to enable ichthyologists to classify these taxa more specifically than "Clupeomorpha *incertae sedis*" or "Teleostei *indeterminate*." The main problems in



fossil clupeomorph classification arise from our poor understanding of the interrelationships of Recent species. Because Recent clupeomorph taxa are more numerous (see above) and always better preserved than fossil taxa, it is considered here to be necessary *first* to classify the Recent forms and *then* to add the fossils to that classification.

The following study is an investigation of clupeomorph interrelationships based on the internal skeletal morphology of this group. Emphasizing the skeleton enables fossils to be included in this study. Preliminary studies (Grande, 1982a) have shown that the skeleton shows many characters useful in the phylogenetic classification of clupeomorphs.

The objectives of this study are to:

1. review briefly some of the previous work on clupeomorph interrelationships and
2. review the skeletal morphology of clupeomorphs and produce materials for a revision of the subgroups of clupeoid fishes.

A large number of clupeomorph taxa (mostly Recent species) are examined in detail (see Materials section) and several osteological features will be presented for all of these species in the numerous tables. It is hoped that this information, together with the related conclusions, can serve as a base for further studies on the interrelationships of Recent and fossil clupeomorph fishes. Most known fossil clupeomorph species are briefly discussed and listed. The general osteology of two Recent clupeoids (*Odaxothrissa vittata*—a pelloneuline, and *Dorosoma cepedianum*—a dorosomatine) is given in the appendix. All taxonomic names used here are included in an index at the end of this paper.

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## BRIEF HISTORY OF CLUPEOMORPH CLASSIFICATION

The detailed classification of clupeomorph fishes has traditionally encompassed many problems. Clupeomorph taxonomy during the eighteenth and nineteenth centuries is summarized by Lönnberg (1924) and will not be discussed here. Problems with these early classifications are similar to the problems with most later ones discussed below, in that most of them are based on primitive characters. In the opinion of the author, the goal of systematists is to attempt to make monophyletic or "natural" groups of organisms based on characters uniquely derived for those groups (see Systematic Methodology section below).

Berg (1940) and several other twentieth-century ichthyologists used the Clupeomorpha (and Clupeiformes) as a nonmonophyletic repository for a wide variety of primitive teleosts. It was, basically a "wastebasket group," used to contain any primitive teleost that did not fit into another, better-characterized teleost subgroup. Berg (1940, p. 417) admitted that: "This order [Clupeiformes] represents an artificial assemblage . . . . In time the Clupeiformes will be, doubtlessly, divided in many orders." Also, Gosline (1971, p. 111) admitted that the Clupeiformes, as he defined them, "are much too diverse to allow any unexceptional diagnosis." The classifications used by Berg (1940), Regan (1929), Svetovidov (1952), Jordan (1923), Garstang (1931), McAllister (1968), Gosline (1971), and others included such groups as †leptolepiforms, †tenothrissiforms, †ichthyodectiforms, gonorynchiforms, salmoniforms, osteoglossomorphs, albuloids, elopoids, alepocephaloids, stomiatoids, and esocoids within Clupeomorpha. Classifying clupeomorphs with any of these other groups implies (at least cladistically) that there is a close relationship between them. Nelson (1973), Greenwood et al. (1966), and others have noted that evidence of such a relationship in the form of shared, derived characters (synapomorphies) is nonexistent. It was not until recently (Greenwood et al., 1966) that clupeomorphs were more clearly diagnosed (that is, diagnosed by apparently unique characters).

Greenwood et al. (1966) defined the Clupeomorpha more rigorously by eliminating

several taxa from the group and recognizing three character "complexes" as unique to the remaining members. The three characters they proposed as unique to this group are: (1) the presence of a recessus lateralis (a chamber in the otic region of the head into which several lateral-line canals open) (see character 9 below and Greenwood et al., 1966, p. 358—unlike in Greenwood et al., the recessus lateralis character is not used here to define Clupeomorpha, but rather only a subgroup of it); (2) an otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase (the swimbladder diverticulum of each side divides within the skull to form two large vesicles which are lodged within ossified bullae of the prootic and pterotic bones—see figs. 3, 32B, and 45B); and (3) the second hypural fused with the first ural centrum at all stages of development and an autogenous first hypural (see figs. 7B, 8, 12, 19, 38, and 51).

Of these three characters the third is not confined exclusively to clupeomorphs because the caudal skeleton condition (including the presence of a complete neural spine on  $pu_2$ ) is also found in characoids (Roberts, 1974, fig. 78). Neither the recessus lateralis nor the diverticulum of the swimbladder into ossified prootic bullae have been reported in any nonclupeomorph group. The recessus lateralis character is used here as a defining character for a clupeomorph subgroup (Clupeiformes) rather than all of Clupeomorpha (see below). (The use of the names "clupeomorph" and Clupeomorpha are used here in the sense of Greenwood et al., 1966; that is, clupeomorphs do not include elopomorphs, gonorynchiforms, hiodontids, or salmoniforms.)

Patterson and Rosen (1977, p. 126) added another clupeomorph character to those of Greenwood et al.—that of the supratemporal commissural sensory canal [extrascapular canal] penetrating the parietal (see also Patterson, 1967, p. 104). This feature is discussed below as character 3.

Clupeomorph characters will be further discussed below, under Systematic Discussion of Clupeomorph Fishes.

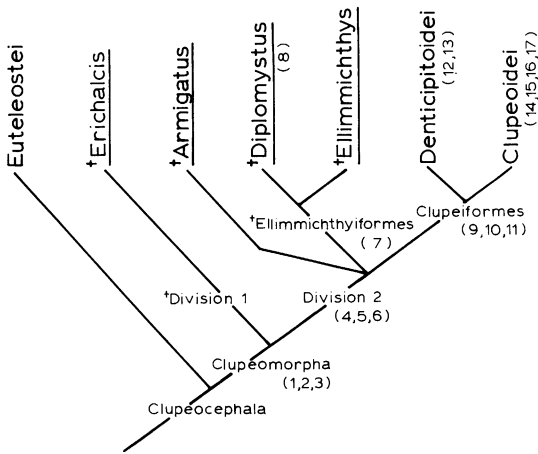


FIG. 1A. Cladogram showing the monophyletic groups of clupeomorph fishes based on osteological characters as interpreted here. Defining characters for Euteleostei and Clupeocephala given in Patterson and Rosen (1977). Characters 1–17 discussed in text. †*Erichalcis*, †*Armigatus*, and †*Elimmichthys* are monotypic taxa.

Within the framework of Greenwood et al.'s Clupeomorpha (based on Recent species), later workers (Patterson, 1967; Patterson and Rosen, 1977; and Grande, 1982a) have added several fossil taxa. In a previous paper (Grande, 1982a) I summarized this information in a cladogram, which is modified here with additional information to make figure 1A. Since publication of that earlier cladogram, I have examined additional and better-preserved material indicating that †*Ornategulum* is probably not a clupeomorph. The major problems with the fossil taxa are more complex than those for the Recent species because of relatively poor preservation in most cases. For example, it is usually difficult or impossible to see bullae or gill arches in fossil clupeomorphs. Also, orientation of specimens is often a serious problem with fossils. For example, fishes that have a very laterally compressed shape in life (like many clupeomorphs) are almost always laterally compressed and crushed as fossils. (When they die and fall to the bottom of a body of water they usually come to rest flat side down prior to their burial and subsequent fossilization.) This makes observation of features on the ventral or dorsal regions of the braincase difficult or impossible. Thus

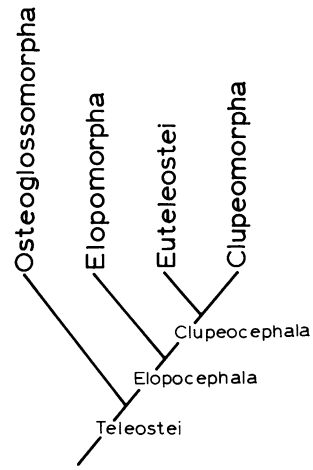


FIG. 1B. Cladogram of Recent teleost fishes after Patterson and Rosen, 1977.

the work required to diagnose and describe a taxon thoroughly is much more difficult for a fossil than for a Recent species. This is another reason why it is more practical to classify the Recent members of a higher taxon first and to add the fossils to the system later.

It should be noticed that the cladogram in figure 1A leaves the majority of the Clupeomorpha (all but one of about 318 Recent species, and most fossil species) within the Clupeoidei. The major problems with the overall classification of clupeomorph fishes today rests within this group.

Within Clupeoidei, if we include only those species retained by Greenwood et al., there are several Recent groups traditionally thought to be "distinct" (not necessarily monophyletic). These are Chirocentridae (wolf herrings); Engraulidae (anchovies); Dussumieriinae (round herrings); Clupeinae (true herrings, pilchards, sprats, sardines); Pellonulinae (no common name); Dorosomatinae (gizzard shads); Alosinae (shads, alewives, menhaden); Pristigasterinae (no common name); and Congothrissinae (no common name). Some of the subfamilies above have been given familial status, and vice versa, by various authors, but most workers refer to these groups in some fashion. Examples of how these groups have been classified by various authors are shown in figure 2. (Numbers of fossil genera and species are given in the section A List of Fossil Clu-



peomorphs.) Estimates of valid *Recent* genera and species in each clupeoid group (based on Whitehead, 1968, 1973; Wongratana, 1980; Nelson and Rothman, 1973; Robins et al., 1980; Poll, 1974; Poll and Roberts, 1976; and G. Nelson, personal commun.) are as follows:

	Genera (number)	Species (number)
Chirocentridae	1	2
Engraulidae	15	130
Dussumieriidae	4	11
Pellonulinae	21	41
Clupeinae	17	61
Dorosomatinae	7	22
Alosinae	8	19
Pristigasterinae	9	30
Congothrissinae	1	1
Total	83	317

The relationships of these groups to one another are poorly known, as indicated by the polychotomous nature of the branching diagrams in figure 2. This is partly the result of the way in which clupeoids have been studied in the past. Several groups (such as the engraulids, dussumieriines, and dorosomatines) were found to be autapomorphic (unique) in some way by various authors, and were classified as distinct groups. Other groups, such as Clupeinae, became repositories for the remaining clupeoids. Synapomorphies for groups such as Clupeinae (as those groups have traditionally been constructed) have yet to be discovered, and the interrelationships of the clupeoid subgroups are virtually unknown.

The clupeoid classification that will be used here is as follows:

- Clupeoidei
  - Pristigasteroidea
  - Engrauloidea
  - Clupeoidea
    - Chirocentridae
    - Clupeidae
      - Pellonulinae (including *Congothrissa*)
      - Dussumieriinae
      - Dorosomatinae
      - Alosinae
      - Clupeinae

This classification best expresses the cladis-

tic interrelationships recognized here based on the skeleton. This classification is similar to that of Nelson (1970a) except for placement of *Chirocentrus*. Within Clupeoidea, derived characters were found only for Pellonulinae and Dussumieriinae. Work is still in progress by the author on the interrelationships of the remaining members. The subfamilies Dorosomatinae, Alosinae, and Clupeinae [which were recognized as clupeid subfamilies by Svetovidov (1952)] are used here merely as groups of convenience, and no implication of their being monophyletic is intended.

The systematics of clupeomorph fishes will be discussed further in two sections below (in descending phylogenetic order). The Clupeomorpha and other higher groups (subordinal or higher) will be discussed in the section Systematic Discussion of Clupeomorph Fishes. This will be followed immediately by a systematic discussion of clupeoids in the section entitled Systematic Discussion of Clupeoid Fishes. These sections will emphasize osteological information.

METHODS

SYSTEMATIC METHODOLOGY: The method of classification used here is phylogenetic analysis (also referred to as cladistics) which was put forth formally by Hennig (1950, 1966). Within a cladistic classification, taxa are grouped hierarchically on the basis of shared derived characters (synapomorphies) rather than on their overall similarity. These characters shared by a specific group are hypothesized to be uniquely derived for that group, thus uniquely defining it. The derived character information is summarized in the most parsimonious way possible by a cladogram. A cladogram does not require any theory of phylogeny, but is simply the most parsimonious (or efficient) ordering of a data matrix. It reflects increasing levels of generality of unique character distributions; and, given the assumption that nature is structured hierarchically, a cladogram is considered to be the best estimate of the true phylogeny. "Derived" characters are identified through ontogeny (the more derived character state is the later state) or by finding unique group characters (the presence of ver-

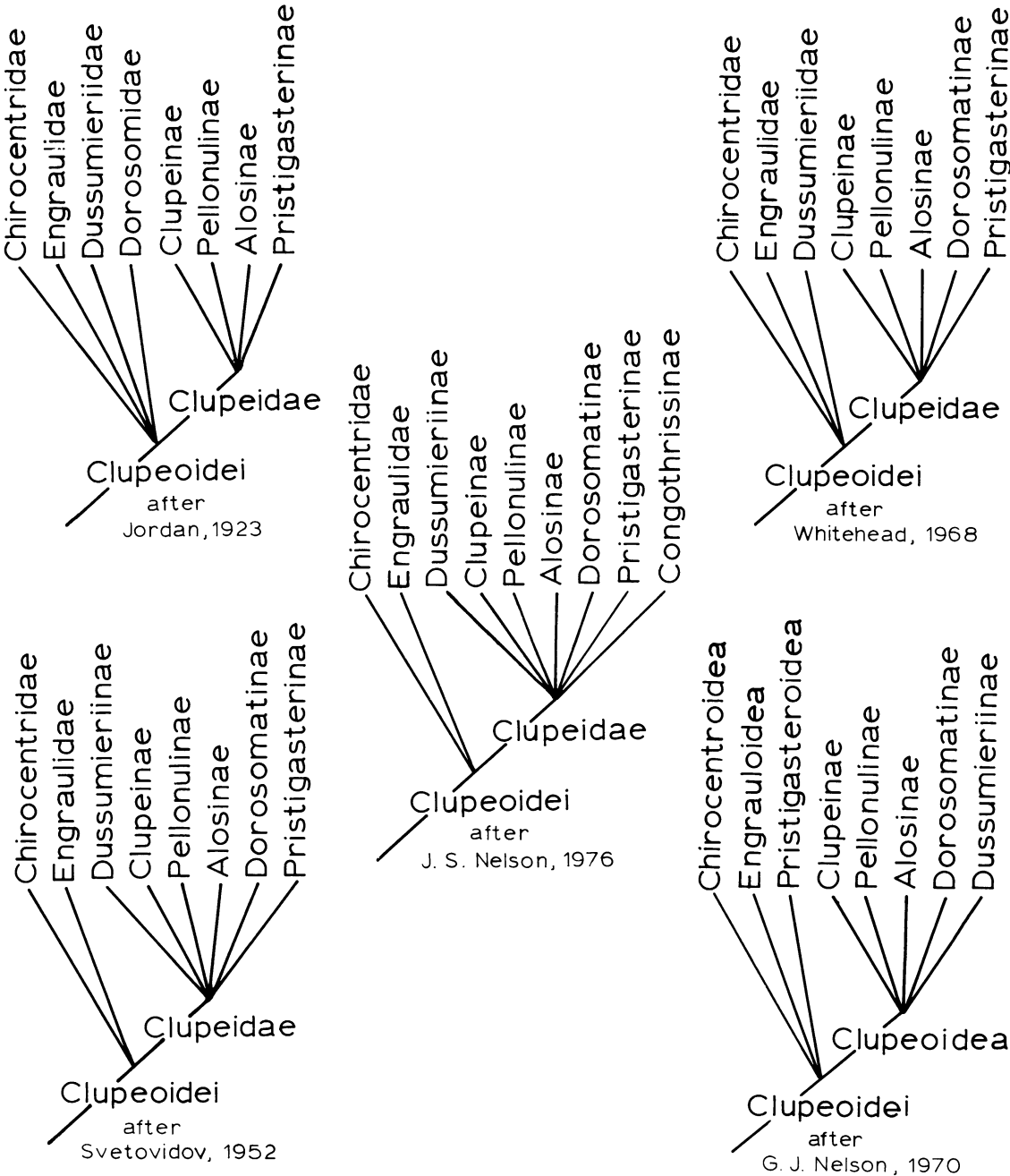


FIG. 2. Clupeoid classifications by various authors.

tebrae in vertebrates, for example). The absence of a derived character (such as the absence of vertebrae in "invertebrates"), unless secondarily lost, is not considered to be indicative of a natural group. A character which is unique to a particular group is also thought

to be derived for that group. When incongruent characters are found at some level in the analysis, the principle of parsimony is used to choose among alternative explanations of the data.

Recognized taxa are those which are

monophyletic (in the sense of Hennig, 1966); a monophyletic group contains all the descendants, and only the descendants, of a common ancestor. Cladistic techniques are described at length in Nelson and Platnick (1981) and Wiley (1981).

**PREPARATION TECHNIQUES:** Cleared and counterstained specimens of Recent clupeiforms were prepared according to the alcian blue-alizarin red staining method of Dingerkus and Uhler (1977). All species of Recent nonengraulid clupeomorphs available to the author, and one species of each engraulid genus available to the author were cleared and stained (see Materials section below). As illustrated by the number of different species used here, this study emphasizes nonengraulid clupeomorph taxa. Wherever possible, several specimens of each species were prepared to examine intraspecific variation (numbers of each species examined here are given in the Materials section). In the few cases where available material could not be cleared and stained, radiographs were prepared to enable a cursory examination of the osteology.

Identification of specimens to species was done (mostly by Gareth Nelson—AMNH) using keys modified from Hildebrand (1963), Poll (1965), Whitehead (various publications), and Wongratana (1980).

Fossil material was prepared, where necessary, using needles under a dissecting microscope. In addition, some material was prepared completely out of the matrix using the epoxy transfer technique of Toombs and Rixon (1959).

Anatomical illustrations were prepared from sketches of structures as viewed through a Wild TYP 256575 camera lucida mounted on a Wild M-8 dissecting microscope. In all drawings, anterior direction faces left unless otherwise noted in plate caption.

**COUNTS, MEASUREMENTS, AND DESCRIPTIVE TERMINOLOGY:** Preural vertebrae were counted anteriorly from the anteriormost vertebra, bearing the first neural spine, back to preural 1 (the centrum bearing the parhypural). Counts of dorsal and anal fin pterygiophores (proximal radials) include the last modified element (the "stay" of Weitzman, 1962, and others). Counts given of pleural ribs are for pairs of ribs and they include the

posterior "floating" ribs, even when the element is reduced in size. Branched epurals are counted as two elements (fused at the base) and are indicated by an asterisk. Names for skeletal structures are mostly those used by Patterson, 1975a (braincase); Patterson and Rosen, 1977 (jaws and caudal skeleton); Nelson, 1970a (gill arches); Grande, 1982a (scutes); and Weitzman, 1962 (other parts of the skeleton).

The names of all fossil taxa mentioned in the text are preceded by a dagger (†). The use of quotation marks around taxonomic names is explained below in the section entitled A List of Fossil Clupeomorphs.

**GENERAL PHYLOGENETIC PLAN FOR CHOOSING OUTGROUPS:** The general teleost classification of Patterson and Rosen (1977) was used here in selecting outgroup species for comparison. That classification system is shown (for the Recent groups) in figure 1B.

## ABBREVIATIONS

### INSTITUTIONAL:

- AM, The Australian Museum, Sydney, New South Wales
- AMNH, American Museum of Natural History, New York
- ANSP, Academy of Natural Sciences, Philadelphia
- BMNH, British Museum (Natural History), London
- CAS, California Academy of Sciences, San Francisco
- CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
- FMNH, Field Museum of Natural History, Chicago
- MCZ, Museum of Comparative Zoology, Cambridge
- MNHN, Museum National d'Histoire Naturelle, Paris
- MRAC, Musée Royal de l'Afrique Centrale, Tervuren
- PU, Museum of Natural History, Princeton University, Princeton, New Jersey
- SMMP, Science Museum of Minnesota, St. Paul, Minnesota
- SU, Stanford University collection, deposited at CAS
- UAVP, The University of Alberta, Canada
- UMMZ, Museum of Zoology, University of Michigan, Ann Arbor
- USNM, National Museum of Natural History, Washington, D.C.



## ANATOMICAL:

- aa, anguloarticular  
 ac, anterior ceratohyal  
 af, auditory fenestra  
 afn, anterior frontal fontnelle  
 AFS, anal fin stay  
 ao, antorbital  
 B, basibranchial  
 BH, basihyal  
 BHO, ossification of the basihyal  
 BHT, basihyal tooth plate  
 bo, basioccipital  
 bpr, prootic bulla  
 bpt, pterotic bulla  
 br, branchiostegal ray  
 BT, basibranchial toothplate  
 C, ceratobranchial  
 ci, circuli (surface ridges)  
 cl, cleithrum  
 cm, coronomeckelian  
 co, coracoid  
 de, dentary  
 DFL, dorsal filament  
 DFS, dorsal fin stay  
 dh, dorsal hypohyal  
 DR, distal radial  
 E, epibranchial  
 ecp, ectopterygoid  
 enpt, endopterygoid  
 ep, epural  
 epo, epioccipital  
 exo, exoccipital  
 ext, extrascapular  
 extc, extrascapular canal  
 fm, foramen magnum  
 fp, pre-epiotic fossa  
 fr, frontal  
 FR, fin ray  
 frc, supraorbital canal  
 fsb, foramen through which anterior swimbladder diverticulum enters neurocranium  
 gsb, groove for cranial diverticulum of swimbladder  
 H, hypobranchial  
 hm, hyomandibular  
 hs, hemal spine  
 hyp, hypural  
 I, infrapharyngobranchials  
 ic, foramen for internal carotid artery  
 ih, interhyal  
 int, intercalar  
 io, infraorbital (io<sub>1</sub> = lachrymal; io<sub>6</sub> = dermo-sphenotic)  
 ioc, infraorbital canal  
 iop, interopercle  
 ks, median keel of abdominal scute  
 le, lateral ethmoid  
 ls, ascending arm of abdominal scute  
 mac, mandibular canal  
 mc, mesocoracoid  
 mes, mesethmoid  
 MP, mediopharyngobranchial  
 MR, middle radial  
 mtp, metapterygoid  
 mx, maxilla  
 na, nasal  
 nac, nasal canal  
 ns, neural spine  
 of, optic fenestra  
 op, opercle  
 or, foramen for orbital artery  
 os, orbitosphenoid  
 pa, parietal  
 pac, parietal canal  
 pal, palatine  
 pb, pelvic bone  
 pbr, pelvic radials  
 pc, posterior ceratohyal  
 pcl, postcleithrum  
 pfn, posterior frontal fontanelle  
 ph, parhypural  
 pmx, premaxilla  
 pop, preopercle  
 popc, preopercular canal  
 PR, proximal radial (in dorsal and anal fins = pterygiophore)  
 pro, prootic  
 ps, parasphenoid  
 pto, pterotic  
 ptoc, temporal canal (pterotic canal)  
 ptp, pterotic spine  
 pts, pterosphenoid  
 ptt, posttemporal  
 pttc, posttemporal canal  
 pu, preural vertebra  
 q, quadrate  
 r, retroarticular  
 rd, radii (grooves)  
 rec, common opening to recessus for infraorbital, preopercular, lateral extrascapular, and pterotic sensory canals  
 rei, opening to recessus for infraorbital sensory canal  
 rep, opening to recessus for preopercular sensory canal  
 rept, opening to recessus for pterotic extension of sensory canal  
 rex, opening to recessus for lateral extrascapular sensory canal  
 s, symplectic  
 sc, scapula  
 smx, supramaxilla  
 so, supraorbital  
 soc, supraoccipital  
 sop, subopercle

sp, sphenotic  
 tf, temporal foramen  
 u, ural vertebra  
 un, uroneural  
 UP, upper pharyngeal toothplate  
 vh, ventral hypohyal  
 vo, vomer  
 VII, foramen for facial nerve  
 IX, foramen for glossopharyngeal nerve  
 X, vagus foramen

### USE OF VERNACULAR NAMES

Vernacular names are uncapitalized and have the particular endings listed below.

## MATERIAL EXAMINED

Skeletal preparations of over 750 clupeomorph specimens representing 94 genera (83 Recent) and 155 species (140 Recent) were prepared and examined in detail to generate data for the cladograms and tables presented in this paper. This sample includes members of nearly all described genera and about half of all described species of Recent clupeomorphs.

In addition to the material listed below (which was examined in detail), specimens or illustrations of over 150 additional fossil species (listed in section entitled A List of Fossil Clupeomorphs) were briefly examined. These fossil species include all species known to the author which belong in Clupeomorpha as defined here.

All Recent material is cleared and stained (see Methods section) unless otherwise indicated. In addition to the clupeomorph material listed below, specimens of †*Ornategulum sardinioides* (AMNH 3820, 3858, 6105, 6475, and 6580; BMNH 47877) (sl = 79–250 mm); *Hiodon tergisus* (AMNH 23754 sw) (sl = 64 mm); *Megalops atlantica* (AMNH 27478 sw) (sl = 80 mm); *Salmo trutta* (AMNH 21164) (sl = 45–80 mm); and various fossil and Recent specimens cited in text were used for outgroup information. Various publications cited in text were also used for outgroup comparison. Much of the information below on Recent type species nomenclature is after Whitehead (various publications) and Hildebrand (1963). Specimens

Names ending in *in* are tribes (such as *ehiravin* for *Ehiravini*).

Names ending in *ine* are subfamilies (such as *clupeine* for *Clupeinae*).

Names ending in *id* are families (such as *clupeid* for *Clupeidae*).

Names ending in *ide* are superfamilies (such as *clupeide* for *Clupeoidea*).

Names ending in *oid* are suborders (such as *clupeoid* for *Clupeoidei*).

Names ending in *form* are orders (such as *clupeiforms* for *Clupeiformes*).

Names ending in *morph* are superorders (such as *clupeomorphs* for *Clupeomorpha*).

within Clupeomorpha examined in detail for this study include the following species:

DIVISION: †CLUPEOMORPHA DIVISION 1  
 ORDER: UNNAMED

†*Erichalcis* Forey, 1975, p. 152 (type species †*E. arcta* Forey, 1975, by monotypy).

†*E. arcta* Forey, 1975—specimens (UAVP 8606: holotype; UAVP 8598, 8628, 8629, and 17535) from the Lower Cretaceous black, marine shales, and limestones of the Loon River Formation, Northwest Territories, Canada (sl = to about 100 mm: most material incomplete).

DIVISION: CLUPEOMORPHA DIVISION 2  
 ORDER: *INCERTAE SEDIS*  
 (NOT CLUPEIFORMES)

†*Armigatus* Grande, 1982, p. 4 (type species †*Clupea brevissimus* Blainville, 1818, by original designation).

†*A. brevissimus* (Blainville, 1818)—12 specimens (AMNH 3465, 3658, 3818, 5775, 5776, and 5811) from the Upper Cretaceous marine deposits of Hajula and Hakel, Lebanon (sl = 53 to 64 mm).

DIVISION: CLUPEOMORPHA DIVISION 2  
 ORDER: †ELLIMMICHTHYIFORMES  
 FAMILY: †ELLIMMICHTHYIDAE

†*Diplomystus* Cope, 1877, p. 808 (type species †*Diplomystus dentatus* Cope, 1877, by original designation).

†*D. dentatus* Cope, 1877—17 specimens (SMMP 78.9.14, AMNH 763, 2477 [holotype], 2480,

2483, 2979, 8109, 8168, 10465, 10466, 10469–10471, 10473–10476) from Early Eocene freshwater lacustrine deposits of the Green River Formation, Wyoming (F-1 and F-2 localities of Grande, 1980) (sl = 27–393 mm).

†*D. birdi* Woodward, 1895—7 specimens (AMNH 5745, 5798, 6113, 10188, 10189, 11106, and 11425) from the Upper Cretaceous marine deposits of Hajula and Hakel, Lebanon (sl = 51–65 mm).

†*D. dubertreti* Signeux, 1951—2 specimens (MNHN 1946-18-17 [the holotype]) from the Upper Cretaceous marine deposits of Sahel Alma, Lebanon (sl = 130 mm); and FMNH PF706, same locality (specimen missing tail section but about the same size as MNHN specimen above).

†*Ellimmichthys* Jordan, 1919, p. 27 (type species †*Diplomystus longicostatus* Cope, 1886, by original designation).

†*E. longicostatus* (Cope, 1886)—6 specimens; 2 specimens (including neotype) on a single slab (AMNH 734) and BMNH 8256–8258, 7109, and 10350; all from the Lower Cretaceous marine deposits along the coast near Itacaranha, Bahia, Brazil (sl = 88–101 mm).

#### DIVISION: CLUPEOMORPHA DIVISION 2

##### ORDER: CLUPEIFORMES

##### SUBORDER: DENTICIPITOIDEI

##### FAMILY: DENTICIPITIDAE

*Denticeps* Clausen, 1959, p. 147 (type species *Denticeps clupeoides* Clausen, 1959, by original designation).

*D. clupeoides* Clausen, 1959—3 specimens (AMNH 53082 sw and FMNH 96513) from a freshwater stream on the Dahomey–Nigerian border, Africa (sl = 18–38 mm).

†*Palaeodenticeps* Greenwood, 1960, p. 6 (type species †*Palaeodenticeps tanganyikae* Greenwood, 1960, by original designation).

†*P. tanganyikae* Greenwood, 1960—2 specimens (BMNH P.42610 [the holotype] and BMNH P.42613) from the middle to late Tertiary freshwater lacustrine deposits near the western margin of the Iramba Plateau, Singida district, Tanganyika Territory (sl = 28 mm).

#### DIVISION: CLUPEOMORPHA DIVISION 2

##### ORDER: CLUPEIFORMES

##### SUBORDER: CLUPEOIDEI

##### SUPERFAMILY: PRISTIGASTEROIDEA

*Chirocentrodon* Günther, 1868, p. 463 (type species by monotypy, *Chirocentrodon taeniatus*

Günther, 1868 = *Pellona bleekermani* Poey, 1867). See Hildebrand 1963, p. 438.

*C. bleekermani* (Poey, 1867)—3 specimens (AMNH 10118 sw) probably from western Atlantic waters off the coast of eastern South America (sl = 78–79 mm).

†*Gastroclupea* Signeux, 1964, p. 291 (type species †*Gastroclupea branisai* Signeux, 1964, by monotypy).

†*G. branisai* Signeux, 1964—8 specimens (MNHN 1963-11-1, 1963-11-2, 1963-11-10, 1963-11-13, 1963-11-14, 1963-11-16, 1963-11-20, and AMNH 8674) from Upper Cretaceous deposits of the El Molino Formation, Bolivia (sl = about 30–50 mm).

*Ilisha* Richardson, 1846, p. 306 (type species by monotypy, *Ilisha abnormalis* Richardson, 1846 = *Alosa elongata* Bennett, 1830). See Whitehead 1970, p. 20.

*I. elongata* (Bennett, 1830)—1 specimen (AMNH 35811 sw) from western Pacific waters off the coast of Fukien Province, China (sl = 127 mm).

*I. africana* (Bloch, 1795)—4 specimens (AMNH 17730 sw) from eastern Atlantic waters of Banana, Congo, western Africa (sl = 43–60 mm).

*I. indica* (Swainson, 1839)—1 specimen (AMNH 53083 sw) probably from Indo-Pacific waters (sl = 71 mm).

*I. furthii* (Steindachner, 1875)—5 specimens (AMNH 11426 sw) from eastern Pacific drainage of the Rio Chucunaque, Panama (sl = 36–42 mm).

*I. amazonica* (Miranda-Ribeiro, 1923)—1 specimen (AMNH 10187 sw) in western Atlantic waters at the mouth of the Rio Trombetas, Brazil (sl = 146 mm).

*Neoopisthopterus* Hildebrand, 1948, p. 6 (type species *Odontognathus tropicus* Hildebrand, 1946, by original designation).

*N. tropicus* (Hildebrand, 1946)—1 specimen (AMNH 53084 sw) probably from eastern Pacific waters off the coast of Panama (sl = 55 mm).

*Odontognathus* Lacépède, 1800, p. 220 (type species *Odontognathus mucronatus* by monotypy).

*O. mucronatus* Lacépède, 1800—3 specimens (AMNH 20749 sw) from Rio de Janeiro, Brazil (sl = 87–147 mm).

*O. panamensis* (Steindachner, 1876)—1 specimen (AMNH 10189 sw) from the Gulf of Nicoya, Costa Rica, western Central America (sl = 146 mm).

*Opisthopterus* Gill, 1861, p. 38 (type species by original designation, *Pristigaster tartoor* Valenciennes, 1847 = *Pristigaster tardoore* Cu-



- vier, 1829). See Whitehead, 1967, pp. 121–122.
- O. valenciennesi* Bleeker, 1872—1 specimen (AMNH 17586 sw) from Sumatra (sl = 43 mm).
- O. equitorialis* Hildebrand, 1946—2 specimens (AMNH 10188 sw) from the Gulf of Nicoya, Costa Rica, western Central America (sl = 120–132 mm).
- Pellona* Valenciennes, 1847, p. 300 [type species designated by Gill, 1861, *Pellona orbignyana* Valenciennes, 1847 = *Pellona flavipinnis* (Valenciennes, 1837)]. See Whitehead, 1967.
- P. ditchela* Valenciennes, 1847—2 specimens (AMNH 18412 sw and USNM 72510) from Java (sl = 79–84 mm).
- P. flavipinnis* (Valenciennes, 1837)—1 specimen (AMNH 39957 sw) from the mouth of Rio Baures (Blanco), Bolivia (sl = 160 mm).
- P. harroweri* (Fowler, 1917)—1 specimen (AMNH 20759 sw) from Rio de Janeiro, Brazil (sl = 64–80 mm).
- Pliosteostoma* Norman, 1923, p. 21 (type species by monotypy *Pristigaster lutipinnis* Jordan and Gilbert, 1882).
- P. lutipinnis* (Jordan and Gilbert, 1882)—(x-ray), 2 specimens (SU 39322) from Banderas Bay, Pacific coast of Mexico (sl = 119–137 mm).
- Pristigaster* Cuvier, 1817, p. 176 (type species by monotypy figured but no specific name given, but *Pristigaster* sp. Cuvier, 1817 = *Pristigaster cayanus* Cuvier, 1829).
- P. cayana* Cuvier, 1829—2 specimens (AMNH 10186 sw) from the coast of Brazil (sl = 83–91 mm).
- Raconda* Gray, 1831, p. 9 (type species by monotypy, *Raconda russeliana* Gray, 1831).
- R. russeliana* Gray, 1831—(x-ray), 1 specimen (ANSP 87573) from the coast of Bombay, India (sl = 178 mm).
- DIVISION: CLUPEOMORPHA DIVISION 2  
ORDER: CLUPEIFORMES  
SUPERORDER: CLUPEOIDEI  
SUPERFAMILY: ENGRAULOIDEA
- Anchoa* Jordan and Evermann, 1927, p. 501 (type species, *Engraulis compressus* Girard, 1858, by original designation).
- A. compressa* (Girard, 1858)—2 specimens (AMNH 2671 sw) from eastern Pacific waters off the coast of San Diego, California (sl = 93–95 mm).
- Anchovia* Jordan and Evermann, 1896, p. 449 (type species, *Engraulis macrolepidotus* Kner and Steindachner, 1865, by original designation).
- A. clupeioides* (Swainson, 1839)—13 specimens (AMNH 40893 sw) from the Corintijn River, Nickerie District, Suriname (sl = 35–47 mm).
- Anchoviella* Fowler, 1911, p. 211 (type species *Engraulis perfasciatus* Poey, 1860, by original designation).
- A. perfasciata* (Poey, 1860)—(x-rays), 7 specimens; 3 (SU 4852) from Jamaica (sl = 49–67 mm) and 4 (SU 4249) from St. Lucia, West Indies (sl = 42–48 mm).
- Cetengraulis* Günther, 1868, p. 383 (type species, *Engraulis edentulus* Cuvier, 1829, designated by Jordan and Evermann, 1896, p. 450).
- C. edentulus* (Cuvier, 1829)—3 specimens (AMNH 37073 sw) from Port au Prince, Haiti (sl = 79–83 mm).
- Coilia* Gray, 1830, fig. 3 (caption only) (type species *Coilia hamiltoni* Gray, 1831 = *Mystus ramcarati* Hamilton-Buchanan, 1822).
- C. rendahli* Jordan and Seale, 1926—1 specimen (AMNH 37035 sw) from western Pacific waters off Foochow, Fukien Province, China (sl = 123 mm).
- Encrasicholina* Fowler, 1938, p. 156 (type species *Encrasicholina punctifer* Fowler, 1938, by original designation).
- E. purpurea* (Fowler, 1900)—6 specimens (AMNH 54601 sw) from Kameoke Bay, Hawaii (sl = 44–67 mm).
- Engraulis* Cuvier, 1817, p. 98 (type species *Clupea encrasicolus* Linnaeus, 1758, designated by Fleming, 1822).
- E. mordax* Girard, 1856—10 specimens (AMNH 54600 sw) from eastern Pacific waters off the coast of California (sl = 52–61 mm).
- Lycengraulis* Günther, 1868, p. 385 (type species *Engraulis grossidens* Cuvier, 1828, designated by Jordan and Evermann, 1896).
- L. grossidens* (Cuvier, 1828)—2 specimens (AMNH 20751 sw) from the Rio de Janeiro, Brazil (sl = 92–97 mm).
- Lycotrissa* Günther, 1868, p. 7 (type species *Engraulis crocodilus* Bleeker, 1851, by monotypy).
- L. crocodilus* (Bleeker, 1851)—(x-ray), 1 specimen (USNM 103302) from Thailand (sl = 189 mm).
- Pterengraulis* Günther, 1868, p. 384 (type species *Clupea atherinoides* Linnaeus, 1758, by monotypy).
- P. atherinoides* (Linnaeus, 1758)—3 specimens (AMNH 48888 sw) from the Rio Orinoco, Venezuela (sl = 36–97 mm).
- Setipinna* Swainson, 1839, p. 292 (type species, *Setipinna megalura* = *Clupea phasa* Hamilton-Buchanan, 1822, designated by Swain, 1882).
- S. papuensis* Munro, 1964—2 specimens

- (AMNH 17551 sw) from the Meraube River, New Guinea (sl = 78–85 mm).
- Stolephorus* Lacépède, 1803, p. 381 (type species, *Stolephorus commersonii* Lacépède, 1803, by subsequent designation—decided by Opinion 93 of the International Commission—see Whitehead, 1967a, pp. 135–136 for explanation).
- S. indicus* (van Hasselt, 1823)—5 specimens (AMNH 32820 sw) from Indian Ocean waters, off the coast of Kenya (sl = 78–94 mm).
- Thrissina* Jordan and Seale, 1925, p. 30 (type species *Clupea baelama* Forskål, 1775, by original designation).
- T. baelama* (Forskål, 1775)—3 specimens (AMNH 27026 sw) from a stream in Guam, west Pacific (sl = 39–104 mm).
- Thryssa* Cuvier, 1829, p. 176 (type species *Clupea setirostris* Broussonet, 1782, designated by Jordan, 1917).
- T. hamiltoni* (Gray, 1835)—1 specimen (AMNH 38188 sw) from Pacific waters off the coast of Tam-Sui, Taiwan and 5 specimens (USNM 217037) from a freshwater stream in Fly Basin, Papua, New Guinea (sl = 27–99 mm).
- DIVISION: CLUPEOMORPHA DIVISION 2  
ORDER: CLUPEIFORMES  
SUBORDER: CLUPEOIDEI  
SUPERFAMILY: CLUPEOIDEA  
FAMILY: CHIROCENTRIDAE
- Chirocentrus* Cuvier, 1817, p. 178 (type species *Clupea dorab* Förskal, 1775, by monotypy).
- C. dorab* (Förskal, 1775)—2 specimens; 1 specimen (UMMZ 180095) from Java and 1 specimen (AMNH 54622 sw) with no locality information (sl = 132–275 mm).
- DIVISION: CLUPEOMORPHA DIVISION 2  
ORDER: CLUPEIFORMES  
SUBORDER: CLUPEOIDEI  
SUPERFAMILY: CLUPEOIDEA  
FAMILY: CLUPEIDAE  
SUBFAMILY: PELLONULINAE
- Clupeichthys* Bleeker, 1855, p. 274 (type species *Clupeichthys goniognathus* Bleeker, 1855, by monotypy).
- C. goniognathus* Bleeker, 1855—1 specimen (MCZ 47178) from the Mekong River, Thailand (sl = 44 mm).
- C. bleekeri* (Hardenberg, 1936)—2 specimens (BMNH 1979: 3 21 145 152) from Kaupas, Borneo (sl = 51–54 mm).
- Clupeoides* Bleeker, 1851, p. 274 (type species *Clupeoides borneensis* by original designation).
- C. papuensis* (Ramsay and Ogilby, 1886)—2 specimens (BMNH 1977: 11 17 1-19) taken from the Fly River, New Guinea (sl = 41–48 mm).
- Congothrissa* Poll, 1964, p. 8 (type species *Congothrissa gossei* by original designation).
- C. gossei* Poll, 1964—3 specimens (MRAC 102019–022) from the Congo River, Congo Basin (sl = 23–26 mm).
- Corica* Hamilton-Buchanan, 1822, p. 253 (type species *Corica soborna* Hamilton-Buchanan, 1822, by monotypy).
- C. laciniata* Fowler, 1935—1 specimen (BMNH 1979: 8 11 850) from Song Khla Lake, Thailand, and 3 specimens (ANSP 89414) from Tachin, Siam (sl = 40–51 mm).
- Cynothrissa* Regan, 1917c, p. 203 (type species *Cynothrissa mento* Regan, 1917c, designated by Jordan, 1920, p. 563).
- C. mento* Regan, 1917c—4 specimens (AMNH 10119 sw [two] and BMNH 1967: 12 29-179 [two]) taken from the Niger River, Jebba, Nigeria (sl = 94–112 mm).
- C. ansorgii* Boulenger, 1916—2 specimens (AMNH 6397 sw) from the lower Congo River, Boma, Congo (sl = 60–66 mm).
- Ehirava* Deraniyagala, 1929, p. 34 (type species *Ehirava fluviatilis* Deraniyagala, 1929, by monotypy).
- E. malabarica* (Day, 1873)—1 specimen (BMNH 1889 2 1 2048) taken from Malabar, India (sl = 45 mm).
- Gilchristella* Fowler, 1935, p. 365 (type species *Spratelloides aestuarius* Gilchrist, 1914, by original designation).
- G. sp.*—2 specimens (BMNH 1973: 2 9 1-30) taken from the Kowie River, South Africa (sl = 39–40 mm).
- Hyperlophus* Ogilby, 1892, p. 26 [type species *Hyperlophus spratellides*, Ogilby, 1892 (by monotypy) = *H. vittatus* (Castelnau, 1875)—see McCulloch, 1917].
- H. vittatus* (Castelnau, 1875)—16 specimens (AMNH 3050 sw) from the east coast of Australia (sl = 56–87 mm).
- H. translucidus* McCulloch, 1917—3 specimens (AM I 16743-001—from Ryde Bridge, New South Wales; AM I 22854-001—from Lane Cove River, New South Wales; and AM uncatalogued—from Sydney Harbour, Parramatta River, New South Wales) (sl = 47–50 mm).
- †*Knightsia* Jordan, 1907, p. 136 (type species †*Knightsia eocaena* Jordan, 1907).
- †*K. eocaena* Jordan, 1907—29 specimens (AMNH 762, 795a, 795b, 796, 810a–810f, 1339, 1800, 4299, 4300, 9842, 10425–10427, 10418–10423, 11101–11103; USNM 4022;

- and SMMP 78.9.9) from Early Eocene freshwater lacustrine deposits of the Green River Formation, Wyoming (F-1 and F-2 localities of Grande, 1980) (sl = 20–135 mm).
- †*K. alta* (Leidy, 1873)—21 specimens (AMNH 1815, 2500, 2682, 2688, 10428–10436, 10442–10447, 10449, and 10452) from Early and Middle Eocene freshwater lacustrine deposits of the Green River Formation, Wyoming (F-1, G-3, and G-4 localities of Grande, 1980) (sl = 48–135 mm).
- †*K. vetusta* Grande, 1982b—10 specimens (AMNH 10406, 10408–10413, and 10415–10417) from Middle Paleocene freshwater deposits of the Tongue River Formation near Bay Horse, Montana (Powder River County) (sl = 55–70 mm).
- Laeviscutella* Poll, Whitehead, and Hopson, 1965, p. 279 (type species *Laeviscutella dekimpei* Poll, Whitehead, and Hopson, 1965, by monotypy).
- L. dekimpei* Poll, Whitehead, and Hopson, 1965—2 specimens (BMNH 1965: 77 10-14) from Lake Nokove, Dahomey, Western Africa (sl = 39–43 mm).
- Limnothrissa* Regan, 1917c, p. 207 (type species *Limnothrissa miodon* Regan, 1917c, by monotypy).
- L. miodon* Regan, 1917c—3 specimens (BMNH 1973 1 2 152-200) from Zambia, Central Africa (sl = 50–72 mm).
- Microthrissa* Boulenger, 1902, p. 26 (type species *Microthrissa royauxi* Boulenger, 1902, by monotypy).
- M. royauxi* Boulenger, 1902—4 specimens (AMNH 5830 sw) from the Zaire (Congo) River, Kisangani (Stanleyville), Zaire, Central Africa (sl = 42–63 mm).
- M. minuta* Poll, 1974—1 specimen (MCZ 50208) from the Zaire (Congo) River, Zaire (sl = 46 mm).
- Nanothrissa* Poll, 1965, p. 309 (type species *Microthrissa parva* Regan, 1917c, by monotypy).
- N. parva* Poll, 1965—4 specimens (MCA 51479) from the Republic of Central Africa, Bangui Market (sl = 35–38 mm).
- N. stewarti* Poll and Roberts, 1976—3 specimens (MCZ 48167) from Lake Mai, near Ipeke, Zaire Basin (sl = 18–20 mm).
- Odaxothrissa* Boulenger, 1899, p. 64 (type species *Odaxothrissa losera* Boulenger, 1899, by monotypy).
- O. losera* Boulenger, 1899—2 specimens (BMNH 1919: 9 10 89-90 with no locality data, and AMNH [an x-ray]) from the Congo (sl = 122 mm).
- O. vittata* Regan, 1917c—6 specimens (MCZ 50349 [four] and ANNH 5890 sw [two]) all from the Zaire River, Zaire, Central Africa (sl = 38–125 mm).
- Pellonula* Günther, 1868, p. 452 (type species *Pellonula vorax* Günther, 1868, by monotypy).
- P. vorax* Günther, 1868—2 specimens (BMNH 1972: 10 18 1-125) from the Ivory Coast, West Africa (sl = 71–80 mm).
- P. afzeliusi* Johnels, 1954—2 specimens (MCZ 48621) from the Ivory Coast, Ghana and 2 specimens (SU 66469) from the Volta River, Ghana (sl = 38–39 mm).
- Poecilothrissa* Regan, 1917c, p. 201 (type species *Poecilothrissa congica*, by monotypy).
- P. congica* Regan, 1917c—2 specimens (BMNH 12 20 28-41) from the Tschungu River, Congo Basin (sl = 48–51 mm).
- Potamalosa* Ogilby, 1896, p. 504 (type species *Clupea richmondia* Macleay, 1880, by monotypy).
- P. richmondia* (Macleay, 1880)—3 specimens (AMNH 1737 sw) probably from New South Wales (sl = 150–156 mm).
- Potamothrissa* Regan, 1917c, p. 203 (type species *Pellonula obtusirostris* Boulenger, 1909, designated by Jordan, 1920, p. 563).
- P. obtusirostris* (Boulenger, 1909)—4 specimens (AMNH 5843) from the Zaire River, Kisangani (Stanleyville), Zaire, Central Africa (sl = 55–63 mm).
- P. acutirostris* (Boulenger, 1909)—1 specimen (BMNH 1962: 12 20 5 6) from the Zaire River, Zaire (sl = 63 mm).
- Spratellomorpha* Bertin, in F. Angel et al., 1946, p. 473 (type species *Sauvagella madagascariensis bianalis* Bertin, 1940, by monotypy).
- S. bianalis* (Bertin, 1940)—1 specimen (BMNH 1968: 4 4 104-110) from Mombasa, Kenya, eastern Africa (sl = 45 mm).
- Sierrathrissa* Thys van den Audenaerde, 1969, p. 386 (type species *Sierrathrissa leonensis* Thys van den Audenaerde, 1969, by original designation).
- S. leonensis* Thys van den Audenaerde, 1969—5 specimens (BMNH 1970: 9 24 177-216) from Volta Lake, Ghana (sl = 21–24 mm).
- Stolothrissa* Regan, 1917c, p. 206 (type species *Stolothrissa tanganicae* Regan, 1917, by monotypy).
- S. tanganicae* Regan, 1917c—2 specimens (BMNH uncatalogued) from Kigoma Bay, Lake Tanganyika, Central Africa (sl = 66–69 mm).
- Thrattidion* Roberts, 1972, p. 2 (type species *Thrattidion noctivagus* Roberts, 1972, by original designation).
- T. noctivagus* Roberts, 1972—3 specimens

(MCA 48162) from the Sanaga River, Cameroon, western Africa (sl = 15–16 mm).

DIVISION: CLUPEOMORPHA DIVISION 2

ORDER: CLUPEIFORMES

SUBORDER: CLUPEOIDEI

SUPERFAMILY: CLUPEOIDEA

FAMILY: CLUPEIDAE

SUBFAMILY: DUSSUMIERIINAE

*Dussumieria* Valenciennes, 1847, p. 467 (type species *Dussumieria acuta* Valenciennes, 1847, by monotypy).

*D. acuta* Valenciennes, 1847—2 specimens (AMNH 17555 sw) from Java, Indonesia (sl = 64–92 mm).

*Etrumeus* Bleeker, 1853, p. 48 (type species *Clupea micropus* Schlegel, 1846 by monotypy).

*E. micropus* (Bleeker, 1853)—2 specimens (AMNH 8840 sw) from western Pacific waters off the coast of Japan (sl = 77–86 mm).

*E. teres* (DeKay, 1842)—10 specimens, 5 (AMNH 736 sw) from Gravesend Bay, New York; and 5 specimens (AMNH 54603 sw) from the western central Atlantic (sl = 32–91 mm).

*E. acuminatus* Gilbert, 1891—6 specimens (AMNH 54602 sw) from eastern Pacific waters off the coast of California (sl = about 115–120 mm).

*Jenkinsia* Jordan and Evermann, 1896, p. 418 (type species by monotypy, *Dussumieria stolidifera* Jordan and Gilbert, 1885).

*J. stolidifera* (Jordan and Gilbert, 1885)—10 specimens (AMNH 2770 sw) from Key West, Florida (sl = 36–61 mm).

*J. lamprotaenia* (Gosse, 1851)—12 specimens (AMNH 28252 sw) from western Atlantic waters in the Bahamas (sl = 30–31 mm).

*Spratelloides* Bleeker, 1851, p. 29 (type species *Clupea argyrotaeniata* Bleeker, 1849b).

*S. delicatulus* (Bennett, 1831)—8 specimens (AMNH 54621 sw) from western Pacific waters (sl = 24–54 mm).

*S. gracilis* (Schlegel, 1846)—1 specimen (AMNH 54605 sw) from western Pacific waters off Peng-Hu, Taiwan (sl = 61 mm).

*S. robustus* Ogilby, 1897—4 specimens (AMNH 54604 sw) from Indo-Pacific waters off the coast of Western Australia (sl = 35–60 mm).

DIVISION: CLUPEOMORPHA DIVISION 2

ORDER: CLUPEIFORMES

SUBORDER: CLUPEOIDEI

SUPERFAMILY: CLUPEOIDEA

FAMILY: CLUPEIDAE

SUBFAMILY: DOROSOMATINAE<sup>1</sup>

*Anodontostoma* Bleeker, 1849b, p. 15 [type species by monotypy *Anodontostoma hasseltii* Bleeker, 1849b = *Anodontostoma chacunda* (Hamilton-Buchanan, 1822)].

*A. chacunda* (Hamilton-Buchanan, 1822)—3 specimens (AMNH 36577 sw) from Daru, Papua New Guinea (sl = 81–89 mm).

*Clupanodon* Lacépède, 1803, p. 465 (type species *Clupea thrissa* designated by Bleeker, 1872, p. 112).

*C. thrissa* (Lacépède, 1803)—3 specimens (AMNH 28122 sw) from Taipei, Taiwan (sl = 49–71 mm).

*Dorosoma* Rafinesque, 1820, p. 171 (type species by monotypy, *Dorosoma notata* Rafinesque, 1820 = *Megalops cepedianum* Lesuer, 1818).

*D. cepedianum* (Lesuer, 1818)—16 specimens (AMNH 37214 sw and AMNH 54606 sw) from the Hudson River, New York (sl = 85–87 mm).

*D. anale* Meek, 1904—2 specimens (AMNH 25673 sw) from the Usumacinta River, Chiapas, Mexico (sl = 81–86 mm).

*D. smithi* Hubbs and Miller, 1941—2 specimens (AMNH 28126 sw) from Rio del Fuerte, near San Blas, Mexico (sl = 97–98 mm).

*Gonialosa* Regan, 1917a, p. 315 (type species *Chatoessus modestus* Day, 1869a, designated by Jordan, 1920, p. 560).

*G. manmina* (Hamilton-Buchanan, 1822)—(x-ray), 2 specimens (ANSP 83988) from the Hughly River, North of Calcutta, India (sl = 56–57 mm).

*Konosirus* Jordan and Snyder, 1900, p. 349 (type species *Chatoessus punctatus* Temminck and Schlegel, 1846, by original designation).

*K. punctatus* (Temminck and Schlegel, 1846)—3 specimens; 2 specimens (AMNH 35812 sw) from Foochow, Fukien Province, China, and 1 specimen (AMNH 27731 sw) from western Pacific waters off the coast of South Korea (sl = 99 mm).

*Nematalosa* Regan, 1917a, p. 313 (type species *Clupea nasus* Bloch, 1795, designated by Jordan, 1920, p. 560).

*N. nasus* (Bloch, 1795)—1 specimen (AMNH 30106 sw) from the Arabian Sea, Bombay, India (sl = 80 mm).

*N. come* (Richardson, 1846)—3 specimens; 1 specimen (AMNH 4363 sw) from Halmahera Island, Indonesia and 2 specimens (AMNH 43405 sw)—no locality data (sl = 38–91 mm).

<sup>1</sup> No character information was found here to indicate this group as monophyletic.



- N. erebi* (Günther, 1868)—9 specimens (AMNH 28097 sw) from Western Australia (sl = 38–71 mm).  
*N. galathea* Nelson and Rothman, 1973—1 specimen (AMNH 28928 sw) from the Andaman Sea, Thailand (sl = 114 mm).  
*N. japonica* Regan, 1917a—1 specimen (AMNH 28124 sw) from Husing, Kao, Taiwan (sl = 128 mm).  
*N. vlaminghi* (Munro, 1956)—1 specimen (AMNH 30112 sw) from Western Australia (sl = 69 mm).  
*Signalosa* Everman and Kendall, 1898, p. 127 (type species, by original designation, *Signalosa atchafalaya* Evermann and Kendall, 1898 = *Dorosoma petenense* Günther, 1866).  
*S. petenense* (Günther, 1866)—23 specimens, 20 (54607 sw) from a stream flowing into Lake Texoma, Oklahoma, and 3 (AMNH 25621 sw) from Rio de la Pasion, Guatemala (sl = 18–67 mm).

## DIVISION: CLUPEOMORPHA DIVISION 2

## ORDER: CLUPEIFORMES

## SUBORDER: CLUPEOIDEI

## SUPERFAMILY: CLUPEOIDEA

## FAMILY: CLUPEIDAE

SUBFAMILY: ALOSINAE<sup>2</sup>

- Alosa* Link, 1790, p. 35 (type species *Clupea alosa* Linnaeus, 1758, designated by Cuvier, 1829, p. 319).  
*A. fallax* (Lacépède, 1803)—2 specimens (AMNH 32853 sw) from the Severn River, Somerset Co., England (sl = 62–64 mm).  
*A. sapidissima* (Wilson, 1811)—5 specimens (AMNH 39234 sw) from the Hudson River, New York (sl = 58–69 mm).  
*Brevoortia* Gill, 1861, p. 37 (type species by original designation, *Brevoortia menhaden* Gill = *Clupea tyrannus* Latrobe, 1802).  
*B. tyrannus* (Latrobe, 1802)—8 specimens (AMNH 27686 sw) from Pine Creek, Fairfield, Connecticut (sl = 38–47 mm).  
*B. patronus* Goode, 1879—3 specimens (AMNH 58618 sw) from Port Aransas, Texas (sl = 31–64 mm).  
*Caspialosa* Berg, 1915, p. 4 (type species *Clupea caspia* Fichwald, 1838).  
*C. tanaica* (Grimm, 1901)—6 specimens; 5 x-rays (AMNH 18046) and 1 cleared and stained specimen (AMNH 18046 sw) (sl = 260–262 mm).  
*Ethmalosa* Regan, 1917a, p. 302 (type species

- Alausa dorsalis* Valenciennes, 1847 = *Clupea fimbriata* Bowdich, 1825, by monotypy).  
*E. fimbriata* (Bowdich, 1825)—1 specimen (AMNH 54619 sw) from Abidjan Harbor, Ivory Coast, western Africa (sl = 75 mm).  
*Ethmidium* Thompson, 1916, p. 458 (type species by original designation, *Clupea notacanthoides* Steindachner, 1870 = *Alausa maculata* Valenciennes, 1847).  
*E. maculatum* (Valenciennes, 1847)—1 specimen (USNM 77314) from Cota, Chile (sl = about 100 mm).  
*Gudusia* Fowler, 1911, p. 207 (type species *Clupanodon chapra* Hamilton-Buchanan, 1822).  
*G. chapra* (Hamilton-Buchanan, 1822)—(x-rays), 2 specimens (ANSP 83993) collected from India, probably from freshwater (sl = 41–42 mm).  
*G. variegata* (Day, 1869b)—1 specimen (AMNH 8355 sw) from the Chindwin River, Monywa, Upper Burma, S.E. Asia (sl = 81 mm).  
*Hilsa* Regan, 1917a, p. 303 (type species *Clupea durbanensis* Regan, 1906).  
*H. kelee* (Cuvier, 1829)—2 specimens; 1 specimen (ANSP 53059-61) from Durban, South Africa and another (AMNH 32828 sw) from Mombasa, Kenya (sl = 87–101 mm).  
*Pomolobus* Rafinesque, 1820, p. 170 (type species *Pomolobus chrysochloris* Rafinesque, 1820, by monotypy).  
*P. aestivalis* (Mitchill, 1814)—5 specimens (AMNH 54617 sw) from the Hudson River, New York (sl = 68–70 mm).  
*P. pseudoharengus* (Wilson, 1811)—5 specimens (AMNH 54620 sw) from Lake Erie, Ohio (sl = 42–57 mm).

## DIVISION: CLUPEOMORPHA DIVISION 2

## ORDER: CLUPEIFORMES

## SUBORDER: CLUPEOIDEI

## SUPERFAMILY: CLUPEOIDEA

## FAMILY: CLUPEIDAE

SUBFAMILY: CLUPEINAE<sup>3</sup>

- Amblygaster* Bleeker, 1849, p. 73 (type species *Amblygaster clupeoides* Bleeker, 1849a, by monotypy).  
*A. leiogaster* (Valenciennes, 1847)—1 specimen (AMNH 17581 sw) from Manado, northern Celebes, western Indopacific (sl = 156 mm).  
*A. sirm* (Walbaum, 1792)—2 specimens (AMNH 19796 sw) from southeastern Celebes, western Indo-Pacific (sl = 104–105 mm).  
*Clupea* Linnaeus, 1758, p. 317 (type species, *Clu-*

<sup>2</sup> No character information was found here to indicate this group as monophyletic.

<sup>3</sup> No character information was found to indicate this group as monophyletic.

- pea harengus* Linnaeus, 1758, by implication).
- C. harengus* Linnaeus, 1758—5 specimens (AMNH 54608 sw) from western Atlantic waters off the coast of New Jersey (sl = 64–84 mm).
- C. pallasii* Valenciennes, 1847—9 specimens; 2 specimens (AMNH 54609 sw) from San Francisco Bay, California, and 7 specimens (AMNH 2703 sw) from eastern Pacific waters around the San Juan Islands off the coast of Washington State (sl = 46–115 mm).
- †“*Clupea*” *catapygoptera* Woodward, 1901 (Agassiz, *nomen nudum*)—12 specimens (AMNH 745, 745G, 791, 1354, 1813, 4105, 4107, 4109, and 4111; and BMNH 13461, 21529, and 41385) from Middle Eocene marine deposits of Monte Bolca, Italy (sl = 43–89 mm).
- Clupeonella* Kessler, 1877, p. 187 (type species *Clupeonella grimmi* Kessler, 1877).
- C. cultriventris* (Nordmann, 1840)—4 specimens (AMNH 36491 sw) from the Black Sea near Sulina (sl = 65–72 mm).
- †*Ellimma* Jordan, 1913, p. 79 (type species †*Ellipes branneri* Jordan, 1907).
- †*E. branneri* (Jordan, 1907)—15 specimens, (AMNH 10046–10060) from the Eocene black shale deposits at Riacho Doce, Alagoas, Brazil (sl = 22–87 mm).
- †*E. elmodenae* Jordan and Gilbert, 1919—CAS 55404 [holotype] and type description (sl of type = 96 mm; specimen now broken—sl from type description).
- Escualosa* Whitley, 1940, p. 402 (type species, by original designation, *Clupea macrolepis* Steindachner, 1879 = *Kowala thoracata* Valenciennes, 1847—see Whitehead, 1964a, p. 43).
- E. thoracata* (Valenciennes, 1847)—6 specimens (AMNH 32502 sw and 32503 sw) from Prachuab, Thailand (sl = 69–71 mm).
- †*Gosiutichthys* Grande, 1982b, p. 15 (type species, †*Gosiutichthys parvus*, by original designation).
- †*G. parvus* Grande, 1982b—56 specimens (AMNH 10456, 10457, and 10458) from early Middle Eocene freshwater deposits of the Green River Formation, just north of the Fontanelle Dam, southwestern Wyoming.
- Harengula* Cuvier and Valenciennes, 1847, p. 277 (type species *Harengula latulus* Cuvier and Valenciennes, 1847 = *Clupea clupeola* Cuvier, 1829—see Rivas, 1963, pp. 386–393).
- H. clupeola* (Cuvier, 1829)—3 specimens (AMNH 30354 sw) from western Atlantic waters off the Bahamas (sl = 60–73 mm).
- H. humeralis* (Cuvier, 1829)—10 specimens (AMNH 28954 sw) from the Bahamas and (AMNH 22010 sw) from western Atlantic waters off the coast of Florida (sl = 33–70 mm).
- H. jaguana* Poey, 1865—5 specimens (AMNH 28283 sw) from western Atlantic waters off Little Abaco, Bahamas (sl = 59–66 mm).
- H. thrissina* Jordan and Gilbert, 1882—3 specimens (AMNH 5475 sw) from eastern Pacific waters off Carmen Island, Gulf of California, Mexico (sl = 62–85 mm).
- Herklotsichthys* Whitley, 1951, p. 67 (type species *Harengula dispilonotus* Bleeker, 1852, by original designation).
- H. dispilonotus* (Bleeker, 1852)—4 specimens (AMNH 54611 sw) from western Pacific waters (sl = 58–75 mm).
- H. castelnaui* (Ogilby, 1897)—4 specimens (AMNH 54610 sw) from a bay near Cooktown, Australia (sl = 44–59 mm).
- H. koningsbergeri* (Weber and DeBeaufort, 1913)—5 specimens (AMNH 49470 sw) from Rio de Janeiro, Brazil (sl = 37–46 mm).
- H. quadrimaculatus* (Rüppell, 1837)—4 specimens (AMNH 32822 sw) from Mombasa, Kenya (sl = 75–100 mm).
- Lile* Jordan and Evermann, 1896, p. 428 (type species *Clupea stolidifera* Jordan and Gilbert, 1882).
- L. stolidifera* (Jordan and Gilbert, 1882)—2 specimens (AMNH 7100 sw) from Tumaco, Columbia (sl = 51–53 mm).
- L. piquitinga* (Schreiner and Ribeiro, 1903)—5 specimens (AMNH 3838 sw) from Natal, Brazil (sl = 60–66 mm).
- Opisthonema* Gill, 1861, p. 37 (type species, by original designation, *Opisthonema thrissa* Gill, 1861 = *Megalops oglina* LeSuer, 1818).
- O. oglinum* (LeSuer, 1818)—5 specimens (AMNH 54613 sw) from Seiste Key, Florida (sl = 53–60 mm).
- O. libertate* (Günther, 1866)—1 specimen (AMNH 14148 sw) from Topolobampo Bay, Mexico (sl = 61 mm).
- O. medirastre* Berry and Barrett, 1963—1 specimen (AMNH 54612 sw) from Pichilique Bay, Baja, California (sl = 63 mm).
- Platanichthys* Whitehead, 1968, p. 478 (type species, *Lile platana* Regan, 1917b, by original designation).
- P. platana* (Regan, 1917b)—2 specimens (BMNH 1969: 11 25 103–117) from Buenos Aires, Argentina (sl = 58–73 mm).
- Ramnogaster* Whitehead, 1964c, p. 324 (type species, *Clupea arcuata* Jenyns, 1842, by original designation).
- R. arcuata* (Jenyns, 1842)—2 specimens (ANSP

- 70406-9) from the Rio Uruguay, Uruguay (sl = 100 mm).
- R. pallida* (DeBuen, 1952)—5 specimens (AMNH 20711 sw) from the Rio de Janeiro, Brazil (sl = 39–48 mm).
- Rhinosardinia* Eigenmann, 1912, p. 445 (type species, *Rhinosardinia serrata* Eigenmann, 1912, by original designation).
- R. serrata* Eigenmann, 1912—4 specimens (AMNH 40923 sw and 40924 sw) from the Corintijn River, Suriname (sl = 18–46 mm).
- R. bahiensis* (Steindachner, 1880)—1 specimen (AMNH 40921 sw) from Suriname (sl = 36 mm).
- Sardinops* Hubbs, 1929, p. 264 (type species, *Melletta caerulea* Girard, 1854, by original designation).
- S. caerulea* (Girard, 1854)—1 specimen (AMNH 5457 sw) from Balenos Bay, Baja California (sl = 108 mm).
- S. melanosticta* (Temminck and Schlegel, 1846)—4 specimens (AMNH 17340 sw) from Japan (sl = 39–45 mm).
- S. neopilchardus* (Steindachner, 1879)—2 specimens (AMNH 48824 sw) from the Swan River, West Australia (sl = 139 mm).
- Sardina* Antipa, 1905, p. 54 (type species, *Clupea pilchardus* Walbaum, 1792, by original designation).
- S. pilchardus* (Walbaum, 1792)—9 specimens from St. George Bay, Lebanon (sl = 50–57 mm).
- Sardinella* Cuvier and Valenciennes, 1847, p. 263 (type species, *Sardinella aurita* Cuvier and Valenciennes, 1847, by original designation).
- S. aurita* Cuvier and Valenciennes, 1847—2 specimens (AMNH 44437 sw) from St. George Bay, Lebanon (sl = 112–116 mm).
- S. anchovia* Cuvier and Valenciennes, 1847—1 specimen (AMNH 1528 sw) from Dominica, West Indies and 4 specimens (AMNH 22552 sw) from Costa Rica (sl = 72–105 mm).
- S. gibbosa* (Bleeker, 1849a)—3 specimens (AMNH 32819 sw) from Mombasa, Kenya (sl = 94–99 mm).
- S. longiceps* Valenciennes, 1847—1 specimen (AMNH 17524 sw) from the East Indies (sl = 83 mm).
- S. maderensis* (Lowe, 1841)—6 specimens (AMNH 44448 sw) from St. George Bay, Lebanon (sl = 68–93 mm).
- S. marquesensis* Berry and Whitehead, 1968—5 specimens (AMNH 43496 sw) from Kaneohe Bay, Hawaii (not endemic to Hawaii—transplanted from the Marquesas) (sl = 47–67 mm).
- S. pinnula* Bean, 1912—3 specimens (AMNH 43473 sw) from Bermuda (sl = 83–102 mm).
- S. sindensis* (Day, 1878)—1 specimen (AMNH 54614 sw) from the Suez Canal, Egypt (sl = 97 mm).
- S. zunasi* Bleeker, 1854)—4 specimens (AMNH 13082 sw) from Kagoshima, Japan (sl = 70–89 mm).
- Sprattus* Girgensohn, 1846, p. 534 (type species, *Sprattus haleciformis* Girgensohn, 1846 = *Clupea sprattus* Linnaeus, 1758).
- S. sprattus* (Linnaeus, 1758)—2 specimens (AMNH 36845 sw) from eastern Atlantic waters off the Cliffs of Dover, Kent, England (sl = 72 mm).
- S. antipodum* (Hector, 1872)—4 specimens (AMNH 54615 sw and 54616 sw) from Indo-Pacific waters off New Zealand (sl = 76–108 mm).
- Strangomera* Whitehead, 1964c, p. 323 (type species, *Clupea bentincki* Norman, 1936, by original designation).
- S. bentincki* (Norman, 1936)—1 specimen (ANSP 69664 67) from eastern Pacific waters off the coast of Angol, Chile (sl = 106 mm).
- Tenuulosa* Fowler, 1934, p. 246 (type species *Alosa reevesii* Richardson, 1846).
- T. toli* (Valenciennes, 1847)—(x-ray), 1 specimen (AMNH 17767) from Canton, China (sl = 68 mm).
- †*Xyne* Jordan and Gilbert, 1919, p. 25 (type species, †*Xyne grex* Jordan and Gilbert, 1919, by original designation).
- †*X. grex* Jordan and Gilbert, 1919—30 specimens (AMNH 11208) from Miocene marine deposits of Lompoc, California (sl = 115–130 mm).

## SYSTEMATIC DISCUSSION OF CLUPEOMORPH FISHES

The higher clupeomorph groups will be discussed in general order corresponding to the cladogram in figure 1A. This information is summarized by the following classification.

### Clupeomorpha

#### †Division 1 (†*Erichalcis arcta*)

#### Division 2

#### †*Armigatus*

†*Ellimmichthyiformes* (†*Ellimmichthys*  
& †*Diplomystus*)

Clupeiformes

Denticipitoidei (*Denticeps* & †*Paleo-*  
*denticeps*)

Clupeoidei

Engrauloidea

Pristigasteroidea

Clupeoidea

Chirocentridae (*Chirocentrus*  
only)

Clupeidae

Pellonulinae

Dussumieriinae

Dorosomatinae<sup>4</sup>

Alosinae<sup>4</sup>

Clupeinae<sup>4</sup>

If fossil taxa are included in the cladogram, the first clupeomorph character of Greenwood et al., 1966 (the presence of a recessus lateralis) no longer defines all of the Clupeomorpha, but instead one of its subgroups called Clupeiformes here (and in Grande, 1982a). The recessus and other character information defining natural groups of clupeomorphs will be discussed below in order corresponding to character numbers given in the cladograms illustrated in figures 1A, 9, 14, 18, and 21. The character information for higher clupeomorph subgroups is discussed in this section and for clupeoid subgroups in the next section.

#### Clupeomorpha (Characters 1, 2, and 3)

1. *Presence of one or more abdominal scutes (including a pelvic scute), each of a single element which crosses the ventral midline of the fish* (discussed by Patterson, 1970a, p. 180; Whitehead, 1963b) (see figs. 36, 49, 10, 11A–11M, 11P–11S, 17, 24, and 25). All species of Clupeomorpha have at least one abdominal scute (the pelvic scute), and most species have a series of these scutes running along the midline of the belly. In *Chirocentrus* the scute is secondarily separated at the midline in adult specimens. Whitehead (1963b) found that in a specimen of 130 mm, the two halves of the scute were joined at the

midline, but in larger fish the two halves were separate. No evidence was found here to support Whitehead's (1963b) theory that the pelvic scute is derived from modified splint bones. Because a secondarily separated pelvic scute is derived for Chirocentridae, this unique type of clupeomorph scute could be potentially useful in identifying fossil members of the family. Previous characters used (absence of abdominal scutes, big teeth, etc.) have all been either plesiomorphic or too ambiguous to be reliable (see discussion of Chirocentridae below).

*Notopterus* (AMNH 43170 sw and AMNH 43430 sw—both *N. chitala*) has abdominal structures that superficially resemble clupeomorph abdominal scutes, but these (even in the smallest individuals observed here) have separate right and left halves, each half with its own median ventral spine. †Pycnodonts also have superficially similar structures, but these are complex (often multiboned) structures which are not homologous to clupeomorph-type abdominal scutes. *Argyropelecus aculeatus* (FMNH 64352; sl = 59–64 mm) shows a type of abdominal scute which is thought here to be independently derived for sternoptychids because of the peculiar ascending arm morphology (see Weitzman, 1974, fig. 111) and because of the distribution of other characters (*Argyropelecus* shows no clupeomorph characters). No nonclupeomorph fishes are known to have clupeomorph-type scutes. The number of abdominal scutes is reduced to one (the pelvic scute) in *Chirocentrus*, dussumieriines, some engrauloids, and some pellonulines; in dussumieriines the scute is modified into a W-shape (see fig. 17).

2. *Otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase, forming ossified bullae in the prootic, and usually also in the pterotic* (discussed and/or illustrated in Cervigón and Velazquez, 1978, fig. 16; O'Connell, 1955; Wohlfahrt, 1936; Greenwood et al., 1966, p. 358) (see figs. 3, 31B, 32B, 44B, 45B). Pterotic bullae are absent in three Recent clupeomorph genera [*Sprattus* and *Clupeonella* (see Whitehead, 1964c) and *Ethmidium* (personal observ., USNM 77314)] and also in the Lower Cre-

<sup>4</sup> Retained as a convenience group only (see above); no characters were found to indicate this is a monophyletic group.

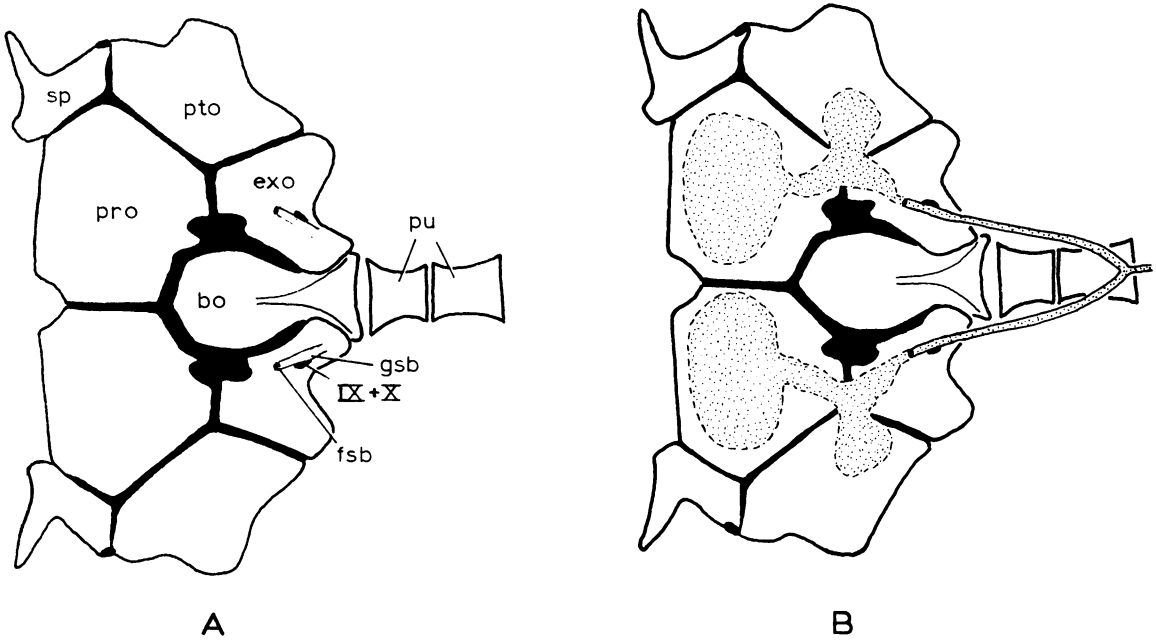


FIG. 3. Ventral view of posterior part of cranium (parasphenoid removed) in *Jenkinsia* (modified after Cervigón and Velazquez, 1978). (A) Diverticulum and bullae omitted; (B) showing diverticulum of swimbladder and bullae (stippled). Bullae and region of diverticulum which is internal (within the prootic, pterotic, and exoccipital) are outlined in dashed lines.

taceous fossil clupeomorph †*Spratticeps* (see Patterson, 1970a), but these fishes all have prootic bullae. Although no well-defined bullae of either type have been observed in †*Erichalcis*, †*Armigatus*, or †*Ellimmichthyiformes*, the presence of at least prootic bullae is suspected. This suspicion arises from the "strawberry appearance" of the surface of the prootic in †*Erichalcis* (Forey, 1975, p. 156) and from inflated areas of thin bone in †*Diplomystus dentatus* (personal observ.) which resemble the fusiform bullae of clupeoids. Although this interpretation needs confirmation with better preserved (and dorsoventrally oriented) specimens, it is assumed that these primitive clupeomorphs had at least rudimentary bullae. Character 2 is unique to the Clupeomorpha and, like character 1, is considered to be one of the most easily recognizable characters of the skeleton.

The bullae are briefly discussed further under character 9, and their functional morphology is discussed at length in Blaxter and Hunter, 1982.

3. *Supratemporal commissural sensory canal primitively passing through parietals, or through parietals and supraoccipital* (discussed in Patterson, 1970a, pp. 177, 179; Patterson and Rosen, 1977, p. 126) (see figs. 27B and 40B). The footnote in Patterson and Rosen, 1977 (p. 126, fn. 2) implies that penetration of the parietal by the supratemporal commissure (the lateral extrascapular canal as illustrated here) is the actual character. It is present in all known clupeomorphs and is thought (Patterson, 1970, p. 177) to be the result of fusion of extrascapular bones to the parietals. In more advanced clupeomorphs (Clupeiformes) the canal also passes through the supraoccipital. As a clupeomorph synapomorphy, character 3 is questionable in that it also occurs in characoids (*Acestro-rhynchus*, *Hoplias*, *Brycon*, and others), osteoglossomorphs (*Papyrocranus*, *Xenomystus*, and others), †*Ornategulum*, and possibly other groups. Nevertheless, it will be retained here until a more detailed survey of this feature is made among teleost fishes.

Clupeomorpha Division 2 (Characters 4, 5, and 6)

4. *Hypural 2 fused with the first ural centrum at all stages of development, and an autogenous first hypural* (discussed by Caven-der, 1966; Gosline, 1960; Greenwood et al., 1966; Patterson and Rosen, 1977) (see figs. 7A, 8, 12, 19, 38, and 51). Although not unique to clupeomorphs (present, for example, in some characoids such as *Saccodon wagneri* illustrated in Roberts, 1974, fig. 78; and in †*Ornategulum sardinioides* illustrated in Forey, 1973b, fig. 7), this condition was not observed in osteoglossomorphs, elopomorphs, or primitive ostariophysans (the primitive ostariophysan caudal skeleton as interpreted from Fink and Fink, 1981, figs. 1 and 23; and from Patterson, 1975b). Ostariophysans are thought by Rosen (1973) and others to be primitive euteleosts. For these reasons, this condition is thought to have been independently derived for both Division 2 clupeomorphs and characoids. Because this condition also occurs outside of Clupeomorpha, it is considered to be a character here only because it is congruent with characters 5 and 6. Primitively, in Division 2 the hypural 1 is merely autogenous (not fused) to the first ural centrum (figs. 8, 7B). In more advanced clupeomorphs (Clupeoidei), hypural 1 is further separated by a "hiatus" as shown in figures 12, 19, 38, and 51. †*Erichalcis arcta* is the only known clupeomorph species where the second hypural is also autogenous.

5. *The presence of a well-defined pre-epiotic fossa* (discussed in Patterson, 1970a, p. 176) (see figs. 27A and 40A). Forey (1975, p. 156) reports the absence of a well-defined pre-epiotic fossa in †*Erichalcis* but it is present in †*Armigatus brevissimus* (Patterson, 1967, p. 104), †*Diplomystus* (personal observ.) and Clupeoidei. No pre-epiotic fossa has been observed in Denticipitoidei, but this is thought to be possibly the result of obliteration by the expansion of the pterotic bulla (Greenwood, 1968a, p. 232). The pre-epiotic fossae in engraulids are often reduced (*Engraulis encrasicolus*—see Ridewood, 1905, pp. 472–473) to nearly absent (*Coilia nasus*—see Ridewood, 1905, p. 477) also due probably to expansion of the pterotic bullae. Pre-epiot-

ic fossa were not observed in any nonclupeomorph teleosts.

6. *The development of dorsal scutes, with a median keel* (discussed in Grande, 1982a; Schaeffer, 1947; Nelson, 1970b; Woodward, 1892). Dorsal scutes, once thought to be restricted to only a few Recent species (Schaeffer, 1947), are now known to occur in most major clupeomorph groups (†*Armigatus*, †*Ellimmichthyiformes*, Clupeoidea, Engrauloidea, and Pristigasteroidea—see tables 1a–10a). Most of these are illustrated in Grande, 1982a. The secondary loss of this element in Denticipitoidei, some Clupeoidea, some Engrauloidea, and some Pristigasteroidea is thought here to be more plausible than independent acquisition in †*Ellimmichthyiformes*, †*Armigatus*, Clupeoidea, Engrauloidea, and Pristigasteroidea.

†*Ellimmichthyiformes* (Character 7)

7. *Lateral expansion of dorsal scute "wings" which give scute a subrectangular shape* (discussed in Grande, 1982a). The placement of †*Ellimmichthys longicostatus* (Cope) with †*Diplomystus* rests on this single character. Its dorsal scute is shaped like an ontogenetically primitive †*Diplomystus* scute (see Grande, 1982a, figs. 9 and 18). †*Diplomystus* and †*Ellimmichthys* both share characters 4–6 with Clupeiformes and †*Armigatus* but lack defining characters which would allow placement of †*ellimmichthyiformes* in either of those groups (see fig. 1A).

†*Ellimmichthyiformes* are known from Early Cretaceous through Middle Eocene time (see Materials section and Grande, 1982a).

†*Diplomystus* (Character 8)

8. *Spines which increase in number ontogenetically on the posterior edge of the dorsal scutes* (see Grande, 1982a; Jordan, 1907, p. 136; Cope, 1884, p. 74). This character is illustrated in Grande, 1982a, fig. 9, and is unique among teleosts.

†*Diplomystus* species interrelationships are discussed in Grande, 1982a. The group, as defined there, contains three species: †*D. dentatus*, †*D. birdi*, and †*D. dubertreti* (see Materials section), but since that publication I have discovered a fourth species which belongs in the genus. This new species is de-



scribed, but yet unnamed ( $\dagger$ *Diplomystus* sp. in Chang and Chow, 1978). Based on the description and the detailed illustrations, this Tertiary species from China is the sister species of  $\dagger$ *D. dentatus* from the Green River Formation, and will be further discussed below.

#### Clupeiformes (Characters 9, 10, and 11)

9. *The presence of a recessus lateralis* (discussed in Greenwood et al., 1966, p. 358; Wohlfahrt, 1936; Greenwood, 1968a) (see figs. 27B and 40B). The recessus lateralis is an intracranial space in the otic region of the skull into which open the supraorbital, infraorbital, preopercular, and temporal (pteryotic) sensory canals. It is separated from the perilymphatic spaces of the ear by a membranous fenestra, and is bounded by the pteryotic and sphenotic, and partly roofed by the frontal.

Osteologically, one of the most obvious changes associated with the development of the recessus is the modification of the dermosphenotic. [Most authors (e.g., Nelson, 1969; and Weitzman, 1962) simply designate whichever infraorbital bone occurs last in the series, as the dermosphenotic.]

Clupeomorphs without a recessus ( $\dagger$ *Armigatus brevissimus*, fig. 4A;  $\dagger$ *Diplomystus*, fig. 4D;  $\dagger$ *Erichalcis* Forey, 1975, p. 166; and  $\dagger$ *Ellimmichthys*) have a well-developed dermosphenotic stretching well forward above the orbit, carrying the infraorbital canal with it. The infraorbital canal branches in the middle of this bone (figs. 4A and 4D) much like in *Hiodon*; some salmonids (see Patterson, 1970, fig. 31); and some ostariophysans (see Fink and Fink, 1981, fig. 7c).

Clupeomorphs that have a recessus (clupeiforms) do *not* have a well-developed dermosphenotic. The clupeiform dermosphenotic is reduced in size and does not contain a branched canal (e.g., figs. 4b, 27, and 40). There appear to be two basic types of clupeiform dermosphenotics: the type found in denticipitoids, and the type found in clupeoids. In denticipitoids the dermosphenotic is dorsal to the opening to the recessus (fig. 4b) and is between the supraorbital canal and the recessus (if Greenwood, 1968a, has correctly identified this bone). In clupeoids, the

dermosphenotic is ventral to the opening to the recessus and does not link the supraorbital canal to the recessus. Instead, in all clupeoids, it directly links the infraorbital canal ventrally to the recessus (e.g., figs. 27 and 40). The denticipitoid dermosphenotic is a hollow, tube-shaped bone, while the dermosphenotic in clupeoids is shaped more like a typical infraorbital bone. The difference in structure and position of the two basic "dermosphenotic" types is so striking that the homology of the bone in *Denticeps* should seriously be questioned. Possibly the bone identified as the dermosphenotic by Greenwood (1968a) is merely a small second ossification of the supraorbital canal, rather than a sixth infraorbital which has changed position. There is no evidence for either possibility over the other (also discussed by Forey, 1975, pp. 168–169). The homology of the nonclupeiform dermosphenotic with that of clupeiforms has also been questioned. For example, Patterson (1967, p. 105) stated that "the [morphology of the dermosphenotic in  $\dagger$ *Armigatus*] suggests that the clupeoid recessus lateralis involves loss of the dermosphenotic." The interpretations of Patterson (1967), Forey (1975), and those given above suggest that the dermosphenotic of clupeomorphs is in need of further study. Perhaps a detailed examination of the ontogeny of the infraorbital series in *Denticeps* (and  $\dagger$ *Diplomystus*, if possible) would clarify the homology of the dermosphenotic.

The recessus lateralis is not known to occur in any nonclupeiform species. The function of this structure is not well understood, but studies by various authors (Wohlfahrt, 1936; Blaxter and Hunter, 1982; Tracy, 1920; Evans, 1935, and others) indicate that together with the bullae and swimbladder modification (character 2) it may form a complex that aids in sound reception and/or maintenance of equilibrium or neutral buoyancy.

10. *Parietals completely separated (medially) by the supraoccipital* (discussed by Patterson, 1970a, p. 177; 1967, p. 103; Whitehead, 1963b) (see figs. 30A and 43A and compare with fig. 5). Although separation of the parietals by the supraoccipital has occurred in various euteleost groups, those instances are thought to have developed independently from the occurrence in

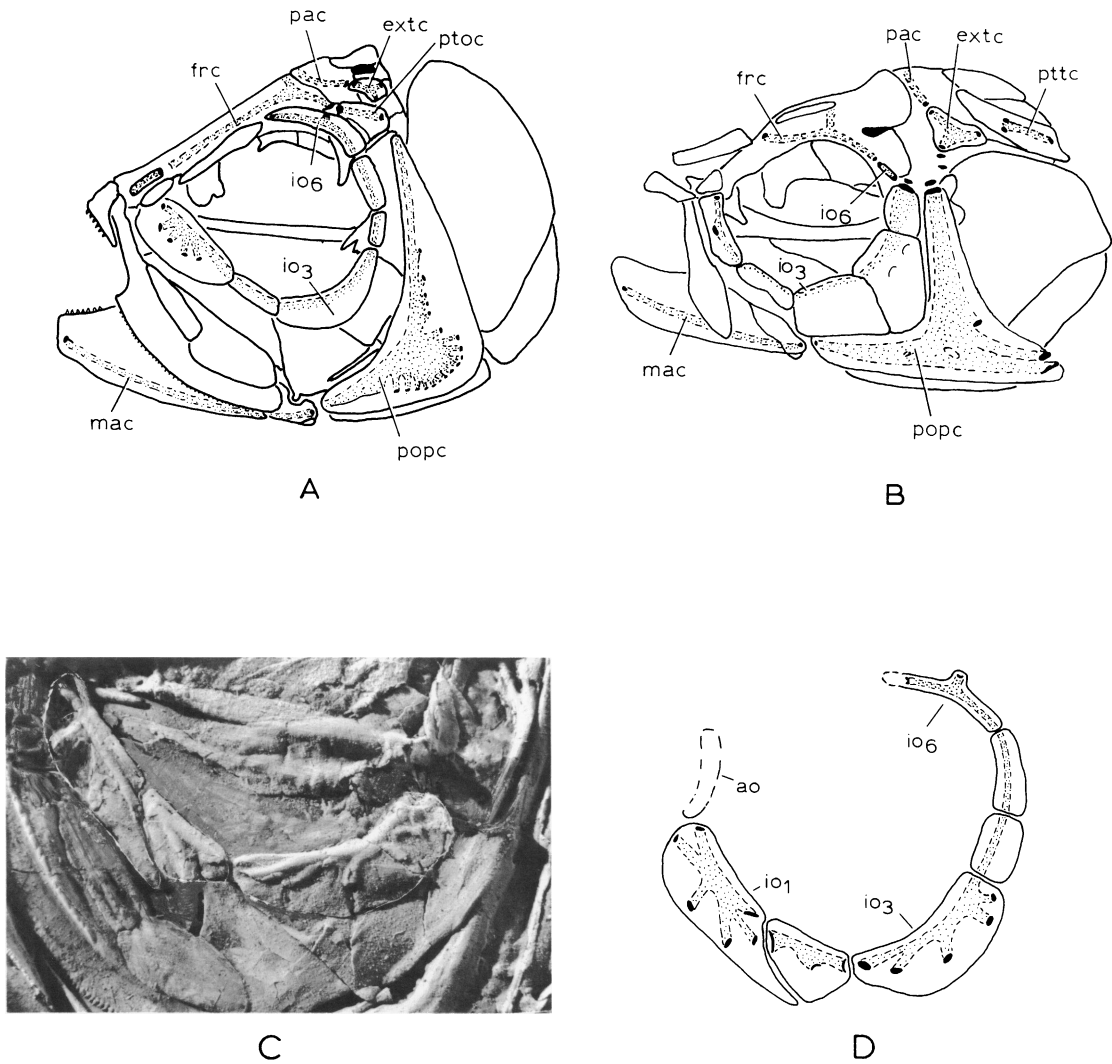


FIG. 4. The sensory canals (stippled) and dermosphenotic (io<sub>6</sub>) of three primitive clupeomorphs. (A) †*Armigatus brevissimus* (modified after Patterson, 1967); (B) *Denticeps clupeoides* (modified after Greenwood, 1968—odontodes omitted); (C) †*Diplomystus dentatus* (region of the first three infraorbitals), latex peel of FMNH PF10232 (sl = 145 mm); and (D) reconstruction of the complete infraorbital series of †*Diplomystus dentatus*, based mostly on FMNH PF10232 (fig. 4C), FMNH PF 10067 (fig. 8B) and AMNH 763 (fig. 7 of Grande, 1982a). The supraorbitally positioned dermosphenotic is relatively large in †*Armigatus* (e.g., fig. 4A) and †ellimmichthyiforms (e.g., fig. 4D), reduced in denticipitoids (e.g., fig. 4B), and reduced and moved to a postorbital position in all clupeoids (e.g., figs. 27 and 40). The dermosphenotic in †*Erichalcis* is unknown and was not preserved in any specimens observed here.

Clupeiformes. Nonclupeiform clupeomorphs (“primitive” clupeomorphs) have parietals in contact medially, anterior to the supraoccipital (†*Erichalcis*—see fig. 5 and Forey, 1975, p. 154; †*Armigatus brevissimus*—see Patterson, 1967, p. 103; and probably †*Diplomystus*—see Grande, 1982a, p. 7) like osteoglossomorphs (Taverne, 1977a, 1978); †ichthyodectiforms (Patterson and Rosen, 1977); elopiforms (Forey, 1973b), †leptolepids (Nybelin, 1974), salmoniforms (Patterson, 1970b), and many other groups of euteleosts.

11. Loss of the beryciform foramen (com-

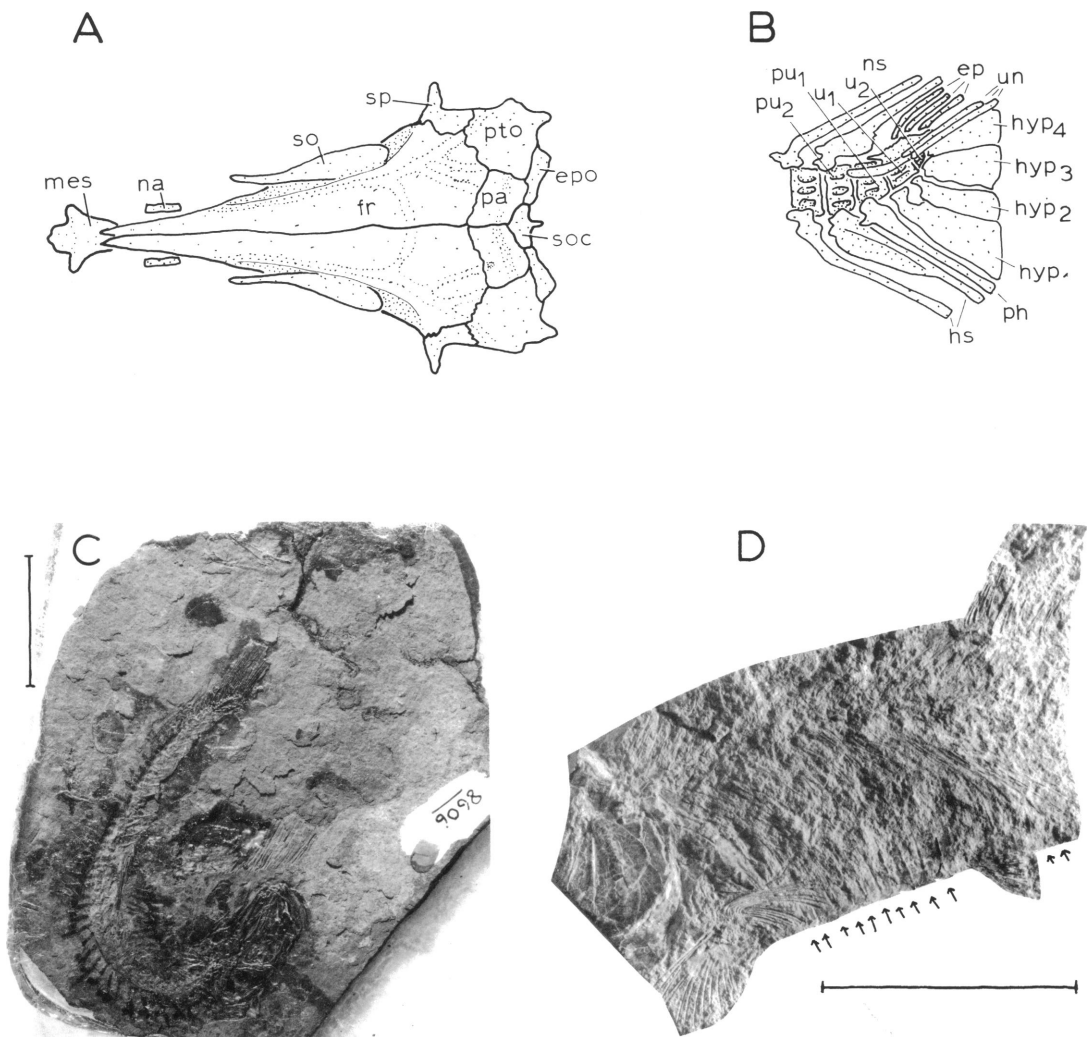


FIG. 5. †*Erichalcis arcta* Forey. (A) Drawing of skull roof (after holotype and Forey, 1975, fig. 1); (B) drawing of caudal skeleton (restoration based on UAVP 8598 and 8629); (C) the first published photograph of holotype UAPP 8606; and (D) UAVP 17535, which clearly shows clupeomorph-type abdominal scutes (arrows). Scale = 2 cm for C and D.

pare fig. 6 with figs. 34A and 47A). Another character probably independently derived for Clupeiformes is the loss of the so-called “Beryciform foramen” of McAllister, 1968, p. 6. The beryciform foramen is a large perforation just above the midsection of the anterior ceratohyal. This opening is found in †*Leptolepis bronni* (=†*L. coryphaenoides*), several percomorph groups (illustrated in McAllister, 1968) and in primitive Clupeomorphs [†*Erichalcis* (Forey, 1975, p. 156); †*Armigatus* (well preserved on AMNH 5776) and †ellim-

michthyiforms (fig. 6, and Grande, 1982a)]. The most parsimonious explanation for the distribution of this feature among Clupeomorpha is that primitively, clupeomorphs had the foramen, and it was secondarily lost in Clupeiformes.

Denticipitoidei (Characters 12 and 13)

12. The presence of odontodes (denticles) covering the dermal bones of the skull (Greenwood, 1960, 1968a; Clausen, 1959)

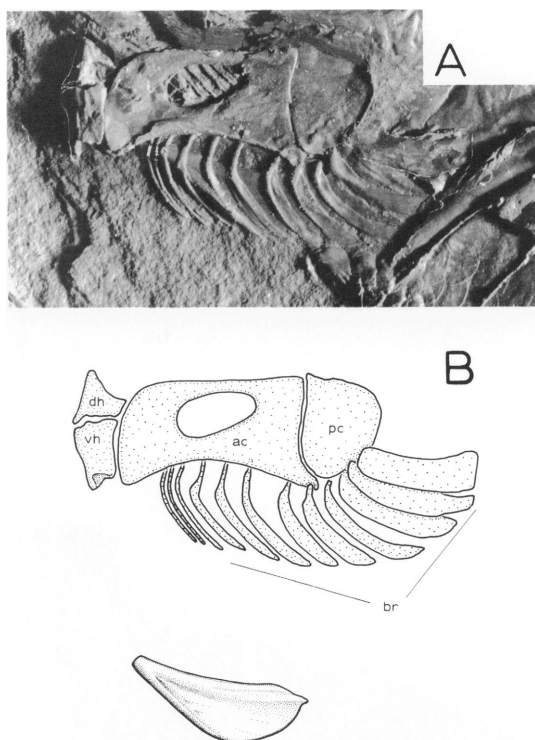


FIG. 6. Branchiostegal apparatus and urohyal of †*Diplomystus dentatus* (FMNH PF10230; 147 mm sl): (A) photograph (urohyal is lying under the branchiostegal rays); and (B) line drawing (with urohyal removed from under branchiostegals and drawn below them). Note the beryciform foramen in the anterior ceratohyal. Lateral view.

(fig. 7A). Among clupeomorphs this character is unique to Denticipitoidei (including only two monotypic genera, *Denticeps* and †*Palaeodenticeps*). Among nonclupeomorph teleosts, similar facial odontodes are known only in certain catfishes, e.g., *Loricaria cataphracta* (AMNH 40081 sw) and *Plecostomus* sp. (AMNH 43453 sw). Baskin (1972, p. 57) also reported these teeth in some trichomycterid, callichthyid, and astroblepid catfishes.

13. *Reduction in number of uroneurals in caudal skeleton to one* (Greenwood, 1968a) (fig. 7B). All other clupeomorphs observed have three uroneurals. The general shape of the *Denticeps* uroneural, and the slight branched appearance of its posterior end, suggest that the three uroneurals have fused in denticipitoids.

Also, *Denticeps* was the only Division 2

clupeomorph observed here to have only five hypurals.<sup>5</sup> Other characters unique to denticipitoids are given and discussed in Greenwood, 1968a. Although *Denticeps* has many peculiar skeletal features, it is clearly a clupeiform clupeomorph because of the presence of pterotic and prootic bullae, abdominal scutes, and a recessus lateralis. The many peculiarities of the skull and caudal skeleton are independently derived features of denticipitoids.

Only a single fossil denticipitoid is described, and it is Middle to Late Tertiary in age (see Materials section and below).

#### Clupeoidei (Characters 14, 15, 16, and 17)

14. *Fusion of the first uroneural with the first preural centrum* (Whitehead, 1963b; Cavender, 1966; Gosline, 1960) (compare figs. 7B and 8 to figs. 12, 19, 38, and 51). This character is absent in denticipitoids (fig. 7B), †ellimmichthyiforms (Grande, 1982a), †*Armigatus* (Patterson, 1967), †*Erichalcis* (Foray, 1975), and most other teleosts. This feature also occurs in many ostariophysans and some more advanced teleosts (Fink and Fink, 1981); although in the Cretaceous fossil chanid, †*Tharrhias*, possibly representing the primitive gonorynchiform condition (Patterson, 1975b), the uroneural is not fused to any centrum. Based on a parsimonious evaluation of the distribution of this character, it is considered independently derived for Clupeoidei.

15. *Reduction in relative size of the first ural centrum* (Cavender, 1966; Grande, 1982a) (compare figs. 7B and 8 with figs. 38 and 51). The first ural centrum in denticipitoids, †ellimmichthyiforms, †*Armigatus*, and †*Erichalcis* is about equal in size or larger than the first preural centrum [as in *Hiodon*, *Salmo*, *Megalops*, †*Ornategulum*, osteoglossoids (Taverne, 1977a, 1978), and most euteleosts that still have independent ural cen-

<sup>5</sup> †*Erichalcis arcta* (in the monotypic †Division 1 of Clupeomorpha) is the only other clupeomorph which appears to have reduced the number of hypurals to 5 (or possibly even 4) but it lacks characters 4–6 (diagnostic of Clupeomorpha Division 2), 9–11 (diagnostic of Clupeiformes), and any other unique similarities with denticipitoids. Therefore, there is no reason to suspect a close relationship between denticipitoids and †*Erichalcis*.

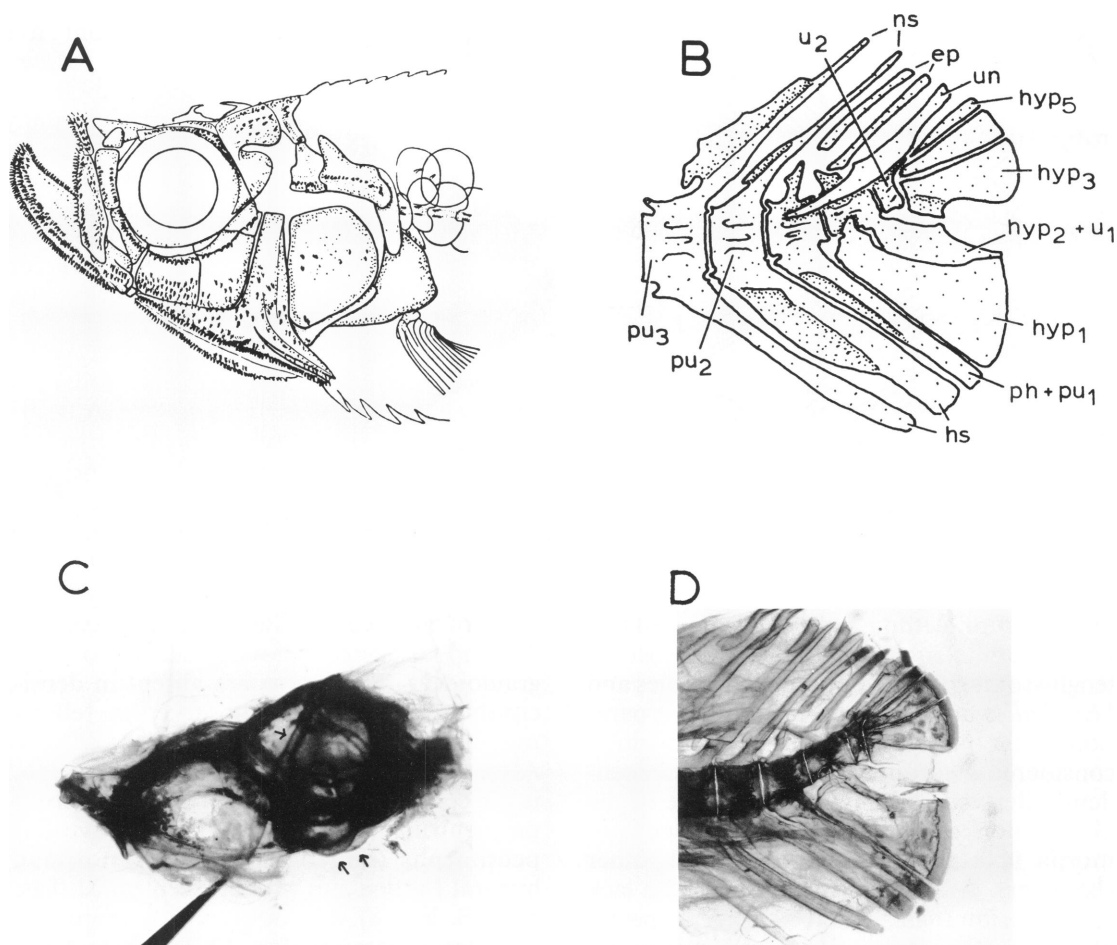


FIG. 7. *Denticeps clupeoides*. (A) Drawing of skull showing the distribution of the odontodes (from Greenwood, 1968a, fig. 1); (B) the caudal skeleton drawn from AMNH 53082 sw (sl = 38 mm); (C) lateral view of the braincase (AMNH 53082) showing the bullae (arrows); and (D) photograph of caudal skeleton drawn in B with the left uroneural removed.

tra (personal observ.)). This centrum is reduced in size in all clupeoids, and is considered here to be a derived character for that group.

16. *Loss of lateral line scales* (Whitehead, 1963b; Grande, 1982a). Although some clupeoids have one or two anterior lateral line scales (at least some species of *Alosa*, *Nematalosa* for example) all clupeoids have lost most or all of the lateral line. Primitive clupeomorphs [denticipitoids, †ellimmichthyiforms, †*Armigatus*, and †*Erichalcis*<sup>6</sup> have a

complete lateral line, going all the way back to the caudal fin as do gonorynchiforms (personal observ. on *Chanos*, *Phractolaemus*, and *Kneria*, AMNH 32991, 33471, and 33478), *Salmo*, *Megalops*, †*Ornategulum*, and osteoglossomorphs]. Lateral line scales going all the way back to the base of the caudal fin were also observed in *Denticeps*.

17. *Separation of the parhypural from the first ural centrum* (Grande, 1982a). †*Armigatus*, †ellimmichthyiforms, and denticipitoids all have the parhypural fused to the first

<sup>6</sup> Although no lateral line pores were observed in the scales of †*Erichalcis arcta*, this species has a series of

specialized modified scales (illustrated in Forey, 1975, fig. 11b) suggesting the presence of a lateral line.

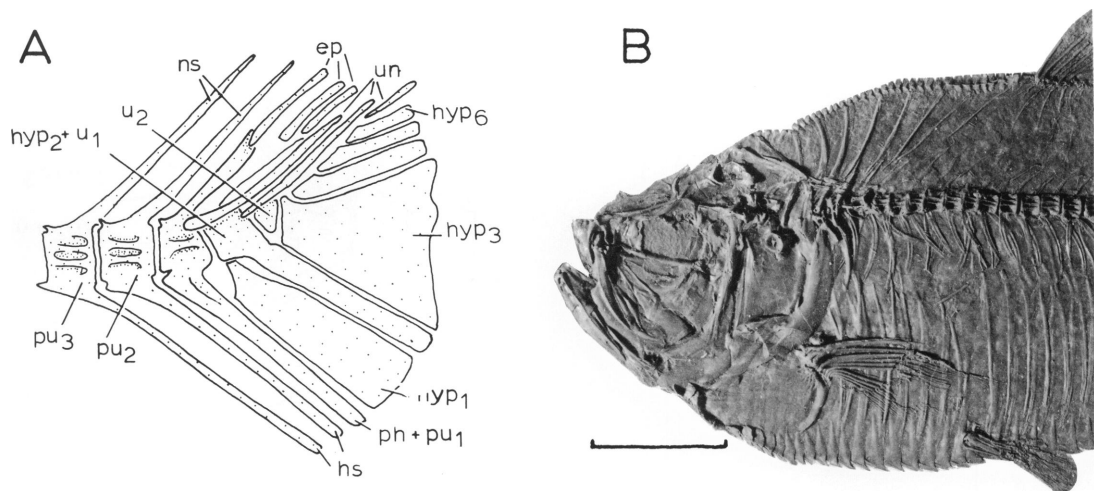


FIG. 8. †*Diplomystus dentatus*. (A) Caudal skeleton (after Cavender, 1966, fig. 4); and (B) latex peel of anterior half of fish (FMNH PF10067, scale = 2 cm). Postcranial skeleton illustrated in figure 11K.

ural centrum. Although the occurrence of this fusion in euteleosts is variable, and most osteoglossomorph and elopomorph species and †*Erichalcis* have no such fusion, the separation of the parhypural from the centrum is considered a secondary separation independently derived for clupeoids, because of the distribution of the feature among clupeomorph taxa and its congruence with other characters. All clupeoids observed here lack such a fusion (figs. 38 and 51) except species of *Dussumieria* and *Etrumeus* (dussumieriines are discussed below).

Another possible character at this level is the occurrence of spines or “pegs” on the

basis of the two middle caudal fin rays (fig. 13, and discussed below in section on Engrauloidea). These pegs are absent in denticipitoids, and were not observed in †ellimichthyiforms, †*Armigatus*, or †*Erichalcis*. Also, a character noted by Cavender, 1966, is the complete separation of hypural 1 from ural centrum 1 in clupeoids. In primitive clupeomorphs (nonclupeoid clupeomorphs), hypural 1 articulates with ural centrum 1 (figs. 5B, 7B, and 8), but in clupeoids there is a complete separation (figs. 12, 19, 38, and 51).

The Clupeoidei will be discussed further in the following section.

## SYSTEMATIC DISCUSSION OF CLUPEOID FISHES

In this section the various family-level clupeoid subgroups will be discussed. The cladogram in figure 9 shows the interrelationships of clupeoid subgroups as interpreted here on the basis of various osteological characters. Characters numbered in the cladogram are explained below, and characters 14, 15, 16, and 17 (of Clupeoidei) are discussed in the previous section (above). Character information will also be given for the construction of cladograms for Pristigasteroidea, Dussumieriinae, and Pellonulinae (figs. 14, 18, and

21). In addition, other osteological information for clupeoids (mostly nonengraulide species) is summarized in Tables 3a and b through 10a and b. Engraulide interrelationships (including a cladogram) and characters are discussed further in Grande and Nelson (in press).

No osteological synapomorphies were discovered here for Dorosomatinae, Clupeinae, or Alosinae; the monophyly of those groups as they have been traditionally constructed (see Whitehead, 1968, for example) is doubt-



ful. In the opinion of the author, one of the greatest remaining problems in clupeomorph systematics is to discover the interrelationships of the members of these three doubtfully monophyletic groups.

#### Engrauloidea (Characters 18 and 19)

18. *Suspensorium inclined obliquely backward* (discussed by Ridewood, 1905 and Whitehead, 1963b). This character (see fig. 10) is unique to anchovies among all teleosts observed here. It is most apparent in the backward inclination of the articular head of the quadrate and the forward inclination of the head of the hyomandibular (compare fig. 10B and figs. 28 and 41).

19. *Mesethmoid projecting in advance of vomer, snout piglike* (Whitehead, 1963b and Ridewood, 1905). This (fig. 10) is probably the most widely used character for identifying anchovies, because it is easily seen even in fresh (unskeletonized) specimens. Like the last character, this one was observed only in engraulides, and in all engraulides examined.

#### Pristigasteroidea (Characters 20 and 21)

20. *Predorsal bones oriented either vertically or inclined anterodorsally* (discussed also in Wongratana, 1980). In all Recent species of the Pristigasteroidea observed here, the predorsal bones have this character (see fig. 11). The Cretaceous †*Gastroclupea* is an exception, but because it appears to have a pristigasteride type of caudal skeleton (character 21 below), and because it is remarkably similar in appearance to the peculiar *Pristigaster* (see Signeux, 1964), it is retained here in Pristigasteroidea at least until better preserved material can be examined. Nearly all other clupeomorphs (and other teleosts) have predorsal bones that are inclined posterodorsally. The only exceptions observed here were in *Ramnogaster arcuata*, a clupeine which has vertical predorsal bones. Because this species lacks other characters diagnostic of Pristigasteroidea, and has characters 22 and 23 (see below), the vertical orientation of predorsal bones in this species is thought to be derived independently of Pristigasteroidea.

21. *Loss of interlobar notch in third hypural of caudal skeleton* (the "diasteme hypural" of Monod, 1967, 1968; also discussed

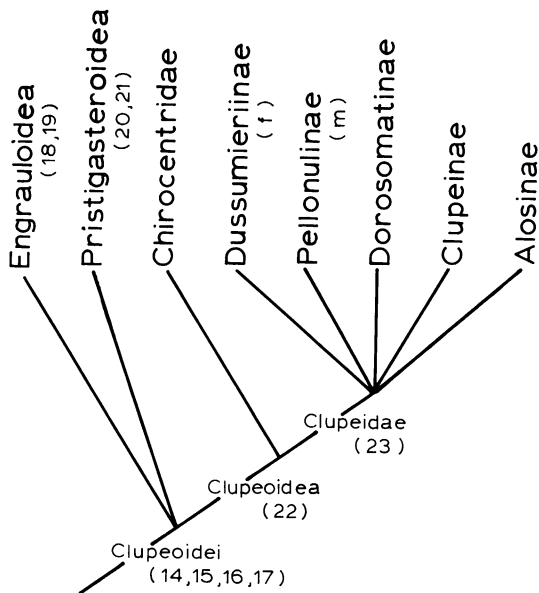


FIG. 9. Cladogram showing the monophyletic (except for Dorosomatinae, Alosinae, and Clupeinae—see text) groups of clupeoid fishes based on osteological characters as interpreted here. Chirocentridae monotypic (one species) and characters 14–23 and f and m discussed in text.

in Wongratana, 1980) (see fig. 12). There is a distinct gap between the second and third hypural of most clupeomorph fishes, usually associated with a distinct notch on the third hypural (also observed on *Megalops*). This gap, which has no caudal rays articulating with it, separates the articulating surfaces of the upper caudal fin lobe from the lower. Among clupeomorphs observed here (tables 1b–10b), the loss of this gap was also found only in †*Diplomystus dentatus* (an †ellimmichthyiform); and *Setipinna*, *Thrissina*, and *Thryssa hamiltoni* (Indo-Pacific anchovies). The gap is only poorly developed in the remaining Indo-Pacific anchovies. Because of the distribution of this character (see figs. 1 and 9), its occurrence in †*D. dentatus* is thought to be independently derived from its occurrence elsewhere. Its occurrence in all Pristigasteroidea and a few Engrauloidea suggests the possibility of a relationship between those two groups; but because Engrauloidea shows no other uniquely derived affinities with Pristigasteroidea or vice versa, the occurrence is thought to be independently derived for both groups. Thus, it is also con-

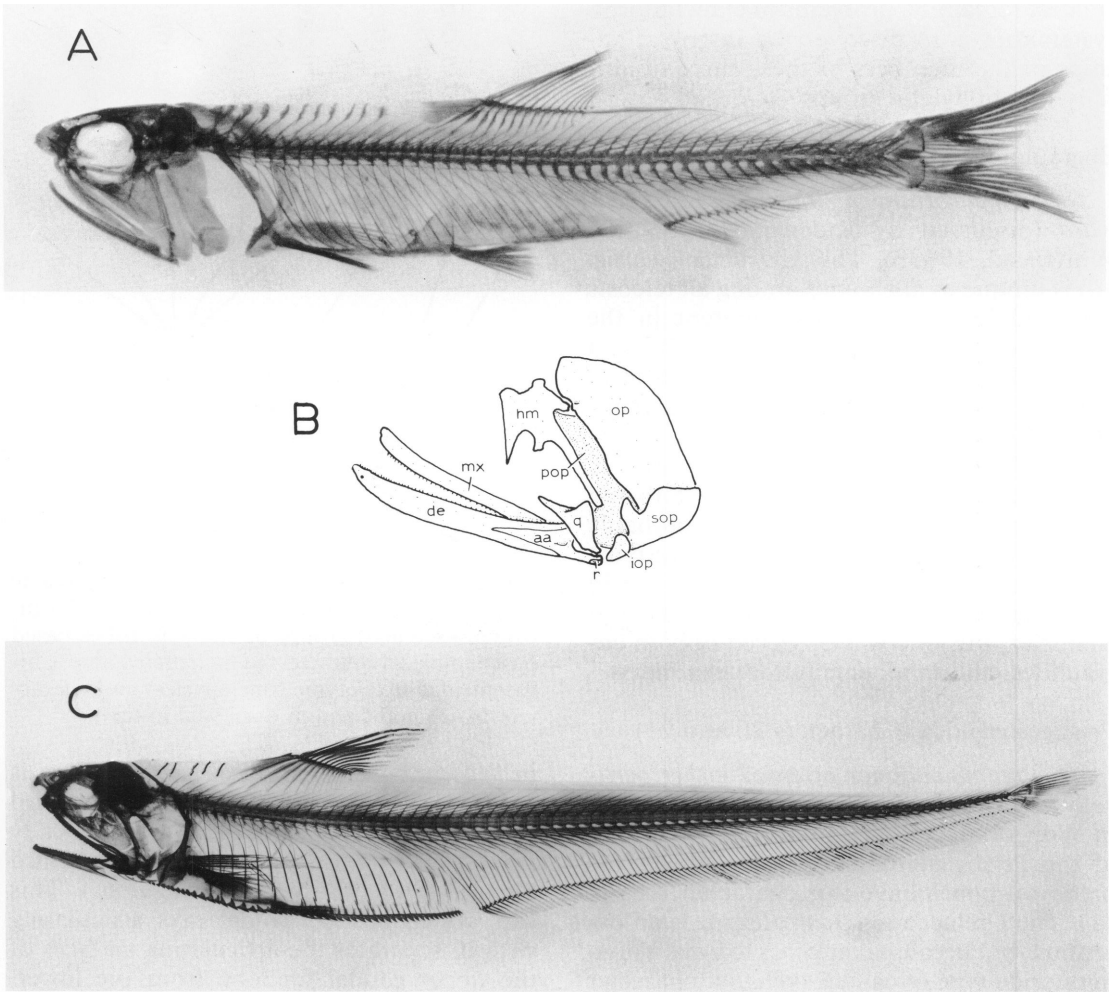


FIG. 10. *Engraulis guineensis* (AMNH 53904 sw) (sl = 68 mm). (A) Cleared and stained specimen (with hypobranchial apparatus and right lateral facial bones removed) showing the piglike nose and oblique orientation of suspensorium; and (B) medial view of jaws, part of suspensorium, and opercular bones, showing anteriorly inclined orientation of quadrate and hyomandibular bones. (C) *Coilia rendahli* (AMNH 10321 sw) (sl = 118 mm), one of the rat-tailed anchovies (with hypobranchial apparatus and right lateral facial bones removed).

sidered to be derived for the Pristigasteroidea. This character will be further discussed below in the discussion on Engrauloidea. Nelson (1967a, p. 392) also discovered what he interpreted as a defining character for Pristigasteroidea in the gill arches. He stated (with illustrations) that: "the members of this [group] are distinctive in having prominent basibranchial dentition, including separate

toothplates fused with B2 and one or more pairs of hypobranchials, an unusual if not unique condition in teleostean fishes." Although this character was not as thoroughly surveyed here as many others (only a few clupeoid species were examined for it), this condition was not observed here in any clupeomorph species outside of Pristigasteroidea.



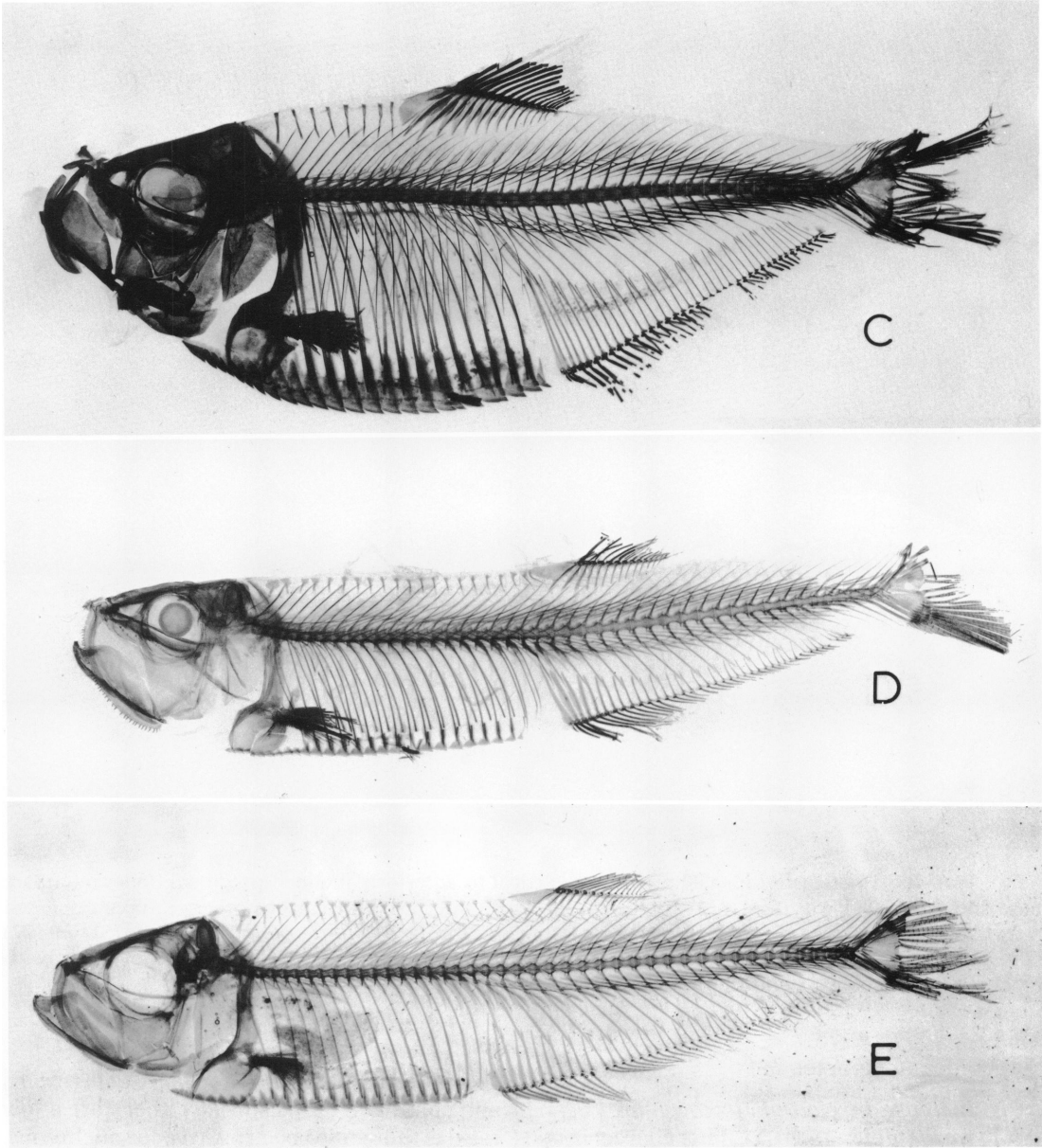


FIG. 11C-E. Pristigasteroidea (see caption for fig. 11A-B). (C) *Pellona harroweri* (AMNH 20759 sw) (sl = 64 mm); (D) *Chirocentrodon bleekermanus* (AMNH 10118 sw) (sl = 78 mm); (E) *Neoapistopterus tropicus* (AMNH 53084 sw) (sl = 55 mm). Figures C-E are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

ae = .49-.66 (X = .56, S.D. = 0.41, N = 14 species); Alosinae = .50-.63 (X = .55, S.D. = .036, N = 12 species); Clupeinae = .52-.66 (X = .59, S.D. = .034, N = 45 species). The general increase in relative abdominal size in clupeomorphs may be related to a general

trend toward a less piscivorous diet in the group.

Nelson (1970a, p. 19) discussed some possible nonosteological characters for Clupeoidea, including a “peculiar type of connection between the swimbladder and gut” (after

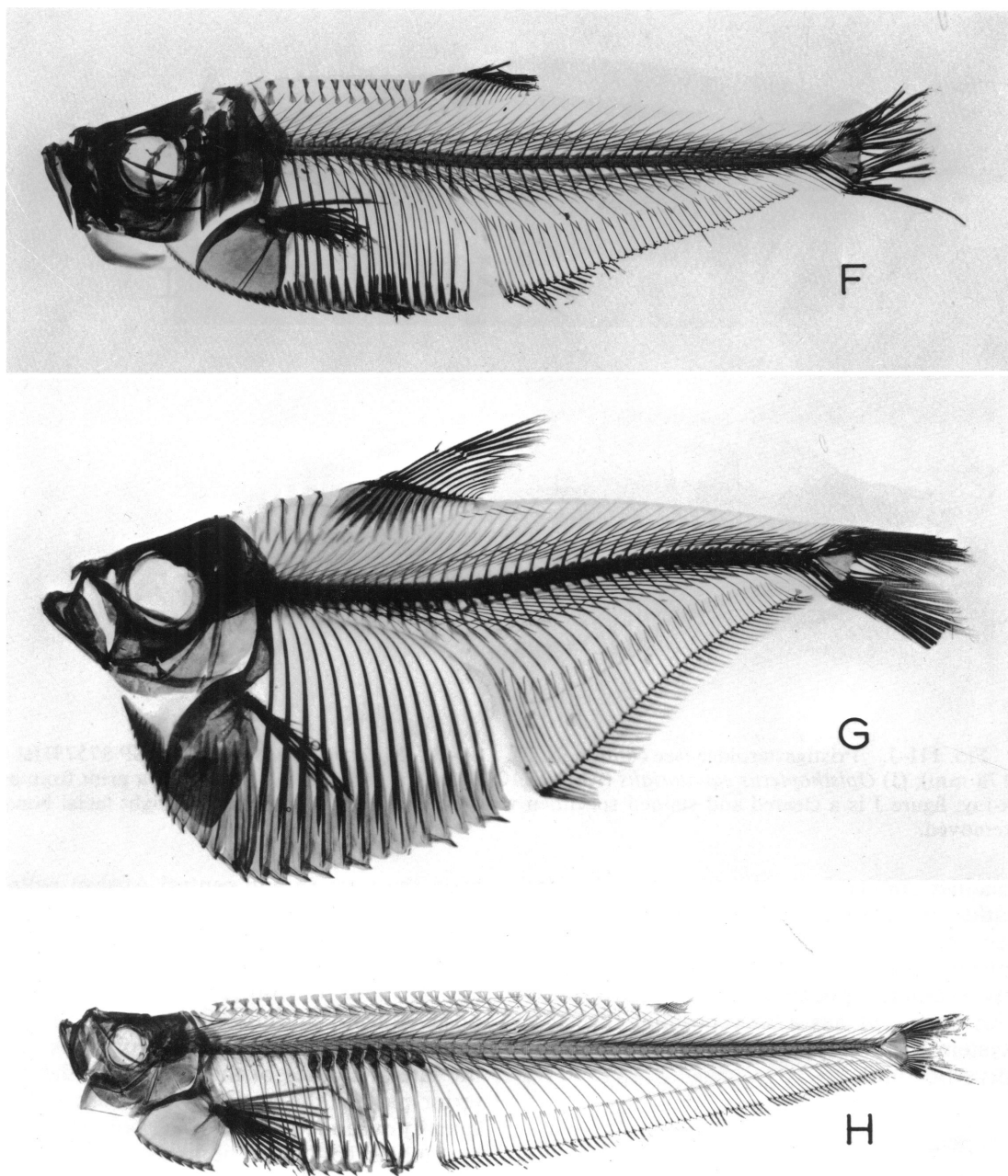


FIG. 11F-H. Pristigasteroidea (see caption for fig. 11A-B). (F) *Ilisha africana* (AMNH 17730 sw) (sl = 55 mm); (G) *Pristigaster cayana* (AMNH 10186 sw) (sl = 83 mm); (H) *Odontognathus mucronatus* (AMNH 20749 sw) (sl = 87 mm). Figures F-H are cleared and stained specimens, with hypobranchial apparatus and right facial bones removed.

Harder, 1957, 1958a, 1958b, and 1960). Pristigasteroidea and "primitive" (in the sense of

Nelson, 1970a) members of Engrauloidea have a ductus pneumaticus (stomach-air-

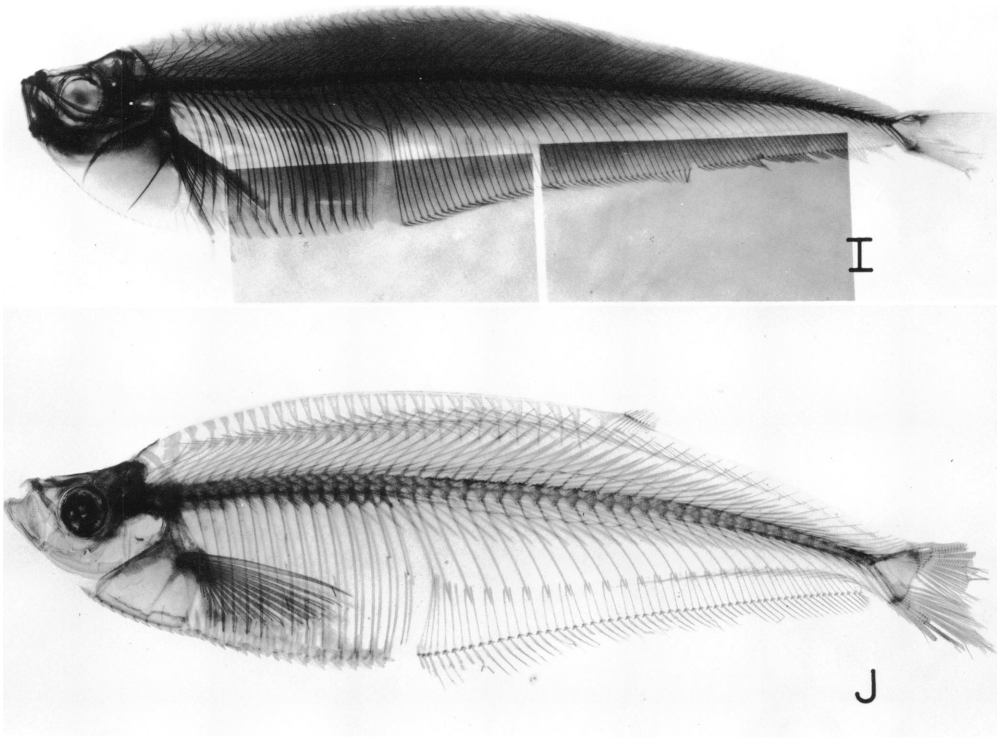


FIG. 11I–J. Pristigasteroidea (see caption for fig. 11A–B). (I) *Raconda russeliana* (ANSP 87573) (sl = 178 mm); (J) *Opisthopterus equatorialis* (AMNH 10188 sw) (sl = 120 mm). Figure I is a print from an x-ray; figure J is a cleared and stained specimen with hypobranchial apparatus and right facial bones removed.

bladder connection) in a more anterior position on the esophagus than other clupeoids (see fig. 6 in Nelson, 1970a). The ductus pneumaticus of *Denticeps* is also in a relatively anterior position (Greenwood, 1968b), but *Denticeps* has a very peculiar digestive system for a clupeiform (i.e., no stomachic diverticulum).

#### Clupeidae (Character 23)

23. *The presence of two long, rodlike postcleithra* (tables 1b–10b). Nearly all members of Clupeoidea observed here (all except for the pello-nuline *Clupeoides papuensis* and the dussumieriines *Dussumieria*, *Jenkinsia*, and *Spratelloides*) have two long, rodlike postcleithra (see figs. 22 and 35C, for example), the anteriormost which articulates either behind the cleithrum with the supracleithrum

as in the western and central African pello-nulines (fig. 35C) or more lateral to the cleithrum as in other members of Clupeoidea (fig. 48C). The drawings by Chapman (1948, figs. 15 and 16) omitted the posteriormost postcleithrum. In those species in which the anterior rodlike postcleithrum articulates with the lateral surface of the cleithrum, the anterior part of the anterior cleithrum is frequently expanded with laminar bone (fig. 48C and tables 1b–10b). The homology of these postcleithra with those of other teleosts is uncertain for two reasons. First of all, some clupeoids (tables 1b–10b) have a third “postcleithrum” (usually scale-shaped) anterior to the two long, rodlike ones or sandwiched between the anterior rodlike one and the cleithrum (fig. 48C). Second of all, the postcleithra of clupeoids articulate to the lateral surface of the cleithrum, while in the other teleosts



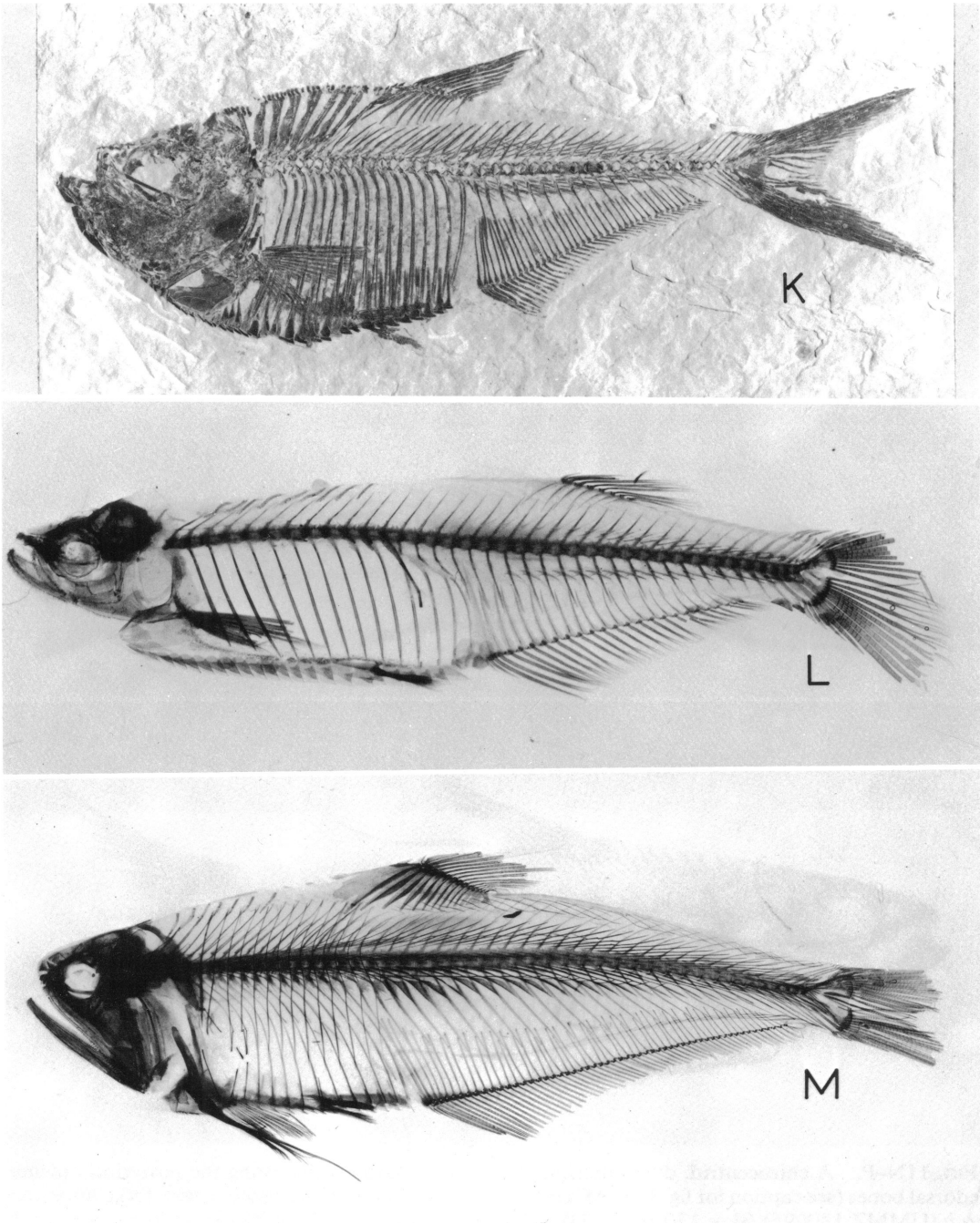


FIG. 11K–M. An †ellimmichthyid, denticipitoid, and engraulide, showing the posteriorly inclined predorsal bones (compare these and figs. 11N–S, 10, 24, 25, 26B, and 39B with fig. 11A–J) and various other features discussed in text. (K) †*Diplomystus dentatus* (SMMP 78, 9, 14) (sl = 70 mm); (L) *Denticeps clupeoides* (AMNH 53082 sw) (sl = 38 mm); (M) *Setipinna godavari* (AMNH uncat.) (sl = 90 mm). Figure K is a prepared fossil; L–M are cleared and stained specimens with hypobranchial apparatus and right facial bones removed. Head somewhat displaced on *Denticeps* specimen.



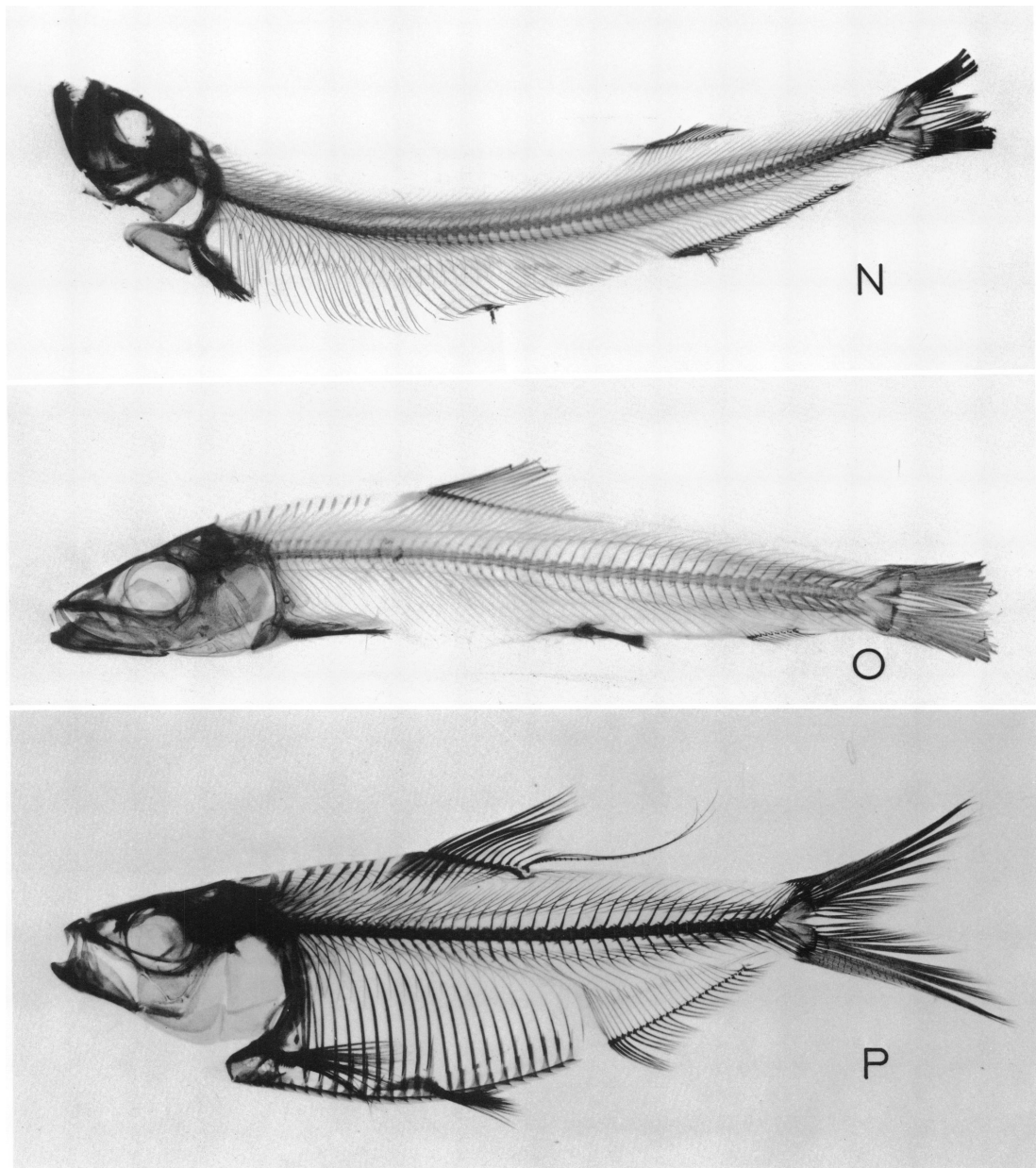


FIG. 11N-P. A chirocentrid, dussumieriine, and dorosomatine all showing the posteriorly inclined predorsal bones (see caption for fig. 11K-M) and various other features discussed in text. (N) *Chirocentrus dorab* (UMMZ 180095) (sl = 130 mm); (O) *Etrumeus micropus* (AMNH 8840 sw) (sl = 78 mm); (P) *Signalosa petenense* (AMNH 25621 sw) (sl = 67 mm). Figures N-P are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

observed here that have postcleithra (*Salmo*, for example) the postcleithra articulate with the medial surface of the cleithrum.

None of the clupeomorphs outside of Clupeidae were observed to have the rodlike postcleithra. No postcleithra were observed

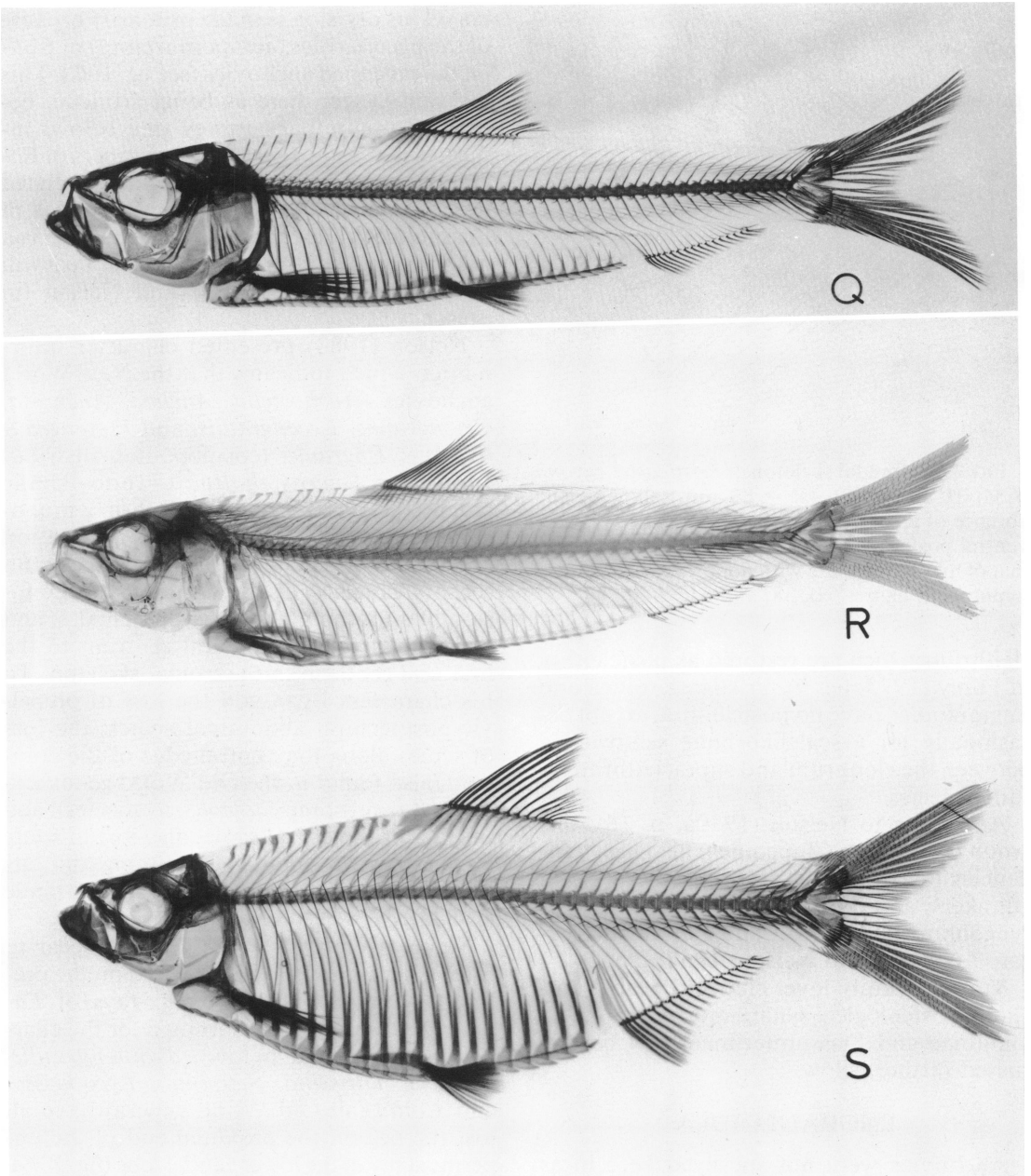


FIG. 11Q–S. An alosine and two clupeines showing the posteriorly inclined predorsal bones (see caption for fig. 11K–M) and various other features discussed in text. (Q) *Pomolobus aestivalis* (AMNH 54617 sw) (sl = 67 mm); (R) *Sardinella aurita* (AMNH 44437) (sl = 117 mm); (S) *Platanichthys platana* (BMNH 1969: 11 25 103-117) (sl = 73 mm). Figures Q–S are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

in *Chirocentrus*, †*Armigatus*, or †ellimmichthyiforms; and denticipitoids have only two small, scalelike bones associated with the up-

per part of the cleithrum (also noted by Greenwood, 1968, p. 147). †*Erichalcis* has three scalelike bones associated with the

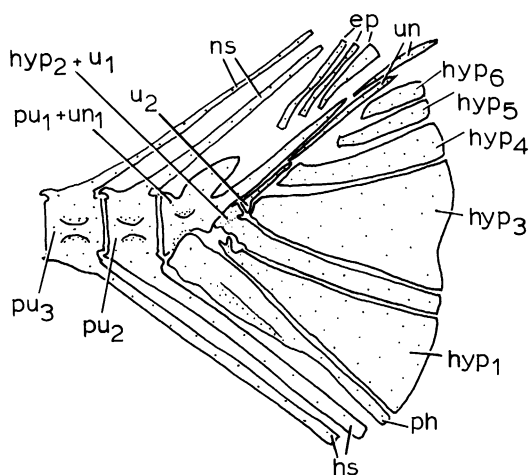


FIG. 12. Caudal skeleton of *Pristigaster cayana* (AMNH 10186 sw) (sl = 83 mm) showing the absence of an interlobar caudal notch in hyp<sub>3</sub> (the ventral posterior edge of hyp<sub>3</sub> is nearly flush with that of hyp<sub>2</sub>). Compare with nonpristigasterid third hypurals in figures 7B, 38, and 51.

cleithrum which are restored as postcleithra in Forey (1975, fig. 9). *Pristigasteroidea* and *Engrauloidea* have no postcleithra, except occasionally for a scalelike bone sandwiched between the cleithrum and supracleithrum in some species.

According to Nelson (1970a, p. 16), this group (=Nelson's Clupeoidea) also has "tendencies toward loss of teeth, proliferation of gillrakers, and development of a mediopharyngobranchial cartilage and epibranchial organs" (surveyed in Nelson, 1967b).

Various family-level clupeoid groups (including osteological synapomorphies for Pellonulinae and Dussumieriinae) will be discussed further below.

### ENGRAULOIDEA

Anchovies were not surveyed here in as much detail as the nonengraulid clupeomorphs. The group was only briefly surveyed here (one species of each genus available—tables 4a and 4b), and only a few brief comments will be made here about them.

Anchovies are currently (Whitehead, 1972, p. 166) divided into two subfamilies; the Coilineae (including only the genus *Coilia*) and Engraulinae (including all the rest of the gen-

era). This division is made primarily because of the peculiarities (autapomorphies) of *Coilia*, the rat-tailed anchovies (see fig. 10C). This division is seen here as being artificial, because a preliminary survey (see below) indicates that some Old World members of Engraulinae are probably more closely related to *Coilia* than to the New World species of Engraulinae, indicating that Engraulinae is a nonmonophyletic group. The higher taxa will be restructured in Grande and Nelson (in press).

Nelson (1983) presented character information which indicates that the New World anchovies (*Anchoviella*, *Anchoa*, *Anchovia*, *Cetengraulis*, *Lycengraulis*, and *Pterengraulis*) plus *Engraulis* (cosmopolitan distribution) plus *Encrasicholina* (=Indo-Pacific species of *Stolephorus*, in part) form a monophyletic group. This character information included a peculiar arrangement of certain sensory canals (Nelson, 1983, fig. 1), the fusion of a toothplate with epibranchial 1, and a fusion of the first preural centrum to the first ural centrum in the caudal skeleton. To his characters I can add the loss of prepelvic-postpectoral abdominal scutes; the loss of scutes along the ventral edge of the coracoid (also found in the Old World genus *Lycotrissa* and some *Stolephorus* species); and the loss of the dorsal scute (also lost in some species of *Stolephorus*), assuming that its presence is primitive, as proposed in Grande (1982a).

Some of the Old World genera appear to form a monophyletic group based on the preliminary survey taken here (x-rays of *Papuengraulis* were also examined for the characters mentioned below). *Papuengraulis*, *Thryssa*, *Thrissina*, *Setipinna*, *Lycotrissa*, and *Coilia* (all Old World genera) have all lost the peg on the proximal end of the uppermost ray of the lower caudal lobe (fig. 13A). This peg is present in the other anchovies as it is in clupeids, *Chirocentrus*, and *Pristigasteroidea*. (It is probably derived for Clupeoidei—see above.) This same group of Old World anchovies has the notch in the third hypural of the caudal skeleton either lost or very poorly developed. The loss of this notch is similar to that found in *Pristigasteroidea* (discussed above in discussion of character

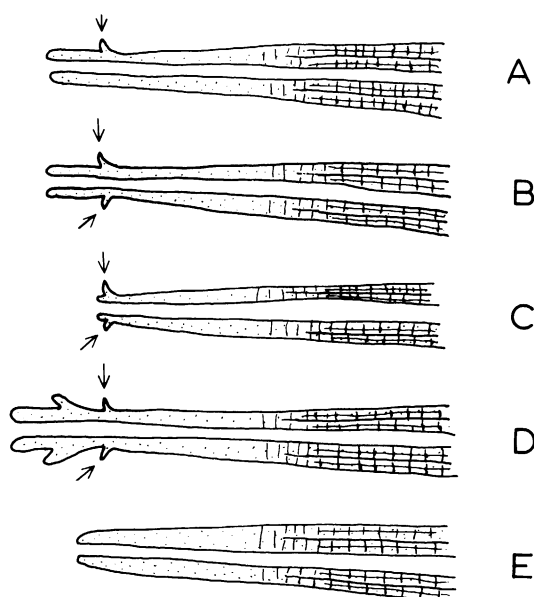


FIG. 13. The bases of the two middle caudal fin rays showing the dorsal and ventral "pegs" (arrows). Among all clupeoid species observed here, only *Setipinna*, *Lycorhissa*, *Papuengraulis*, *Thrissina*, *Coilia*, and *Thryssa* (all Old World anchovies) have lost the ventral peg (A). Other engraulids, most clupeines, pellenulines, and all alosines and dorosomatines, have a two-peg arrangement resembling B. Pristigasterids have a two-peg arrangement like B or C. Chirocentrids look like D and dussumieriines have a somewhat variable condition ranging from B (sometimes with the pegs pointing in a more medial direction) to C (sometimes with the pegs very poorly developed in some specimens). *Denticeps* (E) is representative of the nonclupeoid condition.

21) but thought to be independently derived for this group of anchovies.

Engrauloidea are extremely rare in the fossil record (Whitehead, 1963b, p. 748 and personal observ.). The only fossil anchovy specimens observed here (after examining the fossil fish collections of AMNH, BMNH, FMNH, MNHN, SMMP, and USNM) are several individuals of a single, undescribed species from Miocene deposits of Famagusta, Cyprus (BMNH P 47312, 61224a, and 61224b). This also appears to be the oldest known engraulid. The only described fossil species (other than species based only on oto-

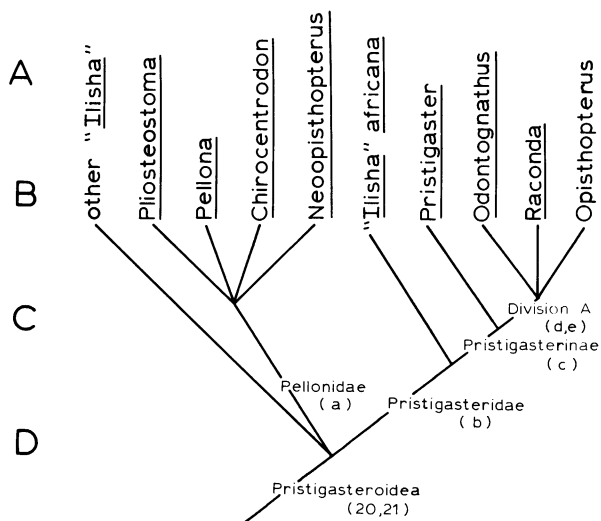


FIG. 14. Cladogram showing the monophyletic groups of pristigasteride fishes based on osteological characters as interpreted here. Characters 20, 21, and a through e discussed in text.

liths) which appears to belong in Engraulidae is (based on several detailed photographs) †*Engraulis macrocephalus* Landini and Menezes, 1978, from the Plio-Pleistocene of Italy. A study of fossil and Recent anchovies with description of a new species is currently in press (Grande and Nelson).

†*Engraulis* "evolans" (Blainville, 1818) from the Eocene Monte Bolca Formation [type specimen MNHN 10944 and counterpart MNHN 10945 (sl = 70 mm) illustrated in Agassiz, 1833–1842, vol. 5, pl. 37b, figs. 1 and 2] was examined here and was found to not even be a clupeomorph. (Previously, Jordan and Seale, 1926, p. 393, also questioned the validity of placing this species in Engraulidae.) The caudal skeleton, which is well preserved, indicates that this fish is a euteleost, probably an exocoetoid. The hypurals are all fused together and there is a massive neural plate attached to  $pu_1$ . The caudal skeleton is very similar to that illustrated for *Exocoetus volitans* by Monod (1968, p. 282). This specimen is still listed as an engraulid in Blot (1980, p. 352)—where the author of the name is miscited ("Volta, 1796" is listed there as author of the Blainville name).

For a group so abundant and widespread today, the scarcity of fossil anchovies is peculiar, especially considering how very common fossil clupeids are (see list below). Possibly this suggests a relatively young age for the group, but it more likely reflects the ecological restrictions of anchovies to high-energy habitats, which do not usually produce articulated, well-preserved fish fossils. Recent anchovies inhabit nearshore marine areas and rivers.

### PRISTIGASTEROIDEA

(Characters a-e)

This group of fishes has been previously classified by Norman (1923) and Berry (1964a). Only one fossil species ( $\dagger$ *Gastroclupea*) is known to the author, and it dates back to the Late Cretaceous. Osteological characters for the group as a whole are discussed above. A cladogram summarizing the osteological characters as interpreted here is given in figure 14. The genus *Ilisha* appears to be a nonmonophyletic group which is in need of revision; because not many of the species were available here, such a revision was not attempted. The subgroups of Pristigasteroidea corresponding to the cladogram in figure 14 are supported here by new characters, and testing of this cladogram with additional characters is needed. The characters in the cladogram are as follows:

#### Character a (of Pellonidae)

*a. Maxillary-premaxillary gap covered by bone* (fig. 15). This gap is covered in two different ways. In *Pliosteostoma* and *Pellona* it is covered by an additional bone in the upper jaw—the hypomaxilla (fig. 15A). In *Chirocentron* and *Neoapistopterus*, the gap is covered by an extension of the maxilla which is possibly a hypomaxilla fused onto the maxilla (fig. 15B). Such a fusion has not been seen ontogenetically, so it is unknown whether the hypomaxilla or the extension of the maxilla is the more derived of the two conditions. Other pristigasterids have a gap as do other clupeomorphs (see figs. 27 and 40 for example). A hypomaxillary bone occurs in only one other known clupeomorph genus—*Haerengula* (Berry, 1964b).

#### Character b (of Pristigasteridae)

*b. Presence of a bony process on the first pleural rib which articulates with the shoulder girdle* (fig. 16). This feature was observed in no other teleost other than this group of pristigasterids. Although some other species (e.g., *Chirocentron*) have a small, laminar expansion near the top of the first pleural rib, it is not as well developed and does not articulate with the cleithrum.

#### Character c (of Pristigasterinae)

*c. Loss of pelvic fins.* The loss of the pelvic fins in this group is thought to be independent of their loss in *Neoapistopterus* because of the coincidence of other characters. No other clupeomorphs were observed to have lost the pelvic fins.

The internal supports for the pelvic fins appear to be also lost in this group. *Raconda russeliana*, which has also lost the dorsal fin, has retained the dorsal internal supports (pterygiophores).

#### Characters d and e (of Pristigasterinae Division A)

*d. More than 23 predorsal bones* (tables 1a-10a). No other clupeomorphs were observed to have more than 22 predorsal bones, and most species have from 7 to 12.

*e. More than 57 anal pterygiophores* (tables 1a-10a). Among all other clupeomorphs, only the rat-tailed anchovies, *Coilia*, have as many anal pterygiophores [104], but that genus has all of the characters of the Engrauloidea and lacks pristigasterid characters. Therefore, the increase in anal pterygiophores is seen as independently derived for this group of pristigasterids.

### CHIROCENTRIDAE

This group currently contains only one genus and two species (Whitehead, 1972, pp. 166-169). Many fossil species (mostly ichthyodectiforms) have also been included in this family by Bardack (1965b), Nybelin (1964), Saint-Seine (1949), and others, but this was done on the basis of primitive character information and ignoring the complex characters uniting *Chirocentrus* with other Recent clupeiforms (discussed in Cavender,

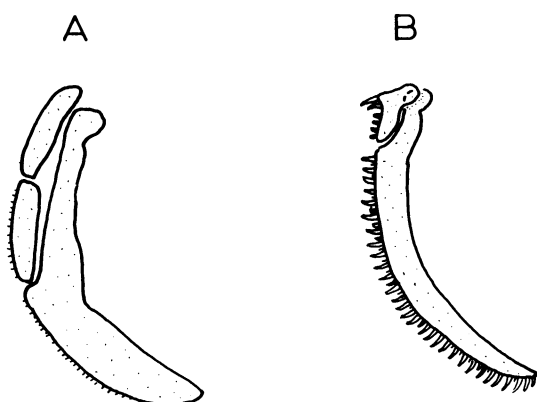


FIG. 15. The absence of the maxillary-premaxillary gap is shown. The gap is covered (A) by a hypomaxillary bone in *Pellona* and (B) by an extension of the maxilla in *Chirocentrodon*. Compare with figures 27 and 40.

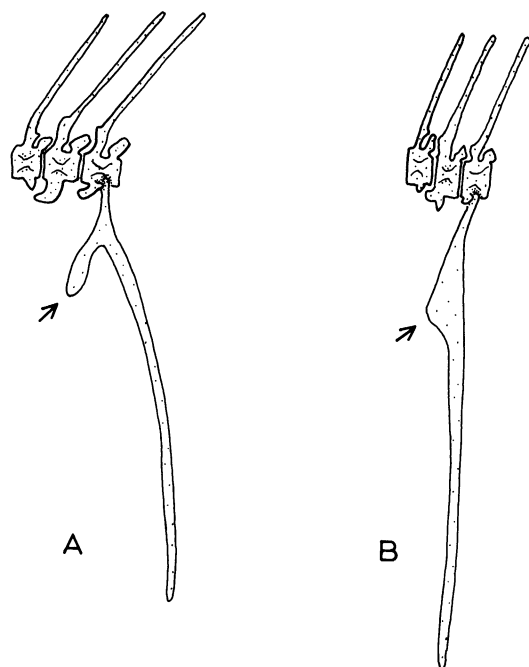


FIG. 16. The three anteriormost vertebrae of some pristigasterids (intermuscular bones omitted) showing the process on the first pleural rib (arrow) extending to and articulating with the pectoral girdle. (A) *Ilisha africana* (AMNH 17730 sw); (B) *Pristigaster cayana* (AMNH 10186 sw). Although *Chirocentrodon* and *Neopisthopterus* have a small laminar expansion of the first pleural rib, it does not articulate with the shoulder girdle.

1966; Patterson, 1967; Patterson and Rosen, 1977; and above). †Ichthyodectiforms lack all the clupeomorph, clupeiform, and clupeoid synapomorphies discussed here. No convincing character information was found here to warrant inclusion of any species other than the two Recent species of *Chirocentrus* in the Chirocentridae. No true chirocentrid fossils are known (no fossil species has been adequately demonstrated to be closely related to *Chirocentrus*).

*Chirocentrus* has traditionally been thought to be a "primitive" clupeomorph and has thus been placed in its own superfamily (Whitehead, 1963b; Nelson, 1970a) or even suborder (Berg, 1940). It has been thought to be more primitive than other living clupeiforms because of its large fanglike teeth, the presence of a second set of pectoral radials (distal radials), the "absence of abdominal scutes," and the presence of a "spiral valve" in the intestine. For reasons discussed below, *Chirocentrus* is not considered here to be so primitive.

The presence of fanglike teeth, if somewhat spotty in its distribution among Recent clupeomorphs, is widespread. Besides, in *Chirocentrus*, this feature is also found in some members of Pellonulinae (see *Odaxothrissa*, fig. 27A); in Pristigasteroidea (*Chirocentrodon*, see fig. 15B and Hildebrand, 1963, fig. 115); in Engrauloidea (*Lycothrissa*); and to a lesser extent in several other clupeoids.

Distal radials in the pectoral girdle are not unique to *Chirocentrus* among living clupeoids, as suggested by Patterson (1967, p. 107) and others. They have been discovered in several species including pellonulines (fig. 35; Yabumoto and Uyeno, 1981, fig. 5; Roberts, 1972, fig. 10), dorosomatines (fig. 48), dussumieriines (Cervigón and Velaquez, 1978, fig. 50), and pristigasterids (Starks, 1930, fig. 5). A preliminary survey here indicates that many or most clupeomorphs have at least two sets of pectoral radials.

The so-called "absence of abdominal scutes" in *Chirocentrus* is not actually an absence; it is merely a reduction. *Chirocentrus* still retains the pelvic scute (as do all clupeomorphs), although it is modified in adults. The reduction of the pelvic scute in *Chirocentrus* (ontogenetic, lateral separation described above under discussion of character

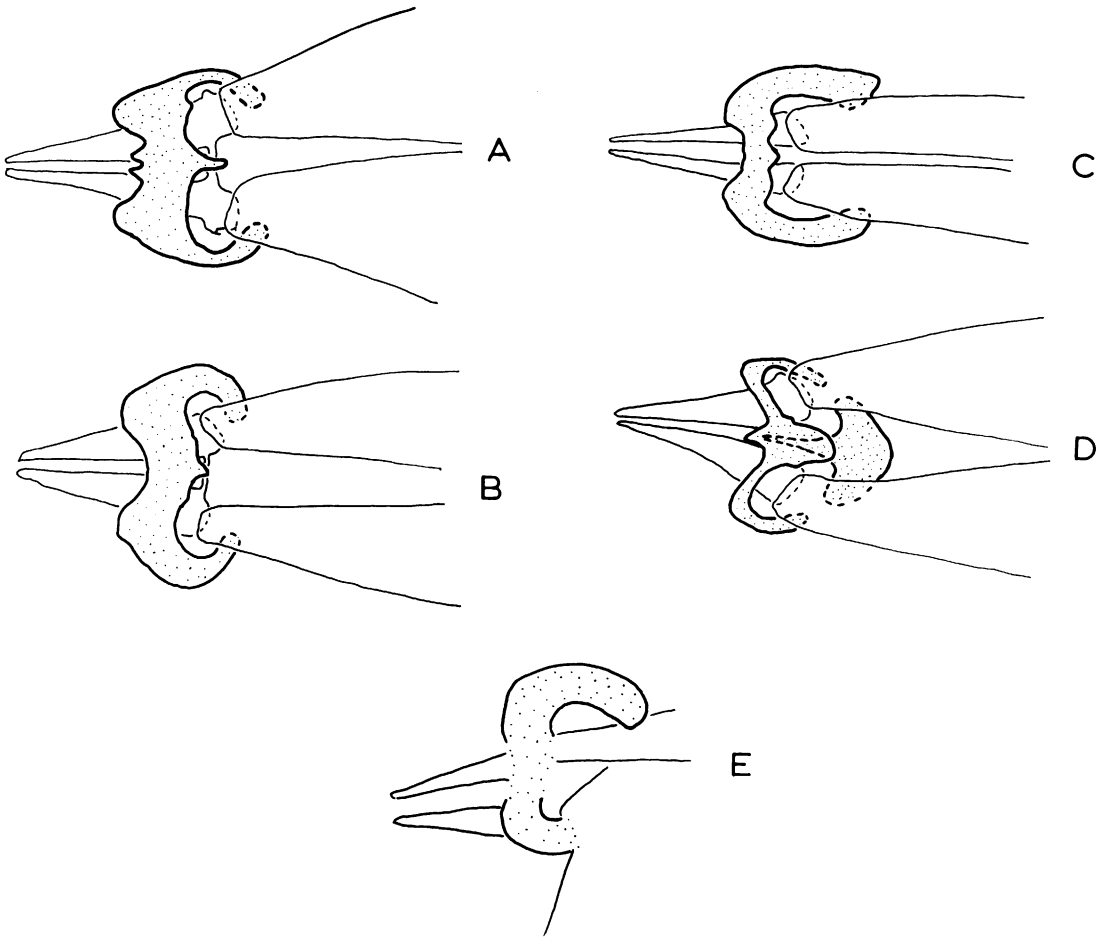


FIG. 17. The W-shaped pelvic scute of dussumieriines. Scutes (stippled) from (A) *Jenkinsia stolifera* (AMNH 2770 sw) (sl = 55 mm); (B) *Spratelloides delicatulus* (AMNH 54621 sw) (sl = 52 mm); (C) *Dussumieria acuta* (AMNH 17555 sw) (sl = 92 mm); (D) *Etrumeus teres* (AMNH 736 sw) (sl = 91 mm); (E) undescribed dussumieriine from the Eocene Monte Bolca Formation (BMNH 37227) (sl = 70 mm). Pelvic girdles and fins in outline with stipple. Figures A–D are ventral views; E is a dorsal view.

1, and in Whitehead, 1963b) is probably a character derived for chirocentrids; the modified scute of the adult (one side illustrated in Whitehead, 1963b, fig. 3d) may be a character useful for identifying true fossil chirocentrids. The lack of nonpelvic abdominal scutes (as in *Chirocentrus*) is not thought to be primitive for Clupeomorpha (see fig. 1) because it also occurs in pellenulines (table 5d), engraulids (table 4b), and dussumieriines (table 6b). Primitive clupeomorphs (†*Erichalcis*, †*Armigatus*, †*Ellimmichthyiformes*, and *Denticipitoidei*) all have a full series of abdominal scutes. The lateral separation of

the pelvic scute in *Chirocentrus* is unique among all clupeomorphs. Abdominal scutes will be further discussed below in the section on Dussumieriinae.

The implication that *Chirocentrus* has a chondrichthyan-type intestinal spiralfalten (a true spiral valve) was questioned by Cohen (1958). The intestinal ringfalten (rings of tissue projecting into the gut) of *Chirocentrus* although spiral in form, is not necessarily homologous with the spiralfalten (Cohen, 1958, p. 98) and probably worth further study.

Therefore, it is thought here that although *Chirocentrus* may be a primitive member of



the superfamily Clupeoidea, there is no reason to consider it a primitive clupeomorph fish.

### DUSSUMIERIINAE (Characters f-l)

This group of fishes has previously been revised by Whitehead (1963a). In his original classification he included the genera *Ehirava*, *Gilchristella*, and *Sauvagella*, which he later (1972, pp. 190–191) removed and placed into the Pellonulinae. He originally placed these Indo-Pacific pellenuline genera within Dussumieriinae (=Whitehead's Dussumieriidae) because of their lack of or poorly developed nonpelvic abdominal scutes; but he later changed his mind when it was discovered that certain West African pellenulines (Poll et al., 1965) also lack nonpelvic abdominal scutes. As noted above, chirocentrids and many anchovy species also lack these scutes. The pellenulines lack the one character that is truly unique to the dussumieriines—the peculiar modified pelvic scute (fig. 17) found only in *Etrumeus*, *Dussumieria*, *Spratelloides*, *Jenkinsia*, and an undescribed Eocene fossil taxon (fig. 17E). This scute, also described by Chapman (1948) and Whitehead (1962b) is unkeeled and W-shaped, immediately anterior to the pelvic fins with the arms of the W extending laterally around the base of the fin rays. The oldest fossils known to the author which are clearly assignable to Dussumieriinae belong to the undescribed Monte Bolca species illustrated in figure 17E. Whitehead (1963a and elsewhere), Nelson (1967a, 1970a), Taverne (1977b), and others have considered dussumieriines to be the most primitive of the clupeids (sister-group to all other clupeid groups) mostly because of their lack of nonpelvic abdominal scutes and the high number of branchiostegal rays in Dussumieriini. Within clupeomorph fishes, these two characters are interpreted here as advanced rather than primitive characters.

Because Clupeomorpha (see fig. 1A) primitively have abdominal scutes (present in all †*Erichalcis*, †*Armigatus*, †*ellimmichthyiforms*, denticipitoids, and pristigasterids), the absence of abdominal scutes in some engraulids, chirocentrids, pellenulines, and dussumieriines is seen here as several independent

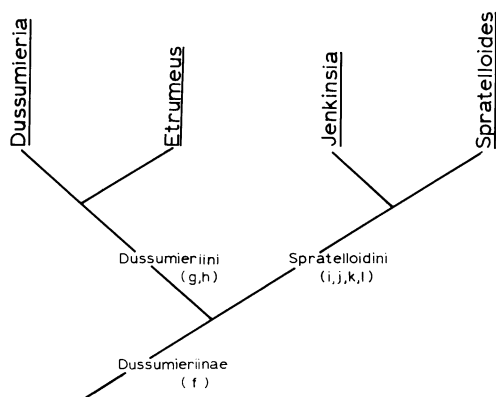


FIG. 18. Cladogram showing the monophyletic groups of dussumieriine fishes. Characters f through l discussed in text.

secondary losses. The presence of a high number of branchiostegal rays is seen here as an advanced clupeomorph character for reasons discussed below (character g).

If we look at the general trend of increasing relative abdominal cavity size among clupeomorphs (discussed above with character 22), the dussumieriines are a relatively derived rather than “primitive” clupeoid group (tables 1a–10a). Svetovidov (1952, p. 98) considered dussumieriines to be “the most advanced” of the clupeoid family level groups.

A cladogram summarizing the osteological characters as interpreted here is given in figure 18. The characters in the cladogram are discussed below.

#### Character f (of Dussumieriinae)

*f.* The presence of a peculiar, unkeeled, W-shaped pelvic scute (fig. 17). Unique to dussumieriines and explained above.

Although several old fossil species have been assigned to Dussumieriinae (or “Dussumieriidae”) such as the Cretaceous †*Clupavus neocomiensis* (by Arambourg, 1954) and the Upper Jurassic †*Luisiella inexcitata* (by Bocchino, 1967), none have ever been demonstrated to be clupeomorphs (as defined here). †*Luisiella* was diagnosed as a clupeomorph because of the presence of ossified centra, and as a dussumieriine because of the absence of scutes. By today’s standards, †*Luisiella* is *Teleostei incertae sedis* and not a clupeomorph, certainly not a dussumieriine.

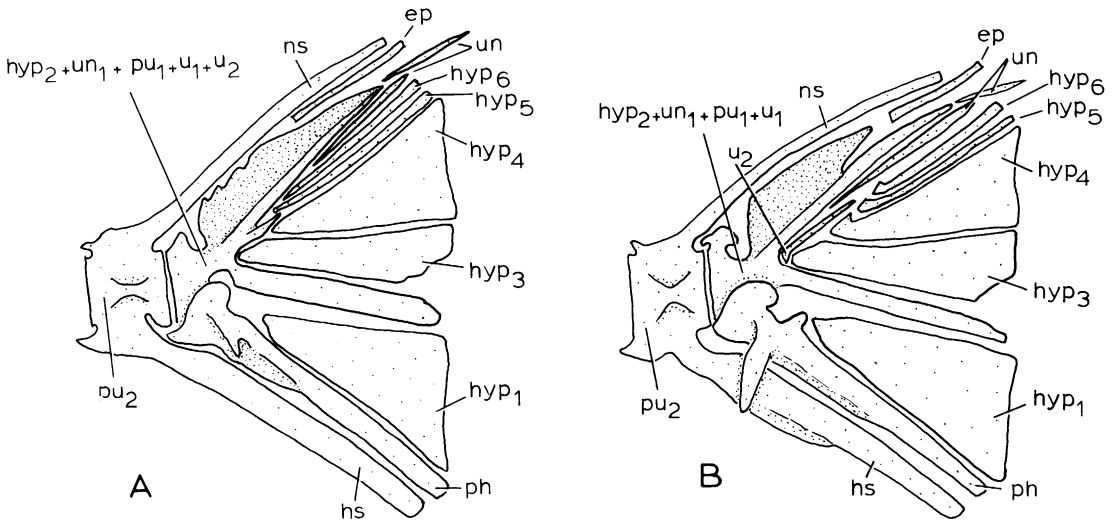


FIG. 19. The caudal skeletons of Spratelloidini showing vertebral fusions and expansion of the fourth hypural as explained in text. (A) *Jenkinsia stolidus* (AMNH 2770 sw) (sl = 53 mm) and (B) *Spratelloides delicatulus* (AMNH 54621 sw) (sl = 51 mm).

There are no clupeomorphs known prior to the Cretaceous (see Grande, 1982a and below). Arambourg (1954) assigned †*Chupavus neocomiensis* (discussed below) to Dussumieriinae also because of the absence of scutes. The absence of scutes in itself is not a reason to assign a fossil to Dussumieriinae (since nonclupeomorphs also are without abdominal scutes). To be a dussumieriine, a fossil must first be demonstrated to be a clupeomorph. The presence of the uniquely derived pelvic scute (character f above) would diagnose a fossil to this group.

Characters g and h (of Dussumieriini)

g. *Extremely high number of branchiostegal rays (14–20)*. Although Whitehead (1963a, p. 367), Nelson (1967, p. 398), and others have considered the high number of branchiostegal rays to be a “primitive” feature of Dussumieriinae, it is considered here to be a character independently derived for the tribe Dussumieriini. The range for this group is higher than in any other known clupeomorph, and only a few engraulid species even overlap this range (see tables 1a–10a). Clupeomorpha primitively have fewer branchiostegal rays (†*Armigatus* = 10–12, †*Erichalcis* = about 9, tellimmichthyiforms = 10–12, denticipitoids = 5, engraulids = 8–15,

pristigasterids = 6, chirocentrids = 8, spratelloidins = 6–8, and other clupeids = 4–9). In the nonclupeomorph species examined, the number is variable (*Salmo trutta* = 11, *Megaloops atlantica* = 24, *Hiodon tergisus* = 8).

h. *Parhypural fused with first preural centrum*. Gosline (1960, fig. 7) was first to note that *Dussumeria acuta* was peculiar among clupeoids in having this feature. It was found here that this fusion is also present in the other species of *Dussumeria* and in *Etrumeus*, but in no other clupeoid. Most non-clupeoid clupeomorphs also have this fusion (see fig. 8 for example) but because chirocentrids, spratelloidins, and all other clupeoids have no such fusion (see figs. 38 and 51, for example), this is considered here to be a character independently derived for the Dussumieriini.

†*Etrumeus boulei* Arambourg, 1927, from Miocene deposits of Oran, Algeria shows the modified pelvic scute indicative of a dussumieriine and a high branchiostegal ray count (greater than 13) indicative of a dussumieriin (specimen MNHN 279 [sl = 200 mm] is a good example).

Characters i–l (of Spratelloidini)

i. *An expansion of the fourth hypural in the caudal skeleton to be roughly symmetrical to*

the first hypural (fig. 19). Among all clupeomorphs (and other teleosts) examined, this character is unique to Spratelloidini.

j. *Reduction of number of epurals to 1* (tables 1a–10a) (fig. 19). Among clupeomorphs, the primitive number of epurals appears to be three. Although several clupeiform species have reduced the number to two, only one other clupeomorph species observed besides *Spratelloides* and *Jenkinsia* (the pellone line *Corica laciniata*) has reduced the number to one exclusively (although a few alosine and clupeine species which usually have two occasionally have one—see tables).

k. *Fusion of the first ural centrum to the first preural centrum* (tables 1b–10b) (fig. 19). This fusion, among clupeomorphs, is confined to this tribe, a group of pellone lines (discussed below), a group of engraulids (discussed above), and one clupeine (*Clupeonella cultiventris*). Because of the distribution of this feature among clupeids and coincidence with other characters, it is considered to be independently derived for the Spratelloidini. *Jenkinsia* also has  $u_2$  fused with  $u_1 + pu_1$  (fig. 19A), and  $u_2$  and  $u_1$  are fused in *Etrumeus* (with no fusion to  $pu_1$ ).

l. *Reduction of infraorbital bones to five*. Among clupeomorphs, the number of infraorbital bones is almost always six, excluding the antorbital (see also, Nelson, 1969) except for *Jenkinsia*, *Spratelloides*, and *Potamalosa* (an Australian pellone line). Yabumoto and Uyeno (1981, fig. 4) reported only five for *Hyperlophus translucidus*, but all specimens of this species examined here had six. It is quite feasible that some *Hyperlophus* specimens could have five since this genus may be closely related to *Potamalosa* (see section below on Pellonulinae). The reduction to five in *Potamalosa* (and that shown for *Hyperlophus translucidus* by Yabumoto and Uyeno, 1981) is different than in Spratelloidini. In *Potamalosa* (fig. 20), it is the result of a fusion between  $io_3$  and  $io_4$  based on the position of the neuromasts and the bones (method used by Nelson, 1969, for determining fusion patterns). The reduction in Spratelloidini is the result of the absence of  $io_6$  (=the dermosphenotic), a bone usually very small in clupeiforms but undetectable in any specimens of *Jenkinsia* or *Spratelloides* observed here.

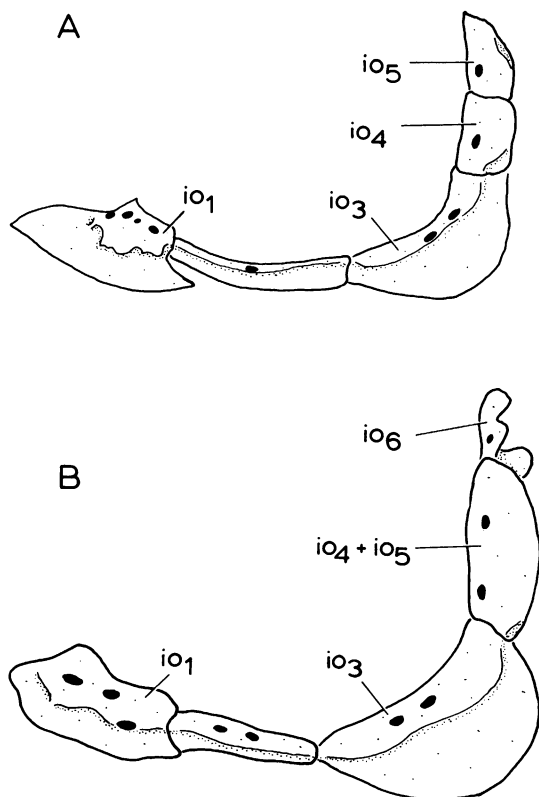


FIG. 20. Infraorbital series in (A) *Potamalosa richmondia* (AMNH 1737 sw) (sl = 150 mm) and (B) *Spratelloides delicatulus* (AMNH 54621 sw) (sl = 51 mm). Positions of neuromasts indicated by large black ovals.

Whitehead (1963b) also noted that in Dussumieriini, the posterior frontal fontanelles are closed in the adults but open in adults of Spratelloidini. It is thought here that additional study of this condition in tellinimichthyiforms and in ontogenetic series of Recent clupeids is needed before it can be determined whether the posterior frontal fontanelles are a primitive or an advanced clupeid character.

†*Spratelloides lemoinei* Arambourg, 1927, from Miocene deposits of Oran, Algeria, is also a member of the Spratelloidini. Several specimens (including the type: MNHN 904, sl = 86 mm) show the W-shaped pelvic scute, indicating that it is a dussumeriine, and others (MNHN 1146 G, sl = 65 mm) also show the expanded fourth hypural, single epural, and  $u_1$ – $pu_1$  fusion indicative of Spratelloidini.

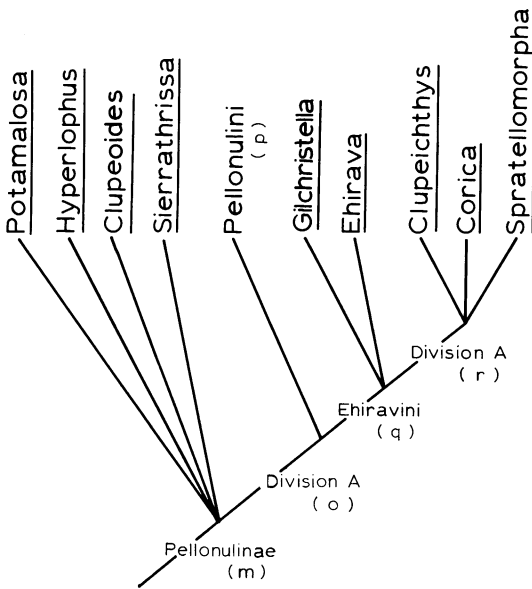


FIG. 21. Cladogram showing the monophyletic groups of pellonuline fishes. Characters m and o through r discussed in text.

#### PELLONULINAE (Characters m, o–r)

This group of fishes has previously been revised by Regan (1971c—African species; 1922—Indo-Pacific species); Poll (1974—African species); and Whitehead (1972—Indo-Pacific species). A cladogram summarizing the osteological characters as interpreted here is given in figure 21 and the characters are discussed below. The monotypic family Congothrissidae erected by Poll (1964) to contain only *Congothrissa gossei* Poll, 1964, is not considered valid here and elsewhere (Roberts, 1972, pp. 21–22; Whitehead, 1968). This species appears to belong with the rest of the African pellonulines (within Pellonulini).

The only fossils known here that are described as pellonulines are several species in the genus †*Knightia* (most species reviewed in Grande, 1982b) and one species in the genus *Pellonula*. †*Knightia* is known from Middle Paleocene through Middle Eocene time in North America and China; and †*Pellonula grasionescui* Ciobanu, 1977, is described from Oligocene deposits of Rumania. Based on an illustration and the type description, I could not determine whether or not †*P. grasionescui* actually belongs in Pello-

nulinae (specimen was unavailable for this study).

#### Characters m and o (of Pellonulinae)

*m.* Loss of anterior supramaxilla (Regan, 1917c, 1922; Whitehead, 1968, 1972). This loss also occurs in some members of Dussumieriinae, Dorosomatinae, and Engrauloidea. Although Whitehead, 1968, reports the clupeine *Platanichthys* as having only one supramaxilla in some specimens, the holotype (Whitehead, 1968, p. 484) and all specimens examined here had two.

Separation of this group based on this character is tenuous, and it may be advisable, after further study, to remove *Potamalosa*, *Hyperlophus*, *Sierrathrissa*, *Clupeoides*, and †*Knightia* from the group, thus leaving only the two groups (Pellonulini and Ehiravini as used here) united by the fusion of the first ural centrum with the first preural centrum (discussed below).

**Character o (of Pellonulinae Division A, containing the Pellonulini and the Ehiravini as used here)**

*o.* Fusion of the first ural centrum with the first preural centrum (tables 1b–10b; fig. 38). This fusion occurs elsewhere only in a group of engraulids (discussed above), the dussumieriine tribe Spratelloidini (also discussed above), and one clupeine, *Clupeonella culiventrifera*. Because there is no other evidence indicating possible close relationship between pellonulines and engraulids, the fusion in Engrauloidea is seen here as independently derived for a group of anchovies.

The presence of a similar vertebral fusion in Spratelloidini does not clearly specify any relationship between dussumieriines and pellonulines because pellonulines do not have the unique pelvic scute of dussumieriines (character f here) and only one tribe of dussumieriines has the vertebral fusion of the pellonuline groups. Thus, unless further evidence clearly indicates a close relationship between Pellonulinae and Dussumieriinae, the fusion of  $pu_1$  and  $u_1$  in Pellonulini and Ehiravini is considered to be independently derived for a group containing those two tribes.

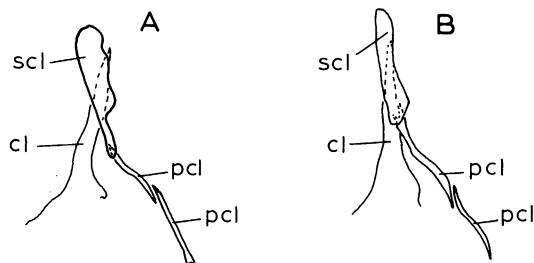


FIG. 22. Articulation of postcleithrum with supracleithrum in (A) *Laeviscutella dekimpei* (BMNH 1965: 77 10-14) (sl = 43 mm). (B) *Hyperlophus vittatus* (AMNH 3050 sw) (sl = 58 mm). Diagram A shows the type of articulation for the western and central African pellowulines as discussed in text. Both are lateral views.

#### Character p (of Pellonulini, the Western and Central African Pellonulines)

*p. Articulation of postcleithrum with supracleithrum well behind cleithrum* (tables 1b-10b, fig. 22). The Pellonulini as recognized here include the genera *Pellonula*, *Microthrissa*, *Nanothrissa*, *Poecilothrissa*, *Sto- lothrissa*, *Limnothrissa*, *Cynothrissa*, *Odaxothrissa*, *Potamothrissa*, *Laeviscutella*, *Congothrissa*, and *Thrattidion*. All of these genera are nearly unique among the clupeomorphs observed here in having the articulation between the posterior end of the supracleithrum and the anterior end of the first rodlike postcleithrum well behind the cleithrum (figs. 22A and 35). This group also appears to be confined to Western and Central Africa, and most of its species are confined to freshwater. The only other observed occurrence of this supracleithrum-postcleithrum articulation was in the ehiravin genera *Clupeichthys* and *Ehirava*. Admittedly, it is also possible that character p, like character o, may instead define a group containing both Ehiravini and Pellonulini (requiring secondary loss of character p in *Gilchristella*, *Corica*, and *Spratellomorpha*); this would leave Pellonulini as paraphyletic (with no known synapomorphies) within Pellonulinae. Nevertheless, the interpretation used here, if somewhat tenuous (influenced by the geographic range of the two main pellowuline groups), is that the articulation was derived for Pellonulini independent of its derivation

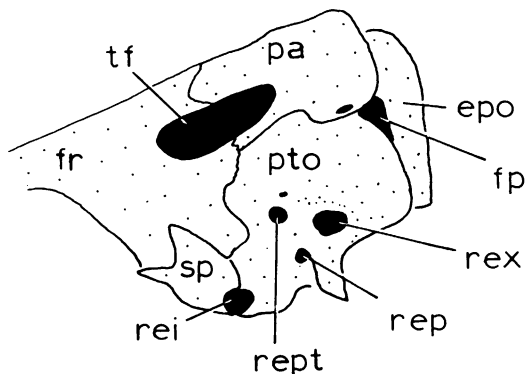


FIG. 23. The openings to the recessus in Ehiravini, demonstrated by *Corica laciniata* (ANSP 89414) (sl = 51 mm). All pellowulines other than ehiravins have a common opening to the recessus for the infraorbital, preopercular, lateral extrascapular, and pterotic sensory canals as illustrated in figures 27 and 30.

in *Ehirava* and *Clupeichthys*. All other groups with the clupeid postcleithra (long, rodlike form discussed above under character 23) have the articulation with the supracleithrum either overlapping or at least close against the cleithrum (figs. 22 and 48).

Character q (of Ehiravini, the Southeastern African-Indo-Pacific pellowulines). (The taxon Ehiravini as used here differs from the usage of Whitehead, 1973, p. 13, in that the genus *Clupeichthys* is included.)

*q. Lateral extrascapular canal, preopercular canal, and a third unnamed canal (apparently connected to some superficial sensory canals on the head) all emptying through independent openings in the pterotic bone leading directly to the recessus chamber (along with a fourth independent opening, for the infraorbital canal, formed by the pterotic and sphenotic bones) (fig. 23).* The recessus lateralis is a very complex feature of clupeiforms (discussed above under character 9) and after further study will probably yield other characters diagnostic of various clupeiform groups. The pellowuline tribe Ehiravini (as used here) shows what is interpreted as a uniquely derived series of openings to the recessus through the pterotic bone. The lateral surface of the pterotic bone is smooth, thin bone completely containing three sepa-

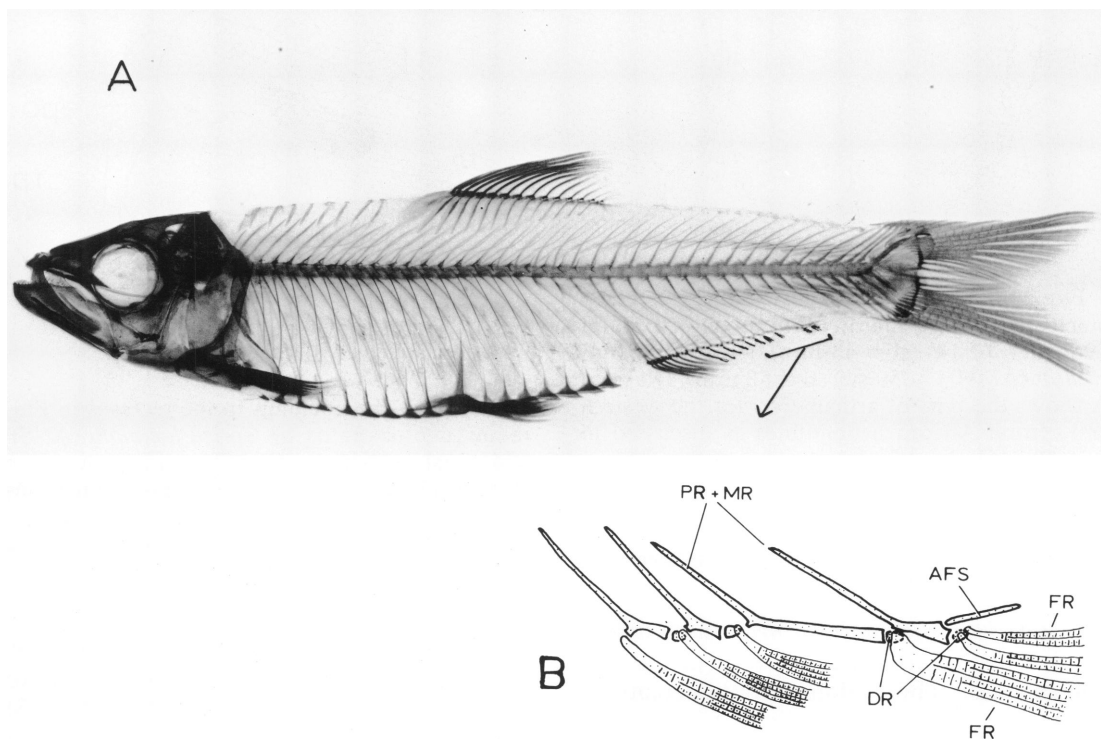


FIG. 24. (A) *Clupeichthys goniognathus* (MCZ 47178) (sl = 44 mm) showing the anal finlet (arrow) and modification of the fin support in certain members of Ehiravini (discussed in text). Posterior anal rays highlighted. (B) Line drawing of the last four sets of anal fin radials and associated fin rays from specimen in A.

rate openings—one for the lateral extrascapular canal, one for the preopercular canal, and a third (apparently connecting a series of superficial head canals to the recessus chamber) anterior to the other two (see fig. 23). A fourth separate opening to the recessus is formed in part by the pterotic and in part by the lateral flange of the sphenotic bone.

In all other pelloneulines (Pelloneulini, *Clupeoides*, *Hyperlophus*, and *Potamalosa*) there is only one single, large opening (see fig. 27B), and in other clupeiforms the condition is variable, but never exactly like the ehiravin condition. The function of the “third opening” in the pterotic bone, and a more complete study and survey of the recessus openings for the sensory canals, is a subject for further study. The Ehiravini appear to be confined to an area from South and Eastern Africa, through the Indo-Pacific, in both fresh and marine waters.

#### Character r (of Ehiravini Division A)

*r.* Anal finlet behind main (anterior) body of anal fin, with associated pterygiophore modifications (fig. 24). This structure is unique among all clupeomorphs examined, and was not observed in any other teleost. †*Scombroclupea macrophthalmala* (Heckel, 1849) from the Late Cretaceous of Lebanon, is a primitive clupeomorph (study in progress) that has several anal finlets; but the associated support structure for each finlet (which contains an autogenous middle radial) is quite different from that of the ehiravin finlet.

#### DOROSOMATINAE, CLUPEINAE, AND ALOSINAE

No osteological characters were discovered that would indicate that any of these three groups individually, or all three groups together, form a monophyletic group. In the

opinion of the author, the greatest remaining problem in clupeomorph systematics is to discover how the members of these three groups are interrelated within Clupeoidei.

Most fossil clupeoids (see list below) are in this group (that is, they are clupeids that do not appear to belong in Dussumieriinae or Pellonulinae). Most fossils that have been described as "*Clupea*" (i.e., " $\dagger$ *Clupea*" *cato-pygoptera* Woodward, 1901; and over 40 others) are in fact *incertae sedis* within this larger group; and none have ever been shown to be more closely related to members of *Clupea* (i.e., *C. harengus* Linnaeus, 1758; and *C. pallasii* Valenciennes, 1847) than to other clupeine genera.

Dorosomatines have been revised by various workers (Regan, 1917a [Worldwide]; Miller, 1960 [New World], Whitehead, 1962a [Old World]; Nelson and Rothman, 1973 [Worldwide]). Among those listed, the only workers who attempted to clearly define the group as monophyletic were Nelson and Rothman (based on nonosteological characters of the digestive tract), although they admit (p. 138) that the group may also contain some species currently classified in Clupeinae and Alosinae. A more general survey is thus

needed to more accurately identify this group. Characters normally used in regional keys (such as Whitehead, 1972) are the presence of a single supramaxillary bone, gizzardlike stomach, filamentous dorsal fin ray, inferior mouth, dentary flared outward, etc. None of these characters are restricted to dorosomatines, and most occur in only part of the group.

Clupeinae and Alosinae are very difficult to diagnose even roughly as distinct groups. Some authors (Regan, 1916; Hildebrand, 1963 and others) have combined parts of Alosinae and Clupeinae, while others (Regan, 1917a; Nelson, 1970a and others) have combined parts of Alosinae with Dorosomatinae. Of the osteological structures surveyed here, no characters were found to clearly diagnose any of these groups. The gill arches of clupeoid fishes (currently under study by the author) may yet reveal some synapomorphic skeletal characters for major groups of clupeids. For example, the mediopharyngobranchial (fig. 46) was found by Nelson (1967a, p. 396) to be unique among clupeomorphs to all alosines, dorosomatines, and some clupeines (although his study sample was somewhat limited). The interrelationships of Clupeidae are still under study by the author.

## ADDITIONAL OSTEOLOGICAL INFORMATION SURVEYED

Tables 1a through 10a and 1b through 10b on pages 282–308 summarize some of the osteological features surveyed in the study sample. An effort was made to study a few specimens, each of a large number of clupeomorph species, rather than many specimens of only a few species. Therefore, intraspecific variation is greater than indicated for several

meristic features (tables 1a–10a). Some of these features are also surveyed elsewhere using additional specimens: dorsal scutes (Grande, 1982a); branchiostegal rays (Nelson, 1970a); supramaxillary bones (Whitehead, 1968), and vertebrae (Nelson, in progress).

## ADDITIONAL COMMENTS ON FOSSIL CLUPEOMORPHS

Much of the literature on fossil clupeomorph fishes is in a confusing state. Several authors (Schaeffer, 1949; Bardack, 1965a; Bochino, 1967; Arratia, 1975; and others) have used the groups Clupeomorpha and Clupeoidei to include almost any teleost fossil which lacks obvious derived characters (such as dorsal spines) suggesting placement elsewhere. This may be partly due to the fact

that many of the good characters diagnosing Clupeomorpha, or some subdivision of it (such as bullae, diverticulum of the swimbladder, recessus lateralis, etc.) are only rarely preserved in fossils. In my opinion, the *incertae sedis* and *indeterminate* categories should be more widely used so as not to disrupt classificatory systems based on Recent and well preserved, diagnosable, fossil spec-

TABLE 1a  
Meristic Information for Some Nonclupeiform Clupeomorphs

Genus Species	Pre- dorsal bones	Dorsal scutes <sup>a</sup>	Bran- chios- tegal rays	Supra- maxil- lary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs- preural verte- brae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
† <i>Erichalcis</i>										
† <i>E. arcta</i>	?	0	≥9	2	18	42	.43	11-12	19	3
† <i>Armigatus</i>										
† <i>A. brevissimus</i>	5-6	11-12 (A)	10-12	2	13	31-32	.41	18-19	28	3
† <i>Diplomystus</i>										
† <i>D. dentatus</i>	7-8	33-36 (A)	12	2	17	41-43	.40	11-12	39-40	3
† <i>D. birdi</i>	6-7	23 (A)	10-11	2	11-12	30	.38	16-17	23-25	3
† <i>D. dubertreti</i>	6-7	20 (A)	?	2	12-13	33-34	.37	23	27	?
† <i>Ellimmichthys</i>										
† <i>E. longicostatus</i>	7	12 (A)	8-9	2	19-22	36-37	.56	12-13	9	3

<sup>a</sup> (A) = between skull and dorsal fin.

imens. For example, †*Ostariostoma wilseyi* Schaeffer, 1949, should be classified Teleostei *incertae sedis* rather than in Clupeoidea. Schaeffer's (p. 15) reason for placing the species in Clupeoidea is "because the general

level of organization indicates this allocation at the present time rather than any other." The type and only known specimen of †*Ostariostoma* shows no derived character indicating it is a clupeomorph, and therefore

TABLE 1b  
Morphological Information for Some Nonclupeiform Clupeomorphs

Genus Species	Presence of pre- pelvic abdominal scutes	Presence of post- pelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind <sup>a</sup>	Presence of two long rod- like post- cleithra	Fusion of caudal vertebrae	Absence of in- terlobar notch on third hypural	Large caniniform teeth in jaw
† <i>Erichalcis</i>								
† <i>E. arcta</i>	+	+	?	—	—	—	—	—
† <i>Armigatus</i>								
† <i>A. brevissimus</i>	+	+	+	—	—	—	+	—
† <i>Diplomystus</i>								
† <i>D. dentatus</i>	+	+	+	—	—	—	+	—
† <i>D. birdi</i>	+	+	+	—	—	—	?	—
† <i>D. dubertreti</i>	+	+	+	—	—	—	?	—
† <i>Ellimmichthys</i>								
† <i>E. longicostatus</i>	+	+	+	—	—	—	—	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).



TABLE 2a  
Meristic Information for Denticipitoidei

Genus Species	Predorsal bones	Dorsal scutes	Bran- chios- tegal rays	Supra- maxil- lary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs- preural verte- brae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Denticeps</i>										
<i>D. clupeioides</i>	11	0	5	0	14	38	.37	7	23	2
† <i>Palaeodenticeps</i>										
† <i>P. tanganyikae</i>	12 (based on Greenwood, 1960)	0	5	0	12	30	.40	8	23	3

should not yet be placed within Clupeomorpha. Other fossil species which are well preserved and relatively common (such as those from the Green River Formation, Monte Bolca, Lebanon, etc.) have a much better chance to be more specifically classified (such as the genus †*Knightia* within Pellonulinae or at least within Clupeidae *incertae sedis*—see Grande, 1982b).

Some fossil species will probably always be classified *incertae sedis* or *indeterminate* at general taxonomic levels because of lack of preservation (i.e., insufficient morphological information). For example, †“*Diplomystus*” *solignaci* Gaudant and Gaudant, 1971 (re-

moved from †*Diplomystus* in Grande, 1982a, p. 19) is known by only a single specimen, which is poorly preserved. It (holotype: MNHN 1970-3, illustrated in Gaudant and Gaudant, 1971) has abdominal scutes and poorly preserved dorsal scutes indicating that it is at least identifiable as belonging in Clupeomorpha. But most of the caudal skeleton and skull are not preserved and the morphology of its dorsal scute is unknown; consequently this species cannot be placed within any clupeomorph subgroup.

The presence of “clupeomorph-type” abdominal scutes (see character 1 above) is probably the most useful character for iden-

TABLE 2b  
Morphological Information for Denticipitoidei

Genus Species	Presence of prepelvic abdominal scutes	Presence of post- pelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind <sup>a</sup> cleithrum	Presence of two long rod- like post- cleithra	Fusion of caudal <sup>b</sup> vertebrae	Absence of in- terlobar notch on third hypural	Large caniniform teeth in jaw
<i>Denticeps</i>								
<i>D. clupeioides</i>	+ <sup>b</sup>	+ <sup>b</sup>	+ <sup>b</sup>	—	—	—	—	—
† <i>Palaeodenticeps</i>								
† <i>P. tanganyikae</i>	+ <sup>b</sup>	+ <sup>b</sup>	+ <sup>b</sup>	—	—	—	—	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).  
<sup>b</sup> All of the abdominal scutes in *Denticeps* and *Paleodenticeps* lack ascending arms.

TABLE 3a  
Meristic Information for Some Pristigasterides (Clupeiidae: Pristigasteroidea)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxil- lary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs- preural verte- brae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Chirocentrodon</i>										
<i>C. bleekermanus</i>	19-21	0	6	2	18	44	.41	15-16 ( $\bar{X}$ = 15.66)	40	3
<i>Neopisthoporus</i>										
<i>N. tropicus</i>	20	0	6	2	16	44	.35	15	42	3
<i>Pliosteostoma</i>										
<i>P. lutipinnis</i>	23	0	6	2	17-18	49-50	.35	14	48-53	2
<i>Pellona</i>										
<i>P. ditchela</i>	7	0	6	2	16-17	42	.39	18-19	33-34	3
<i>P. flavipinnis</i>	9	0	6	2	19	43	.44	19	38	3
<i>P. harroweri</i>	8	0	6	2	13	39	.33	15-16 ( $\bar{X}$ = 15.75)	37-39	3
<i>Odontognathus</i>										
<i>O. mucronatus</i>	30-31 ( $\bar{X}$ = 30.66)	0	6	2	15	52-54	.28	11-12 ( $\bar{X}$ = 11.66)	75-78	3
<i>O. panamensis</i>	28	0	6	2	16	51	.31	12	61	3

TABLE 3a—(Continued)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxil- lary bones	Pleural ribs (pairs)	Pleural verte- brae	Pleural ribs— preural verte- brae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Raconda</i>										
<i>R. russeliana</i>	30	0	6	2	17	61	.28	16	88	3
<i>Opisthopterus</i>										
<i>O. valenciennesi</i>	24	0	6	2	18	51	.35	18	58	3
<i>O. equitorialis</i>	25	0	6	2	16	47	.34	13–14	58–59	3
<i>Pristigaster</i>										
<i>P. cayana</i>	5	2 (B)	6	2	14	43	.33	14–15	46–47	3
<i>Ilisha</i>										
<i>I. africana</i>	11	0	6	2	14–15 ( $\bar{X}$ = 14.75)	42	.35	15	45	3 <sup>b</sup>
<i>I. elongata</i>	14	0	6	2	23	55	.42	18	47	3
<i>I. amazonica</i>	6	0	6	2	14	40	.35	15	46	3
<i>I. furthii</i>	8–9 ( $\bar{X}$ = 8.25)	0	6	2	19–20 ( $\bar{X}$ = 19.25)	50–51 ( $\bar{X}$ = 50.80)	.38	16–17 ( $\bar{X}$ = 16.75)	48–50	3
<i>I. indica</i>	10	0	6	2	16	42	.38	17	39	3
† <i>Gasteroclupea</i>										
† <i>G. branisai</i>	16–17	34–36 (A)	?	2	9	32	.28	12–13	13–14	3

<sup>a</sup> (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.<sup>b</sup> One specimen had the last two epurals fused at their bases, a variable condition common in many clupeoid species.

TABLE 3b  
Morphological Information for Some Pristigasterides (Clupeoidei: Pristigasteroidea)

Genus Species	Presence of prepelvic abdominal scutes	Presence of post- pelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind <sup>a</sup> cleithrum	Presence of two long rod- like post- cleithra	Fusion of caudal vertebrae	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
<i>Chirocentrodon</i>								
<i>C. bleekermanus</i>	+	+	+	—	—	—	+	+
<i>Neopisthopterus</i>								
<i>N. tropicus</i>	+	+	+	—	—	—	+	+
<i>Pliosteostoma</i>								
<i>P. lutipinnis</i>	+	+	+	—	—	—	+	—
<i>Pellona</i>								
<i>P. ditchela</i>	+	+	+	—	—	—	+	—
<i>P. flavipinnis</i>	+	+	+	—	—	—	+	—
<i>P. harroweri</i>	+	+	+	—	—	—	+	—
<i>Odontognathus</i>								
<i>O. mucronatus</i>	+	+	+	—	—	—	+	—
<i>O. panamensis</i>	+	+	+	—	—	—	+	—
<i>Raconda</i>								
<i>R. russeliana</i>	+	+	+	—	—	—	+	—
<i>Opisthopterus</i>								
<i>O. valenciennesi</i>	+	+	+	—	—	—	+	—
<i>O. equitorialis</i>	+	+	+	—	—	—	+	—
<i>Pristigaster</i>								
<i>P. cayana</i>	+	+	+	—	—	—	+	—
<i>Ilisha</i>								
<i>I. africana</i>	+	+	+	—	—	—	+	—
<i>I. elongata</i>	+	+	+	—	—	—	+	—
<i>I. amazonica</i>	+	+	+	—	—	—	+	—
<i>I. furthii</i>	+	+	+	—	—	—	+	—
<i>I. indica</i>	+	+	+	—	—	—	+	—
† <i>Gasteroclupea</i>								
† <i>G. branisai</i>	+	+	+	—	—	?	?	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).

tifying fossils as clupeomorphs. These scutes appear to be unique to Clupeomorpha and are usually well preserved and easy to see on fossil specimens (figs. 8b, 11k, and 25). Many problems arise from the placement of fossils within Clupeomorpha because of some superficial resemblance to *Chirocentrus*, a Recent clupeomorph lacking nonpelvic abdom-

inal scutes. If a fossil lacks the obvious character of nonpelvic abdominal scutes (such as †*Ostariostoma*, †ichthyodectids, etc.) then other clupeomorph characters (such as a pelvic scute, pterotic and/or prootic bullae, a recessus, etc.) must be found before placing the taxon within Clupeomorpha.

Contrary to recent work (Forey, 1973b;

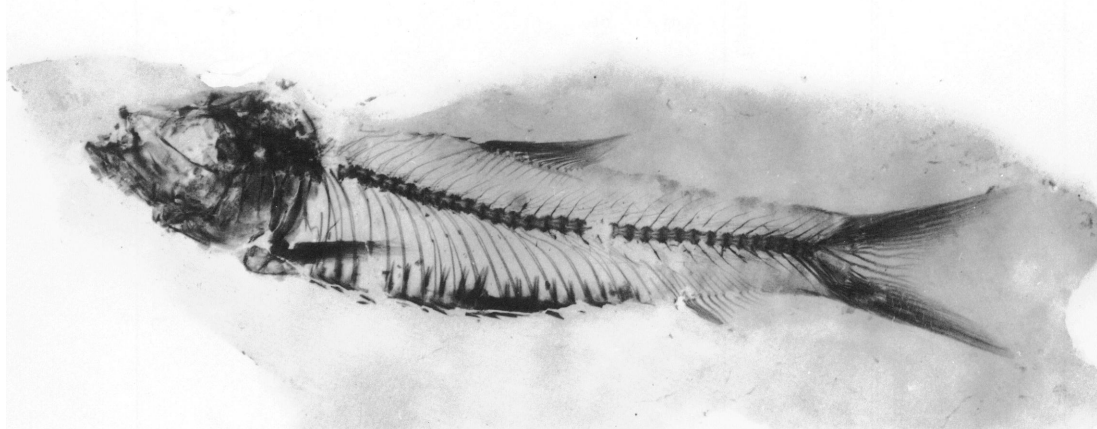


FIG. 25. Positive print made from radiograph of †*Knightia eocaena* from the Early Eocene of the Green River Formation.

Patterson and Rosen, 1977; and Grande, 1982a), the present investigation does not include the genus †*Ornategulum* in Clupeomorpha. Forey (1973b) erected the genus †*Ornategulum* to contain the single species, †“*Clupea*” *sardinioides* Pictet, 1850, and he placed it as Clupeomorpha *incertae sedis*. He identified the taxon as belonging to Clupeomorpha mainly because it has a free first hypural and a fusion between the second hypural and the first ural centrum. Without the presence of additional clupeomorph characters, this caudal skeleton condition (discussed above under character 4) is thought to be insufficient evidence to justify placement of †*Ornategulum* in Clupeomorpha. Forey also stated (p. 1317) that the “presence of a complete neural spine upon  $pu_2$  should be regarded as a distinguishing feature of Clupeomorpha”; but this condition is, in fact, not a clupeomorph character. A complete neural spine on  $pu_2$  also occurs in primitive euteleosts (Fink and Fink, 1981; and personal observ.); *Elopomorphs* (*Megalops*); and *Osteoglossomorphs* (e.g., *Hiodon*). Patterson and Rosen, 1977, and Grande, 1982a, at first accepted Forey’s placement of †*Ornategulum* into Clupeomorpha; and they placed the monotypic genus as the sister-group to all other species in the group because it lacked characters unique to Clupeomorpha. This placement is reconsidered here for the reasons given above (i.e., insufficient evidence

for placement of †*Ornategulum* into Clupeomorpha), and also because †*Erichalcis arcta* Forey, 1975, is thought here to be the sister-group of all other known clupeomorphs. †*Ornategulum* has no scutes and the presence of bullae is doubtful (Forey, 1973b, p. 1308, and personal observ.). †*Erichalcis* has clupeomorph-type abdominal scutes (well preserved on UAVP 17535: see fig. 5D), and according to Forey, 1975, p. 156, “the prootic has a ‘strawberry’ appearance which is very similar to the bullate areas in Recent clupeoid skulls. The presence of a prootic bulla is suspected.” Unlike other clupeomorphs, †*Erichalcis* does not have a fusion between the second hypural and the first ural centrum (fig. 5B), suggesting the possibility that the most primitive clupeomorphs (i.e., Division 1) did not have the fusion (character 4). †*Ornategulum* is therefore left as Clupeocephala *incertae sedis*.

Within Clupeomorpha, the *incertae sedis* category can be used at several levels, again, to promote stability of a system based on more easily diagnosable species. For example, many species that have been assigned to the genus †*Diplomystus* should be assigned only to Clupeomorpha Division 2 *incertae sedis*. Their placement into the tellinmichthyiform genus was done on the basis of superficial primitive similarities (the presence of both dorsal and abdominal scutes). The problems of such placements are dis-

TABLE 4a  
Meristic Information for Some Species of Anchovies (Clupeoidei: Engrauloidea)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxil- lary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs- preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Anchoa</i>										
<i>A. compressa</i>	10-11	0	13	2	17	41	.41	11-12	30	2
<i>Anchovia</i>										
<i>A. clupeioides</i>	15	0	13	2	17	43	.40	14	29-31	2
<i>Anchoviella</i>										
<i>A. perfasciata</i>	9-11	0	11-12	2	20-21	42-44	.48	14-15	16-18	2
<i>Cetengraulis</i>										
<i>C. edentulus</i>	10-11	0	8	1	18	41	.44	15-16	23-25	2
<i>Coilia</i>										
<i>C. grayi</i>	5	1 (C)	11	2	21	75	.28	13	104	2
<i>Encrasiicholina</i>										
<i>E. purpurea</i>	9-10 (usual 10)	0	13	2	22-23	43-44	.52	14	16-17	2
<i>Engraulis</i>										
<i>E. mordax</i>	12-13	0	13	2	23-24	46	.51	15-17	22-23	2
<i>Lycothrissa</i>										
<i>L. crocodilus</i>	10	0	13	1	16	48	.33	12	50	3

TABLE 4a—(Continued)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxil- lary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs— preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Lycengraulis</i>										
<i>L. grossidens</i>	11–12 (usual 12)	0	15	2	20	46	.43	14–15	24–28	2
<i>Pterengraulis</i>										
<i>P. atherinoides</i>	10–11	0	13	2	18–19	45	.41	12–13	32–34	2
<i>Setipinna</i>										
<i>S. papuensis</i>	7	1 (C)	14–15	1	14	48–49	.29	14–15	57–58	3
<i>Stolephorus</i>										
<i>S. indicus</i>	9–10 (usual 9)	0 <sup>b</sup>	14	2	20	43	.46	15	18–20 (usual 19)	2
<i>Thrissina</i>										
<i>T. baelama</i>	7–8	1 (C)	12	2	17	40–41	.42	13–14	29–32	2
<i>Thryssa</i>										
<i>T. hamiltoni</i>	6–7 (usual 7)	1 (C)	12–13	1 <sup>c</sup>	18–19	45–46 (usual 45)	.41	12–13 (usual 13)	37–38	3

<sup>a</sup> (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.<sup>b</sup> Within the genus *Stolephorus*, *S. tri* and *S. macrops* have a single scute; and *S. indicus*, *S. commersonii*, *S. heterolobus*, *S. buccaneeri*, *S. bataviensis*, *S. andhraensis*, and *S. holodon* have no dorsal scutes (Grande, 1982).<sup>c</sup> Most species are known to have two supramaxillary bones (Whitehead, 1968).

TABLE 4b  
Morphological Information for Some Species of Anchovies (Clupeoidei: Engrauloidea)

Genus Species	Presence of prepelvic abdominal scutes	Presence of post- pelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind <sup>a</sup> cleithrum	Presence of two long rod- like post- cleithra	Fusion of caudal vertebrae <sup>b</sup>	Absence of in- terlobar notch on third hypural	Large canini- form teeth in jaw
<i>Anchoa</i>								
<i>A. compressa</i>	—	—	—	—	—	A	—	—
<i>Anchovia</i>								
<i>A. clupeoides</i>	—	—	—	—	—	A	—	—
<i>Anchoviella</i>								
<i>A. perfasciata</i>	—	—	—	—	—	A	—	—
<i>Cetengraulis</i>								
<i>C. edentulus</i>	—	—	—	—	—	A	—	—
<i>Coilia</i>								
<i>C. grayi</i>	+ <sup>c</sup>	+	+	—	—	—	— <sup>d</sup>	—
<i>Encrasicholina</i>								
<i>E. purpurea</i>	—	—	—	—	—	A	—	—
<i>Engraulis</i>								
<i>E. mordax</i>	—	—	—	—	—	A	—	—
<i>Lycothrissa</i>								
<i>L. crocodilus</i>	—	—	—	—	—	—	—	+
<i>Lycengraulis</i>								
<i>L. grossidens</i>	—	—	—	—	—	A <sup>e</sup>	—	—
<i>Pterengraulis</i>								
<i>P. atherinoides</i>	—	—	—	—	—	A	—	—
<i>Setipinna</i>								
<i>S. papuensis</i>	+	+	+	—	—	—	+	—
<i>Stolephorus</i>								
<i>S. indicus</i>	+	—	—	—	—	—	—	—
<i>Thrissina</i>								
<i>T. baelama</i>	+	+	— <sup>f</sup>	—	—	—	+	—
<i>Thryssa</i>								
<i>T. hamiltoni</i>	+	+	+	—	—	—	+	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).  
<sup>b</sup>  $pu_1 + u_1 = A$ ;  $pu_1 + u_1 + u_2 = B$ ; and  $u_1 + u_2 = C$ .  
<sup>c</sup> Some species are known to have no prepelvic scutes (Whitehead, 1972, p. 240).  
<sup>d</sup> Poorly developed.  
<sup>e</sup> Not fused in the small specimens examined here, but reported by Nelson (1983, p. 53) to be fused in large specimens.  
<sup>f</sup> Occasionally one or two scutes are found in this species (Whitehead, 1972, p. 228).



TABLE 5a  
Merisitic Information for the Wolf-Herring (Clupeoidei: Clupeoidea: Chirocentridae)

Genus Species	Pre- dorsal bones	Dorsal scutes	Branchi- ostegal rays	Supra- maxillary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs- preural verte- brae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Chirocentrus</i>										
<i>C. dorab</i>	1	0	8	2	43	73	.59	15	30	2

cussed in Grande, 1982a, and in that paper many species are removed from the genus †*Diplomystus*.

Many fossil clupeids which should be classified as Clupeidae *incertae sedis* or *indet.* remain instead assigned to the genus *Clupea* Linnaeus (such as †“*Clupea*” *catopygoptera* Woodward, 1901; and over 40 other species). Most of them were described in the nineteenth century when most or all known Recent clupeids were classified within that genus. Since that time, with the discovery of many more species and the development of a more complex clupeid classification, Recent clupeids have been assigned to over 50 genera. Describing such fossils as *Clupea* is now somewhat misleading because they are probably not closely related to the legitimate species of the genus (*Clupea harengus* Linnaeus, 1758 [the type] and *C. pallasii* Valenciennes, 1847). It is felt here, that the ten-

uous nature of such a generic assignment should somehow be indicated in the name of these species. This could be done simply by removing the fossils from *Clupea* and placing them in their own monotypic genera; but this would be an unwarranted burden on the literature if they were later found to belong to other preexisting genera. It is preferred here to instead put such genera in quotes (as done above and below). If the species is found later not to be closely related to the other members of the genus it is described in and it appears not to be closely related to species in any other described genus (such as †“*Clupea*” *brevissimus* Blainville, 1818, which is not even in Clupeiformes as used here), it should be placed into a new genus (†*brevissimus* is now in the monotypic genus †*Armigatus*—see Grande, 1982a, p. 4). Below, the systematic position of some additional fossil clupeids will be reviewed.

TABLE 5b  
Morphological Information for the Wolf-Herring (Clupeoidei: Clupeoidea: Chirocentridae)

Genus Species	Presence of pre- pelvic abdominal scutes	Presence of post- pelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind <sup>a</sup> cleithrum	Presence of two long rod- like post- cleithra	Fusion of caudal vertebrae <sup>b</sup>	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
<i>Chirocentrus</i>								
<i>C. dorab</i>	—	—	—	—	—	—	—	+

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).  
<sup>b</sup>  $pu_1 + u_1 = A$ ;  $pu_1 + u_1 + u_2 = B$ ; and  $u_1 + u_2 = C$ .

TABLE 6a  
Meristic Information for Some Pellonulines (Clupeioidei: Clupeidae: Pellonulinae)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxillary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs- preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Spratellomorpha</i>										
<i>S. bialalis</i>	12	0	6	1	23	43	.53	16	16	2
<i>Corica</i>										
<i>C. laciniata</i>	10-12	0	6	1	19-20	39-40	.49	15-16	15-16	1
<i>Clupeichthys</i>										
<i>C. bleekeri</i>	9-10	0	6-7	1	20-21	39	.53	15	19	2
<i>C. sp.</i>	8	0	6	1	20	39	.51	15	17	2
<i>Ehirava</i>										
<i>E. malabarica</i>	10	0	6	1	22	39	.56	14	17	2
<i>Gilchristella</i>										
<i>G. aestuarius</i>	12, 14	0	6-7	1	20-21	40-41	.51	15	19-21	2
<i>Congothrissa</i>										
<i>C. gossei</i>	7	0	4	0	19	40-41	.47	13-14	13-15	2
<i>Cynothrissa</i>										
<i>C. ansorgii</i>	10	0	6	1	23	45	.51	16	17	3
<i>C. mento</i>	10-12	0	6	1	24-25	44-45	.55	16	18-19	3
<i>Laeviscutella</i>										
<i>L. dekimpei</i>	10-11	0	6	1	21-22	41	.52	14	17, 19	3
<i>Limnothrissa</i>										
<i>L. miodon</i>	12	0	7	1	25-26	43-44	.59	14-15	16-17	2

TABLE 6a—(Continued)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxillary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs— preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Nanothrissa</i>										
<i>N. parva</i>	12–13	0	5	1	23	42	.55	12	19–20	3 <sup>b</sup>
<i>N. stewarti</i>	8–9	0	6	1	19–20	37–38	.52	13–14	15–17	2
<i>Odaxothrissa</i>										
<i>O. vittata</i>	10–11	0	6	1	23–24	44	.53	16	19–21 (usual 21)	3
<i>O. losera</i>	10	0	6	1	23	44	.52	16	19	3
<i>Pellonula</i>										
<i>P. vorax</i>	10–11	0	6	1	22	41	.54	15–16	16, 19	3
<i>P. afzeluusi</i>	10–12	0	6	1	20	39–41	.50	15	17–18	2–3 <sup>b</sup>
<i>Poecilothrissa</i>										
<i>P. congica</i>	11	0	5	1	23	43	.53	14–15	17–18	3
<i>Potamothrissa</i>										
<i>P. obtusirostris</i>	9–10 ( $\bar{X}$ = 9.75)	0	5	1	25–26	44–45	.57	14–15	16–17	2
<i>P. acutirostris</i>	9	0	5	1	23	42	.55	13	19	2
<i>Sierrathrissa</i>										
<i>S. leonensis</i>	11–12	0	3	1	22–23	40	.56	13–14	17–18	2
<i>Siolothrissa</i>										
<i>S. tanganicae</i>	11–12	0	6–7	1	25–26	43	.59	15	15	2
<i>Thraitidion</i>										
<i>T. noctivagus</i>	11–12	0	5	0	21	45	.47	13–14	24	3

TABLE 6a—(Continued)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxillary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs— preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Microthrissa</i>										
<i>M. royauxi</i>	7–10 (usual 9–10)	0	5	1	19	40–41	.47	13	22–24 (usual 24)	3
<i>M. minuta</i>	13	0	6	1	23	42	.55	14	20	3 <sup>b</sup>
<i>Clupeoides</i>										
<i>C. papuensis</i>	10–11	0	5	1	21	42	.50	14	18–20	2
<i>Hyperlophus</i>										
<i>H. vitattus</i>	15	28–29 (A)	4	1	28–29	48	.59	16–17	17–19	3
<i>H. translucidus</i>	13	17–18 (A)	4	1	19–20	39–40	.49	15–16	20–22 (20, 20, 22)	3
<i>Potamalosa</i>										
<i>P. richmondia</i>	11	14 (A)	7	1	28	46	.61	16	14	3
† <i>Knightia</i>										
† <i>K. eocaena</i>	7	11–14 (A) (usual 13)	7–8	1	21–23	37–38	.59	11–14 (usual 12–13)	13–15	3
† <i>K. alta</i>	7–8	10–13 (A) (usual 12)	7–8	1	21–23	37	.59	11–13 (usual 12)	13–16	3
† <i>K. vetusta</i>	8	12 (A)	7–8	1	21–22	38–39	.56	13–14	16–17	3

<sup>a</sup> (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.<sup>b</sup> The last two epurals are fused to each other at their bases on some specimens.

TABLE 6b  
Morphological Information for Some Pellonulines (Clupeoidei: Clupeoidea: Clupeidae: Pellonulinae)

Genus Species	Presence of pre- pelvic abdomi- nal scutes	Presence of post- pelvic abdomi- nal scutes	Pos- terior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind clei- thrum <sup>a</sup>	Presence of two long rodlike post- cleithra	A third, scale- shaped post- cleithrum present, anterior to the two long rodlike post- cleithra	Fusion of caudal verte- brae <sup>b</sup>	Absence of inter- lobar notch on third hypural	Large canini- form teeth in jaw
<i>Spratellomorpha</i>									
<i>S. bianalis</i>	—	—	—	—	+	—	A	—	—
<i>Corica</i>									
<i>C. laciniata</i>	+	+	—	—	+	—	A	—	—
<i>Clupeichthys</i>									
<i>C. bleekeri</i>	+	+	—	+	+	—	A	—	+
<i>C. sp.</i>	+	+	—	+	+	—	A	—	+
<i>Ehirava</i>									
<i>E. malabarica</i>	+	—	—	+	+	—	A	—	—
<i>Gilchristella</i>									
<i>G. aestuarius</i>	+	—	—	—	+	—	A	—	—
<i>Congothrissa</i>									
<i>C. gossei</i>	—	—	—	+	+	—	A	—	—
<i>Cynothrissa</i>									
<i>C. ansorgii</i>	+	+	— <sup>d</sup>	+	+	—	A	—	+
<i>C. mento</i>	+	+	— <sup>d</sup>	+	+	—	A	—	+
<i>Laeviscutella</i>									
<i>L. dekimpei</i>	+	+ <sup>c</sup>	—	+	+	—	A	—	—
<i>Limnothrissa</i>									
<i>L. miodon</i>	+	+	—	+	+	—	A	—	—
<i>Nanothrissa</i>									
<i>N. parva</i>	+	+	— <sup>d</sup>	+	+	—	A	—	—
<i>N. stewarti</i>	+	+	— <sup>d</sup>	+	+	—	A	—	—
<i>Odaxothrissa</i>									
<i>O. vittata</i>	+	+	—	+	+	—	A	—	+
<i>O. losera</i>	+	+	—	+	+	—	A	—	+
<i>Pellonula</i>									
<i>P. vorax</i>	+	+	—	+	+	—	A	—	—
<i>P. afzeluisi</i>	+	+	—	+	+	—	A	—	—
<i>Poecilothrissa</i>									
<i>P. congica</i>	+	+	—	+	+	—	A	—	—
<i>Potamothrissa</i>									
<i>P. obtusirostris</i>	+	+	—	+	+	—	A	—	—
<i>P. acutirostris</i>	+	+	—	+	+	—	A	—	—

TABLE 6b—(Continued)

Genus Species	Presence of pre- pelvic abdomi- nal scutes	Presence of post- pelvic abdomi- nal scutes	Pos- terior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind clei- thrum <sup>a</sup>	Presence of two long rodlike post- cleithra	A third, scale- shaped post- cleithrum present, anterior to the two long rodlike post- cleithra	Fusion of caudal verte- brae <sup>b</sup>	Absence of inter- lobar notch on third hypural	Large canini- form teeth in jaw
<i>Sierrathrissa</i>									
<i>S. leonensis</i>	—	+ <sup>e</sup>	—	— <sup>f</sup>	—	—	—	—	—
<i>Stolothrissa</i>									
<i>S. tanganyicae</i>	+	+	—	+	+	—	A	—	—
<i>Thrattidion</i>									
<i>T. noctivagus</i>	+ <sup>e</sup>	+ <sup>e</sup>	—	+	+	—	A	—	—
<i>Microthrissa</i>									
<i>M. royauxi</i>	+	+	+	+	+	—	A	—	—
<i>M. minuta</i>	+	+	— <sup>d</sup>	+	+	—	A	—	—
<i>Clupeoides</i>									
<i>C. papuensis</i>	+	+	—	—	—	—	—	—	—
<i>Hyperlophus</i>									
<i>H. vitattus</i>	+	+	+	—	+ <sup>g</sup>	—	—	—	—
<i>H. translucidus</i>	+	+	+	—	+ <sup>g</sup>	—	—	—	—
<i>Potamalosa</i>									
<i>P. richmondia</i>	+	+	+	—	+ <sup>g</sup>	+	—	—	—
† <i>Knightia</i>									
† <i>K. eocaena</i>	+	+	+	—	+ <sup>g</sup>	?	—	—	—
† <i>K. alta</i>	+	+	+	—	+ <sup>g</sup>	?	—	—	—
† <i>K. vetusta</i>	+	+	+	—	+ <sup>g</sup>	?	—	—	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).  
<sup>b</sup>  $pu_1 + u_1 = A$ ;  $pu_1 + u_1 + u_2 = B$ ; and  $u_1 + u_2 = C$ .  
<sup>c</sup> Lacking ascending arms.  
<sup>d</sup> Only one or two scutes present below coracoid.  
<sup>e</sup> Reduced.  
<sup>f</sup> No postcleithra.  
<sup>g</sup> Anterior end of anterior rodlike postcleithrum expanded.

The oldest clupeomorphs known to the author are Early Cretaceous in age. These include †“*Diplomystus*” *primotinus* Uyeno, 1979, and †“*D.*” *kokuraensis* Uyeno, 1979 from Japan (both excluded from †*Diplomystus* by Grande, 1982a, p. 18; but both are clupeomorphs showing both abdominal and dorsal scutes); †“*Diplomystus*” *goodi* Eastman, 1912 from Western Africa (also removed from †*Diplomystus* by Grande, 1982a,

p. 19; a clupeomorph showing abdominal and dorsal scutes); and †*Ellimmichthys longicostatus* (Cope, 1886) from Brazil (also with both abdominal and dorsal scutes). The above Cope species is an †ellimmichthyiform; the Eastman species is Clupeomorpha Division 2 *incertae sedis*; and based on his (1979) reconstructions, the Uyeno species are possibly clupeoids.

I recently received a paper (Chang and

Chou, 1978) illustrating two fossil clupeomorphs ( $\dagger$ *Diplomystus* sp. and  $\dagger$ *Knightia* sp.) that are described, but not named, from Cenozoic freshwater deposits of eastern China. They are extremely interesting, biogeographically.  $\dagger$ *Diplomystus* sp. (illustrated in Chang and Chou, 1978, text fig. 3 and plate 1, fig. 3), is very likely the closest known relative of  $\dagger$ *Diplomystus dentatus* from Eocene freshwater deposits in Wyoming; and  $\dagger$ *Knightia* sp. (illustrated in Chang and Chou, 1978, text fig. 4 and plate 1, fig. 4) may also be the closest known relative of the western North American species of  $\dagger$ *Knightia* (Paleocene-Eocene). I was unable to obtain any of this material to examine in detail, but the illustrations (including photographs) are clear. These and several other teleost genera which occur in the Green River Formation of western North America appear to show a trans-Pacific pattern of area relationships not visible in the Recent western North American biota (Grande, 1985).

$\dagger$ *Luisiella inexcitata* Bochino, 1967, from the Upper Jurassic of Argentina, is not a clupeomorph. Bochino (1967) suggests that this species is closely related to leptolepiforms and uses the presence of ossified centra as reason for placement in Clupeiformes. She then places the species in Dussumieriidae because it lacks scutes. Here this species is presently *Teleostei incertae sedis* (see discussion under character f). Similarly, no character information has been reported that would indicate that  $\dagger$ *Protoclupea chilensis* Arratia et al., 1975, from the Upper Jurassic of Chile, is a clupeomorph. Like  $\dagger$ *Luisiella*, this species lacks scutes, bullae, and other clupeomorph characters, and should be placed as *incertae sedis* within Teleostei, or possibly within Clupeocephala if it actually has five or six hypurals and a  $u_1$ -hyp<sub>2</sub> fusion as illustrated in Arratia et al. (1975, fig. 6).

One of the goals of the author is to reexamine the fossils that have been described as clupeomorphs and to reassess their placement. It is apparent that the majority of fossil clupeomorphs need redescription, and reevaluation (see the number of nominal fossil species placed in  $\dagger$ "*Clupea*" below, for example). Many fossil species described as "dussumieriids" (preliminary observation) or chirocentrids (Patterson and Rosen, 1977;

and above) do not even appear to be clupeomorphs.

To the revision of the fossil clupeid,  $\dagger$ *Knightia* (Grande, 1982b) the following information can be added. The designated co-types of  $\dagger$ "*Knightia*" *brasiliensis* Woodward, 1939 (BMNH 25259–25266) were examined and they lack dorsal scutes, thus excluding this species from the genus  $\dagger$ *Knightia*. Woodward (1939, p. 430) reported the presence of dorsal scutes in this species "supported by a series of bones like the supports of the median fins" (probably on the basis of BMNH P 25263). After examination here, these were interpreted not as dorsal scutes, but rather as a series of small grooves made by the tops of the predorsal bones. Also,  $\dagger$ "*Clupea*" *vectensis* Newton, 1889, does not (as suggested in Grande, 1982b, p. 14) appear to be closely related to  $\dagger$ *Knightia*, because one specimen (BMNH 39302) clearly shows the presence of two supramaxillary bones in this species. As suggested elsewhere (Grande, 1982b) and above, the known geographic range of  $\dagger$ *Knightia* is western North America and China only. Also, a specimen of an isolated braincase of  $\dagger$ *Knightia eocaena* Jordan, 1907 (BMNH P 61170) was discovered which indicates that  $\dagger$ *Knightia* had both prootic and pterotic bullae as most other Recent clupeids.

Since my initial observation (Grande, 1982a, p. 26) on a single specimen of  $\dagger$ *Gasteroclupea branisai* Signeux, 1964 from Upper Cretaceous deposits of Bolivia (see pristigasteroid, and Materials sections here), I have examined several additional specimens at MNMH and revised the number of dorsal scutes (given as 25 in Grande, 1982a) to about 34–36 (see table 3a). The initial count was inaccurate because it was based on a badly crushed, incomplete specimen. The dorsal scute morphology is basically subtriangular with long, lateral wings. The scute is wider than long, and the shallow apex points anteriorly and overlaps the preceding scute. Each scute has a strong median crest and most bear a median spine. This doubly armored clupeoid shows some striking resemblances to the cypriniform *Gastrolepecus* (see Signeux, 1964, plate 1) in the pectoral fin and fin support, but the caudal skeleton (visible on MNMH 1963-11 and 1963-16) and the dorsal and abdominal scutes indicate that this is



TABLE 7a  
Merisitic Information for Some Round Herrings (Clupeiodei: Clupeoidea: Clupeidae: Dussumieriinae)

Genus Species	Predorsal bones	Dorsal scutes	Branchi- ostegal rays	Supra- maxil- lary bones	Pleural ribs (pairs)	Preural verte- brae	Pleural ribs- preural verte- brae ratio	Dorsal fin pte- rygio- phores	Anal fin pte- rygio- phores	Epurals
<i>Dussumieria</i>										
<i>D. acuta</i>	21-22	0	15	2	37	55-56	.67	19	14	2
<i>Etrumeus</i>										
<i>E. teres</i>	10	0	14	1	34-35	49-50	.70	19	10	3
<i>E. acuminatus</i>	10-12 (usual 11)	0	16	1	40	54	.74	19	9-10	3
<i>E. micropus</i>	11	0	14	1	38	53-54	.71	20	11	3
<i>Jenkinsia</i>										
<i>J. stolidifera</i>	6-8	0	6	1	26	42-44	.61	13	15	1
<i>J. lamprotaenia</i>	6-7	0	6	1	21-22 (usual 22)	38-39	.58	11-12	15	1
<i>Spratelloides</i>										
<i>S. gracilis</i>	11	0	7	2	32	47	.68	11-12	14	1
<i>S. delicatulus</i>	9	0	7	2	27	41-43	.64	12	10	1
<i>S. robustus</i>	9-10	0	7-8	2	31-32 ( $\bar{X}$ = 31.75)	48-50	.65	12	10	1

a clupeoid, probably a member of *Pristigasteroidea*. Additional description of this genus is in progress by M. Gayet (MNMH).

The genus †*Clupavus* (erected by Arambourg, 1950, p. 417) and the †*Clupavidae* were reviewed by Patterson (1970b, pp. 283-288). Patterson found that, of the more than a dozen species referred to the genus (mostly for superficial resemblances), only †*Clupavus maroccanus* Arambourg, 1968 (the type) is a definite †clupavid. Previously (Grande, 1982a, p. 2728) I stated that if Taverne's (1977b) restorations of †*Clupavidae* (=†*C. maroccanus*) were correct, then the family may belong in Clupeiodei (influenced mainly by his fig. 9 of the caudal skeleton). Upon examination of the material (MNHM T 243 G and D—caudal skeleton; and 257 g—skull), I find no sufficient evidence that †clupavids are even clupeomorphs. No bullae were visible in the skull, and the last few infraorbital bones are not preserved (as noted by Taverne, 1977b), so the position and morphology of the dermosphenotic is unknown. There are no scutes or any other characters unique to clupeomorphs. The caudal skeleton, which as figured by Taverne (1977b, fig. 9) resem-

bles the clupeoid condition, is in fact subject to several different interpretive reconstructions. The fossils are all tiny impressions, and the drawings are made on the basis of latex or clay peels. Therefore, dissection of specimens to see underlying bones is not possible. Interpretations on a single specimen can differ strikingly. For example, compare fig. 9 in Taverne, 1977b with figs. 16 and 17 in Gayet, 1981. Taverne illustrates †*Clupavus maroccanus* as having  $u_1$  fused to  $hyp_2$  and  $un_1$  fused to  $pu_1$  (as in clupeoids). Gayet illustrates the species as having neither of the fusions and considers it to be a characid. Both Taverne's and Gayet's restorations are based on the same specimens, MNHN T93 and T243, which were also observed here. Although I disagree with Gayet's (1981, p. 188) conclusion that †clupavids are the sister-group to the Characidae, I agree with her in that there is no apparent close relationship between †clupavids and clupeiforms.

A LIST OF FOSSIL CLUPEOMORPHS

The main list below will include only those nominal fossil species which appear to belong

TABLE 7b  
Morphological Information for Some Round Herrings (Clupeoidei: Clupeoidea: Clupeidae: Dussumieriinae)

Genus Species	Presence of pre- pelvic abdomi- nal scutes	Presence of post- pelvic abdomi- nal scutes	Pos- terior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind clei- thrum <sup>a</sup>	Presence of two long rodlike post- cleithra	A third, scale- shaped post- cleithrum present, anterior to the two long rodlike post- cleithra	Fusion of caudal verte- brae <sup>b</sup>	Absence of inter- lobar notch on third hypural	Large canini- form teeth in jaw
<i>Dussumieria</i>									
<i>D. acuta</i>	—	—	—	—	—	—	—	—	—
<i>Etrumeus</i>									
<i>E. teres</i>	—	—	—	—	+ <sup>c</sup>	+	C	—	—
<i>E. acuminatus</i>	—	—	—	—	+ <sup>c</sup>	+	C	—	—
<i>E. micropus</i>	—	—	—	—	+ <sup>c</sup>	+	C	—	—
<i>Jenkinsia</i>									
<i>J. stolidifera</i>	—	—	—	—	—	—	B	—	—
<i>J. lamprotaenia</i>	—	—	—	—	—	—	B	—	—
<i>Spratelloides</i>									
<i>S. gracilis</i>	—	—	—	—	—	—	A	—	—
<i>S. delicatulus</i>	—	—	—	—	—	—	A	—	—
<i>S. robustus</i>	—	—	—	—	—	—	A	—	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).  
<sup>b</sup>  $pu_1 + u_1 = A$ ;  $pu_1 + u_1 + u_2 = B$ ; and  $u_1 + u_2 = C$ .  
<sup>c</sup> Anterior end of anterior rodlike postcleithrum is broadly expanded with laminar bone.

to Clupeomorpha as used here, rather than all of the fossil taxa which have ever been assigned to “Clupeomorpha.” There are well over 200 fossil taxa which have been described as “clupeomorphs,” but many of them (†ichthyodectids, †leptolepids, †clupavids, †plethodids, †syllaemids, †pachyrhizodontids, etc.) do not belong in Clupeomorpha as defined here. Most of these fossils were described 20 or more years ago, when Clupeomorpha was much less clearly characterized and no more than a wastebasket group (see discussion above under Brief History of Clupeomorph Classification). It included parts of Elopomorpha (e.g., albuloids and elopoids), Osteoglossomorpha (e.g., †*Lycoptera* and *Hiodon*), Euteleostei (e.g., ostariophysans, myctophids), and other taxa. In some early descriptions (e.g., Schaeffer, 1949, and others) Clupeomorpha, Clupeiformes, and

even Clupeoidei were occasionally used as the equivalent of Teleostei *incertae sedis*. Actual specimens of many of the taxa listed below have not yet been examined by the author (indicated as “no specimens examined here”); but based on examination of at least photographs and published illustrations, they appear to belong in Clupeomorpha (they appear to have clupeomorph-type abdominal scutes, bullae, etc.). Species known only by scales, otoliths, or other isolated fragments are not included in the main list, although they are discussed further below. Also, fossils assigned to living species are not listed (e.g., *Dorosoma petenense* reported from the Plio-Pleistocene of New Mexico by Miller, 1982; *Alosa nordmani* reported from the Pontian of eastern Europe by Pauca, 1931). The names are arranged in alphabetical order (except for fossil type species which are listed

TABLE 8a  
Meristic Information for Some Gizzard-Shads (Clupeoidei: Clupeidae: "Dorosomatinae")

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchiostegal rays	Supra-maxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs- preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
<i>Dorosoma</i>										
<i>D. cepedianum</i>	8-9 ( $\bar{X}$ = 8.80)	1-2 (B)	6	2	26	49-50	.53	13-14 <sup>b</sup>	29-32	2
<i>D. anale</i>	9	2 (B)	6	2	47	47	.53	13 <sup>b</sup>	31-35	2
<i>D. smithi</i>	8	?	6	2	22	45	.49	13-14 <sup>b</sup>	25-27	2
<i>Signalosa</i>										
<i>S. petense</i>	8	1 (B)	6	2	22-23	41-42	.54	14 <sup>b</sup>	21-26 (usual 23-25)	2
<i>Anodontostoma</i>										
<i>A. chacunda</i>	8	0	5	1	23	41-42	.55	18	18-19	3
<i>Clupanodon</i>										
<i>C. thrissa</i>	8	23-25 (A)	6	1	26	45	.58	15-16 <sup>b</sup>	24	2-3
<i>Konosirus</i>										
<i>K. punctatus</i>	10	0	6	1	33	50	.66	17 <sup>b</sup>	24	3
<i>Nematalosa</i>										
<i>N. nasus</i>	9	1 (B)	6	1	26	46	.57	15 <sup>b</sup>	20	3
<i>N. come</i>	8	1 (B)	5-6	1	25	44	.57	16 <sup>b</sup>	22	3
<i>N. erebi</i>	8	1 (B)	6	1	23-25	43-44	.54	14-15 <sup>b</sup>	20-21	3
<i>N. galathea</i>	8	1 (B)	6	1	23	44	.52	16 <sup>b</sup>	23	3
<i>N. japonica</i>	8	1 (B)	6	1	29	48	.60	16 <sup>b</sup>	21	3
<i>N. vlaminghi</i>	8	1 (B)	6	1	26	46	.57	15 <sup>b</sup>	22	3
<i>Gonialosa</i>										
<i>G. mannina</i>	9	?	5	1	26	45	.58	14-15	22	2-3

<sup>a</sup> (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

<sup>b</sup> Last dorsal fin ray elongated into a long filament.

TABLE 8b  
Morphological Information for Some Gizzard-Shads (Clupeoidei: Clupeoidea: Clupeidae:  
"Dorosomatinae")

Genus Species	Presence of pre- pelvic abdomi- nal scutes	Presence of post- pelvic abdomi- nal scutes	Posterior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind clei- thrum <sup>a</sup>	Presence of two long rodlike post- cleithra	A third, scale- shaped post- cleithrum present, anterior to the two long rodlike post- cleithra	Fusion of caudal verte- brae <sup>b</sup>	Absence of inter- lobar notch on third hypural	Large canini- form teeth in jaw
<i>Dorosoma</i>									
<i>D. cepedianum</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>D. anale</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>D. smithi</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Signalosa</i>									
<i>S. petense</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Anodontostoma</i>									
<i>A. chacunda</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Clupanodon</i>									
<i>C. thrissa</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Konosirus</i>									
<i>K. punctatus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Nematalosa</i>									
<i>N. nasus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>N. come</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>N. erebi</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>N. galathea</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>N. japonica</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>N. vlaminghi</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Gonialosa</i>									
<i>G. manmina</i>	+	+	+	—	+ <sup>c</sup>	?	—	—	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).  
<sup>b</sup>  $pu_1 + u_1 = A$ ;  $pu_1 + u_1 + u_2 = B$ ; and  $u_1 + u_2 = C$ .  
<sup>c</sup> Anterior end of anterior rodlike postcleithrum is broadly expanded with laminar bone.

first) because the phylogenetic relationships of most species are poorly known. A tentative systematic placement of each species will be made here (in bold face type) as specifically as possible based on available data; but further study of many of these will allow a more specific level of systematic placement (e.g., to family or subfamily instead of merely Clupeiformes *incertae sedis*). Where the previous generic assignment of a species is inaccurate (†“*Clupea*” *vectensis* for example), the first

part of the binomial name (the genus) is placed in quotes. Where an available species name is considered to be a subjective junior synonym of another species of the *same* genus (†*Diplomystus* “*analis*” for example), the *second* part of the binomial is placed in quotes. If an available species name is considered to be a subjective junior synonym of another species of a *different* genus (†“*Diradias* *aratus*” for example) *both* parts of the binomial are placed in quotes. Unavailable names (ju-

TABLE 9a  
Meristic Information for Some Shads (Clupeoidei: Clupeoidea: Clupeidae: "Alosinae")

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs— preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Alosa</i>										
<i>A. fallax</i>	12-13	0	8	2	31	56-57	.55	17	22	1-2
<i>A. sapidissima</i>	11-12 (usual 11)	0	7-8 (usual 7)	2	33	56-57	.58	17-18	19-20	2
<i>Pomolobus</i>										
<i>P. aestivalis</i>	10-11 (usual 10)	1 (B)	7	2	30-31	50-51 (usual 50)	.60	16-17	17-18	1-2 (usual 2)
<i>P. pseudoharengus</i>	9-12	0	7	2	27-28	48	.57	16-17 (usual 16)	17-18	3
<i>Brevoortia</i>										
<i>B. tyrannus</i>	11-12	0	7	2	27	48	.56	20	21-22	1-2
<i>B. patronus</i>	10-11	0	7	2	24-25	45-46	.54	20	21-22	2
<i>Caspialosa</i>										
<i>C. tanaica</i>	10-11	0	8	2	26	48	.54	15-17	18-19	2
<i>Ethmalosa</i>										
<i>E. fimbriata</i>	8	2	6	2	24	43	.56	16	19	3
<i>Ethmidium</i>										
<i>E. maculatum</i>	11	24 (A)	9	2	31	49	.63	19	16	2
<i>Gudusia</i>										
<i>G. chapra</i>	8-9	0	6	2	21	41	.51	15	22	2-3
<i>G. variegata</i>	8	0	6	2	21	42	.50	16	27	3
<i>Hilsa</i>										
<i>H. kelee</i>	7	0	6	2	24	43	.56	17	20	2

<sup>a</sup> (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

TABLE 9b  
Morphological Information for Some Shads (Clupeoidei: Clupeoidea: Clupeidae: "Alosinae")

Genus Species	Presence of pre- pelvic abdomi- nal scutes	Presence of post- pelvic abdomi- nal scutes	Pos- terior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind clei- thrum <sup>a</sup>	Presence of two long rodlike post- cleithra	A third, scale- shaped post- cleithrum present, anterior to the two long rodlike post- cleithra	Fusion of caudal verte- brae <sup>b</sup>	Absence of inter- lobar notch on third hypural	Large canini- form teeth in jaw
<i>Alosa</i>									
<i>A. fallax</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>A. sapidissima</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Pomolobus</i>									
<i>P. aestivalis</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>P. pseudoharengus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Brevoortia</i>									
<i>B. tyrannus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>B. patronus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Caspialosa</i>									
<i>C. tanaica</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Ethmalosa</i>									
<i>E. fimbriata</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Ethmidium</i>									
<i>E. maculatum</i>	+	+	+	—	?	?	—	—	—
<i>Gudusia</i>									
<i>G. chapra</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>G. variegata</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Hilsa</i>									
<i>H. kelee</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).  
<sup>b</sup>  $pu_1 + u_1 = A$ ;  $pu_1 + u_1 + u_2 = B$ ; and  $u_1 + u_2 = C$ .  
<sup>c</sup> Anterior end of anterior rodlike postcleithrum is broadly expanded with laminar bone.

nior homonyms, *nomina nuda*, etc.) are not listed, although they are discussed and given in the taxonomic index. Where objective synonyms occur, only one name will be listed here (so there is only one name listed for each type specimen).  
It is hoped that this list will aid future workers on fossil and Recent clupeomorphs, and that many of the clupeomorph fossils listed below will be redescribed in greater detail. References for all taxonomic name authors cited here are included under Literature Cited, and all taxonomic names used or im-

plied are included in the taxonomic index. There are probably some unintentional omissions in this list (descriptions which I have missed in the literature), but the fossil species which I am aware of that appear to belong in Clupeomorpha as used here are included below.  

†*Alisea* Jordan and Gilbert, 1919

†*Alisea grandis* Jordan and Gilbert, 1919 [from Miocene marine sediments of southern California]. Known by only one dis-

TABLE 10a  
Meristic Information for Some Herrings (Clupeoidei: Clupeidae: Clupeinae)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs— preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>Clupea</i>										
<i>C. harengus</i>	18–19 (usual 18)	0	8	2	35–37 (usual 36)	56–57	.64	17–18 (usual 18)	16–18	2
<i>C. pallasi</i>	15–16 (usual 16)	0	8	2	34–35	52–53	.66	17–18 (usual 18)	15–16	1–2 (usual 2)
<i>Strangomera</i>										
<i>S. bentincki</i>	15	0	7	2	26	44	.59	17	17	2
<i>Sprattus</i>										
<i>S. sprattus</i>	17	0	7	2	28	48	.58	18	19	3
<i>S. antipodum</i>	15	0	7	2	26–27	45–46	.58	17–18	16–18	3
<i>Rammogaster</i>										
<i>R. arcuata</i>	15	0	7	2	23	44	.52	18	22	3
<i>R. pallida</i>	7–8 (usual 8)	0	6	2	24	42	.57	18	17–19	3
<i>Amblygaster</i>										
<i>A. sirm</i>	8	0	6	2	27	43–44	.62	19–20	17–18 <sup>b</sup>	3
<i>A. leiogaster</i>	8	0	6	2	25	44	.57	18	17 <sup>b</sup>	3
<i>Clupeonella</i>										
<i>C. cultiventris</i>	11	0	7	2	23–24	42	.56	15	18–21	1–2 (usual 2)
<i>Sardinops</i>										
<i>S. caerulea</i>	10	0	7	2	33	52	.63	18	17 <sup>b</sup>	2–3
<i>S. melanosticta</i>	10	0	7	2	31–32	51	.62	18–19	17–18 <sup>b</sup>	3
<i>S. neopilchardus</i>	10	0	7	2	32	50	.64	18–19	17–18 <sup>b</sup>	3
<i>Sardina</i>										
<i>S. pilchardis</i>	10–11 (usual 11)	0	7	2	30–31	50–51	.60	17–18	17–19 <sup>b</sup>	3
<i>Sardinella</i>										
<i>S. aurita</i>	9–10	0	6	2	30	48	.63	18	17 <sup>b</sup>	2



TABLE 10a—(Continued)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi-ostegal rays	Supra-maxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs—preural vertebrae ratio	Dorsal fin pterygio-phores	Anal fin pterygio-phores	Epurals
<i>S. anchovia</i>	9–10 (usual 9)	0	6	2	29	46–47	.62	17	16–17 <sup>b</sup>	3 <sup>c</sup>
<i>S. longiceps</i>	9	0	6	2	28	47	.60	?	16 <sup>b</sup>	3 <sup>c</sup>
<i>S. gibosa</i>	9	0	6	2	27–28	45–47	.60	17	18–19 <sup>b</sup>	3
<i>S. maderensis</i>	9	0	6	2	27–28 (usual 27)	46–47 (usual 46)	.59	18–19 (usual 18)	17–20 <sup>b</sup>	3
<i>S. marquesensis</i>	8	0	6	2	26–27 (usual 27)	44	.61	18–19 (usual 18)	16–18 <sup>b</sup>	2–3 (usual 3)
<i>S. pinnula</i>	9	0	6	2	27–28	46	.60	16	16–17 <sup>b</sup>	3 <sup>d</sup>
<i>S. sindensis</i>	9	0	6	2	29	47	.62	16	18 <sup>b</sup>	3
<i>S. zunasi</i>	8	0	6	2	25	43–44	.58	17–18	17–19 <sup>b</sup>	3
<i>Escualosa</i>										
<i>E. thoracata</i>	10	0	4	2	22	40	.55	15	17–19	2
<i>Harengula</i>										
<i>H. clupeiola</i>	7	1 (B)	6	2	25–26	41–42	.61	16–17	17	2–3 (usual 3)
<i>H. humeralis</i>	7	1 (B)	6	2	23	40	.58	16–17	16–19	3
<i>H. jaguana</i>	7	1 (B)	6	2	25	41	.61	16–17 (usual 17)	16–18	3
<i>H. thrissina</i>	7	1 (B)	6	2	25–26	42	.61	17	14–15	3
<i>Herklotsichthys</i>										
<i>H. dispilonotus</i>	7	1 (B)	6	2	22–23 (usual 22)	39	.56	18	17–18	3
<i>H. castelnaui</i>	8	1 (B)	6	2	23–24 (usual 23)	41	.56	16–18	17–19	3
<i>H. koningsbergeri</i>	10	1 (B)	6	2	19–21 (usual 20)	39–40 (usual 40)	.50	13–14	19–23	3
<i>H. quadrimaculatus</i>	8	1 (B)	6	2	25–26 (usual 26)	43–44	.60	18	17–18	2–3
<i>Lile</i>										
<i>L. stolidifera</i>	9–10 (usual 9)	0	6	2	24	42–43	.56	17	17–18	3

TABLE 10a—(Continued)

Genus Species	Predorsal bones	Dorsal scutes <sup>a</sup>	Branchi- ostegal rays	Supra- maxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs— preural vertebrae ratio	Dorsal fin pterygio- phores	Anal fin pterygio- phores	Epurals
<i>L. piquitinga</i>	8	0	6	2	23	40	.58	15–17 (usual 16)	15–17	2
<i>Opisthonema</i>										
<i>O. libertate</i>	8	1 (B)	6	2	28	46	.61	18 <sup>d</sup>	19	3
<i>O. medirastre</i>	?	1 (B)	6	2	28	47	.60	19 <sup>d</sup>	18	3
<i>O. oglinum</i>	7–9	1 (B)	6	2	27–28	45–46	.60	18–19 <sup>d</sup>	21–22 (usual 21)	3
<i>Platanichthys</i>										
<i>P. platana</i>	10–11	0	5–6	2	21–22	40–41	.53	13	19–20	3
<i>Rhinosardinia</i>										
<i>R. bahiensis</i>	12	0	5	2	24	43	.56	15	16	2
<i>R. serrata</i>	10	0	5	2	20–21	36–38	.55	13–14	14	2
<i>Tenualosa</i>										
<i>T. toli</i>	8	1 (B)	?	2	27	44	.61	18	17	3
† <i>Gosiutichthys</i>										
† <i>G. parvus</i>	6–7	10–13 (usual 12–13)	7–8	2	20–21	34–36	.59	10–11	10–13	3
† <i>Ellimma</i>										
† <i>E. branneri</i>	6–7	9–11	7	2	17	31–32	.54	13	13	2–3
† <i>E. elmodenae</i>	14	0	?	2	26	44	.59	16–18	18	?
† <i>Xyne</i>										
† <i>X. grex</i>	?	0	?	2	26	44	.59	?	?	3
†“ <i>Clupea</i> ” (Monte Bolca)										
†“ <i>C.</i> ” <i>catopygoptera</i>	8	0	7	2	21–22	41	.53	14–15	15–17	3

<sup>a</sup> (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore.

<sup>b</sup> Last two anal fin rays elongated.

<sup>c</sup> Several specimens have the last two epurals fused together at their bases.

<sup>d</sup> Last dorsal fin ray elongated into a long filament.

TABLE 10b  
Morphological Information for Some Herrings (Clupeoidei: Clupeoidea: Clupeidae: “Clupeinae”)

Genus Species	Presence of pre- pelvic abdomi- nal scutes	Presence of post- pelvic abdomi- nal scutes	Pos- terior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum <sup>a</sup>	Presence of two long rodlike post- cleithra	A third, scale- shaped post- cleithrum present, anterior to the two long rodlike post- cleithra	Fusion of caudal verte- brae <sup>b</sup>	Absence of inter- lobar notch on third hypural	Large canini- form teeth in jaw
<i>Clupea</i>									
<i>C. harengus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>C. pallasii</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Strangomera</i>									
<i>S. bentincki</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Sprattus</i>									
<i>S. sprattus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. antipodum</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Ramnogaster</i>									
<i>R. arcuata</i>	+	+	+	—	?	+	—	—	—
<i>R. pallida</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Amblygaster</i>									
<i>A. sirm</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>A. leiogaster</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Clupeonella</i>									
<i>C. cultiventris</i>	+	+	+	—	+ <sup>c</sup>	+	A	—	—
<i>Sardinops</i>									
<i>S. caerulea</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. melanosticta</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. neopilchardus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Sardina</i>									
<i>S. pilchardis</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Sardinella</i>									
<i>S. aurita</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. anchovia</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. longiceps</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. gibosa</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. maderensis</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. marquesensis</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. pinnula</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. sindensis</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>S. zunasi</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Escualosa</i>									
<i>E. thoracata</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Harengula</i>									
<i>H. clupeola</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—

TABLE 10b—(Continued)

Genus Species	Presence of pre- pelvic abdomi- nal scutes	Presence of post- pelvic abdomi- nal scutes	Pos- terior edge of coracoid lined with scutes	Articu- lation of post- cleithra with supra- cleithrum well behind clei- thrum <sup>a</sup>	Presence of two long rodlike post- cleithra	A third, scale- shaped post- cleithrum present, anterior to the two long rodlike post- cleithra	Fusion of caudal verte- brae <sup>b</sup>	Absence of inter- lobar notch on third hypural	Large canini- form teeth in jaw
<i>H. humeralis</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>H. jaguana</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>H. thrissina</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Herklotsichthys</i>									
<i>H. dispilonotus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>H. castelnaui</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>H. koningsbergeri</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>H. quadrimaculatus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Lile</i>									
<i>L. stoliifera</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>L. piquitinga</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Opisthonema</i>									
<i>O. libertate</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>O. medirastrae</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>O. oglinum</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Platanichthys</i>									
<i>P. platana</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Rhinosardinia</i>									
<i>R. bahiensis</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>R. serrata</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
<i>Tenuulosa</i>									
<i>T. toli</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
† <i>Gosiutichthys</i>									
† <i>G. parvus</i>	+	+	+	—	+ <sup>c</sup>	+	—	—	—
† <i>Ellimma</i>									
† <i>E. branneri</i>	+	+	+	—	?	?	—	?	—
† <i>E. elmodenae</i>	+	+	+	—	+ <sup>c</sup>	?	?	?	—
† <i>Xyne</i>									
† <i>X. grex</i>	+	+	+	—	+	?	—	—	—
†“ <i>Clupea</i> ” (Monte Bolca)									
†“ <i>C.</i> ” <i>catopygoptera</i>	+	+	+	—	+ <sup>c</sup>	?	—	—	—

<sup>a</sup> With a well-defined space between the postcleithra and the cleithrum (see fig. 22).

<sup>b</sup>  $pu_1 + u_1 = A$ ;  $pu_1 + u_1 + u_2 = B$ ; and  $u_1 + u_2 = C$ .

<sup>c</sup> Anterior end of anterior rodlike postcleithrum is moderately to broadly expanded with laminar bone.

torted, incomplete specimen lacking head and much of body (holotype SU 135, il-

lustrated in Jordan and Gilbert, 1919, pl. 17, fig. 3). Type species for genus by mono-

typy. It is doubtful whether this poorly preserved specimen warranted description as a new taxon. **Clupeidae**.

*Alosa* Link, 1790

(When the interrelationships of alosines, clupeines, and dorosomatines are better understood, most of the fossil species described in *Alosa* will probably be removed from that genus.)

†*Alosa aralensis* Chisara, 1977 [from Oligocene deposits of Russia]. No specimens were examined here, but type and other specimens are illustrated in figs. 1–3 of original description. **Clupeidae**.

†*Alosa baykali* Rückert-Ülkümen, 1965 [from Miocene marine deposits of Turkey]. No specimens were examined here, but illustrations (holotypes and paratypes) are in pl. 25, figs. 27 and 28 of original description. Material is at the Geological Institute of the Univ. of Istanbul. **Clupeidae**.

†*Alosa crassa* Sauvage, 1873 [from Miocene marine deposits of Oran, northern Africa; and Crete, Italy]. Abundant in the collections of MNHN; some material is also at BMNH and AMNH. Several MNHN specimens are illustrated in Arambourg, 1927. Redescribed and figured also in Gaudant, 1980. Thought by Woodward (1901, p. 151) to be a subjective junior synonym of †*A. numidica*. **Clupeidae**.

†*Alosa elongata* Agassiz [non Bennett, 1830], 1843 [from Miocene marine deposits of Oran, northern Africa]. Abundant at MNHN. Several nearly complete specimens from MNHN are illustrated in Arambourg, 1927. Thought by Woodward (1901, p. 151) to be a subjective junior synonym of †*A. numidica*. **Clupeidae**.

†*Alosa fortipinnata* Rückert-Ülkümen, 1965 [from Miocene marine deposits of Turkey]. No specimens were examined here, but the holotype is illustrated in pl. 25, fig. 24 of original description and is deposited at Geol. Inst. Univ. Istanbul. **Clupeidae**.

†*Alosa genuina* Danil'chenko, 1960 [from ?Oligocene or Miocene marine deposits of the Caucasus Mts., USSR]. No specimens were examined here, but a nearly complete specimen (the holotype) is illustrated in the type description (pl. 19, fig. 5). Also described and illustrated (reconstructed line

drawing) in Danil'chenko (1980, p. 18 and fig. 7). Material in the Paleontological Inst., Acad. Sci., Moscow, USSR. **Clupeidae**.

†*Alosa numidica* Sauvage, 1873 [from Miocene marine deposits of Oran, Northern Africa]. Thought by Arambourg, 1927, p. 18, to be a subjective junior synonym of †*A. elongata*. Type specimen is at MNHN (fig. 66 in type description). Referred to *Clupea* in Woodward, 1901, p. 151. **Clupeidae**.

†*Alosa ovalis* Rückert-Ülkümen, 1965 [from Miocene marine deposits of Turkey]. No specimens were examined here, but several specimens (including holotype) are illustrated in pl. 26, figs. 34–36 of original description and deposited at Geol. Inst. of the Univ. Istanbul. **Clupeidae**.

†*Alosa pinarhisarensis* Rückert-Ülkümen, 1965 [from Miocene marine deposits of Turkey]. No specimens were examined here, but specimens (including holotype) are illustrated in pl. 25, fig. 31 and pl. 26, figs. 32–33 of original description. Specimens deposited at Geol. Inst. of the Univ. Istanbul. **Clupeidae**.

†*Alosa renoui* Sauvage, 1873 [from Miocene deposits of Oran, Northern Africa]. Thought by Arambourg, 1927, pl. 18 to be a subjective junior synonym of †*A. elongata*, and by Woodward (1901, p. 152) to be a subjective junior synonym of †*A. numidica*. Type of MNHN. **Clupeidae**.

†*Alosa sculptata* (Weiler, 1920) [from Miocene marine deposits of Germany]. No specimens examined here, but one is illustrated in Weiler, 1928, pl. 3, fig. 5; and another in Andelković, 1963, pl. 1, fig. 4. Originally described in "*Meletta*." **Clupeidae**.

†*Alosa weileri* Rückert-Ülkümen, 1960 [from Miocene marine deposits of Turkey]. No specimens were examined here, but illustrations are in pl. 13, figs. 1 and 2 of original description. Material deposited at the Geol. Inst. of the Univ. Istanbul. **Clupeidae**.

†*Alosina* Wagner, 1860

†*Alosina salmonea* Wagner, 1860 [from Middle Oligocene deposits of Bavaria]. Thought by Woodward (1901) not to be distinguishable from "*Clupea*." Described by Weiler (1932, p. 310) as †*Etrumeus salmoneus*.

Holotype (nearly complete fish not examined here) is in the Paleontological Museum in Munich. Type species for genus by original designation. **Clupeidae**.

†*Armigatus* Grande, 1982a

†*Armigatus brevissimus* (Blainville, 1818) [from Upper Cretaceous (Cenomanian) marine limestone deposits of Lebanon]. Discussed in Grande, 1982a; a common species represented in most major museum collections. Type species for genus; by original designation. Also reported from the Cenomanian of Morocco, Yugoslavia, and Italy (Arambourg, 1954; Erasmo, 1946; and Leonardi, 1966). Originally described in "*Clupea*," and later included in †*Diplomystus* by some authors. **Clupeomorpha Division 2: *incertae sedis*, but not in Clupeiformes or †*Diplomystus*.**

†*Austroclupea* Bardack, 1961

†*Austroclupea zuninoi* Bardack, 1961 [from ?Miocene or Pliocene freshwater deposits of Argentina]. Many specimens are at AMNH and Yacimientos Petroliferos Fiscales, Buenos Aires, Argentina. Two nearly complete specimens are illustrated in Bardack, 1961, figs. 1 and 2. Type species for genus by original designation. **Clupeidae**.

*Caspialosa* Berg, 1915

†*Caspialosa praecursor* Bogachev, 1928 [from Late Tertiary marine deposits of Azerbaydzhan, USSR]. No specimens were examined here, but one is illustrated in original description. Also discussed in Danil'chenko, 1972. Described in Danil'chenko, 1980, as *Alosa*. **Clupeidae**.

*Chatoessus* Cuvier, 1829

(=*Dorosoma* Rafinesque, 1820, see Whitehead, 1967a, p. 96.)

†*Chatoessus brevis* Steindachner, 1859 [from Miocene marine deposits in Croatia]. No specimens examined here, but one is illustrated in pl. 3 of type description. Thought by Kramberger (1883, p. 77) to be a junior synonym of †"*Clupea*" *doljeana* Kramberger, 1883. **Clupeidae**.

†*Chatoessus humilis* Steindachner, 1859

[from Miocene marine deposits in Croatia]. No specimens were examined here, but one is illustrated in pl. 3 of type description. Thought by Kramberger (1883, p. 77) to be a synonym of †"*Clupea*" *doljeana* Kramberger, 1883. **Clupeidae**.

†*Chatoessus tenuis* Steindachner, 1859 [from Miocene marine deposits in Croatia]. No specimens were examined here, but one is illustrated in pl. 3 of type description. Thought by Kramberger (1883, p. 77) to be a synonym of †"*Clupea*" *doljeana* Kramberger, 1883. **Clupeidae**.

*Clupea* Linnaeus, 1758

(Few if any of the following species actually belong in the genus phylogenetically.)

†"*Clupea*" *antiqua* Pictet, 1858 [from the Early Cretaceous (Neocomian) of Switzerland]. No specimens were observed here, but several are illustrated in pl. 4, figs. 7–13 of the type description. **Clupeomorpha: *incertae sedis*.**

†"*Clupea*" *arcuata* Kner, 1863 [from Miocene marine sediments of Croatia, Yugoslavia; and Chiavon, Italy]. No specimens were examined here, but a nearly complete fish is illustrated and described in Bassani (1889, pl. 2, fig. 2). Discussed in Woodward (1901, p. 154). Placed in *Alosa* by Erasmo (1930, p. 30). Material at Museo Civico di Storia Naturale, Verona, Italy. **Clupeidae**.

†"*Clupea*" *bassanii* Franceschi, 1922 [from Oligocene marine deposits of Chiavon, Italy]. No specimens were examined here, but two somewhat distorted specimens are illustrated in pl. 14, figs. 3a and 3b of the type description. **Clupeidae**.

†"*Clupea*" *breviceps* Heckel, 1853a [from Oligocene marine deposits of Chiavon, Italy]. Material at Court Museum of Vienna, Austria (including holotype) and at Museo Civico di Storia Naturale, Verona, Italy. No specimens examined here, but a nearly complete fish is illustrated and redescribed in Bassani, 1889. **Clupeidae**.

†"*Clupea*" *catopygoptera* Woodward, 1901 (*Agassiz nomen nudum*) [from Eocene marine sediments of Monte Bolca, Italy]. This was the first clupeomorph species reported from Monte Bolca (Agassiz, 1844). Lioy

(1866) described another 11 clupeid species from Monte Bolca (10 of these are also listed in Woodward, 1901, p. 158, and Blot, 1980, pp. 351–352). Unfortunately, these 11 species all appear to be *nomina dubia*. Based on material examined here, there are definitely more than one species of clupeoid represented at Monte Bolca (including a dussumieriine discussed above). The clupeoid fauna from this locality is badly in need of revision and description. None of the material examined belongs in *Clupea*. Monte Bolca clupeids are well represented in most major museum collections.

#### **Clupeidae.**

†“*Clupea*” *crenata* (Heckel, 1850) [from Oligocene-Miocene deposits in Austria, Germany, Poland, and France]. Discussed by Woodward, 1901, p. 151. Several specimens at BMNH. Originally described in the genus *Meletta*, but transferred to *Clupea* by Woodward, 1901. Thought by Jerzmańska (1960), Szymczyk (1978), and others to be a subjective junior synonym of †*Clupea sardinites* Heckel. **Clupeidae.**

†“*Clupea*” *dentex* Blainville, 1818 [from Miocene marine deposits of Italy]. No specimens were examined here, but this species is illustrated in Agassiz, 1844, vol. 5, part 2, pl. 61, figs. 4 and 5. **Clupeidae.**

†“*Clupea*” *doljeana* Kramberger, 1883 [from Miocene marine deposits of Croatia, Yugoslavia (type) and Turkey (Rückert-Ülkumen, 1965)]. No specimens were examined here, but one is illustrated in Kramberger, 1883, pl. 14, fig. 4. Thought to belong in *Alosa* by Erasmo (1930, p. 27).

#### **Clupeidae.**

†“*Clupea*” *elongata* Steindachner, 1860 [from Miocene marine deposits of Croatia, Yugoslavia]. No specimens were examined here. Represented by a partial specimen (illustrated in pl. 1, fig. 1 of original description). Specimen deposited in the Court Museum of Vienna, Austria. **Clupeidae.**

†“*Clupea*” *fontannesii* Sauvage, 1880 [from Miocene sediments of Drome, France]. No specimens were examined here, but some are illustrated in pl. 7, figs. 1–3 of original description. **Clupeidae.**

†“*Clupea*” *gervaisi* de Botella, 1868 [from Pliocene? deposits of Murcia, Spain]. No specimens were examined here, but some

are illustrated (by incomplete material) in original description (pl. 11, figs. 8–11). **Clupeidae.**

†“*Clupea*” *gorjensis* Huica and Gheorghiu, 1962 [from Miocene marine sediments of Romania]. No specimens were examined here, but one is illustrated in Andelković, 1964, pl. 1, fig. 5; and the holotype is illustrated in fig. 1 of the type description. **Clupeidae.**

†“*Clupea*” *gracillima* Bassani, 1889 [from Oligocene marine deposits of Chiavon, Italy]. No specimen was examined here, but a nearly complete fish (holotype) is illustrated in type description. Numerous specimens in the collections of Court Museum, Vienna, Austria and Museo Civico di Storia Naturale, Verona, Italy. Discussed in Woodward, 1901, p. 155. **Clupeidae.**

†“*Clupea*” *grandonii* Bassani, 1889 [from Oligocene marine sediments of Chiavon, Italy]. No specimens were examined here, but a nearly complete fish (holotype) is illustrated in Bassani, 1889, pl. 3, fig. 4. Material at Museo Civico di Storia Naturale, Verona, Italy. **Clupeidae.**

†“*Clupea*” *haidingeri*, Heckel, 1850 [from Miocene sediments of Vienna.] No specimens were examined here, but one is illustrated in type description, pl. 21. In the collection of the Imperial Geological Survey, Vienna (an incomplete specimen). **Clupeidae.**

†“*Clupea*” *heckeli* (Rzehak, 1881) [from Tertiary sediments of Europe]. No specimens were examined here, but several are illustrated in figs. 1–5 of the type description. Originally described in the genus *Meletta*. Thought by Woodward (1901, p. 151) to be a subjective junior synonym of †“*C.*” *crenata*. **Clupeidae.**

†“*Clupea*” *heterocerca* Kramberger, 1883 [from Miocene sediments of Croatia, Yugoslavia]. No specimens were examined here, but one is illustrated in pl. 13, fig. 9 of original description. In the collection of the Imperial Geological Survey, Vienna (an incomplete specimen). Thought to be *Alosa* by Rückert-Ülkumen, 1965, p. 330. **Clupeidae.**

†“*Clupea*” *hungarica* Gorjanović-Kramberger, 1902 [from Miocene (Pontian) deposits of Hungary]. No specimens were ob-

served here, but one is illustrated in the type description. **Clupeidae.**

†“*Clupea*” *inflata* Vukotinović, 1870 [from Tertiary marine sediments of Croatia, Yugoslavia, and Chiavon, Italy]. No specimens were examined here, but one is illustrated in Andelković, 1969, fig. 1; discussed in Woodward, 1901, p. 156; and Bassani, 1889, p. 39. **Clupeidae.**

†“*Clupea*” *intermedia* Kramberger, 1885 [from Miocene marine deposits of Croatia, Yugoslavia]. No specimens were examined here. Holotype is said to be an “imperfect fish” in the Museum of the Imperial Geological Survey, Vienna (Woodward, 1901, p. 156). No specimen or illustration observed here, so determination omitted. This species is included in this list, nevertheless, because Woodward included it in his list of “*Clupea*” fossils (p. 156) and indicated that he examined at least an illustration of the type. It is therefore probably a **clupeoid**.

†“*Clupea*” *lanceolata* von Meyer, 1851 [from Lower Miocene freshwater sediments of Wurtemberg, Germany]. Thought by Woodward (1901, p. 150) to be a subjective junior synonym of †“*C.*” *humilis*. Thought by Andelković (1969) to also be present in Yugoslavia. Cotypes are illustrated in von Meyer, 1851, pl. 14, fig. 2 and pl. 16, fig. 11. **Clupeidae.**

†“*Clupea*” *latissima* Bassani, 1889 [from Oligocene marine deposits of Chiavon, Italy]. No specimen was examined here, but the holotype (a nearly complete specimen) is illustrated in Bassani, 1889, pl. II, fig. 4). This species is also discussed in Woodward, 1901, p. 156. **Clupeidae.**

†“*Clupea*” *linderi* Priem, 1912 [from Pliocene marine sediments of France]. No specimens were observed here, but the type (a complete skeleton) is illustrated in pl. 6, fig. 36 of the type description (coll. de Paleontologie de l'École nationale des Mines). **Clupeidae.**

†“*Clupea*” *longimana* (Heckel, 1850b) [from Oligocene-Miocene deposits of Austria, Germany and France]. Thought by Woodward (1901, p. 151) to be a subjective junior synonym of †“*C.*” *crenata*. Also described in Weiler (1932, p. 318). Originally

described in the genus *Meletta*. No specimens were examined here, but one is illustrated in pl. 9, fig. 5 of type description. **Clupeidae.**

†“*Clupea*” *lorcae* Sauvage, 1878 [from Pliocene sediments of Murcia, Spain]. No specimen was examined here, but the fragmentary type is illustrated in pl. 11, fig. 5 of original description. **Clupeidae.**

†“*Clupea*” *maceki* Kramberger, 1883 [from Miocene marine sediments of Croatia]. No specimens were examined here, but an incomplete specimen is illustrated in pl. 13, figs. 10 and 11 of the original description. Type is in the Geological Museum, University of Agram, Yugoslavia. **Clupeidae.**

†“*Clupea*” *melettaeformis* Steindachner, 1860 [from Miocene marine sediments of Croatia, Yugoslavia]. No specimens were examined here, but a partial specimen is illustrated in pl. 13, fig. 12 of type description. Holotype is in Court Museum, Vienna. **Clupeidae.**

†“*Clupea*” *mucronata* Kramberger, 1895 [from Miocene marine sediments of Croatia, Yugoslavia]. No specimens were examined here, but a nearly complete fish is illustrated in pl. 11, fig. 3 of original description. Also described by Weiler (1932, p. 314) as †*Alosa* cf. *mucronata*. **Clupeidae.**

†“*Clupea*” *ombonii* Bassani, 1889 [from Oligocene marine sediments of Chiavon, Italy]. No specimens were examined here, but a nearly complete fish (holotype) is illustrated in Bassani, 1889, pl. 3, fig. 4. Numerous specimens are at Museo Civico di Storia Naturale, Verona, Italy; and Geological Museum, University of Padua. **Clupeidae.**

†“*Clupea*” *parisoti* (Sauvage, 1870b) [from ?Oligocene-Miocene deposits of France]. Thought by Woodward (1901, p. 151) to be a subjective junior synonym of †“*C.*” *crenata*. Originally described in the genus *Meletta*. No specimens were examined here, but one is illustrated in pl. 9, fig. 6 of type description. **Clupeidae.**

†“*Clupea*” *sagorensis* Steindachner, 1863 [from Upper Tertiary marine sediments from Croatia, Yugoslavia; and Chiavon, Italy]. No specimens examined here, but a nearly complete fish is illustrated in Bas-



- sani, 1889, pl. 3, fig. 5. Material in Court Museum, Vienna, Austria and Museo Civico di Storia Naturale, Verona, Italy. Discussed in Woodward, 1901, p. 157. Thought to be *Alosa* by Rückert-Ülkümen, 1965, p. 329. **Clupeidae.**
- †“*Clupea*” *sahleri* (Sauvage, 1870b) [from ?Oligocene-Miocene deposits of France]. Thought by Woodward (1901, p. 151) to be a subjective junior synonym of †“*C.*” *crenata*. Originally described in the genus *Meletta*. Not examined here, but illustrated in pl. 9, fig. 4 of type description. **Clupeidae.**
- †“*Clupea*” *sarmatica* Böhm, 1942 [from Upper Tertiary marine deposits of Hungary]; no specimens were examined here, but one is illustrated in original description. Described as a subspecies of †“*C.*” *voinovi* Pauca. **Clupeidae.**
- †“*Clupea*” *scheuchzeri* Blainville, 1818 [from the Oligocene marine black shales of Canton Glarus, Switzerland]. These fishes are frequently distorted, and are in a slatelike matrix that is very difficult to prepare. Well represented in several European museums including BMNH and MNHN. **Clupeidae.**
- †“*Clupea*” *spinosa* Rückert-Ülkümen, 1965 [from Miocene sediments of Pinarhisar, Turkey]. Holotype (not examined here) illustrated in pl. 23, fig. 11 of original description, and is deposited in collection of Geol. Inst., Univ. Istanbul. **Clupeidae.**
- †“*Clupea*” *styriaca* (Steindachner, 1863) [from Miocene deposits of Styria, Austria]. No specimens were examined here. Holotype is said to be an “imperfect fish” in the Imperial Geological Survey, Vienna (Woodward, 1901, p. 156). Originally described in the genus *Meletta*. No illustration observed here, so determination omitted. This species is included in this list, nevertheless, because Woodward included it in his list of “*Clupea*” fossils (p. 157) and indicated that he examined at least an illustration of the type. Therefore, it is probably a clupeoid.
- †“*Clupea*” *tanegashimaensis* Saheki, 1929 [from Upper Tertiary deposits of Japan]. None examined here. **Clupeidae.**
- †“*Clupea*” *tenuissima* Agassiz, 1844 (in Ag. 1833–1844) [from Miocene deposits of Ragusa, Sicily]. No specimens were examined here, but an incomplete specimen is illustrated in pl. 61, fig. 3 of Agassiz, 1844. According to Woodward, 1901, p. 154, the type specimen is supposed to be [at BMNH] but is not recognizable. Because the type is lost, it was not determined whether †“*Clupea*” *tenuissima* Ag. is conspecific with †“*Diplomystus*” *tenuissimus* de Stephano, 1918 (=a myctophoid—see below). One of the two specimens of †“*C.*” *tenuissima* illustrated in Agassiz (1844, pl. 5, fig. 5) appears to be a clupeid. **Clupeidae.**
- †“*Clupea*” *tiejei* David, 1943 [from Upper Miocene marine sediments of southern California]. Known by one nearly complete specimen illustrated in David, 1943, pl. 12. Holotype given in type description as “no. 200 Tm. Univ. S. Calif. Coll. Paleont.” With only about 47 vertebrae and about 13 predorsal bones, this species is not likely to belong to the genus †*Clupea*. **Clupeidae.**
- †“*Clupea*” *vectensis* Newton, 1889 [from Oligocene lacustrine deposits of the Isle of Wight]. This species was mistakenly placed in †*Diplomystus* by Woodward (1889, p. 230 and 1901, p. 146) due to a misunderstanding about the genera †*Knightia* and †*Diplomystus* (discussed in Grande, 1982a, pp. 19, 4 and 5). Redescription of species and placement in new genus currently in press by J. Gaudant. Material uncommon, and mostly at BMNH, MNHN, and AMNH. **Clupeidae.**
- †“*Clupea*” *ventricosa* von Meyer, 1851 [from Lower Miocene freshwater sediments of Wurtemberg, Germany]. Thought by Woodward (1901, p. 150) to possibly be a subjective junior synonym of †“*C.*” *humilis* (=†*Clupeonella humilis*). Cotypes illustrated in von Meyer, 1851, pl. 14, figs. 1a, 1b. Specimens are also deposited at BMNH. **Clupeidae.**
- †“*Clupea*” *voinovi* Paucă, 1929 [from ?Oligocene-Miocene sediments of eastern Europe]. No specimens examined here, but one is illustrated in Andelković, 1969, pl. 1, fig. 2. **Clupeidae.**
- †“*Clupea*” *voironensis* Pictet, 1858 [from the Early Cretaceous (Neocomian) of Switzerland]. No specimens observed here, but several illustrations are in pl. 5, figs. 1–10

of the type description. **Clupeomorpha: incertae sedis.**

*Clupeonella* Kessler, 1877

†*Clupeonella binagadensis* Bogachev, 1938 [from Miocene deposits of Armenia]. No specimens were observed here, but one is illustrated in fig. 1 of the type description.

**Clupeidae.**

†*Clupeonella humilis* (von Meyer, 1851) [from Lower Miocene freshwater sediments of Wurtemberg, Germany]. Originally described in *Clupea*. Discussed in Woodward, 1901, pp. 150–151 as *Clupea*. Redescribed by Menner (1949) and Danil'chenko (1972, 1980) in *Clupeonella*. Fairly common in most major museum collections. **Clupeidae.**

†*Clupeonella mediocris* Bogachev, 1955 [from Upper Tertiary sediments of eastern Europe]. No specimens were examined here, but one is illustrated in fig. 1 of the type description. Also described in Danil'chenko, 1980, p. 14. **Clupeidae.**

†*Clupeonella pliocena* Bogachev, 1913 [from Late Tertiary marine deposits of Armenia]. Also discussed by Danil'chenko, 1972, p. 200. **Clupeidae.**

†*Clupeonella pliocenica* Menner, 1949 [from Upper Miocene sediments of Russia]. No specimens were observed here, but one is illustrated in original description. Also described by Danil'chenko, 1980. **Clupeidae.**

†*Clupeonella vexata* Bogachev, 1938 [from Late Tertiary (Pontian) marine deposits of Armenia]. No specimens were observed here, but some are illustrated in figs. 2–4 of the type description. Also discussed in Danil'chenko, 1972, p. 200, and 1980, p. 13. **Clupeidae.**

†*Clupeops* Sauvage, 1880

†*Clupeops insignis* Sauvage, 1880 [from Miocene deposits of Drome, France]. Thought by Woodward (1901, p. 159) to be indistinguishable from "*Clupea*." No specimens examined here, but a partial specimen is illustrated in pl. 7, figs. 4 and 5 of original description. Type species of genus by original designation. **Clupeidae.**

†*Diplomystus* Cope, 1877

[†*Copeichthys* Dollo, 1904, is an objective junior synonym of this genus (Jordan, 1907, p. 137).]

†*Diplomystus dentatus* Cope, 1877 [from Lower and Middle Eocene freshwater deposits of Wyoming]. Discussed above, and redescribed in Grande, 1982a. A very common species represented in most major museums, particularly FMNH. Type species for genus by original designation.

†**Ellimmichthyidae.**

†*Diplomystus " analis "* Cope, 1877; a subjective junior synonym of †*D. dentatus* from the same locality (as explained by Grande, 1980). Type specimen (illustrated in Cope, 1884, pl. 7, fig. 4) is USNM 4004.

†**Ellimmichthyidae.**

†*Diplomystus birdi* Woodward, 1895 [from Upper Cretaceous (Cenomanian) marine limestone deposits of Lebanon]. Discussed above, and redescribed in Grande, 1982a. A relatively uncommon species well represented in a few museums (AMNH, BMNH, MNHN). †**Ellimmichthyidae.**

†*Diplomystus dubertreti* Signeux, 1951 [from Upper Cretaceous (Santonian) marine chalk deposits of Lebanon]. Discussed above, and redescribed in Grande, 1982a. An extremely rare species known by only three specimens (2 at MNHN, 1 at FMNH). †**Ellimmichthyidae.**

†*Diplomystus " pectorosus "* Cope, 1877; a subjective junior synonym of †*D. dentatus* from the same locality (as explained by Grande, 1980). Type specimen (illustrated in Cope, 1884, pl. 10, fig. 3) is USNM 4020. **Ellimmichthyidae.**

†*Diplomystus " theta "* Cope, 1874; a subjective synonym of †*D. analis* [=†*D. dentatus*] as explained by Cope (1884, p. 77) and Grande (1980, p. 90). Holotype is lost. **Ellimmichthyidae.**

†*Diplomystus* n. sp. A. Described but unnamed by Chang and Chow, 1978 [from Early Tertiary deposits of eastern China]. A nearly complete specimen (deposited in the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica) is illustrated in pl. 1, fig. 3 of the description. **Ellimmichthyidae.**

†"*Diplomystus*" *coverhamensis* Chapman,

1918 [from Upper Cretaceous deposits of New Zealand]. Not †*Diplomystus* for reasons discussed in Grande, 1982a. Type and only known specimen (illustrated in Chapman, 1918, pl. 8, fig. 4) is in the collection of the National Museum, Wellington, New Zealand (not observed here). **Clupeomorpha Division 2: *incertae sedis*.**

†“*Diplomystus*” *dartevellei* Casier, 1965 [from Lower Cretaceous deposits of Zaire]. Discussed in Grande, 1982a, where it is removed from †*Diplomystus* (no new generic name proposed). No specimens were examined here, but some are illustrated in Taverne, 1976, figs. 1–3. All known material is at RMAC. **Clupeomorpha Division 2: *incertae sedis*.**

†“*Diplomystus*” *goodi* Eastman, 1912 [from Lower Cretaceous black limestone and shale deposits of West Africa]. Discussed in Grande, 1982a, p. 19; and in Taverne, 1975. Removed from †*Diplomystus* by Grande, 1982a, but not given a new generic name. Well represented in several museum collections including AMNH, BMNH, FMNH, and CMNH. **Clupeomorpha Division 2: *incertae sedis*.**

†“*Diplomystus*” *kasachstanicus* Khisarova, 1974 [from Upper Cretaceous sediments of Alma-ata, USSR]. Also described by Danil’chenko, 1980, p. 7. Reported in descriptions as having oval, keeled dorsal scutes with no pectinations. No specimens were examined here, but two extremely poor illustrations are in pl. 1, figs. 1 and 3 of the type description. Holotype (spec. no. 827) is deposited in the Institute of Zoology, Academy of Sciences, Kazakhstan, SSR. This species does not belong in †*Diplomystus*. **Clupeomorpha Division 2: *incertae sedis*.**

†“*Diplomystus*” *kokuraensis* Uyeno, 1979 [from Lower Cretaceous lacustrine shales, Kyushu Island, Japan]. Discussed in Grande, 1982a, and there removed from †*Diplomystus* (no new generic name was proposed). Specimens were not examined by author, but information and illustrations in the original description exclude this species from †*Diplomystus*. All known material is at the Kitakyushu Museum of Natural History, Japan. **Clupeomorpha Division 2: *incertae sedis*.**

†“*Diplomystus*” *marmorensis* Woodward, 1904 (in Newton, 1904) [from Miocene sediments of Turkey]. Discussed in Grande, 1982a and there removed from †*Diplomystus* and placed as *Clupeoidei incertae sedis* (no new generic name was proposed). Only one known specimen (BMNH P10015). **Clupeidae.**

†“*Diplomystus*” *minutus* Khisarova, 1974 [from Upper Cretaceous sediments of Alma-ata, USSR]. Also described in Danil’chenko, 1980, pp. 7–8. Reported in descriptions as having oval or rounded dorsal scutes. No specimens were examined here, but two extremely poor illustrations are in pl. 1, figs. 2 and 4 of the type description. This species does not belong in †*Diplomystus*. Holotype (spec. no. 1051) is deposited in the Institute of Zoology, Academy of Sciences, Kazakhstan, SSR. **Clupeomorpha: *incertae sedis*.**

†“*Diplomystus*” *primotinus* Uyeno, 1979 [from Lower Cretaceous lacustrine shales, Hyushu Island, Japan]. Discussed in Grande, 1982a, and there removed from †*Diplomystus* (no new generic name proposed). Specimens were not examined here, but information and illustrations in the original description exclude this species from †*Diplomystus*. All known material is at the Kitakyushu Museum of Natural History, Japan. **Clupeomorpha Division 2: *incertae sedis*.**

†“*Diplomystus*” *solignaci* Gaudant and Gaudant, 1971 [from Upper Cretaceous limestone deposits of Tunisia, North Africa]. Discussed in Grande, 1982a, and there removed from †*Diplomystus* but not given a new generic name. Only one known specimen (MNHN 1970-3). **Clupeomorpha Division 2: *incertae sedis*.**

†*Diradias* Jordan, 1924

†“*Diradias aratus*” Jordan, 1924; a subjective junior synonym of †*Ganolytes cameo* (as explained by David, 1943, pp. 94 and 5), from upper Miocene marine sediments of southern California. Type specimen (illustrated in Jordan, 1924, pl. F) is SU 600. Type species for genus by original designation. **Clupeidae.**

†“*Diradias fenestralis*” Jordan, 1925; a sub-

jective junior synonym of †*Ganolytes cameo* (as explained by David, 1943, pp. 94 and 5), from Upper Miocene marine sediments of southern California. Type specimen (illustrated in Jordan, 1925, pl. 1) is SU 759. **Clupeidae**.

*Dussumieria* Valenciennes, 1847

†*Dussumieria? elami* Arambourg, 1966 [from Oligocene marine deposits in Iran]. No specimens showing preservation of pelvic abdominal area, caudal skeleton, or bullae were observed here, so I could not verify that this species was even a clupeomorph. Type and only known specimen is illustrated in Arambourg, 1966, pl. 1, fig. 5 (an incomplete specimen missing parts mentioned above).

*Engraulis* Cuvier, 1817

†*Engraulis macrocephalus* Landini and Menesini, 1978 [from Plio-Pleistocene marine deposits of Calabria, Italy]. Originally described as a subspecies of *E. encrasicolus*. Seven nearly complete specimens illustrated in pl. 1, figs. 1–7 of type description. The illustrated specimens and about 20 others are deposited at the Istituto di Geologia e Paleontologia dell'Università di Pisa. **Engrauloidea**.

†*Ellimma* Jordan, 1913

†*Ellimma branneri* (Jordan, 1910) [from ?Upper Eocene, estuarine black shale deposits of Alagoas, Brazil]. A double armored species originally described in the preoccupied genus *Ellipes*, and later transferred to a new genus †*Ellimma*. Discussed above and in Grande, 1982b. Abundant in collections of AMNH and BMNH. Type species of genus by original designation. **Clupeidae**.

†*Ellimma "riacensis"* (Jordan, 1919c); a subjective junior synonym of †*E. branneri* from the same locality (as explained by Schaeffer, 1947). Known by the type (CMNH 5248/4, illustrated in Jordan, 1910, pl. 10) and some material at SU. **Clupeidae**.

†*Ellimmichthys* Jordan, 1919c

†*Ellimmichthys longicostatus* (Cope, 1886) [from Lower Cretaceous estuarine black limestone deposits of Bahia, Brazil]. A relatively uncommon species represented in only a few museums (AMNH, BMNH, and Museo Nacional Brazil). This species was originally described as belonging to †*Diplo-mystus*, but later placed in a new genus for reasons explained in Jordan, 1919a, and Grande, 1982a. Type species of genus, by original designation. The name *Ellipes* as applied to this species (Jordan, 1910) was found to be a junior homonym and thus unavailable (see Jordan, 1919c). †**Ellimmichthyidae**.

†*Entringus* Jordan, 1907

†*Entringus scintillans* Jordan, 1907 [from Upper Miocene marine sediments of southern California]. Redescribed by David (1943, pp. 6–9). Small ventral scutes are present, and the modified pelvic scute has not been reported, making placement of this species in Dussumeriidae tenuous. Very abundant in collections of CAS and SU. Jordan (1907) at first reported the presence of a complete lateral line in this species, but later (1919c, p. 5) admitted he was mistaken about this. Jordan placed this species first (1907) in †Leptolepidae, later (1919c) in †Pholidophoridae, and then (1921) in his clupeoid family †Ganolytidae. David (1943) recognized this species as a clupeoid. Type species for genus by monotypy. **Clupeidae**.

†*Eoknightia* Taverne, 1976

†*Eoknightia caheni* Taverne, 1976 [from Lower Cretaceous deposits of Zaire]. A double armored clupeomorph not closely related to †*Knightia* as name implies (it is described as having two supramaxillary bones). No specimens examined here, but illustrations are in Taverne, 1976. Known only by one poorly preserved specimen at MRAC. If Taverne's reconstruction is correct, this species is a clupeoid. Type species of genus, by original designation. **Clupeomorpha Division 2: incertae sedis**.

†*Eosardinella* Sato, 1966

†*Eosardinella hishinaiensis* Sato, 1966 [from Upper Miocene marine sediments of Northeastern Japan]. No specimens examined here, but the species is well illustrated in original description. Specimens are deposited at Kurosawajiri Technical High School, Japan. Type species by original designation. Appears to be closely related to the clupeine, *Sardinella*. **Clupeidae**.

†*Epelichthys* Jordan, 1925

†*Epelichthys michaelis* Jordan, 1925 [from Upper Miocene marine sediments of southern California]. The type for this species (an incomplete, distorted fish illustrated in Jordan, 1925, pl. 20c) is lost according to David, 1943. Only two specimens of this species were reported (SU 777: holotype; and SU 775). Type species for genus by original designation. **Clupeidae**.

†*Erichalcis* Forey, 1975

†*Erichalcis arcta* Forey, 1975 [from Lower Cretaceous (Albian) marine deposits of the Northwest Territories, Canada]. Discussed above; material is deposited at UAVP. Type species of genus, by original designation. †**Clupeomorpha Division 1: †Erichalcidae**.

*Etrumeus* Bleeker, 1853

†*Etrumeus boulei* Arambourg, 1925 [from Miocene marine deposits of Oran, northern Africa]. This species is discussed above in text. Several specimens are deposited at MNHN and several of these nearly complete specimens are illustrated in Arambourg, 1927. **Clupeidae: Dussumieriinae: Dussumieriini**.

*Etrumeus hafizi* Arambourg, 1943 [from Oligocene marine deposits in Iran]. Known by one nearly complete specimen and some scales at MNHN (both specimens illustrated in Arambourg, 1966). **Clupeidae: Dussumieriinae**.

†*Ganoessus* Jordan, 1920

†*Ganoessus clepsydra* (Jordan and Gilbert, 1919) [from Upper Miocene marine sediments of southern California]. Originally described in †*Ganolytes*, but later put into †*Ganoessus* by Jordan, 1920, p. 571. According to David (1943, p. 94), all material for this species is deposited at SU except for the holotype (illustrated in Jordan and Gilbert, 1919, pl. 11, fig. 1), which is lost. Type species for genus by original designation. **Clupeidae**.

†*Ganolytes* Jordan, 1919c

†*Ganolytes cameo* Jordan, 1919c [from Upper Miocene marine sediments of southern California]. Discussed and redescribed in David (1943, pp. 3–6) and illustrated in Jordan, 1919c, pl. 2, fig. 3 and pl. 4, figs. 1 and 2 (fragmentary material) and in David, 1943, pl. 1, fig. 1 (nearly complete specimen). This species is known by several specimens at SU, CAS, and Calif. Inst. Technol. Coll. Vert. Paleont. This is the type species of the genus, by monotypy. Jordan (1921, p. 241) proposed a new family (†*Ganolytidae*) to contain this species because of what he thought were peculiar scales. David (1943, p. 5) recognized these as typical clupeid scales, and placed the species back in *Clupeidae*. **Clupeidae**.

†*Gasteroclupea* Signeux, 1964

†*Gasteroclupea branisai* Signeux, 1964 [from Upper Cretaceous sediments of Bolivia]. Mentioned above in text; currently being redescribed by M. Gayet. A few specimens are at AMNH (one illustrated in Schaeffer, 1963, fig. 6) and several are at MNHN. Type species for genus by original designation. **Pristigasteroidea**.

†*Gosiutichthys* Grande, 1982b

†*Gosiutichthys parvus* Grande, 1982b [from Middle Eocene lacustrine sediments of Wyoming]. Common in several museum collections, particularly AMNH and FMNH. Type species of genus by original designation. **Clupeidae**.

†*Haplospondylus* Cabrera, 1927

†*Haplospondylus clupeioides* Cabrera, 1927 [from Lower Cretaceous sediments of Santa Cruz, Argentina]. No specimens were examined here, but the type and only known specimen (a skeleton lacking the caudal region, number 25.xl.24.1 of the Dept. de Paleon. del Museo do La Plata) is illustrated in the original description. This species was originally described as a †“leptolepid,” but there are no characters given in the description that would indicate that this species belongs in †Leptolepidae, and the type specimen appears to have clupeomorph-type abdominal scutes (see illustration in type description; and Cione, in preparation). This species is currently being studied in more detail by A. L. Cione (Museo de La Plata). Montypic genus. **Clupeomorpha**, *incertae sedis*.

*Hilsa* Regan, 1917a

†*Hilsa elegans* (Gabelaya, 1976) [from Pliocene sediments of Russia]. No specimens were examined here, but in the type description three specimen illustrations (pl. 2, figs. 1–3) and a line drawing (fig. 2) are given. Originally described in *Alosa*, but later placed into *Hilsa* by Danil’chenko, 1980. **Clupeidae**.

†*Hilsa lata* (Gabelaya, 1976) [from Pliocene sediments of Russia]. No specimens were examined here, but in the type description four specimen illustrations (pl. 3, figs. 1–4) and a rough line drawing (fig. 3) are given. Originally described in *Alosa*, but later placed into *Hilsa* by Danil’chenko, 1980. **Clupeidae**.

†*Hilsa oblonga* (Gabelaya, 1976) [from Pliocene sediments of Russia]. No specimens were examined here, but some are illustrated in pl. 4, figs. 1–4 of type description. Originally described in *Alosa*, but later placed into *Hilsa* by Danil’chenko, 1980. **Clupeidae**.

†*Hilsa torosa* (Gabelaya, 1976) [from Pliocene sediments of Russia]. No specimens were examined here, but some are illustrated in pl. 5, figs. 1 and 2 of type description. Originally described in *Alosa*, but later placed into *Hilsa* by Danil’chenko, 1980. **Clupeidae**.

†*Histiurus* Costa, 1850

†*Histiurus elatus* Costa, 1850 [from Lower Cretaceous (Aptian or Albian) marine sediments in Italy]. A double armored clupeomorph (no specimens examined here) that, based on descriptions and illustrations (e.g., Erasmo, 1915, pl. 9, fig. 2), does not belong in †*Knightia* (as suggested by Jordan, 1919a, p. 245) of †*Diplomystus* (as suggested by Woodward, 1901, p. 139). Type species for genus, by original designation. Erasmo (1915, p. 43) thought this species to be subjective junior synonym of †*Armigatus brevissimus* (Blainville). **Clupeomorpha Division 2: incertae sedis**.

†*Histiurus seriolooides* Costa, 1864 [from Lower Cretaceous (Aptian or Albian) marine sediments in Italy]. This species (no specimens examined here), based on description (Costa, 1865), does not belong in †*Knightia* (as suggested by Jordan, 1919a, p. 245) or †*Diplomystus* (as suggested by Woodward, 1901, p. 139). Erasmo (1915, p. 43) thought this species to be a subjective junior synonym of †*Armigatus brevissimus* (Blainville). **Clupeomorpha Division 2: incertae sedis**.

†*Histiurus ventricosus* Costa, 1865 [from Lower Cretaceous (Aptian or Albian) marine sediments in Italy]. This species (no specimens examined here), based on description and illustrations (Costa, 1865; and Erasmo, 1915, pl. 9, fig. 3), does not belong in †*Knightia* (as suggested by Jordan, 1919a, p. 245) or †*Diplomystus* (as suggested by Woodward, 1901, p. 139). Erasmo (1915, p. 43) thought this species to be a subjective junior synonym of †*Armigatus brevissimus* (Blainville). **Clupeomorpha Division 2: incertae sedis**.

†*Horaclupea* Borkar, 1973a

†*Horaclupea intertrappea* Borkar, 1973 [from Late Paleocene or Early Eocene freshwater lacustrine deposits of Saurashtra, India]. Material (not examined here) consists of 10 specimens deposited at the Maharashtra Association for the Cultivation of Science. Type species for genus by original designation. **Clupeidae**.

†“*Horaclupea*” *geei* (Hora, 1937) [from Eocene marine deposits of Pakistan]. Orig-

inally described as *Clupea*, but transferred to †*Horachupea* by Borkar (1973b). Material not examined here, but holotype is illustrated in Hora, 1937: figs. 1, 2 and 3, and pl. 15, figs. 4, 5 and 6. Probably not closely related to †*Horachupea intertrappea*, but not *Clupea* either. Material is deposited in the collection of the Geological Survey of India. **Clupeidae.**

†*Knightia* Jordan, 1907

†*Knightia eocaena* Jordan, 1907 [from Lower Eocene lacustrine sediments of Wyoming, Colorado, and Utah]. Redescribed in Grande, 1982b. Extremely common in most major museum collections. The names †*Clupea humilis* and †*Clupea pusilla* were both applied to this species by Leidy and Cope, but both names were junior homonyms (Jordan, 1907; Grande, 1982b) and thus invalid. The name †*Diplomystus humilis* is also invalid for reasons explained in Grande, 1982b. Type species of genus by original designation. **Clupeidae: Pellonulinae.**

†*Knightia alta* (Leidy, 1873) [from Lower Eocene lacustrine sediments of Wyoming, Colorado, and Utah]. Redescription in Grande, 1982b. Common in most major museum collections. This species has also been placed in *Clupea* (Leidy, 1873) and †*Diplomystus* (Cope, 1877) but it belongs in neither of those genera, as demonstrated by Grande (1982a, 1982b) and Jordan (1907). **Clupeidae: Pellonulinae.**

†*Knightia "copei"* Tanner, 1925; a subjective junior synonym of †*K. alta* from the same locality (as explained in Grande, 1980 and 1982b). Type specimen is illustrated in Tanner, 1925, fig. 6, pl. 3 (University of Utah, number 11). **Clupeidae: Pellonulinae.**

†*Knightia vetusta* Grande, 1982b [from lacustrine limestone in the Middle Paleocene, Montana]. Uncommon in museum collections. Well represented in the AMNH collection; also represented in FMNH collection. **Clupeidae: Pellonulinae.**

†*Knightia* n. sp. A. Described but unnamed by Chang and Chow, 1978 [from Early Tertiary deposits of eastern China]. A nearly complete specimen (deposited in the In-

stitute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica) is illustrated in pl. 1, fig. 4 of the description.

**Clupeidae: Pellonulinae.**

†“*Knightia*” *brasiliensis* Woodward, 1939 [from ?Pliocene freshwater deposits of Maranhao, Brazil]. For reasons discussed above, this species must be removed from †*Knightia* (no new genus is proposed here without further study). Eight specimens are deposited at BMNH. **Clupeidae.**

†*Knightia ? yuyanga* Liu, 1963 [from Eocene lacustrine shales of Hupei, China]. No specimens were examined here except for the illustration in the original description. Very similar in appearance to †*Knightia*, but known only by one incomplete specimen (lacking caudal region) which is in the Institute of Vertebrate Palaeontology and Paleoanthropology, Academia Sinica, China. **Clupeidae.**

†*Lembicus* Jordan, 1925

†*Lembicus meiklejohni* Jordan, 1925 [from Upper Miocene marine sediments of southern California]. Known by only one incomplete specimen (holotype SU 691, illustrated in Jordan, 1925, pl. 11a). David (1943, pp. 94–95) suggested that this fish may belong in †*Ganoessus*. Type species for genus by original designation. **Clupeidae.**

†*Nolfia* Taverne, 1976

†*Nolfia kwangoensis* Taverne, 1976 [from Lower Cretaceous deposits of Zaire]. No specimens were examined here, but an illustration of the type is in Taverne, 1976. Known only by a partial postcranial skeleton at MRAC. Type species of genus, by original designation. **Clupeomorpha Division 2: incertae sedis.**

*Opisthonema* Gill, 1861

†*Opisthonema antethrissa* Ciobanu, 1977 [from Oligocene marine deposits of Rumania]. No specimens were examined here, but holotype (a well-preserved complete skeleton) is illustrated in pl. 11, fig. 1 of the type description. Material deposited at

Muzeului de stiinte naturale, Piatra Neamt, Rumania. **Clupeidae**.

†*Opisthonema palosverdensis* David, 1943 [from Upper Miocene marine sediments of southern California]. Known by only a single, nearly complete, specimen (not examined here) illustrated in David, 1943, fig. 15. Holotype is no. 10101, in the Calif. Inst. Technol. Coll. Vert. Paleont. **Clupeidae**.

†*Opisthonema persicum* Arambourg, 1966 [from Oligocene marine deposits of Iran]. Described in detail by Arambourg in type description. Several specimens at MNHN (illustrated in Arambourg, 1966). **Clupeidae**.

†*Palaeodenticeps* Greenwood, 1960

†*Palaeodenticeps tanganyikae* Greenwood, 1960 [from Oligocene lacustrine shales, Tanganyika Territory, Central Africa]. Described in detail by Greenwood, 1960. All known material is deposited at BMNH except for one latex peel at FMNH (original specimens are impressions only). Type species of genus, by original designation. **Denticipitidae**.

†*Paraclupea* Du, 1950

†*Paraclupea chetungensis* Du, 1950 [from Lower Cretaceous sediments of Chekiang Province, China]. No specimens examined here except by illustrations (showing the clupeomorph abdominal scutes and dorsal scutes) from Sun (1956, figs. 1–4). This species is clearly a clupeomorph. All known material is in the Laboratory of Vertebrate Paleontology, Academia Sinica, China. Type species of genus by original designation. Placed in its own monotypic family by Chang and Chou, 1977. **Clupeomorpha Division 2: incertae sedis**.

†*Paretrumeus* Danil'chenko, 1980

†*Paretrumeus avitus* Danil'chenko, 1980 [from Lower Oligocene deposits of Russia]. No specimens were observed here, but the type and one referred specimen (both nearly complete skeletons) and a line drawing reconstruction are illustrated in the original description. Danil'chenko (1980, p. 22)

noted the presence of prootic and pterotic bullae of about equal size, but did not mention whether or not the specimens show the W-shaped pelvic scute. Therefore, although this species is probably a clupeomorph, whether or not it belongs in *Dussumieriinae* is uncertain. **Clupeomorpha: ?Dussumieriinae**.

*Pellonula* Gunther, 1868

†“*Pellonula*” *grasionescui* Ciobanu, 1977 [from Oligocene marine deposits of Rumania]. No specimens were examined here, but the holotype (a nearly complete specimen) is illustrated in pl. 14, fig. 2 of the type description. Material deposited at Muzeului de stiinte naturale, Piatra Neamt, Rumania. Based on illustration and description of this material, this species may not belong in *Pellonulinae*. **Clupeidae: ?Pellonulinae**.

*Pomolobus* Rafinesque, 1820

†*Pomolobus antiquus* (Smirnov, 1935) [from Oligocene marine deposits of the Caucasus Mts., USSR]. No specimens were examined here, but two nearly complete specimens (including lectotype) are redescribed and illustrated in Danil'chenko, 1960. Originally described as †“*Clupea*” *ventricosa antiqua*, but later redescribed in the genus †*Pomolobus* by Danil'chenko, 1960, pp. 11–12. Also described in Danil'chenko, 1980, p. 17. Several specimens are deposited in the Paleontological Inst., Acad. Sci., Moscow, USSR. **Clupeidae**.

†*Pomolobus curtus* Danil'chenko, 1960 [from Oligocene marine deposits of the Caucasus Mts., USSR]. No specimens were examined here, but a nearly complete fish (the holotype) is illustrated in pl. 20, fig. 3 of type description. Also described and illustrated (reconstructed line drawing) in Danil'chenko, 1980, pp. 15–16 and fig. 5. Several specimens are deposited in the Paleontological Inst. Acad. Sci., Moscow, USSR. **Clupeidae**.

†*Pomolobus facilis* Danil'chenko, 1960 [from Oligocene marine deposits of the Caucasus Mts., USSR]. No specimens were examined here but two nearly complete specimens (including holotype) are illustrated in



pl. 21, figs. 1 and 2 of type description. Also described and illustrated (reconstructed line drawing) in Danil'chenko, 1980, pp. 16–17 and fig. 6. Specimens are deposited at Paleontological Inst., Acad. Sci., Moscow, USSR. **Clupeidae**.

†*Primisardinella* Danil'chenko, 1968

†*Primisardinella gentrix* Danil'chenko, 1968 [from Upper Paleocene deposits of Turkistan, USSR]. No specimens were examined here, but several complete specimens are illustrated in text fig. 1 and pl. 23, figs. 1–4 of original description. Also described in Danil'chenko, 1980, p. 8. Type species for genus by original description. **Clupeidae**.

†*Pseudochilsa* Menner, 1949

†*Pseudochilsa brevicauda* (Lednev, 1914) [from Miocene deposits of Apspheron Peninsula, USSR]. Originally described as †“*Diplomystus*,” but later placed in a new genus by Menner. Also described and illustrated (reconstructed line drawing) in Danil'chenko, 1980, pp. 19–20 and fig. 8. Type species for genus by original designation (Menner, 1949). **Clupeidae**.

†*Quisque* Jordan, 1920

†*Quisque gilberti* Jordan, 1920 [from Upper Miocene marine sediments of southern California]. Known by a few SU specimens (not examined here). Most of description in Jordan, 1921, p. 245. Evidently Jordan was not familiar with a wide variety of clupeomorph skeletons, because he gives as the diagnosis from †*Quisque* “the presence of very strong ventral scutes” (1921, p. 246). As shown by fig. 11, many different clupeomorphs have strong ventral scutes. There is no published picture of this species other than a restored drawing in Jordan showing few skeletal details. Type species for genus by original designation. **Clupeidae**.

†*Sahelinia* Arambourg, 1927

†*Sahelinia gregaria* (de Bosniaski, 1878) [from Upper Miocene marine deposits of Sicily, Italy and Oran]. Originally this name was indicated to be in “*Clupea*,” but Ar-

ambourg (1927, p. 31) found this species to be a dussumieriid, and placed it in a new genus. Several specimens are illustrated in Arambourg (1925, pl. 4, figs. 2, 3, 4, and 5; and 1920, pl. 5, figs. 9 and 10). Type species of genus. Erasmo, 1930, p. 32, and Leonardi, 1959, p. 124 retain this species in “*Clupea*.” Material at MNHN. **Clupeidae: Dussumieriinae**.

*Sardina* Antipa, 1905

†*Sardina necteodosciobanensis* Ciobanu, 1977 [from Oligocene marine deposits of Rumania]. No specimens were examined here, but the holotype (a well-preserved complete skeleton) is illustrated in pl. 9, fig. 1 of the type description. Material deposited at Muzeului de stiinte naturale, Piatra Neamt, Rumania. **Clupeidae**.

†*Sardina prisca* Danil'chenko, 1969 [from Miocene marine sediments of southern Russia]. No specimens were examined here, but the holotype is illustrated in original description. Also described in Danil'chenko, 1980, pp. 14–15. Many specimens in the Paleontological Inst., Acad. Sci., Moscow, USSR. **Clupeidae**.

*Sardinella* Valenciennes, 1847

†*Sardinella beogradensis* Anđelković, 1967 [from Miocene deposits of Yugoslavia]. No specimens were examined here, but an illustration of the type is in pl. 1 of original description. **Clupeidae**.

†*Sardinella brouweri* Beaufort, 1923 [from Miocene marine limestone deposits of South Celebes]. No specimens were observed here, but the type and only known specimen (lacking the anterior half of the head) is illustrated in the type description. **Clupeidae**.

†*Sardinella denticulata* Ciobanu, 1977 [from Oligocene marine deposits of Rumania]. No specimens were examined here, but the holotype (a nearly complete skeleton) is illustrated in pl. 8, fig. 1 of the type description. Material deposited at Muzeului de stiinte naturale, Piatra Neamt, Rumania. **Clupeidae**.

†*Sardinella engrauliformis* Danil'chenko, 1960 [from ?Oligocene or Miocene marine deposits of the Caucasus Mts., USSR]. No

- specimens were examined here, but three nearly complete specimens (including lectotype) are illustrated in Danil'chenko, 1960, pl. 19, figs. 1 and 2. Although Danil'chenko, 1960 cites Smirnov as the original author of this species name (†"*Clupea engrauliformis* Smirnov, 1935," from Upper Maikop deposits of the USSR), Smirnov's name is a junior homonym of †"*Clupea*" *engrauliformis* Liroy, 1866, from Monte Bolca, Italy (currently a *nomen dubium* but nevertheless an available name). Therefore, Smirnov's name is unavailable. Danil'chenko (1960) described (and designated a type specimen for) †*Sardinella engrauliformis*, and should be considered the first author of the name. Also described in Danil'chenko, 1980, p. 10. Several specimens are in the Paleontological Inst., Acad. Sci., Moscow, USSR. **Clupeidae.**
- †*Sardinella milanovskii* Menner, 1949 [from Pliocene marine deposits of Russia]. No specimens were examined here. Also described in Danil'chenko, 1980, p. 11, and described and illustrated in Gabelaya, 1976, pp. 19–21, fig. 1, pl. 1 figs. 1–4. **Clupeidae.**
- †*Sardinella perrata* Danil'chenko, 1970, in Iosifova and Danil'chenko, 1970 [from Miocene marine deposits of central Russia]. No specimens were examined here, but two specimens (including holotype) are illustrated in fig. 3 of original description. Also described in Danil'chenko, 1980, p. 11. **Clupeidae.**
- †*Sardinella rata* Danil'chenko, 1960 [from Tertiary marine deposits of the Caucasus Mts., USSR]. No specimens were examined here, but a nearly complete specimen (holotype) is illustrated in pl. 18, fig. 1 of original description. Also, reconstructed line drawing and additional description is in Danil'chenko (1980, pp. 8–9, fig. 4). Numerous specimens are deposited in the Paleontological Inst., Acad. Sci., Moscow, USSR. **Clupeidae.**
- †*Sardinella sardinites* (Heckel, 1850) [from Upper Miocene marine deposits of Croatia and Oligocene marine deposits of Poland]. Originally described in the genus "*Melleta*." Later (Gorjanović-Kramberger, 1884, p. 76; Woodward, 1901, p. 152; Jerzmańska, 1960, p. 31; Szymczyk, 1978, p. 394) described in *Clupea*, and most recently, described in *Sardinella* by Danil'chenko, 1980, p. 9. Represented by three nearly complete specimens at BMNH. Type and referred specimens are deposited at Court Museum, Vienna. **Clupeidae.**
- †*Sarmatella* Menner, 1949
- †*Sarmatella vucotinovici* (Kramberger, 1884) [from Upper Miocene deposits of Croatia, Yugoslavia]. Originally described in "*Clupea*." No specimens were examined here, but some material is illustrated in pl. 13, figs. 7 and 8 of original description. Also described in Danil'chenko, 1980, p. 14. Type specimen is deposited at University of Agram, Yugoslavia. Type species for genus by original designation (Menner, 1949). **Clupeidae.**
- †*Scombroclupea* Kner, 1863
- †*Scombroclupea "pinnulata"* Kner, 1863 [from Upper Cretaceous (Cenomanian) marine deposits of Yugoslavia]. Thought by most workers (i.e., Woodward, 1901; Erasmo, 1946) to be a subjective junior synonym of †*S. macrophthalma* (Heckel). †*Scombroclupea pinnulata* is the type species for the genus and the holotype is deposited in the University of Vienna. **Clupeomorpha: incertae sedis.**
- †*Scombroclupea macrophthalma* (Heckel, 1849) [from Upper Cretaceous (Cenomanian) marine limestone deposits of Lebanon and Yugoslavia]. Currently being studied by the author. Caudal skeleton (yet undescribed) difficult to examine because it is overlain by a massive uroneural somewhat resembling the stegural of certain osmerids. A common species represented in most major museum collections by specimens from Lebanon. This genus is easily distinguished by the series of separate finlets in the anal fin. Originally described in "*Clupea*," but this species is not a clupeoid. **Clupeomorpha: incertae sedis.**
- †*Scombroclupea ? murlii* Sahni and Choudhary, 1971 [from Lower Eocene marine deposits of Rajasthan, India]. Known only by three partial specimens (not examined here) deposited at Lucknow University, Museum of Geology, India. Description and illustrations are insufficient to determine if

this species actually belongs in †*Scombro-clupea*. **Clupeomorpha: *incertae sedis*.**

*Spratelloides* Bleeker, 1851

†*Spratelloides lemoinei* Arambourg, 1927 [from Miocene marine deposits of Oran, northern Africa]. This species is discussed above in text. Several specimens are deposited at MNHN and several of these are illustrated in Arambourg, 1927. Andelković's (1969, p. 134) placement of this species in the engraulid genus *Stolephorus* is clearly incorrect. Gaudant (1979) reports the occurrence of this species also in the Miocene of Italy. **Clupeidae: Dussumieriinae: Spratelloidini.**

†*Spratticeps* Patterson, 1970a

†*Spratticeps gaultinus* Patterson, 1970a [from Lower Cretaceous (Albian) sediments of Folkestone, England]. Known only from isolated braincases which are described in detail by Patterson, 1970a. This species has large prootic (but no pterotic) bullae, and the parietals are separated by the supra-occipital. All four known specimens are deposited in England (BMNH and Institute of Geological Sciences). Type species by original designation. **Clupeiformes: *incertae sedis*.**

†*Xenothrissa* Jordan, 1925

†*Xenothrissa aphrasta* Jordan, 1925 [from Upper Miocene marine sediments of southern California]. Thought by David (1943, pp. 120, 121) to be a subjective junior synonym of †*Ganolytes aratus* (= †*Diradias aratus* Jordan). Holotype is an incomplete skeleton illustrated in pl. 2 of original description and is deposited at SU. Type species by original designation. **Clupeidae.**

†*Xyne* Jordan and Gilbert, 1919

†*Xyne grex* Jordan and Gilbert, 1919 [from Upper Miocene marine sediments of southern California]. Discussed above and in David, 1943, pp. 89–92. According to David (1943) species of the genus †*Xyrinius* Jordan and Gilbert are subjective junior synonyms of this species. This species

is extremely abundant (though not usually well preserved) and can be found in most museum collections in North America. Type species for genus, by original designation. **Clupeidae.**

†*Xyne "fitgeri"* Jordan and Gilbert, 1920; a subjective synonym of †*Xyne grex* as explained by David (1943, p. 90) and implied by Jordan, 1921, p. 243). From Upper Miocene marine sediments of southern California, the holotype (illustrated in Jordan and Gilbert, pl. 5) is an SU specimen (not examined here). **Clupeidae.**

†*Xyrinius* Jordan and Gilbert, 1919

†*Xyrinius houshi* Jordan and Gilbert, 1919 [from Upper Miocene marine sediments of southern California]. According to David (1943, p. 90) this species may be a subjective junior synonym of †*Xyne grex*. The holotype (illustrated in Jordan and Gilbert, 1919, pl. 31, fig. 3) is deposited at SU. Originally described as a labrid (based only on a somewhat distorted, incomplete specimen). Type species of genus by original designation. **Clupeidae.**

†*Xyrinius barbarae* (Jordan and Gilbert, 1919) [from Upper Miocene marine sediments of southern California]. According to David (1943, p. 90) this species may be a subjective junior synonym of †*Xyne grex*. The holotype (illustrated in Jordan and Gilbert, 1919, pl. 9, fig. 3) should be at SU, but now appears to be lost. Jordan and Gilbert first described this species in the genus †*Ellimma*, but Jordan (1921) transferred it to †*Xyrinius*. **Clupeidae.**

†*Xyrinius elmodenae* (Jordan and Gilbert, 1919) [from Upper Miocene marine sediments of southern California]. According to David (1943, p. 90) this species may be a subjective junior synonym of †*Xyne grex*. The holotype (illustrated in Jordan and Gilbert, 1919, pl. 12, fig. 1) is at CAS. Jordan and Gilbert first described this species in the genus †*Ellimma*, but Jordan (1921) transferred it to †*Xyrinius*. **Clupeidae.**

The above list of fossil clupeomorphs includes 156 species described in over 50 genera; 36 of those genera (type indicated for each) contain only fossil species. Many other species which have been described as clu-

peomorphs are excluded from the above list for various reasons discussed in the above text, and in the section below.

COMMENTS ON SOME OTHER  
SPECIES NOT INCLUDED  
IN ABOVE LIST

Taxonomic names based only on scales, otoliths or other isolated fragments are not listed above because they are thought, at present, to be of relatively little use in phylogenetic studies (although when scales and otoliths are found associated with skeletons, they have as much potential as any other piece of the skeleton to contribute valuable character information). Some species not listed above which are based only on scales are:

- †“*Alosa*” *ganolytoides* David, 1946a
- †*Bramlettia chicoensis* (Cockerell, 1919)  
(monotypic genus of David, 1946b, originally described in the genus *Pomolobus*)
- †“*Clupea*” *grandisquama* (Steindachner, 1864) (originally described in the genus *Meletta*)
- †*Driverius cretaceus* David, 1946b (monotypic genus)
- †*Pseudotringus kreyenbagius* David, 1946a (monotypic genus)
- †*Wisslerius sardinelloides* David, 1946a (monotypic genus)

Some species not listed above which are based only on otoliths are:

- †“*Alosa*” *incisa* Stinton, 1977
- †*Archengraulis productus* Stinton, 1968
- †“*Clupea*” *bonii* Anfossi and Mosna, 1971
- †“*Clupea*” *gidjakensis* Pobedina et al., 1956
- †“*Clupea*” *gratus* Pobedina et al., 1956
- †“*Clupea*” *pulchra* Smigielska, 1966
- †“*Clupea*” *suzini* Pobedina, 1954
- †“*Clupea*” *tarchanicus* Pobedina, 1954
- †“*Clupea*” *testis* Koken, 1891
- †“*Clupea*” *trolli* Papp and Thenius, 1954
- †“*Clupea*” *weileri* Smigielska, 1966
- †“*Chirocentrus*” *exilis* Stinton, 1977
- †“*Coilia*” *planata* Stinton, 1962
- †“*Dussumieria*” *amussa* Stinton, 1977
- †“*Etrumeus*” *undatus* Stinton, 1977
- †“*Harengula*” *regularis* Stinton, 1977
- †“*Harengula*” *similis* Stinton, 1977
- †“*Ilisha*” *lerichei* Nolf and Capetta, 1980

- †“*Ilisha*” *nijsseni* Nolf and Steurbaut, 1979
- †“*Opisthonema*” *collatum* Stinton, 1977
- †“*Pomolobus*” *circularis* Stinton, 1977
- †“*Sardinella*” *extensa* Stinton, 1977
- †“*Sardinella*” *spatiosa* Stinton, 1977
- †“*Setipinna*” *retusa* Stinton, 1962
- †“*Stolephorus*” *furculus* Stinton, 1977
- †“*Stolephorus*” *productus* Stinton, 1977

It is recommended that descriptions based on such fragments should either not be given new species names (i.e., remain classified as *incertae sedis* at some higher taxonomic level) or that the new names be specially indicated so as not to disrupt classifications based on more complete fossil and Recent material (as †“<Genus *Clupeidarum*> *orbiculatus*” in Nolf and Capetta, 1980). The taxonomic literature will then be easier to review for broad phylogenetic studies. The genera, or genera-equivalent names †*Clupeidarum* [see Nolf, var. pub. and others] and †*Clupeiformorum* [see Gaemers and van Hinsbergh, 1978] are used exclusively for supposed clupeomorph species known only by otoliths. The many species described in these “taxa” [mostly in †*Clupeidarum* or †*Otolithus* (*Clupeidarum*)] are not listed in this paper.

Liroy (1866) ascribed the following names from Monte Bolca:

- †“*Clupea*” *cephalus*
- †“*Clupea*” *chrysosoma*
- †“*Clupea*” *denticiformis*
- †“*Clupea*” *engrauliformis*
- †“*Clupea*” *microcephala*
- †“*Clupea*” *minutissima*
- †“*Clupea*” *ophthalmica*
- †“*Clupea*” *polyachanthina*
- †*Ptericephalina elongata*
- †*Ptericephalina macrogastrina*
- †*Uropterina platyrachis*

These names are also listed in Blot, 1980. Liroy designated no type specimens and published no illustrations for these names, and his brief descriptions are insufficient to permit recognition of the taxa that the names apply to. Therefore, these names are currently left as *nomina dubia*.

Arambourg (1925) found the following species, originally described in “*Clupea*,” to be myctophiforms:

- †“*Clupea*” *bosniaskii* Bonomi, 1896
- †“*Clupea*” *ecnomi* Sauvage, 1873
- †“*Clupea*” *macrocerca* Bonomi, 1896
- †“*Clupea*” *megapteryx* Sauvage, 1873
- †“*Clupea*” *meneghinii* Capellini, 1878
- †“*Clupea*” *microsoma* Sauvage, 1870a
- †“*Clupea*” *modainensis* Bonomi, 1896
- †“*Clupea*” *opisthopteryx* Sauvage, 1873
- †“*Clupea*” *saulos* Sauvage, 1870
- †“*Clupea*” *sauvagei* Capellini, 1878
- †“*Clupea*” *trinacridis* Sauvage, 1873
- †“*Clupea*” *xenophanis* Sauvage, 1873
- †“*Clupea*” *zanclea* Sauvage, 1873
- †*Sardinella caudata* Sauvage, 1870 = †“*Clupea*” *caudata* (Sauvage, 1873)

Arambourg (1927, p. 42) also found †“*Diplomystus*” *tenuissimus* de Stefano, 1918 to be myctophiform.

These specimens are all from Miocene marine deposits of Sicily and Italy. Erasmo (1930) disagreed with Arambourg and thought that some of these species belonged in *Alosa*. I prefer to follow the views of Arambourg here. The type and associated specimens for most of these species were examined (some on the basis of photographs) here, and found to be distorted, very incomplete specimens which provide no convincing evidence to warrant their placement in Clupeomorpha. Similarly, the following species were found to be indeterminable fragments not necessarily assignable to Clupeomorpha:

- †“*Clupea*” *glyptopoma* Franceschi, 1922
- †“*Clupea*” *lawleyi* Capellini, 1878
- †“*Clupea*” *lesinensis* Kramberger, 1886
- †“*Clupea*” *lundgreni* Davis, 1890
- †“*Clupea*” *praesardinites* (Rzehak, 1881) (originally described in the genus *Meletta*).

Woodward (1901, p. 153) also mentions †“*Clupea*” *leptostea* as a name written by Agassiz on a BMNH specimen from Monte Bolca. This name is published without description in Agassiz (1835, p. 306 and 1844, vol. 5, pt. 2, p. 120) and regarded as the type for the genus †*Ptericephalina* Lioy 1866 (discussed above in this section). Eastman (1905, p. 11) described this species as †*Channoides leptostea* Eastman (ex. Ag. Mss.). Specimens assigned to †*C. leptostea* by Woodward (1901) and Eastman (1905) have been found to be

different species. One specimen (BMNH 37227) attributed to †*Clupea leptostea* (Woodward, 1901, p. 153) is identified here (fig. 17E) as a dussumieriine. Other specimens assigned to †*Clupea leptostea* or †*Channoides leptostea* have been found to be ostariophysans (Patterson, 1984b).

Several fossil herrings were originally described in the Recent genus, *Meletta* (a junior synonym of *Sprattus*—see Whitehead, 1967a, p. 20). Woodward transferred all of these species to “*Clupea*,” and they are tentatively listed that way above. Woodward also removed the so-called †“*Clupea*” *laticauda* Pictet, 1850, from Clupeomorpha; he first placed it in †Enchodontidae (1901, p. 158), and later assigned it to a new genus, †*Hakelia* (1942b, p. 554). Woodward (1901, p. 158) also referred to †“*Clupea*” *goldfussi* Agassiz, 1844 as “an unknown fish from the neighbourhood of Bingen.”

The following monotypic genera of Jordan and Gilbert (originally described as “dussumieriids” and an engraulid) were found by David (1943) and others not to be clupeomorphs:

- †*Quaestia* Jordan and Gilbert, 1919
- †*Rhomurus* Jordan, 1919
- †*Sternbergia* Jordan and Gilbert, 1925
- †*Lygisma* Jordan and Gilbert, 1919
- †*Engraulites* Jordan and Gilbert, 1925 (in Jordan, 1925)
- †*Smithites* Jordan and Gilbert, 1919

The species of these six genera were all described from Miocene deposits of California. Three additional generic names in the literature are applied to †*Smithites* Jordan and Gilbert: †*Jorbertia* White and Moy-Thomas, 1941; †*Jobertina* Fowler, 1958, non Pellegrin, 1908; and †*Hayina* Fowler, 1958. White and Moy-Thomas (1941) substituted †*Jorbertia* for *Smithites* which was preoccupied by a mollusk genus (Fowler, 1958). Fowler evidently misread the White and Moy-Thomas name, thought it was preoccupied by †*Jobertina* Pellegrin (a characoid fish), and substituted the name †*Hayina*.

†“*Clupea*” *gaudyri* Pictet and Humbert, 1866, from the Cenomanian of Lebanon (placed in the genus †*Scombroclupea* by Woodward, 1901) was redescribed in detail

and shown to be a salmoniform, by Patterson (1970b). Patterson placed this species in a new monotypic genus, †*Gaudryella*. In the same paper, Patterson (1970b, p. 289) discussed †“*Scombroclupea*” *scutata* Woodward, 1908 (from Neocomian marine deposits of Brazil). Woodward (1942) placed this species in a new monotypic genus, †*Scombroclupoides*, and considered it to be a clupeoid because he found traces of an abdominal scute. Patterson found the so-called “abdominal scute” to be the front part of the left opercle and subopercle, and noted that there was no evidence to indicate that this species was a clupeomorph.

No evidence could be found to warrant inclusion in Clupeomorpha of several other genera, including: †*Pseudoberyx*, †*Histiothrissa*, and †*Halecopsis* (all discussed, with references, in Woodward, 1901; and †*Halecopsis* discussed also in Patterson, 1984a, p. 134); †*Neohalecopsis* Weiler, 1928 (discussed in Patterson, 1984a, p. 134); †*Mesoclupea* Ping and Yen, 1933 (also redescribed in Chang, 1963); †*Jhingrania* Misra and Saxena, 1964; †*Iquius* Jordan, 1919b; †*Paleoclupea* Dante, 1942; †*Crossognathus* Pictet, 1858

(discussed in Patterson and Rosen, 1977, pp. 131–135); and †*Clupeopsis* Casier, 1946. Likewise, †*Quisque bakeri* Jordan, 1922, does not appear to be a clupeomorph. These taxa (described as “clupeoids” by various authors) should all be excluded from Clupeomorpha. I was unable to make a determination on †*Audenaerdia* Taverne, 1973 based on illustrations there, and was unable to see any specimens or detailed photographs of this species.

The fossil record of Engrauloidea (anchovies) is extremely sparse, and only one of the described species (†*Engraulis macrocephalus*) known here was adequately demonstrated to belong to that group. Some [e.g., †“*Engraulis*” *evolans* (Blainville, 1818)—discussed above] do not even belong in Clupeomorpha. Other species (†“*Engraulis*” *brevipinnis* Heckel, 1853b and †“*Engraulis*” *longipinnis* Heckel, 1853b) also appear to be misclassified as engraulids. A second true fossil anchovy species represented by nearly complete skeletons is described by Grande and Nelson (in press). Grande and Nelson also review all known species which have been described as fossil engraulids and discuss further the anomalous scarcity of fossil anchovies.

## SUMMARY AND CONCLUSIONS

This study of the osteology and interrelationships of clupeomorph fishes used an extremely large and diverse collection of clupeomorph skeletons. This made possible not only a very broad survey for new synapomorphies, but also a more complete testing of synapomorphic characters previously proposed on the basis of smaller, less complete study samples. The skeletal anatomy of two Recent clupeomorph species illustrated in the appendix are meant to act as a reference for future descriptive papers on clupeomorph skeletal anatomy. Much of the meristic and some of the morphological information surveyed here is summarized in the 20 tables of the text; and the characters thought to be synapomorphies will be briefly summarized below. For more detailed explanation of the synapomorphies (or group diagnostic characters) see the systematic discussion sections above. The subgroups contained in the taxa discussed below are given in the cladograms

in figures 1A, 9, 14, 18, and 21, and character numbers below correspond to numbers in those cladograms. Based on the results of this survey, I propose the following classification and characterization.

**Superorder Clupeomorpha**—clupeocephalans which have:

1. one or more abdominal scutes, each primitively consisting of a single (unpaired) element which crosses the ventral midline of the fish;
2. an otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and then expands to form ossified bullae in the prootic and usually also in the pterotic;
3. supratemporal commissural sensory canal primitively passing through parietals and supraoccipital.

Clupeomorpha contains two subgroups here: Division 1 (including only one species,

†*Erichalcis arcta*) and Division 2 (containing all other known clupeomorphs).

**Clupeomorpha Division 2**—clupeomorphs which have:

4. hypural 2 fused with the first ural centrum, and an autogenous first hypural;
5. a well-defined pre-epiotic fossa;
6. dorsal scutes (at least primitively) with a median keel.

Clupeomorpha Division 2 contains three subgroups here: †*Ellimmichthyiformes* (including only the genera †*Ellimmichthys* and †*Diplomystus*); an unnamed group containing the single species †*Armigatus brevissimus* (considered a group here only because no evidence could be found to include it in †*Ellimmichthyiformes* or *Clupeiformes*, but it was found to be a member of *Clupeomorpha* Division 2); and *Clupeiformes* (containing all other members of *Clupeomorpha* Division 2). These three groups presently represent an unresolved trichotomy within *Clupeomorpha* Division 2.

**Order †Ellimmichthyiformes**—Division 2 clupeomorphs which have:

7. a peculiar dorsal scute morphology (see above).

This order contains one species of †*Ellimmichthys* and four species of †*Diplomystus*. As shown by Grande, 1982a, several species must be removed from the genus †*Diplomystus* to make it monophyletic and thus useful for systematic studies. †*Diplomystus* is also diagnosed by a unique dorsal scute morphology (character 8 described above and in Grande, 1982a).

**Order Clupeiformes**—Division 2 clupeomorphs which have:

9. a recessus lateralis;
10. the parietals completely separated (medially) by the supraoccipital; and
11. no berycyform foramen from the anterior carotohyal.

*Clupeiformes* contains two subgroups here: *Denticipitoidei* (containing two monotypic genera—one fossil) and *Clupeoidei* (containing the rest of the *Clupeiformes*).

**Suborder Denticipitoidei**—clupeiforms which have:

12. odontodes (teeth) covering the dermal bones of the skull; and

13. the number of uroneurals in caudal skeleton reduced to only one.

Several other skeletal features unique to denticipitoids are listed in Greenwood, 1968.

**Suborder Clupeoidei**—clupeiforms which have:

14. a fusion of the first uroneural with the first preural centrum;
15. a reduction in relative size of the first ural centrum;
16. most or all of the lateral line scale canals lost;
17. a separation of the parhypural from the first ural centrum (except for *Dussumieria* and *Etrumeus* where fusion is probably secondary and derived for *Dussumieriini*).

Also derived for *Clupeoidei* is the space between hypural 1 and ural centrum 1 (in other clupeomorphs hyp<sub>1</sub> articulates with u<sub>1</sub>). *Clupeoidei* contains three subgroups here (an unresolved trichotomy): *Engrauloidea*, *Pristigasteroidea*, and *Clupeoidea*.

**Superfamily Engrauloidea**—*Clupeoidei* which have:

18. a suspensorium that is inclined obliquely backward; and
19. an overhanging snout with the mesethmoid projecting in advance of the vomer.

**Superfamily Pristigasteroidea**—*Clupeoidei* which have:

20. vertically or anterodorsally inclined predorsal bones;
21. the absence of the interlobar notch in the third hypural.

Nelson (1967a) also considered the peculiar type of basihyal dentition of this group as possibly unique among teleosts. Within *Pristigasteroidea*, the interrelationships are in need of further study. The genus *Ilisha* is not monophyletic and should be reexamined and revised. Some subgroups of *pristigasterides* have characters that appear to be unique, at least among clupeomorphs, such as **Pristigastriidae** (as used here) which all have a bony process on the first pleural rib which articulates with the shoulder girdle. *Pristigasterides* are still under study by the author.

**Superfamily Clupeoidea**—*Clupeoidei* which have:

22. a relatively large pleural rib to preural vertebrae ratio (thought to reflect a general trend of increasing relative abdominal cavity size in the group).

This trend has also occurred (convergently) in some specialized members of Engrauloidea. Clupeoidea contains two subgroups: Chirocentridae (with one genus and two species) and Clupeidae (containing all the rest of Clupeoidea).

**Clupeidae** is unique among clupeomorphs in having two rodlike postcleithra. Within Clupeidae, two subgroups can be osteologically characterized (Dussumieriinae and Pellonulinae). Most of the rest of Clupeidae ("Dorsomatinae," "Alosinae," and "Clupeinae") may be found to be characterized by the presence of mediopharyngobranchials, but the gill arches have yet to be thoroughly surveyed in the study sample. The interrelationships of Clupeidae are still under study by the author. No valid osteological characters diagnostic of Alosinae, Dorosomatinae, or Clupeinae (as those groups have traditionally been defined) could be found here.

The subfamily **Dussumieriinae** is unique in having a peculiar, unkeeled, W-shaped pelvic scute. Within Dussumieriinae there are two subgroups: Dussumieriini (containing *Dussumieria* and *Etrumeus*) and Spratelloidini (containing *Spratelloides* and *Jenkinsia*).

The tribe **Dussumieriini** contains those dussumieriids which have an extremely high number of branchiostegal rays, and a fusion of the parhypural to preural centrum 1.

The tribe **Spratelloidini** contains those dussumieriids which have an expansion of the fourth hypural, a reduction in number of epurals to one, a fusion of the first ural centrum to the first preural centrum, and a reduction of the number of infraorbital bones to five.

The subfamily **Pellonulinae** is problematical. This group has traditionally been defined as including those clupeids lacking an anterior supramaxillary bone. The problem is that some dussumieriines and Old World dorosomatines also lack the anterior supramaxillary (outside Clupeidae and within Clupeomorpha some engrauloids also lack the

anterior supramaxillary). If we accept the lack (or loss) of this bone as being independently derived for the Pellonulinae (character m above, as traditionally defined), then there appears to be a large subgroup (unnamed here) within the subfamily which can be defined by the fusion of the first ural centrum with the first preural centrum (character o above). This group would exclude only three Recent and one fossil pellonuline genera, and could itself be subdivided into two subgroups: Pellonulini (containing about 12 genera) and Ehiravini (containing 5 genera).

The tribe **Pellonulini** is characterized by a peculiar arrangement of the postcleithra (character p above), and includes the monotypic genus *Congrothrissa* (originally described in its own monotypic family, "Congothrissidae"). The tribe **Ehiravini** is characterized by the morphology of the sensory openings to the recessus (character q above), and contains a subgroup (Division A here) characterized by the possession of an anal finlet.

The monophyly of the traditional clupeid groups "Alosinae," "Dorosomatinae," and "Clupeinae" as they have been defined is thought to be doubtful. No valid osteological characters could be found for them and they are used here only as groups of convenience. As explained above, there may be a monophyletic group containing most of the members of these three groups, characterized by the presence of a mediopharyngobranchial, but this problem is still under study.

Many fossil clupeomorphs can more easily be reviewed, redescribed, and more accurately classified with the comparative skeletal information compiled here in the form of cladograms, tables, and line drawings. The state of the literature on nearly complete fossil clupeomorph species has been relatively inadequate, partly because many of the paleontologists who have worked on fossil clupeomorphs have been reluctant or unable to examine thoroughly the Recent fishes, and also because many neoichthyologists are reluctant or unable to work with fossil material. Fishes are fishes, whether they are fossil or Recent species; therefore broad systematic studies of any taxonomic group should con-



tain both Recent and adequately preserved fossil species. It is the opinion of the author that, in general, the more taxa that are examined, the more confident a systematist can be of his character information (i.e., the more taxa included in the study sample, the more tests he has of the structure of his cladogram and the distribution of characters on it). Recent material (if available) will generally be more useful than fossil material in systematic studies of major group intrarelationships, because of one main practical (nontheoretical) reason—Recent material is always, and without exception, better preserved (and therefore, easier to work with) than fossil materials. The descriptive work of a paleontologist is harder than that of a neontologist (if the paleontologist is working with whole animals) because he may have to examine hundreds of fossil specimens to extract the osteological information that the neontologist can get from a single Recent specimen. And no fossil has the complete preservation of all the soft anatomy as Recent specimens do.

By using skeletal characters to diagnose monophyletic clupeomorph groups, investigators can incorporate fossils into the classificatory system with reasonable accuracy.

Those fossil species that were found to belong in Clupeomorpha (over 150 nominal species) are listed above. Many other fossils originally described as “clupeids” or “clupeoids” were found not even to be clupeomorphs. Most fossil taxa classified within Clupeomorpha, particularly those without scutes, should be reevaluated (and redescribed). The paleontologist can properly classify or diagnose fossil teleosts (such as clupeomorphs) only with a broad knowledge of the Recent fauna. Continued study is needed to resolve fully the interrelationships of Clupeidae, but the cladograms and character explanations here demonstrate that a phylogenetic classification of clupeomorph fishes based on the skeleton is feasible.

The major phylogenetic problems left among clupeomorph fishes (if we consider the largest problems to be those groups with the largest number of unresolved taxa) are seen here as (1) solving the interrelationships of Engrauloidea; (2) discovering the relationships of the members of Clupeinae, Alosinae and Dorosomatinae; and (3) testing the cladograms here based on the skeleton, by doing similar comprehensive studies of the muscle, internal organ, and nervous systems of clupeiform fishes.

## APPENDIX: THE OSTEOLOGY OF *ODAXOTHRISSA* AND *DOROSOMA*

The osteology of two clupeid species is illustrated here. Although many of the following plates are referred to earlier in the text, they are presented here as two sets. In most cases, cartilages have been omitted (unless stated otherwise in caption).

The first species (figs. 26–38) is the African pellenuline, *Odaxothrissa vittata* Regan, illustrated from drawings of AMNH 5890 sw (sl = 125 mm). The second species (figs. 39–

51) is the North American dorosomatine, *Dorosoma cepedianum* (Lesueur), illustrated from drawings of AMNH 37214 sw (sl = 77 mm).

It is hoped that these two sets of drawings will add to the descriptive information on these two species, will demonstrate some of the osteological variation between clupeoid taxa, and will be used as a general reference for clupeid skeletal anatomy.

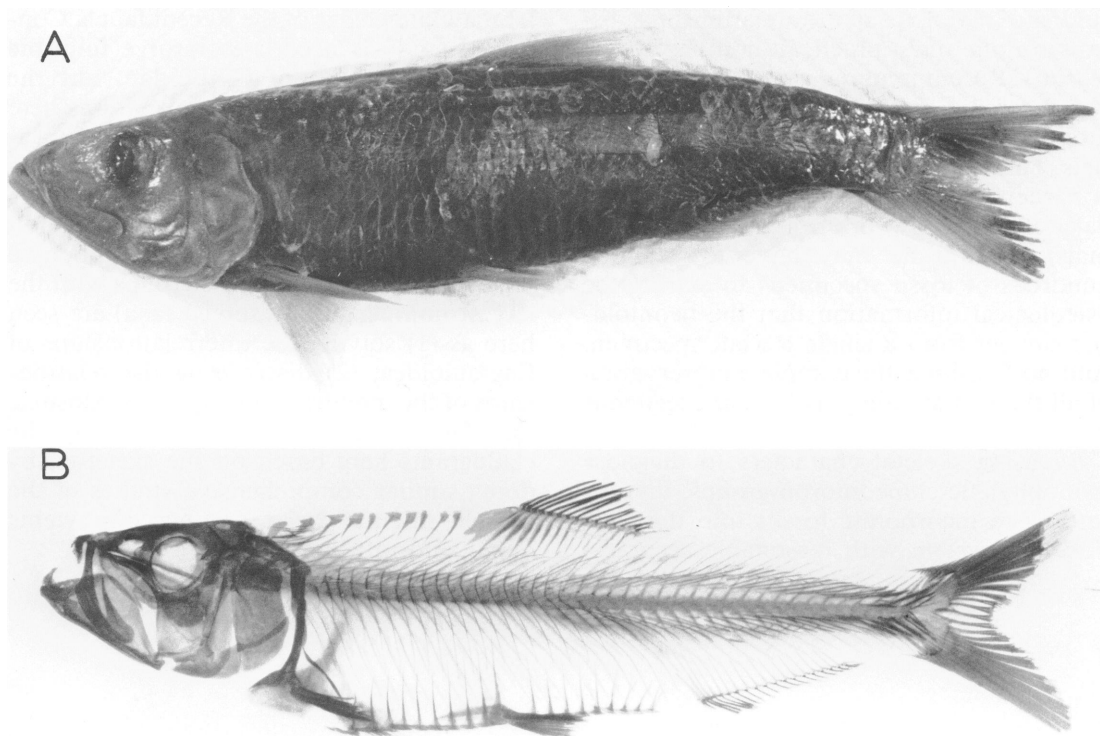


FIG. 26. *Odaxothrissa vittata* Regan, 1917 (AMNH 5890) (sl = 125 mm). (A) Preserved; (B) the same specimen cleared and stained, with hypobranchial apparatus and right lateral facial bones removed. Anatomical abbreviations used in the following diagrams (figs. 27–38) of this species are explained on pages 242–243.

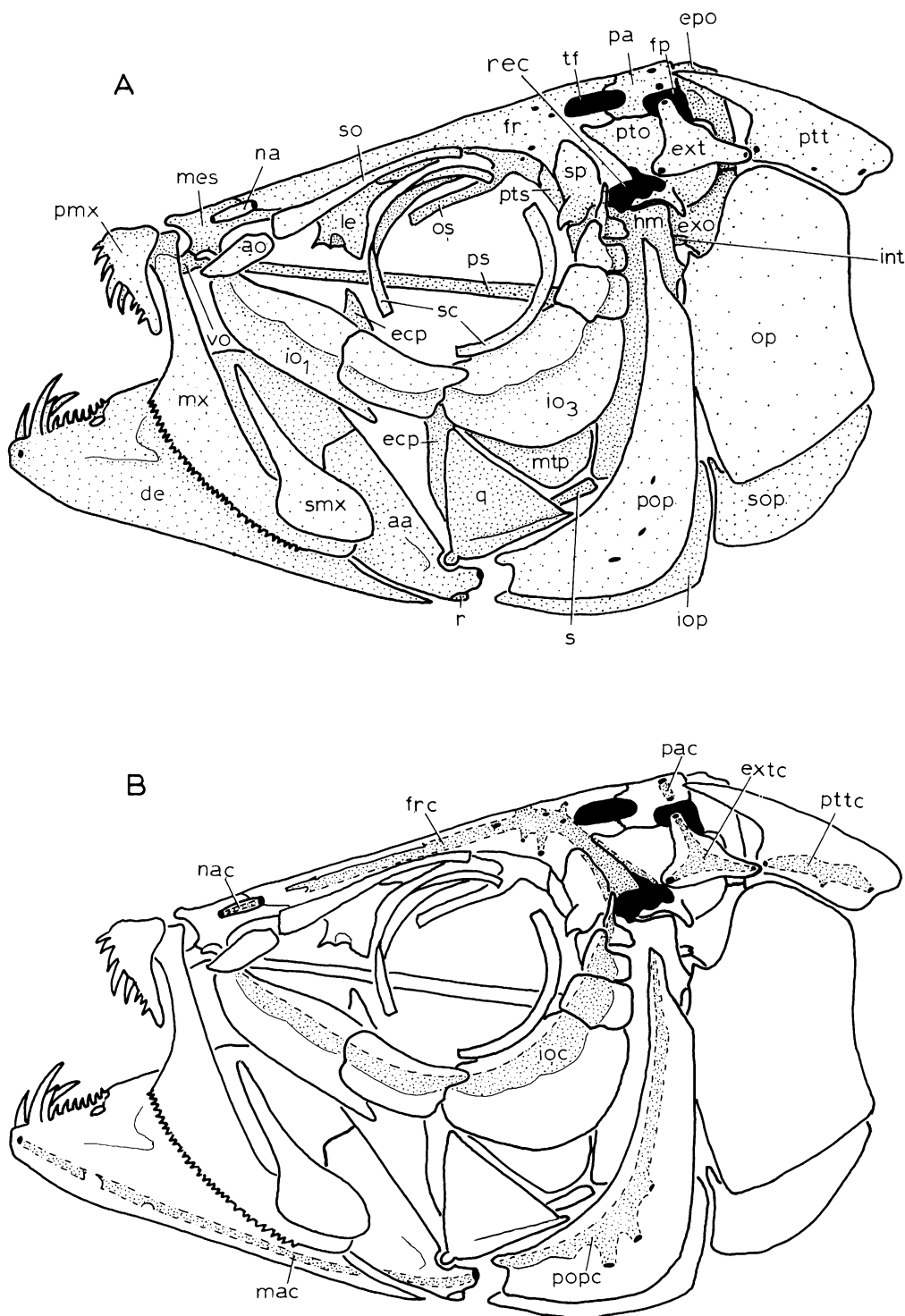


FIG. 27. *Odaxothrissa vittata*. (A) Lateral view of skull; (B) same, showing sensory canals (stippled). Note the small dermosphenotic (io<sub>6</sub>), lying anteroventral to the common opening to the recessus.

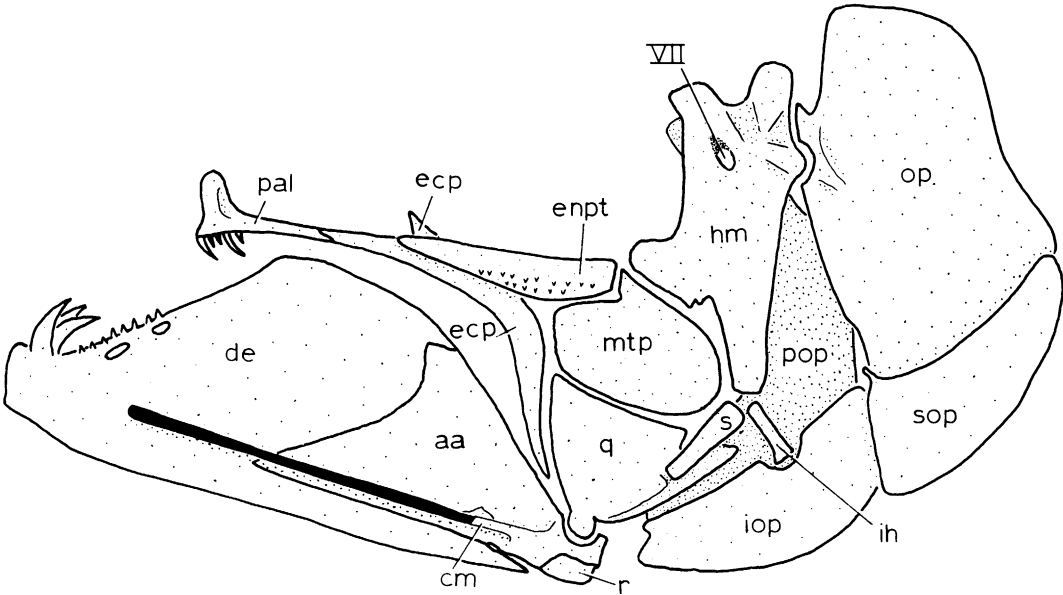


FIG. 28. *Odaxothrissa vittata*, medial view of the lower jaw, opercular bones, and suspensorium. Coronomeckelian cartilage in black.

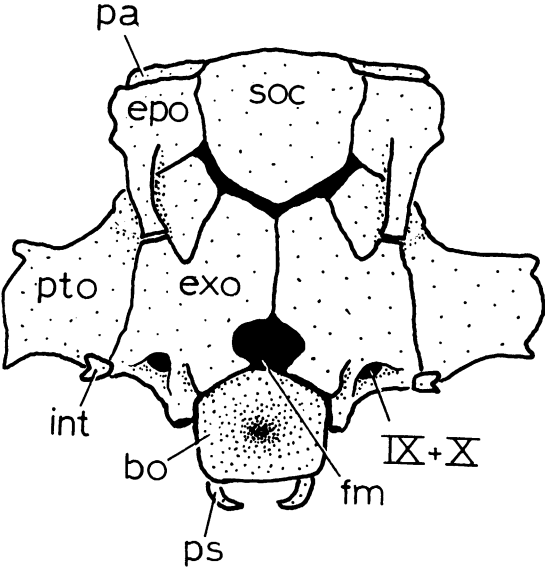


FIG. 29. *Odaxothrissa vittata*, posterior view of cranium. Condyle for first vertebra consists entirely of the basioccipital (denticipitoids were the only clupeiforms observed here to have a tripartite condyle as shown in Greenwood, 1968, fig. 13).

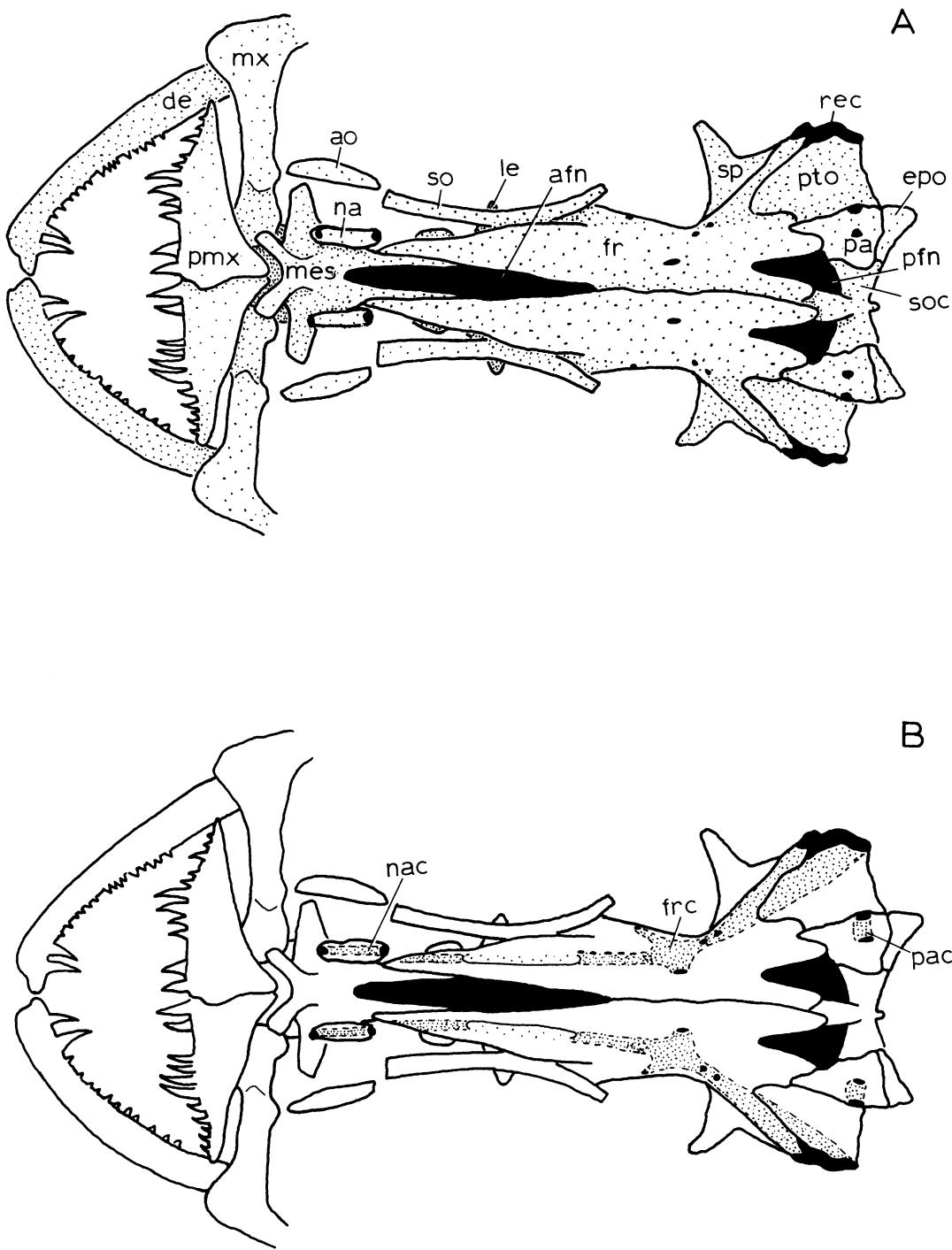


FIG. 30. *Odaxothrissa vittata*. (A) Dorsal surface of skull roof, with part of upper and lower jaw, nasals, antorbitals, and supraorbitals; (B) same, showing sensory canals (heavy stipple = enclosed canals, light stipple = open canals). Jaws slightly flattened dorsoventrally.

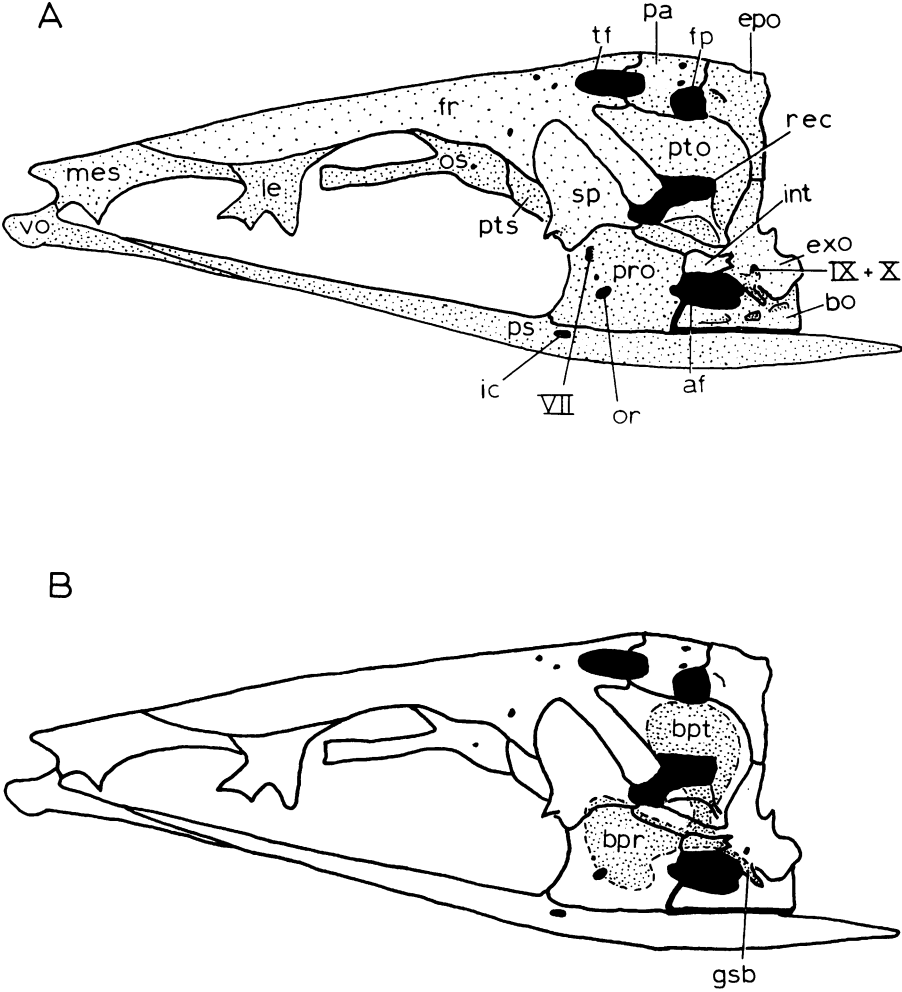


FIG. 31. *Odaxothrissa vittata*. (A) Lateral view of cranium; (B) same, showing bullae (stippled) as seen through bone.

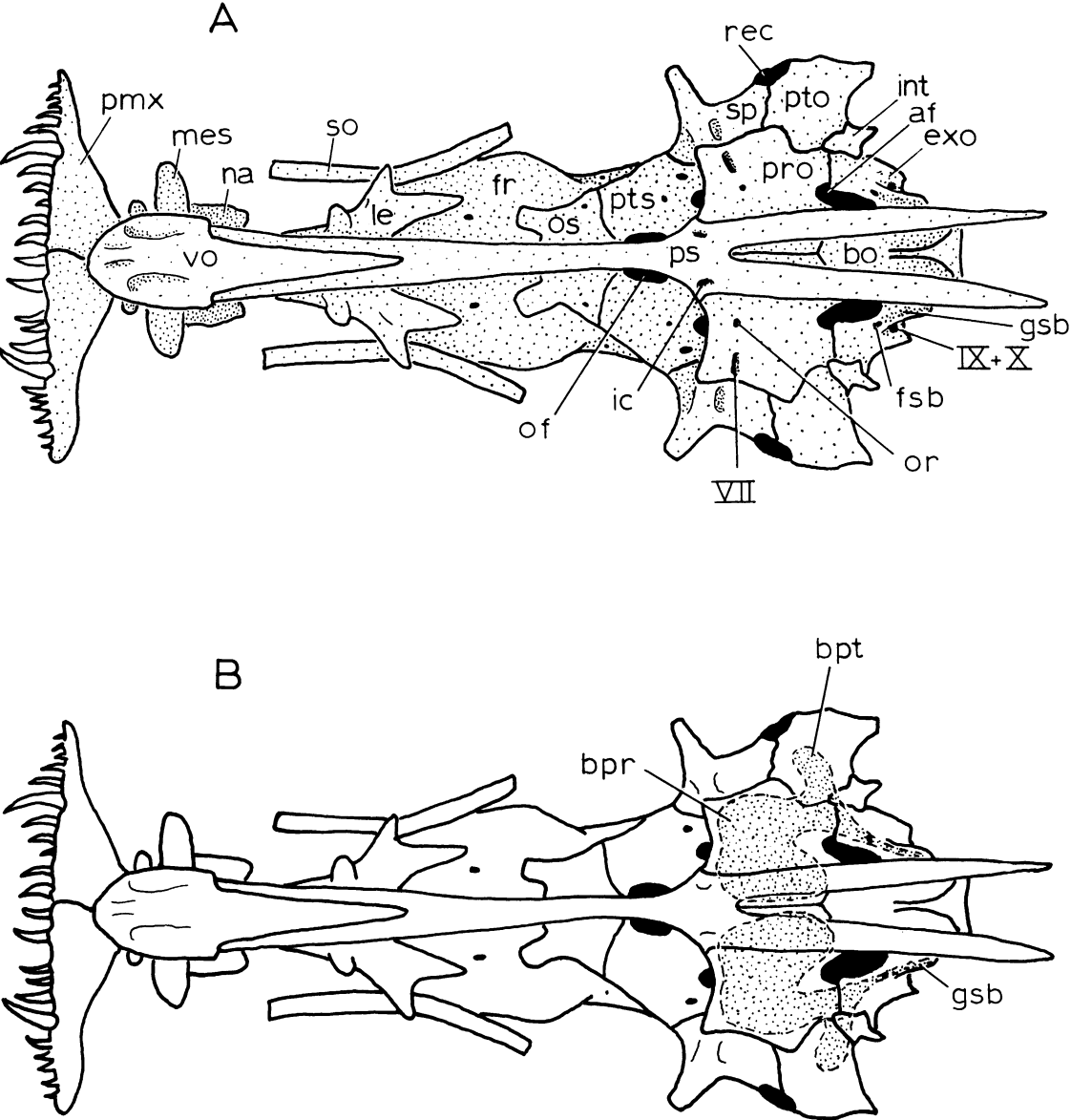


FIG. 32. *Odaxothrissa vittata*. (A) Ventral view of cranium; (B) same, showing position of bullae (stippled) as seen through bone.

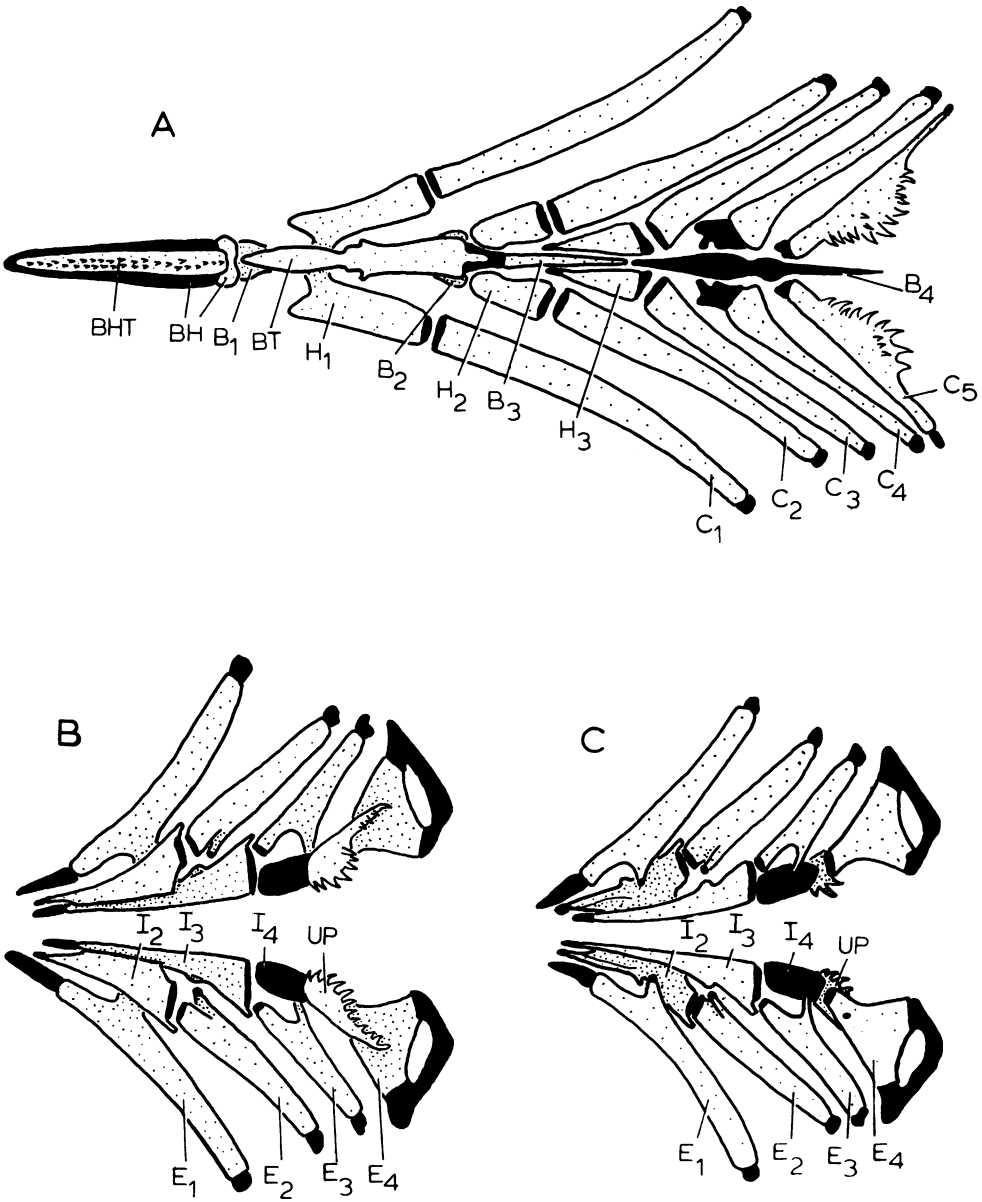


FIG. 33. *Odaxothrissa vittata*, gill arches (cartilage in black). Drawn flattened under a glass slide in glycerine. (A) Oral surface of ventral arches; (B) oral surface of dorsal arches; (C) aboral (dorsal) surface of dorsal arches.



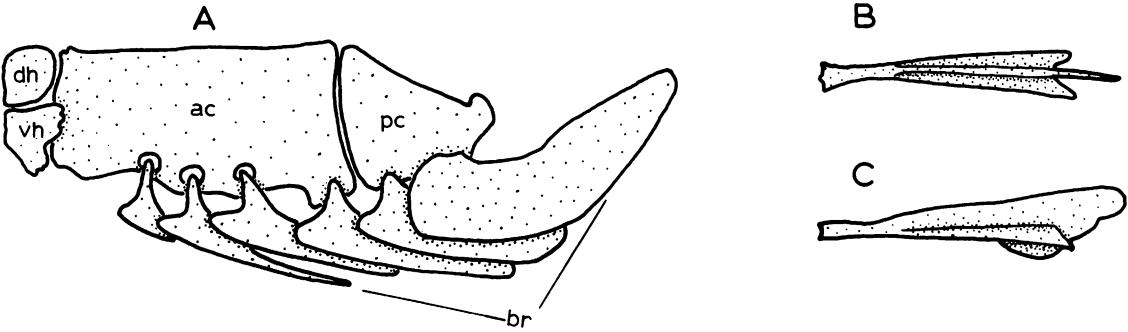


FIG. 34. *Odaxothrissa vittata*. (A) Lateral view of branchiostegal support and rays; (B) dorsal view of urohyal; (C) lateral view of urohyal.

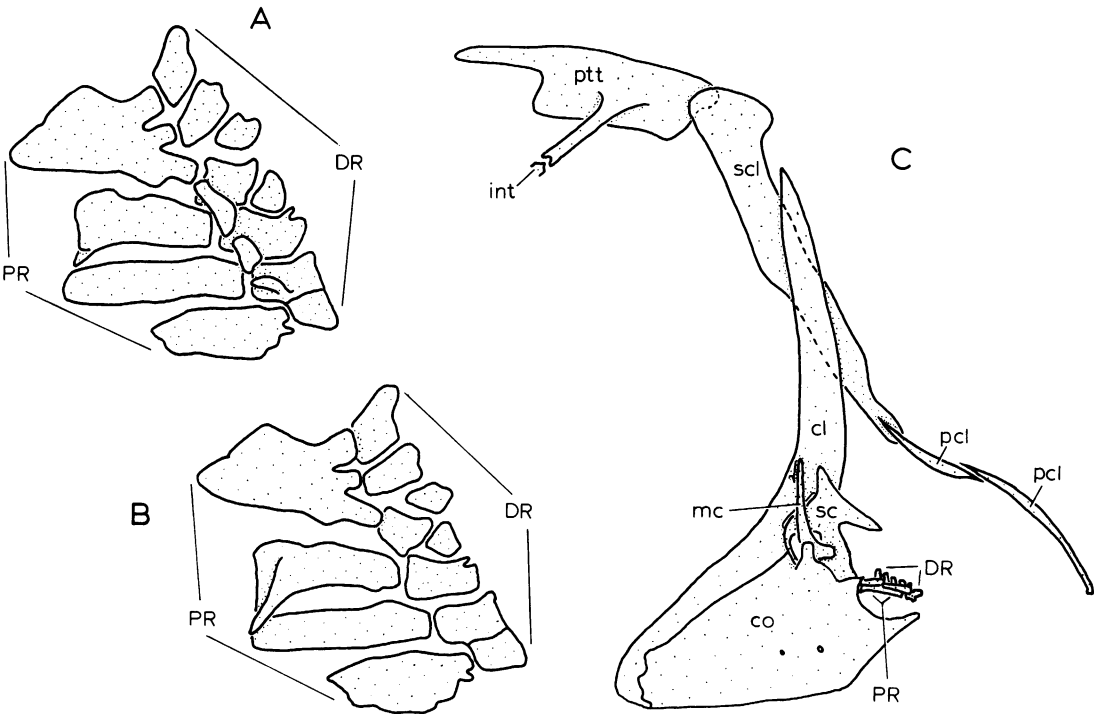


FIG. 35. *Odaxothrissa vittata*. (A) Pectoral radials, enlarged from C, oblique dorsolateral view; (B) pectoral radials enlarged from C, oblique dorsomedial view; (C) pectoral girdle, medial view, finrays omitted. Anterior for A and B points to upper left.

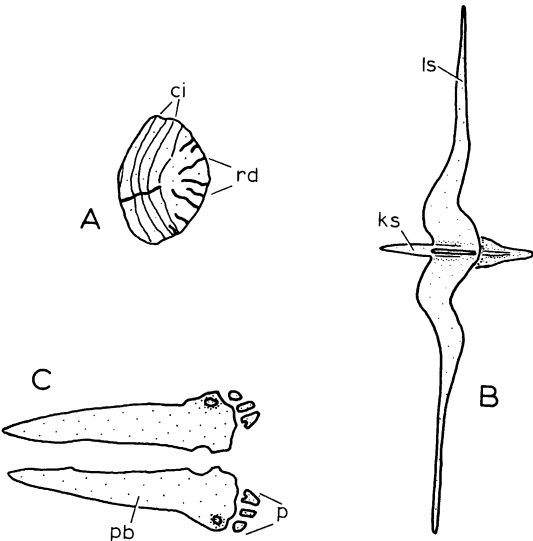


FIG. 36. *Odaxothrissa vittata*. (A) Flank scale; (B) ventral view of pelvic scutes flattened under a glass slide; (C) dorsal view of both pelvic girdles (right and left side separated at median contact).

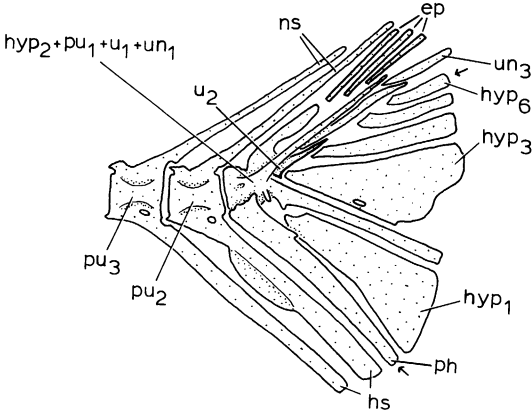


FIG. 38. *Odaxothrissa vittata*, caudal skeleton. Arrows point to articulation with uppermost and lowermost principal fin rays.

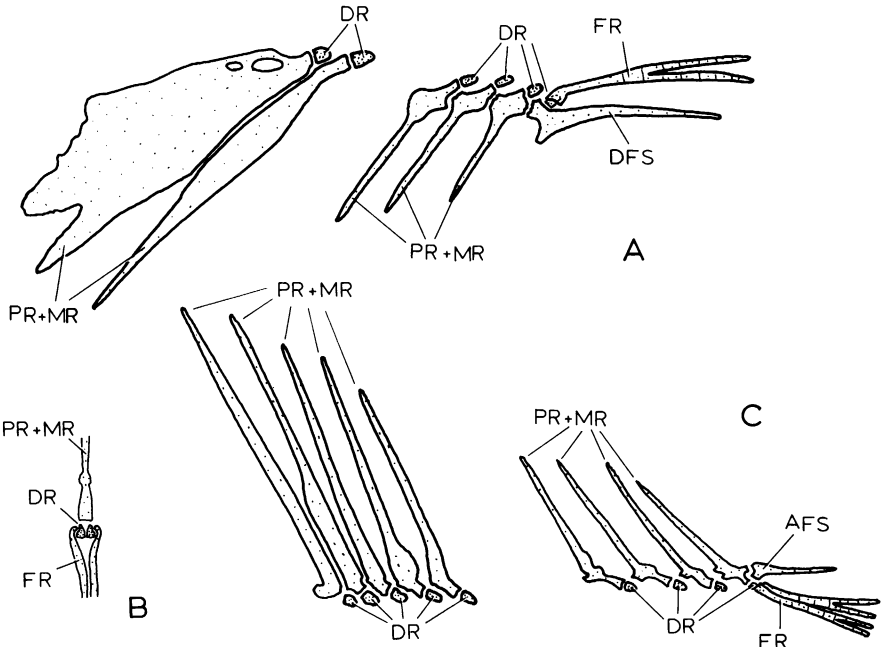


FIG. 37. *Odaxothrissa vittata*, median fin ray supports (most of the fin rays omitted). (A) Lateral view of anteriormost and posteriormost dorsal fin ray supports; (B) anterior view of the base of the eighth anal fin ray; (C) lateral view of anteriormost and posteriormost anal fin ray supports.

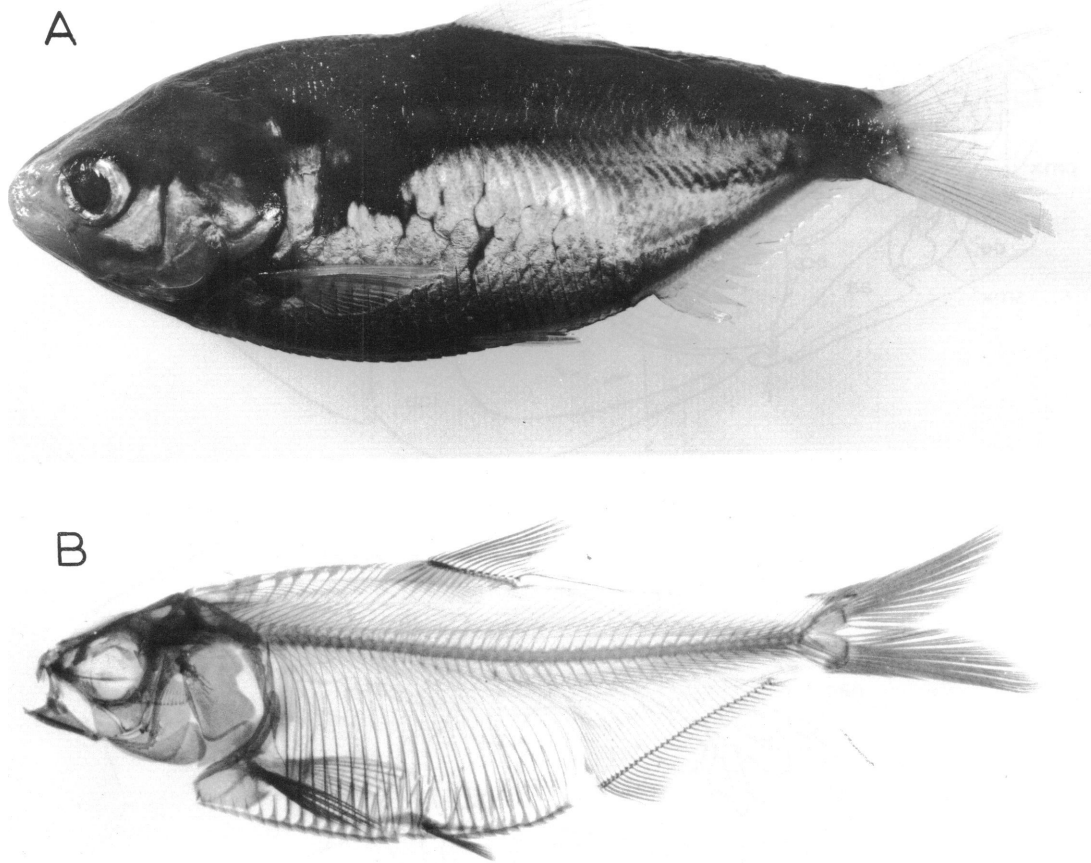


FIG. 39. *Dorosoma cepedianum* (Lesuer) (AMNH 37214) (sl = 77 mm). (A) Preserved; (B) the same specimen cleared and stained with hypobranchial apparatus and right lateral facial bones removed. Anatomical abbreviations used in the following diagrams (figs. 40–50) can be found on pages 242–243.

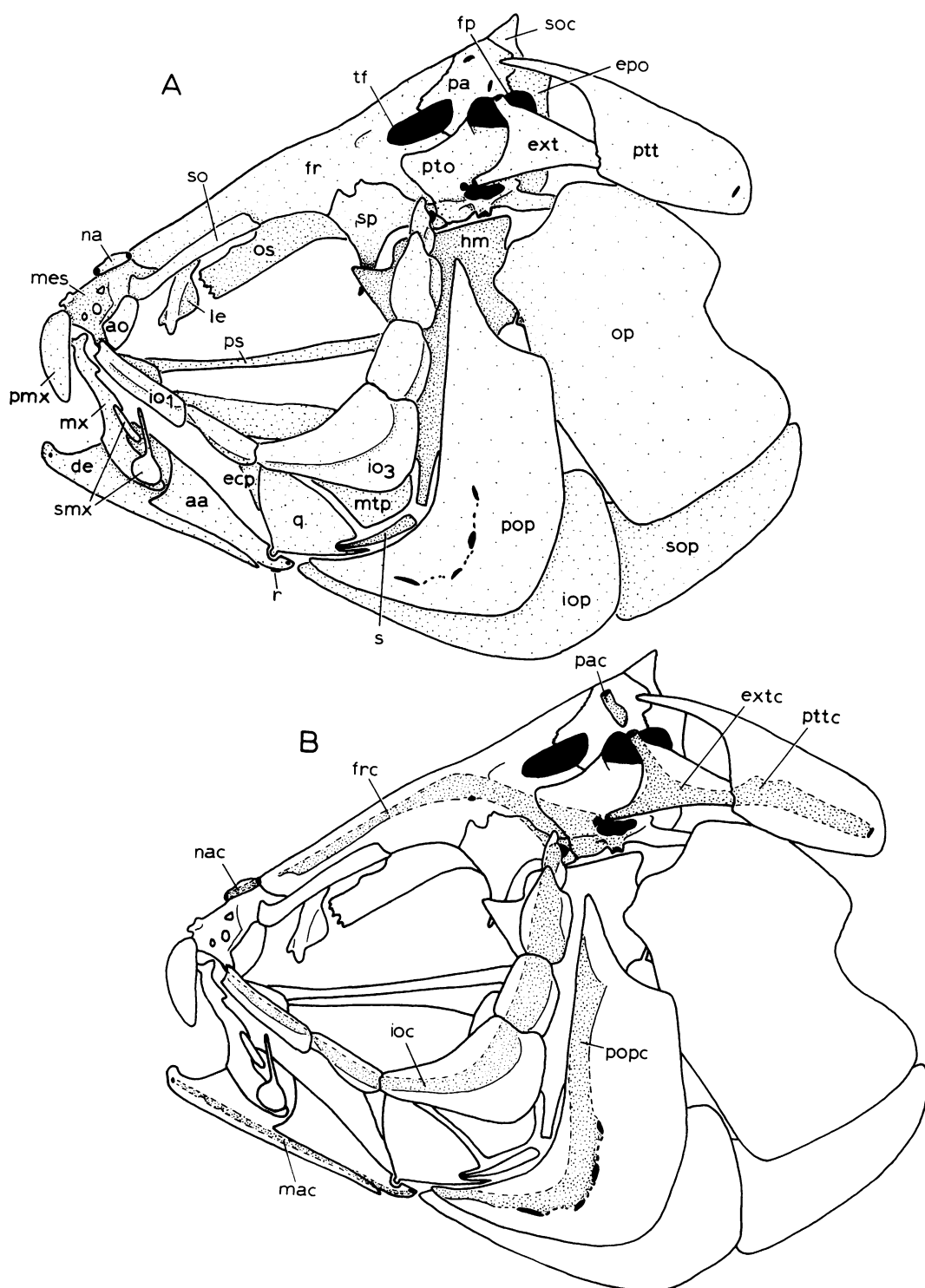


FIG. 40. *Dorosoma cepedianum* (sclerotic bones removed). (A) Lateral view of skull; (B) same, showing sensory canals (stippled). Note the small dermosphenotic (=io<sub>6</sub>), lying ventral to the opening to the recessus for the infraorbital canal.

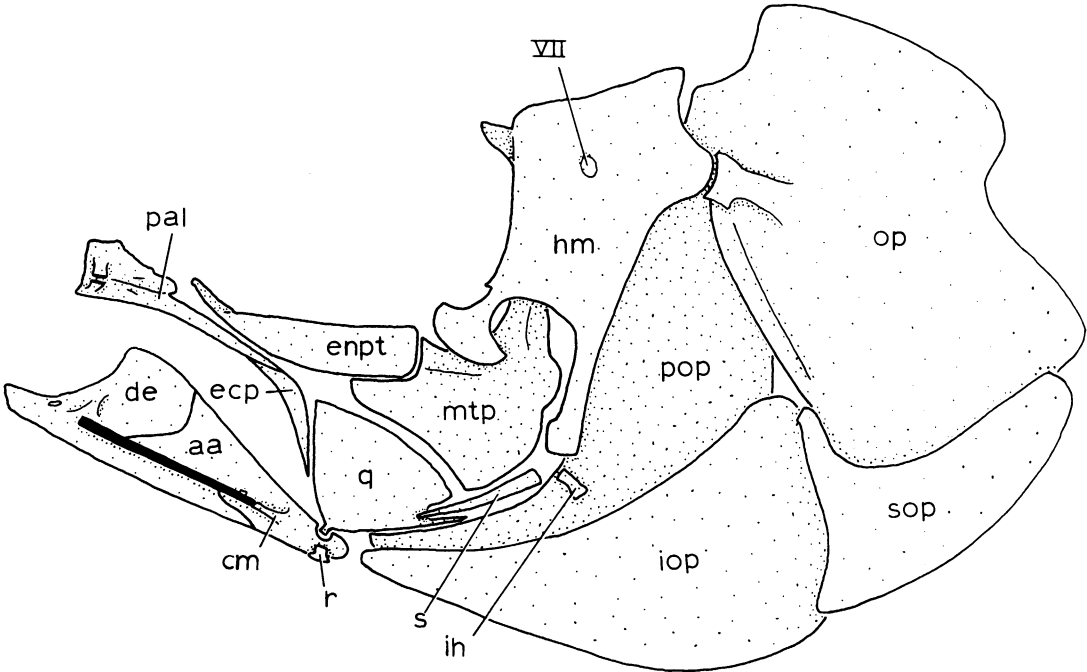


FIG. 41. *Dorosoma cepedianum*, medial view of the lower jaw, opercular bones, and suspensorium. Coronomeckelian cartilage in black.

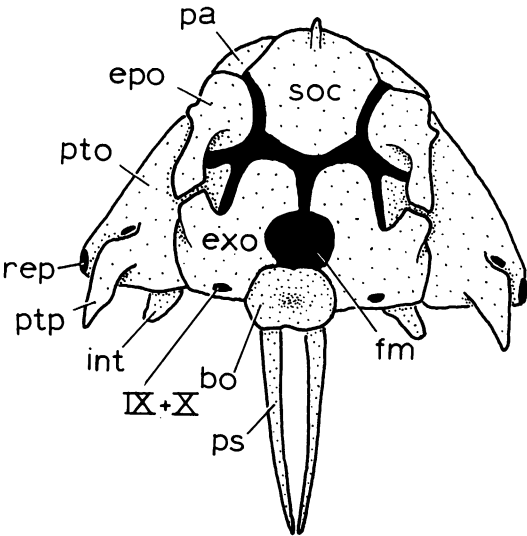


FIG. 42. *Dorosoma cepedianum*, posterior view of cranium.

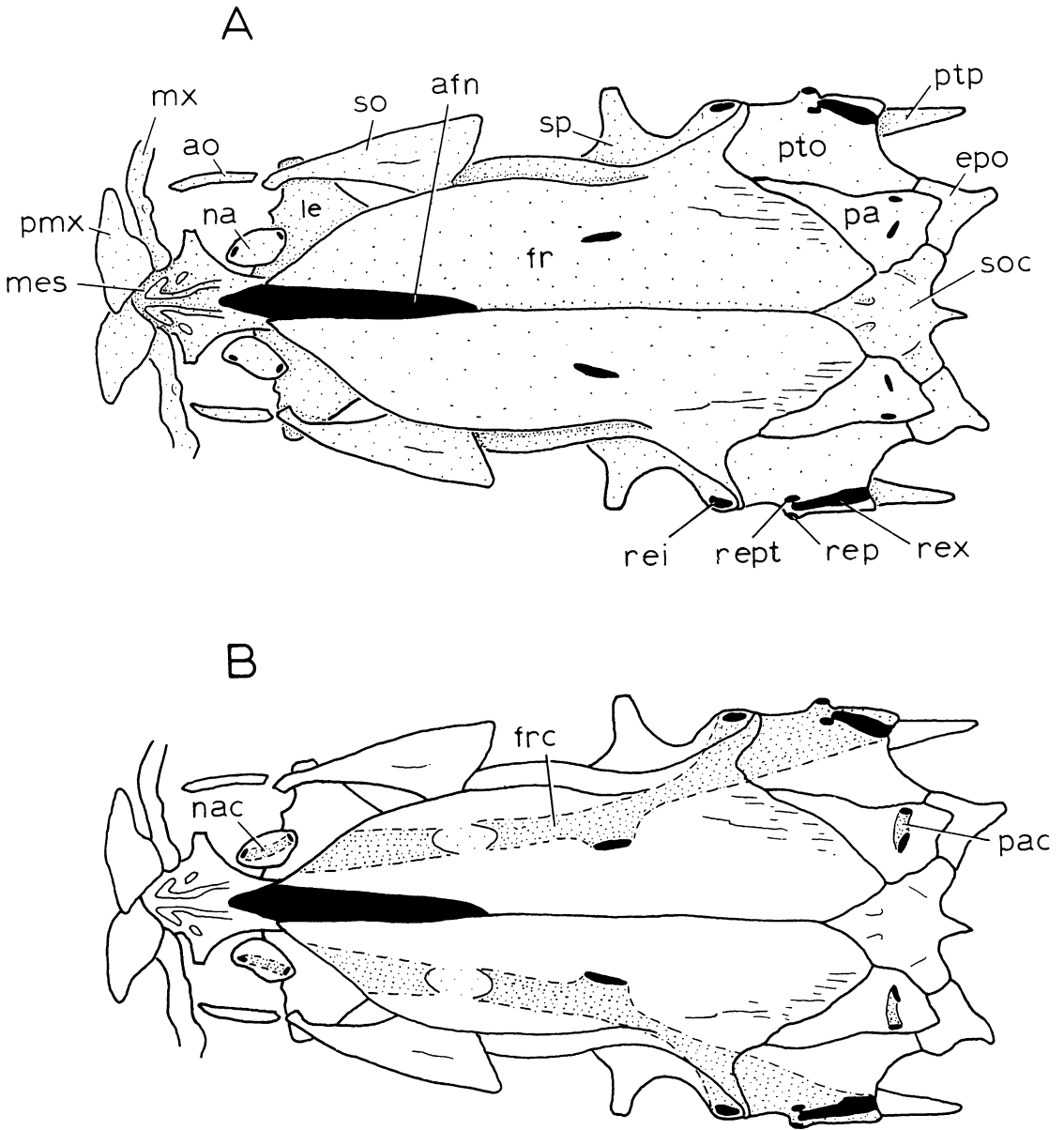


FIG. 43. *Dorosoma cepedianum*. (A) Dorsal surface of skull roof, with part of upper jaw, nasals, antorbitals, and supraorbitals; (B) same, showing sensory canals (heavy stipple = enclosed canals, light stipple = open canals). Upper jaws slightly flattened dorsoventrally.

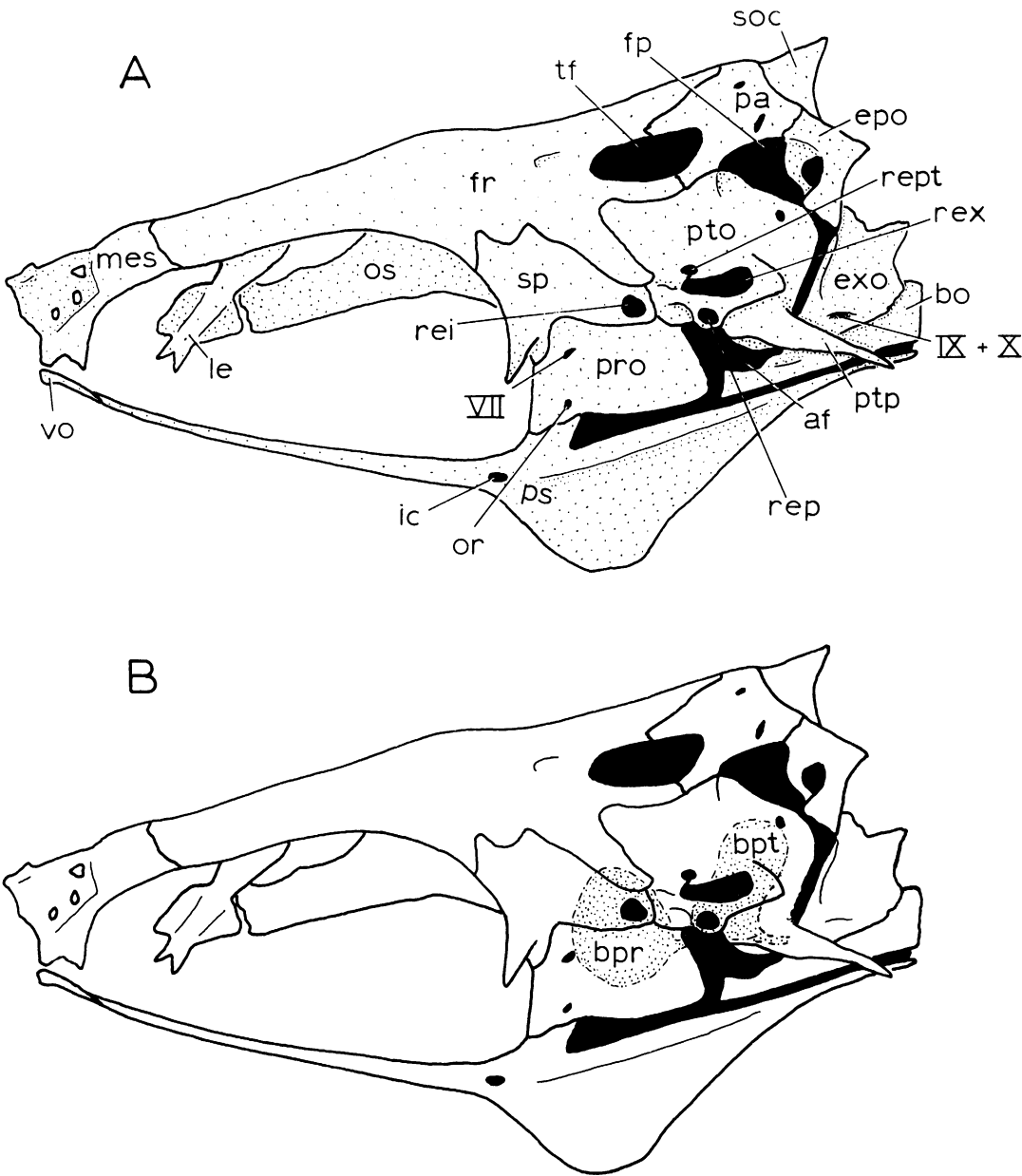


FIG. 44. *Dorosoma cepedianum*. (A) Lateral view of cranium; (B) same, showing bullae (stippled) as seen through bone.

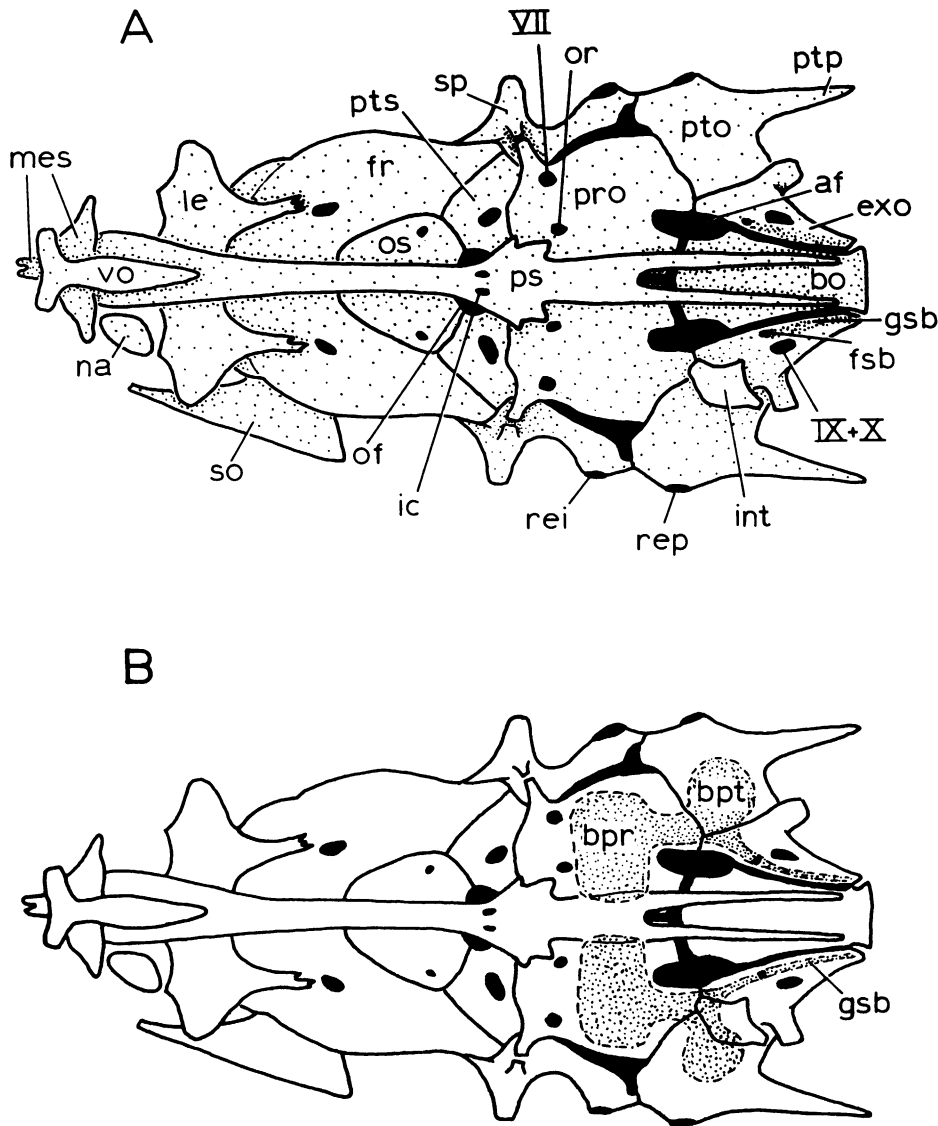


FIG. 45. *Dorosoma cepedianum*. (A) Ventral view of cranium; (B) same, showing position of bullae (stippled) as seen through bone.



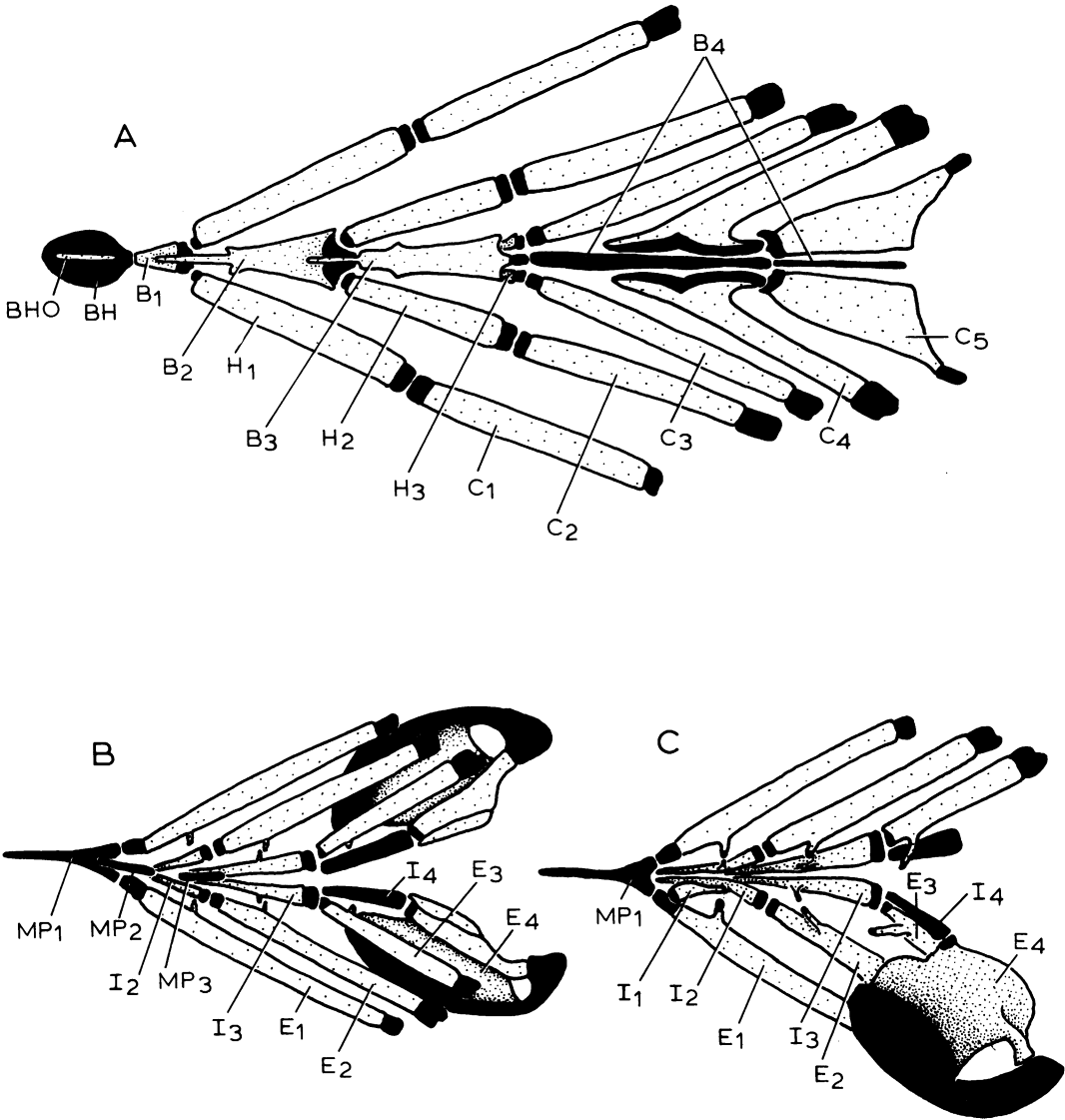


FIG. 46. *Dorosoma cepedianum*, gill arches (cartilage in black). Drawn flattened under a glass slide in glycerine. (A) Oral surface of ventral arches (B4 appears to be separated into anterior and posterior sections); (B) oral surface of dorsal arches; (C) aboral (dorsal) surface of dorsal arches (4th epibranchial and 1st infraorbital on right side removed).

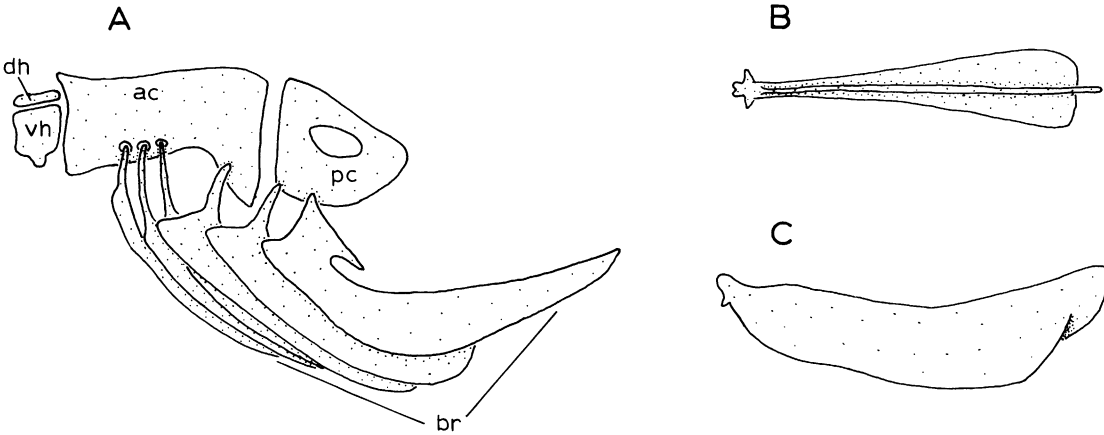


FIG. 47. *Dorosoma cepedianum*. (A) Lateral view of branchiostegal support and rays; (B) dorsal view of urohyal; (C) lateral view of urohyal.

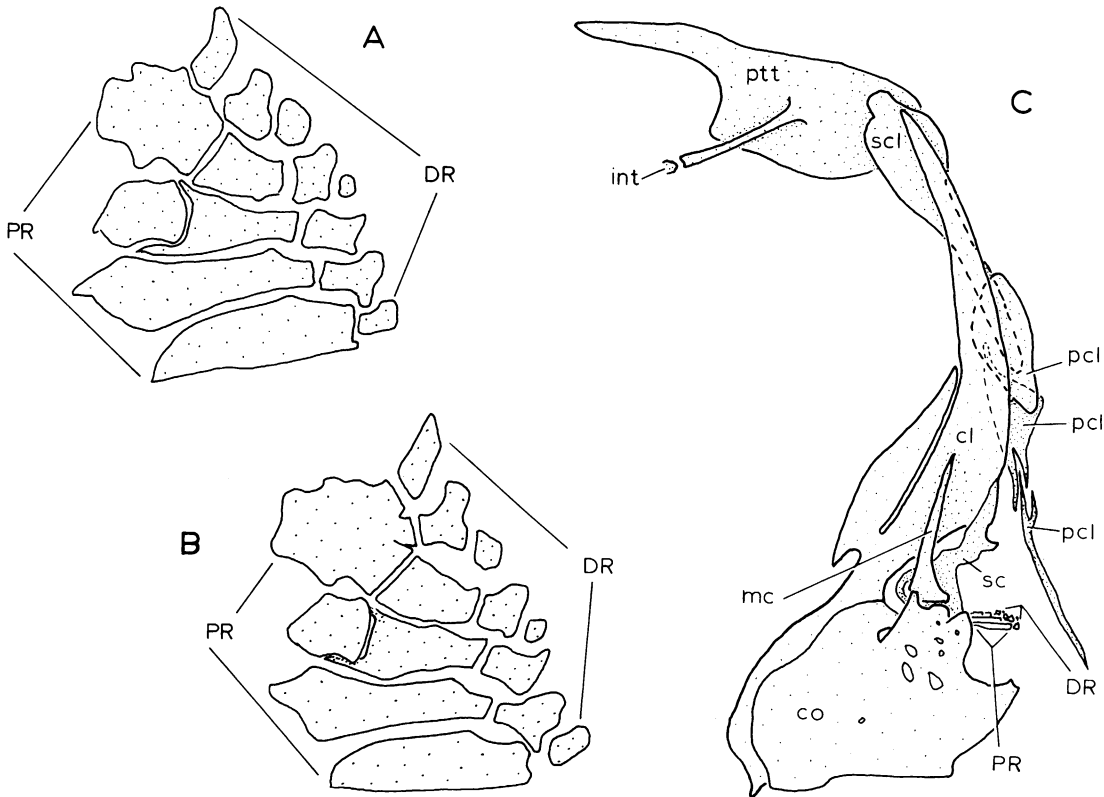


FIG. 48. *Dorosoma cepedianum*. (A) Pectoral radials, enlarged from C, oblique dorsolateral view; (B) pectoral radials enlarged from C, oblique dorsomedial view; (C) pectoral girdle, medial view. Anterior for A and B points to upper left. Finrays omitted.

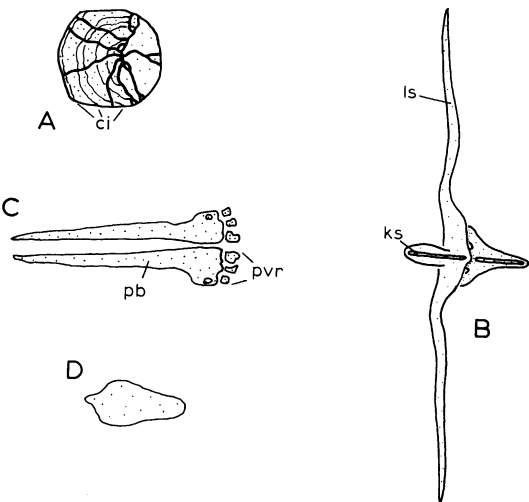


FIG. 49. *Dorosoma cepedianum*. (A) Flank scale; (B) ventral view of pelvic scutes flattened under glass slide; (C) dorsal view of pelvic girdles; (D) dorsal scute.

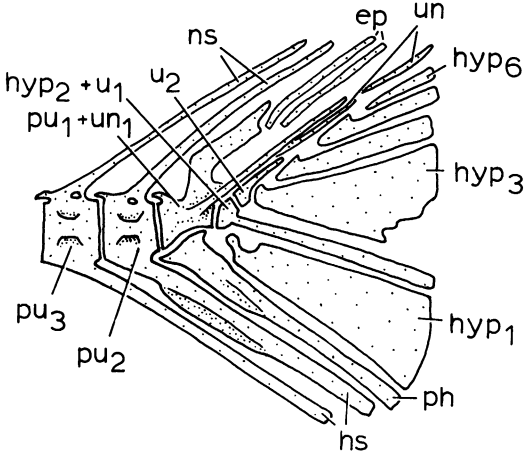


FIG. 51. *Dorosoma cepedianum*, caudal skeleton. Arrows point to articulation with uppermost and lowermost principal fin rays.

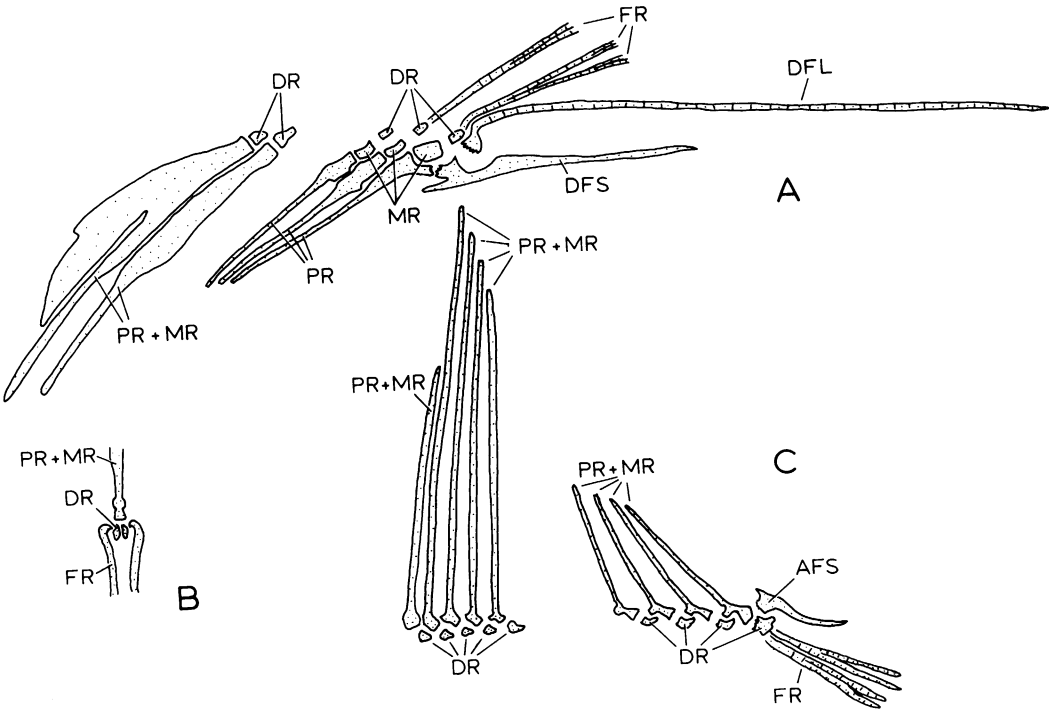


FIG. 50. *Dorosoma cepedianum*, median fin ray supports (most of the fin rays omitted). (A) Lateral view of anteriormost and posteriormost dorsal fin ray supports; (B) anterior view of the base of the eighth anal fin ray; (C) lateral view of anteriormost and posteriormost anal fin ray supports. Bases of fin rays removed on A and C.

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## TAXONOMIC INDEX

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