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

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

by

LANCE GRANDE

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of Doctor
of Philosophy, The City University of New York

1983

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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TABLE OF CONTENTS

Non-clupeiform clupeomorphs

Denticipitoidei

Pristigasteroidea

Engrauloidea

Chirocentridae

Pellonulinae

Dussumieriinae

Dorosomatinae

Alosinae

Clupeinae

LIST OF TABLES

LIST OF FIGURES

1968--odontodes omitted). The supraorbitally positioned dermosphenotic is large in +Armigatus and +ellimmichthyiforms (as in A); highly reduced in denticipitoids (as in B); and absent (or moved to a post orbital position) in all clupeoids (as in figs. 27A and 40A). The dermosphenotic of +Ornategulum has not been described and was not observed here.

Fig. 5. The skull roof of +Ornategulum sardinioides (after Forey 1973).

Fig. 6. Middle radials in the anal fins of A) +Diplomystus dentatus (AMNH 1330 - sl=375 mm; 7th and 8th radial sets with fin rays) and B) +Diplomystus birdi (AMNH 11425 - sl=51 mm; 3rd radial set with fin ray). Portion of fin ray which normally covers distal radial is removed in both A and B.

Fig. 7. A) The skull of Denticeps clupeoides showing the distribution of the odontodes (from Greenwood, 1968: fig. 1); B) The caudal skeleton of Denticeps clupeoides drawn from AMNH 53082 sw (sl=38 mm).

Fig. 8. The caudal skeleton of +Diplomystus dentatus, after Cavender (1966: fig. 4).

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 genus) and characters 14-23 and f and m discussed in text.

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 pig-like nose and oblique orientation of suspensorium; B) medial view of jaws, part of suspensorium and opercular bones, showing anteriorally 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).

Fig. 11 A-B. Pristigasterids, showing the vertical to anteriorly inclined predorsal bones (compare these and figs. 11 C-J with figs. 11 K-S, 10, 24, 25, 26B, and 39B) and various other features discussed in text. A) *Ilisha elongata* (AMNH 35811 sw) (sl=127 mm); B) *Pliosteostoma lutipinnis* (SU 39322) (sl=119 mm). Fig. B , a print from a radiograph; fig. A, a cleared and stained specimen with hypobranchial apparatus and right facial bones removed.

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

Fig. 11 F-H. Pristigasterids (see caption for fig. 11 A-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). Figs. F-H are cleared and stained specimens, with hypobranchial apparatus and right facial bones removed.

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

Fig. 11 K-M. An $^+$ellimmichthyid, denticipitoid, and engraulid, showing the posteriorly inclined predorsal bones (compare these and figs. 11 N-S, 10, 24, 25, 26B and 39B with figs. 11 A-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 tenuifilis* (AMNH 55085 sw) (sl=90 mm). Fig. 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. 11 N-P. A chirocentrid, dussumieriine and dorosomatine all showing the posteriorly inclined predorsal bones (see caption for figure 11 K-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). Figs. N-P are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

Fig. 11 Q-S. An alosine and two clupeines showing the posteriorly inclined predorsal bones (see caption for figure 11 K-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). Figs. Q-S are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

Fig. 12. Caudal skeleton of Pristigaster cayana (AMNH 10186 sw) (sl=83 mm) showing the absence of an interlobar caudal notch in hyp_3 (the ventral posterior edge of hyp_3 is nearly flush with that of hyp_2). Compare with non-pristigasterid third hypurals in figs. 7B, 38 and 51.

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, Lycothrissa, Papuengraulis, Thrissina, Coilia and Thrissa (all old world anchovies) have lost the ventral peg (A). Other engraulids, most clupeines, pellonulines 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). Pristigasterids have either condition B or C. Denticeps (E) is representative of the non-clupeoid condition.

Fig. 14. Cladogram showing the monophyletic groups of pristigasterid fishes based on osteological characters as interpreted here. Characters 20, 21, a through f discussed in text.

Fig. 15. Showing the absence of the maxillary-premaxillary gap. The gap is covered A) by a hypomaxillary bone in Pellona and B) by an extension of the maxilla in Chirocentrodon. Compare with figs. 27 and 40.

Fig. 16. The three anterior most 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 Neoopisthopterus have a small laminar expansion of the first pleural rib, it does not articulate with the shoulder girdle.

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 without stipple. Figs. A-D are ventral views; E is a dorsal view.

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

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

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.

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

Fig. 22. Articulation of postcleithrum with supracleithrum in A) *Laeviscutella dekimpei* (BMNH 1965:7 7

10-14) (sl=43 mm); B) Hyperlophus vittatus (AMNH 3050 sw) (sl=58 mm). Figure A shows the type of articulation for the western and central African pellonulines as discussed in text. Both are lateral views.

Fig. 23. Showing the openings to the recessus in Ehiravini, demonstrated by Corica laciniata (ANSP 89414) (sl=51 mm). All pellonulines 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.

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.

Fig. 25. Positive print made from radiograph of +Knightia eocaena from the Early Eocene of the Green River Formation.

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.

Fig. 27. *Odaxothrissa vittata* A) lateral view of skull; B) same, showing sensory canals (stippled).

Fig. 28. *Odaxothrissa vittata*, medial view of the jaws, opercular bones and suspensorium. Coronomeckelian cartilage in black.

Fig. 29. *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. 30. *Odaxothrissa vittata*, A) lateral view of cranium; B) same, showing bullae (stippled) as seen through bone.

Fig. 31. *Odaxothrissa vittata*, posterior view of cranium.

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 dorso-lateral view; B) pectoral radials enlarged from C, oblique dorso-medial view; C) pectoral girdle, medial view. Anterior for A and B points to upper left.

Fig. 36. Odaxothrissa vittata, A) flank scale; B) ventral view of two abdominal scutes below pelvic fin (the pelvic scutes) drawn flattened under a glass slide in glycerine; C) dorsal view of both pelvic girdles flattened under a glass slide (right and left side separated at posterior median contact).

Fig. 37. Odaxothrissa vittata, median fin ray supports (most of the fin rays ommitted): A) lateral view of anterior most and posterior most dorsal fin ray supports;

B) anterior view of the base of the eighth anal fin ray; C) lateral view of anterior most and posterior most anal fin ray supports.

Fig. 38. Odaxothrissa vittata, caudal skeleton. Arrows point to ariculation with uppermost and lowermost principal fin rays.

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.

Fig. 40. Dorosoma cepedianum (sclerotic bones removed), A) lateral view of skull; B) same, showing sensory canals (stippled).

Fig. 41. Dorosoma cepedianum, medial view of the jaws, opercular bones and suspensorium. Coronomeckelian cartilage in black.

Fig. 42. 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. 43. Dorosoma cepedianum, A) lateral view of cranium; B) same, showing bullae (stippled) as seen through bone .

Fig. 44. Dorosoma cepedianum, posterior view of cranium.

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 (B_4 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 infrapharyngobranchial 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 dorso-lateral view; B) pectoral

radials enlarged from C, oblique dorso-medial view; C) pectoral girdle, medial view. Anterior for A and B points to upper left.

Fig. 49. Dorosoma cepedianum, A) flank scale (heavy lines=grooves or "radii"); B) ventral view of two abdominal scutes below pelvic fin (the pelvic scutes drawn flattened under a glass slide, in glycerine); C) dorsal view of both pelvic girdles flattened under a glass slide. D) Dorsal view of dorsal scutes.

Fig. 50. Dorosoma cepedianum, median fin ray supports (most of the fin rays omitted): A) lateral view of anterior most and posterior most dorsal fin ray supports; B) anterior view of the base of the eighth anal fin ray; C) lateral view of anterior most and posterior most anal fin ray supports. Bases of fin rays removed on A and C.

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

ABSTRACT

The Clupeomorpha are a diverse, widespread group of fishes containing about 317 Recent and about 100 known fossil species. They are known as far back as the 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.

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. Cladograms for Pristigasteroidea, Dussumieriinae and Pellonulinae based on osteological characters are also given.

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.

Skeletal preparation of over 750 clupeomorph specimens representing 92 genera (82 Recent) and 155 species (140 Recent) were examined here for the character information above and for several other morphological and meristic features (such as number of predorsal bones, branchiostegal rays, etc) summarized in part by tables 1a to 10a and 1b to 10b. The osteology of a pellonuline (*Odaxothrissa vittata*) and a dorosomatine (*Dorosoma cepedianum*) is also descriptively illustrated in detail.

It is hoped that this work will serve as a base for future phylogenetic studies on clupeomorph fishes by paleoichthyologists and Recent ichthyologists 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 herring-like fishes, are a diverse widespread group of fishes containing about 317 Recent and possibly 100 known 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 worlds total 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 containing highly useful keys for identification of species (based mainly on external morphology) and solving many nomenclatorial problems in the clupeomorph literature, these works have not really addressed the problem of how clupeomorph groups are related to each other.

The state of phylogenetic literature on fossil clupeomorphs is even worse. 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 _incertae sedis_". The main problems in fossil clupeomorph classification arise from our poor understanding of the interrelationships of Recent species. Because Recent clupeomorph taxa are much more numerous (see above) and always better preserved than fossil taxa, it is considered here to be most reasonable to study the Recent forms first and place the fossils later, than to do the reverse.

The following study is an attempt to investigate the problem of clupeomorph interrelationships by examining 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) briefly review 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. Using osteological characters

should enable fossil clupeomorphs to be included in the classification.

A large number of clupeomorph taxa (mostly Recent species) are examined here (see Materials section) and several osteological features will be presented for all of these species in the numerous tables presented here. It is hoped that this information together with conclusions expressed here can serve as a base for further studies on the interrelationships of Recent and fossil clupeomorph fishes. The general osteology of two Recent clupeoids (*Odaxothrissa vittata* - a pellonuline, and *Dorosoma cepedianum* - a dorosomatine) is given in the appendix.

BRIEF HISTORY OF CLUPEOMORPH CLASSIFICATION

The detailed classification of clupeomorph fishes has traditionally represented many problems. Clupeomorph taxonomy during the 18th and 19th century is summarized by Lonnberg (1924:43-62) 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 20th century ichthyologists used the Clupeomorpha (and Clupeiformes) as a non-monophyletic repository for a wide variety of primitive teleosts. Berg (1940, p.417) admitted that:

> "This order [Clupeiformes] represents an artificial assemblage...In time the Clupeiformes will be, doubtlessly, divided in many orders."

Gosline (1971, p.111) admitted that the Clupeiformes, as he defined it, "are much too diverse to allow any unexceptional diagnosis." The classification used by Berg, as well as many others (Gosline, 1971; Regan, 1929; Svetovidov, 1952) included elopoids (*Elops* and *Megalops*) albuloids and alepocephaloids within the Clupeomorpha. Other classifications (eg. Jordan, 1923; Garstang, 1931; McAllister, 1968) included osteoglossomorphs (particularly *Hiodon*), gonorynchiforms, and other groups as well. 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 non-existent. 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., 1966:358); 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 swim-bladder 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 figures 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 non-clupeomorph 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 comissural 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, in the "SYSTEMATIC DISCUSSION OF CLUPEOMORPH FISHES" section.

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. The major problems with the fossil taxa are more complex than those for the Recent species because relatively poor preservation is an added factor 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. The work required to thoroughly diagnose and describe a taxon is much more difficult to do 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 (fig. two), 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 two. Numbers of Recent genera and species in each clupeoid group (based on Whitehead 1968a, 1973; Wongratana 1980; Nelson and Rothman 1973; Robins _et_ _al_., 1980; Poll, 1974; Poll and Roberts, 1976; and G. Nelson pers. comm) are as follows:

Chirocentridae	-	1 genus,	2 species
Engraulidae	-	15 genera,	130 species
Dussumieriidae	-	4 genera,	11 species
Pellonulinae	-	21 genera,	41 species
Clupeinae	-	16 genera,	61 species
Dorosomatinae	-	7 genera,	22 species
Alosinae	-	8 genera,	19 species
Pristigasterinae	-	9 genera,	30 species
Congothrissinae	-	1 genus,	1 species
TOTAL		82 genera	317 species

The relationships of these groups to one another are poorly known, as indicated by the polychotomous nature of the branching diagrams in figure two. 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 cladistic 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 entitled "SYSTEMATIC DISCUSSION OF CLUPEOMORPH FISHES". This will be followed immediatly 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. A cladogram 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 which group a character is unique to (the presence of vertebrae 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 non-engraulid 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 non-engraulid clupeomorph taxa. Wherever possible, several specimens of each species were prepared to examine intraspecific variation (numbers of each species examined here are given in materials section below). 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--A.M.N.H.) 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 anterior-most vertebra, bearing the first neural spine, back to preural 1 (the centra 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 asterick. Names for skeletal structures are mostly those used by Patterson, 1975 (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 preceeded by a dagger(+).

General phylogenetic plan for choosing outgroups.--The teleost classification of Patterson and Rosen (1977) was used here in selecting outgroup species for comparison. That classificatory 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.
FMNH, Field Museum of Natural History, Chicago.
MCZ, Museum of Comparative Zoology, Cambridge.
MNHN, Museum National d'Histoire Naturelle, Paris.
MRAC, Musee 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
UMMZ, Museum of Zoology, University of Michigan, Ann Arbor
USNM, National Museum of Natural History, Washington, D.C.

Anatomical:

aa, angulo-articular

ac, anterior ceratohyal

af, auditory fenestra

AFS, anal fin stay

afn, anterior frontal fontnelle

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

epo, epioccipital

exo, exoccipital

ext, extrascapular

extc, extrascapular canal

fm, foramen magnum

fp, pre-epiotic fossa

fr, frontal

frc, supraorbital canal

FR, fin ray

fsb, foramen through which anterior swim-bladder diverticulum enters neurocranium

gsb, groove for cranial diverticulum of swim-bladder

H, hypobranchial

hyp, hypural

hm, hyomandibular

hs, hemal spine

I, infrapharyngobranchials

ic, foramen for internal carotid artery

ih, interhyal

int, intercalar

io, infraorbital

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

pmx, premaxilla

pop, preopercle

popc, preopercular canal

PR, proximal radial (in dorsal and anal fins = pterygiophore)

pro, prootic

ps, parasphenoid

pto, pterotic

ptoc, 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

The following format is used for vernacular name usage here. Besides being uncapitalized, these names have particular endings listed below.

Names ending in _in_ are for tribe names (such as ehiravin for Ehiravini).

Names ending in _ine_ are for subfamily names (such as clupeine for Clupeinae).

Names ending in _id_ are for family names (such as clupeid for Clupeidae).

Names ending in _oid_ are for subordinal names (such as clupeoid for Clupeoidei).

Names ending in _form_ are for ordinal names (such as clupeiforms for Clupeiformes).

Names ending in _morph_ are for superordinal names (such as clupeomorphs for Clupeomorpha).

MATERIAL EXAMINED

The following is a list of clupeomorph skeletal preparations used for this study. All Recent material is cleared and stained (see methods section) unless otherwise indicated. Genera are listed in alphabetical order within each family level taxon. Most species are listed in chronological order within each genus, except for the type species (if it was examined here) which is listed first. In addition to the clupeomorph material listed below, specimens of Hiodon tergisus (AMNH 23754 SW), (sl=64 mm), Megalops atlantica (AMNH 27478 SW) (sl=80 mm), and Salmo trutta (AMNH 21164) (sl=45 to 80 mm), and various publications cited in text were used for outgroup information. A few additional fossil specimens are listed in the text below. Much of the information (below) on Recent type species nomenclature is after Whitehead (various publications) and Hildebrand (1963).

CLUPEOMORPHA

+Unnamed clupeomorph order (Division 1)

+Ornategulum Forey, 1973, p.1304 (type species +Clupea sardinioides Pictet, 1850, by original designation).

+O. sardinioides (Pictet, 1850) - 5 specimens (AMNH 3820, 3858, 6105, 6475 and 6580) from the Upper Cretaceous marine deposits of Hajula and Hakel Lebanon (sl=79 to 250 mm).

+Clupeomorpha Division 2 incertae sedis.

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

+A. brevissimus (Blainville, 1818) - 12 specimens (AMNH3465, 3658, 3818, 5775, 5776, and 5811) from the Upper Cretaceous marine deposits of Hajula and Hakel, Lebanon (sl=53 to 64 mm).

+Elimmichthyiformes
+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 to 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 to 65 mm).

+D. dubertreti Signeux, 1951 - 1 specimen (1946-18-17 [the holotype]) from the Upper Cretaceous marine deposits of Sahel Alma, Lebanon (sl=130 mm).

+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 to 101 mm).

Clupeiformes

Denticipitoidei

Denticipitoidae

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

D. clupeoides Clausen, 1959 - 2 specimens (AMNH 53082 sw)from a freshwater stream on the Dahomey-Nigerian border, Africa (sl=18 to 38 mm).

+*Paleodenticeps* Greenwood, 1960, p. 6 (type species +*Paleodenticeps tanganikae* Greenwood, 1960, by original designation).

+*P. tanganikae* 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).

Clupeiformes

Clupeoidei

Pristigasteroidea

Chirocentrodon Gunther, 1868, p463 (type species by monotypy, *Chirocentrodon taeniatus* Gunther, 1868 = *Pellona bleekeriana* Poey, 1867). See Hildebrand 1963: 438.

C. bleekerianus (Poey, 1867) - 3 specimens (AMNH 10118 sw) probably from western Atlantic waters off the coast of eastern South America (sl=78 to 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: 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 to 60 mm).

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

I. furthii (Steindachner, 1875) - 5 specimens (AMNH 11426 sw) from eastern Pacific drainage of the Rio Chucunaque, Panama (sl=36 to 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 Lacepède, 1800, p.220 (type species Odontognathus mucronatus by monotypy).

O. mucronatus Lacepède, 1800 - 3 specimens (AMNH 20749 sw) from Rio de Janeiro, Brazil (sl=87 to 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 Cuvier 1829). See Whitehead 1967: 121-122.

O. valenciennesi Bleeker, 1872 - 1 specimen (AMNH 17586 sw) from Sumatra (sl=43 mm).

O. equatorialis Hildebrand, 1946 - 2 specimens (AMNH 10188 sw) from the Gulf of Nicoya, Costa Rica, western Central America (sl=120 to 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 to 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 to 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 to 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).

Clupeiformes

Clupeoide

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 to 95 mm).

Anchovia Jordan and Evermann, 1896, p.449 (type species, *Engraulis macrolepidotus* Kner and Steindachner, 1864, by original designation).

A. clupeoides (Swainson, 1839) - 13 specimens (AMNH 40893 sw) from the Corintijn River, Nickerie District, Suriname (sl=35 to 47 mm).

Anchoviella Fowler, 1911, p.211 (type species *Engraulis perfasciatus* Poey, 1860, by original designation).

A. perfasciatus (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: 450).

C. edentulus (Cuvier, 1829) - 3 specimens (AMNH 37073 sw) from Port au Prince, Haiti (sl=79 to 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 (s44 to 67 mm).

Engraulis Cuvier, 1817, p.98 (type species *Clupea encrasicolus* Linne, 1758, designated by Flemming, 1822).

E. mordax Girard, 1856 - 10 specimens (AMNH 54600 sw) from eastern Pacific waters off the coast of California (sl=52 to 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 to 97 mm).

Lycothrissa Günther, 1868, p.7 (type species *Engraulis crocodilus* Bleeker, 1851, by monotypy).

L. crocodilis (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 to 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 to 85 mm).

Stolephorus Lacepède, 1803, p.381 (type species, Stolephorus commersonii Lacepède, 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 to 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 to 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 to 99 mm).

Clupeiformes
Clupeoidei
Clupeoidea
Chirocentridae

Chirocentrus Cuvier, 1817, p.178 (type species *Clupea dorab* Forskål, 1775, by monotypy).

C. *dorab* (Forskål, 1775) - 2 specimens, one UMMZ 180095) from Java and one AMNH 54622 sw) with no locality information (sl=130 to 275 mm).

Clupeiformes
Clupeoidei
Clupeoidea
Clupeidae
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 to 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 to 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 to 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 to 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 to 112 mm).

C. *ansorgii* Boulenger, 1916 - 2 specimens (AMNH 6397 sw) from the lower Congo River, Boma, Congo (sl=60 to 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 to 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 to 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 to 50 mm).

+*Knightia* Jordan, 1907, p.136 (type species +*Knightia 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 to 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 to 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 to 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: 7 7 10-14) from Lake Nokove, Dahomey, Western Africa (sl=39 to 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 to 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 to 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 to 38 mm).

N. *stewarti* Poll and Roberts, 1976 - 3 specimens (MCZ 48167) from Lake Mai, near Ipeke, Zaire Basin (sl=18 to 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 AMNH 5890 sw [two]) all from the Zaire River, Zaire, Central Africa (sl=38 to 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 to 80 mm).

P. afzeluisi Johnels, 1954 - 2 specimens MCZ 48621) from the Ivory Coast, Ghana and 2 specimens (SU 66469) from the Volta River, Ghana (sl=38 to 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 to 51 mm).

Potamalosa Ogilby, 1896, p.504 (type species Clupea richmondia Macleay, 1879, by monotypy).

P. richmondia (Macleay, 1879) - 3 specimens (AMNH

1737 sw) probably from New South Wales (sl=150 to 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 to 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 Angel, F. etal 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 Tanganiyika, Central Africa (sl=66 to 69 mm).

Thrattidion Roberts, 1972, p.2 (type species *Thrattidion tanganicae* Roberts, 1972, by original designation).

T. noctivagus Roberts, 1972 - 3 specimens (MCA 48162) from the Sanaga River, Cameroon, western Africa (sl=15 to 16 mm).

Clupeiformes
  Clupeoidei
    Clupeoidea
      Clupeidae
        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 to 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 to 86 mm).

E. teres (DeKay, 1842) - 10 specimens, five (AMNH 736 sw) from Gravesend Bay, New York; and five specimens (AMNH 54603 sw) from the mid-central Atlantic (sl=32 to 91 mm).

E. acuminatus Gilbert, 1891 - 5 specimens (AMNH 54602 sw) from eastern Pacific waters off the coast of California (sl=about 115 to 120 mm).

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

J. stolifera (Jordan and Gilbert, 1885) - 10 specimens (AMNH 2770 sw) from Key West, Florida (sl=36 to 61 mm).

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

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

S. delicatulus (Bennett, 1831) - 8 specimens (AMNH 54621 sw) from western Pacific waters (sl=24 to 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 Indopacific waters off the coast of Western Australia (sl=35 to 60 mm).

Clupeiformes

Clupeoidei

Clupeoidea

Clupeidae

Dorosomatinae*

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 to 89 mm).

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

C. thrissa (Lacepède, 1803) - 3 specimens (AMNH 28122 sw) from Taipei, Taiwan (sl=49 to 71 mm).

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

*no character information was found here to indicate this group as monophyletic.

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

D. anale Meek, 1904 - 2 specimens (AMNH 25673 sw) from the Usumacinata River, Chiapas, Mexico (sl=81 to 86 mm).

D. smithi Hubbs and Miller, 1941 - 2 specimens (AMNH 28126 sw) from Rio del Furte, near San Blas, Mexico (sl=97 to 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 to 57 mm).

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

K. punctatus (Temmunck and Schlegel, 1846) - 3 specimens; two (AMNH 35812 sw) from Foochow, Fukien Province,China, and one (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, one (AMNH 4363 sw) from Halmahera Island, Indonesia and two (AMNH 43405 sw) - no locality data (sl=38 to 91 mm).

N. erbi (Günther, 1868) - 9 specimens (AMNH 28097 sw) from Western Australia (sl=38 to 71 mm).

N. galatheae 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 atchafalayae 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 to 67 mm).

Clupeiformes
Clupeoidei
Clupeoidea
Clupeidae
Alosinae*

Alosa Link, 1790, p.35 (type species Clupea alosa Linnaeus, 1758, designated by Cuvier 1829, p.319).

A. falax (Lacepède, 1803) - 2 specimens (AMNH 32853 sw) from the Severn River, Somerset Co., England

*no character information was found here to indicate this group as monophyletic.

(sl=62 to 64 mm).

A. sapidissima (Wilson, 1811) - 5 specimens (AMNH 39234 sw) from the Hudson River, New York (sl=58 to 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 to 47 mm).

B. patronus Goode, 1879 - 3 specimens (AMNH 58618 sw) from Port Aransas, Texas (sl=31 to 64 mm).

Caspialosa Berg, 1915, p.4 (type species Clupea caspia Fichwald, 1838).

C. tanaica (Grimm, 1901) - 6 specimens, five x-rays (AMNH 18046) and one cleared and stained specimen (AMNH 18046 sw) (sl=260 to 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 to 42 mm).

G. variegata (Day, 1869b) - 1 specimen (AMNH 8355 sw) from the Chindwin River, Monywa, Upper Burma, S.E. Asia (sl=81 mm).

<u>Hilsa</u> Regan, 1917a, p.303 (type species <u>Clupea</u> <u>durbanensis</u> Regan, 1906).

<u>H</u>. <u>kelee</u> (Cuvier, 1829) - 2 specimens, one (ANSP 53059-61) from Durban, South Africa and another (AMNH 32828 sw) from Mombasa, Kenya (sl=87 to 101 mm).

<u>Pomolobus</u> Rafinesque, 1820, p.170 (type species <u>Pomolobus</u> <u>chrysochloris</u> Rafinesque, 1820, by monotypy).

<u>P</u>. <u>aestivalis</u> (Mitchill, 1814) - 5 specimens (AMNH 54617 sw) from the Hudson River, New York (sl=68 to 70 mm).

<u>P</u>. <u>pseudoharangus</u> (Wilson, 1811) - 5 specimens (AMNH 54620 sw) from Lake Erie, Ohio (sl=42 to 57 mm).

Clupeiformes
Clupeoidei
Clupeoidea
Clupeidae
Clupeinae*

<u>Amblygaster</u> Bleeker, 1849, p.73 (type species <u>Amblygaster</u>

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*no character information was found to indicate this group as monophyletic.

clupeoides Bleeker, 1849, by monotypy).

A. *liogaster* (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 Indopacific (sl=104 to 105 mm).

Clupea Linnaeus, 1758, p.317 (type species, *Clupea 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 to 84 mm).

C. *pallasii* Valenciennes, 1847 - 9 specimens, two (AMNH 54609 sw) from San Francisco Bay, California, and seven (AMNH 2703 sw) from eastern Pacific waters around the San Juan Islands off the coast of Washington State (sl=46 to 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 to 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 to 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 to 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 to 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 Fontenelle 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 to 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 to 70 mm).

_H_. _jaguana_ Poey, 1865 - 5 specimens (AMNH 28283 sw) from western Atlantic waters off Little Abaco, Bahamas (sl=59 to 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 to 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 to 75 mm).

_H_. _castelnaui_ (Ogilby, 1897) - 4 specimens (AMNH 54610 sw) from a bay near Cooktown, Australia (sl=44 to 59 mm).

_H_. _koningbergeri_ (Weber and DeBeaufort, 1913) - 5 specimens (AMNH 20711 sw) from Rio de Janeiro, Brazil (sl=37 to 46 mm).

_H_. _quadrimaculatus_ (Rüppell, 1837) - 4 specimens (AMNH 32822 sw) from Mombasa, Kenya (sl=75 to 100 mm).

Lile Jordan and Evermann, 1896, p.428 (type species _Clupea stolifera_ Jordan and Gilbert, 1882).

_L_. _stolifera_ (Jordan and Gilbert, 1882) - 2 specimens (AMNH 7100 sw) from Tumaco, Columbia (sl=51 to 53 mm).

_L_. _piquitinga_ (Schreiner and Ribeiro, 1903) - 5 specimens (AMNH 3838 sw) from Natal, Brazil (sl=60 to 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 to 60 mm).

_O_. _libertate_ (Günther, 1866) - 1 specimen (AMNH 14148 sw) from Topolobampo Bay, Mexico (sl=61 mm).

<u>O</u>. <u>medirastre</u> Berry and Barrett, 1963 - 1 specimen (AMNH 54612 sw) from Pichilinque Bay, Baja, California (sl=63 mm).

<u>Platanichthys</u> Whitehead, 1968, p.478 (type species, <u>Lile platana</u> Regan, 1917b, by original designation).

<u>P</u>. <u>platana</u> (Regan, 1917b) - 2 specimens (BMNH 1969: 11 25 103-117) from Buenos Aries, Argentina (sl=58 to 73 mm).

<u>Ramnogaster</u> Whitehead, 1964c, p.324 (type species, <u>Clupea arcuata</u> Jenyns, 1842, by original designation).

<u>R</u>. <u>arcuata</u> (Jenyns, 1842) - 2 specimens (ANSP 70406-9) from the Rio Uruguay, Uruguay (sl=100 mm).

<u>R</u>. <u>pallida</u> (DeBuen, 1952) - 5 specimens (AMNH 20711 sw) from the Rio de Janeiro, Brazil (sl=39 to 48 mm).

<u>Rhinosardinia</u> Eigenmann, 1912, p.445 (type species, <u>Rhinosardinia</u> <u>serrata</u> Eigenmann, 1912, by original designation).

<u>R</u>. <u>serrata</u> Eigenmann, 1912 - 4 specimens (AMNH 40923

sw and 40924 sw) from the Corintijn River, Suriname (sl=18 to 46 mm).

R. *bahiensis* (Steindachner, 1880) - 1 specimen (AMNH 40921 sw) from Suriname (sl=36 mm).

Sardinops Hubbs, 1929, p.264 (type species, *Maletta caerulea* Girard, 1854, by original designation).

S. *caerulea* (Girard, 1854) - 1 specimen (AMNH 5457 sw) from Balenos Bay, Baja, California (sl=108 mm).

S. *melanostricta* (Temminck and Schlegel, 1846) - 4 specimens (AMNH 17340 sw) from Japan (sl=39 to 45 mm).

S. *neopilchardus* (Steindachner, 1879) - 2 specimens (AMNH 48824 sw) from the Swan River, West Australia (sl=139 mm).

S. *pilchardus* (Walbaum, 1792) - 9 specimens from St. George Bay, Lebanon (sl=50 to 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 to 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 to 105 mm).

S. gibbosa (Bleeker, 1849a) - 3 specimens (AMNH 32819 sw) from Mombasa, Kenya (sl=94 to 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 to 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 to 67 mm).

S. pinnula Bean, 1912 - 3 specimens (AMNH 43473 sw) from Bermuda (sl=83 to 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 to 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 Indopacific waters off New Zealand (sl=76 to 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).

Tenualosa 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 to 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 (+*Ornategulum sardinioides*)
  - Division 2
    - +*Armigatus*
    - +Ellimmichthyiformes (+*Ellimmichthys* & +*Diplomystus*)
    - Clupeiformes
      - Denticipitoidei (*Denticeps* & +*Paleodenticeps*)
      - Clupeoidei
        - Engrauloidea
        - Pristigasteroidea
        - Clupeoidea
          - Chirocentridae (*Chirocentrus* only)
          - Clupeidae
            - Pellonulinae
            - Dussumieriinae

Dorosomatinae*

Alosinae*

Clupeinae*

When we include fossil taxa in our cladogram, the first clupeomorph character of Greenwood *et al*. (the presence of a recessus lateralis) no longer defines all of the Clupeomorpha, but instead defines a part of it called Clupeiformes here (and in Grande, 1982a). The recessus and other character information thought here to define 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.

Characters 1, 2 and 3 (defining Clupeomorpha):

(1) *Hypural 2 fused with the first ural centrum at all stages of development, and an autogenous first hypural* (discussed by Cavender, 1966; Gosline, 1960; Greenwood et al., 1966; Patterson and Rosen, 1977) (see figures 8, 12,

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*This is retained as a convenience group only (see above), no characters were found to indicate this is a monophyletic group.

19, 38 and 51). Although not unique to clupeomorphs (present in some characoids such as *Saccodon wagneri* illustrated in Roberts, 1974: fig. 78 for example) it is nearly so, and 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). 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 clupeomorphs and characoids.

(2) *Otophysic connection involving a diverticulum of the swim-bladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase, forming ossified bullae in the prootic, and usually also in the pterotic* (discussed and/or illustrated in Cervigon and Velazquez, 1978: fig. 16; O'Connell, 1955; Wohlfahrt, 1936; Greenwood, *et al*., 1966, p. 358) (see figures 3, 30B, 32B, 43B, 45B). Pterotic bullae are absent in three Recent clupeomorph genera, [*Sprattus* and *Clupeonella* (see Whitehead, 1964c) and *Ethmidium* (personal observation, USNM 77314)] and also in the Upper Cretaceous fossil clupeomorph $^{+}$*Spratticeps* (see Patterson, 1970), but these fishes all have prootic bullae. Although no well defined bullae of either type have been observed in $^{+}$*Ornategulum* (Forey, 1973, p. 1308), $^{+}$*Armigatus*

(+*Diplomystus* of Patterson 1970, p. 179) +*Ellimmichthys* or +*Diplomystus* (personal observation), inflated areas of thin bone have been reported in the exoccipital (Forey, 1973, p. 1309 and here, p. 157 for +*Ornategulum* ; personal observation for +*Diplomystus*) which resemble the fusiform bullae of clupeoids. Although this interpretation needs confirmation with better preserved (and dorso-ventrally oriented) specimens, it will be assumed that these primitive clupeomorphs had at least rudimentary bullae. Character 2 is unique to the Clupeomorpha and is considered to be one of the most easily recognizable defining characters.

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 and supraoccipital* (discussed in Patterson, 1970, p. 177, 179; Patterson and Rosen, 1977, p. 126) (see figure 27B and 40B). The footnote in Patterson and Rosen, 1977 (p. 126, footnote 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 (although Forey, 1973, p. 1305, does not illustrate this in +*Ornategulum*, Patterson and Rosen [1977, p. 126] reported it present in

this genus). It is thought (Patterson, 1970, p. 177) to be the result of fusion of extrascapular bones to the parietals. As a clupeomorph character this is questionable in that it also occurs in characoids (*Acestrorhynchus*, *Hoplias*, *Brycon*, and others), osteoglossomorphs (*Papyrocranus*, *Xenomystus* and others), and possibly other groups. Nevertheless, it will be retained here until a more detailed survey of this feature is made among teleost fishes.

Characters 4, 5 and 6 (defining Division 2 of Clupeomorpha):

(4) *Presence of one or more abdominal scutes, each of a single element which crosses the ventral midline of the fish* (discussed by Patterson, 1970, p. 180; Whitehead, 1963) (see figures 36 and 49). All species in Division 2 of Clupeomorpha except for *Chirocentrus* 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. *Notopterus* (AMNH 43170 sw and AMNH 43430 sw-both *N. chitala*) has abdominal structures that superficially resemble clupeomorph abdominal scutes, but these have separate right and left halves, each half with its own median ventral spine. No non-clupeomorph fishes are known to have clupeomorph-type abdominal scutes. The number of abdominal scutes is reduced to one (the pelvic scute) in

dussumieriines, some engrauloids and some pellonulines; in dussumieriines the scute is modified into a W-shape (see figure 17). The absence of any scute in Chirocentrus is thought to be the result of secondary loss, because the independent derivation of abdominal scutes in +ellimmichthyiforms, denticepitoids, pristigasterids, engraulids and clupeids seems much less likely. +Ornategulum (the sistergroup to the rest of the Clupeomorpha) has no abdominal scutes, so the presence of these structures is thought to be uniquely derived for Division 2 of the Clupeomorpha.

(5) The presence of a well-defined pre-epiotic fossa (discussed in Forey, 1973, p. 1316; Patterson, 1967, p. 104) (see figures 27A and 40A). Forey (1973, p. 1316) reports the absence of a well defined pre-epiotic fossa in +Ornategulum, but it is present in +Armigatus brevissimus (Patterson, 1967, p. 104), +Diplomystus (pers. 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, 1968, p. 232). The pre-epiotic fossae in engraulids are often reduced (Engraulis encrasicholus - 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-epiotic fossa were not observed in

any non-clupeomorph teleosts.

(6) *The development of dorsal scutes, with a median keel* (discussed in Grande 1982a; Schaeffer, 1947; Nelson, 1970; 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.

Character 7 (defining +Ellimmichthyiformes):

(7) *Lateral expansion of dorsal scute "wings" which give scute a subrectangular shape* (discussed in Grande, 1982a). The placement of +*Ellimmichthyiformes 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 the defining characters for Clupeiformes or +*Armigatus* (see figure

1A).

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

Character 8 (defining +Diplomystus):

(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.

Characters 9, 10 and 11 (defining Clupeiformes):

(9) The presence of a recessus lateralis (discussed in Greenwood *et al*., 1966: p. 358; Wohlfahrt, 1936; Greenwood, 1968) (see figures 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 pterotic lateral-line canals. It is separated from the perilymphatic spaces of the ear by a membranous fenestra, and is bounded by the pterotic 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 (the last infraorbital bone).

Clupeomorphs without a recessus (+*Armigatus brevissimus* - see Patterson, 1967: pp. 102, 103; +*Diplomystus* - see Grande, 1982a: p. 10; and probably +*Ornategulum* - see Forey, 1973: pp. 1302, 1310, 1311; and +*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 (fig. 4A and Grande 1982a: fig. 7) much like in *Hiodon*; some salmonids (see Patterson, 1970, fig. 31); and some ostariophysans (see Fink and Fink, 1981: fig. 7c).

In clupeomorphs with a recessus (Clupeiformes) the dermosphenotic is either highly reduced, without the middle branch of its canal, and not stretching well forward above the orbit (Denticipitoidei - see fig. 4B and Greenwood, 1968: fig. 4) or moved to a post- to suborbital position, no longer between the recessus and the supraorbital canal (Clupeoidei - see fig. 27B and 40B). In denticipitoids, the recessus is, in a sense, incomplete, because there is no opening to it directly from the supraorbital canal. Instead, this canal is connected to the recessus via a tubular dermosphenotic (see fig. 4B). In clupeoids, there is no dermosphenotic in this position, and the supraorbital canal empties directly into the recessus. The opening at the end of the infraorbital canal is relatively close to the opening of the preopercular canal;(compare figures 27B and 40B with figure 4A). This has led some authors (Patterson, 1967: p. 103) to suggest that the dermosphenotic bone of non-clupeiform clupeomorphs and denticipitoids has actually been lost in clupeoids (for example, compare the clupeoids in figs. 27B and 40B with the denticipitoid and †*Armigatus* in fig. 4). Many or most authors (Nelson, 1969; Weitzman, 1962) simply designate whichever infraorbital bone occurs last in the series, as the dermosphenotic. Patterson's (1967) interpretation implies that the "dermosphenotic" of clupeoids is not necessarily homologous with that of many non clupeoids.

So, in summary, osteologically, the recessus appears to show a sort of transformation series in Clupeiformes. An incomplete recessus is present in Denticipitoidei, and a complete recessus, including the infraorbital canal is present in Clupeoidei (explained above). Even within those species with a complete recessus (clupeoids) there is a great deal of osteological variation in structure, some of which will be discussed below in Pellonulinae, and some of which is still under study by the author.

The recessus lateralis is not known to occur in any non-clupeiform 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 swim-bladder 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, 1970: p. 177; 1967: p. 103; Whitehead, 1963b) (see figs. 29A and 42A and compare with fig. 5). Although separation of the parietals by the supraoccipital has occurred in various euteleost groups, those instances are thought to be independently derived from the occurrence in Clupeiformes. Non-clupeiform clupeomorphs ("primitive" clupeomorphs) have parietals in contact medially, anterior to the supraoccipital ($^{+}$*Ornategulum* - see fig. 5 and Forey, 1973: p. 1316; $^{+}$*Armigatus brevissimus* - see Patterson, 1967: p. 103; and probably $^{+}$*Diplomystus* - see Grande, 1982a: p. 7) like in osteoglossomorphs (Taverne, 1977, 1978); $^{+}$ichthyodectiforms (Patterson and Rosen, 1977); elopiforms (Forey, 1973b), $^{+}$leptolepids (Nybelin, 1974), and salmoniforms (Patterson, 1970b) and many other euteleosts.

(11) *Loss of middle radials in anal fin* (see figures 37 and 50. Primitive (non-clupeiform) clupeomorphs appear to have had distinct middle radials in the anal fin (observed in $^{+}$*Ornategulum sardinoides* [AMNH 6475: sl=86

mm]; $^{+}$Armigatus brevissimus [AMNH 3898, 5320, 5754: sl=61 to 87 mm]; $^{+}$Ellimmichthys [BMNH P 7109] and $^{+}$Diplomystus [fig. 5]). In the anal fin of all clupeiforms observed, these elements are no longer seen as distinct elements.[1] In clupeiforms the anal middle radials appear to be fused to the anal proximal radials. Although this fusion was not observed ontogenetically in the anal fin, the comparative osteology suggests it (compare the anal fin supports in fig. 5 with figs. 37 and 50). There is ontogenetic evidence that fusion of middle radials to proximal radials takes place in the dorsal fin supports of some species. In specimens of Microthrissa royauxi (AMNH 5830 sw), the smallest specimen (sl=42 mm) shows the presence of two dorsal middle radials unfused with their corresponding proximal radials, but the three larger specimens (sl=62-63 mm) show no unfused middle radials. Small specimens of Odaxothrissa vittata (MCZ 50349: sl=38-52 mm) also still show several unfused dorsal middle radials not observed in a large specimen (AMNH 5890 sw: sl=125 mm). In some species (fig. 50A) the posterior part of the dorsal fin shows unfused middle radials and the anterior part of the fin has fused radials, with a

[1] Although Yabumoto and Uyeno (1981: fig. 5F) reported an unfused anal middle radial in Hyperlophus vittatus, none of the 16 cleared and stained specimens observed here had any.

graded series of incomplete to complete fusion running in between.

Because the middle radials are still unfused in the anal fins of $^{+}$ellimmichthyiforms, $^{+}$*Armigatus*, and $^{+}$*Ornategulum* (see above); *Megalops* and *Salmo* (pers. observ.); and at least some osteoglossoids (Tavern, 1977: p. 107), it is proposed that among clupeomorphs loss of the middle anal radial (probably by fusion to the proximal radial) is independently derived for the Clupeiformes (even though siluriforms and some other ostariophysans have also lost this element according to Fink and Fink, 1981: p. 19).

Another character possibly 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 (illustrated in Grande 1982a: fig. 8A). Besides $^{+}$*Leptolepis bronni* and several percomorph groups (illustrated in McAllister, 1968) this opening is also found in $^{+}$*Ornategulum* (Forey, 1973: p. 1310); $^{+}$*Armigatus* (well preserved on AMNH 5776) and $^{+}$ellimmichthyiforms (Grande, 1982a). It was not observed in any clupeiform. Although it is possible that this was independently derived for $^{+}$*Ornategulum* and $^{+}$*Armigatus* plus $^{+}$ellimmichthyiforms (thus possibly uniting the last two groups) it seems more likely that the loss of this feature in Clupeiformes is independently derived for that group. This suggests that the presence of the foramen is derived (primitively) for Clupeomorpha or possibly Clupeocephala if its presence is also the primitive euteleost condition.

Characters 12 and 13 (defining Denticipitoidei):

(12) The presence of odontodes (denticles) covering the dermal bones of the skull (Greenwood, 1960, 1968; Clausen, 1959) (figure 7A). Present in both *Denticeps* and +*Paleodenticeps*, the two known monotypic genera in this suborder, this feature is unique among clupeomorphs, and among teleosts is known also only in some catfishes [such as *Loricaria cataphracta* (AMNH 40081 sw) and *Plecostomus* sp. (AMNH 43453 sw)]. Baskin (1972: p. 57) also reports these teeth in at least some trichomycterid, callichthyid, and astroblepid catfishes.

(13) Reduction in number of uroneurals in caudal skeleton to one (Greenwood, 1968) (fig. 7B). All other clupeomorphs observed have three uroneurals. *Denticeps* was also the only clupeomorph observed here to have only five hypurals.

Other characters unique to denticipitoids are given and discussed in Greenwood, 1968.

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

Characters 14, 15, 16 and 17 (defining Clupeoidei):

(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), $^+$*Ornategulum* (Forey, 1973), and most 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 $^+$*Ornategulum* is about equal in size or larger than the first preural centrum (as in *Hiodon*, *Salmo*, *Megalops*, osteoglossoids [Taverne, 1977, 1978], and most euteleosts that still have independent ural centra (pers. observ.).

This centrum is reduced in size in all clupeoids, and is considered here to be a defining character of 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 $^{+}$*Ornategulum*) have a complete lateral line, going all the way back to the caudal fin as do gonorynchiforms, (pers. observ. on *Chanos*, *Phractolaemus* and *Kneria*, AMNH 32991, 33471 and 33478), *Salmo*, *Megalops*, and osteoglossomorphs.

(17) *Separation of the parhypural from the first ural centrum* (Grande, 1982a). $^{+}$*Ornategulum*, $^{+}$*Armigatus*, $^{+}$ellimmichthyiforms, denticipitoids all have the parhypural fused to the first ural centrum. Although the occurrence of this fusion in euteleosts is variable, and most osteoglossomorph and elopomorph species 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 coincidence with other characters. All clupeoids observed here lack such a fusion (figs. 38 and 51) except species of *Dussumieria* and *Etrumeus* (dussumieriines 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 $^{+}$ellimmichthyiforms, $^{+}$*Armigatus*, or $^{+}$*Ornategulum*.

The Clupeoidei will be discussed further in the following section.

SYSTEMATIC DISCUSSION OF CLUPEOID FISHES

The cladogram in figure 9 shows the interrelationships of clupeoid subgroups as interpreted here by various osteological characters. Some of these, and other information surveyed from a large number of species (mostly non-engrauloid species) are given in the tables of below. Besides the characters given in figure 9 (explained below) osteological characters were found which are interpreted as synapomorphies for dussumierines and pellonulines. Character information will also be given for the construction of cladograms for Pristigasteroidea, Dussumieriinae and Pellonulinae.

No osteological synapomorphies could be discovered here for Dorosomatinae, Clupeinae or Alosinae, and the monophyly of those groups as they have been traditionally constructed (see Whitehead 1968, for example) is doubtful. 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. Below, the character information for the cladogram in figure 9 will be presented, and then the various family-level groups will be discussed.

Characters 14, 15, 16 and 17 (defining Clupeoidei): discussed in previous section.

Characters 18 and 19 (defining Engrauloidea):

(18) Suspensorium inclined obliquely backward (discussed by Ridewood, 1905 and Whitehead, 1963b). This character (see fig. 10) is unique to engrauloids 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 pig-like (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 engrauloids, and in all engrauloids examined.

Characters 20 and 21 (defining Pristigasteroidea):

(20) Predorsal bones oriented either vertically or inclined antero-dorsally (discussed also in Wongratana, 1980). In all Recent species of the Pristigasteroidea observed here, the predorsal bones showed this feature (see fig. 11). The Cretaceous +Gastroclupea is an exception, but because it appears to have a pristigasterid

type of caudal skeleton (character 21 below) and because it is remarkably similar to the peculiar genus, *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 postero-dorsally. The only exceptions observed here were in *Ramnogaster arcuata*, which appeared to have 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 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 Indopacific 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 considered here to be derived for the Pristigasteroidea. This character will be further discussed below in the discussion on Engrauloidea.

Nelson (1967: 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 this) this condition was not observed here in any clupeomorph species outside of Pristigasteroidea.

Character 22 (defining Clupeoidea):

(22) Increase in pleural rib to preural vertebrae ratio (tables 1a through 10a). This character is thought here to reflect a general trend of increasing relative abdominal cavity size among clupeomorphs. In the clupeomorph species observed, group ratios were as follows: +Ornategulum = .47; +Armigatus = .41; +Diplomystus = .37-.40; +Ellimmichthys = .56; Denticipitoidei = .37-.40; Pristigasteroidea = .28-.44; Engrauloidea = .27-.51; Clupeoidea = .47-.71. The ratio for Engrauloidea observed here is .27-45 ($\bar{x}$=.39, SD=.058, N=12 genera) except for some specialized New World forms (Cetengraulis, and some Engraulis species) so a low ratio is thought to be primitive for anchovies. +Ellimmichthys also has a high ratio (see above) but this monotypic genus is not thought to be a generalized +ellimmichthyiform, and the high ratio for this species is thought to be independently derived (an autapomorphy in the sense of Hennig, 1966). Among Clupeoidea the ratios observed are as follows: Chirocentridae = .59; Pellonulinae = .49-.61 ($\bar{x}$=.53, S.D.=.039, N=31 species); Dussumieriinae = .58-.74 ($\bar{x}$=.66, S.D.=.050, N= 9 species); Dorosomatinae = .49-.66 ($\bar{x}$=.56, S.D.=.041, N=14 species); Alosinae = .50-.63 ($\bar{x}$=.55, S.D.=.036, N=12 species); Clupeinae = .52-.66 ($\bar{x}$=.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 non-osteological characters for Clupeoidea, including a 'peculiar type of connection between the swimbladder and gut" (after Harder, 1957, 1958a, 1958b, and 1960). Pristigasteroidea and "primitive" (in the sense of Nelson 1970a) members of Engrauloidea have a ductus pneumaticus (stomach-airbladder 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 because Denticeps has a very peculiar digestive system for a clupeiform (i.e., no stomachic diverticulum) such comparisons are difficult to make.

Character 23 (defining Clupeidae):

(23) The presence of two long rod-like postcleithra (tables 1b-10b). Nearly all members of Clupeoidea observed here (all except for the pellonuline Clupeoides papuensis and the dussumieriines Dussumieria, Jenkinsia and Spratelloides) have two long rod-like postcleithra (see figs. 35C and 48 for example), the anterior most which articulates either behind the cleithrum with the supracleithrum as in the western and central African pellonulines (fig. 35C) or more lateral to the cleithrum

as in other members of Clupeoidea (fig. 48). The drawings by Chapman (1948: figs. 15 and 16) have omitted the posterior-most postcleithrum. In those species in which the anterior rod-like postcleithrum articulates with the lateral surface of the cleithrum, the anterior part of the anterior cleithrum is frequently expanded with laminar bone (fig. 48 and tables 1b-10b). The homology of these post cleithra 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 rod-like ones or sandwiched between the anterior rod-like 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 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 was observed to have the rod-like postcleithra. No postcleithra were observed in Chirocentrus, +Armigatus, +ellimmichthyiforms, or +Ornategulum; and denticipitoids have only two small scale-like bones associated with the upper part of the cleithrum (also noted by Greenwood, 1968: p. 147). Pristigasteroidea and Engrauloidea have no postcleithra, except occasionally for a scale like bone sandwiched between the cleithrum and supracleithrum in some species.

According to Nelson 1970a: p. 16, this group (=his 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 synopomorphies for Pellonulinae and Dussumieriinae) will be further discussed below.

ENGRAULOIDEA: Anchovies were not surveyed here in as much detail as the non-engraulid 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 Coilinae (including only the genus Coilia) and Engraulinae (including all the rest of the genera). 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 Engraulinae is a non-monophyletic group.

Nelson (1983) presented character information which indicated 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) formed 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 we 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 *Lycothrissa* and some *Stolephorus* species); and the loss of the dorsal scute (also lost in some species of *Stolephorus*) assuming its presence to be 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*, *Lycothrissa* 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 engraulids 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 21) but thought to be independently derived for this group of anchovies.

Engraulids are extremely rare in the fossil record (Whitehead, 1963b: p. 748 and personal observation). The only fossil anchovie observed here (after examining the fossil fish collections of AMNH, BMNH, FMNH, MNHN, SMMP, and USNM) was a specimen from Miocene deposits of Famagusta, Cyprus (BMNH P. 47312). This also appears to be the oldest known engraulid.

Two specimens of "+*Engraulis*" *evolans* Agassiz, 1843, from the Eocene Monte Bolca Formation (type specimen MNHN 10944, sl=70 mm - illustrated in Agassiz, 1833-1842: vol. 5, pl. 37b, figs. 1 and 2; and referred specimen MNHN 10945, sl=51 mm) were examined and were found to not even be clupeomorphs. The caudal skeletons, which are well preserved in the above specimens, indicate that they are euteleosts, very possibly exocoetoids. 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* *volitous* by Monod (p. 282). The holotype of "+*Engraulis*" *evolans* Agassiz, 1843 was also used as the holotype for "$^+$Exocoetus" exiliens Volta, 1796. Volta's (1796: p.164 and plate 34, fig. 5) systematic placement of the specimen is considered here to be more accurate than that of Agassiz. This specimen is still listed as an engraulid in Blot, 1980: p. 352 - where the author of the name is missited ("Volta, 1796" is listed there as author of the Agassiz name).

For a group so abundant and widespread today, the scarcity of fossil anchovies is peculiar, especially considering how very common fossil clupeids are. Possibly this suggests a relatively young age for the group, but the phylogenetic data here suggests otherwise.

PRISTIGASTEROIDEA: This group of fishes has been previously classified by Norman (1923) and Berry (1964a). 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 non-monophyletic group which is in need of revision. Because not many of the species were available here, such a revision was not attempted. The higher groups of Pristigasteroidea corresponding to the cladogram in figure 14 will not be named here, until further revision of the group is undertaken, and additional character information found. The characters in the cladogram are as follows:

(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 the occurrence of an additional bone in the upper jaw--the hypomaxilla (fig. 15A). In *Chirocentrodon* and *Neopisthopteris* 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 most other clupeomorphs (see figs. 27 and 40 for example). A hypomaxillary bone occurs in only one other known clupeomorph genus-*Harengula* (Berry, 1964b).

(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., *Chirocentrodon*) 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.

(c) *Loss of pelvic fins*. The loss of the pelvic fins in this group is thought to be independent of their loss in *Neopisthopterus* 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 lost the dorsal fin externally, has retained the internal supports (pterygiophores).

(d) Greater 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) Greater than 57 anal pterygiophores (tables 1a-10a). Among all other clupeomorphs, only the rat-tailed anchovies, Coilia, have this 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 (discussed in Patterson, 1967 and Patterson and Rosen, 1977) and ignoring the complex characters uniting Chirocentrus with other Recent clupeiforms (discussed 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 fang-like 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.

The presence of fang-like teeth if somewhat spotty in its distribution among Recent clupeomorphs, is widespread. Besides *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); Engrauloidea (*Lycothrissa*); and to a lesser extent in several other clupeoids.

The presence of distal radials in the pectoral girdle is 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 (Cervigon and Velazquez, 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 absence of abdominal scutes (except for the pelvic scute) in clupeomorphs is not thought to be primitive for Clupeomorpha, Division 2 (see fig. 1). Besides *Chirocentrus*, their absence also occurs in pellonulines (table 5b), engraulids (table 4b) and dussumieriines (table 6b). The absence of a pelvic scute in *Chirocentrus* is unique among all Clupeomorpha Division 2, and because *Chirocentrus* is clearly a clupeoid (see above) the loss of this structure is thought to be secondarily derived for that genus. Abdominal scutes will be further discussed below in the section on Dussumieriinae.

The implication that *Chirocentrus* has a chondrichthyian type intestinal Spiralfalten (a true spiral valve) was thought by Cohen (1958) to be questionable. 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: 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: 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 pellonuline genera within Dussumieriinae (=his Dussumieriidae) because of their lack of or poorly developed abdominal scutes, but later changed his mind when it was discovered that certain West African pellonulines (Poll et al. 1965) also lack abdominal scutes. It should also be noted that chirocentrids and many anchovie species also lack abdominal scutes (see above section on Engrauloidea). The pellonulines lack the one character that is truly unique to the dussumieriines--the pecular modified pelvic scute (fig. 17) found only in Etrumeus, Dussumieria, Spratelloides and Jenkinsia. This scute, described and figured 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. Whitehead (1963a and elsewhere); Nelson (1967a, 1970a); Taverne (1977) and others have considered dussumieriines to be the most primitive of the clupeids, (sistergroup to all other clupeid groups) mostly because of their lack of 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 Division 2 (see fig. 1A) primitively have abdominal scutes (present in all +Armigatus, +ellimmichthyiforms, denticipitoids, and pristigasterids), the absence of abdominal scutes in some engraulids, chirocentrids, pellonulines and dussumieriines is seen here as several independent 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) also considered dussumieriines to "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 (defining 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 inexcutata* (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. There are no clupeomorphs known prior to the Cretaceous (see Grande 1982a and below). Arambourg (1954) assigned +*Clupavus neocomiensis* 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 all non-clupeomorphs also are without abdominal scutes). The presence of the uniquely derived pelvic scute (character f above) would diagnose a fossil to this group.

Character g and h (defining Dussumieriini):

(g) *Extremely high number of branchiostegal ray (14-20)*. Although Whitehead (1963a: p. 367) Nelson (1967a: p. 398) and other have considered the high number of branchiostegal rays to be a "primitive" feature of dussumieriines, 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 clupeomorph of Division 2 (fig. 1A) and only a few engraulid species even overlap this range (see tables 1a-10a). Clupeomorpha, Division 2 primitively have fewer branchiostegal rays (+*Armigatus* = 10-12, +ellimmichthyiforms = 10-12, denticipitoids = 5, engraulids = 8-15, pristigasterids = 6, chirocentrids = 8, spratelloidins = 6-8, and other clupeids = 4-9. In the non-clupeomorph species examined, the number is variable (*Salmo trutta* = 11, *Megalops atlantica* = 24, *Hiodon tergisus* = 8).

(h) *Parhypural fused with first preural centrum*. Gosline (1960: fig. 7) was first to note that *Dussumieria acuta* was peculiar among clupeoids in having this feature. It was found here that this fusion is also present in the other species of *Dussumieria* and in *Etrumeus*, but in no other clupeoid. 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 Dussumierini.

+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).

Character i, j, k and l (defining (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 2, only one other clupeomorph species observed besides Spratelloides and Jenkinsia (the pellonuline Corica laciniata) has reduced the number to 1 exclusively (although a few alosine and clupeine species which usually have 2 occasionally have 1 - see tables).

(k) Fusion of the first ural centrum to the first preureal centrum (tables 1b-10b) (fig. 19). This fusion, among clupeomorphs, is confined to this tribe, a group of pellonulines (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). U_2 and U_1 are also fused in *Etrumeus* (with no fusion to PU_1).

(1) *Reduction of infraorbital bones to 5*. Among clupeomorphs, the number of infraorbital bones is almost always 6 excluding the antorbital (see also Nelson, 1969) except for *Jenkinsia*, *Spratelloides*, and *Potamalosa* (an Australian pellonuline). Yabumoto and Uyeno (1981: fig. 4) reported only 5 for *Hyperlophus translucidus*, but all specimens of this species examined here had 6. It is quite feasible that some *Hyperlophus* specimens could have 5 since this genus may be closely related to *Potamalosa* (see section below on Pellonulinae). The reduction to 5 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 io3 and io4 based on the position of the neuromasts and position of the bones (method used by Nelson 1969 for determining fusion patterns). The

reduction in Spratelloidini is the result of the absence of io6 (=the dermosphenotic) a bone usually very small in clupeiforms but undetectable in any specimens of _Jenkinsia_ or _Spratelloides_ observed here.

Whitehead (1963b) also noted that in Dussumierini, 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 +ellimmichthyiforms and in ontogenetic series of Recent clupeids is needed before it can be determined whether the posterior frontal fontanells 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 it is a dussumeriine, and others (MNHN 1146 G, sl=65mm) also show the expanded 4th hypural, single epural, and u_1-pu_1 fusion indicative of Spratelloidini.

PELLONULINAE: This group of fishes has previously been revised by Regan (1917c-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. The characters in the cladogram 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).

Character m (defining 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 (defining an unnamed group containing the Pellonulini and the Ehiravini as used here).

(o) Fusion of the first ural centrum with the first preural centrum (tables 1b-10b; figure 38). This fusion occurs elsewhere only in a group of engraulids (discussed above), the dussumieriine tribe Spratelloidini (also discussed above) and one clupeine, Clupeonella cultiventris. 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 have 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.

Character p (defining 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*, *Stolothrissa*, *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 rod-like postcleithrum well behind the cleithrum (figs. 22 and 35). This group also appears to be confined to Western and Central Africa, almost exclusively in freshwaters. 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 (p) in *Gilcrestella*, *Corica* and *Spratellomorpha*; which would leave Pellonulini as paraphyletic (with no known synapormorphies) within Pellonulinae. Nevertheless, the interpretation used here, if somewhat tenuous (influenced by the geographic range of the two main pellonuline groups) is that the articulation was derived for Pellonulini independent of its derivation in *Ehirava* and *Clupeichthys*. All other groups with the clupeid postcleithra (long rod-like 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 (defining Ehiravini, the Southeastern African-Indo-Pacific pellonulines). The Ehiravini as used here differ 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 connecting 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 frontal 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 pellonuline tribe Ehiravini (as used here) shows what is interpeted 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 separate openings - one for the lateral extrascapular canal, one for the preopercular canal and a third opening (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 frontal bone.

In all other pellonulines, (Pellonulini, _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 to the sensory canals, is a subject for further study. The Ehiravini appears to be confined to an area from South and Eastern Africa, through the Indo-Pacific, in both fresh and marine waters.

Character r (defining an unnamed group of ehiravins).

(r) _Anal finlet behind main body of (anterior) anal fin, with associated pterygiophore modifications (fig. 24)_. This structure is unique among all clupeomorphs examined, and was not observed in any other teleost.

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 are in this group (that is they are cluepids that do not appear to belong in Dussumieriinae or Pellonulinae). Most fossils that have been described as "*Clupea*" (*i.e.* "$^{+}$*Clupea*" *catopygoptera* de Zigno, 1874; "$^{+}$*Clupea*" *humilis* von Meyer, 1851; and several 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*. *harangus* Linn., 1758; and *C*. *pallasii* Val., 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 non-osteological 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, gizzard-like stomach, filamentous dorsal fin ray, inferior mouth, dentary flared outward, etc. None of these characters are restricted to dorosomatines, and most occur in only some of the group.

Clupeinae and Alosinae are very difficult to even roughly diagnose 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 (1967: pp. 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 below 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).

Table 1a. Meristic information for some non-clupeoform clupeomorphs

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
†*Ornategulum*										
†*O. sardinioides*	12	0	17	2	24	51	.47	13	7	3
†*Armigatus*										
†*A. brevissimus*	5-6	11-12	10-12	2	13	31-32	.41	18-19	28	3
†*Diplomystus*										
†*D. dentatus*	7-8	33-36	12	2	17	41-43	.40	11-12	39-40	3
†*D. birdi*	6-7	23	10-11	2	11-12	30	.38	16-17	23-25	3
†*D. dubertreti*	6-7	20	?	2	12-13	33-34	.37	23	27	?
†*Ellimmichthys*										
†*E. longicostatus*	7	12	8-9	2	19-22	36-37	.56	12-13	9	3

[1] (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

Table 1b. Morphological information for some non-clupeoform clupeomorphs.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
†*Ornategulum*								
† *O. sardinioides*	-	-	-	-	-	-	-	-
†*Armigatus*								
†*A. brevissimus*	+	+	+	-	-	-	+	-
†*Diplomystus*								
†*D. dentatus*	+	+	+	-	-	-	+	-
†*D. birdi*	+	+	+	-	-	-	?	-
†*D. dubertreti*	+	+	+	-	-	-	?	-
†*Ellimmichthys*								
†*E. longicostatus*	+	+	+	-	-	-	-	-

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

Table 2a. Meristic information for Denticipitoidei.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Denticeps										
D. clupeoides	11	0	5	0	14	38	.37	7	23	2
†Paleodenticeps										
†P. tanganikae	12 (based on Greenwood 1960)	0	5	0	12	30	.40	8	23	3

---

[1] (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

Table 2b. Morphological information for Denticipitoidei.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind[1] cleithrum	Presence of two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Denticeps								
D. clupeoides	+[3]	+[3]	+[3]	-	-	-	-	-
†*Paleodenticeps*								
†*P. tanganikae*	+[3]	+[3]	+[3]	-	-	-	-	-

---

[1] with a well defined space between the postcleithra and the cleithrum (see figure 22).

[2] $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

[3] all of the abdominal scutes in *Denticeps* and *Paleodenticeps* lack ascending arms.

Table 3a. Meristic information for some pristigasterines (Clupeoidei: Pristigasteroidea)

Genus *Species*	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Chirocentrodon										
C. bleekerianus	19-21	0	6	2	18	44	.41	15-16 ($\bar{x}$=15.66)	40	3
Neoopisthopterus										
N. tropicus	20	0	6	2	16	44	.35	15	42	3
Pliosteostoma										
P. lutipinnis	23	0	6	2	17-18	49-50	.35	14	48-53	2
Pellona										
P. ditchela	7	0	6	2	16-17	42	.39	18-19	33-34	3
P. flavapinnis	9	0	6	2	19	43	.44	19	38	3
P. harroweri	8	0	6	2	13	39	.33	15-16 ($\bar{x}$=15.75)	37-39	3
Odontognathus										
O. mucronatus	30-31 ($\bar{x}$=30.66)	0	6	2	15	52-54	.28	11-12 ($\bar{x}$=11.66)	75-78	3
O. panameusis	28	0	6	2	16	51	.31	12	61	3

Table 3a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
<u>Raconda</u>										
<u>R. russelliana</u>	30	0	6	2	17	61	.28	16	88	3
<u>Opisthopterus</u>										
<u>O. valenciennesi</u>	24	0	6	2	18	51	.35	18	58	3
<u>O. equitorialis</u>	25	0	6	2	16	47	.34	13-14	58-59	3
<u>Pristigaster</u>										
<u>P. cayana</u>	5	2(B)	6	2	14	43	.33	14-15	46-47	3
<u>Ilisha</u>										
<u>I. africana</u>	11	0	6	2	14-15 ($\bar{x}$=14.75)	42	.35	15	45	3[2]
<u>I. elongata</u>	14	0	6	2	23	55	.42	18	47	3
<u>I. amazonica</u>	6	0	6	2	14	40	.35	15	46	3
<u>I. furthii</u>	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
<u>I. indica</u>	10	0	6	2	16	42	.38	17	39	3

Table 3a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
†*Gasteroclupea*										
†*G. branisai*	16-17	34-36(A)	?	2	9	32	.28	12-13	13- 14	3

---

1 (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

2 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 pristigasterines (Clupeoidei: Pristigasteroidea)

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Chirocentrodon								
C. bleekerianus	+	+	+	-	-	-	+	+
Neoopisthopterus								
N. tropicus	+	+	+	-	-	-	+	+
Pliosteostoma								
P. lutipinnis	+	+	+	-	-	-	+	-
Pellona								
P. ditchela	+	+	+	-	-	-	+	-
P. flavapinnis	+	+	+	-	-	-	+	-
P. harroweri	+	+	+	-	-	-	+	-
Odontognathus								
O. mucronatus	+	+	+	-	-	-	+	-
O. panamensis	+	+	+	-	-	-	+	-
Raconda								
R. russelliana	+	+	+	-	-	-	+	-

Table 3b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind[1] cleithrum	Presence of two long rod-like postcleithra	Fusion of caudal vertebrae [2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Opisthopterus								
O. valenciennesi	+	+	+	-	-	-	+	-
O. equitorialis	+	+	+	-	-	-	+	-
Pristigaster								
P. cayana	+	+	+	-	-	-	+	-
Ilisha								
I. africana	+	+	+	-	-	-	+	-
I. elongata	+	+	+	-	-	-	+	-
I. amazonica	+	+	+	-	-	-	+	-
I. furthii	+	+	+	-	-	-	+	-
I. indica	+	+	+	-	-	-	+	-
†*Gasteroclupea*								
†*G. branisai*	+	+	+	-	-	?	?	-

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

Table 4a. Meristic information for some species of anchovies (Clupeoidei: Engrauloidea).

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Anchoa										
A. compressa	10-11	0	13	2	17	41	.41	11-12	30	2
Anchovia										
A. clupeoides	15	0	13	2	17	43	.40	14	29-31	2
Anchoviella										
A. perfasciata	9-11	0	11-12	2	20-21	42-44	.48	14-15	16-18	2
Cetengraulis										
C. edentulus	10-11	0	8	1	18	41	.44	15-16	23-25	2
Coilia										
C. grayi	5	1(c)	11	2	21	75	.28	13	104	2
Encrasicholina										
E. purpurea	9-10 (usually 10)	0	13	2	22-23	43-44	.52	14	16-17	2
Engraulis										
E. mordax	12-13	0	13	2	23-24	46	.51	15-17	22-23	2
Lycothrissa										
L. crocodilus	10	0	13	1	16	48	.33	12	50	3

Table 4a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Lycengraulis										
L. grossidens	11-12 (usually 12)	0	15	2	20	46	.43	14-15	24-28	2
Pterengraulis										
P. atherinoides	10-11	0	13	2	18-19	45	.41	12-13	32-34	2
Setipinna										
S. papuensis	7	1(C)	14-15	1	14	48-49	.29	14-15	57-58	3
Stolephorus										
S. indicus	9-10 (usually 9)	0[2]	14	2	20	43	.46	15	18-20 (usually 19)	2
Thrissina										
T. baelama	7-8	1(C)	12	2	17	40-41	.42	13-14	29-32	2
Thryssa										
T. hamiltoni	6-7 (usually 7)	1(C)	12-13	1[3]	18-19	45-46 (usually 45)	.41	12-13 (usually 13)	37-38	3

[1] (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only;

(C) = above first dorsal pterygiophore only.

[2] 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).

[3] most species are known to have 2 supramaxillary bones (Whitehead 1968).

Table 4b. Morphological information for some species of anchovies (Clupeoidei: Engrauloidea).

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind[1] cleithrum	Presence of two long rod-like postcleithra	Fusion of caudal vertebrae [2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
<u>Anchoa</u>								
<u>A</u>. <u>compressa</u>	-	-	-	-	-	A	-	-
<u>Anchovia</u>								
<u>A</u>. <u>clupeoides</u>	-	-	-	-	-	A	-	-
<u>Anchoviella</u>								
<u>A</u>. <u>perfasciata</u>	-	-	-	-	-	A	-	-
<u>Cetengraulis</u>								
<u>C</u>. <u>edentulus</u>	-	-	-	-	-	A	-	-
<u>Coilia</u>								
<u>C</u>. <u>grayi</u>	+[3]	+	+	-	-	-	- (poorly developed)	-
<u>Encrasicholina</u>								
<u>E</u>. <u>purpurea</u>	-	-	-	-	-	A	-	-
<u>Engraulis</u>								
<u>E</u>. <u>mordax</u>	-	-	-	-	-	A	-	-
<u>Lycothrissa</u>								
<u>L</u>. <u>crocodilus</u>	-	-	-	-	-	-	-	+

Table 4b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Lycengraulis								
L. grossidens	-	-	-	-	-	A[4]	-	-
Pterengraulis								
P. atherinoides	-	-	-	-	-	A	-	-
Setipinna								
S. papuensis	+	+	+	-	-	-	+	-
Stolephorus								
S. indicus	+	-	-	-	-	-	-	-
Thrissina								
T. baelama	+	+	-[5]	-	-	-	+	-
Thryssa								
T. hamiltoni	+	+	+	-	-	-	+	-

---

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

3 some species are known to have no prepelvic scutes (Whitehead 1972, p.240).

4 not fused in the small specimens examined here, but reported by Nelson (1983, p.53) to be fused in large specimens.

5 occasionally 1 or 2 scutes are found in this species (Whitehead 1972, p.228).

Table 5a. Meristic information for the wolf-herring (Clupeoidei: Clupeoidea: Chirocentridae)

Genus Species	Predorsal bones	Dorsal scutes	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	**Epurals**
Chirocentrus										
C. dorab	1	0	8	2	43	73	.59	15	30	2

Table 5b. Morphological information for the wolf-herring (Clupeoidei: Clupeoidea: Chirocentridae)

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum [1]	Presence of two long rod-like postcleithra	Fusion of caudal vertebrae [2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
<u>Chirocentrus</u>								
<u>C. dorab</u>	-	-	-	-	-	-	-	+

---

[1] with a well defined space between the postcleithra and the cleithrum (see figure 22).

[2] $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

Table 6a. Meristic information for some pellonulines (Clupeoidei: Clupeoidea:Clupeidae: Pellonulinae)

Genus Species	Predorsal bones	[1]Dorsal scutes	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Spratellomorpha										
S. bianalis	12	0	6	1	23	43	.53	16	16	2
Corica										
C. laciniata	10-12	0	6	1	19-20	39-40	.49	15-16	15-16	1
Clupeichthys										
C. bleekeri	9-10	0	6-7	1	20-21	39	.53	15	19	2
C. sp.	8	0	6	1	20	39	.51	15	17	2
Ehirava										
E. malabarica	10	0	6	1	22	39	.56	14	17	2
Gilcrestella										
G. aestuarius	12,14	0	6-7	1	20-21	40-41	.51	15	19-21	2
Congothrissa										
C. gossei	7	0	4	0	19	40-41	.47	13-14	13-15	2
Cynothrissa										
C. ansorgii	10	0	6	1	23	45	.51	16	17	3
C. mento	10-12	0	6	1	24-25	44-45	.55	16	18-19	3

Table 6a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Laeviscutella										
L. deKimpei	10-11	0	6	1	21-22	41	.52	14	17,19	3
Limnothrissa										
L. miodon	12	0	7	1	25-26	43-44	.59	14-15	16-17	2
Nanothrissa										
N. parva	12-13	0	5	1	23	42	.55	12	19-20	3*
N. stewarti	8-9	0	6	1	19-20	37-38	.52	13-14	15-17	2
Odaxothrissa										
O. vittata	10-11	0	6	1	23-24	44	.53	16	19-21 (usually 21)	3
O. losera	10	0	6	1	23	44	.52	16	19	3
Pellonula										
P. vorax	10-11	0	6	1	22	41	.54	15-16	16,19	3
P. afzeluisi	10-12	0	6	1	20	39-41	.50	15	17-18	2-3*
Poecilothrissa										
P. congica	11	0	5	1	23	43	.53	14-15	17-18	3

Table 6a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Potamothrissa										
P. obtusirostris	9-10 ($\bar{x}$=9.75)	0	5	1	25-26	44-45	.57	14-15	16-17	2
P. acutirostris	9	0	5	1	23	42	.55	13	19	2
Sierrathrissa										
S. leonensis	11-12	0	3	1	22-23	40	.56	13-14	17-18	2
Stolothrissa										
S. tanganicae	11-12	0	6-7	1	25-26	43	.59	15	15	2
Thrattidion										
T. noctivagus	11-12	0	5	0	21	45	.47	13-14	24	3
Microthrissa										
M. royauxi	7-10 (usually 9-10)	0	5	1	19	40-41	.47	13	22-24 (usually 24)	3
M. minuta	13	0	6	1	23	42	.55	14	20	3*
Clupeoides										
C. papuensis	10-11	0	5	1	21	42	.50	14	18-20	2
Hyperlophus										
H. vitattus	15	28-29(A)	4	1	28-29	48	.59	16-17	17-19	3
H. translucidus	13	17-18(A)	4	1	19-20	39-40	.49	15-16	20-22 (20,20,22)	3

Table 6a continued.

<u>Genus</u> <u>Species</u>	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
<u>Potamalosa</u>										
<u>P. richmondia</u>	11	14(A)	7	1	28	46	.61	16	14	3
†<u>Knightia</u>										
†<u>K. eocaena</u>	7	11-14(A) (usually 13)	7-8	1	21-23	37-38	.59	11-14 (usually 12-13)	13-15	3
†<u>K. alta</u>	7-8	10-13(A) (usually 12)	7-8	1	21-23	37	.59	11-13 (usually 12)	13-16	3
†<u>K. vetusta</u>	8	12(A)	7-8	1	21-22	38-39	.56	13-14	16-17	3

---

[1] (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

* 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 prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Spratellomorpha									
S. bianalis	-	-	-	-	+	-	A	-	-
Corica									
C. laciniata	+	+	-	-	+	-	A	-	-
Clupeichthys									
C. bleekeri	+	+	-	+	+	-	A	-	+
C. sp.	+	+	-	+	+	-	A	-	+
Ehirava									
E. malabarica	+	-	-	+	+	-	A	-	-
Gilcrestella									
G. aestuarius	+	-	-	-	+	-	A	-	-
Congothrissa									
C. gossei	-	-	-	+	+	-	A	-	-

Table 6b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Cynothrissa									
C. ansorgii	+	+	-[4]	+	+	-	A	-	+
C. mento	+	+	-[4]	+	+	-	A	-	+
Laeviscutella									
L. deKimpei	+	+[3]	-	+	+	-	A	-	-
Limnothrissa									
L. miodon	+	+	-	+	+	-	A	-	-
Nanothrissa									
N. parva	+	+	-[4]	+	+	-	A	-	-
N. stewarti	+	+	-[4]	+	+	-	A	-	-
Odaxothrissa									
O. vittata	+	+	-	+	+	-	A	-	+
O. losera	+	+	-	+	+	-	A	-	+

Table 6b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithrap.	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Pellonula									
P. vorax	+	+	-	+	+	-	A	-	-
P. afzeluisi	+	+	-	+	+	-	A	-	-
Poecilothrissa									
P. congica	+	+	-	+	+	-	A	-	-
Potamothrissa									
P. obtusirostris	+	+	-	+	+	-	A	-	-
P. acutirostris	+	+	-	+	+	-	A	-	-
Sierrathrissa									
S. leonensis	-	+ (reduced)	-	(no postcleithra)	-	-	-	-	-
Stolothrissa									
S. tanganicae	+	+	-	+	+	-	A	-	-
Thrattidion									
T. noctivagus	+ (reduced)	+ (reduced)	-	+	+	-	A	-	-
Microthrissa									
M. royauxi	+	+	+	+	+	-	A	-	-
M. minuta	+	+	-[4]	+	+	-	A	-	-

Table 6b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
<u>Clupeoides</u>									
<u>C</u>. <u>papuensis</u>	+	+	-	-	-	-	-	-	-
<u>Hyperlophus</u>									
<u>H</u>. <u>vitattus</u>	+	+	+	-	+[5]	-	-	-	-
<u>H</u>. <u>translucidus</u>	+	+	+	-	+[5]	-	-	-	-
<u>Potamalosa</u>									
<u>P</u>. <u>richmondia</u>	+	+	+	-	+[5]	+	-	-	-
†<u>Knightia</u>									
†<u>K</u>. <u>eocaena</u>	+	+	+	-	+[5]	?	-	-	-
†<u>K</u>. <u>alta</u>	+	+	+	-	+[5]	?	-	-	-
†<u>K</u>. <u>vetusta</u>	+	+	+	-	+[5]	?	-	-	-

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

3 lacking ascending arms.

4 only one or two scutes present below coracoid

5 anterior end of anterior rod like postcleithrum expanded.

Table 7a. Meristic information for some round herrings (Clupeoidei: Clupeoidea: Clupeidae: Dussumieriinae)

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Dussumieria										
D. acuta	21-22	0	15	2	37	55-56	.67	19	14	2
Etrumeus										
E. teres	10	0	14	1	34-35	49-50	.70	19	10	3
E. acuminatus	10-12 (usually 11)	0	16	1	40	54	.74	19	9-10	3
E. micropus	11	0	14	1	38	53-54	.71	20	11	3
Jenkinsia										
J. stolifera	6-8	0	6	1	26	42-44	.61	13	15	1
J. lamprotaenia	6-7	0	6	1	21-22 (usually 22)	38-39	.58	11-12	15	1
Spratelloides										
S. gracilis	11	0	7	2	32	47	.68	11-12	14	1
S. delicatulus	9	0	7	2	27	41-43	.64	12	10	1
S. robustus	9-10	0	7-8	2	31-32 ($\bar{x}$=31.75)	48-50	.65	12	10	1

[1] (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

Table 7b. Morphological information for some round herrings (Clupeoidei: Clupeoidea: Clupeidae: Dussumieriinae)

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
<u>Dussumieria</u>									
<u>D</u>. <u>acuta</u>	-	-	-	-	-	-	-	-	-
<u>Etrumeus</u>									
<u>E</u>. <u>teres</u>	-	-	-	-	+[3]	+	C	-	-
<u>E</u>. <u>acuminatus</u>	-	-	-	-	+[3]	+	C	-	-
<u>E</u>. <u>micropus</u>	-	-	-	-	+[3]	+	C	-	-
<u>Jenkinsia</u>									
<u>J</u>. <u>stolifera</u>	-	-	-	-	-	-	B	-	-
<u>J</u>. <u>lamprotaenia</u>	-	-	-	-	-	-	B	-	-
<u>Spratelloides</u>									
<u>S</u>. <u>gracilis</u>	-	-	-	-	-	-	A	-	-
<u>S</u>. <u>delicatulus</u>	-	-	-	-	-	-	A	-	-
<u>S</u>. <u>robustus</u>	-	-	-	-	-	-	A	-	-

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

3 anterior end of anterior rod-like postcleithrum is broadly expanded with laminar bone.

Table 8a. Meristic information for some gizzard-shads (Clupeoidei: Clupeoidea: Clupeidae: "Dorosomatinae")

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Dorosoma										
D. cepedianum	8-9 (x=8.80)	1-2(B)	6	2	26	49-50	.53	13-14[2]	29-32	2
D. anale	9	2(B)	6	2	47	47	.53	13[2]	31-35	2
D. smithi	8	?	6	2	22	45	.49	13-14[2]	25-27	2
Signalosa										
S. petense	8	1(B)	6	2	22-23	41-42	.54	14[2]	21-26 (usually 23-25)	2
Anodontostoma										
A. chacunda	8	0	5	1	23	41-42	.55	18	18-19	3
Clupanodon										
C. thrissa	8	23-25(A)	6	1	26	45	.58	15-16[2]	24	2-3
Konosirus										
K. punctatus	10	0	6	1	33	50	.66	17[2]	24	3
Nematalosa										
N. nasus	9	1(B)	6	1	26	46	.57	15[2]	20	3

Table 8a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
N. come	8	1(B)	5-6	1	25	44	.57	16[2]	22	3
N. erebi	8	1(B)	6	1	23-25	43-44	.54	14-15[2]	20-21	3
N. galatheae	8	1(B)	6	1	23	44	.52	16[2]	23	3
N. japonica	8	1(B)	6	1	29	48	.60	16[2]	21	3
N. vlaminghi	8	1(B)	6	1	26	46	.57	15[2]	22	3
Gonialosa										
G. manmina	9	?	5	1	26	45	.58	14-15	22	2-3

[1] (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only; (C) = above first dorsal pterygiophore only.

[2] 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 prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Dorosoma									
D. cepedianum	+	+	+	-	+[3]	+	-	-	-
D. anale	+	+	+	-	+[3]	+	-	-	-
D. smithi	+	+	+	-	+[3]	+	-	-	-
Signalosa									
S. petense	+	+	+	-	+[3]	+	-	-	-
Anodontostoma									
A. chacunda	+	+	+	-	+[3]	+	-	-	-
Clupanodon									
C. thrissa	+	+	+	-	+[3]	+	-	-	-
Konosirus									
K. punctatus	+	+	+	-	+[3]	+	-	-	-
Nematalosa									
N. nasus	+	+	+	-	+[3]	+	-	-	-
N. come	+	+	+	-	+[3]	+	-	-	-

Table 8b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
N. erebi	+	+	+	-	+[3]	+	-	-	-
N. galatheae	+	+	+	-	+[3]	+	-	-	-
N. japonica	+	+	+	-	+[3]	+	-	-	-
N. vlaminghi	+	+	+	-	+[3]	+	-	-	-
Gonialosa									
G. manmina	+	+	+	-	+[3]	?	-	-	-

---

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

3 anterior end of anterior rod-like postcleithrum is broadly expanded with laminar bone.

Table 9a. Meristic information for some shads (Clupeoidei: Clupeoidea: Clupeidae: "Alosinae")

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Alosa										
A. fallax	12-13	0	8	2	31	56-57	.55	17	22	1-2
A. sapidissima	11-12 (usually 11)	0	7-8 (usually 7)	2	33	56-57	.58	17-18	19-20	2
Pomalobus										
P. aestivalis	10-11 (usually 10)	1(B)	7	2	30-31	50-51 (usually 50)	.60	16-17	17-18	1-2 (usually 2)
P. pseudoharengus	9-12	0	7	2	27-28	48	.57	16-17 (usually 16)	17-18	3
Brevoortia										
B. tyrannus	11-12	0	7	2	27	48	.56	20	21-22	1-2
B. patronus	10-11	0	7	2	24-25	45-46	.54	20	21-22	2
Caspialosa										
C. tanaica	10-11	0	8	2	26	48	.54	15-17	18-19	2
Ethmalosa										
E. fimbriata	8	2	6	2	24	43	.56	16	19	3
Ethmidium										
E. maculatum	11	24(A)	9	2	31	49	.63	19	16	2

Table 9a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Gudusia										
G. chapra	8-9	0	6	2	21	41	.51	15	22	2-3
G. variegata	8	0	6	2	21	42	.50	16	27	3
Hilsa										
H. kelee	7	0	6	2	24	43	.56	17	20	2

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[1] (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 prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Alosa									
A. fallax	+	+	+	-	+[3]	+	-	-	-
A. sapidissima	+	+	+	-	+[3]	+	-	-	-
Pomalobus									
P. aestivalis	+	+	+	-	+[3]	+	-	-	-
P. pseudoharengus	+	+	+	-	+[3]	+	-	-	-
Brevoortia									
B. tyrannus	+	+	+	-	+[3]	+	-	-	-
B. patronus	+	+	+	-	+[3]	+	-	-	-
Caspialosa									
C. tanaica	+	+	+	-	+[3]	+	-	-	-
Ethmalosa									
E. fimbriata	+	+	+	-	+[3]	+	-	-	-

Table 9b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Ethmidium									
E. maculatum	+	+	+	-	?	?	-	-	-
Gudusia									
G. chapra	+	+	+	-	+[3]	+	-	-	-
G. variegata	+	+	+	-	+[3]	+	-	-	-
Hilsa									
H. kelee	+	+	+	-	+[3]	+	-	-	-

---

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 $PU_1 + U_1 = A$; $PU_1 + U_1 + U_2 = B$; and $U_1 + U_2 = C$.

3 anterior end of anterior rod-like postcleithrum is broadly expanded with laminar bone.

Table 10a. Meristic information for some herrings (Clupeoidei: Clupeoidea: Clupeidae: "Clupeinae")

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Clupea										
C. harengus	18-19 (usually 18)	0	8	2	35-37 (usually 36)	56-57	.64	17-18 (usually 18)	16-18	2
C. pallasii	15-16 (usually 16)	0	8	2	34-35	52-53	.66	17-18 (usually 18)	15-16	1-2 (usually 2)
Strangomera										
S. bentincki	15	0	7	2	26	44	.59	17	17	2
Sprattus										
S. sprattus	17	0	7	2	28	48	.58	18	19	3
S. antipodum	15	0	7	2	26-27	45-46	.58	17-18	16-18	3
Ramnogaster										
R. arcuata	15	0	7	2	23	44	.52	18	22	3
R. pallida	7-8 (usually 8)	0	6	2	24	42	.57	18	17-19	3
Amblygaster										
A. sirm	8	0	6	2	27	43-44	.62	19-20	17-18[2]	3
A. leiogaster	8	0	6	2	25	44	.57	18	17[2]	3

Table 10a continued.

Genus *Species*	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Clupeonella										
C. cultiventris	11	0	7	2	23-24	42	.56	15	18-21	1-2 (usually 2)
Sardinops										
S. caerulea	10	0	7	2	33	52	.63	18	17[2]	2-3
S. melanosticta	10	0	7	2	31-32	51	.62	18-19	17-18[2]	3
S. neopilchardus	10	0	7	2	32	50	.64	18-19	17-18[2]	3
S. pilchardis	10-11 (usually 11)	0	7	2	30-31	50-51	.60	17-18	17-19[2]	3
Sardinella										
S. aurita	9-10	0	6	2	30	48	.63	18	17[2]	2
S. anchovia	9-10 (usually 9)	0	6	2	29	46-47	.62	17	16-17[2]	3[4]
S. longiceps	9	0	6	2	28	47	.60	??	16[2]	3[4]
S. gibosa	9	0	6	2	27-28	45-47	.60	17	18-19[2]	3
S. maderensis	9	0	6	2	27-28 (usually 27)	46-47 (usually 46)	.59	18-19 (usually 18)	17-20[2]	3

Table 10a continued.

Genus Species	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
S. marquesensis	8	0	6	2	26-27 (usually 27)	44	.61	18-19 (usually 18)	16-18[2]	2-3 (usually 3)
S. pinnula	9	0	6	2	27-28	46	.60	16	16-17[2]	3[4]
S. sindensis	9	0	6	2	29	47	.62	16	18[2]	3
S. zunasi	8	0	6	2	25	43-44	.58	17-18	17-19[2]	3
Escualosa										
E. thoracata	10	0	4	2	22	40	.55	15	17-19	2
Harengula										
H. clupeola	7	1(B)	6	2	25-26	41-42	.61	16-17	17	2-3 (usually 3)
H. humeralis	7	1(B)	6	2	23	40	.58	16-17	16-19	3
H. jaguana	7	1(B)	6	2	25	41	.61	16-17 (usually 17)	16-18	3
H. thrissina	7	1(B)	6	2	25-26	42	.61	17	14-15	3
Herklotsichthys										
H. dispilonotus	7	1(B)	6	2	22-23 (usually 22)	39	.56	18	17-18	3
H. castelnaui	8	1(B)	6	2	23-24 (usually 23)	41	.56	16-18	17-19	3

Table 10a continued.

Genus Species	Predorsal bones	Dorsal scutes^1	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
H. koningsbergeri	10	1(B)	6	2	19-21 (usually 20)	39-40 (usually 40)	.50	13-14	19-23	3
H. quadrimaculatus	8	1(B)	6	2	25-26 (usually 26)	43-44	.60	18	17-18	2-3
Lile										
L. stolifera	9-10 (usually 9)	0	6	2	24	42-43	.56	17	17-18	3
L. piquitinga	8	0	6	2	23	40	.58	15-17 (usually 16)	15-17	2
Opisthonema										
O. libertate	8	1(B)	6	2	28	46	.61	18^3	19	3
O. medirastre	?	1(B)	6	2	28	47	.60	19^3	18	3
O. oglinum	7-9	1(B)	6	2	27-28	45-46	.60	18-19^3	21-22 (usually 21)	3
Platanichthys										
P. platana	10-11	0	5-6	2	21-22	40-41	.53	13	19-20	3
Rhinosardinia										
R. bahiensis	12	0	5	2	24	43	.56	15	16	2
R. serrata	10	0	5	2	20-21	36-38	.55	13-14	14	2

Table 10a continued.

Genus *Species*	Predorsal bones	Dorsal scutes[1]	Branchiostegal rays	Supramaxillary bones	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-Preural vertebrae ratio	Dorsal fin pterygiophores	Anal fin pterygiophores	Epurals
Tenualosa										
T. toli	8	1(B)	?	2	27	44	.61	18	17	3
†*Gosiutichthys*										
†*G. parva*	6-7	10-13 (usually 12-13)	7-8	2	20-21	34-36	.59	10-11	10-13	3
†*Ellimma*										
†*E. branneri*	6-7	9-11	7	2	17	31-32	.54	13	13	2-3
†*E. elmodenae*	14	0	?	2	26	44	.59	16-18	18	?
†*Xyne*										
†*X. grex*	?	0	?	2	26	44	.59	?	?	3
†"*Clupea*" (Monte Bolca)										
†"*C.*" *catopygoptera*	8	0	7	2	21-22	41	.53	14-15	15-17	3

1 (A) = between skull and dorsal fin; (B) = between skull and first predorsal bone only;
(C) = above first dorsal pterygiophore.

2 last two anal fin rays elongated.

3 last dorsal fin ray elongated into a long filament.

4 several specimens have the last two epurals fused together at their bases.

Table 10b. Morphological information for some herrings (Clupeoidei: Clupeoidea: Clupeidae: "Clupeinae")

<u>Genus</u> <u>Species</u>	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
<u>Clupea</u>									
<u>C. harengus</u>	+	+	+	-	+[3]	+	-	-	-
<u>C. pallasii</u>	+	+	+	-	+[3]	+	-	-	-
<u>Strangomera</u>									
<u>S. bentincki</u>	+	+	+	-	+[3]	+	-	-	-
<u>Sprattus</u>									
<u>S. sprattus</u>	+	+	+	-	+[3]	+	-	-	-
<u>S. antipodum</u>	+	+	+	-	+[3]	+	-	-	-
<u>Ramnogaster</u>									
<u>R. arcuata</u>	+	+	+	-	?	+	-	-	-
<u>R. pallida</u>	+	+	+	-	+[3]	+	-	-	-
<u>Amblygaster</u>									
<u>A. sirm</u>	+	+	+	-	+[3]	+	-	-	-
<u>A. leiogaster</u>	+	+	+	-	+[3]	+	-	-	-

Table 10b continued.

Genus *Species*	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum^1	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae^2	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Clupeonella									
C. cultiventris	+	+	+	-	+^{3}	+	A	-	-
Sardinops									
S. caerulea	+	+	+	-	+^{3}	+	-	-	-
S. melanosticta	+	+	+	-	+^{3}	+	-	-	-
S. neopilchardus	+	+	+	-	+^{3}	+	-	-	-
S. pilchardis	+	+	+	-	+^{3}	+	-	-	-
Sardinella									
S. aurita	+	+	+	-	+^{3}	+	-	-	-
S. anchovia	+	+	+	-	+^{3}	+	-	-	-
S. longiceps	+	+	+	-	+^{3}	+	-	-	-
S. gibosa	+	+	+	-	+^{3}	+	-	-	-
S. maderensis	+	+	+	-	+^{3}	+	-	-	-
S. marquesensis	+	+	+	-	+^{3}	+	-	-	-

Table 10b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
S. pinnula	+	+	+	-	+[3]	+	-	-	-
S. sindensis	+	+	+	-	+[3]	+	-	-	-
S. zunasi	+	+	+	-	+[3]	+	-	-	-
Escualosa									
E. thoracata	+	+	+	-	+[3]	+	-	-	-
Harangula									
H. clupeola	+	+	+	-	+[3]	+	-	-	-
H. humeralis	+	+	+	-	+[3]	+	-	-	-
H. jaguana	+	+	+	-	+[3]	+	-	-	-
H. thrissina	+	+	+	-	+[3]	+	-	-	-
Herklotsichthys									
H. dispilonotus	+	+	+	-	+[3]	+	-	-	-
H. castelnaui	+	+	+	-	+[3]	+	-	-	-

Table 10b continued.

Genus *Species*	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
H. koningsbergeri	+	+	+	-	+[3]	+	-	-	-
H. quadrimaculatus	+	+	+	-	+[3]	+	-	-	-
Lile									
L. stolifera	+	+	+	-	+[3]	+	-	-	-
L. piquitinga	+	+	+	-	+[3]	+	-	-	-
Opisthonema									
O. libertate	+	+	+	-	+[3]	+	-	-	-
O. medirastre	+	+	+	-	+[3]	+	-	-	-
O. oglinum	+	+	+	-	+[3]	+	-	-	-
Platanichthys									
P. platana	+	+	+	-	+[3]	+	-	-	-
Rhinosardinia									
R. bahiensis	+	+	+	-	+[3]	+	-	-	-
R. serrata	+	+	+	-	+[3]	+	-	-	-

Table 10b continued.

Genus Species	Presence of prepelvic abdominal scutes	Presence of postpelvic abdominal scutes	Posterior edge of coracoid lined with scutes	Articulation of postcleithra with supracleithrum well behind cleithrum[1]	Presence of two long rod-like postcleithra	A third, scale-shaped postcleithrum present, anterior to the two long rod-like postcleithra	Fusion of caudal vertebrae[2]	Absence of interlobar notch on third hypural	Large caniniform teeth in jaw
Tenualosa									
T. toli	+	+	+	-	+[3]	+	-	-	-
†Gosiutichthys									
†G. parva	+	+	+	-	+[3]	+	-	-	-
†Ellimma									
†E. branneri	+	+	+	-	?	?	-	?	-
†E. elmodenae	+	+	+	-	+[3]	?	?	?	-
†Xyne									
†X. grex	+	+	+	-	+	?	-	-	-
†"Clupea" (Monte Bolca)									
†C. catopygoptera	+	+	+	-	+[3]	?	-	-	-

1 with a well defined space between the postcleithra and the cleithrum (see figure 22).

2 PU_1+U_1 = A; $PU_1 + U_1 + U_2$ = B; and $U_1 + U_2$ = C.

3 anterior end of anterior rod-like postcleithrum is moderately to broadly expanded with laminar bone.

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; and others) have used the groups Clupeomorpha and Clupeoidei to include most 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, diverticululum of the swimbladder, recessus lateralis, etc.) are only rarely preserved in fossils. In the opinion of the author the _incertae sedis_ category should be more widely used so not to disrupt classificatory systems based on Recent and well preserved, diagnosable, fossil specimens. For example, +_Ostariostoma wilseyi_ Schaeffer, 1949, should be classified Teleostei, _incertae sedis_ rather than in Clupeoidea. Schaeffer's (p. 15) reason for placement in Clupeoidea is given as "because the general level of organization indicates this allocation at the present time rather than any other." It (latex cast of type, PV 14728) shows no derived character indicating it is a clupeomorph, and therefore 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* at a very general level because of lack of preservation (*i.e*. insufficient morphological information). For examaple $^+$"*Diplomystus*" *solignaci* Gaudant and Gaudant, 1971 (removed 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 it is at least *incertae sedis* within Clupeomorpha Div. 2. But most of the caudal skeleton and skull are not preserved and the morphology of its dorsal scute is unknown; consequently this species cannot presently be placed within any clupeomorph div. 2 subgroup.

The presence of abdominal scutes is probably the most useful character for identifying fossils as clupeomorphs, because this appears to be unique to clupeomorphs, and are usually well preserved and easy to see on fossil specimens (fig. 25). Many problems arise from the placement of fossils within Clupeomorpha because of some superficial resemblance to *Chirocentrus*, a scuteless Recent clupeomorph. If a fossil lacks the obvious character of abdominal scutes (such as +*Ostariostoma*, +ichthyodectids, etc.) then other characters (such as a pterotic and/or prootic bullae, a recessus, etc) should be found before placing the taxon within Clupeomorpha. A character frequently used to identify scuteless fossil taxa as being clupeomorphs is the caudal skeleton character (see character 1 above). An example of such a usage is for +*Ornategulum* (see Forey, 1973). As discussed above, this feature is almost, but not entirely, unique to clupeomorph fishes and should be used in conjunction with other character information if possible (Forey, 1973: p. 1317 also mentions possible evidence of diverticulum of swim-bladder and [p. 1309] prootic bullae). One specimen of +*Ornategulum* observed here (BMNH P 47877 - a transfer preparation of a skull) shows a sphericle swelling of thin bone in the prootic region which strongly resembles a prootic bulla.

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, most species that have been assigned to the genus +*Diplomystus* should be assigned only to Clupeomorpha Division 2 *incertae sedis*. Their placement into the

+ellimmichthyiform genus was done on the basis of superficial primitive similarities (the presence of both dorsal and abdominal scutes). The problems of such placements are discussed in Grande, 1982a, and in that paper many species are removed from the genus +*Diplomystus*.

Many fossil clupeids which should presently be classified as Clupeidae *incertae sedis* remain instead assigned to the genus *Clupea* Linnaeus (such as +"*Clupea*" *humilis* von Meyer, 1851; +"*Clupea*" *catopygoptera* Woodward, 1901; and over a dozen other species). Most of them were described in the 19th 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. The fossils described as *Clupea* are 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 tenuous 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). This convention is adopted here whenever the implied generic relationship of a fossil is in doubt. If the species is found later not to be closely related to the other members of the genus it is described in (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.

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 II *incertae sedis*; and based on his (1979) reconstructions, the Uyeno species are probably clupeoids.

Luisiella inexcutata 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. He then places the species in Dussumieriidae because it lacks scutes. Here this species is presently Teleostei *incertae sedis* (see discussion under character f).

One of the future goals of the author is to re-examine most of the fossils that have been described as clupeomorphs and to reasses their placement. So far, although several fossil species have been examined (here; and Grande 1982a and 1982b) the majority have yet to be seen. Many fossil species described as "dussumieriids" (preliminary observation) or chirocentrids (Patterson and Rosen, 1977) do not even appear to be clupeomorphs.

To the revision of the fossil clupeid, +*Knightia* (Grande, 1982b) the following information can be added. The designated cotypes of +"*Knightia*" *brasiliensis* Woodward, 1939 (BMNH 25259-25266) were examined and they lack dorsal scutes, thus excluding this species from the genus +*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, +"*Clupea*" *vectensis* Newton, 1889, does not (as suggested in Grande, 1982b: p. 14) appear to be closely related to +*Knightia*, because one specimen (BMNH 39302) clearly shows the presence of two supramaxillary bones in this species. As suggested elsewhere (Grande 1982b), the known geographic range of +*Knightia* is Western North America only. Also, a specimen of an isolated braincase of +*Knightia eocaena* Jordan, 1907, (BMNH P 61170) was discovered which indicates that +*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 +*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 preceeding 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 *Gastropelecus* (see Signeux, 1964: plate 1) in the pectoral fin and fin support, but the head and caudal skeleton (visible on MNMH 1963-11 and 1963-16) like the dorsal and abdominal scutes, indicate that this is 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 an undoubted $^{+}$clupavid. Previously (Grande, 1982a: p. 2728) I stated that if Taverne's (1977b) restorations of $^{+}$Clupavidae (=$^{+}$*C. maroccanus*) were correct, than the family may belong in Clupeoidei (influenced mainly by his fig. 9 of the caudal skeleton). Upon examination of the material (MNHM T. 243 G and D - caudal skeleton; and 257g - skull) there appears to be 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) resembles the clupeoid condition, is in fact subject to several different interpretive reconstructions. The fossils are all tiny impressions, and drawings are made using latex or clay peels. Therefore dissection of specimens to see underlying bones is not possible. Inpterpretations on a single specimen can differ strikingly [see fig. 9 in Taverne, 1977b and compare with figs. 16 and 17 in Gayet, 1981 for example. Tavern illustrates $^+$C. 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 restorations are based on essentially the same specimens, 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.

SUMMARY AND CONCLUSIONS

This study of the osteology and interrelationships of clupeomorph fishes used the largest, most diverse collection of clupeomorph skeletons ever prepared. This made possible not only a survey of a very large study sample for new synapomorphies, but also the 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 figs. 1A, 9, 14, 18 and 21, and character numbers below correspond to numbers in those cladograms.

The superorder Clupeomorpha can be diagnosed by: 1)hypural 2 fused with the first ural centrum, and an autogenous first hypural; 2) the presence of an otophysic connection involving a diverticulum of the swim-bladder that penetrates the exoccipital and then expands to form ossified bullae in the prootic and usually also in the pterotic; and 3) the supratemporal commisural sensory canal primitively passing through parietals and supraoccipital. Clupeomorpha contains two subgroups here: Division 1 (including only one species, +Ornategulum sardinioides) and Division 2 (containing all other known clupeomorphs).

Clupeomorpha Division 2 can be diagnosed by: 4) the presence of one or more abdominal scutes, each of a single (unpaired) element which crosses the ventral midline of the fish; 5) the presence of a well-defined pre-epiotic fossa; and 6) the presence of 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.

The order +Ellimmichthyiformes cam be diagnosed by: 7) the peculiar morphology of its dorsal scutes (see above), and contains one species of $^{+}$*Ellimmichthys* and three 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.

The order Clupeiformes can be diagnosed by several characters including: 9) the presence of a recessus lateralis; 10) the parietals being completely separated (medially) by the supraoccipital; and 11) the loss of middle radials in the anal fin supports. Clupeiformes contains two subgroups here: Denticipitoidei (containing two monotypic genera - one fossil) and Clupeoidei (containing the rest of the Clupeiformes).

The suborder Denticipitoidei can be diagnosed by: 12) the presence of odontodes (teeth) covering the dermal bones of the skull and 13) reduction in number of uroneurals in caudal skeleton to only one. Several other skeletal features unique to denticipitoids are listed in Greenwood, 1968.

The suborder Clupeoidei can be diagnosed within clupeomorpha by: 14) the fusion of the first uroneural with the first preural centrum; 15) reduction in relative size of the first ural centrum, 16) the loss of most or all of the lateral line scale canals and 17) separation of the parhypural from the first ural centrum (except for *Dussumieria* and *Etrumeus* where fusion is probably secondary and derived for *Dussumierini*). Also derived for Clupeoidei is the space between hypural 1 and ural centrum 1 (in other clupeomorphs hyp 1 articulates with U1). Clupeoidei contains three subgroups here (an unresolved trichotomy): Engrauloidea, Pristigasteroidea and Clupeoidea.

The superfamily Engrauloidea (the anchovies) can be diagnosed by several osteological characters including: 18) a suspensorium that is inclined obliquely backward and 19) the presence of a overhanging snout with the mesethoid projecting in advance of the vomer.

The superfamily Pristigasteroidea is thought to have at least two synapomorphic characters including: 20) vertically or antero-dorsally inclined predorsal bones and 21) the absence of the interlobar notch in the third hypural. Nelson (1967) also considered the peculiar type of basihyal dention of this group as possibly unique among teleosts. Within the Pristigasteroidea, the interrelationships are in need of futher study. The genus *Ilisha* is not monophyletic and should be reexamined and revised. Some subgroups of pristigasteroids have characters that appear to be unique, at least among clupeomorphs, such as Pristigasteridae (as used here) which all have a bony process on the first pleural rib which articulates with the shoulder girdle. Pristigasteroids are still under study by the author.

The superfamily Clupeoidea appears to be derived among clupeomorph fishes in having 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 the presence of two rod-like postcleithra. Within Clupeidae, two subgroups can be osteologically diagnosed (Dussumieriinae and Pellonulinae). Most of the rest of Clupeidae ("Dorosomatinae", "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: Dussumierini (containing Dussumieria and Etrumeus) and Spratelloidini (containing Spratelloides and Jenkinsia).

The tribe Dussumierini can be diagnosed by the presence of an extremely high number of branchiostegal rays (within clupeomorpha) and the fusion of the parhypural to preural centrum 1 (within Clupeiformes).

The tribe Spratelloidini can be diagnosed by the expansion of the fourth hypural, reduction in number of epurals to 1, fusion of the first ural centrum to the first preural centrum, and reduction of the number of infraorbital bones to 5.

The subfamily Pellonulinae is somewhat more 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 diagnosed by a peculiar arrangement of the postcleithra, and includes the monotypic genus Congothrissa (originally described in its own monotypic family, "Congothrissidae"). The tribe Ehiravini is diagnosed by the morphology of the sensory openings to the recessus, and contains a subgroup (Division A here) diagnosed 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, diagnosable by the presence of a mediopharyngobranchial, but this problem is still under study.

With the comparative skeletal information compiled here, in the form of cladograms, many fossil clupeomorphs can more easily be reviewed, redescribed, and accurately classified. The state of the literature on nearly complete fossil clupeomorph species has been relatively inadequate, mainly because many paleontologists are unwilling or unable to examine thoroughly the Recent fishes, and many neoichthyologists are reluctant to work with fossil material for various reasons. Fishes are fishes, whether they are fossil or Recent species, and therefore systematic studies of any taxonomic groups should contain both Recent and all of the adquately preserved fossil species. In general, the more taxa that are examined, the more sure the 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). Although I would not recommend ignoring adequately preserved fossil material, the Recent material will generally be more useful in systematic studies of group interrelationships, because of one main practical (non-theoretical) 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 relatively 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 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.

Hopefully, at least with fishes (which tend to be quite well preserved as fossils) the distinction between paleoichthyology and neoichthyology will become less and less important, theoretical differences between systematists will become less important, and systematic specialists will beome concerned once more with the comparative anatomical studies of groups of fossil and Recent animals.

It has been shown by this survey of clupeomorph species that osteological characters can be used to diagnose many monophyletic clupeomorph groups. By using skeletal characters, fossils can be incorporated into the classificatory system with reasonable accuracy. 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 and 2) discovering the relationships of the members of Clupeinae, Alosinae and Dorosomatinae (currently under study by the author), 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 pellonuline, *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* (Lesuer), 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.

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FIGURES AND CAPTIONS

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. +*Ornategulum*, +*Armigatus* and +*Ellimmichthys* are monotypic taxa.

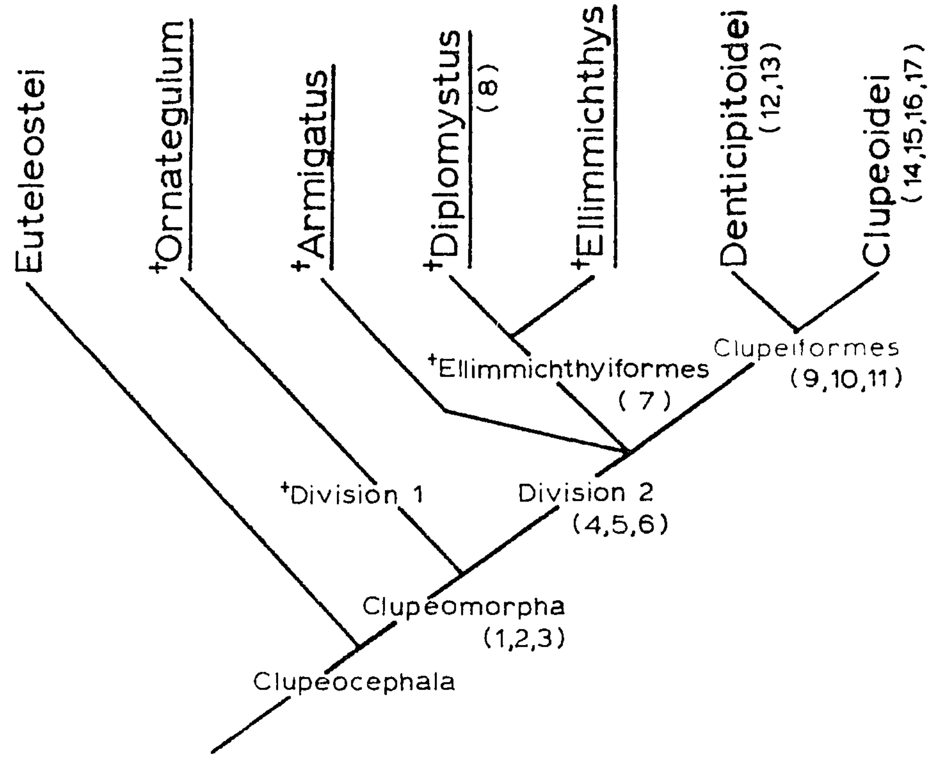

Euteleostei
+Ornategulum
+Armigatus
+Diplomystus
(8)
+Ellimmichthys
Denticipitoidei
(12,13)
Clupeoidei
(14,15,16,17)
+Ellimmichthyiformes
(7)
Clupeiformes
(9,10,11)
+Division 1
Division 2
(4,5,6)
Clupeomorpha
(1,2,3)
Clupeocephala

Figure 1A

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

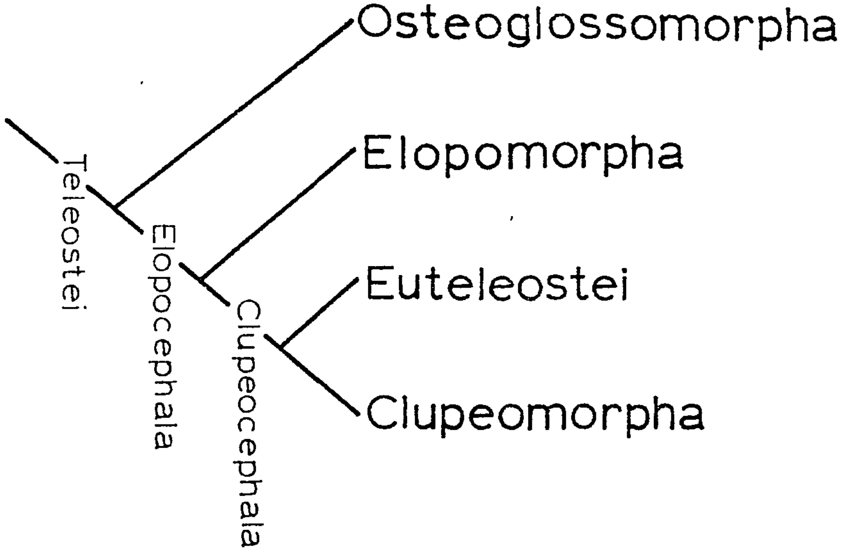

Osteoglossomorpha
Elopomorpha
Euteleostei
Clupeomorpha
Teleostei
Elopocephala
Clupeocephala

Figure 1B

Fig. 2. Clupeoid classifications by various authors.

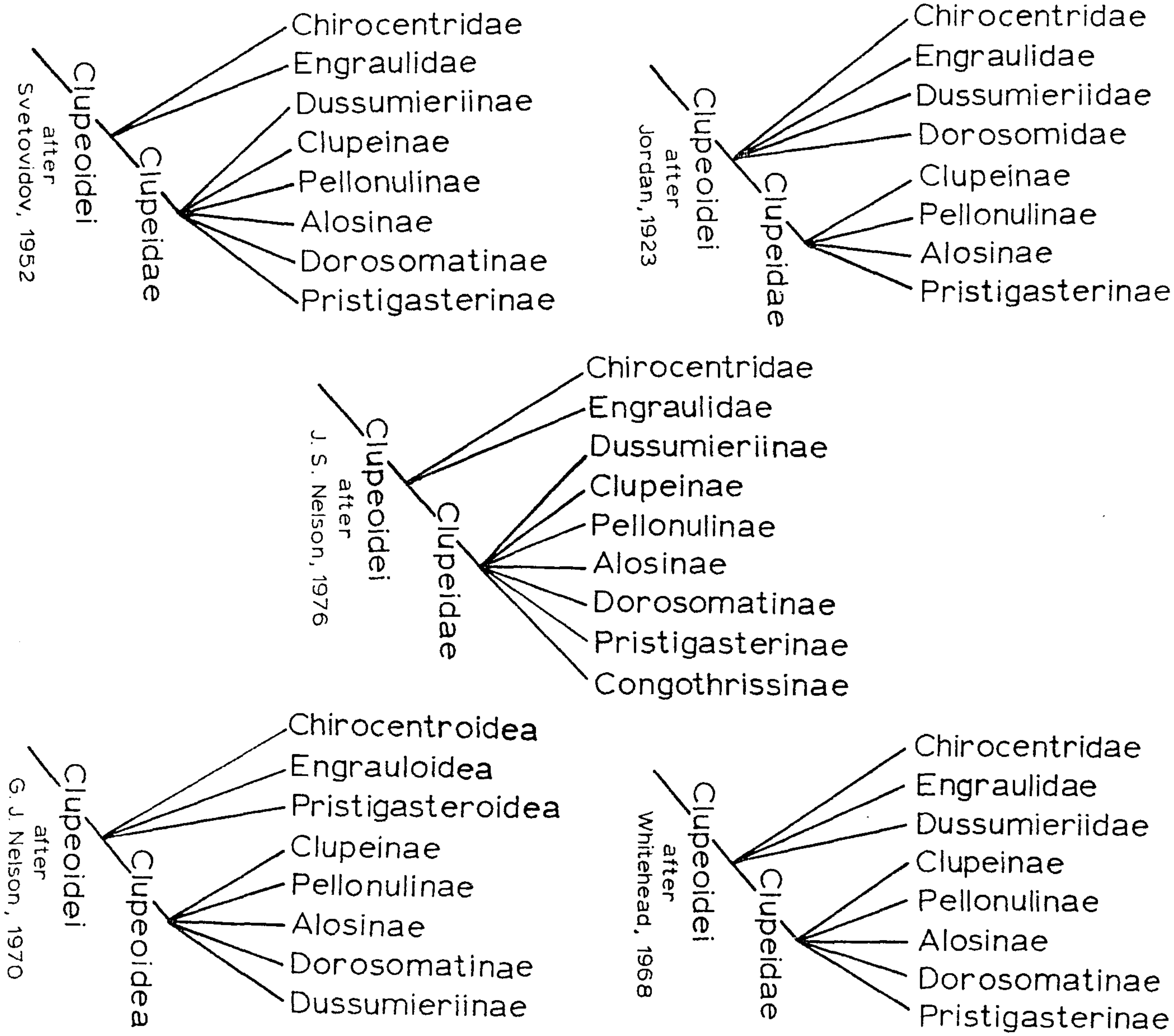
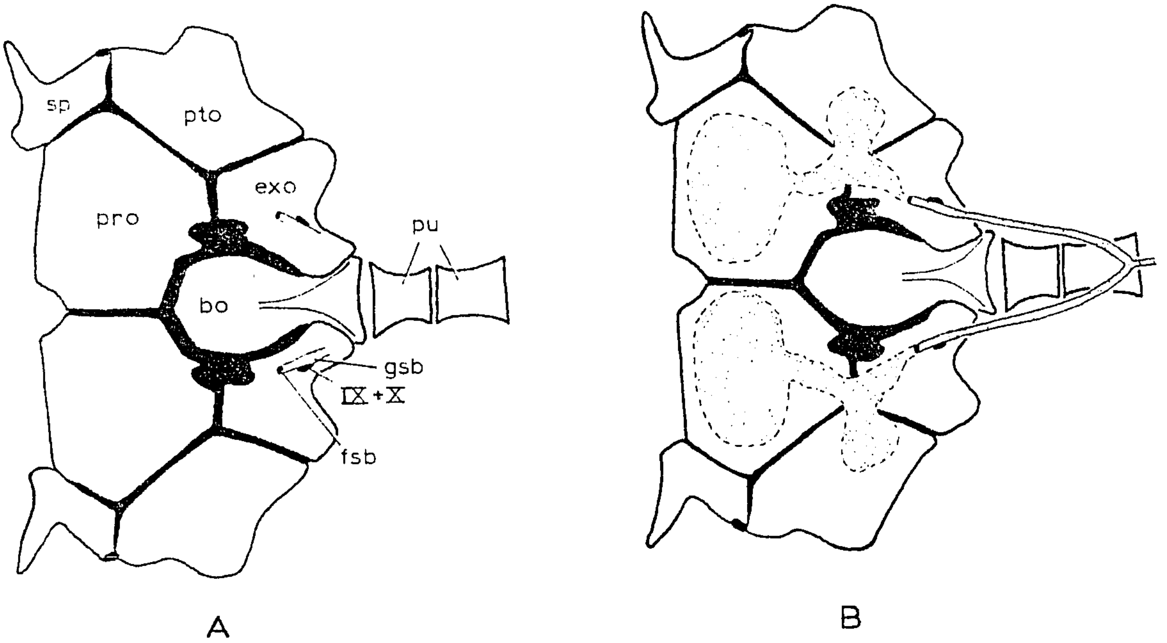

Clupeoidei
after
Svetovidov, 1952
Clupeidae
Chirocentridae
Engraulidae
Dussumieriinae
Clupeinae
Pellonulinae
Alosinae
Dorosomatinae
Pristigasterinae
Clupeoidei
after
Jordan, 1923
Clupeidae
Chirocentridae
Engraulidae
Dussumieriidae
Dorosomidae
Clupeinae
Pellonulinae
Alosinae
Pristigasterinae
Clupeoidei
after
J. S. Nelson, 1976
Clupeidae
Chirocentridae
Engraulidae
Dussumieriinae
Clupeinae
Pellonulinae
Alosinae
Dorosomatinae
Pristigasterinae
Congothrissinae
Clupeoidei
after
G. J. Nelson, 1970
Clupeoidea
Chirocentroidea
Engrauloidea
Pristigasteroidea
Clupeinae
Pellonulinae
Alosinae
Dorosomatinae
Dussumieriinae
Clupeoidei
after
Whitehead, 1968
Clupeidae
Chirocentridae
Engraulidae
Dussumieriidae
Clupeinae
Pellonulinae
Alosinae
Dorosomatinae
Pristigasterinae

Figure 2

Fig. 3. Ventral view of posterior part of cranium (parasphenoid removed) in _Jenkinsia_ (modified after Cervigon 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.

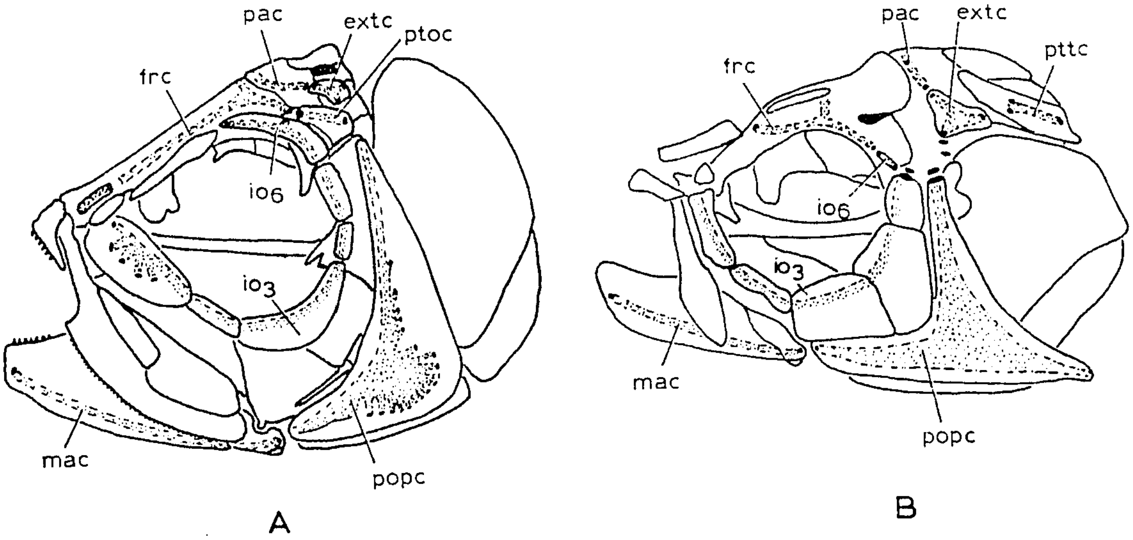


A

B

Figure 3

Fig. 4. The sensory canals (stippled) and dermosphenotics (io 6) of two primitive clupeomorphs; A) +Armigatus brevissimus (modified after Patterson, 1967); and B) Denticeps clupeoides (modified after Greenwood, 1968--odontodes omitted). The supraorbitally positioned dermosphenotic is large in +Armigatus and +ellimmichthyiforms (as in A); highly reduced in denticipitoids (as in B); and absent (or moved to a post orbital position) in all clupeoids (as in figs. 27A and 40A). The dermosphenotic of +Ornategulum has not been described and was not observed here.


pac
extc
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popc
A
pac
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B

Figure 4

Fig. 5. The skull roof of +Ornategulum sardinioides (after Forey 1973).

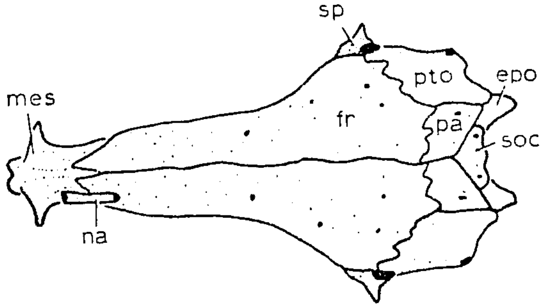


Figure 5

Fig. 6. Middle radials in the anal fins of A) +*Diplomystus dentatus* (AMNH 1330 - sl=375 mm; 7th and 8th radial sets with fin rays) and B) +*Diplomystus birdi* (AMNH 11425 - sl=51 mm; 3rd radial set with fin ray). Portion of fin ray which normally covers distal radial is removed in both A and B.

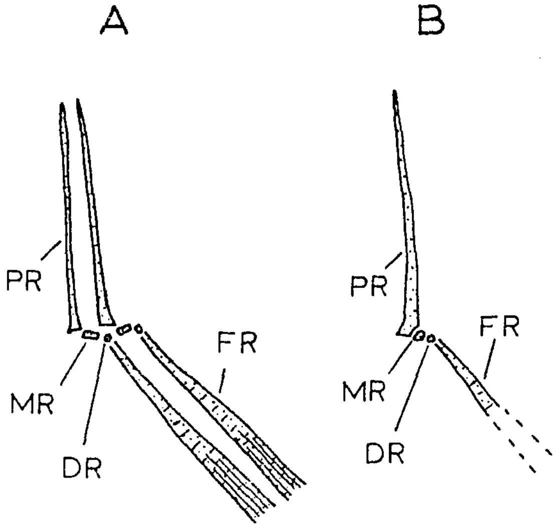


Figure 6

Fig. 7. A) The skull of Denticeps clupeoides showing the distribution of the odontodes (from Greenwood, 1968: fig. 1); B) The caudal skeleton of Denticeps clupeoides drawn from AMNH 53082 sw (sl=38 mm).

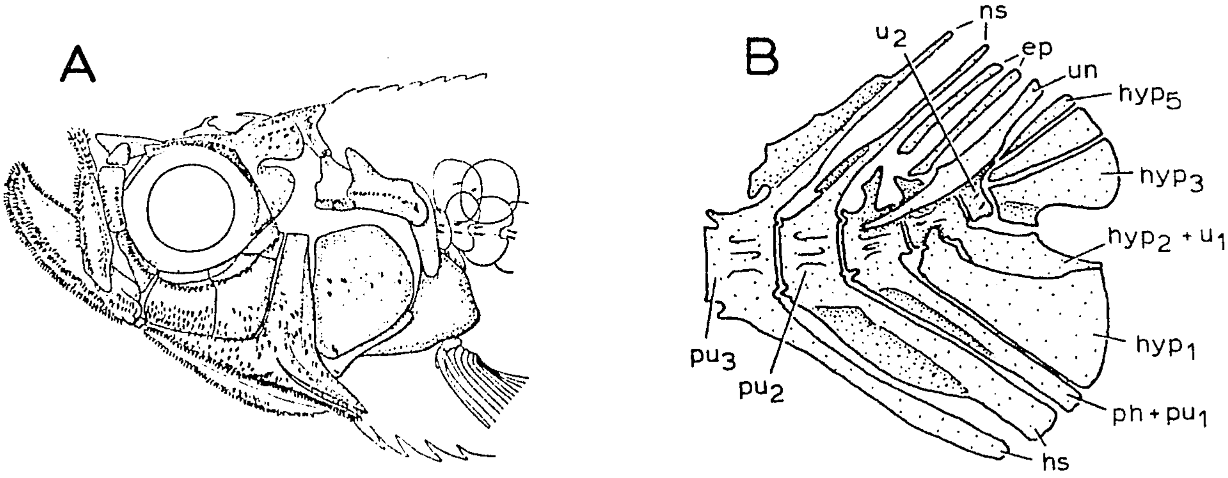


Figure 7

Fig. 8. The caudal skeleton of +*Diplomystus dentatus*, after Cavender (1966: fig. 4).

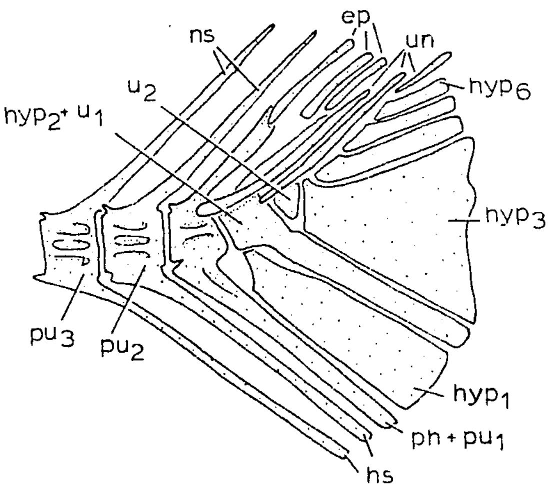


Figure 8

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 genus) and characters 14-23 and f and m discussed in text.

Figure 9

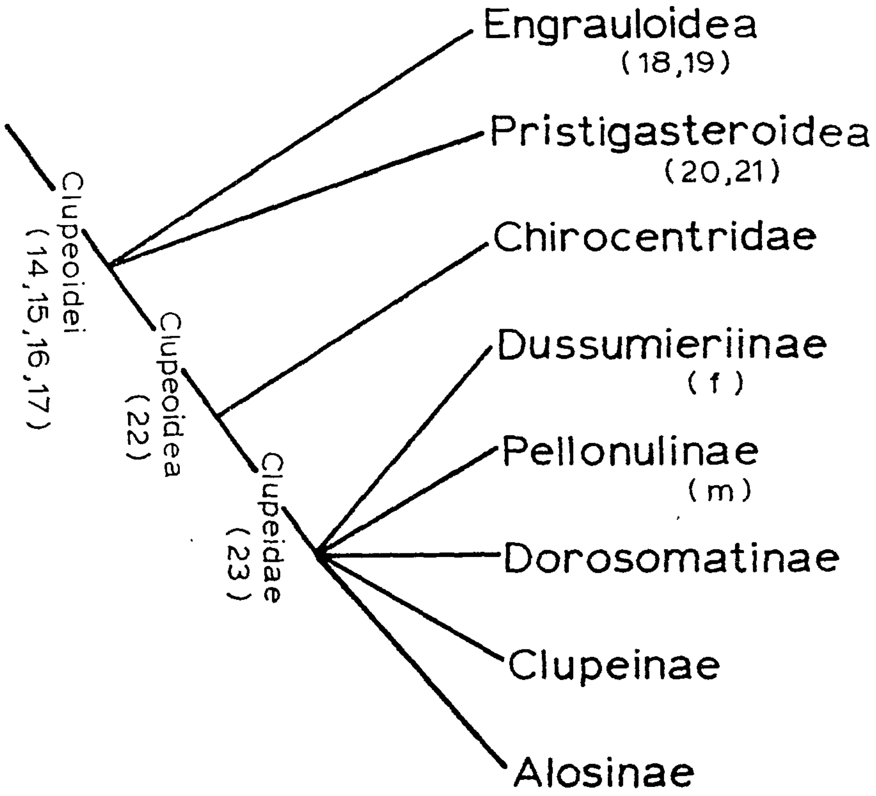

Engrauloidea
(18,19)
Pristigasteroidea
(20,21)
Chirocentridae
Dussumieriinae
(f)
Pellonulinae
(m)
Dorosomatinae
Clupeinae
Alosinae
Clupeoidei
(14,15,16,17)
Clupeoidea
(22)
Clupeidae
(23)

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 pig-like nose and oblique orientation of suspensorium; B) medial view of jaws, part of suspensorium and opercular bones, showing anteriorally 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).

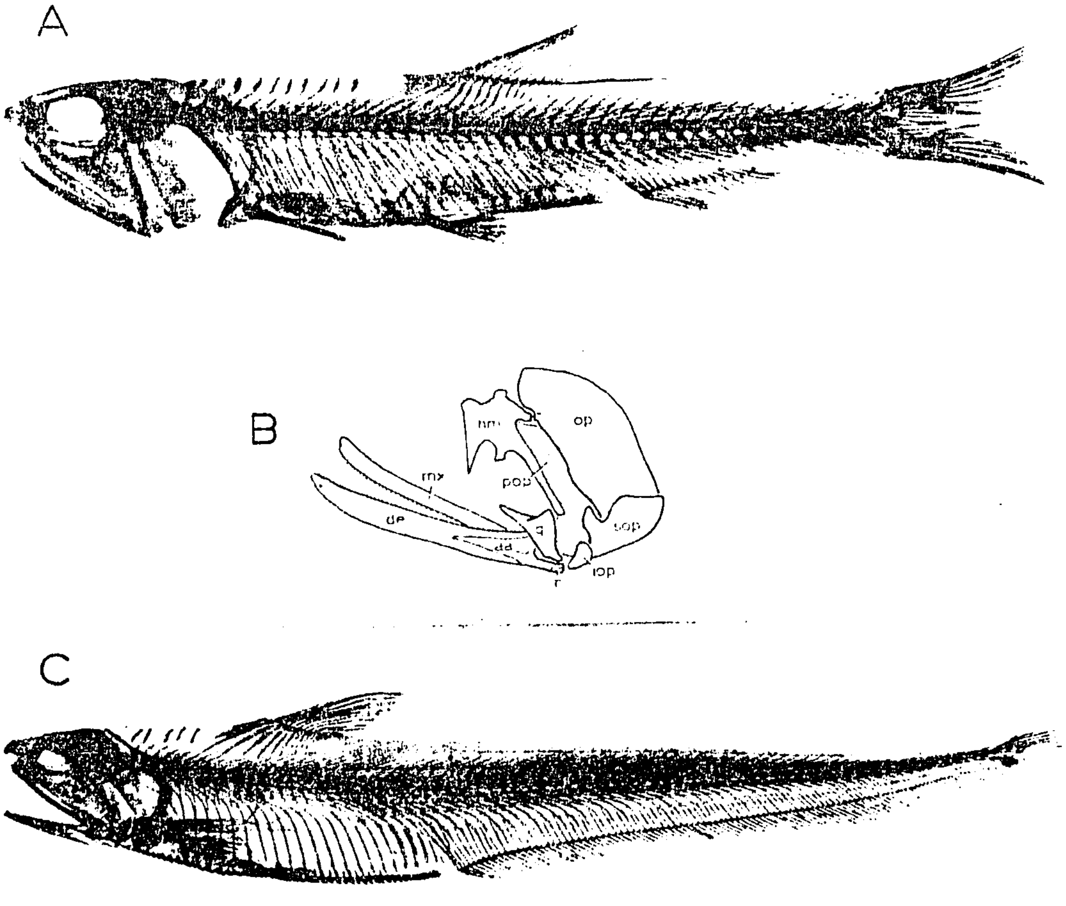


Figure 10

Fig. 11 A-B. Pristigasterids, showing the vertical to anteriorly inclined predorsal bones (compare these and figs. 11 C-J with figs. 11 K-S, 10, 24, 25, 26B, and 39B) and various other features discussed in text. A) Ilisha elongata (AMNH 35811 sw) (sl=127 mm); B) Pliosteostoma lutipinnis (SU 39322) (sl=119 mm). Fig. B, a print from a radiograph; fig. A, a cleared and stained specimen with hypobranchial apparatus and right facial bones removed.

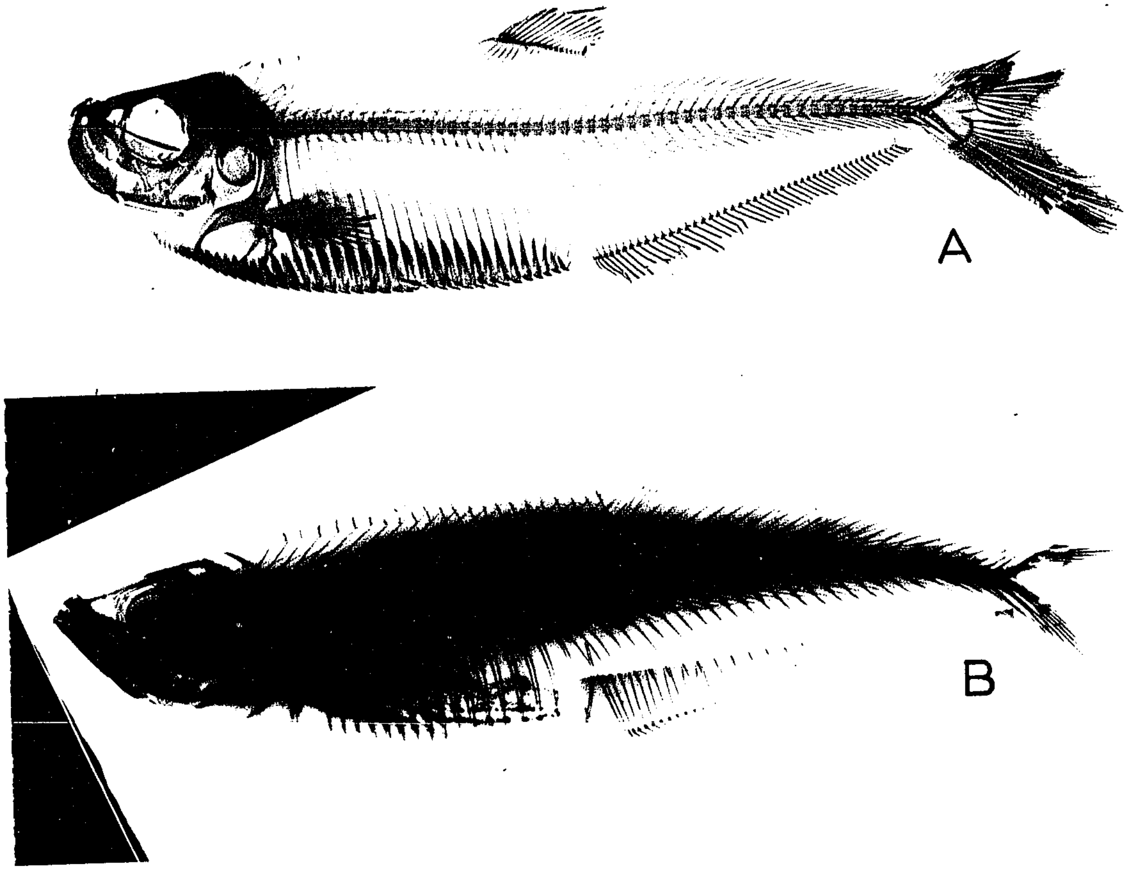


Figure 11 A-B

Fig. 11 C-E. Pristigasterids (see caption for fig. 11 A-B). C) Pellona harroweri (AMNH 20759 sw) (sl=64 mm); D) Chirocentrodon bleekerianus (AMNH 10118 sw) (sl=78 mm); E) Neopisthopteris tropicus (AMNH 53084 sw) (sl=55 mm). Figs. C-E are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

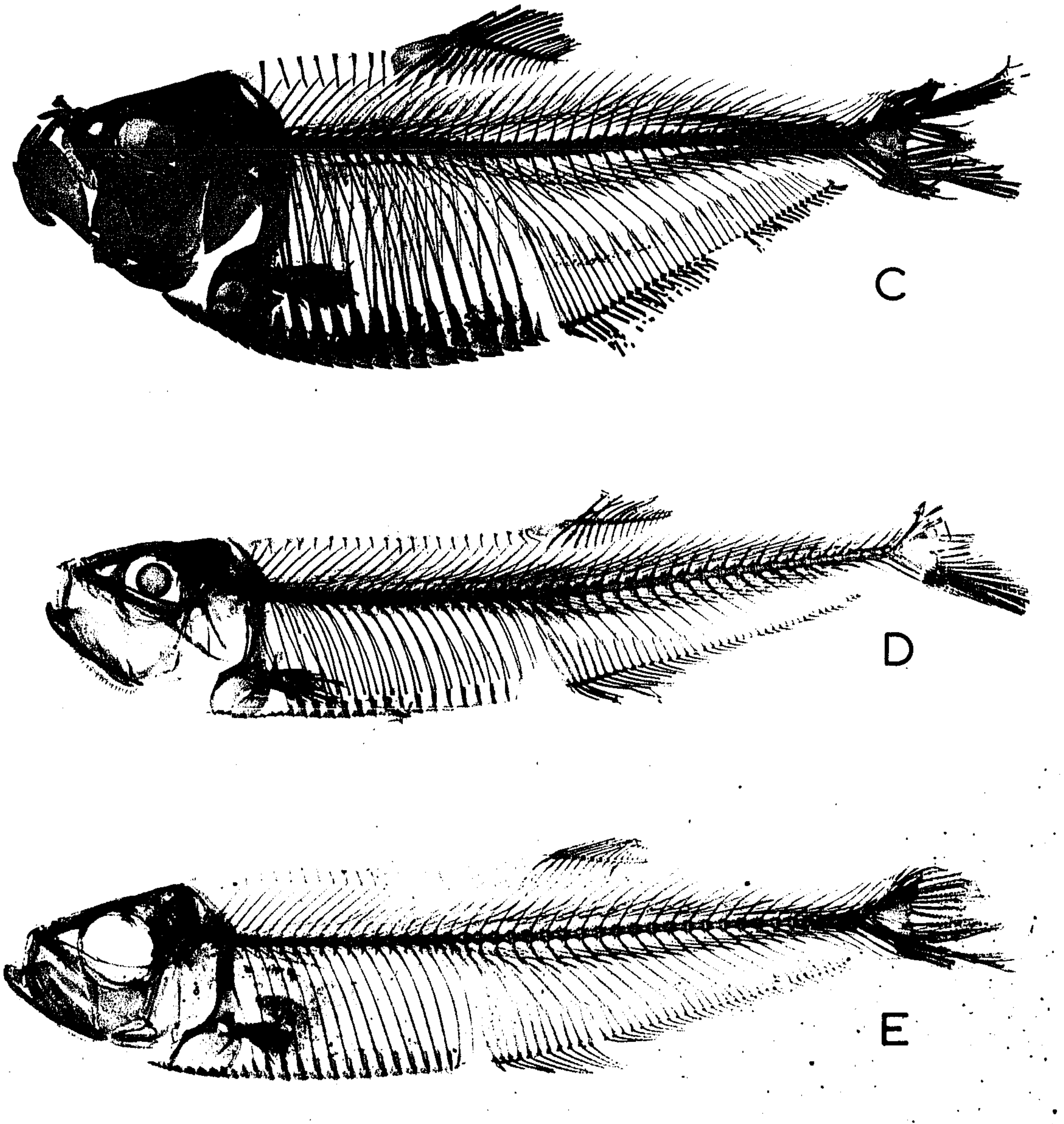


Figure 11 C-E

Fig. 11 F-H. Pristigasterids (see caption for fig. 11 A-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). Figs. F-H are cleared and stained specimens, with hypobranchial apparatus and right facial bones removed.

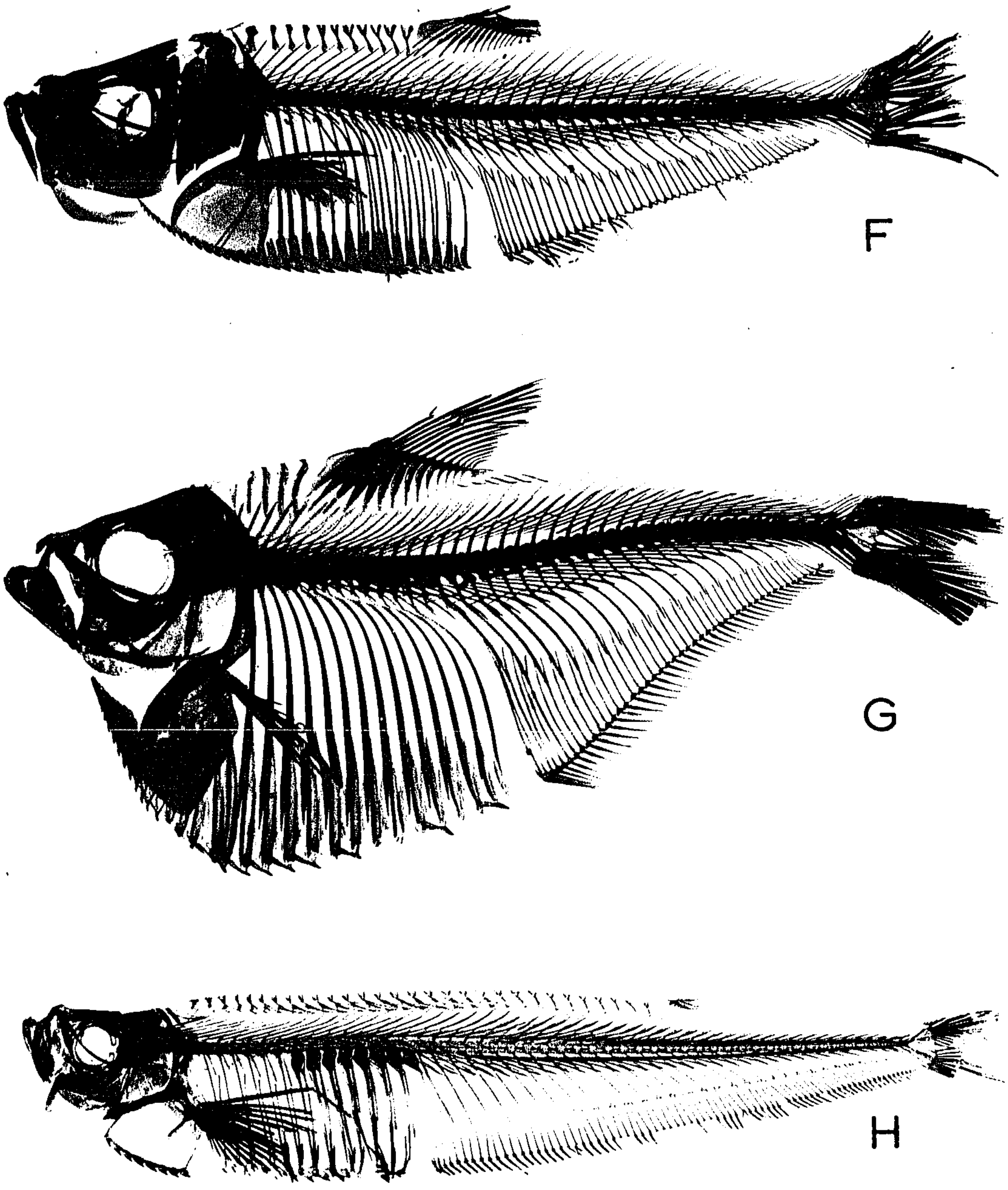


Figure 11 F-H

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

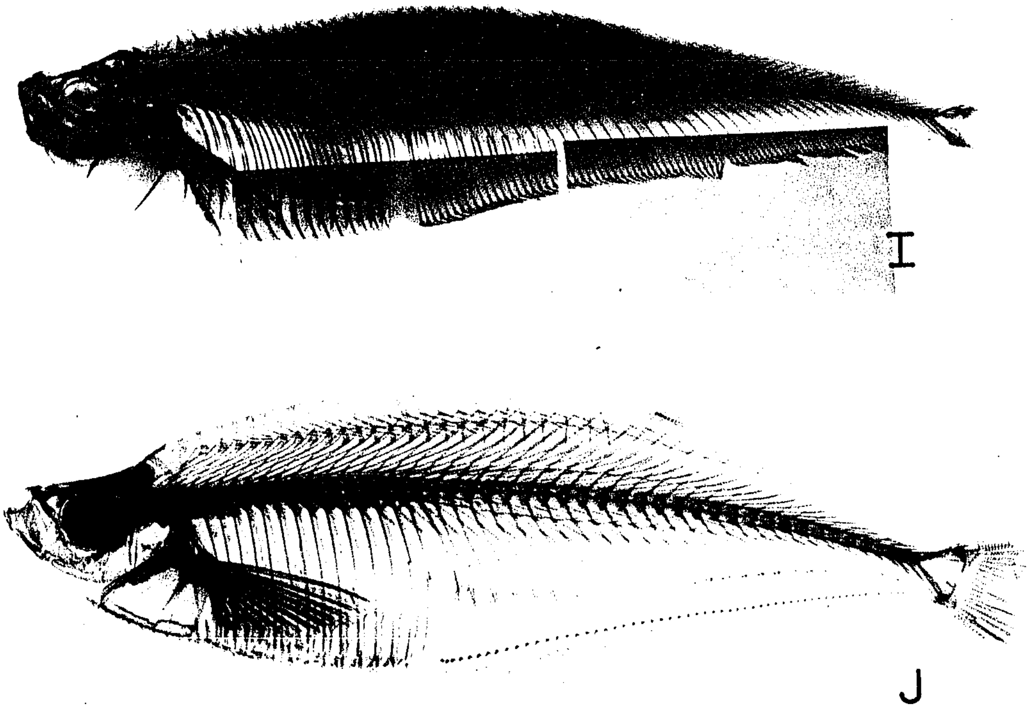


Figure 11 I-J

Fig. 11 K-M. An +ellimmichthyid, denticipitoid, and engraulid, showing the posteriorly inclined predorsal bones (compare these and figs. 11 N-S, 10, 24, 25, 26B and 39B with figs. 11 A-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). Fig. 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.

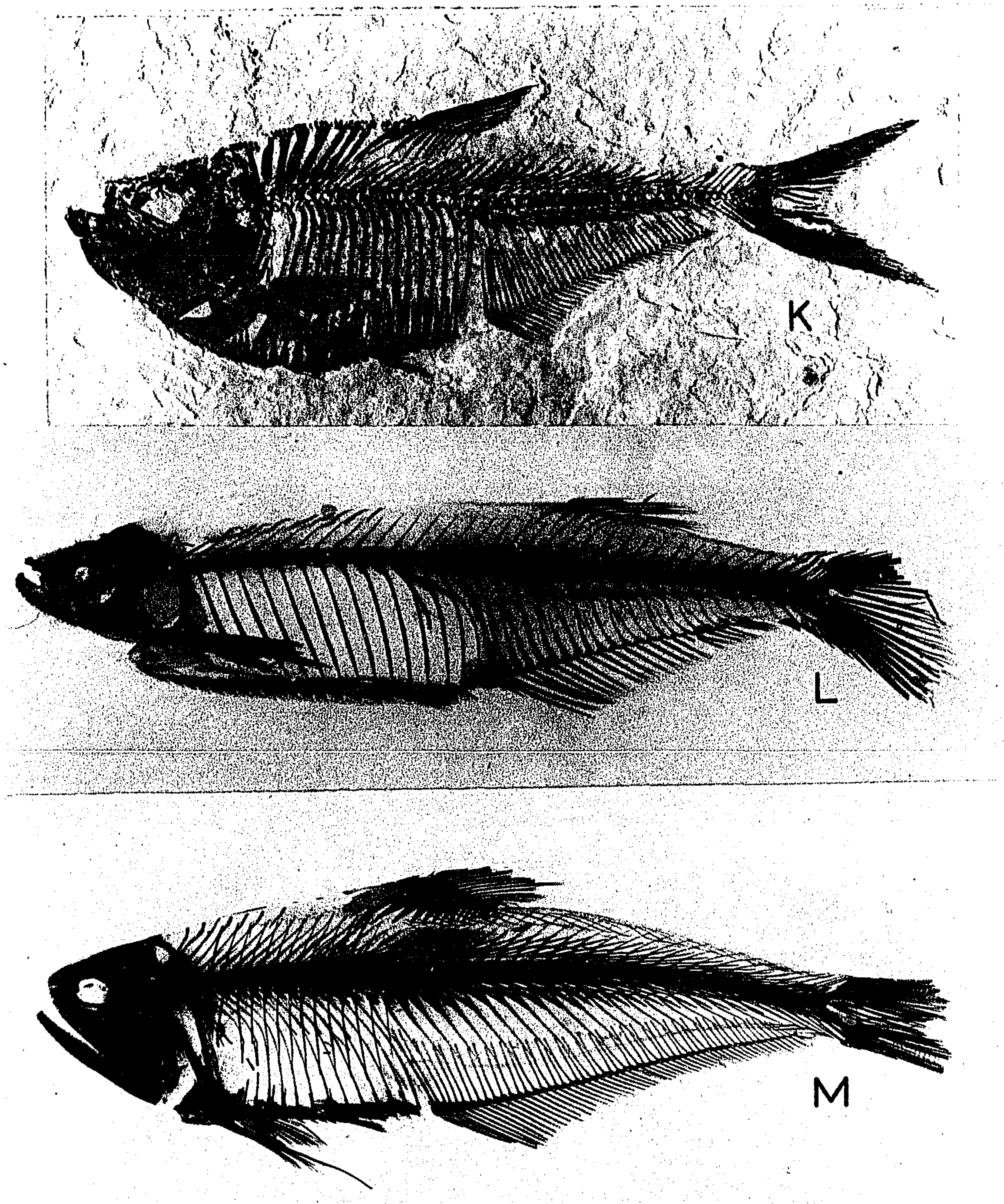


Figure 11 K-M

Fig. 11 N-P. A chirocentrid, dussumieriine and dorosomatine all showing the posteriorly inclined predorsal bones (see caption for figure 11 K-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). Figs. N-P are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

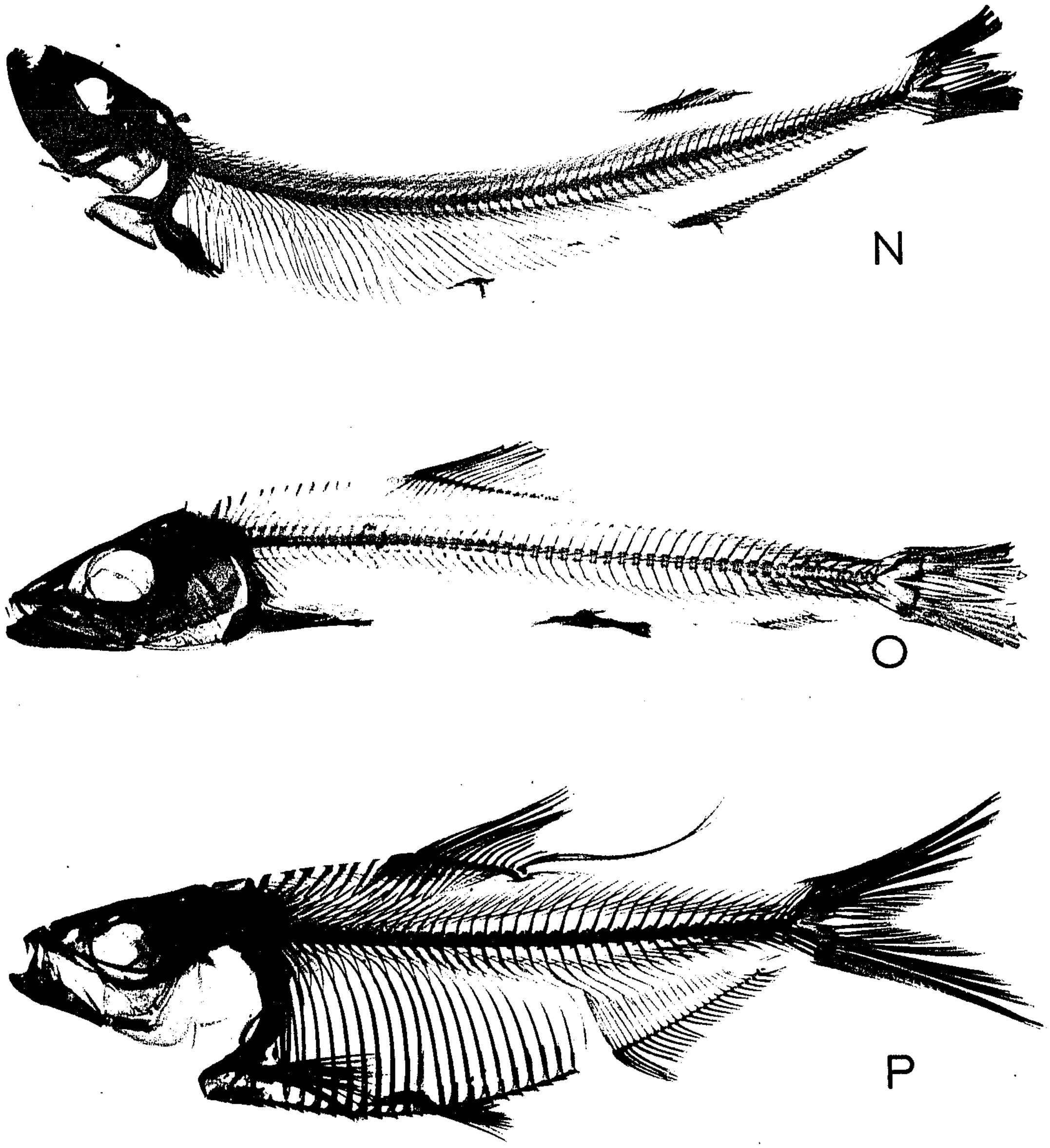


Figure 11 N-P

Fig. 11 Q-S. An alosine and two clupeines showing the posteriorly inclined predorsal bones (see caption for figure 11 K-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). Figs. Q-S are cleared and stained specimens with hypobranchial apparatus and right facial bones removed.

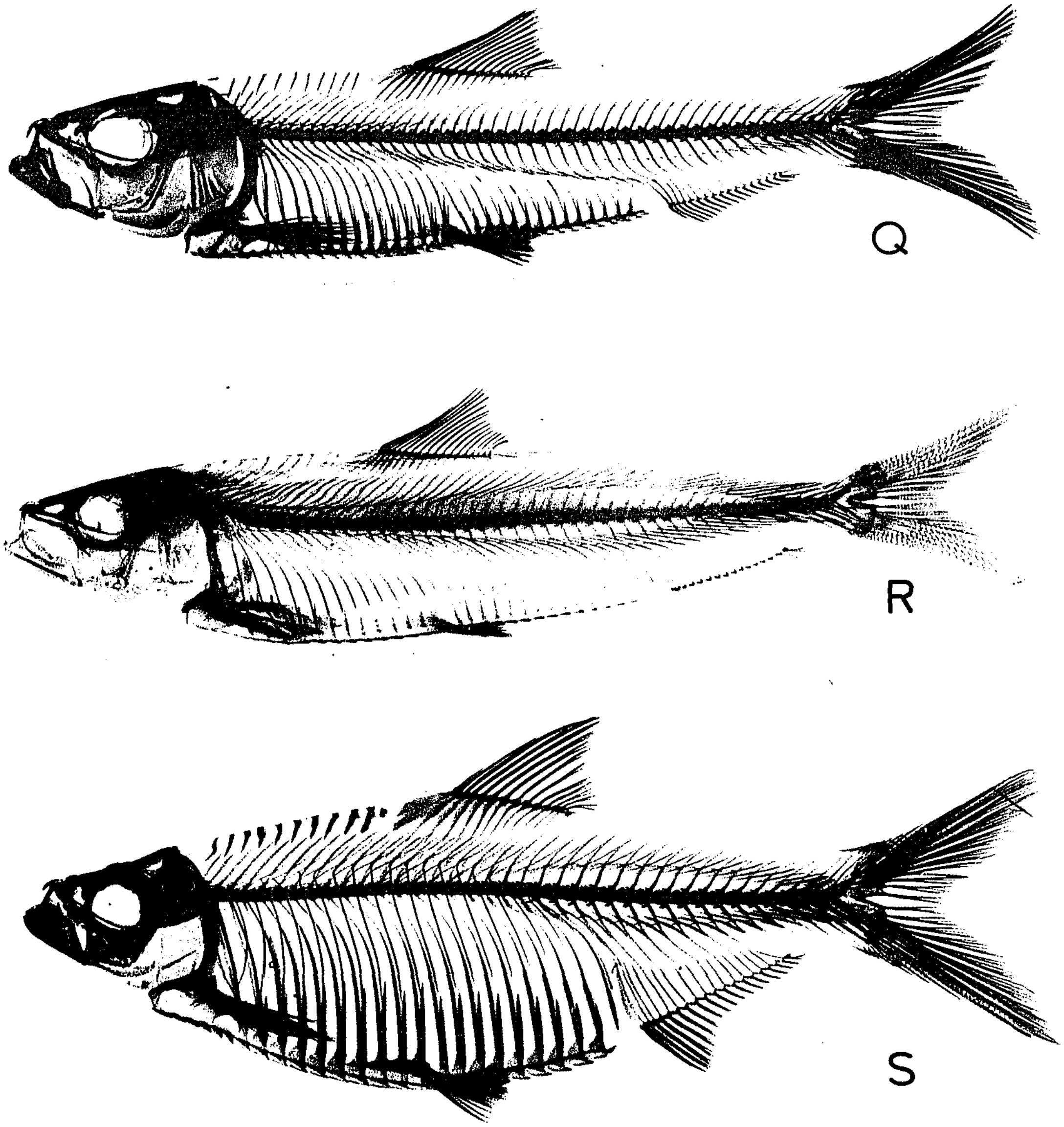


Figure 11 Q-S

Fig. 12. Caudal skeleton of Pristigaster cayana (AMNH 10186 sw) (sl=83 mm) showing the absence of an interlobar caudal notch in hyp_3 (the ventral posterior edge of hyp_3 is nearly flush with that of hyp_2). Compare with non-pristigasterid third hypurals in figs. 7B, 38 and 51.

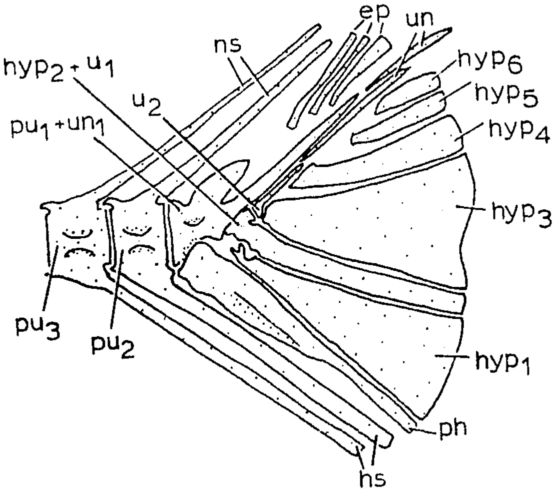

ep
un
ns
hyp2+u1
hyp6
hyp5
u2
pu1+un1
hyp4
hyp3
pu3
pu2
hyp1
ph
hs

Figure 12

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*, *Lycothrissa*, *Papuengraulis*, *Thrissina*, *Coilia* and *Thrissa* (all old world anchovies) have lost the ventral peg (A). Other engraulids, most clupeines, pellonulines 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). Pristigasterids have either condition B or C. *Denticeps* (E) is representative of the non-clupeoid condition.

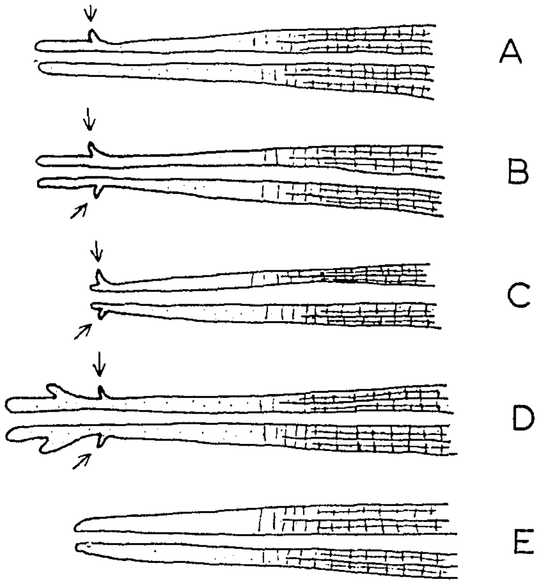


Figure 13

Fig. 14. Cladogram showing the monophyletic groups of pristigasterid fishes based on osteological characters as interpreted here. Characters 20, 21, a through f discussed in text.

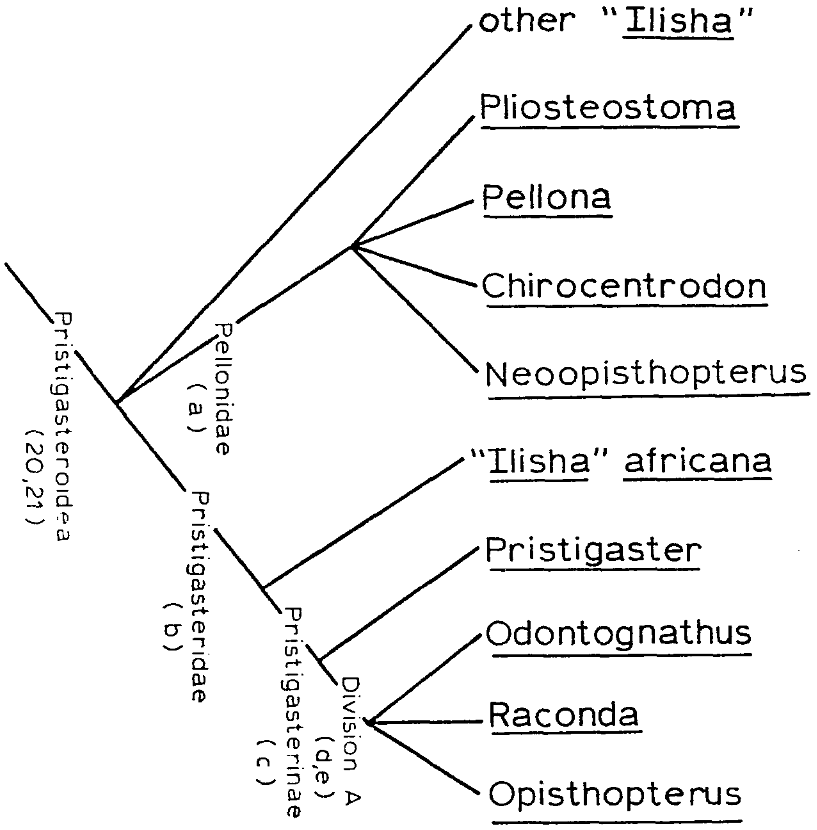

other "Ilisha"
Pliosteostoma
Pellona
Chirocentrodon
Neoopisthopterus
"Ilisha" africana
Pristigaster
Odontognathus
Raconda
Opisthopterus
Pristigasteroidea (20,21)
Pellonidae (a)
Pristigasteridae (b)
Pristigasterinae (c)
Division A (d,e)

Figure 14

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

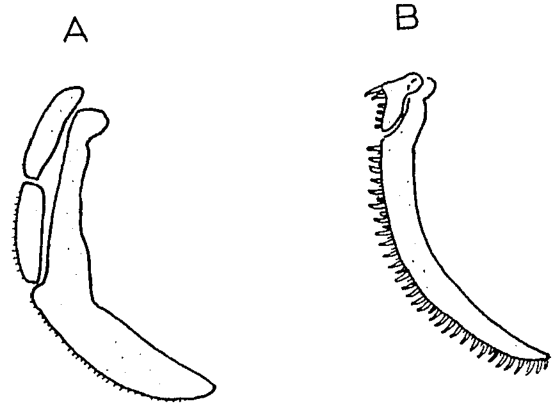


Figure 15

Fig. 16. The three anterior most 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 *Neopisthopter~~i~~us* have a small laminar expansion of the first pleural rib, it does not articulate with the shoulder girdle.

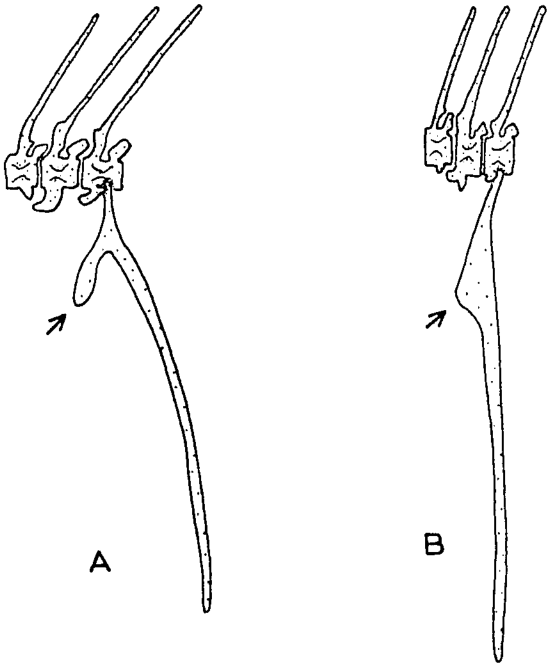


Figure 16

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 without stipple. Figs. A-D are ventral views; E is a dorsal view.

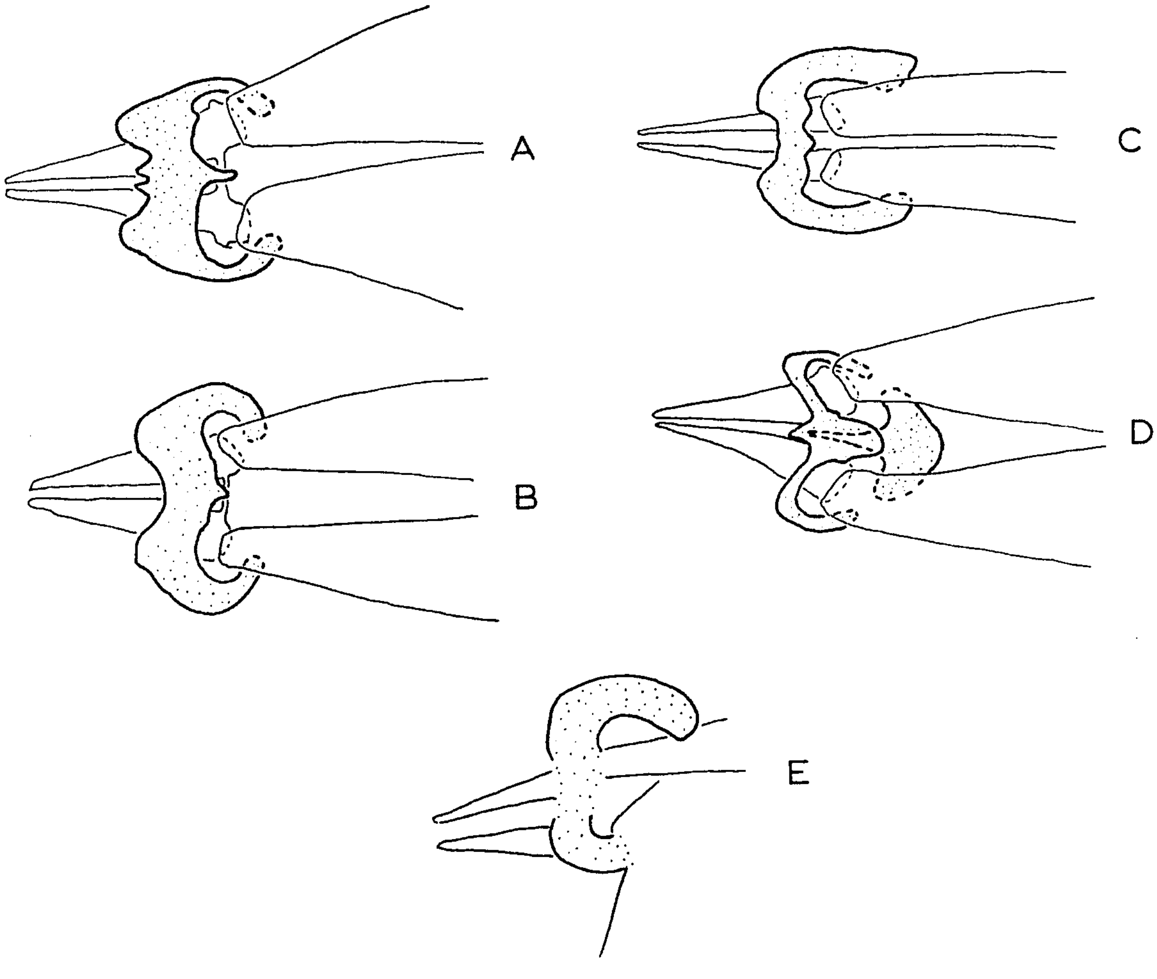


Figure 17

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

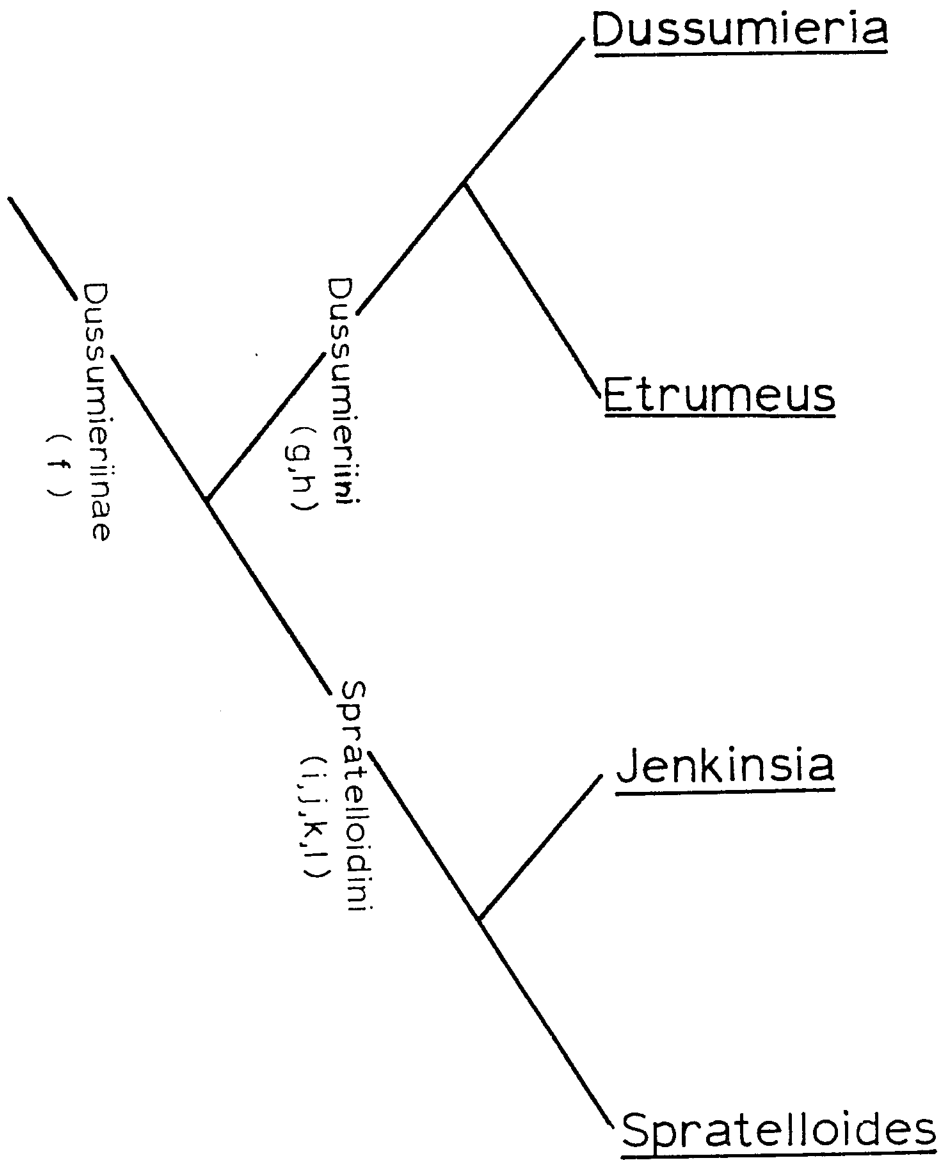
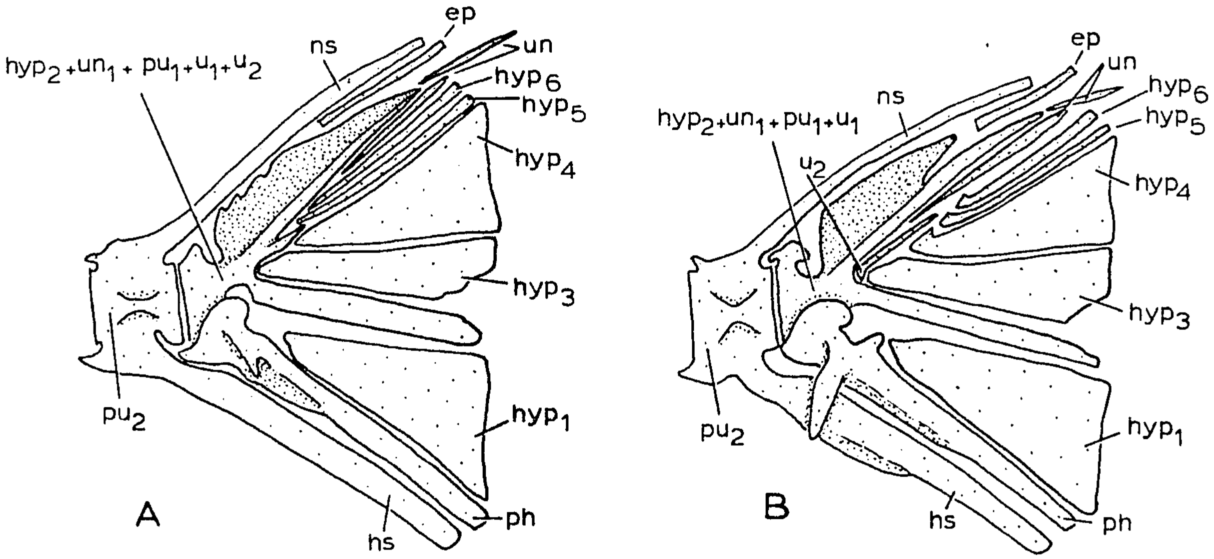

Dussumieria
Etrumeus
Jenkinsia
Spratelloides
Dussumieriinae
(f)
Dussumieriini
(g,h)
Spratelloidini
(i,j,k,l)

Figure 18

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


hyp2+un1+pu1+u1+u2
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pu2
hs
ph
B

Figure 19

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.

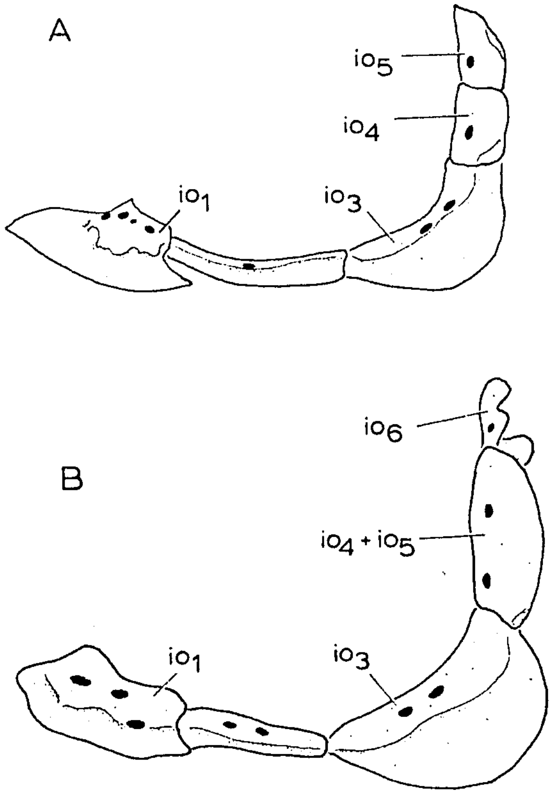

Figure 20

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

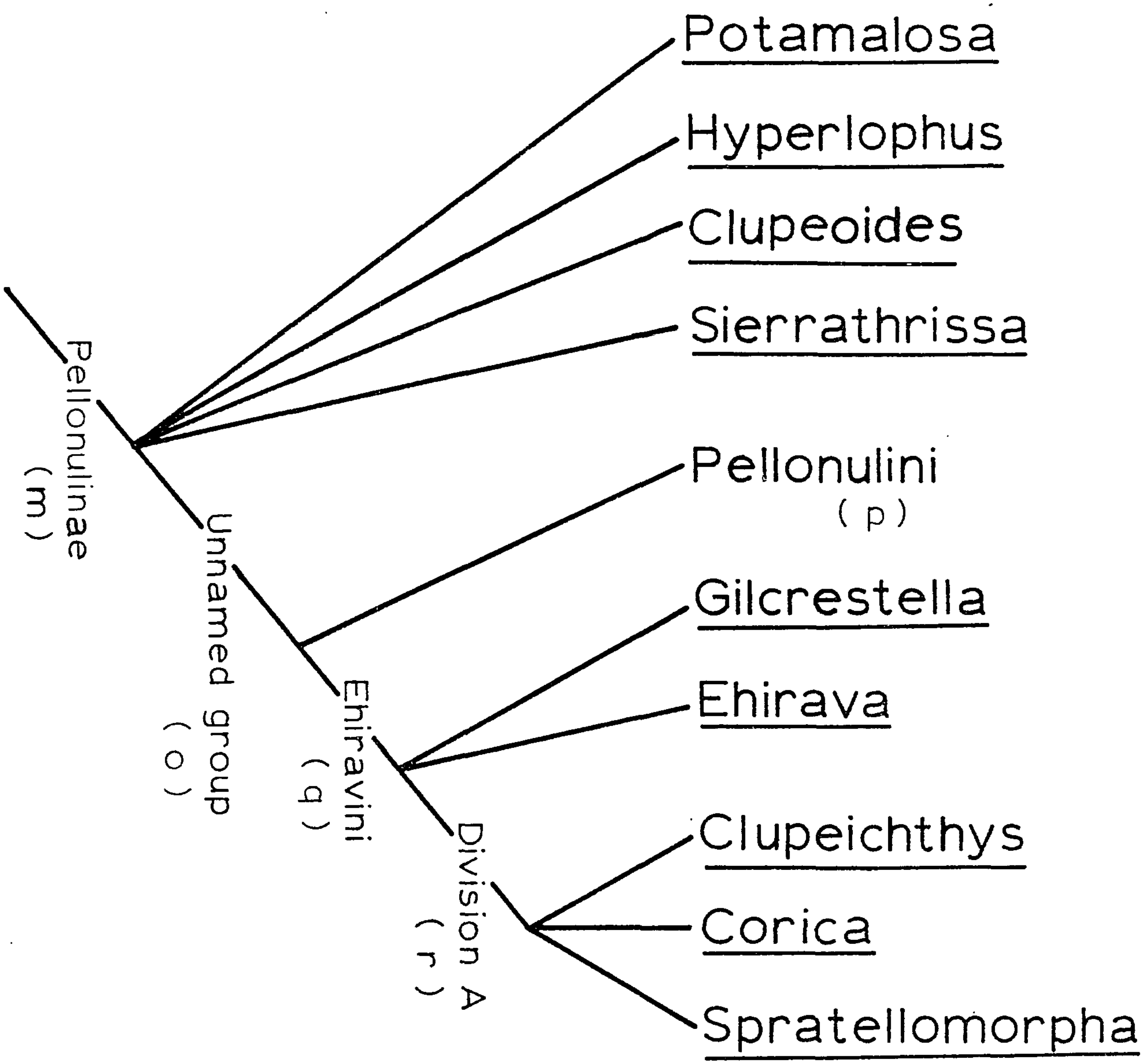
Potamalosa
Hyperlophus
Clupeoides
Sierrathrissa
Pellonulini
(p)
Gilcrestella
Ehirava
Clupeichthys
Corica
Spratellomorpha
Pellonulinae
(m)
Unnamed group
(o)
Ehiravini
(q)
Division A
(r)

Figure 21

Fig. 22. Articulation of postcleithrum with supracleithrum in A) Laeviscutella dekimpei (BMNH 1965:7 7 10-14) (sl=43 mm); B) Hyperlophus vittatus (AMNH 3050 sw) (sl=58 mm). Figure A shows the type of articulation for the western and central African pellonulines as discussed in text. Both are lateral views.

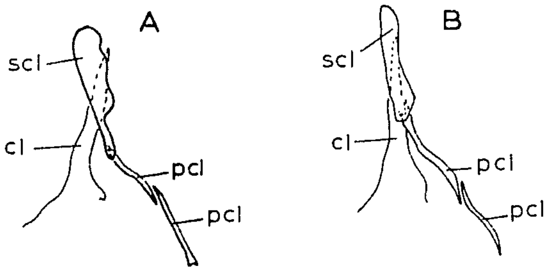

Figure 22

Fig. 23. Showing the openings to the recessus in Ehiravini, demonstrated by Corica laciniata (ANSP 89414) (sl=51 mm). All pellonulines 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.

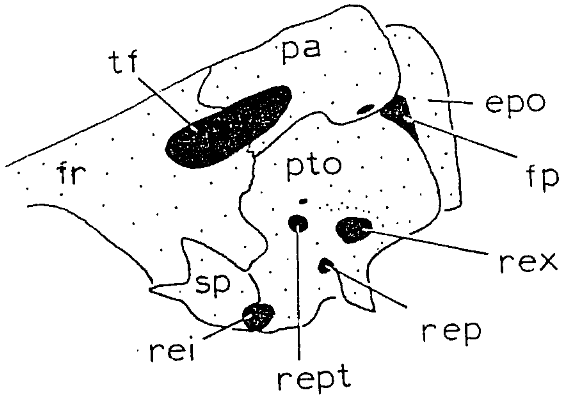

Figure 23

Fig. 24. A) *Clupeichthys gonignathus* (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.

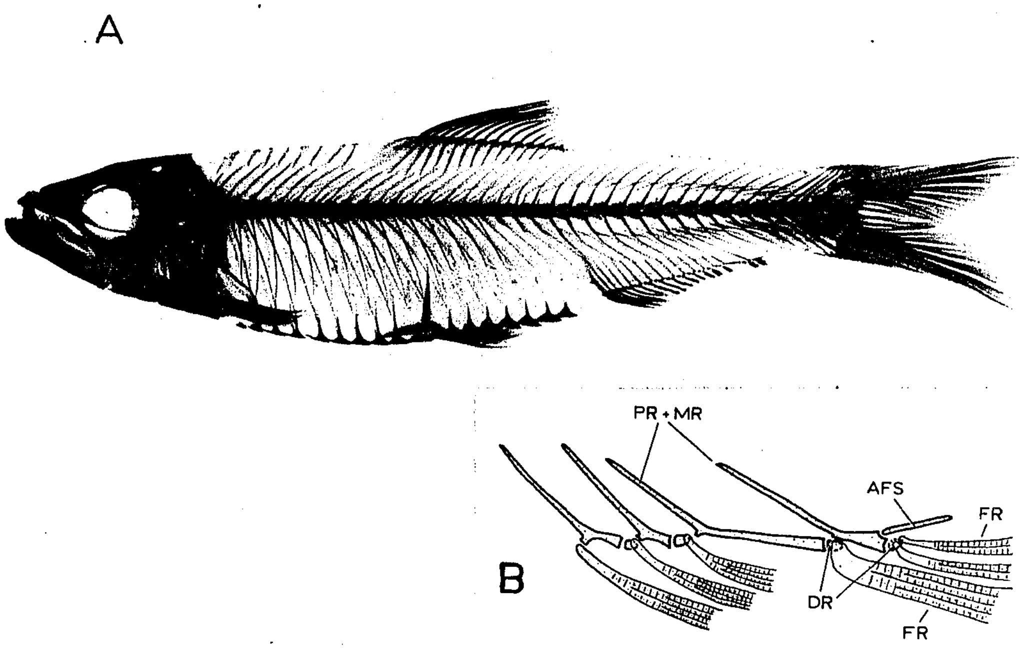

Figure 24

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

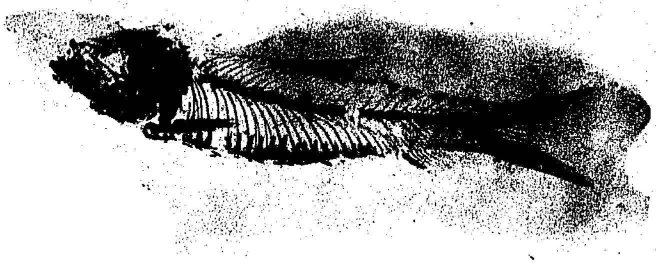

Figure 25

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.

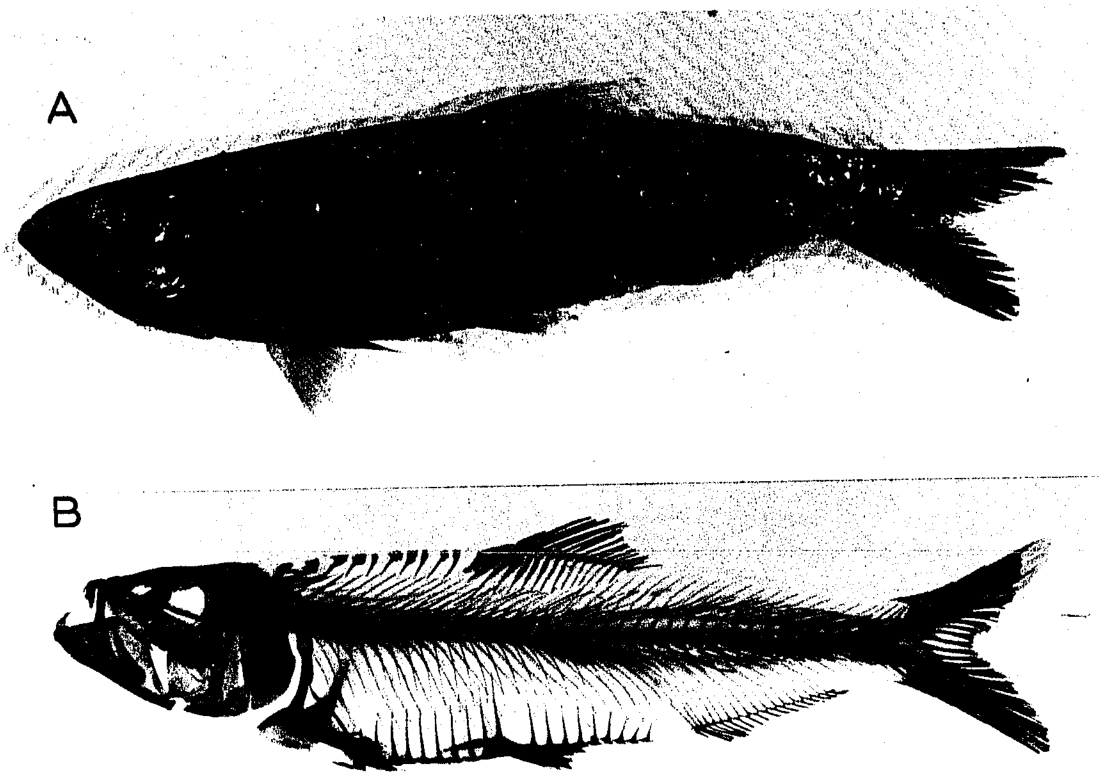

Figure 26

Fig. 27. *Odaxothrissa vittata* A) lateral view of skull; B) same, showing sensory canals (stippled).

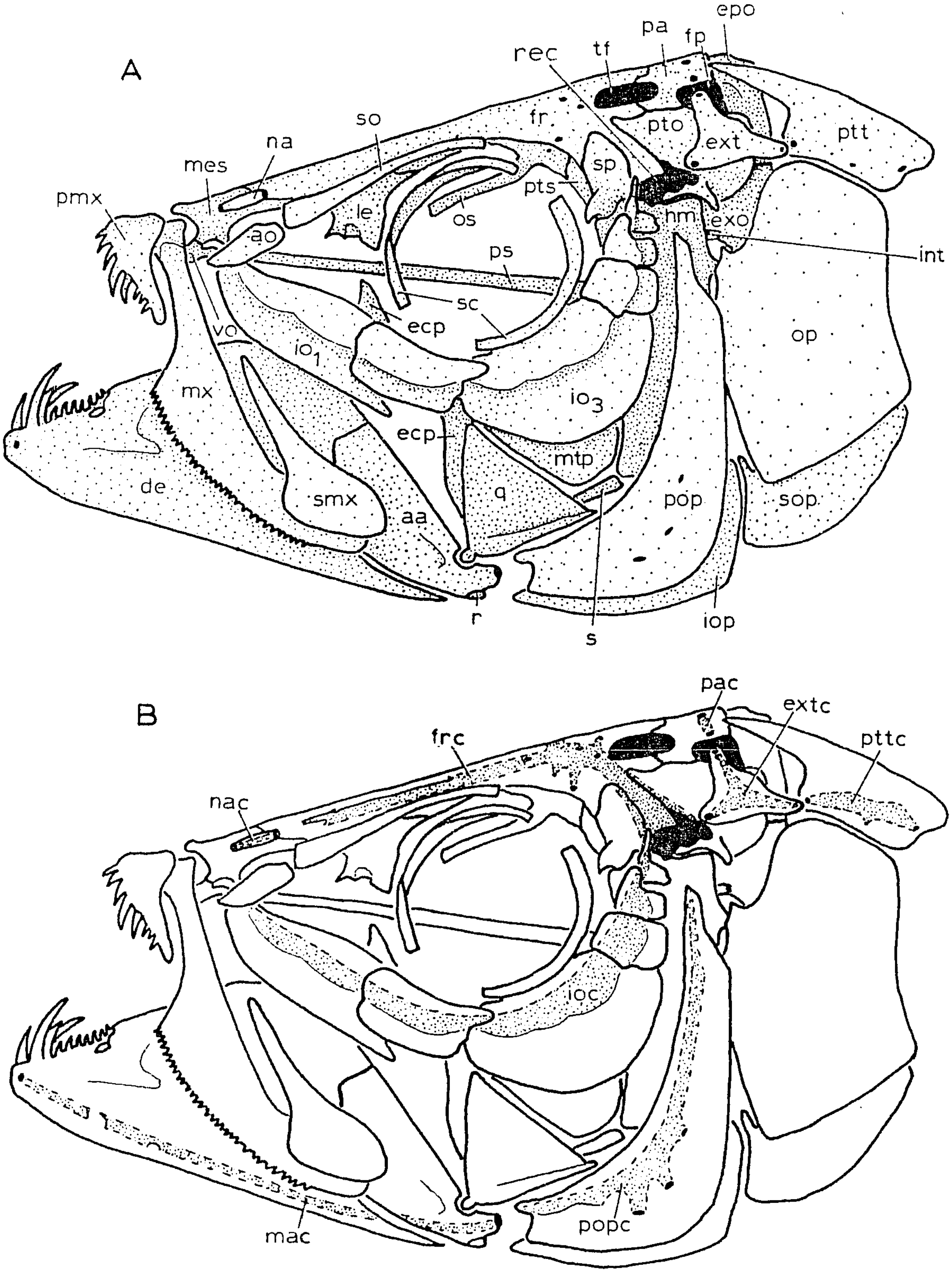
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Figure 27

Fig. 28. _Odaxothrissa_ _vittata_, medial view of the jaws, opercular bones and suspensorium. Coronomeckelian cartilage in black.

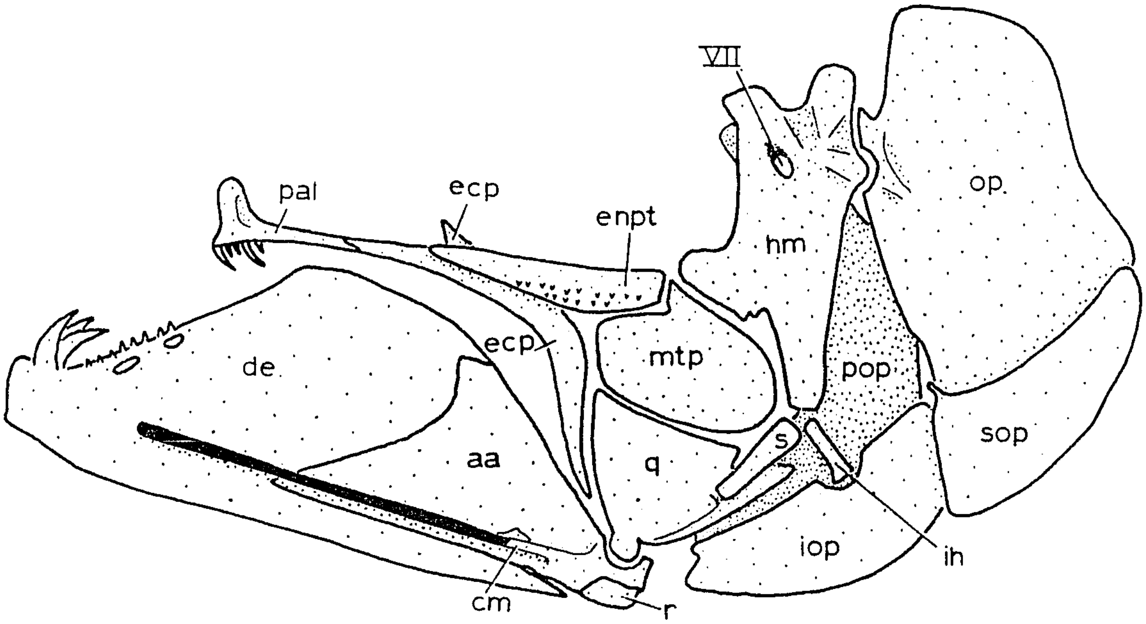

Figure 28

Fig. 29. 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.

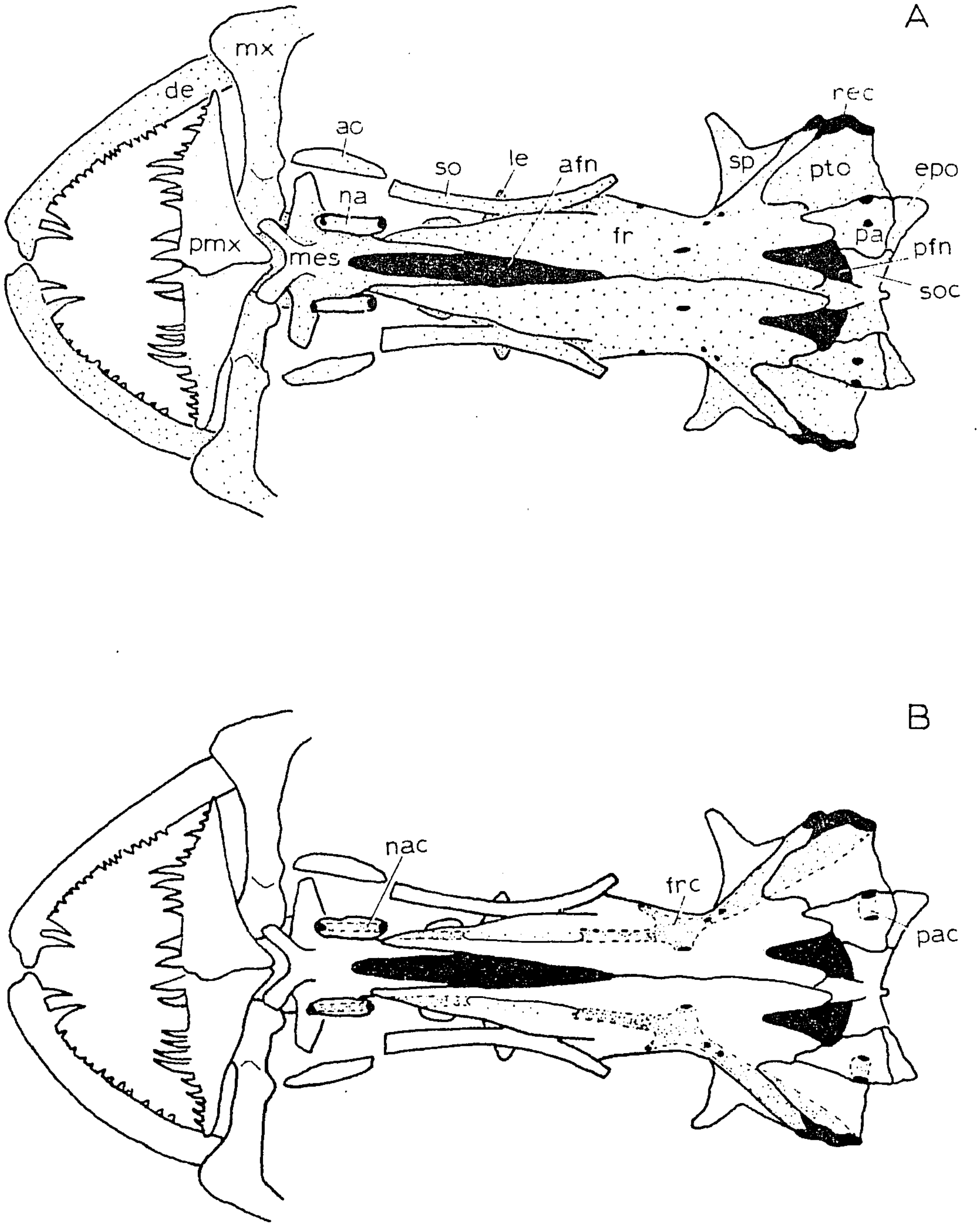
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Figure 29

Fig. 30. *Odaxothrissa vittata*, A) lateral view of cranium; B) same, showing bullae (stippled) as seen through bone.

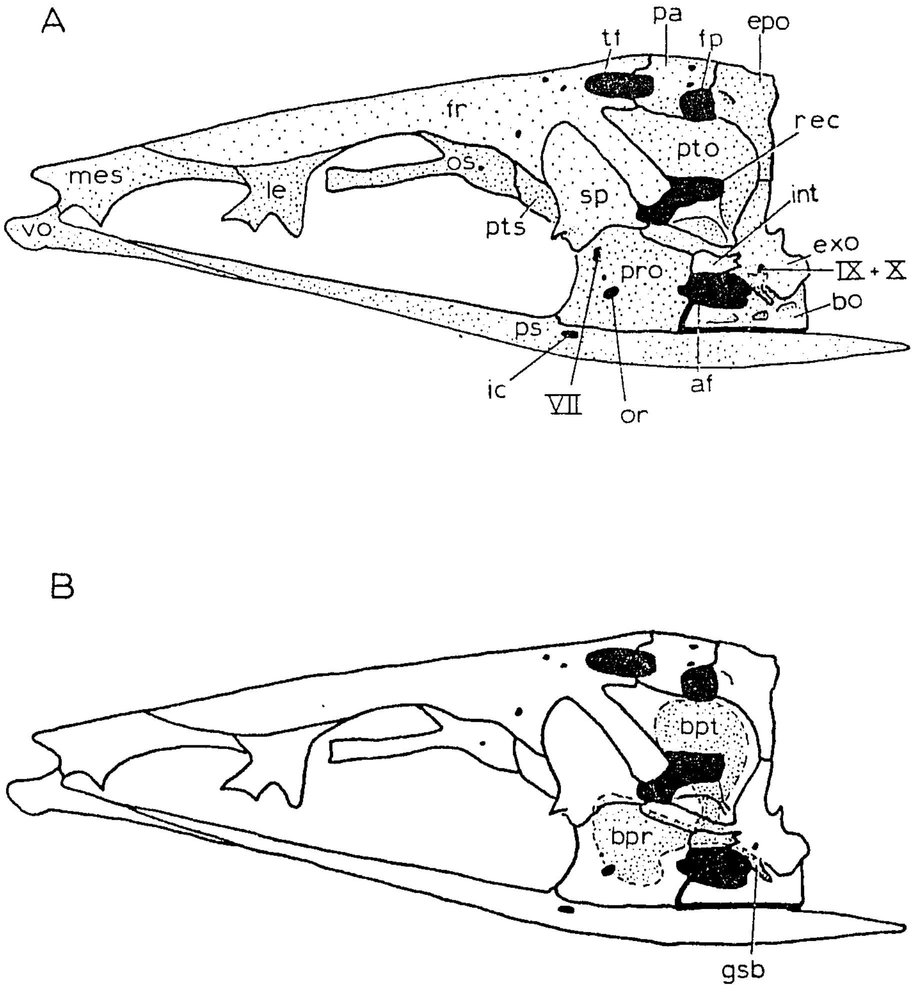
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Figure 30

Fig. 31. Odaxothrissa vittata, posterior view of cranium.

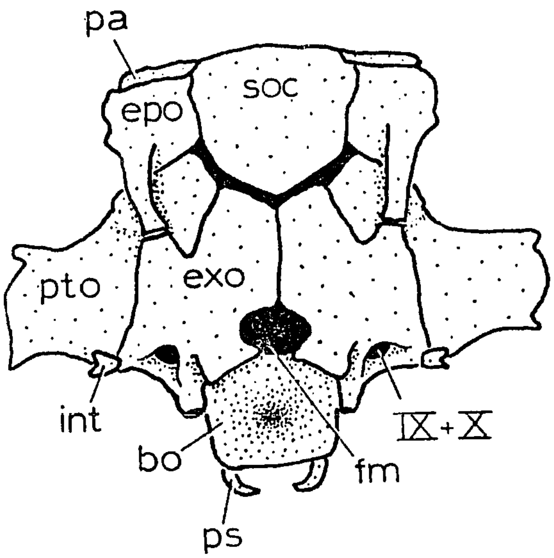
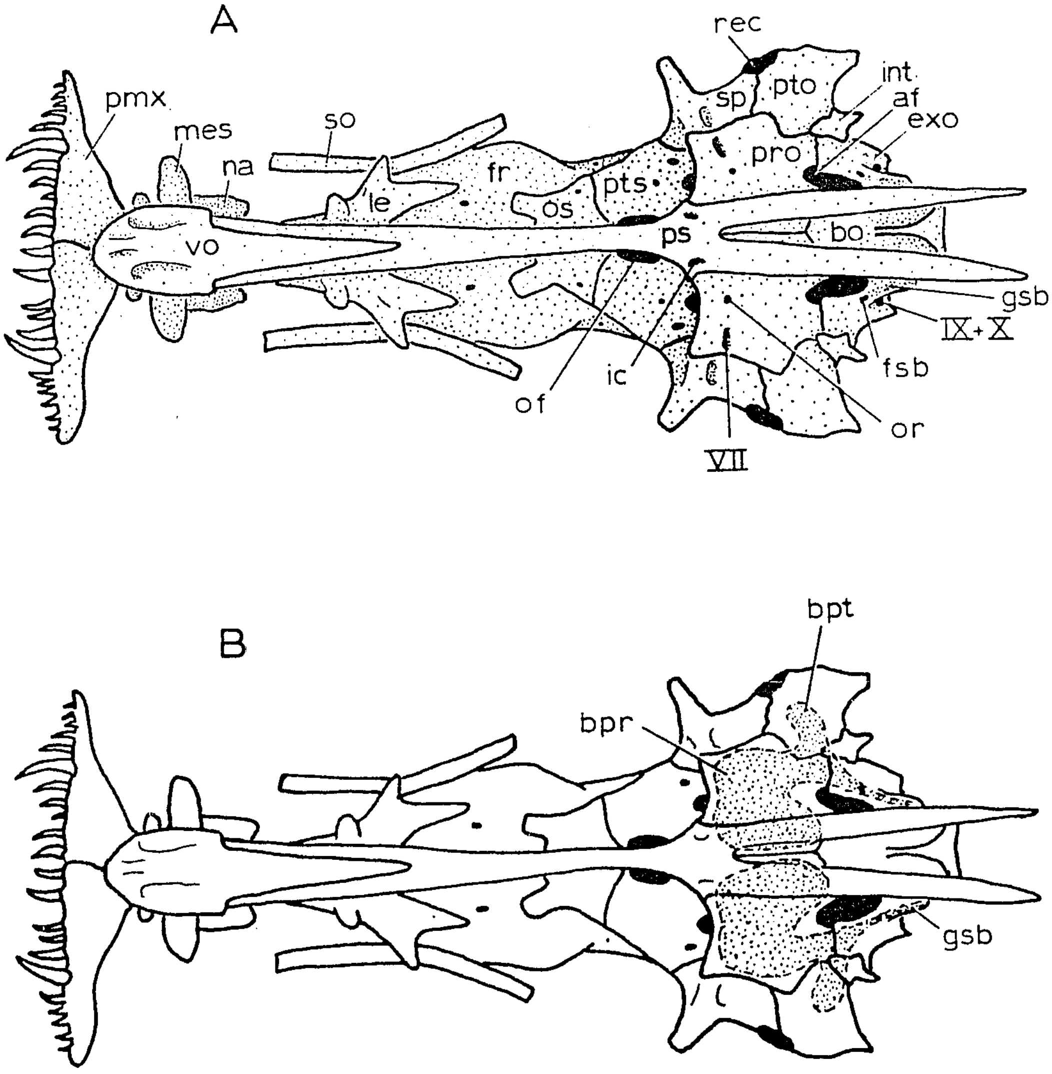


Figure 31

Fig. 32. Odaxothrissa vittata, A) ventral view of cranium; B) same, showing position of bullae (stippled) as seen through bone.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gsb
IX+X
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or
VII
B
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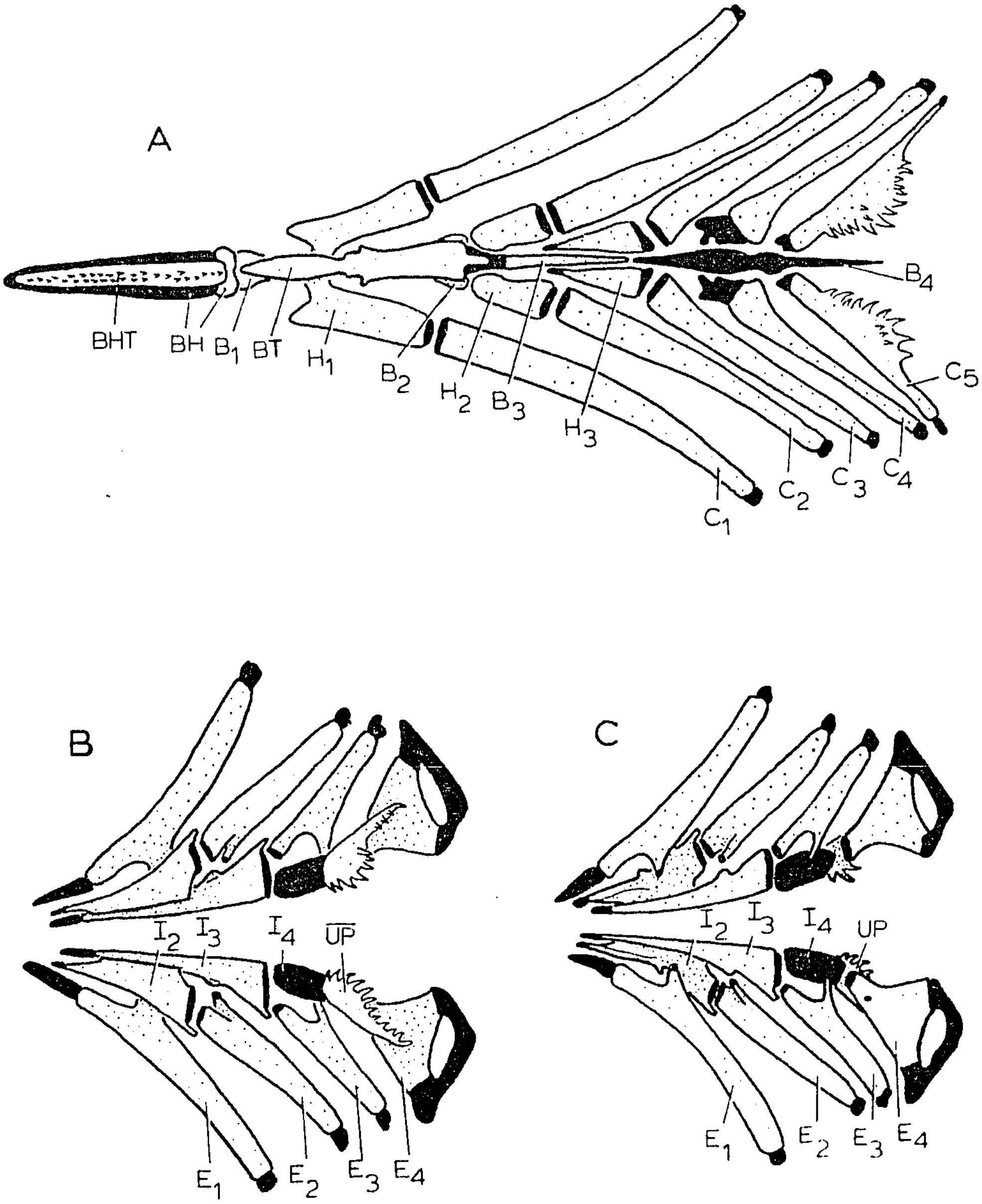
Figure 32

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.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B_1
BT
H_1
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H_2
B_3
H_3
B_4
C_5
C_1
C_2
C_3
C_4
B
I_2
I_3
I_4
$\overline{UP}$
E_1
E_2
E_3
E_4
C
I_2
I_3
I_4
UP
E_1
E_2
E_3
E_4

Figure 33

Fig. 34. *Odaxothrissa vittata*, A) lateral view of branchiostegal support and rays; B) dorsal view of urohyal; C) lateral view of urohyal.

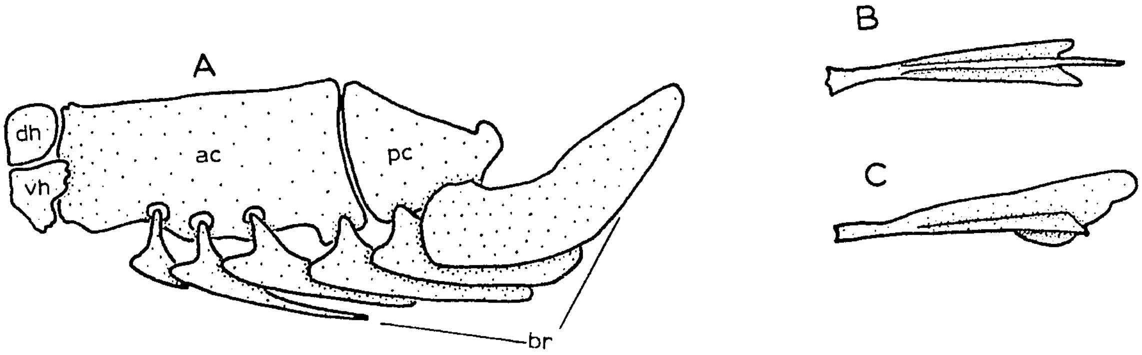


Figure 34

Fig. 35. Odaxothrissa vittata, A) pectoral radials, enlarged from C, oblique dorso-lateral view; B) pectoral radials enlarged from C, oblique dorso-medial view; C) pectoral girdle, medial view. Anterior for A and B points to upper left.

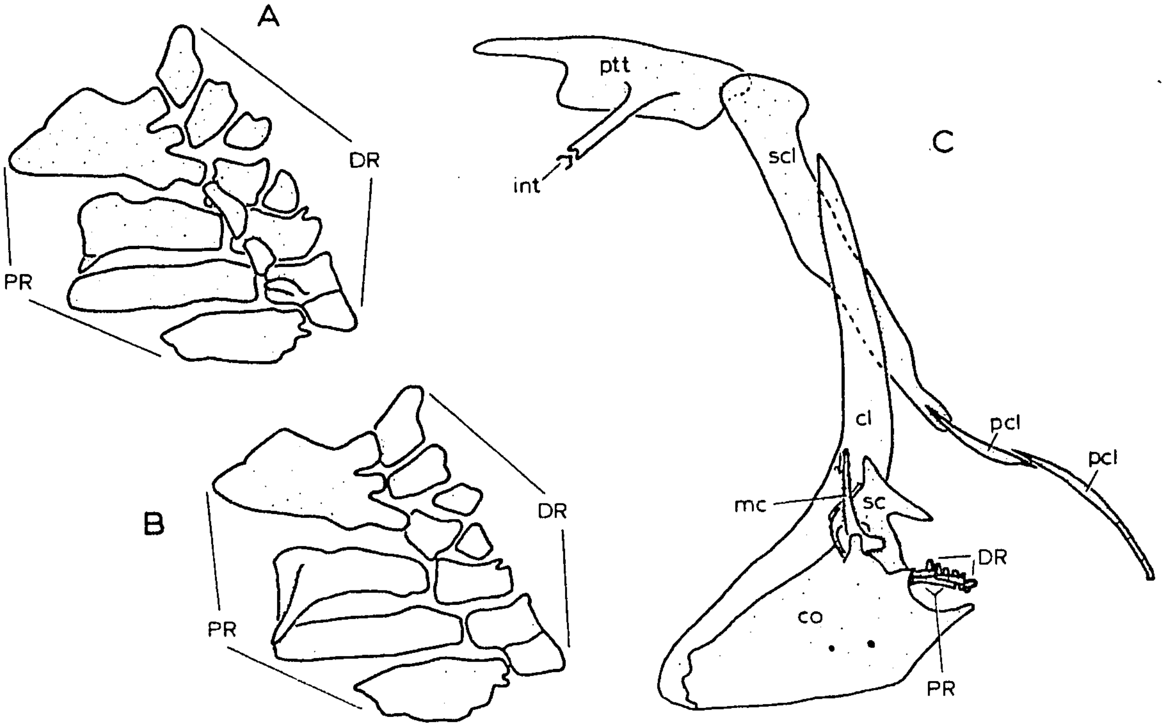


Figure 35

Fig. 36. Odaxothrissa vittata, A) flank scale; B) ventral view of two abdominal scutes below pelvic fin (the pelvic scutes) drawn flattened under a glass slide in glycerine; C) dorsal view of both pelvic girdles flattened under a glass slide (right and left side separated at posterior median contact).

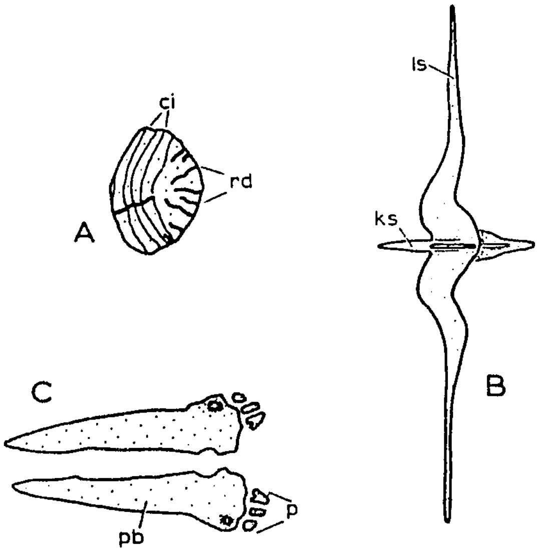


Figure 36

Fig. 37. *Odaxothrissa vittata*, median fin ray supports (most of the fin rays ommitted): A) lateral view of anterior most and posterior most dorsal fin ray supports; B) anterior view of the base of the eighth anal fin ray; C) lateral view of anterior most and posterior most anal fin ray supports.

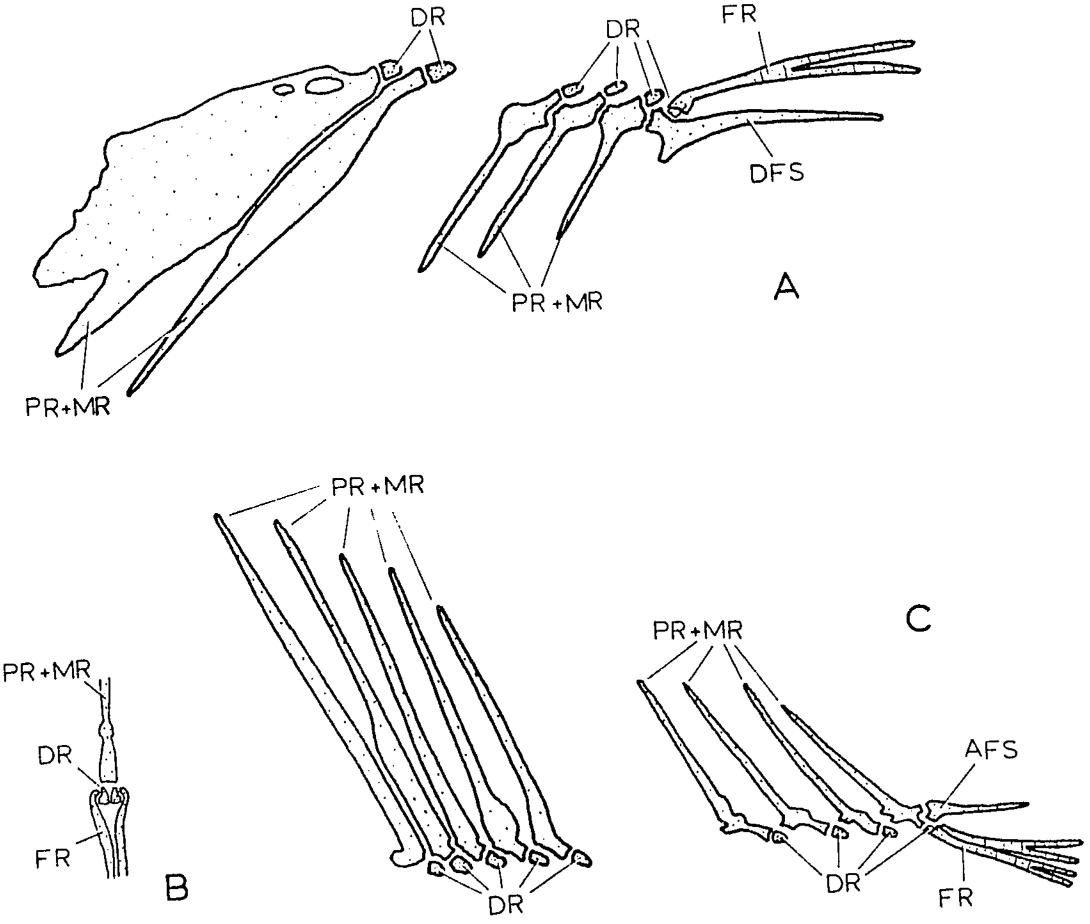


Figure 37

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

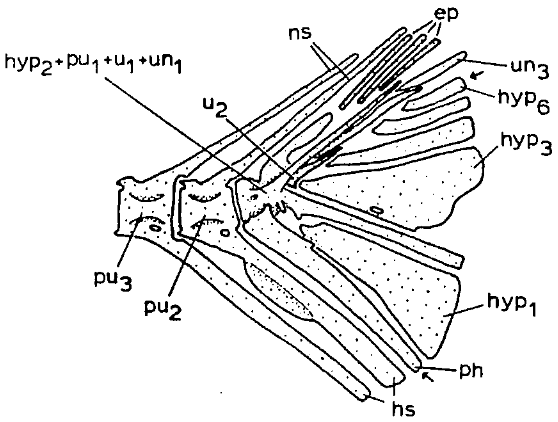


Figure 38

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.

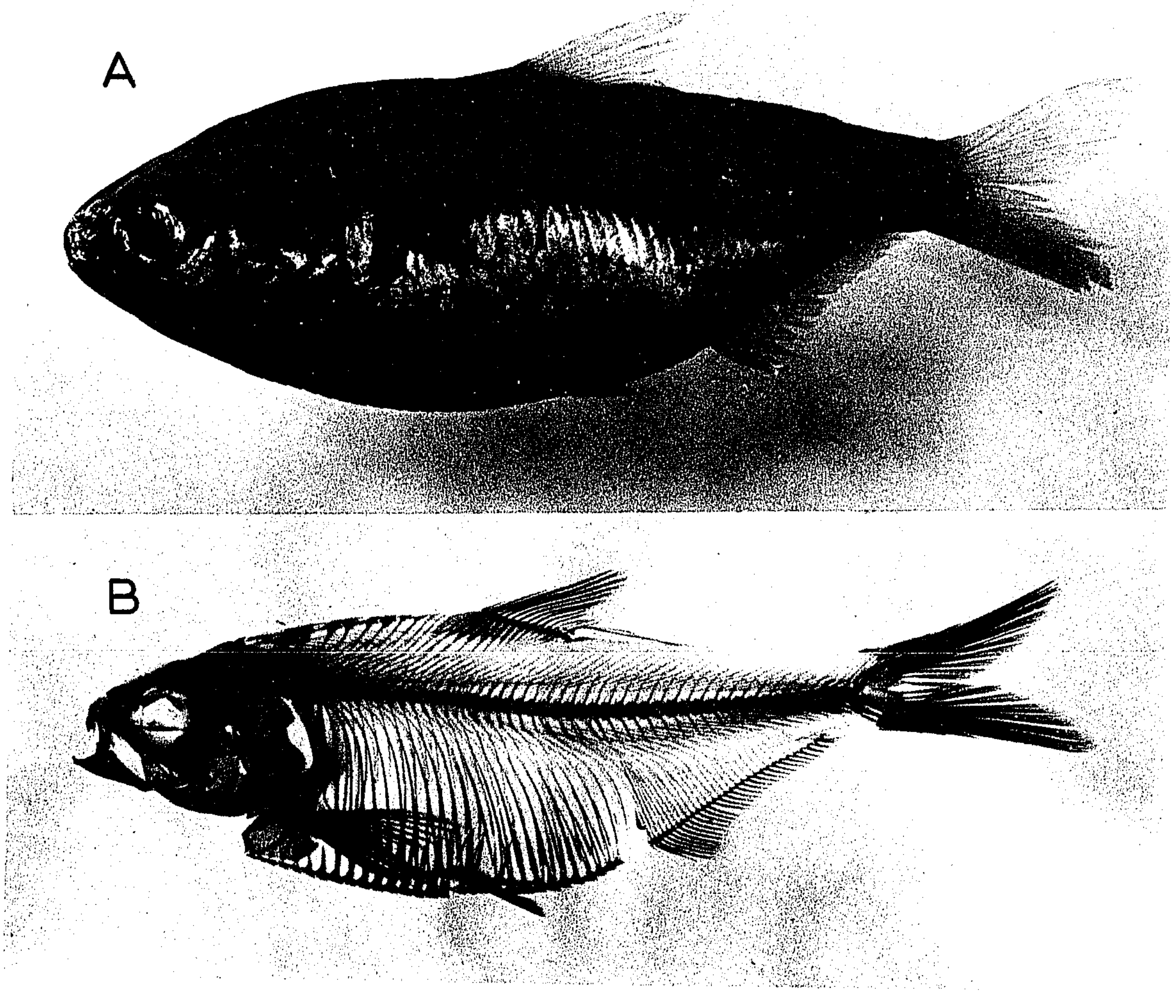
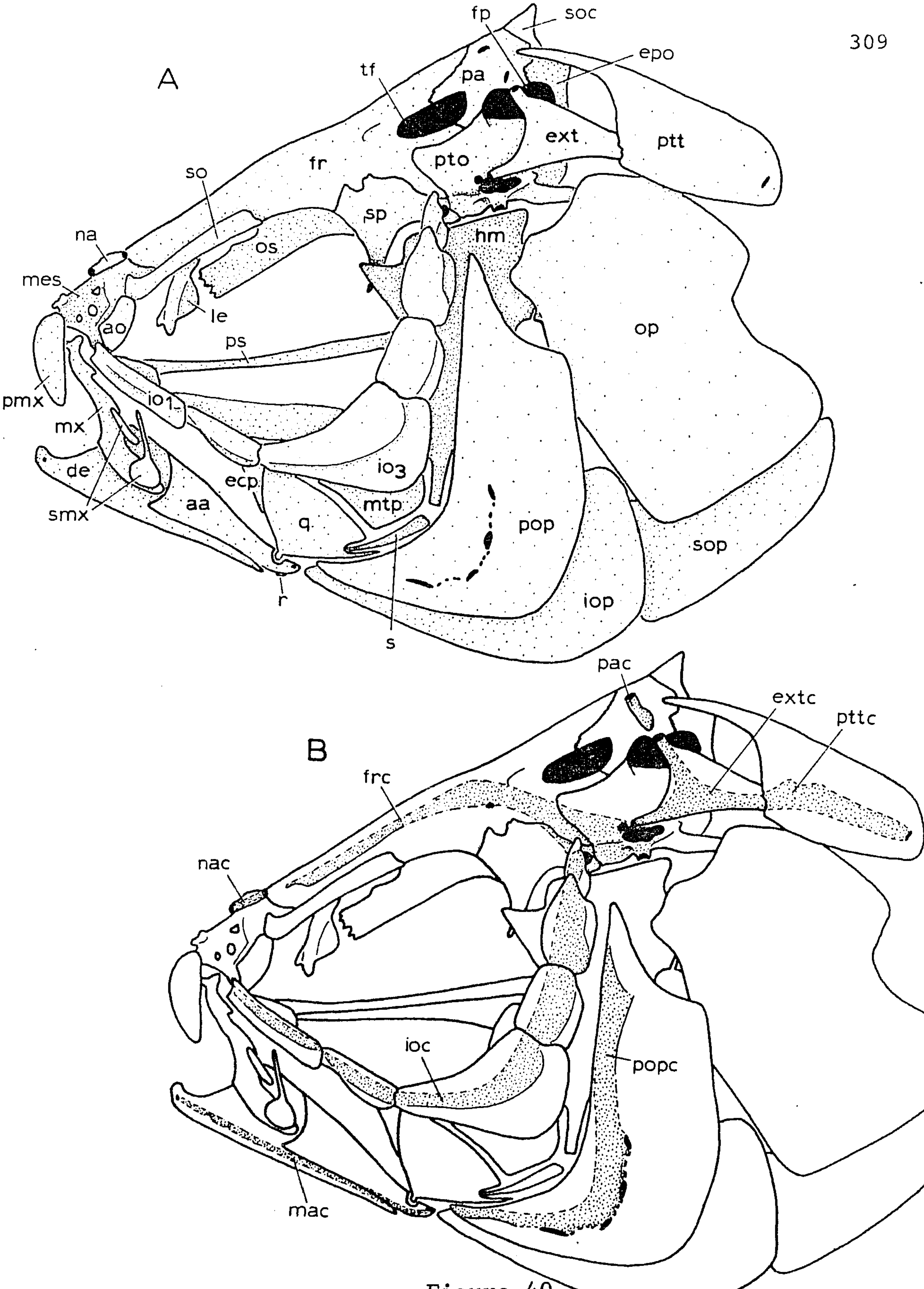


Figure 39

Fig. 40. Dorosoma cepedianum (sclerotic bones removed), A) lateral view of skull; B) same, showing sensory canals (stippled).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mtp
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aa
q
pop
sop
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extc
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Figure 40

Fig. 41. *Dorosoma cepedianum*, medial view of the jaws, opercular bones and suspensorium. Coronomeckelian cartilage in black.

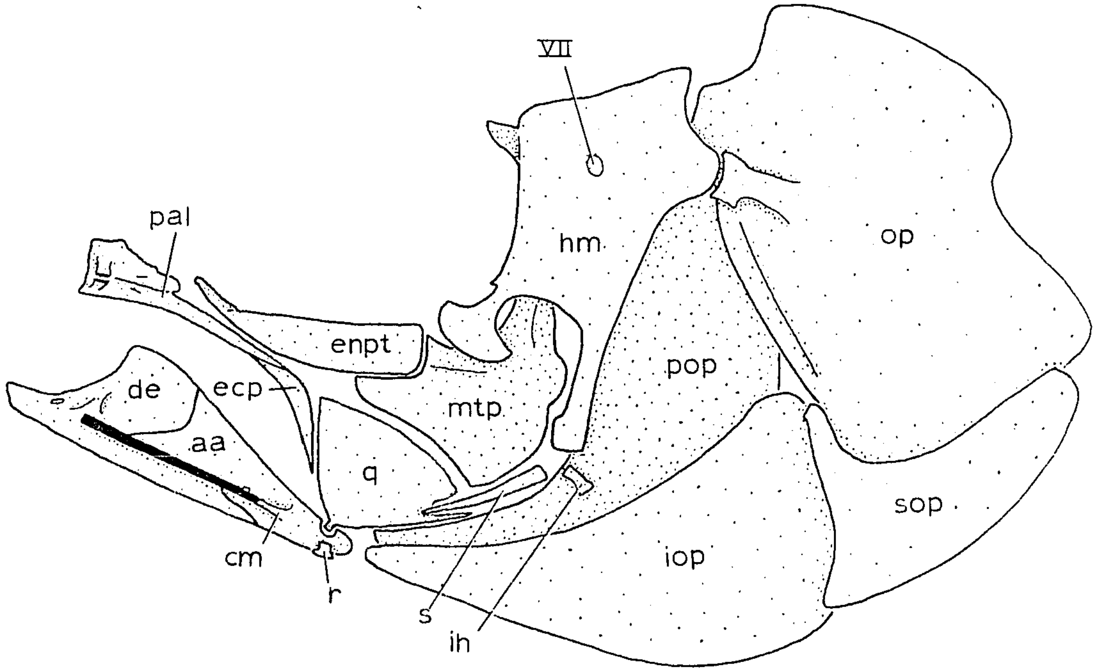

Figure 41

Fig. 42. *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.

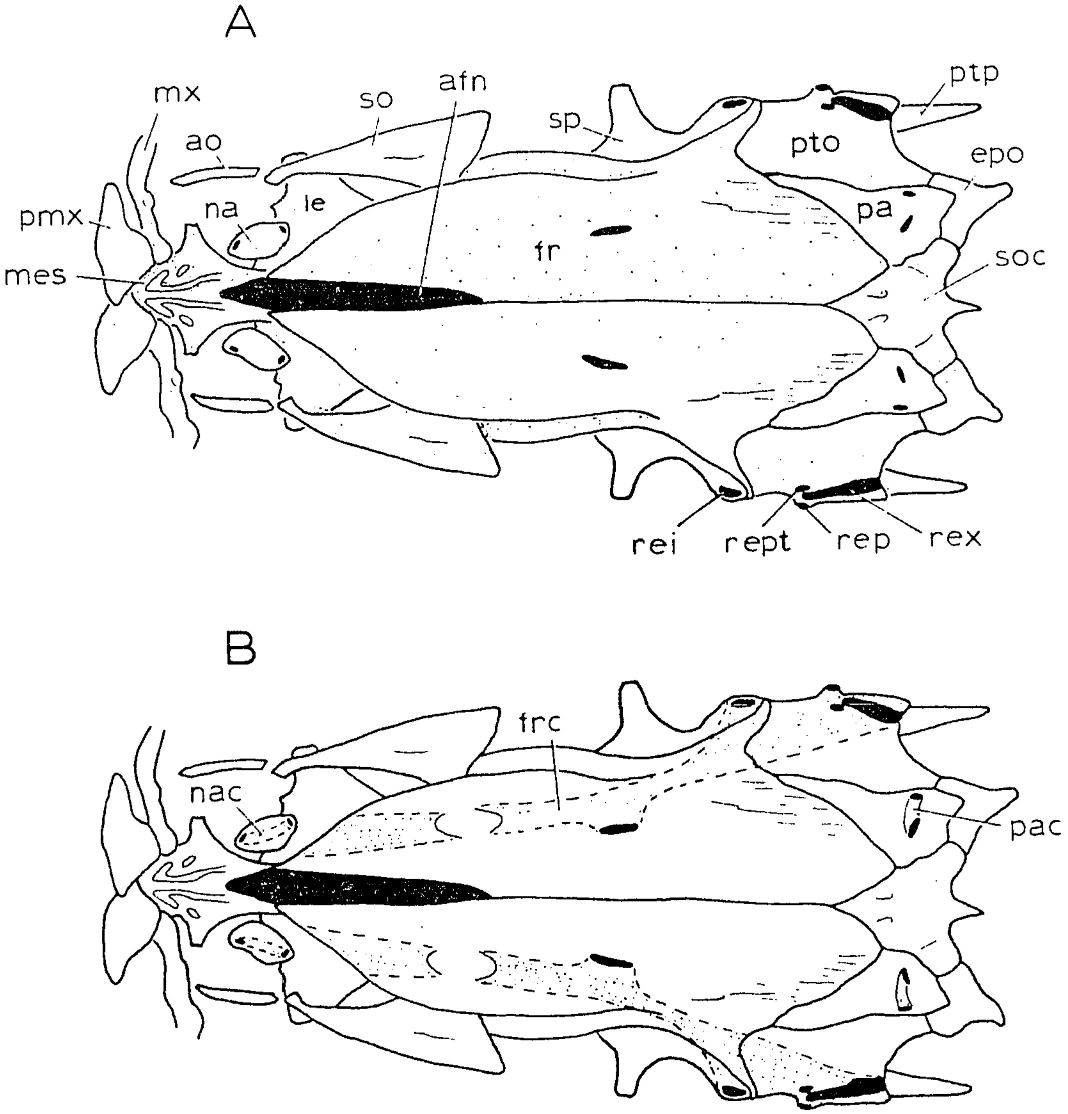
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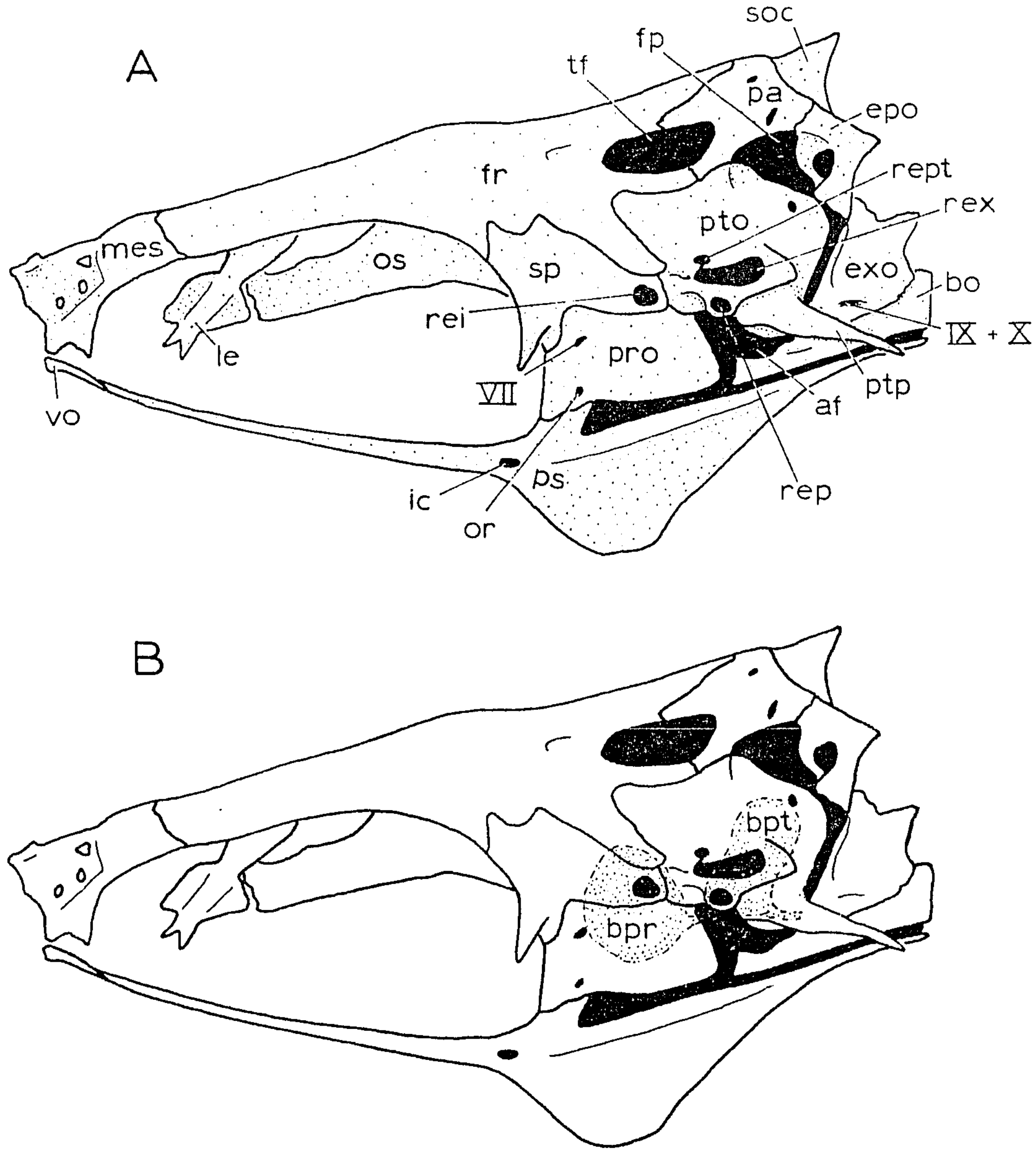
Figure 42

Fig. 43. *Dorosoma cepedianum*, A) lateral view of cranium; B) same, showing bullae (stippled) as seen through bone .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pro
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Figure 43

Fig. 44. *Dorosoma cepedianum*, posterior view of cranium.

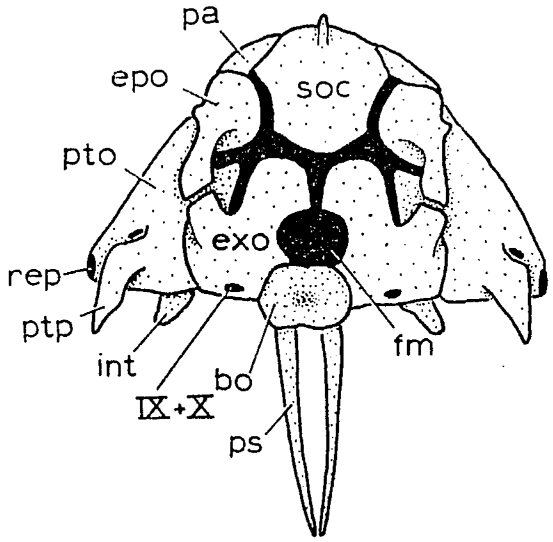
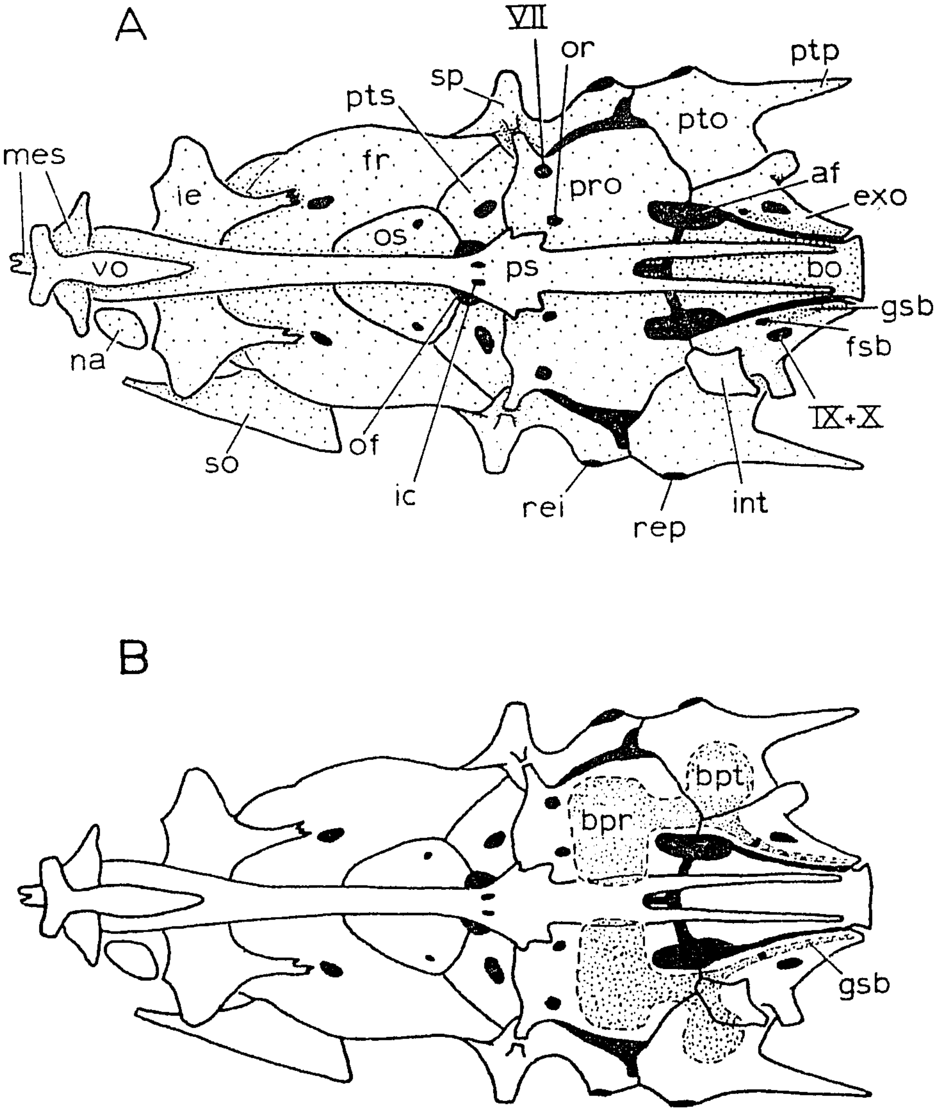


Figure 44

Fig. 45. *Dorosoma cepedianum*, A) ventral view of cranium; B) same, showing position of bullae (stippled) as seen through bone.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na
IX+X
so
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rep
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bpt
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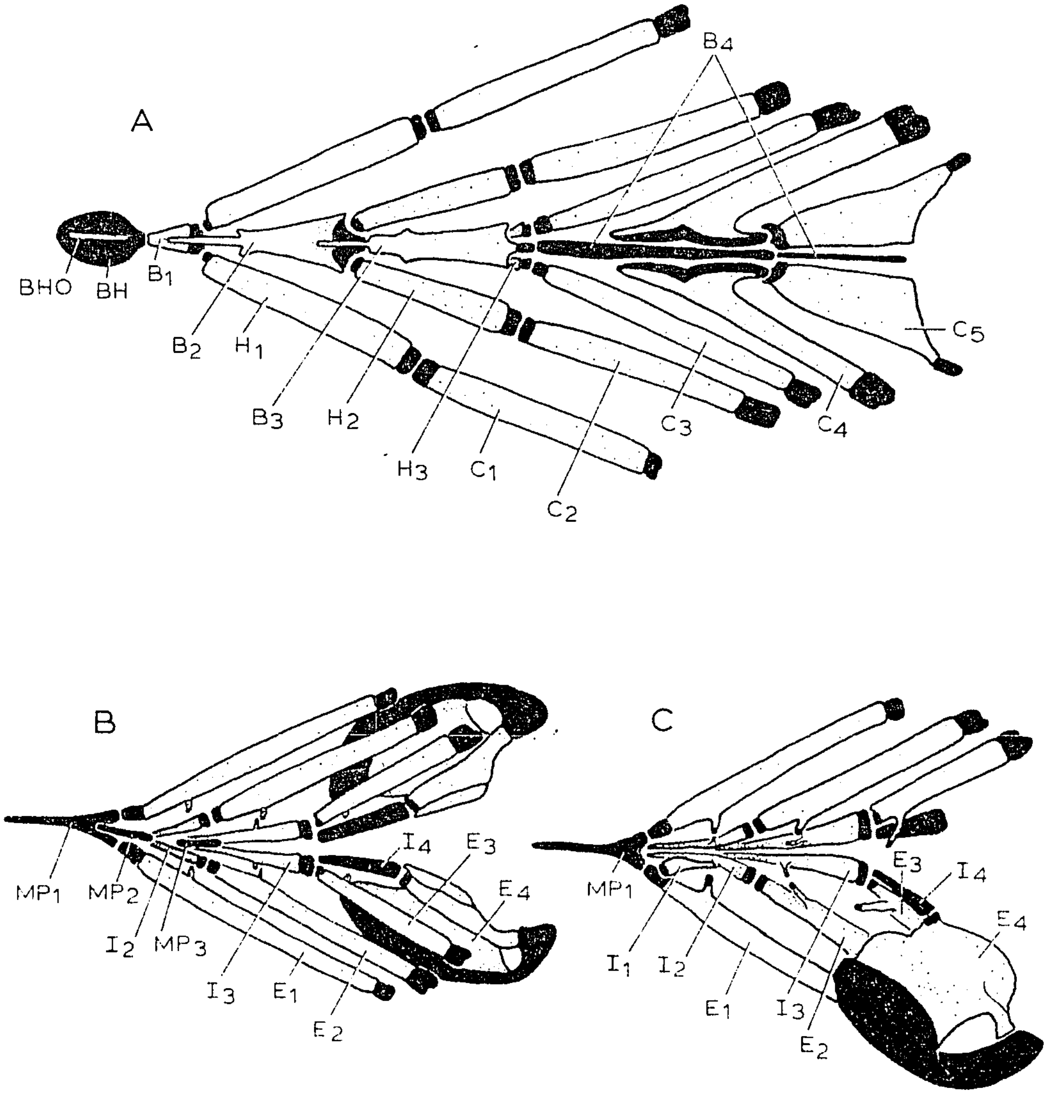
gsb

Figure 45

Fig. 46. *Dorosoma cepedianum*, gill arches (cartilage in black). Drawn flattened under a glass slide in glycerine. A) Oral surface of ventral arches (B_4 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).


A
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BH
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B3
H2
H3
C1
C2
C3
C4
C5
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MP2
I2
MP3
I3
E1
E2
I4
E3
E4
C
MP1
I1
I2
E1
I3
E2
E3
I4
E4

Figure 46

Fig. 47. Dorosoma cepedianum, A) lateral view of branchiostegal support and rays; B) dorsal view of urohyal; C) lateral view of urohyal.

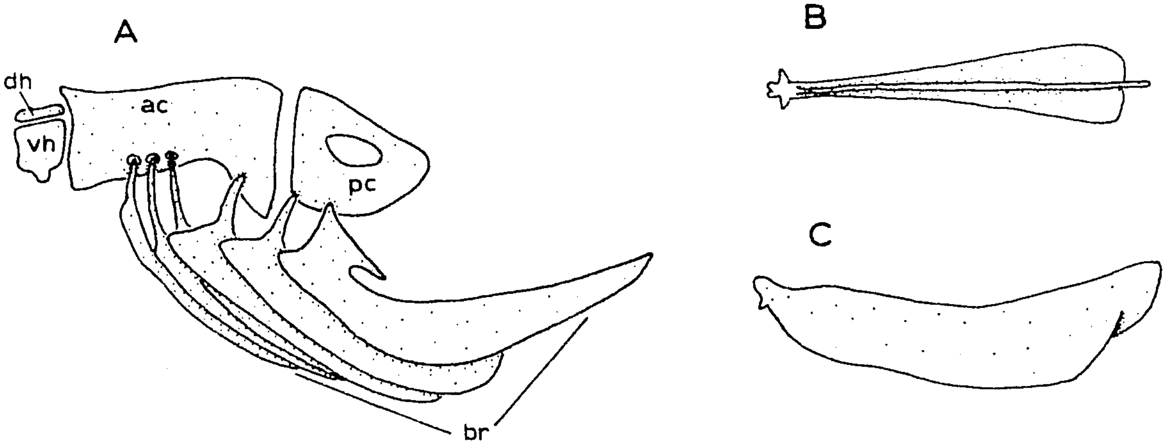


Figure 47

Fig. 48. Dorosoma cepedianum, A) pectoral radials, enlarged from C, oblique dorso-lateral view; B) pectoral radials enlarged from C, oblique dorso-medial view; C) pectoral girdle, medial view. Anterior for A and B points to upper left.

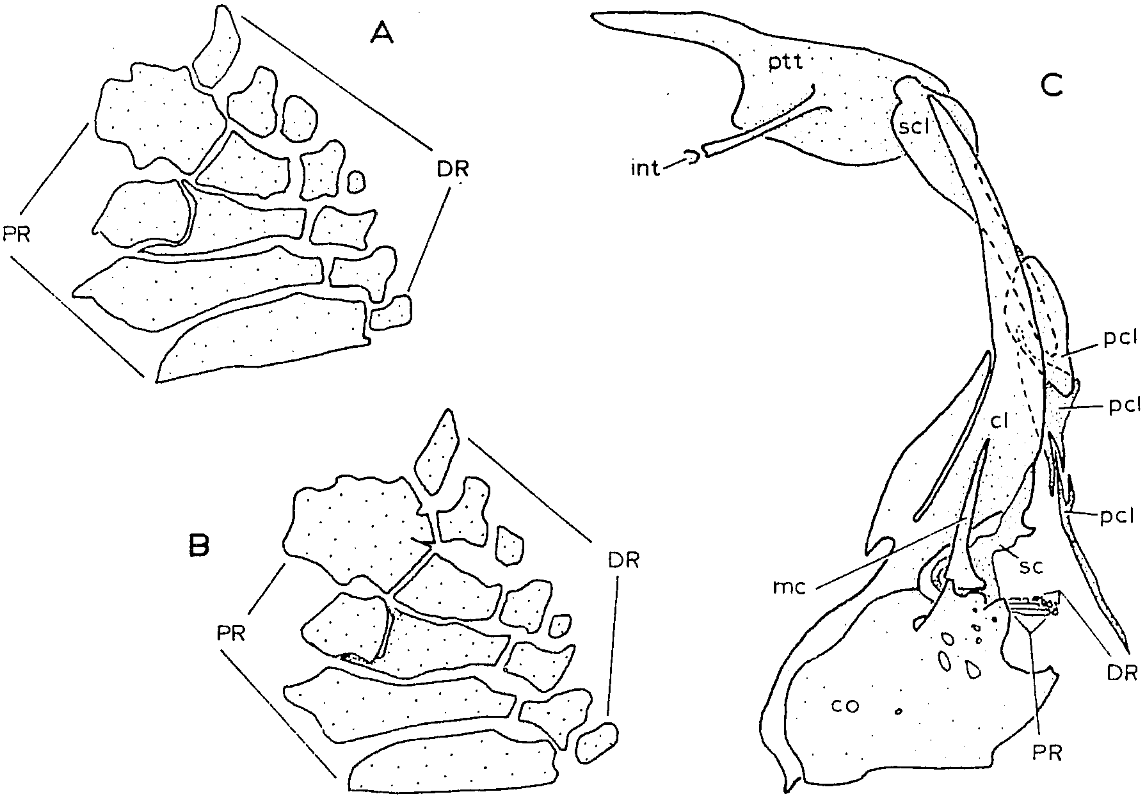


Figure 48

Fig. 49. Dorosoma cepedianum, A) flank scale (heavy lines=grooves or "radii"); B) ventral view of two abdominal scutes below pelvic fin (the pelvic scutes drawn flattened under a glass slide, in glycerine); C) dorsal view of both pelvic girdles flattened under a glass slide. D) Dorsal view of dorsal scutes.

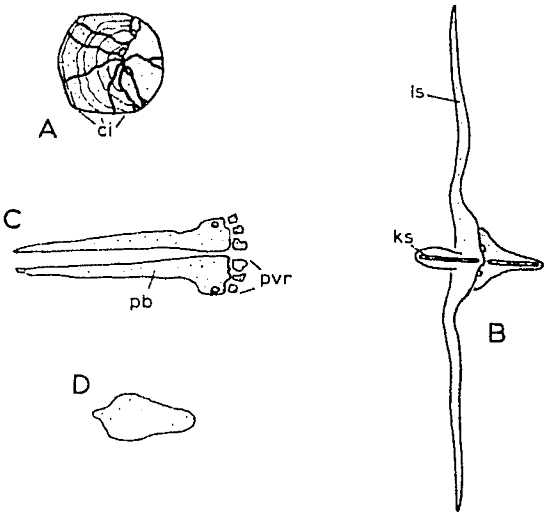
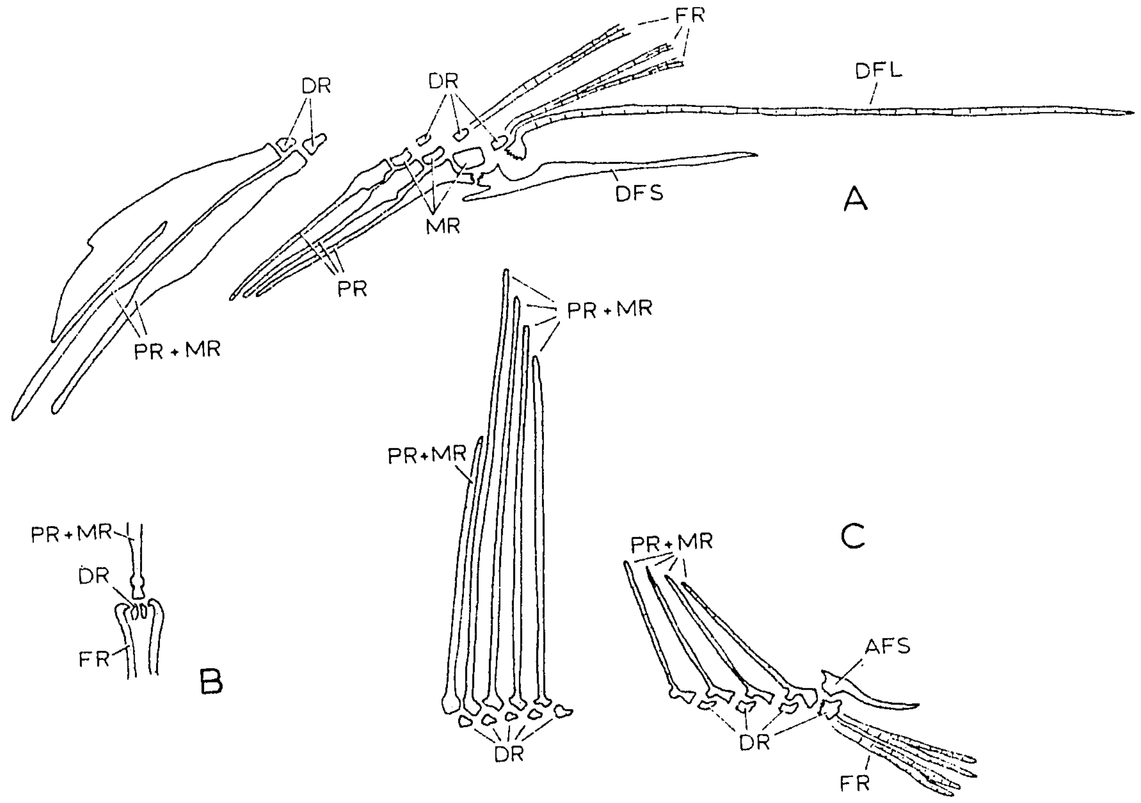


Figure 49

Fig. 50. Dorosoma cepedianum, median fin ray supports (most of the fin rays omitted): A) lateral view of anterior most and posterior most dorsal fin ray supports; B) anterior view of the base of the eighth anal fin ray; C) lateral view of anterior most and posterior most anal fin ray supports. Bases of fin rays removed on A and C.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PR + MR
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PR+MR
PR+MR
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PR+MR
AFS
DR
FR

Figure 50

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

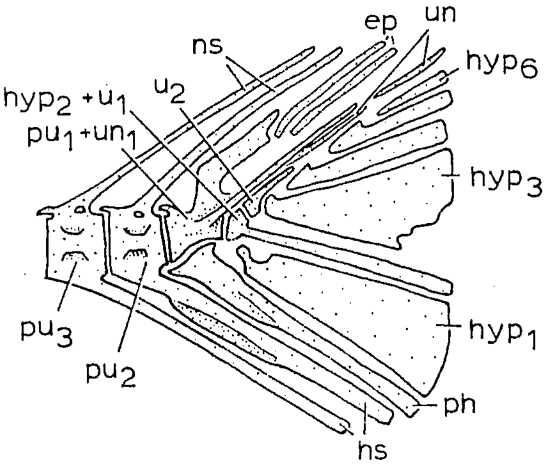

Figure 51