

Phylogeny of the Genera and Families
of Zeiform Fishes, with
Comments on Their Relationships with
Tetraodontiforms and Caproids

JAMES C. TYLER,
BRUCE O'TOOLE,
and
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ABSTRACT

Tyler, James C., Bruce O'Toole, and Richard Winterbottom. Phylogeny of the Genera and Families of Zeiform Fishes, with Comments on Their Relationships with Tetraodontiforms and Caproids. *Smithsonian Contributions to Zoology*, number 618, 110 pages, 90 figures, 2 tables, 2003.—This cladistic study, using 103 putatively informative characters (mostly osteological) of representatives of all of the genera of zeiforms, a primitive tetraodontiform, both genera of caproids, and numerous outgroups, strongly supports the monophyly of zeiforms. The possible relationship of zeiforms with tetraodontiforms and caproids is ambiguous; it is supported in three of the four analyses (data ordered with and without most meristic features and data unordered with most meristic features) but not in the one that we consider the most rational and best justified (data unordered without most meristic features).

Within zeiforms, there is strong support for a phylogeny that requires a substantially different arrangement of genera within a new concept of six monophyletic families (three with subfamilies) in two suborders.

The genus *Cyttus* (Cytoidei, Cyttidae) is shown to be the sister group to all other zeiforms (Zeioidei). The study indicates that the zeiform families, as recognized herein, have the following phylogenetic sequence: Cyttidae (*Cyttus*)—Oreosomatidae (Pseudocyttinae, *Pseudocyttus*; Oreosomatinae, *Alloctytus*, *Oreosoma*, *Neocyttus*)—Parazenidae (Parazeninae, *Parazen*; *Cytopsinae*, *Cytopsinae*, *Stethopristes*)—Zeniontidae (*Zenion*, *Capromimus*, *Cytmimus*)—Grammicolepididae (Macrurocyttinae, *Macrurocyttus*; Grammicolepidinae, *Xenolepidichthys*, *Grammicolepis*)—Zeidae (*Zeus*, *Zenopsis*).

The newly composed families and subfamilies are systematically defined, and keys to them are provided.

Examples of nearly all of the features used in the phylogenetic analyses and systematic accounts are illustrated.

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Phylogeny of the Genera and Families of Zeiform Fishes, with Comments on Their Relationships with Tetraodontiforms and Caproids

*James C. Tyler, Bruce O'Toole,
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Introduction

Zeiformes (dories), such as *Zeus faber* (the John Dory or St. Peter's fish), have been known since ancient times. Linnaeus (1758) placed *Zeus* (sensu lato) in his Thoracici, along with many groups considered today to be acanthopterygians. In this he was followed by Cuvier (1817) and by Cuvier and Valenciennes (1835), although the latter placed *Zeus* and *Capros* in a chapter separate from those dealing with other acanthopterygians, such as scombroids, lamprids, carangids, and others. Günther (1860) erected the Cyttina (*Zeus*, *Cyttus*, *Oreosoma*) as one of five groups in his family Scombridae (the other four being the Scombrina, Nomeina, Stromateina, and Coryphaenina). Gill (1863) erected the Zenoidae (equivalent to Günther's Cyttina) as distinct from his Scombroidae, and he proposed two subfamilies, the Zeinae (*Zeus*, *Zenopsis*, *Cyttus*, *Cyttopsis*) and the Oreosomatinae (*Oreosoma*). Gill did not speculate on the relationship of the Zenoidae and Scombroidae to other families. Starks (1898) concluded that zeids were related to chaetodontoids and acanthuroids and not to scombroids. Jordan and Evermann (1898) considered the relationship of zeids to other families to be uncertain, with similarities to both berycoids (based on their increased number of pelvic-fin rays) and acanthuroids (based on their close attachment of the posttemporal to the skull).

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Holt (1894) suggested that zeiforms might be related to the Heterosomata (flatfishes) (although he also hinted that flatfishes might have other relatives). Thilo (1901) also believed that the Heterosomata (pleuronectiforms) were related to zeids. Boulenger (1902), quoting Holt (1894), independently arrived at the same conclusion as Thilo; thus, he placed the Zeidae (along with the †Amphistiidae and the Pleuronectidae) in Division III (Zeorhombi) of his Acanthopterygia. Boulenger's definition of the zeids included a few specialized characters, but it was based mostly on primitive features. He suggested that the Zeorhombi were derived from a common ancestor with the Berycidae. In 1904, Boulenger reiterated this view.

Regan (1910) proposed a close relationship between zeiforms (his Zeidae) and caproids (his Caproidae), recognized them as the order Zeomorphi, and related them to berycoids, stating that they differed only in certain specializations. Regan's views were followed by Gregory (1933).

Norman (1934) disagreed with Thilo's (1901) and Boulenger's (1902, 1904) assessment that zeiforms were related to flatfishes, but he did not present an alternative hypothesis. Ford (1938) agreed with Norman, noting that the differences in their vertebral morphology did not support an association between flatfishes and zeids. Ford commented on the similarity of the bifurcate first neural arch and spine supporting the first pterygiophore in both *Zeus* and *Capros*.

Berg (1940) simply listed his Zeiformes after the berycoids. He included three families, the Zeidae, Grammicolepididae, and Caproidae, and stated that caproids bore some resemblance to chaetodontoids and ephippids. Myers reviewed the grammicolepidids (1937) and oreosomatids (1960) and made many preceptive surmises about generic groupings of other zeiforms.

Patterson (1968) regarded zeiforms (including caproids) to be the apomorphic sister group to berycoids (including stepha-

noberyciforms), with the two together being the sister group to percomorphs. Winterbottom (1974) suggested that at least some zeiforms might be related to tetraodontiforms. Rosen (1984) provided evidence for a group comprising caproids, tetraodontiforms, and zeiforms, with the latter two being sister groups (see "Previous Phylogenetic Analyses of Zeiforms," below, for details).

Most recently, Johnson and Patterson (1993) tentatively suggested that zeiforms (excluding caproids) are the sister group to beryciforms (excluding stephanoberyciforms) plus percomorphs. They went on to state that *Zenion* and *Parazen* might be the more primitive zeiform taxa (morphologically) and provided the only cladistically based statement of relationships among zeiform families to date. They also offered considerable evidence for the monophyly of the Zeiformes (see "Previous Phylogenetic Analyses of Zeiforms" for details); in the present work we add substantially to that evidence.

Most authors (e.g., Heemstra, 1980, 1986; Tighe and Keene, 1984; Karrer and Heemstra, 1986) presently recognize five families of zeiforms (or six families if caproids are included among zeiforms, as in Eschmeyer, 1990, and Nelson, 1994), usually with the following included genera:

PARAZENIDAE (*Parazen* only)

ZENIONTIDAE (either *Zenion* only or with the enigmatic *Macrurocyttus* also included, in which case the family name Macrurocyttidae is sometimes used)

GRAMMICOLEPIDIDAE (*Grammicolepis*, *Xenolepidichthys*)

OREOSOMATIDAE (*Allocyttus*, *Neocyttus*, *Oreosoma*, *Pseudocyttus*)

ZEIDAE (*Capromimus*, *Cyttomimus*, *Cytopsopsis*, *Cyttus*, *Stethopristes*, *Zenopsis*, *Zeus*)

Among the genera usually assigned to the Zeidae, the placement of *Capromimus* and *Cyttomimus* has been considered questionable (Heemstra, 1980), although they are accepted in that family by Bray (1983). In fact, the family Zeidae has become the convenient repository for all of the zeiform genera that could not be easily placed in any of the other four families.

The genus *Daramattus*, with two South African nominal species, has sometimes been recognized as distinct from *Grammicolepis* within the Grammicolepididae (e.g., Heemstra, 1980), but we agree with Karrer and Heemstra (1986) that the two species of *Daramattus* are both synonyms of *Grammicolepis brachiusculus*.

We have examined the osteology of representatives of all of the above valid genera of zeiforms, and most of the species of zeiforms. The only zeiform species that we at least tentatively consider to be valid that we have not osteologically examined are *Allocyttus guineensis*, valid according to Karrer (1986); *Cytopsopsis cypho*, valid according to Paxton and Hanley (1989) and Bray (1983); *Zenopsis* sp., a new species from the South China Sea and western Australia being described by Yamada, Nakabo, and Bray (MS); and several species of *Neocyttus*, a genus recently revised by Yearsley and Last (1998), who show that in addition to the common *N. rhomboidalis* examined

herein, there are four other valid species, *N. acanthorhynchus* (also considered valid by Heemstra, 1980, and Karrer, 1986), *N. helgae*, *N. psilorhynchus*, and an as yet unnamed taxon.

For several other zeiform species we have examined only radiographs or very limited dry skeletal materials, and our data on these are insufficient for them to be included in our study: *Allocyttus folletti*, *Zenion leptolepis* (either this species has several synonyms, such as *longipinnis* and *japonicus*, in the Indo-western Pacific, or there are more than two valid species of *Zenion*), *Zenopsis oblongus*, and *Zeus capensis* (see "Material").

The nomenclature of the species of zeiforms studied herein is relatively stable, and we do not list their often lengthy synonymies. For such synonymies, see the publications of P.C. Heemstra, C. Karrer, and D.J. Bray cited above, and the following: Heemstra (1999), Karrer (1990), Karrer and Post (1990), Quéro (1973), and Wheeler (1973).

The fossil zeiforms are under study by one of us (JCT) and are not treated herein, mainly because most of the features in our matrix of phylogenetically informative characters cannot be determined in the fossils. The three earliest known zeiforms, however, belong to morphologically primitive genera (see Figure 89 for the Upper Cretaceous *Cretazeus*) that cannot be placed in any of the extant families. These are a single species, *Cretazeus rinaldi* (Tyler et al., 2001), from the Upper Cretaceous (upper Campanian-lower Maastrichtian) of Nardò, Italy, about 72 million years ago (m.y.a.), and two species, *Protozeus kuehnei* and *Archaeozeus skamolensis* (both Bonde and Tyler, in Tyler et al., 2001) from the upper Paleocene-lower Eocene boundary (Mo-clay, Fur Formation) of Denmark, about 58–59 m.y.a. We have examined the holotype (Instituto Superior Técnico (IST), Laboratório de Geologia Aplicada, Lisboa, IST 559, 9 mm SL) of the putative zeiform *Palaeocyttus princeps* Gaudant (1977, 1978) from the Middle Cretaceous of Portugal and agree with Patterson (1993a, 1993b), who noted that it differs substantially from zeiforms, and with Bonde and Tyler (MS) that it is not a zeiform but is probably a beryciform.

All other zeiform fossils are of Oligocene (about 36 m.y.a. for the oldest) or younger age and are zeids that can probably be placed in either the extant *Zeus* or *Zenopsis* (see Figure 90 for one of the typical Oligocene species of *Zenopsis*), and certainly within the *Zeus* + *Zenopsis* clade (Baciu, Bannikov, and Tyler, in prep.).

By comparison, the earliest known tetraodontiforms are a clade of three Upper Cretaceous taxa (the oldest, from Hakel, Lebanon, is from about 95 m.y.a.); this clade is the sister group to the clade comprising all other tetraodontiforms (Eocene to present, the oldest from about 58 m.y.a.) (Tyler and Sorbini, 1996). Caproids are known only as early as the lower middle Eocene (Monte Bolca, Italy, about 50 m.y.a.) (Sorbini, 1983; Sorbini and Bottura, 1988), with taxa that are similar enough to the extant species that they presently are contained in extant genera (but at least the earliest caproid, the Monte Bolca *Antigonina veronensis* Sorbini, lacks a few derived features of the

extant species of *Antigonia* and could be placed in its own genus). We have examined the holotype (Museum National d'Histoire Naturelle, Paris, HDJ-73-17, 20 mm SL) of the putative caproid *Microcapros libanicus* Gayet (1980a, 1980b) from the Middle Cretaceous of Lebanon and agree with Zehren (1989, MS), Bannikov (1991), and Patterson (1993a, 1993b) that it is a trachichthyid, not a caproid.

All of the taxa of the earliest known caproids, zeiforms, and tetraodontiforms are relatively much smaller in size than the fossils of each of these groups from subsequent periods and of the extant species of each. These earliest taxa, however, are fully ossified, and the specimens of each apparently are at least young adults: 21.0 mm standard length (SL) for the Eocene caproid *Antigonia veronensis*; 15.4–53.1 mm SL for the Upper Cretaceous zeiform *Cretazeus rinaldi*; 8.5–10.5 mm SL for the two upper Paleocene species of zeiforms; and ~10–24.5 mm SL for the three Upper Cretaceous species of tetraodontiforms. This leads us to suspect that paedomorphic processes were important in the early evolution of all three groups (Tyler and Sorbini, 1996, had suggested this previously for tetraodontiforms alone).

The primary purpose of the present study is to elucidate the intrarelationships of zeiform fishes, and the characters selected for inclusion in the analyses reflect this (see "Analytical Protocols"). In order to evaluate the relationships between zeiform taxa, we needed to postulate outgroups of the zeiforms for purposes of character evaluation. We have examined representatives of most of the higher-level groups that have been suggested as possible sister groups of zeiforms. We did not include pleuronectiforms, a group that seems to us an unlikely candidate, but this possibility will be the topic of a subsequent study.

We evaluate the evidence supporting zeiform monophyly, revisit the question of caproid, zeiform, and tetraodontiform relationships, and propose a hypothesis of the intrarelationships of zeiform taxa based on a cladistic evaluation of the osteological features of 20 zeiform and 10 outgroup species. We then compare our hypotheses with the results of various other previous studies. Finally, we systematically define all of the familial and subfamilial categories of zeiforms recognized herein.

This study had its origins in 1992, when two of us (JCT and RW) and G. David Johnson of the Smithsonian Institution agreed to attempt a brief preliminary analysis of zeiform relationships for possible inclusion in a forthcoming volume on fish phylogeny. Because of the press of time, that preliminary work used a single exemplar for each of the then-recognized five families of zeiforms, and the results were deemed insufficient for publication; however, some of the phylogenetically interesting features of zeiforms described herein were first discovered in conjunction with G. David Johnson.

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Methods

TERMINOLOGY.—All lengths are standard length (SL) unless otherwise stated, and these are given to the nearest whole millimeter (mm), except for the larval stages discussed in the following section, which are given in tenths of a millimeter. CI=consistency index and RI=retention index (capitalized when referring to overall tree statistics; lower-case when referring to individual character statistics). HPU=haemal spine of preural centrum, PB=pharyngobranchial, PU=preural centrum, NPU=neural spine of preural centrum, UP=upper pharyngeal tooth-plate.

We use Arabic numbers for the characters and character states in our analyses, and (in brackets) Roman numbers for characters discussed from the literature (see “Previous Phylogenetic Analyses of Zeiforms”).

We use the terms Zeiformes and zeiforms for the five families most commonly assigned to that order, herein expanded to six families, with zeiforms not including caproids (or tetraodontiforms).

The term Zeomorphi is ambiguous, and we do not use it herein. As proposed by Regan (1910), the order Zeomorphi in-

cluded two families, the Zeidae for all zeiforms and the Caproidae for *Capros* and *Antigonia*. Myers (1937, 1960) followed Regan in considering the Zeomorphi to include both zeiforms (with five families) and caproids. Greenwood et al. (1966) recognized the Zeiformes (with Zeomorphi as a synonym) with the traditional five families of zeiforms plus caproids, and the inclusion of caproids with zeiforms was followed by Eschmeyer (1990) and Nelson (1994). Rosen (1984), however, used Zeomorphi as a division comprising the five families of zeiforms, which he proposed as the sister group to the division Plectognathi (i.e., the traditional tetraodontiform fishes), with the Zeomorphi (=zeiforms) + Plectognathi (=tetraodontiforms) clade as the sister group to the family Caproidae, and with the caproids + Zeomorphi + Plectognathi constituting the order Tetraodontiformes, a very different usage than traditional for the terms tetraodontiform and zeomorph. Zehren (1987) followed Rosen (1984) in the use of Zeomorphi = zeiform, but others have not. Stiassny and Moore (1992) used “zeoid” for the zeiform lineage within a higher category of a problematic “zeiform radiation” that included caproids, zeoids = zeiforms sensu stricto, and plectognaths = tetraodontiforms. The term Zeomorphi remains available for some higher category that includes the Zeiformes.

If a species is of a monotypic genus or if a genus has only a single species examined in this work, that taxon is often referred to by the generic name alone.

Length of the upper jaw is measured from the midline border of the premaxilla to the ventral end of the maxilla.

The distinction between the abdominal and caudal series of vertebrae is relatively clear in most zeiforms, with the first caudal vertebra having a much longer haemal spine than those preceding it, and it supports along its anterior border the first one or more anal-fin pterygiophores. The distinction, however, is more subjective in some zeiforms, especially in zeids and oreosomatids, because the haemal spines of several vertebrae overlap the lateral surface of the proximal end of the large first anal-fin pterygiophore, and these haemal spines only gradually increase in length. In these cases, the first caudal vertebra is considered to be that in which the haemal spine is alongside the rear half of the lateral surface of the upper end of the first anal-fin pterygiophore, and which is followed by the much longer haemal spine of the second caudal vertebra, with numerous anal-fin pterygiophores between the short haemal spine of the first caudal vertebra and the longer spine of the second (see lateral-view illustrations of the entire skeletons of an oreosomatid and a zeid, Figures 16, 73). For tetraodontiform fishes we retain herein the traditional distinction between abdominal and caudal vertebral series, which is based on the first caudal vertebra being the first in the series with a much longer haemal spine than those preceding it, even though it apomorphically supports the first anal-fin pterygiophore along its posterior border rather than its anterior border as in zeiforms, caproids, and most other fishes.

The caudal peduncular vertebrae are defined as all those, including the urostylar centrum, posterior to the last vertebra with neural or haemal spines supporting dorsal- or anal-fin pterygiophores.

For the specialized scales found in some zeiforms, we follow the currently used terminology of “buckler” for the greatly enlarged (**many times** larger than the other scales on the body) and thickened scale plates found variously along the dorsal- and anal-fin bases and along the ventral midline from the isthmus to the anus in genera of several families, and “scutes” for the only slightly enlarged (no more than about twice the size of the surrounding scales) modified scales with a zipper-like overlapping arrangement along the ventral midline in the Cyttidae. We have no evidence about any possible developmental or phylogenetic differences between the scales in these convenient morphological categories.

The terms interneural space and interhaemal space are used in the revised sense of Birdsong et al. (1988), Baldwin and Johnson (1993), and Bannikov and Tyler (1995), with the first space being that between the first and second neural or haemal spines, and the preneural and prehaemal spaces being those in front of the first neural and haemal spines.

Statements about ribs (pleural ribs) and epineural bones are based on ossified elements and do not include what are sometimes ligamentous elements (for which see Patterson and Johnson, 1995). We note that all zeiforms lack ossified ribs on the first four abdominal vertebrae, with the exception of *Grammicolepis brachiusculus*, in which slender ossified ribs are present from the third abdominal vertebra posteriorly (as shown long ago by Shufeldt, 1888).

The term principal caudal-fin rays is used in the traditional sense of relatively long, articulated (cross-striated) rays, which nearly always have a single uppermost and a single lowermost unbranched ray and branched rays between them, in contrast to the procurrent rays, which are shorter and more spine-like and are usually nonarticulated in acanthomorph fishes. The single exception is *Parazen pacificus*, in which there are two long, articulated, but unbranched rays above and below the branched rays.

Both *Capros* and *Antigonina* are sometimes said to have 12 principal rays, but based on the usual definition of principal rays being the branched rays plus the single uppermost unbranched ray and the single lowermost unbranched ray, *Capros* has 14 principal rays (12 branched + 2 unbranched) and *Antigonina* has 12 (10 branched + 2 unbranched).

We agree with Johnson and Patterson (1993) in their refutation of the persistent legend that some zeiforms have eight branchiostegal rays, like most beryciforms and stephanoberyciforms, rather than seven as in most perciforms. All specimens of zeiforms examined herein have $3 + 4 = 7$ branchiostegals, with the single exception of *Macrurocyttus acanthopodus*, in which five of seven specimens have $2 + 4 = 6$ branchiostegals and two specimens have $3 + 4$ (therefore, it is coded with the majority condition of six rays).

We characterize Bremer branch support values (see “Analytical Protocols”) as follows: 1 = weak, 2 = moderate, 3 = good, 4 = strong, and 5 or higher = very strong.

The term “consistent” synapomorphy is used to denote those character states that are unambiguous, non-reversed, and non-parallel (i.e., exhibit no homoplasy) within both the 20 zeiform taxa and the 10 outgroup taxa. As is always the case, the use of the terms synapomorphy, apomorphy, and plesiomorphy and our statements regarding homoplasy indicate only relative relationships. The terms are restricted to the relationships between the taxa represented in the analyses and pertain only to those taxa being considered for the clade under discussion.

In addition to the species examined among our outgroups, we have consulted Zehren (1979) and Kotlyar (1996) for information on beryciforms and Tyler (1980) for tetraodontiforms; our osteological terminology follows those works, except for a few recently changed usages (e.g., supraneural instead of predorsal, following Mabee, 1988; rib instead of pleural rib, and epineural instead of epipleural, following Patterson and Johnson, 1995, and Johnson and Patterson, 2001, in contrast to Gemballa and Britz, 1998). For the systematics of the genera traditionally assigned to the Zeidae, we have consulted the excellent study by Bray (1983).

ZEIFORM PROCURRENT CAUDAL-FIN RAYS.—In all extant zeiforms the principal caudal-fin rays are preceded by one to eight procurrent rays, except in *Macrurocyttus acanthopodus*, in which there are no procurrent rays (procurrent rays are also absent in the Upper Cretaceous *Cretazeus* and the upper Paleocene *Protozeus*, but a single procurrent may be present in the upper Paleocene *Archaeozeus*). The absence of procurrent rays in the numerous specimens of *Macrurocyttus*, all of which are 45 mm SL or smaller (and in *Cretazeus*, 15–53 mm SL, and the very small specimens of *Protozeus*, 9–11 mm SL) should be considered a derived feature and not a developmental condition because the full complement of procurrent and principal rays in extant zeiforms is usually formed at very small sizes. We have found the procurrent rays fully developed in postlarval or early juvenile specimens for all of the several species of zeiforms for which we have available specimens even smaller than those of any of the above-mentioned species that lack procurrent rays. For example, in the well-ossified skeleton of a cleared and stained 8.9 mm SL specimen of *Zenion hololepis* (see “Material”); the caudal skeleton of this specimen is illustrated in Johnson and Patterson, 1993:597, fig. 21), the full adult complement of 13 principal rays, three procurrent rays above the principals, and two below the principals is present. We have also examined a large series of alcohol-preserved postlarval and early juvenile specimens of *Z. hololepis* from the collections of the Museum of Comparative Zoology (MCZ), Harvard University. This series (MCZ 41617, 60752, 85102–85112, 87021) has 15 specimens of 6.4–20.2 mm SL, with four of them (6.4–8.3 mm) even smaller than the smallest specimen of even *Protozeus*, and all of these small specimens of *Z. hololepis* have the full adult complement of 2 or 3 procurrent rays

above and below and 13 principal rays. Likewise, a series of six alcohol-preserved specimens of *Xenolepidichthys dalgleyshi* of 8.4–18.7 mm SL (MCZ 57867, 57869, 57871, 57872, 84958, 84959) and a single cleared and stained specimen of ~8.9 mm SL (see “Material”) all have the full adult complement of one procurrent ray above and below and 15 principal rays, and two specimens of *Parazen pacificus* of 12.5–18.7 mm SL (MCZ 85099, 85100) have the full adult complement of 7 or 8 procurrent rays above and below and 13 principal rays.

The only small specimen of a zeiform fish we have examined in which the caudal fin is not fully formed is a cleared and stained 7.0 mm SL specimen of *Zenopsis* sp. (see “Material;” this specimen is mentioned by Johnson and Patterson, 1993:596, as *Zeus* sp., 10 mm SL). The entire skeleton is unossified, and the caudal skeleton is not yet fully formed even in cartilage; the caudal fin has five rays in the upper lobe and seven in the lower lobe. Adults of the several species of *Zenopsis* have one procurrent and six principal rays above and one procurrent and seven principal rays below; therefore, the 7.0 mm specimen of *Zenopsis* sp. has not yet developed two of the uppermost rays and one of the lowermost rays.

ZEID PELVIC FIN.—The first element in the pelvic fin of *Zeus* and *Zenopsis* has been interpreted variously as a spine (especially in *Zeus*) or a ray (usually in *Zenopsis*). Based on adult morphology, we consider the first element in the pelvic fin of *Zeus* to be a spine because it is divided basally into two halves for only a short distance; otherwise it is a single piece, unsegmented and unbranched, although this spine is less robust and more flexible than that in many other zeiforms with an unquestioned pelvic-fin spine. The pelvic-fin spine in *Zeus* is followed by six typical rays in *Z. capensis* and usually by seven in *Z. faber* (sometimes only six rays in the latter). Also based on adult morphology, we consider the first element in the pelvic fin of *Zenopsis* to be a ray because it is divided into two halves throughout its length, even though it is unsegmented and unbranched; this element is followed by five other more typical rays, which are segmented and, with increasing specimen size, branched. The single developmental stage we have examined of any of the species of these two genera is a 7 mm SL larval stage of *Zenopsis* sp. (Dana Collection 3915 II), and it is insufficient to settle the issue. Irrespective of its developmental history, the first element in the pelvic fin of *Zenopsis* is significantly different from that of *Zeus*; therefore, we code it differently between the two taxa.

It is clear from the above that we do not know the true homology of the spinous compared with the ray-like first pelvic-fin element in *Zeus* and *Zenopsis*; this may eventually be determined in relation to the reduction of the free pelvic radials between the bases of the rays (see Johnson, 1992; Stiassny and Moore, 1992; Johnson and Patterson, 1993). We note, however, that the first element of the zeiform pelvic fin, whether solid or divided into two halves, segmented or unsegmented, is most parsimoniously interpreted as a spine or a transformed spine. This interpretation involves a single step, a change in morphol-

ogy from spine-like to ray-like. The alternative involves at least four steps: loss of the spine, loss of the arrector muscles associated with the spine, promotion of the first pelvic-fin ray to the position of the spine, and recreation of the arrector muscles to serve the “new” leading element of the pelvic fin. Arrector muscles in teleosts are always associated (in those taxa for which information is available) with the leading element of the pelvic fin where this structure is present and unreduced.

CODING CONVENTIONS.—Meristic and other characters exhibiting variability are used under the following conventions. When one particular count or state is far more common than any other for all of the specimens examined of a species, that count or state is the one used in the analyses. When two or more counts or states are about equally common among the specimens examined for a species, the character is considered to be polymorphic (and marked “p” in the data-set matrix (Table 1) unless the variability is confined to a single character state having a range of values, e.g., total number of vertebrae). In the table of meristic features (Table 2), the most common count for a character, if there is one, is underlined. When the materials of a particular species encompass a broad range of sizes, statements about morphological features are based on the larger specimens available (which, for the cleared and stained materials, are often large juveniles or young adults), except when significant ontogenetic changes are evident in a feature (e.g. size of the beryciform foramen and suturing between the ceratohyal and epihyal) and so recorded for the materials examined. Features of the few cleared and stained larval and post-larval stages examined (for *Morone*, *Zenion*, *Xenolepidichthys*, and *Zenopsis*) are mentioned only where appropriate (e.g., development of procurrent caudal-fin rays).

ANALYTICAL PROTOCOLS.—This study primarily investigates the relationships of zeiform taxa with one another, and secondarily the putative sister-group relationship between zeiforms and tetraodontiforms. Therefore, the morphological features selected for study are mostly those that were found to differ between various zeiform taxa and between zeiforms and a representative of a phylogenetically basal clade of tetraodontiforms. We have not included many of the features (such as in Stiassny and Moore, 1992, and Johnson and Patterson, 1993, and contained references) that might clarify relationships between the lower acanthomorph outgroups used herein and zeiforms. Thus, our lack of resolution in the relationships of zeiforms and the outgroups in some of our analyses is not surprising.

In rooting the trees, 10 potential outgroups were considered, because a well-corroborated sister group for zeiforms has not been established. Although tetraodontiforms and caproids have been most frequently cited in recent years as potential and sequential sister groups for zeiforms, the evidence for this is equivocal (particularly for caproids, for which, additionally, monophyly has yet to be convincingly demonstrated). All 10 potential outgroups gave the same branching sequence within zeiforms when selected as the single outgroup. *Melamphaes*

was selected to root our analyses because it is generally regarded as a member of a group placed near the base of the acanthomorph tree. Thus, even though *Melamphaes* is in certain ways an apomorphic basal acanthomorph, we believe it is a more objective choice for rooting the trees than a taxon that might be either a questionable sister group of zeiforms or one derived either **earlier or** later than the common ancestor of zeiforms. Moreover, even representatives of the more basal clades of tetraodontiforms are so osteologically apomorphic as to be of somewhat limited value in the polarization of zeiform characters.

We recognize the limitations in using a single species to represent a large higher category (e.g., *Morone* representing percoids, and *Parahollardia* representing tetraodontiforms) and that our hypothesis-testing is of the relationships only of the included taxa (or, rather, of a limited number of specimens that we presume adequately represent a species).

Data were gathered on 124 morphological features for 20 zeiform and 10 outgroup taxa. Of these features, 17 were discarded from further consideration early in the study for a variety of reasons; they were either too intraspecifically variable or too subjective to determine consistently between taxa, or they over-emphasized certain repetitive configurations, such as the number of pterygiophores between neural and haemal spines of long sequences of successive vertebrae.

Of the remaining 107 putatively informative characters examined, the number was further reduced to 103 (Table 1) by removing four characters that were autapomorphic and thus phylogenetically uninformative: presence/absence of nasals (absent only in *Parahollardia lineata* and all other tetraodontiforms), presence/absence of teeth on the premaxilla (absent only in *Oreosoma atlanticum*), length of the gill opening (reduced to a short slit only in *Parahollardia lineata* and all other tetraodontiforms), and number of unbranched principal caudal-fin rays (increased from two to four only in *Parazen pacificus*).

A second, more restricted, data set was produced by removing 11 meristic characters. Serially repeated, or "number line," characters, such as meristic features, are difficult to interpret in phylogenetic analyses (Murphy and Doyle, 1998). In addition, meristic characters can be problematic because of the effects of varying developmental condition (see "Meristic Character-State Evolution," below).

The 11 meristic characters (93 through 103) are as follows: total number of vertebrae, number of abdominal vertebrae, number of vertebrae in the caudal peduncle, number of principal caudal-fin rays, number of procurrent caudal-fin rays, number of dorsal-fin spines, number of vacant interneural spaces, number of anal-fin spines, number of pectoral-fin rays, total number of pelvic-fin elements, and number of branchiostegal rays.

The data for the 20 zeiforms and 10 outgroups were analyzed both as the full data set of 103 characters and as a reduced data set of 92 characters. All of these characters and their states are defined at the beginning of the "Results" section.

Most multistate characters were coded and ordered as linear transformation series; the exceptions to this are noted in the character-state descriptions. The data set was also examined with all characters as unordered transformation series. The data were analyzed using Hennig86 (Farris, 1988). Because of the large number of taxa in the data set, implicit enumeration ("ie") was not appropriate; therefore, the Wagner trees were created by multiple passes through the data matrices ("mh"), and then branch breaking and swapping ("bb*") was applied to find the most parsimonious tree(s). Before analysis in Hennig86, the order of taxa in all data matrices was randomized using the Joyride program in Random Cladistics (Siddal, 1997).

In all four analyses (ordered and unordered, both with and without 11 meristic characters), *Melamphaes* served as the primary outgroup and rooted the trees. The polymorphic data were analyzed using mutation coding as it applies to morphological characters (Murphy, 1993). The polymorphic cells were coded as unknown ("?") in the initial analyses, then the characters were optimized onto the resulting tree(s), and the polymorphic data were reassessed. Each polymorphic cell was either recoded, representing the novel evolutionary state (i.e., the mutation), or left unchanged, if the transformation was unresolved or ambiguous. The entire data set was then reanalyzed and the remaining polymorphic cells were reassessed in the same manner. This process was repeated until there were no changes in the data set.

Characters were optimized using the accelerated transformation (ACCTRAN) option in CLADOS (Nixon, 1992), in which reversals are favored over parallelisms for homoplastic characters. Ambiguous character optimizations (i.e., ACCTRAN maps the character differently than in delayed transformation, DELTRAN) are noted in the section "Phylogenetic Results." The support for each clade, as branch-support values (Bremer, 1988, 1994), were evaluated using the "branch support" option in NONA (Goloboff, 1993).

Ten thousand trees were generated that were a maximum of 15 steps longer than the most-parsimonious tree; consensus trees were derived from these to determine branch support. These represent the number of extra steps needed to be added to the most-parsimonious tree that will collapse that branch in the strict consensus of all trees of that length and shorter. These values are considered to be good indicators of ranked nodal support (Doyle, 1998).

TREE CHARACTERISTICS.—Using the full data set of 103 characters, the ordered analysis resulted in six trees of 581 steps (CI=40, RI=65); the strict consensus tree is shown in Figure 1. The unordered analysis resulted in a single most-parsimonious tree of 482 steps (CI=47, RI=64), which is shown in Figure 2.

Using the reduced data set of 92 characters, the ordered analysis resulted in 11 trees of 386 steps (CI=43, RI=66); the strict consensus tree is shown in Figure 3. The unordered analysis resulted in 26 trees of 354 steps (CI=46, RI=68); the strict consensus tree is shown in Figure 4.

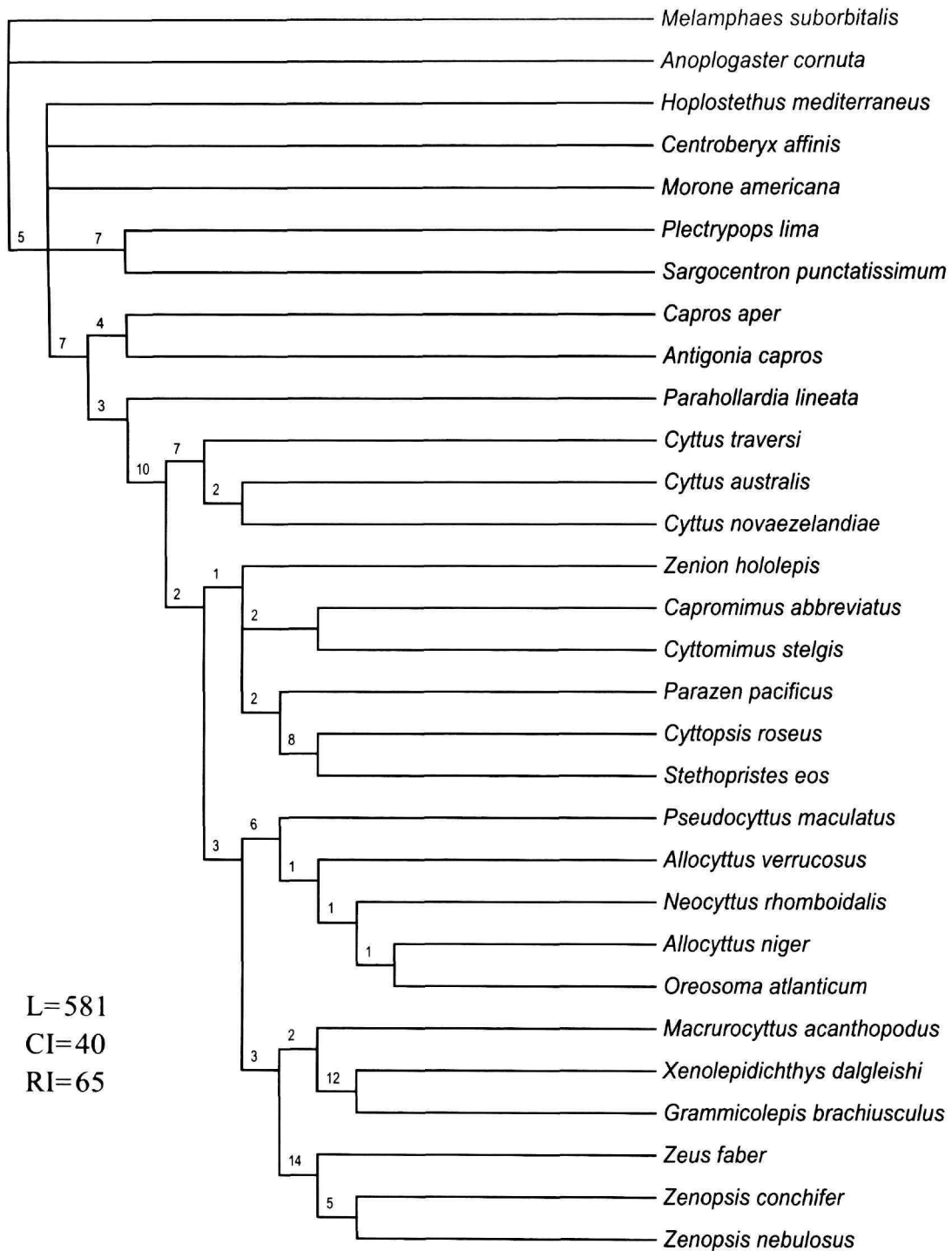


FIGURE 1.—Strict consensus of the six most-parsimonious trees resulting from an ordered analysis of the complete data set of 103 characters. Branch support indices (Bremer, 1994) are shown above all relevant branches. The tree is rooted at *Melamphaes*.

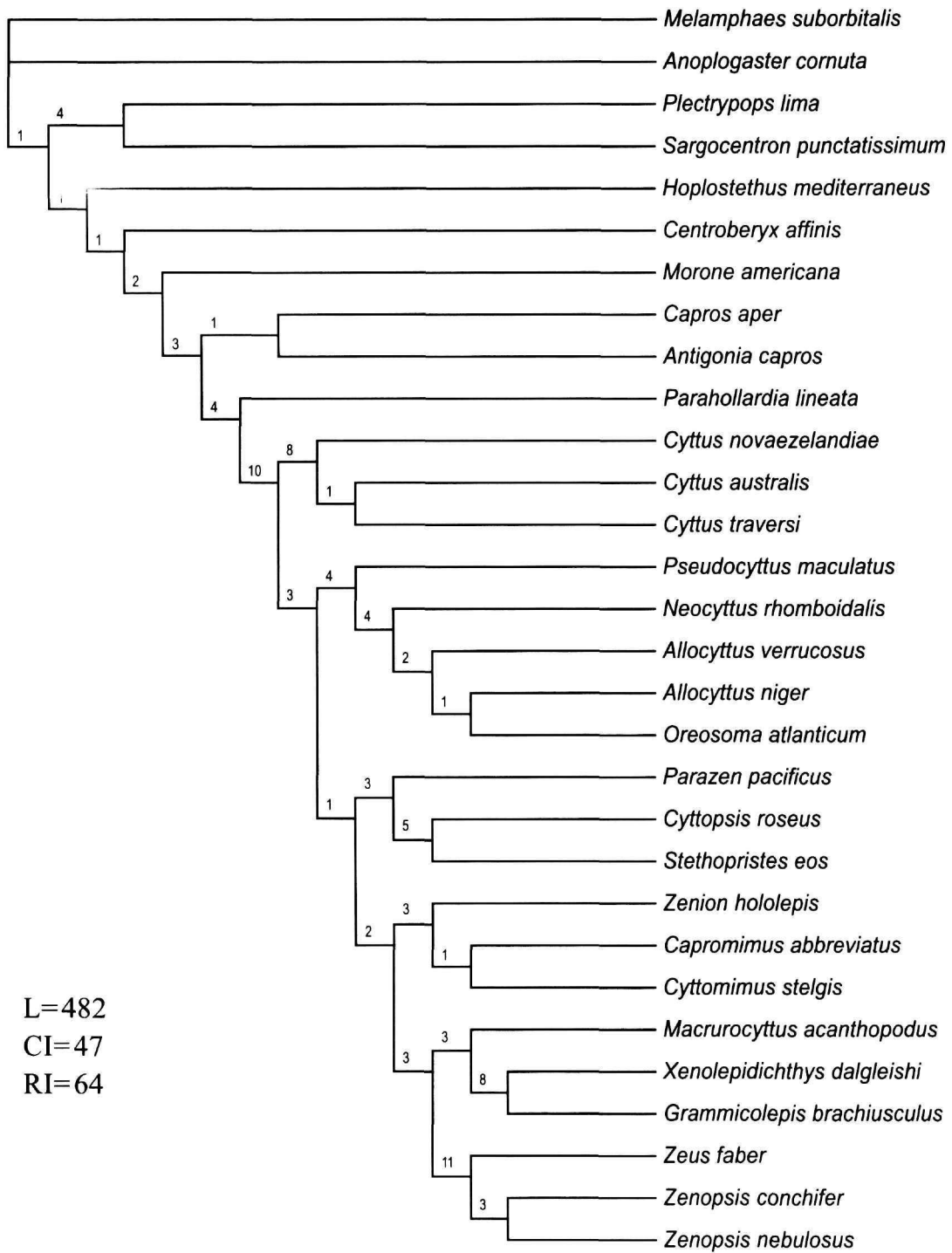


FIGURE 2.—Single most-parsimonious tree resulting from an unordered analysis of the complete data set of 103 characters. Branch support indices (Bremer, 1994) are shown above all relevant branches. The tree is rooted at *Melamphaes*.

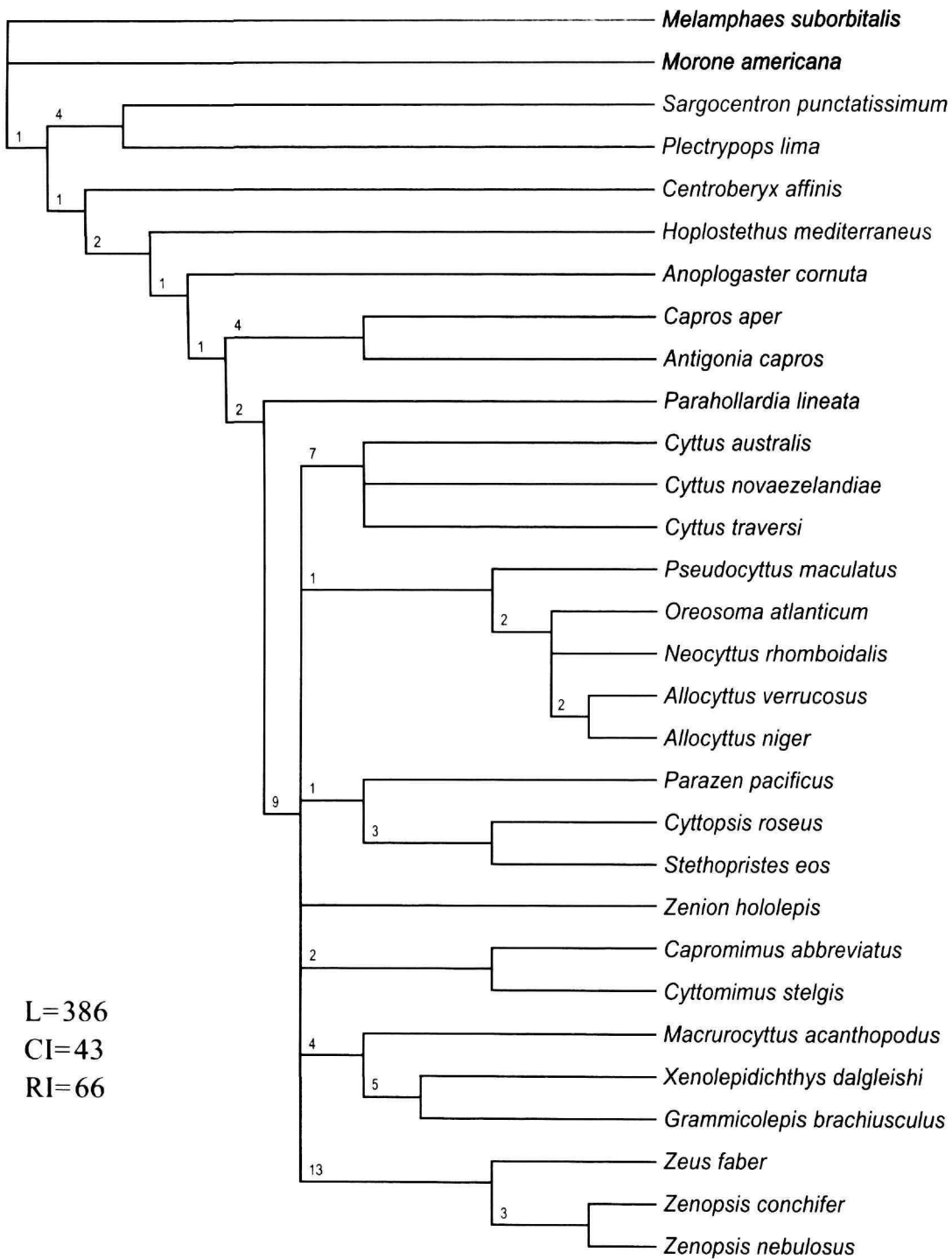


FIGURE 3.—Strict consensus of the 11 most-parsimonious trees resulting from an ordered analysis of the reduced data set of 92 characters. Branch support indices (Bremer, 1994) are shown above all relevant branches. The tree is rooted at *Melamphaes*.

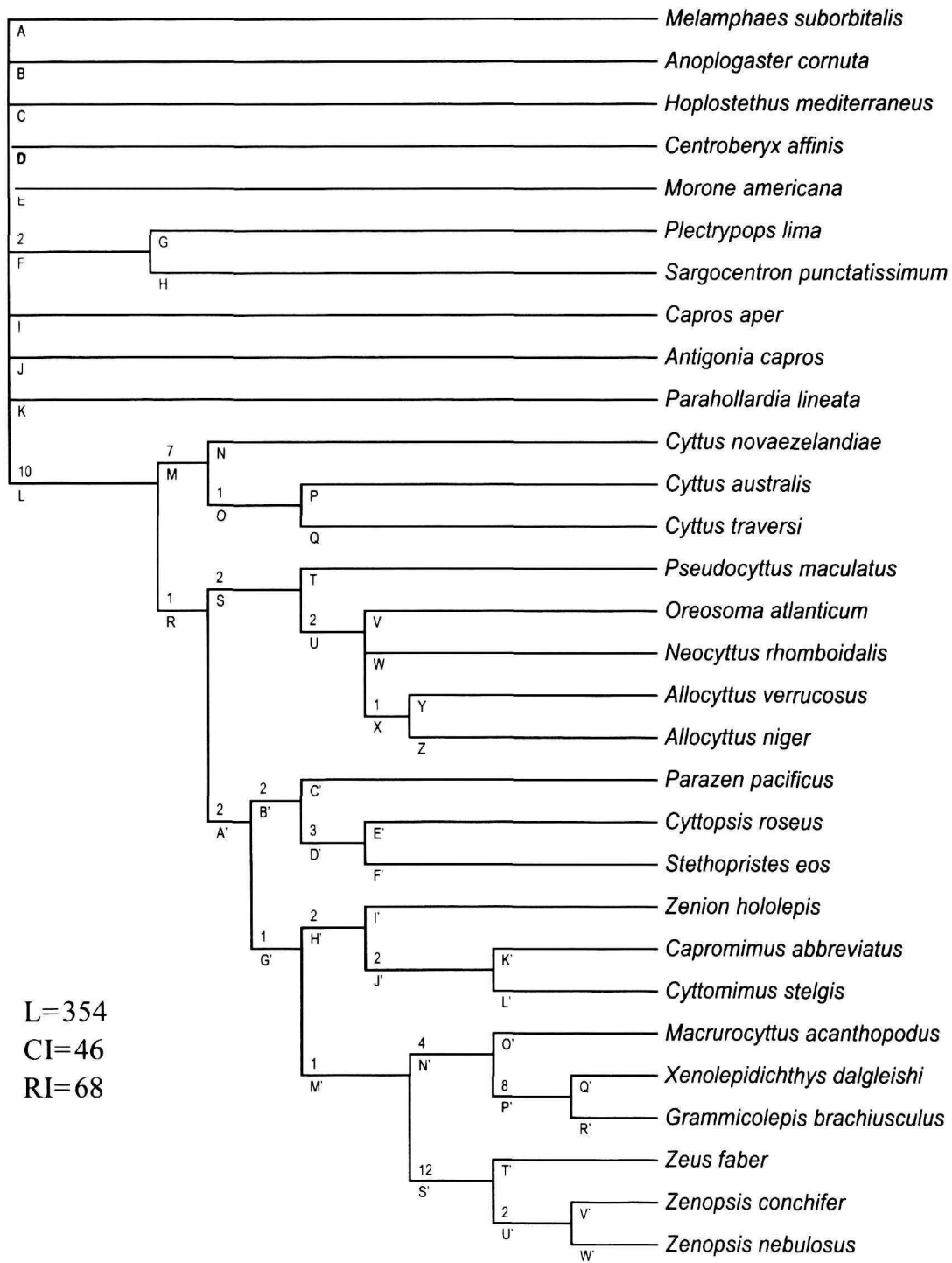


FIGURE 4.—Strict consensus of the 26 most-parsimonious trees resulting from an unordered analysis of the reduced data set of 92 characters. Branch support indices (Bremer, 1994) are shown above all relevant branches. Letters below branches refer to the list of character-state transformations in the Appendix. The tree is rooted at *Melamphaes*.

In Figures 1–4, branch-support values (Bremer, 1988, 1994) are indicated above all nonterminal branches, and in Figure 4 the letters below the branches represent the character transformations, which are given in the Appendix.

The character-state distributions generated by CLADOS for the reduced data set (Figures 3, 4) are considered here to be more rational than those for the full data set because of the problematic nature of many meristic characters, especially in zeiforms (see “Meristic Character-State Evolution”). Additionally, for the reduced data set, the unordered tree (Figure 4) is better justified than the ordered tree (Figure 3), because we have no unequivocal ontogenetic or other data that might allow us to order individual transformation series. Not surprisingly, our attempts at ordering were largely unsuccessful and resulted in trees that were longer than that given in Figure 4. Extra steps were especially apparent for multistate characters. The unordered, reduced-data-set tree (Figure 4) is 32 steps shorter than the tree generated with the ordered, reduced data set (Figure 3). The 11 meristic characters, although not used in constructing the trees, are included in the character distributions used to evaluate nodal support (Figure 5), but they are not included in branch-support calculations.

The use of consensus trees in reconstructing character evolution is somewhat problematic (Maddison, 1989), because the length of the consensus tree may be longer than the most-parsimonious trees. The consensus tree of the unordered, reduced data set (Figure 4) is 39 steps longer than any of the 26 most-parsimonious trees. These extra steps result from the need to interpret the characters that map on the large, basal polytomy and on the single trichotomy of the consensus tree. The large polytomy occurs in the outgroups, so the extra steps added here do not affect our conclusions about zeiforms. Characters 36 and 58, however, both require additional steps on the consensus tree within zeiforms because of the trichotomy involving *Oreosoma*, *Neocyttus*, and *Alloctytus* (Figure 4). By analyzing the evolution of these characters on all 26 equally parsimonious trees, we find that they reconstruct different distributions, and, thus, they should be used with caution to support this group.

The degree of congruence of the 11 meristic characters removed from the analyses was evaluated by optimizing them onto the consensus tree resulting from the unordered analysis of the reduced data set (Figure 4) (see “Meristic Character-State Evolution” and Figure 5). This resulted in one meristic character being congruent with the phylogeny, four others remaining questionable, and six being rejected for future use in zeiforms.

Statements about monophyly of the various taxa are based only on the analysis of the unordered, reduced data set (Figure 4) for the species examined (see “Material”).

MERISTIC CHARACTER-STATE EVOLUTION.—Many of the serially repeated structures of zeiforms have significant variability within and between geographic populations of a species, especially for the soft dorsal- and anal-fin rays. This variability is from a combination of genetic factors and environmental

factors, such as temperature and oxygen levels during early life-history stages (Lindsay, 1988), acting on the genomes within a population, and from differences in these factors between populations. It is almost impossible on the basis of the highly limited samples of zeiforms available from museum specimens alone (collected at diverse places and at different times, and rarely a statistically significant sample of any one population at one time), in the absence of information on developmental conditions and population dynamics, to separate how much of the observed meristic variation is phenotypic versus genetic.

The soft dorsal- and anal-fin rays are sufficiently variable intraspecifically, including within the few large samples available of the same population of some of the zeiform taxa examined, that no attempt was made to use interspecific differences in the counts of soft fin-rays.

Moreover, among zeiforms even some of the usually more conservative and consistent structures, such as fin spines, are relatively more variable, and there is more lability between spines and rays than in most other acanthomorphs. For example, the first element in the pelvic fin of two closely related genera (*Zeus* and *Zenopsis*) is spine-like in one and ray-like in the other; the anal-fin spines vary between four and five in *Zeus faber* and between two and three or between three and four in several species of oreosomatids; the pelvic-fin rays may vary by one element in several species of several families; the relatively low number of abdominal vertebrae varies by one and occasionally two units in several taxa of oreosomatids and zeids (but partially because of difficulty in definition; see “Terminology”); and even the relatively conservative principal caudal-fin ray count is variable in one species (*Macrurocyttus acanthopodus*).

We realize that the more qualitative features, such as the shapes and sizes of bones, that are the basis for other characters used in this study also exhibit variability, but this is usually of a lesser degree than with many of the meristic characters, and the range of conditions is contained within our definition of the character. We recognize that the variability in qualitative characters is more difficult and subjective to determine and describe than it is for easily quantified meristic features, and that this accounts for variability in qualitative features usually not being taken into consideration. But because many of the meristic features are especially variable in zeiforms, and we cannot distinguish between the phenotypic and genetic components of that variability, their value in a phylogenetic analysis is perhaps questionable, and shared conditions may not be due exclusively to homology.

Therefore, we think it is reasonable to exclude most of the fin and vertebral meristic characters from the analyses and then to optimize them onto the cladogram to test congruence. By comparing the distribution of each of these characters with respect to the phylogeny of the group, we can either accept or reject this a priori assumption. If the character is congruent (high *ci* and *ri*) with the phylogeny, then the observed variation is

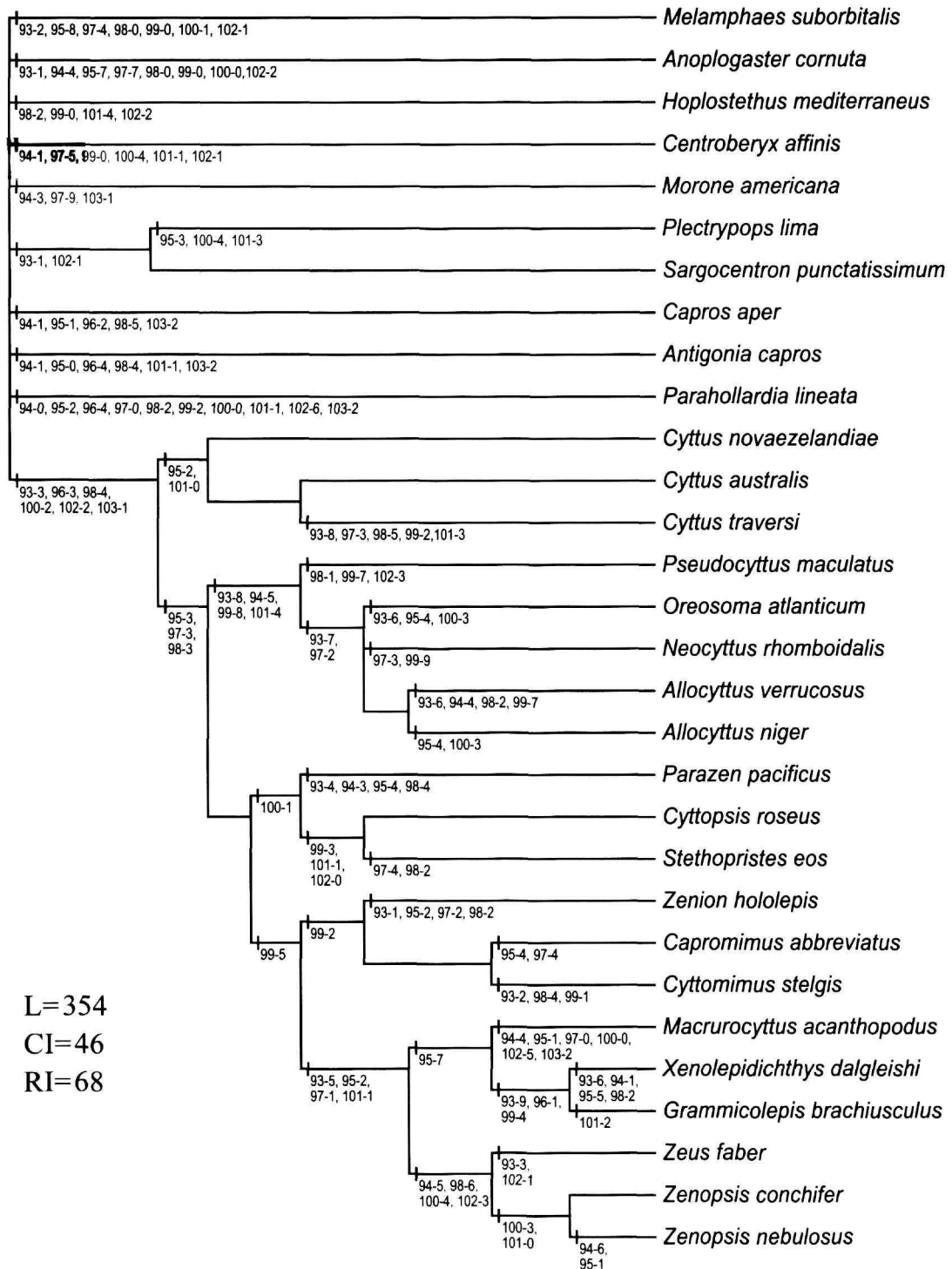


FIGURE 5. Optimization of the 11 meristic characters (characters 93-103) onto the strict consensus tree of the unordered reduced data set of 92 characters in FIGURE 4, to test for congruence with the phylogeny. The tree is rooted at *Melamphaes*.

most likely a function of genealogy and the shared states are homologous. If the character is not congruent (low *ci* and *ri*), then the variation may be a function of something other than phylogeny, and the shared states may be convergent.

The 11 meristic characters (characters 93 through 103) that were excluded from the data set were optimized onto the cladogram (Figure 5) to determine their congruence with our hypothesis of genealogy (Figure 4). Each character was optimized separately, and the *ci* and *ri* are noted for each character so that conclusions can be drawn about their congruence with the phylogeny. The values of these indices are compared with those of the unordered consensus tree (*CI*=46, *RI*=68), with "good" and "poor" defined as higher or lower than those values, respectively. This test of congruence will only determine to what degree the observed variation reflects phylogeny, and, to that extent, the usefulness of a character in a phylogenetic analysis. Many of these characters are regularly used in systematic characterizations, and their great utility for that purpose is not being questioned.

Character 93, total number of vertebrae (*ci* = 56, *ri* = 53, 16 steps for 9 states). This character exhibits a moderate amount of homoplasy, as shown by the seven extra steps needed to map its distribution. The synapomorphy support, *ri*, is also moderate. Therefore, the usefulness of this character in this phylogenetic analysis remains uncertain.

Character 94, number of abdominal vertebrae (*ci* = 46, *ri* = 22, 13 steps for 6 states). This character exhibits a moderate amount of homoplasy, six extra steps, and poor synapomorphy support. The poor synapomorphic support results from mapping character-state transitions on many terminal branches (e.g., *Centroberyx* and *Morone*).

Character 95, number of caudal-peduncle vertebrae (*ci* = 38, *ri* = 21, 18 steps for 8 states). This character also exhibits a large amount of homoplasy, six extra steps, and poor synapomorphy support.

Character 96, number of principal caudal-fin rays (*ci* = 80, *ri* = 87, 5 steps for 4 states). This character exhibits little homoplasy; for this group of fishes the number of caudal-fin rays is a good indicator of phylogeny.

Character 97, number of procurrent caudal-fin rays (*ci* = 50, *ri* = 36, 14 steps for 7 states). This character exhibits a moderate amount of homoplasy and poor synapomorphy support.

Character 98, number of dorsal-fin spines (*ci* = 35, *ri* = 21, 17 steps for 6 states). This character exhibits a large amount of homoplasy and little synapomorphy support.

Character 99, total number of vacant interneural spaces (*ci* = 53, *ri* = 46, 12 steps for 9 states). This character exhibits a moderate amount of homoplasy and moderate synapomorphy support.

Character 100, number of anal-fin spines (*ci* = 33, *ri* = 46, 12 steps for 4 states). This character exhibits a large amount of homoplasy and poor synapomorphy support.

Character 101, number of pectoral-fin rays (*ci* = 33, *ri* = 46, 12 steps for 4 states). This character exhibits a large amount of homoplasy and moderate synapomorphy support.

Character 102, total number of pelvic-fin elements (*ci* = 41, *ri* = 30, 12 steps for 5 states). This character exhibits a moderate amount of homoplasy and poor synapomorphy support.

Character 103, number of branchiostegal rays (*ci* = 33, *ri* = 50, 6 steps for 2 states). This character exhibits a large amount of homoplasy and moderate synapomorphy support.

Of these, only character 96, number of principal caudal-fin rays, is congruent with our hypothesis of phylogeny. This character is presumably affected by variation in developmental conditions acting on differential genomes between semi-isolated populations, but this variation does not mask the phylogenetic signal.

Four of the other meristic characters are of uncertain utility: total number of vertebrae (93), number of procurrent caudal-fin rays (97), total number of vacant interneural spaces (99), and number of branchiostegal rays (103). These characters presumably are also affected by the interaction of developmental conditions on population genomes, but we cannot determine if the variation between taxa is a result of phylogeny or some other factor. Because we cannot determine if these shared traits are due to convergence or homology, the value of these characters in this phylogenetic analysis remains questionable.

The remaining six meristic characters show very little congruence with the hypothesis of phylogeny, and they have poor synapomorphic support: number of abdominal vertebrae (94), number of caudal-peduncle vertebrae (95), number of dorsal-fin spines (98), number of anal-fin spines (100), number of pectoral-fin rays (101), and total number of pelvic-fin elements (102). There is little evidence that these character-state distributions reflect the phylogeny of these fishes.

ILLUSTRATIONS.—Instead of detailed descriptions of the comparative osteological features and character states of zeiforms, we provide illustrations of representatives of each of the six families recognized herein. For each family, an illustration of the lateral view of the entire skeleton of a representative species is given, as well as detailed figures of phylogenetically informative features of its skeleton or skeletal features in comparison with those of other species of the same or subsequently treated families. These detailed illustrations are labeled with the character number separated by a dash from the state number; in the figure legends, some of the character numbers are given only abbreviated descriptions. To preserve the unimpeded overall configuration of the bony parts in the lateral views of the entire skeleton of representative species, pointer lines are not used for the mostly self-evident character states given in the legends. Illustrations of entire skeletons were prepared from outlines based on projections from 35 mm photographic slides of intact whole skeletons (all cleared and stained except one dry skeleton and one radiograph) and refined by microscopic examination of the specimen; all detailed illustrations were drawn using a camera lucida microscope attachment.

All of the osteological illustrations are arranged at the back of this publication in phylogenetic sequence: Cyttidae, Oreosomatidae, Parazenidae, Zeniontidae, Grammicolepididae, and Zeidae.

Scale bars in the illustrations are in mm. A single scale bar for multiple figures applies to all of the parts.

Lateral views of details of the skeleton are of the left-side parts unless otherwise stated.

Gill rakers are not shown in the branchial arch illustrations.

Cartilages and dense fibrous tissue in the branchial arches and elsewhere in the skeleton are not consistently illustrated; when shown, these areas are outlined and are either open, without stippling, or have mechanical stippling or parallel or wavy lines.

Material

Specimens examined are listed for each species in the following order: catalog number, number of specimens, standard length (mm), general geographic region of specimen collection, and type of preparation, with CS = cleared and stained (usually counter stained for cartilage), D = dry skeletal preparation, and R = radiograph. CS specimens are listed first, followed by D and R specimens; within each of these categories, specimens are listed alphabetically by institutional abbreviation, which follow Leviton et al. (1985). The zeiform species are listed alphabetically within the new family arrangements proposed herein, followed by the outgroup species. Author names for species are given here rather than throughout the text.

ZEIFORMES

CYTTIDAE

Cyttus australis (Richardson). AMS I.32386001, 1 (60), Australia, CS. AMNH 91908, 1 (302), Australia, D; AMNH 91910, 1 (233), Australia, D; AMNH 91932, 1 (250), Australia, D. USNM 177052, 2 (168, 183), Australia, R.

Cyttus novaeseelandiae (Arthur). AMNH 95882, 1 (155), Australia, D; AMNH 95891, 1 (162), Australia, D. USNM 320593, 1 (263), New Zealand, R.

Cyttus traversi Hutton. AMNH 92029, 1 (316), Australia, D; AMNH 92052, 1 (215), Australia, D; AMNH 99777, 1 (455), Australia, D; AMNH 99778, 1 (445), Australia, D. USNM 308020, 1 (105), Walters Shoal, Indian Ocean, R; USNM 320583, 1 (263), New Zealand, R.

OREOSOMATIDAE

Alloctytus folletti Myers. USNM 306419, 1 (250), Alaska, R. Data from radiograph insufficient to include species in data matrix and analyses.

Alloctytus niger James, Inada, and Nakamura. AMNH 98405, 1 (315), Australia, D; AMNH 98407, 1 (315), Australia, D; AMNH 98408, 1 (350), Australia, D; AMNH 98629, 1 (320), Australia, D; AMNH 98630, 1 (325), Australia, D; AMNH 98634, 1 (345), Australia, D.

Alloctytus verrucosus (Gilchrist). AMS I.18712002, 1 (83), Australia, CS; AMS I.20068031, 2 (89, 90), Australia, CS. AMNH 95091, 1 (252), Australia, D; AMNH 95651, 1 (280), Australia, D; AMNH 95652, 1 (260), Australia, D; AMNH 95653, 1 (265), Australia, D. USNM 216741, 5 (272–300), Madagascar, R; USNM 307599, 3 (174–182), Madagascar, R; USNM 320678, 1 (250), Madagascar, R; USNM 320709, 2 (275, 279), Madagascar, R.

Neocytus rhomboidalis Gilchrist. AMS I.20099029, 1 (87), Australia, CS; AMS I.21812002, 1 (81), Australia, CS. AMNH 91743, 1 (295), Australia, D; AMNH 91746, 1 (232), Australia, D; AMNH 93612, 1 (243), Australia, D; AMNH 93613, 1 (255), Australia, D; AMNH 95080, 1 (248), Australia, D. USNM 320680, 1 (187), Australia, R.

Oreosoma atlanticum Cuvier. AMS I.21370034, 1 (32), Australia, CS; AMS I.25127008, 1 (133), Australia, CS; AMS I.25933013, 1 (109), Australia, CS. AMNH 99737, 1 (119), Australia, D.

Pseudocytus maculatus Gilchrist. AMNH 95075, 1 (195), Australia, D; AMNH 95088, 1 (255), Australia, D.

PARAZENIDAE

Cyttopsis roseus (Lowe). AMNH 29460, 2 (74, 75), Nicaragua, CS; AMS I.19840010, 1 (46), Australia, CS; CAS 38408, 1 (81), Gabon, CS; USNM 187873, 1 (72), Costa Rica, CS; USNM 304460, 2 (62, 67), Nicaragua, CS. USNM 50562, 1 (130), Japan, R (holotype of synonymous *Cyttopsis itea* Jordan and Fowler); USNM 102129, 1 (182), Puerto Rico, R; USNM 204892, 2 (385, 412), Cuba, R; USNM 227636, 1 (92), locality unknown, R; USNM 227936, 1 (193), Colombia, R; USNM 240051, 1 (95), Bermuda, R.

Parazen pacificus Kamohara. AMNH 29459, 1 (105), Florida, CS; CAS 38404, 1 (96), Nicaragua, CS; USNM 187077, 1 (104), Puerto Rico, CS; USNM 187892, 1 (110), Panama, CS. USNM 157874, 1 (93), Cuba, R; USNM 187077, 2 (96, 97), Puerto Rico, R; USNM 187892, 1 (128), Panama, R; USNM 927761, 1 (174), Columbia, R. Osteology well described by Kotlyar (2001).

Stethopristes eos Gilbert. USNM 226570, 2 (91, 97), Chile, CS. USNM 51626, 1 (107), Hawaii, R (holotype); USNM 226570, 2 (102, 116), Chile, R; USNM 334054, 2 (108, 110), Chile, R.

ZENIONTIDAE

Capromimus abbreviatus (Hector). AMS I.23650001, 1 (61), New Zealand, CS. USNM 334056, 1 (68), New Zealand, R.

Cyttomimus stelgis Gilbert. USNM 306156, 1 (76), Somalia, CS. AMS I.20651018, 2 (73, 81), Australia, R; USNM 51622, 1 (76), Hawaii, R (holotype); USNM 226569, 2 (46, 67), Chile, R; USNM 334055, 3 (55–66), Chile, R.

Zenion hololepis (Goode and Bean). CAS 38409, 1 (70), Bahamas, CS; CAS 76856, 2 (70, 73), no locality, CS; Dana Collection (Copenhagen). station 3744 II, uncataloged, 1 (9), western North Atlantic, CS (well-ossified larval stage); USNM 187864, 3 (50–73), Panama, CS; USNM 307305, 2 (45, 48), Madagascar, CS. USNM 138338, 9 (52–69), Philippines, R; USNM 138339, 1 (54), Philippines, R; USNM 138340, 1 (45), Philippines, R; USNM 138341, 1 (32), Philippines, R; USNM 327842, 4 (60–70), Venezuela, R; USNM 334057, 5 (47–58), Chile, R.

Zenion leptolepis (Gilchrist and von Bonde). USNM 320058, 10 (43–49), Liberia, R; USNM 320059, 3 (83–90), Liberia, R. Data from radiographs insufficient to include species in data matrix and analyses.

GRAMMICOLEPIDIDAE

Grammicolepis brachiusculus Poey. AMNH 99621, 1 (285), Australia, D. USNM 84098, 1 (226), Hawaii, R (holotype of synonymous *Vesposus egregius* Jordan); USNM 102129, 1 (182), Puerto Rico, R; USNM 204892, 2 (385, 412), Cuba, R; USNM 227636, 1 (92), no locality, R; USNM 227936, 1 (193), Colombia (Atlantic), R; USNM 240051, 1 (95), Bermuda, R. Osteology well described by Shufeldt (1888).

Macrurocyttus acanthopodus Fowler. MNHN 1994-1072, 1 (43), New Caledonia, stained, not cleared; USNM 93144, 5 neurocrania 13–14 mm long (vomere to basioccipital) and assorted disarticulated bones from type specimen series (in 14 glass vials), only one specimen, alcohol preserved, intact (removed and recataloged as USNM 331213, see following entry), Philippines, stained, not cleared, all flesh absent. MNHN 1994-1052, 2 (37, 39), New Caledonia, R; MNHN 1994-1073, 3 (37–45), New Caledonia, R; USNM 331213, 1 (~36), Philippines, R (a type specimen, but cataloging data and data published by Fowler (1934) conflict; impossible to determine whether it is the holotype). Rarely collected; see Nyako and Amaoka (1996) for redescription of species.

Xenolepidichthys dalgleishi Gilchrist. AMNH 29455, 4 (70–75), Nicaragua, CS; CAS 38403, 1 (70), Nicaragua, CS; CAS 38406, 1 (75), Colombia, CS; MCZ 57872, 1 (~8–9), Caribbean, CS; USNM 320013, 1 (64), Hon-

duras, CS; USNM 320015, 3 (59–77), Honduras, CS; USNM 320016, 2 (59, 64), Panama, CS. USNM uncatologed, 4 (77–90), Honduras, R; USNM 328266, 4 (69–75), Honduras, R; YPM (BOC) 517, 1 (82), Belize, R; YPM (BOC) 518, 2 (73, 81), Belize, R; YPM (BOC) 524, 1 (85), Belize, R.

ZEIDAE

Zenopsis conchifer (Lowe). CAS 47401, 1 (54), Florida, CS; FMNH 67090, 3 (44–58), Florida, CS; USNM 117280, 2 (51, 81), Florida, CS. AMNH 4451, 1 (126), New York, D; AMNH 56447, 1 (368), New York, D; AMNH 56833, 1 (405), New York, D.

Zenopsis nebulosus Schlegel. AMNH 92291, 1 (325), Australia, D; AMNH 95024, 1 (335), Australia, D; AMNH 95028, 1 (340), Australia, D.

Zenopsis oblongus Parin. USNM 334160, 2 (one partial skeleton, front of head missing, ~280 mm SL; one cranium from specimen of similar size), Nazca Ridge, southeast Pacific, D. USNM 353898, 1 (347), Salaty-Gomez Ridge, southeast Pacific, R. Data from radiograph and two incomplete skeletons insufficient to include species in data matrix and analyses.

Zenopsis sp. Dana Collection (Copenhagen), station 3915 II, uncatologed, 1 (7), western North Atlantic, CS (weakly ossified larval stage, probably of *Z. conchifer*).

Zeus capensis Valenciennes. USNM 330849, 7 (173–193), South Africa, R. Data from radiographs insufficient to include species in data matrix and analyses.

Zeus faber Linnaeus. USNM 307842, 2 (48, 67), Tunisia, CS; USNM 320014, 2 (59, 89), Tunisia, CS; USNM 320063, 1 (80), Guinea, CS. AMNH 22707, 1 (300), Japan, D; AMNH 91448, 1 (230), Australia, D; AMNH 95054, 1 (280), Australia, D; AMNH 95055, 1 (270), Australia, D; USNM 176975, 1 (215), Australia, D. USNM 328597, 1 (223), Kenya, R.

OUTGROUPS

TRIACANTHODIDAE

Parahollardia lineata (Longley). ANSP 93375, 1 (62), Florida, CS; ANSP 97637, 3 (79–84), Louisiana, CS; ANSP 100473, 1 (46), Florida, CS; USNM 280326, 1 (121), Louisiana, CS. Osteology described in detail by Tyler (1968, 1980).

CAPROIDAE

Antigonia capros Lowe. AMNH 21929, 1 (48), Florida, CS; AMNH 29461, 3 (31–43), Nicaragua, CS; FMNH 64378, 1 (50), Nicaragua, CS; USNM 289209, 4 (30–47), Colombia, CS; USNM 320064, 2 (38, 40), Colombia, CS. Osteology of related *A. combatia* Berry and Rathjen described by Zehren (1987). Osteology of *A. rubescens* (Günther) compared with that of chaetodontoids by Starks (1902).

Capros aper (Linnaeus). USNM 268912, 5 (40–73), Morocco, CS; USNM 289207, 3 (48–65), Tunisia, CS; USNM 320065, 2 (57, 58), Morocco, CS. Osteology briefly described by Tortonese (1948); described in great detail by Zehren (MS).

HOLOCENTRIDAE

Plectrypops lima Valenciennes. USNM 288860, 1 (61), Tonga, CS; USNM 334646, 2 (50, 52), Fiji, CS.

Sargocentron punctatissimum (Cuvier). USNM 259019, 2 (53, 61), New Guinea, CS; USNM 269081, 2 (54, 70), Fiji, CS.

MORONIDAE

Morone americana Gill. ROM 369CS, 2 (40, 44), no locality, CS; ROM 373CS, 1 (115), Ontario, CS; ROM 1064CS, 1 (86), Ontario, CS; USNM 109851, 3 (42–46), Virginia, CS; USNM 187300, 1 (77), Maryland, CS; USNM 322796, 30 (7–12), reared larvae, CS. ROM 2605, 1 (320), Ontario, D.

BERYCIDAE

Centroberyx affinis (Günther). USNM 176984, 1 (110), Australia, CS. Osteology described in detail by Zehren (1979). Osteology treated by Kotlyar (1996).

TRACHICHTHYIDAE

Hoplostethus mediterraneus (Cuvier and Valenciennes). USNM 306630, 1 (61), Somalia, CS; USNM 306631, 2 (50, 61), Somalia, CS. Osteology treated by Kotlyar (1996).

ANOLOGASTERIDAE

Anoplogaster cornuta (Valenciennes). USNM 214217, 1 (38), Mississippi, CS; USNM 240793, 1 (43), Bermuda, CS; USNM 244922, 1 (26), Bermuda, CS; VIMS uncatologed, 1 (93), no locality, CS. USNM 215619, 1 (103), Hawaii, R; USNM 240772, 2 (97, 124), Bermuda, R; USNM 343725, 1 (80), Florida, R. Osteology described in detail by Zehren (1979).

MELAMPHAIDAE

Melamphaes suborbitalis (Gill). USNM 218556, 1 (62), South Africa, CS; USNM 218562, 1 (63), South Africa, CS. Osteology well described by Kotlyar (1999).

Results

PHYLOGENY

Characters and Character States

The 103 characters and their states (coded as ordered transformation series where we deem it appropriate) are organized and discussed according to anatomical regions. Characters for which we are not confident about possible transformation series, and therefore treat as unordered, are indicated as such. The distribution of the character states among the taxa analyzed is given in Table 1.

Cranium

CHARACTER 1.—Parietal: present (0); absent (1).

CHARACTER 2.—Basisphenoid: present as a long, oblique shaft connecting parasphenoid and prootic in front of posterior myodome (0); present as a short shaft at front of roof of posterior myodome (1); absent (2).

CHARACTER 3.—Vomer teeth: present (0); absent (1).

CHARACTER 4.—Parasphenoid opening into posterior myodome: absent (0); present (1).

CHARACTER 5.—Honeycomb bone sculpturing on skull, opercles, and lachrymal-infraorbitals: absent (0); present (1).

CHARACTER 6.—Supraocular serrations on frontal: present (0); absent (1).

CHARACTER 7.—Otolith shape and size: moderately large to large, rounded or slightly to deeply indented on one or both sides, or oblong with humps (0); tiny, trilobed (bow-tie shaped) (1).

We have examined zeiform and outgroup otoliths for this work but have not illustrated them; for illustrations of zeiform otoliths see Stinton (1967), Nolf (1985), Nolf and Cappetta (1988), Smale et al. (1995), and Schwarzhan (1996).

CHARACTER 8.—Size and depth of lachrymal: large, deep, height about two to four times in the length (0); moderately deep, height about five to seven times in the length (1); slender (2); absent (–).

CHARACTER 9.—Number of infraorbitals (well-developed elements exclusive of lachrymal, dermosphenotic, and variable rudiments): none (0); three or four (1); five or six (2); seven or eight (3); nine or 10 (4); 11 or 12 (5).

CHARACTER 10.—Depth of most infraorbitals: relatively slender and tubular (0); deep, with large pores and bridges or open lacunae between upper and lower edges (1); deep, with serrate vertical supporting flanges (2); absent (—).

There is no reason to believe that this multistate character is an ordered transformation series; therefore, it was treated as unordered throughout the analyses.

CHARACTER 11.—Dermosphenotic: an ossification distinctly separate from sphenotic, sometimes relatively free from skull (0); fused or highly integrated with sphenotic (1); absent as an identifiable part of sphenotic (2).

CHARACTER 12.—Mouth size: large, alveolar process of premaxilla longer than lateral ethmoid depth (0); small, alveolar process much less than lateral ethmoid depth (1).

CHARACTER 13.—Postmaxillary process: present (0); absent (1).

CHARACTER 14.—Alveolar process of the premaxilla: simple (0); ventrally indented to form pair of blunt lobes (1); deeply bifurcated ventrally (2).

CHARACTER 15.—Ascending process of the premaxilla: reaching to a level in front of orbit or about to front of orbit and lateral ethmoid, no more than one-fifth into orbit (0); reaching distinctly behind lateral ethmoid to about one-third into orbit (1); reaching to about one-half into orbit (2); reaching to rear of orbit (3).

CHARACTER 16.—Palatine teeth: present (0); absent (1).

CHARACTER 17.—Ectopterygoid teeth: present (0); absent (1).

CHARACTER 18.—Articulation of palatine with cranium: main axis of palatine relatively parallel, or only moderately oblique, to body axis and with fixed, dual articulation with lateral ethmoid and ethmo-vomerine region (0); palatine usually oriented distinctly obliquely to axis of body and with a single, pivotal, articulation with lateral ethmoid, resulting in considerable mobility (1).

CHARACTER 19.—Metapterygoid size and articulation: relatively large, length about three-quarters or more that of the quadrate and articulating with it (0); reduced, length about one-half or less of that of the quadrate and not articulating with it (1); absent (2).

CHARACTER 20.—Symplectic ventral flange: absent (0); present (1).

CHARACTER 21.—Dentary cartilages (on lateral surface of dentary): absent or unconsolidated (0); two cartilages of moderate length, each attached anteriorly to dentary and lying sequentially one behind the other, first shorter than second (1); two cartilages of moderate length, each attached anteriorly to dentary and lying sequentially one behind the other, about equal in size or first cartilage only slightly shorter than second (2); well-developed, long complex consisting of two pieces,

posterior end of anterior piece connecting to anterior end of second piece (3); single rod-like cartilage lying along lateral surface of dentary and attaching to it anteriorly (4). Treated as unordered throughout analyses.

CHARACTER 22.—Serrations on lower border of dentary: none (0); single barb near symphysis (1); multiple serrations behind symphysis (2). Treated as unordered throughout analyses.

CHARACTER 23.—Open gill slit between fourth and fifth ceratobranchials: present (0); absent (1).

CHARACTER 24.—Number of gills: 4 complete gills (one complete gill of 2 hemibranchs on each complete gill arch), or 8 hemibranchs (0); 3½ gills, or 7 hemibranchs, with no hemibranch on the rear of the fourth ceratobranchial (1). See following character (25) for comments on correlated features.

CHARACTER 25.—Number of series of gill rakers on branchial arches: 4½, a series present along rear of fourth gill slit (at least dorsally), i.e., along anterior border of fifth ceratohyal (0); 4, no series along rear border of fourth gill slit (1); 3½, no series along posterior border of fourth ceratobranchial and none along rear border of fourth gill slit (2).

We recognize that characters 23–25 may be correlated and actually represent only a single character; however, because we lack clear evidence supporting that assumption, we treat them separately.

CHARACTER 26.—Uncinate process on first epibranchial: absent (0); present (1).

CHARACTER 27.—Interarcual cartilage: absent (0); present (1).

CHARACTER 28.—Second pharyngobranchial suspensory shaft: short or absent (0); moderately long (1); long, about one-half to two-thirds length of first pharyngobranchial (2).

CHARACTER 29.—Third pharyngobranchial suspensory shaft: short or absent (0); moderately long (1); long, almost as long as shaft of second pharyngobranchial (2).

CHARACTER 30.—Position of upper surface of first basibranchial: level with dorsal surfaces of basihyal and second basibranchial, at least posteriorly (0); entirely below level of dorsal surfaces of basihyal and second basibranchial (1).

CHARACTER 31.—Fourth upper pharyngeal toothplate: present (0); absent (1).

CHARACTER 32.—Fifth ceratobranchial: toothed (0); toothless (1).

CHARACTER 33.—Beryciform foramen: present as completely enclosed opening (0); represented by deep groove along lateral surface of ceratohyal, often onto dorsal hypohyal (1); represented by deep concavity on dorsal surface of ceratohyal (2); absent, no lateral groove and no deep dorsal concavity (no deeper than ventral concavity) (3). Treated as unordered throughout analyses.

CHARACTER 34.—Placement of heads of rear group of branchiostegal rays: over surface or along ventral edges of both the ceratohyal and epihyal (0); clustered along ossified posterior border of ceratohyal (1).

The distinction is somewhat subjective, as mentioned in the "Previous Phylogenetic Analyses of Zeiforms" under Rosen (1984).

CHARACTER 35.—Prominent notches on lower border of ceratohyal: present for heads of some branchiostegal rays in anterior group (0); absent (1).

CHARACTER 36.—Ceratohyal-epihyal articulation: exclusively through cartilage (0); through cartilage but with bony interdigitated articulations in some specimens, especially with increasing specimen size (1); bony interdigitated articulations in all specimens at all sizes (2).

CHARACTER 37.—Depth of anterior end of epihyal: equal, or about equal, to depth of adjacent part of ceratohyal (0); distinctly less deep than adjacent part of ceratohyal (1).

The distinction is somewhat subjective, as mentioned in the "Previous Phylogenetic Analyses of Zeiforms" under Rosen (1984).

CHARACTER 38.—Urohyal size: small to moderate, no longer than ceratohyal (0); large, longer than ceratohyal (1).

Vertebral Column and Median Fins

CHARACTER 39.—First vertebra in caudal peduncle with a modified neural or haemal spine: PU2 (0); PU3 (1).

CHARACTER 40.—Association of neural arch and spine of first vertebra with skull: neural arch and spine not closely applied to skull (0); neural arch and spine closely applied to skull, primarily to exoccipitals (1).

Johnson and Patterson (1993) noted certain differences between the caproid and zeiform conditions of this character, but these differences do not necessarily refute homology of the feature in these groups.

CHARACTER 41.—Articulation of second and next few anterior abdominal vertebrae with skull-first vertebra: not flexible (0); flexible, vertebrae linked laterally and ventrally by ligamentous bands, appearing as ventral straps by transmitted light in lateral view (1).

CHARACTER 42.—Dorsal extension of neural spine of first vertebra when neural arch and spine closely applied to skull: neural spine extending only slightly, or not at all, dorsally above its attachment to skull (0); neural spine with a long dorsal portion free from skull beyond curvature of supraoccipital and exoccipitals (1); first neural arch and spine not closely applied to skull (-).

CHARACTER 43.—Proximal attachment of Baudelot's ligament: to basioccipital (0); to first vertebra (1); to exoccipitals (2); to both basioccipital and first vertebra (3). Treated as unordered throughout analyses.

Our coding does not indicate polarity, and we accept Johnson and Patterson's (1993) analysis showing that the primitive acanthomorph condition is having the origin on the first vertebra (our state 1). See "Previous Phylogenetic Analyses of Zeiforms" under Johnson and Patterson (1993).

CHARACTER 44.—Neural spine orientation: all (or all but first few) abdominal neural spines oriented posterodorsally (0); several posterior abdominal and/or anterior caudal neural spines oriented anterodorsally, or at least vertically (1).

CHARACTER 45.—Haemal arch and spine vacuities: no prominent vacuities (0); vacuities of moderate size primarily in haemal arches of many posterior abdominal vertebrae and often in those of anterior caudal vertebrae (1); large vacuities in haemal arches or spines of many posterior abdominal vertebrae and often in those of anterior caudal vertebrae (2). Treated as unordered throughout the analyses.

CHARACTER 46.—Abdominal haemal spines: many vertebrae, especially posteriorly, with a transverse bony bridge below haemal canal and prominent process in the midline below bridge (0); haemal arches with a transverse bony bridge below haemal canal but no median spine below bridge, but short vertical projections may occur below bridge on each side (1).

CHARACTER 47.—Ossified ribs: present on most abdominal vertebrae behind fourth (0); present only on last few abdominal vertebrae (1); present only on a few middle abdominal vertebrae (2); absent (3); present on all abdominal vertebrae except first (4); present on all abdominal vertebrae except first two (5). Treated as unordered throughout analyses.

CHARACTER 48.—Ossified epineurals: present on most abdominal vertebrae or their ribs (0); present on a few anterior abdominal vertebrae (1); present on a few middle abdominal vertebrae (2); absent (3). Treated as unordered throughout analyses.

CHARACTER 49.—Length of the neural spine of PU2: long (0); absent to short (1).

CHARACTER 50.—Hypurapophysis: present (0); absent (1).

CHARACTER 51.—Number of epurals: three (0); two (1); one (2).

CHARACTER 52.—Articulation of proximal end of parhypural to orostylar centrum: strongly embracing centrum (0); slightly removed from and not embracing centrum (1); laterally expanded as a specialized peg on each side of parhypural, with pegs fitting into sockets on each side of centrum (2). Treated as unordered throughout analyses.

CHARACTER 53.—Degree of hypural fusion ("+" indicates fused together): 4-6 separate hypural elements (0); hypurals 1 + 2 fused to centrum and hypurals 3 + 4 free from centrum (1); hypurals 1 + 2 + 3 + 4 fused to centrum (2); hypurals 1 + 2 and 3 + 4 separate and both plates free from centrum (3); hypurals 1 + 2 free from centrum and hypurals 3 + 4 + 5 either free or fused to centrum (4); all hypurals fused to centrum and hypural 5 not free (5). Treated as unordered throughout analyses.

CHARACTER 54.—Uroneural: present (0); absent (1).

CHARACTER 55.—Stegural (sensu Rosen, 1984): present (0); absent (1).

CHARACTER 56.—Extra-caudal ossicle (sensu Fujita, 1990; an extra bone between HPU2 and HPU3) in haemal spine of PU2: absent in all specimens (0); present in at least some specimens (1).

CHARACTER 57.—Dorsal-fin-spine locking mechanism: absent (0); present between first and second dorsal-fin spines (1); present between second and third dorsal-fin spines (2); present between first, second, and third dorsal-fin spines (3); no dorsal-fin spines (–). Treated as unordered throughout analyses.

CHARACTER 58.—Number of groups of vacant interneural spaces (when two or more spaces vacant): one (0), treated as not applicable; two (1); three (2); four (3); only one or no spaces vacant (–).

CHARACTER 59.—Number of dorsal-fin pterygiophores anterior to neural spine of fourth abdominal vertebra: none (0); two (1); three (2); four (3).

CHARACTER 60.—Placement of first pterygiophore of spinous dorsal fin: behind first interneural space (behind second or subsequent neural spines) (0); in first interneural space (between first and second neural spines, or preneural space if first neural arch and spine not closely applied to skull) and often slanted forward (1).

CHARACTER 61.—Position of base of first dorsal-fin pterygiophore in first interneural/preneural space: middle to rear, not contacting skull or neural arch and spine of first vertebra (0); front, contacting skull and first vertebra between sides of neural arch and spine (1); first pterygiophore not in first interneural space (–).

CHARACTER 62.—Distal radials of spinous dorsal fin: large, ossified (0); reduced, absent, or cartilaginous (1); dorsal-fin spines absent (–). See comments under chain-link dorsal-fin spine articulation in Johnson and Patterson (1993).

CHARACTER 63.—Symmetry of soft dorsal- and anal-fin pterygiophores: asymmetrical (0); symmetrical (1).

CHARACTER 64.—Number of supraneurals: none (0); one (1); two (2); three (3).

CHARACTER 65.—Cartilage at distal end of supraneural: present (0); absent (1); no supraneurals (–).

CHARACTER 66.—Anal-fin-spine locking mechanism: absent, when two or more spines are present (0); present between first and second spines (1); one or no spines (–).

CHARACTER 67.—Articulation of first anal-fin spine with pterygiophore: unfused (0); fused in some populations or at larger specimen sizes (1); fused in all specimens (2); anal-fin spines absent (–).

We do not have early developmental evidence about this apparent fusion, and we infer it on the basis of adult comparative morphology.

CHARACTER 68.—Length of second anal-fin spine: moderate to long, more than one-half length of first spine (0); short, less than one-half length of first spine (1); second spine absent (–).

CHARACTER 69.—Number of anal-fin pterygiophores in prehaemal space (anterior to haemal spine of first caudal vertebra): three (0); two (1); one (2); none (3); indeterminate (?).

This count is difficult to determine in many specimens because of the shortness of the haemal spines of the first and second caudal vertebrae and their close association along the top rear of the large first anal-fin pterygiophore.

CHARACTER 70.—Number of anal-fin pterygiophores in first interhaemal space (between haemal spines of the first and second caudal vertebrae): none (0); one (1); two (2); three (3); four (4); five (5); indeterminate (?) (see character 69).

CHARACTER 71.—Number of anal-fin pterygiophores in second interhaemal space (between haemal spines of the second and third caudal vertebrae): none (0); two (1); three (2); four (3); indeterminate (?) (see character 69).

CHARACTER 72.—Number of anal-fin pterygiophores anterior to haemal spine of third caudal vertebra: three (0); four (1); five (2); six (3); seven (4); eight (5); nine (6); 10 (7); 11 (8); indeterminate (?).

CHARACTER 73.—Dorsal-, anal-, and pectoral-fin rays: branched (0); unbranched (1).

Paired Fin Girdles

CHARACTER 74.—Lateral flange on lowermost pectoral-fin radial: absent (0); present (1).

CHARACTER 75.—Number of separate bony elements in postcleithrum: two (0); one (1).

CHARACTER 76.—Flanges on the single postcleithrum: absent (0); one along posterior border, may be laterally flared, (1); two postcleithra (–).

We have no evidence on whether the single postcleithrum results from the fusion of two postcleithra or from the loss of one or the other postcleithrum.

CHARACTER 77.—Supracleithral serrations: absent (0); present along posterior border, this border sometimes laterally flared (1).

CHARACTER 78.—Ventral end of supracleithrum: simple (0); deeply bifurcate (1).

CHARACTER 79.—Cleithral process above articulation with postcleithrum: absent (0); present as prominent prong (1).

CHARACTER 80.—Extrascapulars: one long bone, sometimes forming an open tube, more or less closely held to skull and integrated in line with the crest (often spiny) between the posttemporal and parietal (0); two tubular bones, not closely held to skull except at larger specimen sizes (1); three more-or-less tubular bones (2); absent (3); one very small bone not integrated into skull (4). Treated as unordered throughout analyses.

CHARACTER 81.—Pelvic fin position: about midway between anus and pectoral-fin base (0); slightly behind pectoral-fin base (1); under or anterior to pectoral-fin base (2).

CHARACTER 82.—Pelvic-fin spines: present (0); absent (1).

CHARACTER 83.—Anterolateral processes of the medial (lower) surfaces of the pelvic-fin rays: absent (0); present as prongs from medial surfaces of ray bases (1); present as broad flanges from ray bases (2). Treated as unordered throughout analyses.

CHARACTER 84.—Pelvic-fin-ray serrations: absent (0); present on crests on anterior or upper and/or lower posterior surfaces of several rays (1); present on broad flanges from me-

dial (lower) surface of several rays (2). Treated as unordered throughout analyses.

CHARACTER 85.—Basipterygia articulation: medial processes of basipterygia broadly overlap at level of pelvic fin (0); in contact in midline of middle region but with little or no overlap (1); not in close contact in middle region but often in contact at anterior ends (2); tightly adherent or partially fused along broad area of midline contact (3). Treated as unordered throughout analyses.

CHARACTER 86.—Posterior process of the pelvis, behind pelvic-fin base: short to moderately long, shaped like a moderately broad to broad plate or flattened shaft, usually slightly to distinctly obliquely oriented, with or without flanges and retrorse projections (0); long and rod-like, moderately separated from its opposite member along midline (1); long, tapering shaft in contact or fused with its opposite member along midline (2).

Scales

CHARACTER 87.—Scales on most of body: moderate-sized to small, spiny “ctenoid” (spinoid) scales (0); moderate-sized to small, cycloid scales (1); scales greatly elongate vertically (2); scales absent (excluding enlarged buckler-like scales), or with only lateral-line scales (3). Treated as unordered throughout analyses. For scale morphology in zeiforms and related taxa, see Roberts (1993).

CHARACTER 88.—Buckler-like scales (see “Terminology”): absent (0); present only from isthmus to anus (1); present mid-abdominally and from rear end of spinous dorsal fin to end of soft dorsal-fin base (2); present mid-abdominally and from below spinous dorsal-fin base (usually from front to middle region) to end of soft dorsal-fin base (3); present mid-abdominally from pelvic fin to the anus (4). Treated as unordered throughout analyses.

CHARACTER 89.—Scute-like scales (see “Terminology”): absent (0); present from isthmus to pelvic-fin base and sometimes more posteriorly (1).

CHARACTER 90.—Scales along bases of dorsal- and anal-fin rays: present, usually as a low sheath of scales lacking spiny processes (0); absent, nearby scales without spiny projections and not extending beyond lateral expansions of distal ends of dorsal- and anal-fin pterygiophores (1); absent, but spiny processes present on scales alongside lateral expansions of distal ends of dorsal- and anal-fin pterygiophores (2). Treated as unordered throughout analyses.

Miscellaneous

CHARACTER 91.—Hyperostosis: absent (0); present in supraoccipital and first dorsal-fin pterygiophore of some specimens (1); present in prepelvic scale bucklers (2). Treated as unordered throughout analyses.

CHARACTER 92.—Extended prejuvenile stage, with late ossification, thickened dermal connective tissue, expanded abdomen, and hillocks or cone-like scales: absent (0); present, (1).

Meristic Data

CHARACTER 93.—Total number of vertebrae: 26 or fewer (0); 27 or 28 (1); 29 or 30 (2); 31 or 32 (3); 33 or 34 (4); 35 or 36 (5); 37 or 38 (6); 39 or 40 (7); 41 or 42 (8); 43 or more (9).

CHARACTER 94.—Number of abdominal vertebrae: nine or fewer (0); 10 (1); 11 (2); 12 (3); 13 (4); 14 (5); 15 (6).

CHARACTER 95.—Number of vertebrae in caudal peduncle: three (0); four (1); five (2); six (3); seven (4); eight (5); nine (6); 10 (7); 11 or more (8).

CHARACTER 96.—Number of principal caudal-fin rays: 16 or more (0); 15 (1); 14 (2); 13 (3); 12 (4).

CHARACTER 97.—Number of procurrent caudal-fin rays (including number in both the dorsal and ventral sides, if different): none (0); one (1); two (2); three (3); four (4); five (5); six (6); seven (7); eight (8); nine or more (9). See “Zeiform Procurrent Caudal-Fin Rays” for discussion of specimen size and development of procurrent rays.

CHARACTER 98.—Number of dorsal-fin spines: four or fewer (0); five (1); six (2); seven (3); eight (4); nine (5); 10 or more (6).

CHARACTER 99.—Total number of vacant interneural spaces below dorsal-fin base, posterior to first dorsal-fin pterygiophore: none (0); one (1); two (2); three (3); four (4); five (5); six (6); seven (7); eight (8); nine (9).

CHARACTER 100.—Number of anal-fin spines: none (0); one (1); two (2); three (3); four (4); five (5).

CHARACTER 101.—Number of pectoral-fin rays: 11 or 12 (0); 13 or 14 (1); 15 or 16 (2); 17 or 18 (3); 19 or 20 (4); 21 or 22 (5).

CHARACTER 102.—Total number of pelvic-fin elements: nine (0); eight (1); seven (2); six (3); five (4), not applicable to listed taxa; four (5); three (6).

CHARACTER 103.—Number of branchiostegal rays: eight, 4 + 4 (0); seven, 3 + 4 (1); six, 2 + 4 (2).

Phylogenetic Results

The following character optimizations are based solely on the character distributions on the unordered consensus tree derived from the reduced data set (Figure 4). Character-state changes are given for the relevant nodes. When the character is further derived or reversed in the members of the clade, this is noted. When the character is further derived or reversed in members of another clade convergently, the reader is directed to the relevant optimization number for further details. Character states with further change are only explicitly given where ambiguity is possible (e.g., they are not given for binary characters).

Characters (e.g., optimization numbers 10–17) stated herein to be convergent between zeiforms and the representative tetra-

odontiform (*Parahollardia*) and the two genera of caproids (*Capros* and *Antigonia*) are potential synapomorphies of the putative higher clades involving those taxa (as in Figures 1–3), although these clades are not supported by the unordered analysis of the reduced data set (Figure 4).

MONOPHYLY OF ZEIFORMES (branch L in Figure 4 and the Appendix).—The following nine consistent synapomorphies diagnose a monophyletic zeiform clade.

1. Palatine usually oriented obliquely to axis of body and with a single, pivotal articulation with lateral ethmoid, resulting in considerable mobility (18-1); see also Johnson and Patterson (1993).
2. Three and one-half gills, seven hemibranchs (24-1).
3. Dorsal-, anal-, and pectoral-fin rays unbranched (73-1); convergent in one family (Monacanthidae) of tetraodontiforms not included in this study.
4. No uncinat process on first epibranchial (26-0).
5. Continuous median cartilage present below frontals, extending between ethmoid cartilage and pterospheoids.

This is not included in the data set because the character could not be determined in many of our specimens of zeiforms, but we agree with Johnson and Patterson (1993) that this is a highly probable synapomorphy of zeiforms. For our documentation of this, see "Previous Phylogenetic Analyses of Zeiforms" under Johnson and Patterson (1993).

6. No open gill-slit between fourth and fifth branchial arches (23-1).
7. Metapterygoid reduced in size and not articulating with quadrate (19-1); see also Johnson and Patterson (1993); metapterygoid lost in *Macrurocyttus*.
8. Parhypural slightly removed from and not embracing urostylar centrum (52-1); see also Johnson and Patterson (1993); further derived, to state 2, in *Xenolepidichthys* + *Grammicolepis*.
9. Hypurals 1 + 2 + 3 + 4 fused and fused to centrum (53-2); autapomorphy, to state 5, in *Macrurocyttus*; further derived, to state 1, in *Oreosoma* + (*Neocyttus* + *Allocyttus*) and *Parazen*.

The following 17 characters indicate zeiform monophyly but exhibit homoplasy.

10. Long neural spine on PU2 (49-0); see also Rosen (1984); convergent in *Parahollardia*.
11. Stegural absent (55-1); see also Rosen (1984); convergent in *Parahollardia*.
12. Distal radials of spinous dorsal fin absent or present only as tiny cartilaginous or partially ossified structures under the last few spines (62-1); see also Johnson and Patterson (1993); convergent in *Parahollardia*.

Johnson and Patterson's (1993) analysis did not include tetraodontiforms, but we have found that both zeiforms and tetraodontiforms have this condition.

13. Hypurapophysis absent (50-1); convergent in *Parahollardia*; reversal in *Cyttus traversi*, *Parazen*, *Cyttomimus*, and *Xenolepidichthys* + *Grammicolepis*.
 14. Palatine teeth absent (16-1); convergent in *Melamphaes*, *Antigonia*, and *Parahollardia*.
 15. Neural spine closely applied to skull (40-1); convergent in *Capros*, *Antigonia*, and *Parahollardia*.
 16. Anterior end of epihyal distinctly less deep than adjacent part of ceratohyal (37-1); convergent in *Capros*, *Antigonia*, and *Parahollardia*; reversal in *Stethopristes*, *Zenion* + (*Cyttomimus* + *Capromimus*), and *Macrurocyttus*.
 17. First pterygiophore of spinous dorsal fin inserted in first interneural space, i.e., between first and second neural spines (60-1); convergent in *Sargocentron*, *Capros*, *Antigonia*, and *Parahollardia*.
 18. Three and one-half series of gill-rakers (25-2); convergent in *Anoplogaster* and *Plectrypops* + *Sargocentron*.
 19. Prominent notches on lower border of ceratohyal (35-0); convergent in *Centroberyx* and *Plectrypops* + *Sargocentron*; reversal in *Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*).
 20. Uroneural absent (54-1); convergent in *Melamphaes* and *Anoplogaster*.
 21. Fourth upper pharyngeal toothplate absent (31-1); see also Johnson and Patterson (1993); convergent in *Hoplostethus*.
 22. Articulation of first few vertebrae with skull flexible, vertebrae linked laterally and ventrally by ligamentous bands (41-1); see also Johnson and Patterson (1993); convergent in *Hoplostethus*.
 23. Two dentary cartilages of moderate length, first shorter than second (21-1); further derived, to state 2, in *Parazen* and *Zenion*; further derived, to state 0, in *Xenolepidichthys* + *Grammicolepis*, and convergent in *Anoplogaster*.
 24. Several posterior abdominal and/or anterior caudal neural spines oriented anterodorsally or at least vertically (44-1); convergent in *Antigonia*; reversal in *Parazen* and *Zenion*.
 25. One supraneural (64-1); convergent in *Anoplogaster*; further derived, to state 0, in *Parazen* and *Zeus* + *Zenopsis*, and convergent in *Capros* and *Parahollardia*.
 26. Two epurals (51-1); reversal, to state 2, in *Stethopristes* and (*Zenion* + (*Capromimus* + *Cyttomimus*)) + ((*Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*)) + (*Zeus* + *Zenopsis*)), and convergent in *Parahollardia*; convergent secondary gain, to state 1, in *Zenion* and *Xenolepidichthys* + *Grammicolepis*.
- The following three characters are optimized as supporting the clade; however, their support is questionable because of unknown data or optimization ambiguity.
27. Baudelot's ligament attached to first vertebra (43-1); see also Johnson and Patterson (1993); convergent in *Melamphaes*; further derived, to state 2, in *Zeus* + *Zenopsis*.

Because of the large number of taxa coded as unknown (?), character 43-1 is questionable. For our documentation of this, see "Previous Phylogenetic Analyses of Zeiforms" under Johnson and Patterson (1993).

28. Vomerine teeth present (3-0); convergent in *Centroberyx*, *Morone*, *Plectrypops* + *Sargocentron*, and *Capros*; reversal in *Pseudocyttus*, *Oreosoma*, and *Macrurocyttus* + (*Grammicolepis* + *Xenolepidichthys*). Ambiguous optimization.
 29. Infraorbitals relatively slender and tubular (10-0); convergent in *Morone*, *Sargocentron*, and *Antigonia*; further derived, to state 2, in *Zenion*, and convergent in *Anoplogaster* and *Hoplostethus*; reversal, to state 1, in *Oreosomatidae*. Ambiguous optimization.
- When optimized onto the tree, the following six characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.
30. Thirteen principle caudal-fin rays (96-3); further derived, to state 1, in *Xenolepidichthys* + *Grammicolepis*.
 31. Eight dorsal-fin spines (98-4); convergent in *Antigonia*; further derived, to state 3, in all zeiforms except genus *Cyttus*; further derived, to state 5, in *Cyttus traversi*; further derived, to state 1, in *Pseudocyttus*; further derived, to state 2, in *Alloctytus verrucosus*, *Stethopristes*, *Zenion*, and *Xenolepidichthys*, and convergent in *Hoplostethus* and *Parahollandia*; reversal, to state 6, in *Zeus* + *Zenopsis*; reversal, to state 4, in *Parazen* and *Cyttomimus*.
 32. Seven pelvic-fin elements (102-2); convergent in *Anoplogaster* and *Hoplostethus*; further derived, to state 0, in *Cyttopsis* + *Stethopristes*; further derived, to state 5, in *Macrurocyttus*; further derived, to state 1, in *Zeus*, and convergent in *Melamphaes*, *Centroberyx*, and *Plectrypops* + *Sargocentron*; reversal, to state 3, in *Pseudocyttus* and *Zeus* + *Zenopsis*.
 33. Seven branchiostegal rays (103-1); convergent in *Morone*; further derived, to state 2, in *Macrurocyttus*, and convergent in *Capros*, *Antigonia*, and *Parahollandia*.
 34. Two anal-fin spines (100-2); further derived, to state 1, in *Parazen* + (*Cyttopsis* + *Stethopristes*), and convergent in *Melamphaes*; further derived, to state 0, in *Macrurocyttus*, and convergent in *Anoplogaster* and *Parahollandia*; further derived, to state 4, in *Zeus* + *Zenopsis*, and convergent in *Centroberyx* and *Plectrypops*; reversal, to state 3, in *Oreosoma*, *Neocyttus*, *Alloctytus niger*, and *Zenopsis*.
 35. Thirty-one or 32 vertebrae (93-3); further derived, to state 8, in *Cyttus traversi* and *Oreosomatidae*; further derived, to state 7, in *Oreosoma* + *Neocyttus* + *Alloctytus*; further derived, to state 6, in *Oreosoma*, *Alloctytus verrucosus*, and *Xenolepidichthys*; further derived, to state 4, in *Parazen*; further derived, to state 2, in *Cyttomimus*, and convergent in *Melamphaes*; further derived, to state 5, in (*Macrurocyttus* + (*Xenolepidichthys* + *Grammicole-*

pis)) + (*Zeus* + *Zenopsis*); further derived, to state 9, in *Xenolepidichthys* + *Grammicolepis*; further derived, to state 1, in *Zenion*, and convergent in *Anoplogaster* and *Plectrypops* + *Sargocentron*; reversal, to state 3, in *Zeus*.

Thus, zeiform monophyly is evidenced by 35 synapomorphies, of which 32 are informative (three other characters, 27–29, may support the clade). The Bremer value of 10, the second highest in the analysis, indicates very strong support for the monophyly of the Zeiformes.

MONOPHYLY OF *Cyttus*: CYTTOIDEI, CYTTIDAE (branch M in Figure 4 and the Appendix).—Three consistent synapomorphies support the monophyly of the three species of *Cyttus* and its higher categories.

36. Vacuities of moderate size in haemal arches of posterior abdominal vertebrae and often in those of more anterior caudal vertebrae (45-1).
37. Ascending process of premaxilla reaching back about one-half into orbit (15-2).
38. Scute-like scales present from isthmus to pelvic-fin base (89-1).

The following five characters exhibit homoplasy but nevertheless support the monophyly of *Cyttus*.

39. Upper surface of first basibranchial entirely below level of dorsal surface of basihyal and second basibranchial (30-1); convergent in *Xenolepidichthys* + *Grammicolepis*; see optimization number 140 for details.
40. Anterolateral processes of pelvic-fin rays present as prongs from medial surfaces of ray bases (83-1); convergent in *Zeus* + *Zenopsis*.
41. Lateral flange present on lowermost pectoral-fin radial (74-1); convergent in *Cyttopsis* + *Stethopristes*.
42. Ossified epineurals on a few anterior vertebrae (48-1); convergent in *Hoplostethus*, *Oreosoma*, and *Zeus* + *Zenopsis*; see optimization number 158 for details.
43. No ossified ribs (47-3); convergent in *Parahollandia*, *Cyttomimus*, and *Macrurocyttus*.

The following three characters may support a monophyletic *Cyttus* and its higher categories, but some information is polymorphic or optimization is uncertain.

44. Multiple serrations on dentary behind symphysis (22-2); convergent in *Anoplogaster*, *Plectrypops*, *Capros*, *Oreosoma* + *Neocyttus* + *Alloctytus*, *Zenion* + (*Capromimus* + *Cyttomimus*), and *Grammicolepis*; further derived, to state 1, in *Cyttus novaezealandiae*, and convergent in *Cyttopsis* and *Zeus*. *Cyttus novaezealandiae* assigned state 1 by mutation coding. Ambiguous optimization.
45. Many abdominal haemal spines with a prominent process in midline below bridge under haemal canal (46-0); convergent in *Anoplogaster*, *Hoplostethus*, and (*Parazen* + (*Cyttopsis* + *Stethopristes*)) + ((*Zenion* + (*Capromimus* + *Cyttomimus*)) + ((*Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*)) + (*Zeus* + *Zenopsis*))); see optimization number 77 for details. Ambiguous optimization.

46. Seven or 8 infraorbitals (9-3); polymorphic in *Cyttus australis* (9-2,3) and *C. novaezelandiae* (9-3,4). Although specimens of both species exhibit state 3, other specimens exhibit states 2 or 4; thus character may not support clade.

When optimized onto the tree, the following two characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

47. Eleven or 12 pectoral-fin rays (101-0); convergent in *Zenopsis*; further derived, to state 3, in *Cyttus traversi*, and convergent in *Plectrypops*.
 48. Five vertebrae in caudal peduncle (95-2); convergent in *Parahollardia*, *Zenion*, and (*Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*)) + (*Zeus* + *Zenopsis*); see optimization number 127 for details.

The Bremer value of seven, one of the highest in the analysis, indicates very strong support for the monophyly of *Cyttus* and its higher categories (Cytoidei, Cyttidae).

MONOPHYLY OF *Cyttus australis* AND *Cyttus traversi* (branch O in Figure 4 and the Appendix).—Within the genus *Cyttus*, no consistent synapomorphies group *Cyttus australis* with *Cyttus traversi* to the exclusion of *Cyttus novaezelandiae*. One character, however, that has convergently arisen within other zeiforms and within some of the non-zeiform taxa supports this group.

49. Serrations present along posterior border of supracleithrum (77-1); convergent in *Centroberyx*, *Plectrypops*, *Capros*, *Antigonia*, *Oreosoma* + *Neocyttus* + *Allocyttus*, and *Zenion* + (*Cyttomimus* + *Capromimus*).

This unnamed clade is supported by a single character, which exhibits homoplasy. This is reflected in a Bremer value of one, indicating only weak support for the monophyly of this clade. Bray (1983) placed two of the three species of *Cyttus*, *C. australis* and *C. novaezelandiae*, in the subgenus *Cyttus* and the third, *C. traversi*, in the subgenus *Rhombocyttus*. Our evidence, although weak, is not in agreement with this subgeneric grouping.

MONOPHYLY OF *Pseudocyttus*, *Oreosoma*, *Neocyttus*, *Allocyttus*, *Parazen*, *Cyttopsis*, *Stethopristes*, *Zenion*, *Capromimus*, *Cyttomimus*, *Macrurocyttus*, *Xenolepidichthys*, *Grammicolepis*, *Zeus*, AND *Zenopsis*: ZEIOIDEI (branch R in Figure 4 and the Appendix).—The remainder of the zeiforms form a monophyletic clade supported by seven characters. None of these characters are consistent synapomorphies; they all exhibit a certain amount of homoplasy, with several reversals or convergences.

50. Third pharyngobranchial suspensory shaft moderately long (29-1); further derived, to state 2, in *Allocyttus niger* and *Parazen*; reversal, to state 0, in *Oreosoma* and *Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*).

51. Anal-fin-spine locking mechanism between first and second spines (66-1); reversal in *Grammicolepis*; *Parazen*, *Cyttopsis*, *Stethopristes*, and *Macrurocyttus* with 1 or no spines (–) and cannot be coded for this character.

The following characters may support this clade, but optimization is uncertain.

52. Second pharyngobranchial suspensory shaft long (28-2); further derived, to state 1, in *Oreosomatidae* and *Cyttopsis*; reversal, to state 2, in *Allocyttus niger*; reversal, to state 0, in *Oreosoma* and *Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*). Ambiguous optimization.
 53. Ossified ribs present only on last few abdominal vertebrae (47-1); further derived, to state 0, in *Zeus* + *Zenopsis*; further derived, to state 3, in *Capromimus* + *Cyttomimus* and *Macrurocyttus*, and convergent in *Parahollardia* and *Cyttus*; further derived, to state 2, in *Capromimus*; reversal, to state 5, in *Grammicolepis*. Ambiguous optimization.

When optimized onto the tree, the following characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

54. Seven dorsal-fin spines (98-3); further derived, to state 1, in *Pseudocyttus*; further derived, to state 2, in *Allocyttus verrucosus*, *Stethopristes*, *Zenion*, and *Xenolepidichthys*, and convergent in *Hoplostethus* and *Parahollardia*; reversal, to state 6, in *Zeus* + *Zenopsis*; reversal, to state 4, in *Parazen* and *Cyttomimus*.
 55. Six vertebrae in caudal peduncle (95-3); convergent in *Plectrypops*; further derived, to state 1, in *Macrurocyttus* and *Zenopsis nebulosus*; further derived, to state 7, in *Macrurocyttus* + (*Grammicolepis* + *Xenolepidichthys*), and convergent in *Anoplogaster*; further derived, to state 4, in *Oreosoma*, *Allocyttus niger*, *Parazen*, and *Capromimus*; further derived, to state 2, in *Zenion* and (*Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*)) + (*Zeus* + *Zenopsis*); reversal, to state 5, in *Xenolepidichthys*. Occurrence of polymorphic state 1 in some specimens of *Zeus* and *Zenopsis conchifer* not relevant at this level of analysis.
 56. Three procurate caudal-fin rays (97-3); convergent in *Cyttus traversi*; further derived, to state 1, in (*Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*)) + (*Zeus* + *Zenopsis*); further derived, to state 0, in *Macrurocyttus*, which is convergent in *Parahollardia*; further derived, to state 4, in *Stethopristes* and *Capromimus*; reversal, to state 2, in *Zenion* and *Oreosoma* + *Neocyttus* + *Allocyttus*; reversal, to state 3, in *Neocyttus*. Ambiguous optimization.

The Bremer value of one indicates only weak support for the monophyly of the Zeioidei.

MONOPHYLY OF *Pseudocyttus*, *Oreosoma*, *Neocyttus*, AND *Alloctytus*: OREOSOMATIDAE (branch S in Figure 4 and the Appendix).—There is one consistent synapomorphy that supports the monophyly of this family.

57. Extended prejuvenile stage present, with a unique combination of many derived morphologies (92-1).

There are also three characters that exhibit homoplasy but nevertheless support the monophyly of the family.

58. Two dorsal-fin pterygiophores anterior to neural spine of fourth abdominal vertebra (59-1); convergent in *Centroberyx*, *Morone*, *Parahollardia*, and *Xenolepidichthys* + *Grammicolepis*.
59. Most infraorbitals deep, with large pores and bridges or open lacunae (10-1); reversal.
60. Second pharyngobranchial suspensory shaft moderately long (28-1); convergent in *Cyttopsis*; reversal, to state 0, in *Oreosoma*; convergent, to state 2, in *Alloctytus niger*.

When optimized onto the tree, the following four characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

61. Nineteen or 20 pectoral-fin rays (101-4); convergent in *Hoplostethus*.
62. Eight vacant interneural spaces (99-8); further derived, to state 7, in *Pseudocyttus* and *Alloctytus verrucosus*; autapomorphy, to state 9, in *Neocyttus*. Ambiguous optimization.
63. Forty-one or 42 vertebrae in total (93-8); convergent in *Cyttus traversi*; further derived, to state 7, in *Oreosoma* + *Neocyttus* + *Alloctytus*; further derived, to state 6, in *Oreosoma* and *Alloctytus verrucosus*, and convergent in *Xenolepidichthys*. Ambiguous optimization.
64. Fourteen abdominal vertebrae (94-5); convergent in *Zeus* + *Zenopsis*; further derived, to state 4, in *Alloctytus verrucosus*, and convergent in *Anoplogaster* and *Macrurocyttus*; see optimization number 163 for details. Ambiguous optimization.

The Bremer value of two indicates moderate support for the monophyly of the family Oreosomatidae.

MONOPHYLY OF *Oreosoma*, *Neocyttus*, AND *Alloctytus*: OREOSOMATINAE (branch U in Figure 4 and the Appendix).—Seven characters, when optimized, support the monophyly of this clade. None of these is a consistent synapomorphy, as all have arisen convergently in other taxa.

65. Hypurals 1 + 2 fused and fused to centrum and hypurals 3 + 4 fused and free from centrum (53-1); convergent in *Parazen*.
66. Dorsal-fin-spine locking mechanism between first, second, and third spines (57-3); convergent in (*Zenion* + (*Capromimus* + *Cyttomimus*)) + ((*Macrurocyttus* + (*Grammicolepis* + *Xenolepidichthys*)) + (*Zeus* + *Zenopsis*)); see optimization number 92 for details.

67. Dentary with multiple serrations behind symphysis (22-2); convergent in *Anoplogaster*, *Plectrypops*, *Capros*, *Cyttus*, *Zenion* + (*Capromimus* + *Cyttomimus*), and *Grammicolepis*.

68. Serrations along posterior border of supracleithrum (77-1); convergent in *Centroberyx*, *Plectrypops*, *Capros*, *Antigonia*, *Cyttus australis* + *Cyttus traversi*, and *Zenion* + (*Capromimus* + *Cyttomimus*).

The following optimized character supports this clade because of the trichotomy involving *Oreosoma*, *Neocyttus*, and *Alloctytus*.

69. Ceratohyal-epihyal articulation through cartilage but with interdigitated articulation in some specimens (36-1); convergent in *Cyttus australis* and *Zeus*. Character supports grouping of *Neocyttus* and *Alloctytus*. Ambiguous optimization.

When optimized onto the tree, the following two characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

70. Thirty-nine or 40 vertebrae (93-7); further derived, to state 6, in *Oreosoma* and *Alloctytus verrucosus*, and convergent in *Xenolepidichthys*. Ambiguous optimization.
71. Two procurrent caudal-fin rays (97-2); reversal, with independent convergent reversal in *Zenion*; reversal, to state 3, in *Neocyttus*, with independent convergent reversal in *Cyttus traversi*. Ambiguous optimization.

Thus, the support of one of these characters is not self-evident, but it is optimized as supporting the clade because of the trichotomy. The Bremer value of two indicates moderate support for the monophyly of the subfamily Oreosomatinae.

MONOPHYLY OF *Alloctytus verrucosus* AND *Alloctytus niger* (branch X in Figure 4 and the Appendix).—The monophyly of this clade is supported by three homoplasious characters.

72. Five anal-fin pterygiophores anterior to haemal spine of third caudal vertebra (72-2); convergent in *Cyttus traversi* and *Macrurocyttus*.
73. Beryciform foramen represented by deep groove along lateral surface of ceratohyal (33-1); convergent in *Plectrypops* + *Sargocentron*, *Parazen*, and *Macrurocyttus*. Polymorphic in these two species of *Alloctytus* (33-0,1), but character assigned state 1 by mutation coding.
74. Three groups of vacant interneural spaces (58-2); convergent in (*Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*)) + (*Zeus* + *Zenopsis*). *Alloctytus verrucosus* assigned state 2 by mutation coding. Ambiguous optimization.

The Bremer value of one indicates only weak support for the monophyly of this unnamed clade.

MONOPHYLY OF *Parazen*, *Cyttopsis*, *Stethopristes*, *Zenion*, *Capromimus*, *Cyttomimus*, *Macrurocyttus*, *Xenolepidichthys*,

Grammicolepis, *Zeus*, AND *Zenopsis* (branch A' in Figure 4 and the Appendix).—The monophyly of this clade is supported by three homoplasious characters.

75. Six anal-fin pterygiophores anterior to haemal spine of third caudal vertebra (72-3); convergent in *Centroberyx*; further derived, to state 1, in *Cyttopsis* + *Stethopristes*, and convergent in *Melamphaes*; further derived, to state 2, in *Macrurocyttus*, and convergent in *Allocyttus* and *Cyttus traversi*; reversal, to state 4, in *Capromimus* and *Zenopsis nebulosus*.
76. Basipterygia not in close contact in middle region (85-2); convergent in *Anoplogaster*; further derived, to state 0, in *Parazen*, *Zenion* + (*Cyttomimus* + *Capromimus*), and *Macrurocyttus*.

The support from the next character for this clade is questionable because of ambiguity in optimization.

77. Many abdominal haemal spines with a prominent process in midline below bridge under haemal canal (46-0); convergent in *Anoplogaster*, *Hoplostethus*, and *Cyttus*; reversal, to state 1, in *Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*); reversal, to state 0, in *Xenolepidichthys*. Ambiguous optimization.

The Bremer value of two indicates moderate support for the monophyly of this unnamed clade.

MONOPHYLY OF *Parazen*, *Cyttopsis*, AND *Stethopristes*: PARAZENIDAE (branch B' in Figure 4 and the Appendix).—The monophyly of this clade is supported by one consistent synapomorphy and four others that exhibit homoplasy.

78. Large haemal-spine vacuities in many posterior abdominal vertebrae (45-2).
79. Pelvic-fin spines absent (82-1); convergent in *Anoplogaster* and *Zenopsis*.
80. Two separate postcleithra (75-0); convergent in *Melamphaes*, *Centroberyx*, *Morone*, *Plectrypops* + *Sargocentron*, and *Parahollandia*.
81. Anterolateral processes of medial surfaces of pelvic-fin rays present as broad flanges from ray bases (83-2); convergent in *Hoplostethus* and *Capromimus* + *Cyttomimus*.

When optimized onto the tree, the following character supports this clade, but it is not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

82. One anal-fin spine (100-1); convergent in *Melamphaes*.

The Bremer value of two indicates moderate support for the monophyly of the family Parazenidae.

MONOPHYLY OF *Cyttopsis* AND *Stethopristes*: CYTTOPSINAE (branch D' in Figure 4 and the Appendix).—One consistent synapomorphy supports the monophyly of this clade.

83. Buckler-like scales present from isthmus to anus (88-1).

The following four homoplasious characters support the monophyly of this clade.

84. Four anal-fin pterygiophores anterior to haemal spine of third caudal vertebra (72-1); convergent in *Melamphaes*.
85. Lateral flange on lowermost pectoral-fin radial (74-1); convergent in *Cyttus*.
86. Scales on most of body cycloid and of moderate to small size (87-1); convergent in *Melamphaes*, *Cyttus novaezealandiae*, and *Zeus*.
87. Scales absent along bases of dorsal- and anal-fin rays, and nearby scales without spiny projections and not extending beyond lateral expansions of distal ends of pterygiophores (90-1); convergent in *Anoplogaster* and *Zeus* + *Zenopsis*.

The following character may support the monophyly of this clade, but its optimization is ambiguous.

88. No ossified epineurals (48-3); convergent in *Anoplogaster* and *Macrurocyttus*; autapomorphy, to state 2, in *Cyttopsis*. Ambiguous optimization.

When optimized onto the tree, the following three characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

89. Three vacant interneural spaces (99-3).
90. Nine pelvic-fin elements (102-0).
91. Thirteen or 14 pectoral-fin rays (101-1); convergent in *Centroberyx*, *Antigonia*, *Parahollandia*, and (*Macrurocyttus* + (*Grammicolepis* + *Xenolepidichthys*)) + (*Zeus* + *Zenopsis*); see optimization number 118 for details.

The Bremer value of three indicates good support for the monophyly of the subfamily Cyttopsinae.

MONOPHYLY OF *Zenion*, *Capromimus*, *Cyttomimus*, *Macrurocyttus*, *Xenolepidichthys*, *Grammicolepis*, *Zeus*, AND *Zenopsis* (branch G' in Figure 4 and the Appendix).—All five of the characters that support this clade exhibit homoplasy.

92. Dorsal-fin-spine locking mechanism between first, second, and third spines (57-3); convergent in *Oreosoma* + *Neocyttus* + *Allocyttus*; further derived, to state 2, in *Capromimus* + *Cyttomimus* and *Macrurocyttus* + (*Grammicolepis* + *Xenolepidichthys*).
93. Scales absent along bases of dorsal- and anal-fin rays, but spiny processes present on scales alongside lateral expansions of distal ends of pterygiophores (90-2); further derived, to state 1, in *Zeus* + *Zenopsis*, and convergent in *Anoplogaster* and *Cyttopsis* + *Stethopristes*.

The following two characters may support the monophyly of the clade, but their optimization is ambiguous.

94. No flange present on the single postcleithrum (76-0); convergent in *Anoplogaster*; reversal in *Cyttomimus*. Ambiguous optimization.
95. One epural (51-2); convergent in *Parahollandia* and *Stethopristes*; reversal, to state 1, in *Zenion* and *Xenolepidichthys* + *Grammicolepis*. Ambiguous optimization.

When optimized onto the tree, the following character supports this clade, but it is not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

96. Five vacant interneural spaces (99-5); further derived, to state 2, in *Zenion* + (*Capromimus* + *Cyttomimus*), and convergent in *Parahollardia* and *Cyttus traversi*; further derived, to state 4, in *Xenolepidichthys* + *Grammicolepis*; reversal, to state 1, in *Cyttomimus*. Ambiguous optimization.

The Bremer value of one indicates only weak support for the monophyly of this unnamed clade.

MONOPHYLY OF *Zenion*, *Capromimus*, AND *Cyttomimus*: ZENIONTIDAE (branch H' in Figure 4 and the Appendix).—All eight of the characters that support this clade exhibit homoplasy.

97. Dentary with multiple serrations behind symphysis (22-2); convergent in *Anoplogaster*, *Plectrypops*, *Capros*, *Cyttus*, *Oreosoma* + *Neocyttus* + *Allocyttus*, and *Grammicolepis*.
98. Serrations present along posterior border of supracleithrum (77-1); convergent in *Centroberyx*, *Plectrypops*, *Capros*, *Antigonia*, *Cyttus australis* + *Cyttus traversi*, and *Oreosoma* + *Neocyttus* + *Allocyttus*.
99. Anterior end of epihyal equal, or about equal, to depth of adjacent part of ceratohyal (37-0); reversal, with independent convergent reversals in *Stethopristes* and *Macrurocyttus*.

The following four characters only questionably support this clade.

100. Medial processes of basiptyrgia broadly overlap at level of pelvic fin (85-0); convergent in *Parazen* and *Macrurocyttus*. Ambiguous optimization.
101. Beryciform foramen represented by deep concavity on dorsal surface of ceratohyal (33-2); convergent in *Parahollardia*. Polymorphic (33) in *Zenion* for states 0 and 1 but not 2, thus distribution of states supports clade only indirectly, through homoplasy. Ambiguous optimization.
102. Alveolar process of premaxilla ventrally indented (14-1); reversal in *Cyttomimus*. Ambiguous optimization.
103. Second anal-fin spine short (68-1); convergent in *Xenolepidichthys*; reversal in *Cyttomimus*. Ambiguous optimization.

When optimized onto the tree, the following character supports this clade, but it is not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

104. Two vacant interneural spaces (99-2); convergent in *Parahollardia* and *Cyttus traversi*; reversal, to state 1, in *Cyttomimus*.

The Bremer value of two indicates moderate support for the monophyly of the family Zeniontidae.

MONOPHYLY OF *Capromimus* AND *Cyttomimus* (branch J' in Figure 4 and the Appendix).—All six characters that support this clade exhibit homoplasy.

105. Ascending process of premaxilla reaching distinctly behind lateral ethmoid to about one-third into orbit (15-1); convergent in *Parazen*.
106. Three anal-fin pterygiophores in second interhaemal space (71-2); convergent in *Morone*, *Capros*, and *Parazen*.
107. Seven anal-fin pterygiophores anterior to haemal spine of third caudal vertebra (72-4); reversal, with independent convergent reversal in *Zenopsis nebulosus*.
108. Anterolateral process of medial surfaces of pelvic-fin rays present as broad flanges (83-2); convergent in *Hoplostethus* and *Parazen* + (*Capromimus* + *Cyttomimus*).

The following two characters only questionably support this clade.

109. No ossified ribs (47-3); convergent in *Parahollardia*, *Cyttus*, and *Macrurocyttus*; autapomorphy, to state 2, in *Capromimus*. Ambiguous optimization.
110. Dorsal-fin-spine locking mechanism between second and third spines (57-2); convergent in *Macrurocyttus* + (*Grammicolepis* + *Xenolepidichthys*). Ambiguous optimization.

The Bremer value of two indicates moderate support for the monophyly of this unnamed clade.

MONOPHYLY OF *Macrurocyttus*, *Xenolepidichthys*, *Grammicolepis*, *Zeus*, AND *Zenopsis* (branch M' in Figure 4 and the Appendix).—All eight characters that support the monophyly of this clade exhibit homoplasy.

111. Scales absent (excluding buckler-like scales), or with only lateral-line scales (87-3); further derived, to state 2, in *Xenolepidichthys* + *Grammicolepis*; further derived, to state 1, in *Zeus*, and convergent in *Melamphaes*, *Cyttus novaezelandiae*, and *Cyttopsis* + *Stethopristes*.
112. Basisphenoid absent (2-2); convergent in *Melamphaes* and *Parahollardia*; further derived, to state 1, in *Xenolepidichthys* + *Grammicolepis*.
113. Lachrymal moderately deep (8-1); convergent in *Plectrypops* + *Sargocentron*; further derived, to state 2, in *Zenopsis*.

The support from the next character is questionable.

114. Three groups of vacant interneural spaces (58-2); convergent in *Allocyttus*; reversal, to state 1, in *Xenolepidichthys* + *Grammicolepis*. Ambiguous optimization.

When optimized onto the tree, the following four characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

115. One procurrent caudal-fin ray (97-1); further derived, to state 0, in *Macrurocyttus*, and convergent in *Parahollardia*.

116. Thirty-five or 36 vertebrae (93-5); further derived, to state 9, in *Xenolepidichthys* + *Grammicolepis*; further derived, to state 6, in *Xenolepidichthys*, and convergent in *Oreosoma* and *Alloctytus verrucosus*; reversal, to state 3, in *Zeus*.
117. Five vertebrae in caudal peduncle (95-2); convergent in *Parahollardia*, *Cyttus*, and *Zenion*; further derived, to state 7, in *Macrurocyttus* + (*Xenolepidichthys* + *Grammicolepis*), and convergent in *Anoplogaster*; further derived, to state 1, in *Macrurocyttus* and *Zenopsis nebulosus*, and convergent in *Capros*; reversal, to state 5, in *Xenolepidichthys*.
118. Thirteen or 14 pectoral-fin rays (101-1); convergent in *Centroberyx*, *Antigonia*, *Parahollardia*, and *Cyttopsis* + *Stethopristes*; further derived, to state 0, in *Zenopsis*, and convergent in *Cyttus*; reversal, to state 2, in *Grammicolepis*.

The Bremer value of one indicates only weak support for the monophyly of this unnamed clade.

MONOPHYLY OF *Macrurocyttus*, *Xenolepidichthys*, AND *Grammicolepis*: GRAMMICOLEPIDIDAE (branch N' in Figure 4 and the Appendix).—One consistent synapomorphy supports the monophyly of this clade.

119. Fifth ceratobranchial toothless (32-1).

The following five homoplasious characters support the monophyly of this clade.

120. Neural spine of first vertebra with long dorsal portion free from skull beyond curvature of supraoccipital and exoccipitals (42-1); convergent in *Zenion*.
121. Vomerine teeth absent (3-1); reversal, with independent convergent reversals in *Pseudocyttus* and *Oreosoma*.
122. Second pharyngobranchial suspensory shaft short or absent (28-0); reversal, with independent convergent reversal in *Oreosoma*.
123. Third pharyngobranchial suspensory shaft short or absent (29-0); reversal, with independent convergent reversal in *Oreosoma*.
124. No prominent notches on lower border of ceratohyal (35-1); reversal.

The following two characters are of questionable support.

125. Most haemal arches of abdominal vertebrae with transverse bony bridge below haemal canal but no median spine below bridge (46-1); reversal, to state 0, in *Xenolepidichthys*. Ambiguous optimization.
126. Dorsal-fin-spine locking mechanism between second and third dorsal-fin spines (57-2); convergent in *Capromimus* + *Cyttomimus*. Ambiguous optimization.

When optimized onto the tree, the following character supports this clade, but it is not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

127. Ten vertebrae in caudal peduncle (95-7); convergent in *Anoplogaster*; further derived, to state 1, in *Macrurocyt-*

tus, and convergent in *Zenopsis nebulosus*; reversal, to state 5, in *Xenolepidichthys*.

The Bremer value of four indicates strong support for the monophyly of the family Grammicolepididae.

MONOPHYLY OF *Xenolepidichthys* AND *Grammicolepis*: GRAMMICOLEPIDIDAE (branch P' in Figure 4 and the Appendix).—Three consistent synapomorphies support the monophyly of this clade.

128. Proximal end of parhypural laterally expanded as specialized pegs, with pegs fitting into sockets on sides of centrum (52-2).
129. Scales on most of the body greatly elongate vertically (87-2).
130. Basisphenoid present as a short shaft at front of roof of posterior myodome (2-1).

The following eight homoplasious characters support the monophyly of this clade.

131. Mouth small (12-1); convergent in *Antigonia* and *Parahollardia*.
132. Symplectic ventral flange present (20-1); convergent in *Melamphaes*, *Sargocentron*, and *Zenion*.
133. Two dorsal-fin pterygiophores anterior to neural spine of fourth abdominal vertebra (59-1); convergent in *Centroberyx*, *Morone*, *Parahollardia*, and Oreosomatidae.
134. Pelvic-fin-ray serrations on crests on anterior or upper and/or lower posterior surfaces of several rays (84-1); convergent in *Anoplogaster*, *Capros*, and *Antigonia*.
135. Postmaxillary process absent (13-1); reversal, and convergent in *Centroberyx* and *Parahollardia*.
136. Hypurapophysis present (50-0); reversal, and convergent in *Cyttus traversi*, *Parazen*, and *Cyttomimus*.
137. Two epurals (51-1); reversal, and convergent in *Zenion*.
138. Dentary cartilage absent or unconsolidated (21-0); convergent in *Anoplogaster*.

The following two characters are optimized as supporting the clade, but only questionably.

139. Two groups of vacant interneural spaces (58-1); reversal. Ambiguous optimization.
140. First basibranchial entirely below level of dorsal surfaces of basihyal and second basibranchial (30-1); convergent in *Cyttus*; *Grammicolepis* unknown. Ambiguous optimization.

When optimized onto the tree, the following three characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

141. Fifteen caudal-fin rays (96-1).
142. Four vacant interneural spaces (99-4).
143. Forty-three or 44 vertebrae (93-9); further derived, to state 6, in *Xenolepidichthys*, and convergent in *Oreosoma* and *Alloctytus verrucosus*. Ambiguous optimization.

Even with the uncertainty of support from several of the above characters, the Bremer value of eight is the third highest

in the entire cladogram, indicating very strong support for the monophyly of the subfamily Grammicolepidinae.

MONOPHYLY OF *Zeus* AND *Zenopsis*: ZEIDAE (branch S' in Figure 4 and the Appendix).—The following nine consistent synapomorphies support the monophyly of this family.

144. Otolith tiny, trilobed (7-1).
145. Alveolar process of premaxilla deeply bifurcate ventrally (14-2).
146. Baudelot's ligament attached to exoccipitals (43-2).
147. Extra-caudal ossicle in haemal spine of PU2 of at least some specimens (56-1).
148. Four dorsal-fin pterygiophores anterior to neural spine of fourth abdominal vertebra (59-3).
149. Ventral end of supracleithrum deeply bifurcate (78-1).
150. Ossified ribs on most abdominal vertebrae behind fourth vertebra (47-0).
151. Cleithral processes a prong above articulation with postcleithrum (79-1).
152. Posterior process of pelvis long, rod-like, moderately separated from its opposite member along midline (86-1).

The following five homoplasious characters support the monophyly of this clade.

153. Dermosphenotic fused or closely consolidated with sphenotic (11-1); convergent in *Capros*.
154. Two extrascapular bones, not held closely to skull (80-1); convergent in *Antigonia* and *Morone*.
155. Anterolateral processes of pelvic-fin rays present as prongs from medial surfaces of ray bases (83-1); convergent in *Cyttus*.
156. Scales absent along bases of dorsal- and anal-fin rays, nearby scales without spiny projections (90-1); convergent in *Anoplogaster* and *Cyttopsis* + *Stethopristes*.
157. No supraneurals (64-0); convergent in *Capros*, *Parahollardia*, and *Parazen*.

The following five characters are optimized as supporting the monophyly of the group, but only questionably.

158. Ossified epineurals present on a few anterior abdominal vertebrae (48-1); convergent in *Hoplostethus*, *Cyttus*, and *Oreosoma*; reversal, to state 0, in *Zenopsis conchifer*. Ambiguous optimization.
159. Bony interdigitated articulations between ceratohyal-epihyal in specimens of all sizes (36-2); convergent in *Morone* and *Antigonia*; further derived, to state 1, in *Zeus*, and convergent in *Cyttus australis* and *Oreosoma* + *Neocyttus* + *Alloctytus*. Ambiguous optimization.
160. Buckler-like scales present mid-abdominally and from below front to middle region of spinous dorsal-fin base to end of soft dorsal-fin base (88-3); autapomorphy, to state 2, in *Zeus*. Ambiguous optimization.
161. Supraocular serrations on frontal absent (6-1); convergent in *Melamphaes*, *Morone*, *Sargocentron*, and *Parahollardia*; polymorphic in *Zenopsis* (states 0, 1).

162. Eleven or 12 infraorbitals (9-5); further derived, to state 4, in *Zenopsis conchifer*; polymorphic in *Zeus* (states 2, 3). Character does not clearly support clade without optimization.

When optimized onto the tree, the following four characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

163. Fourteen abdominal vertebrae (94-5); convergent in Oreosomatidae; autapomorphy, to state 6, in *Zenopsis nebulosus*.
164. Four anal-fin spines (100-4); convergent in *Centroberyx* and *Plectrypops*; reversal, to state 3, in *Zenopsis*, with independent convergent reversals in *Oreosoma* and *Alloctytus niger*. Ambiguous optimization.
165. Six elements in pelvic-fin (102-3); reversal, with independent convergent reversal in *Pseudocyttus*; further derived, to state 1, in *Zeus*, and convergent in *Melamphaes*, *Centroberyx*, and *Plectrypops* + *Sargocentron*. Ambiguous optimization.
166. Ten or more dorsal-fin spines (98-6); reversal; polymorphic in *Zenopsis* (*Z. nebulosus*, states 4, 5; *Z. conchifer* states 4, 5, 6).

The Bremer value of 12, which is the highest in the analysis, indicates very strong support for the monophyly of the family Zeidae.

MONOPHYLY OF *Zenopsis conchifer* AND *Zenopsis nebulosus* (branch U' in Figure 4 and the Appendix).—One consistent synapomorphy supports the monophyly of *Zenopsis*.

167. Lachrymal slender (8-2).

The following two homoplasious characters support the monophyly of this clade.

168. First vertebra in caudal peduncle with modified haemal or neural spine PU2 (39-0); convergent in *Parahollardia*, *Parazen*, and *Macrurocyttus*.
169. Pelvic-fin spines absent (82-1); convergent in *Anoplogaster* and *Parazen* + (*Cyttopsis* + *Stethopristes*).

When optimized onto the tree, the following two characters support this clade, but they are not used in the construction of the tree, and this support is not used in the calculation of the branch-support value.

170. Eleven or 12 pectoral-fin rays (101-0); convergent in *Cyttus*.
171. Three anal-fin spines (100-3); reversal, with independent convergent reversals in *Oreosoma* and *Alloctytus niger*.

The Bremer value of two indicates moderate support for the monophyly of this unnamed clade.

Previous Phylogenetic Analyses of Zeiforms

A number of workers have contributed to the study of the phylogeny of zeiforms. Roman numerals in brackets distinguish the characters used in those previous analyses of zeiform

relationships from the characters and their states described herein, which are listed as Arabic numerals in parentheses.

Rosen (1984:31) listed seven characters (not eight, as stated on p. 44 of that work) as indicating monophyly of caproids, zeiforms, and tetraodontiforms. We include six of these characters in our study of the relationships of these groups. Our analysis based on the unordered reduced data set (Figure 4) neither supports nor rebuts this clade, because of the large polytomy among the outgroups, but the other three analyses (Figures 1–3) do support it, and we offer the following comments on Rosen's (1984:31) characters, using the same numerical scheme that he employed.

[I]. "Saccular otolith (sagitta) higher than long and constricted fore and aft in the region of the sulcus." This characterization of overall shape does not apply to many zeiforms or tetraodontiforms, and among caproids it applies to *Capros* but not to *Antigonia*. Moreover, the significance of the gross shape of otoliths is very difficult to interpret and can usually be employed only in conjunction with detailed study of surface features. Many zeiforms and tetraodontiforms have a relatively rounded or oval-shaped sagitta, similar to that of beryciforms. Otolith shape corresponds to our character (7), in which the obviously derived state of reduced size and bow-tie shape supports only the clade of *Zeus* + *Zenopsis*. Therefore, we reject the otolith shape character of zeiforms in general as evidence of monophyly at Rosen's ordinal level.

[II]. "Dorsal and anal fin radials symmetrical,..." This corresponds to our character (63), which would be a synapomorphy of this putative clade of caproids, zeiforms, and tetraodontiforms; however, it occurs convergently in *Anoplogaster*.

[III]. "Radial supporting first dorsal fin spine robust, columnar, inserted ventrally between the neural arches of the first vertebrae [sic] and the occipital bones of the skull to which they are firmly united." Because the first pterygiophore does not lie in the space between the skull and the first neural arch in all the taxa studied herein, it is more appropriate to separate Rosen's character into two distinct characters, as we have done in our characters (60) and (61). The placement of the first pterygiophore of the spinous dorsal-fin (60) supports this putative clade; however, it is convergently derived in *Sargocentron*. The position of the base of the first dorsal-fin pterygiophore in the first interneural space (61) would also be a synapomorphy of this putative clade of caproids, zeiforms, and tetraodontiforms, but there is a secondary loss of contact between the pterygiophore and the neural arch and spine in *Parazen*.

[IV]. "Parasphenoid with a tunnel-like opening to the posterior myodome." This is not discussed in the text by Rosen. The derived condition of this character (4) applies to *Morone*, caproids, and tetraodontiforms. As optimized on our cladogram (Figure 4), the presence of a tunnel-like opening in this area does not support the clade, and this derived condition is not present in any of the zeiform taxa.

[V]. "Interoperculum elongate, bladelike or feather-shaped." There is so much variation in the shape of the interopercle

among zeiforms that this characterization applies only to some taxa. We do not think that caproids share the stated condition, although *Parahollardia* does. We find no way to characterize the variation in the shape of the interopercle in a way that would be useful in defining any of the three groups, let alone as a monophyletic assemblage.

[VI]. "Premaxillary ascending and articular processes elongate and intimately united above a distinct neck that separates them from a very short alveolar process." The variety of premaxillary shapes in zeiforms is so great that we find no unequivocal way to characterize the configuration of the premaxilla by region. Rosen's own figures of premaxillary shape (1984, figs. 27–29) in selected species of caproids, zeiforms, and tetraodontiforms do not all conform to his definition. Rosen and Patterson (1990, figs. 12–15) and Johnson (1982, figs. 2–20) show premaxillae similar to those of zeiforms in many groups of acanthomorphs. We were able, however, to code the extent of the elongation of the ascending process of the premaxilla (15) for all taxa. This character is not a synapomorphy of zeiforms or any other higher categories. Moreover, we are unable to characterize premaxillary shape in any way that suggests it is a synapomorphy of the putative clade of caproids, zeiforms, and tetraodontiforms.

[VII]. "Caudal fin with 15 or fewer principal rays." This is our character (96). We agree that this character occurs, although not uniquely among acanthomorphs, in each of the caproids, zeiforms, and tetraodontiforms and is supportive of this putative clade.

We accept four (II, VII, and the two characters within III) of Rosen's characters as support for this putative clade of caproids, zeiforms, and tetraodontiforms, but only Rosen's character VII is a consistent synapomorphy of the group within the species in our data set. To this we add that the neural arch and spine of the first vertebra is closely applied to the skull (40). Thus, two consistent synapomorphies support the putative clade of caproids, zeiforms, and tetraodontiforms.

We emphasize that although the present study is unable to draw any definitive conclusion regarding the status of this putative clade of caproids, zeiforms, and tetraodontiforms, there are several characters that do support it (Figures 1–3).

Zehren (1991:61A), in a brief one paragraph abstract, stated that caproids are monophyletic based on "seven apomorphies, including ornamentation of the preopercle, frontal and supra-cleithrum," without listing all seven characters (but with the three ornamentation characters counted separately; S. Zehren, pers. comm., 16 Oct 1998). We are unable to find any consistent synapomorphies that define this clade of two genera (*Capros* and *Antigonia*). Other derived features, exhibiting homoplasy, support the caproid clade in three (Figures 1–3) of our four analyses; however, this clade is not supported in the analysis (Figure 4) that we propose as the most rational.

Rosen (1984:31–32) gave four putative synapomorphies (not five, as stated on p. 44) of tetraodontiforms and zeiforms.

[VIII]. "Caudal skeleton with a full spine on the second preural centrum and a greatly reduced first uroneural with no stegural." We regard the first (49) and third (55) of these as valid possible synapomorphies for the putative clade of zeiforms and tetraodontiforms, albeit hardly unique to these fishes. A relatively well-developed uroneural (54) is present among tetraodontiforms in triacanthoids and in the primitive tetraodontoid *Triodon* and thus would not support this putative clade.

[IX]. "Greatest depth of caudal peduncle less than 13 percent of standard length." The statement itself is generally true for both zeiforms and tetraodontiforms, but it is also true for some members of the outgroups (e.g., *Centroberyx* 12%; *Capros* 11%–12%). Thus, we have little confidence in this character as evidence for higher-level relationships among these taxa.

[X]. "Hyoid apparatus with the posterior ceratohyal [=our epihyal] very short and shallower than the adjoining part of the anterior ceratohyal; the bases of the four posterior branchiostegals clustered on the posteroventral margin of the ossified anterior ceratohyal." The first part of this character (37) could be a synapomorphy of this putative clade, although the distinction is somewhat subjective, and, because in our interpretation the condition is also present in *Capros* and *Antigonia*, it would be a synapomorphy at a higher level (but we stress the subjectivity of the character states). We also find the positioning of the branchiostegal bases to be somewhat subjective, and in our interpretation (34), Rosen's derived condition seems to characterize *Capros* and *Parahollardia*, but not *Antigonia* and zeiforms.

[XI]. "Interoperculum long and very slender, acinaciform, and only loosely bound to the preoperculum by connective tissue." We find this subcondition of Rosen's character V to be just as variable within zeiforms and tetraodontiforms as the other interopercular shape characterization, and we find no useful way to define it as a shared derived feature of the two groups.

Rosen (1984:33) listed six synapomorphies of tetraodontiform taxa.

[XII]. "No anal spines." This condition (100) supports the monophyly of tetraodontiforms, but this loss is convergent in *Anoplogaster* and *Macrurocyttus*.

[XIII]. "Caudal fin with 12 or fewer principal rays." The condition of 15 or fewer caudal-fin rays (96) supports a putative clade of caproids, zeiforms, and tetraodontiforms. Within this clade, tetraodontiforms can be characterized as having 12 or fewer principal rays; however, this condition is convergent in *Antigonia*.

[XIV]. "No infraorbitals." This condition (9) is a synapomorphy of tetraodontiforms, but the infraorbitals are absent convergently in *Macrurocyttus*.

[XV]. "No parietals." As with the infraorbitals, the lack of parietals (1) is a synapomorphy of tetraodontiforms, but the parietals are absent convergently in *Macrurocyttus*.

[XVI]. "Small, slitlike gill opening just anterior to the pectoral fin base." We accept this condition as a consistent synapo-

morphy of tetraodontiforms (no character number is assigned to this feature because it is autapomorphic in our data set for *Parahollardia*; see "Analytical Protocols").

[XVII]. "Pelvic girdles closely joined along their lengths and the pelvic-fin rays reduced or absent." The joining of the pelvic girdle along its length (85) is a synapomorphy of tetraodontiforms. We regard the reduction or loss of the pelvic-fin ray as a separate character, but it was not used in the present study because it is autapomorphic in our data set for *Parahollardia*.

Thus, of the six synapomorphies listed by Rosen for tetraodontiforms, we find that only two are non-homoplasious synapomorphies, but they represent three synapomorphies because Rosen's character XVII should be divided into two separate characters.

Rosen provided a single putative synapomorphy to link the ostraciid boxfishes with tetraodontoids. Klassen (1995) pointed out that this single character is far outweighed by the 20 synapomorphies that ostracioids share with balistoids and by the 15 synapomorphies uniting tetraodontoids that are not found in ostracioids, citing the evidence presented in Winterbottom (1974, not referred to by Rosen) and Winterbottom and Tyler (1983). Rosen (1984) did not propose any synapomorphies for zeiform taxa.

Regarding tetraodontiforms, we note that nearly all of the 32 character states identified in the present study as autapomorphies of the representative tetraodontiform, *Parahollardia lineata*, in branch K of Figure 4 and the Appendix, likewise are synapomorphies for the clade comprising all of the extant families of tetraodontiforms, or of the putative zeiform + tetraodontiform clade, or of that clade plus caproids. Many of these tetraodontiform apomorphies involve reductions, simplifications, or loss of structures. These are as follows, with those that are potential synapomorphies of the putative larger clade involving zeiforms, and in many cases caproids, marked with an asterisk after the character state: parietal absent (1-1); basisphenoid absent (2-2); parasphenoid opening into posterior myodome (4-1); supraocular serrations on frontal absent (6-1); infraorbitals absent (9-0); dermosphenotic absent (11-2); mouth small (12-1); postmaxillary process absent (13-1); palatine teeth absent (16-1); four series of gill rakers (25-1); interarcual cartilage present (27-1); beryciform foramen represented by deep concavity on dorsal surface of ceratohyal (33-2); heads of branchiostegal rays clustered along posterior border of ceratohyal (34-1); anterior end of epihyal distinctly less deep than adjacent part of ceratohyal (37-1*); PU2 first caudal peduncle vertebra with modified haemal or neural spines (39-0); neural arch and spine of first vertebra closely applied to skull (40-1*); ossified ribs absent (47-3*); PU2 neural spine long (49-0*); hyurapophysis absent (50-1*); one epural (51-2); stegural absent (55-1*); two dorsal-fin pterygiophores anterior to fourth neural spine (59-1); first dorsal-fin pterygiophore inserted in first interneural (or preneural) space (60-1*); distal radials of spinous dorsal fin absent (62-1*); supraneurals absent (64-0); no anal-fin pterygiophores in prehaemal space (69-3); one anal-fin

pterygiophore in first interhaemal space (70-1); three anal-fin pterygiophores anterior to third caudal haemal spine (72-0); two elements in postcleithrum (75-0); extrascapulars absent (80-3); basipterygia tightly adherent or fused along broad area of midline contact (85-3); and long, tapering shaft-like posterior process of pelvis (86-2). Two other characters not listed under branch K are higher-level potential synapomorphies of the putative caproid + zeiform + tetraodontiform clade, these being base of first dorsal-fin pterygiophore in contact with the skull and first vertebra (61-1*), and symmetrical radials (63-1*). Additionally, the following meristic features are apomorphies of *Parahollardia* and represent synapomorphies for the clade comprising all of the extant families of tetraodontiforms: nine or fewer (actually eight in *Parahollardia*) abdominal vertebrae (94-0); 12 caudal-fin principal rays (96-4); no procurrent caudal-fin rays (97-0); six dorsal-fin spines (98-2); two vacant interneural spaces (99-2); no anal-fin spines (100-0); three pelvic-fin elements (one spine and two reduced rays) (102-6); and total number of vertebrae reduced to 20, which in our coding is subsumed in the 26 or fewer category (93-0). See Tyler and Sorbini (1996) for a smaller number of synapomorphies applicable to all fossil and extant tetraodontiforms and for those that distinguish the most basal tetraodontiform clade of three Upper Cretaceous families from all other, Eocene to present, families of tetraodontiforms.

The most cogent analysis of zeiform characteristics previously available is that of Johnson and Patterson (1993), who listed numerous characters as uniting all zeiforms. With most of these we agree, but several others apply either at a different level of universality or may form part of a larger transformation series, and several have convergently arisen in other groups.

The synapomorphies listed by Johnson and Patterson (1993) are as follows.

[I]. "Baudelot's ligament originating high on the exoccipital, immediately under the vagus foramen." The condition of this character (43) is unknown in half of the zeiform species studied herein because of poor ligament visibility in some of the cleared and stained material (or previous dissections in the vicinity of Baudelot's ligament having damaged it) and the disappearance of the ligament in most of the dry skeletal material. In most of the zeiform taxa in which the determination can be made, Baudelot's ligament originates on the first vertebra (43-1), and our study indicates that it is this derived condition that is ancestral for zeiforms (most outgroup taxa have the origin of the ligament on the basioccipital, 43-0). Among zeiforms, only *Zeus* and *Zenopsis* have a further derived condition of the ligament originating on the exoccipital (43-2). Thus, Baudelot's ligament originating on the first vertebra is a synapomorphy for zeiforms, but this character's support for the monophyly of zeiforms is somewhat questionable because of the large number of taxa in which it presently is unknown.

We code *Melamphaes* 43-1 for this character, convergent with the zeiform synapomorphy, because in both cases the ori-

gin of the ligament is on the first vertebra. The conditions could be considered different, however, because in *Melamphaes* the origin is on the middle to lower part of the centrum whereas in the zeiform ancestral condition it is higher and more anterior, on an anterior process of the first vertebra just above the posterior end of the basioccipital. In *Zeus* and *Zenopsis* the origin has simply moved a little further forward and upward, to a point on the exoccipital just above and in front of the anterior process of the first vertebra.

[II]. "The dorsal fin endoskeleton has the distal portions of the proximal-middle radials laterally expanded, and there are no distal radials in the spinous portion except as tiny cartilaginous or partially ossified structures under the last few spines." We find the degree of expansion of the distal portions of the proximal-middle pterygiophore to be especially subjective and difficult to define. The degree of distal expansion of the pterygiophores varies greatly in the outgroups, ranging from highly expanded in *Plectrypops* and *Sargocentron* to not expanded in *Melamphaes*. Within zeiforms, *Cyttus* and *Parazen* do not have the distal end of the pterygiophores expanded, whereas oreosomatids have the distal end slightly expanded (the low, thin lateral flange along much of the length of the soft dorsal- and anal-fin pterygiophores in *Parazen* forms a lateral prong distally, but we do not consider this comparable to a more general expansion of the distal end of the pterygiophores). The remaining zeiforms do have distally expanded pterygiophores, even though the degree of expansion varies. Because of the subjectivity in delineating character states, we did not include this part of the character in our study.

The second part of this character, no distal radials in the spinous portion except as tiny cartilaginous or partially ossified structures under the last few spines (62-1), is found in all zeiforms, but it is also found in *Parahollardia* and all other tetraodontiforms. Johnson and Patterson (1993) did not include tetraodontiforms in their study, but this character would be a synapomorphy for a putative clade of zeiforms and tetraodontiforms.

[III]. "The palatine has a specialized, mobile articulation with the ectopterygoid, which is truncated dorsally, and the metapterygoid is extremely reduced." We agree that the palatine articulation (18-1) is unique in zeiforms, and the reduced metapterygoid (19-1) also is a synapomorphy of the group.

[IV]. "The anterior vertebral centra have an unusually flexible articulation, and ribs, when present, never occur anterior to the fourth vertebra." The flexible articulation of the anterior centra with the skull (41-1) has arisen convergently in *Hoplostethus*. It is true that ossified ribs (47) are nearly always absent from the first four vertebrae of zeiforms (the one exception being *Grammicolepis*, where ribs begin on the third vertebra), but our study indicates that the absence of all ossified ribs (47-3) defines *Cyttus*, *Cyttomimus*, *Macrurocyttus*, and *Parahollardia* and that the remaining zeiforms secondarily have ossified ribs on at least some of the more posterior vertebrae; only members of two of the most derived clades of zeiforms, the grammicole-

pidid *Grammicolepis* and the zeids *Zeus* + *Zenopsis*, have ossified ribs on most of the abdominal vertebrae, posterior to the second and to the fourth vertebra, respectively.

[V]. "There is a distinctive configuration of the dorsal gill arch elements, including upright columnar processes on PB2 and PB3, and absence of PB4 and UP4 (Rosen, 1973, figs. 101, 102; 1984, figs. 22, 23)." We agree that most zeiforms have a distinctive derived condition of upright columnar processes on PB2 and PB3 (28, 29) and that all zeiforms have PB4 and UP4 absent (31-1). But there is much variation between zeiform species in the length of the columnar processes on PB2 and PB3, from relatively short or barely discernible and certainly not prominent, as in *Cyttus* and a few other taxa (28-0, 29-0), to especially long and prominent (28-2, 29-2). To distinguish these different conditions, we use three codes for the length of the processes: short or absent (state 0), moderately long (state 1), or long (state 2). Because the relatively short condition of some taxa, like *Cyttus* and a few other zeiforms, is difficult to distinguish from the short to essentially absent condition of the processes in the outgroups (e.g., barely discernible or essentially absent in *Capros* compared with very short in *Antigonina*), we code both the relatively short to absent conditions as 0. Thus, our study does not recognize the columnar-process character as a synapomorphy of zeiforms, and only the moderately long to long processes are phylogenetically informative for some clades within zeiforms. A more detailed analysis than attempted here of the morphology of the upper pharyngeal bones, including differences in how PB2 and PB3 are held together and how both are held to the shaft-like suspensory PB1, will surely yield a wealth of useful characters.

[VI]. "Below the frontals there is a continuous median cartilage extending between the ethmoid cartilage and pterosphe-noids." We exclude this feature from our data base because we could not determine it in many of the zeiform taxa (such as the species represented in our materials only by dry skeletons or poorly counter-stained specimens). We accept it, however, as a highly probable zeiform synapomorphy because we find this long cartilage well back into the orbit close to the pterosphe-noids in *Capromimus*, *Cyttomimus*, *Cyttus*, *Parazen*, *Xenolepidichthys*, *Zenion*, *Zenopsis*, and *Zeus*, and it is absent in *Antigonina*, *Capros*, and *Parahollardia*.

[VII]. "In the caudal skeleton there is a full neural spine on PU2, two epurals, and the parhypural is truncated proximally." The presence of a full neural spine on PU2 (49-0) is not unique to zeiforms in our data set. This condition occurs in *Parahollardia* and would be a synapomorphy for a putative clade of zeiforms and tetraodontiforms, as suggested by Rosen (1984). The condition of two epurals in the caudal skeleton (51-1) does support a zeiform clade; however, many zeiforms have a further reduction to one epural (as does *Parahollardia*). The derived condition of the parhypural (52-1) supports a zeiform clade.

Thus, most of the many characters given by Johnson and Patterson (1993) as uniting zeiforms do support the clade, some consistently and some with homoplasy: palatine articulation;

reduced metapterygoid; two epurals or fewer; parhypural slightly removed from and not embracing the centrum; probably some rendition of the PB2 and PB3 columnar process character when further studied, even though our coding may presently mask this possible synapomorphy; absence of PB4 and UP4; flexible articulation of the anterior vertebrae; attachment of Baudelot's ligament (although a different state is ancestral); and median cartilage under the frontal in the orbit. Two others support a putative clade of zeiforms and tetraodontiforms: no spinous dorsal-fin distal radials and long NPU2.

In addition to these characters, the reduction in number of supernumerary dorsal-fin spines from two to one has been suggested as a synapomorphy for zeiforms (Patterson, 1992; Tyler and Sorbini, 1996; Tyler, 1998). Although there is a single supernumerary spine in all zeiforms (see Figures 6, 16, 24, 33, 39, 48, 57, 60, 70, 73, 74, 89, 90), compared with two in caproids and tetraodontiforms, this condition has arisen convergently among the outgroups studied herein in *Plectrypops* + *Sargocentron* and in *Melamphaes*. Because this character is highly variable among lower acanthomorphs, and this homoplasy is reflected among our outgroups, we did not include it in our data set even though it clearly is a synapomorphy of zeiforms.

Bannikov (1991), in disagreement with Rosen's (1984) contention that caproids were related to zeiforms and tetraodontiforms, argued for the close relationship of caproids with acanthuroids and the Eocene genus *Acanthonemus* (from Monte Bolca, Italy) and the placement of caproids among Perciformes. The focus of Bannikov's noncladistic analysis was on caproids and acanthuroids, and not on zeiforms, and we do not further comment on it here because our own results concerning caproid relationships are ambiguous.

Stiassny and Moore (1992) suggested characters that group zeiforms (including caproids), scorpaeniforms, and perciforms together in a group called "Higher Percomorpha." Their analysis was based on a single osteological system, albeit a highly complex one, the anatomy of the pelvic girdle and its various attachments, and it did not examine the majority of the taxa involved in the present study. Additionally, the results presented were in the form of a majority-rule tree, an Adams consensus tree (both of the preceding without topological constraints), and selected trees. The only use of a strict consensus tree was to summarize two (of the 154) most parsimonious trees, under topological constraints to enforce monophyly of two taxa, one of which was their zeiforms (i.e., zeiforms *sensu stricto*, as used herein, plus caproids). Our strict consensus tree of all of the 154 most parsimonious trees based on the data presented by Stiassny and Moore (1992, table 1), and unconstrained topologically, resulted in a large polytomy with a single resolved node. This node, with a branch support value of only one, supports a trichotomy of caproids (i.e., excluding zeiforms), scorpaeniforms, and perciforms.

Thus, although the finely detailed anatomical study of the pelvis by Stiassny and Moore (1992) suggested characters sup-

porting a grouping of zeiforms and caproids with scorpaeniforms and perciforms, the analysis does not in fact support this clade without the a priori constraints.

Two of the characters used by Stiassny and Moore (1992) support a grouping of zeiforms and caproids: [VI] the presence of an inter-pelvic ligament, which is also present in holocentrids, scorpaeniforms, and perciforms; and [VII] the absence of an autogenous lateral pelvic radial in adults, which is shared with at least atheriniforms, lampridids, scorpaeniforms, and perciforms (but not holocentrids). A third character [VIII], the shape of the pelvis in cross section, links caproids (i.e., excluding zeiforms), scorpaeniforms, and perciforms.

The present study, which mainly investigates relationships within zeiforms, includes only the few features of the pelvic girdle anatomy that differ between zeiform species. Few of these features were used by Stiassny and Moore (1992), and we omit several of the pelvic features used in their study of acanthomorph relationships. Because of the different taxa and anatomical features examined in our respective studies, and the limited extent of the phylogenetic conclusions relative to zeiforms that can be drawn from Stiassny and Moore's (1992) analysis, their conclusions were not useful in our attempts to identify a closely related potential outgroup for zeiforms (as used herein, excluding caproids).

Colgan et al. (2000) included two species (one represented by three geographically different populations) of zeiforms among a broad array of taxa in an analysis of basal acanthomorphs that used 12S rDNA and 16S rDNA and was based on a minimum length, strict consensus tree of the combined data set. Among the results were the *Zeus faber* from Italy being the sister group of the scombroid *Rexea*, and these two forming the sister group of a monophyletic trichotomy consisting of *Zeus faber* from Australia, *Z. faber* from Japan, and *Cyttus australis*. This strange aspect of that study is not further considered here.

Wiley et al. (2000) examined the relationships of lower acanthomorphs based on a maximum-parsimony, total-evidence analysis of sections of the 12S mitochondrial ribosomal gene, the 28S ribosomal nuclear gene, and 38 morphological transformation series. They found that Zeiformes formed the sister group of Gadiformes (a relationship not previously proposed, and one not tested in our study). This putative gadiform-zeiform relationship was recovered in only one of the three maximum parsimony trees generated for each data set individually (Wiley et al., 2000, fig. 8). Unfortunately, the subsections of this figure have been transposed, with the tree from the morphological data represented as fig. 8a, and not fig. 8c as the legend states (F. Santini, pers. comm., 15 Jan 2001). This has led to minor discrepancies in the text. For example, they state (p. 344) that the morphological tree "did little better" than the DNA data in playing a role in tree resolution, when in fact it resolves fewer nodes than either of the trees derived from the DNA sets. It is clear to us, and to E.O. Wiley (pers. comm., 8 Feb 2001), that the possibility of gadiform-zeiform relationship needs much further testing before giving it much credence.

Phylogenetic Summary

The monophyly of the zeiform fishes is very strongly supported in all four of the analyses, with branch support values of 10 for both of the unordered trees, with and without most meristic features (Figures 2, 4, respectively), and for the ordered tree with meristics (Figure 1), and with a support value of nine for the ordered tree without most meristics (Figure 3). The tree statistics in all four of the analyses, however, indicate a moderate amount of homoplasy for the ordered trees (assuming the trees do reflect the actual sequence of evolution of these taxa), caused in part by our lack of accuracy in ordering the multistate characters.

The four analyses of the data set produced trees that are different from one another, but many parts of the topology are shared among all four trees. Three of the analyses (Figures 1–3) support Rosen's (1984) putative clade of caproids, zeiforms, and tetraodontiforms and also support a clade of zeiforms and tetraodontiforms; the fourth analysis (Figure 4), which we contend is the best justified and most rational, leaves these relationships unresolved.

In the unordered consensus tree of the reduced data set (Figure 4), the beryciforms (sensu Johnson and Patterson, 1993) may be paraphyletic, with their relationships unresolved. The only relationship resolved in the outgroups is the clade of *Plectrypops* + *Sargocentron*.

Our hypothesis (Figure 4) of zeiform interrelationships neither supports nor rejects that of either Johnson and Patterson (1993), in which zeiforms (excluding caproids) are the sister group of beryciforms (excluding stephanoberyciforms) plus percomorphs, or Rosen (1984), in which caproids are the sister group to a tetraodontiform + zeiform clade. Three of the four analyses (Figures 1–3), however, support Rosen's hypothesis, even though the analysis that we propose as most rational does not (Figure 4; the most conservative interpretation of the data, with the fewest assumptions made).

Within zeiforms, the Cyttidae (Cyttoidei, genus *Cyttus*) is the first group to split off the main branch, and it forms the sister group to the remaining zeiforms in three of the four analyses and has very strong support in all four analyses. The next clade, which occurs in three of the four analyses, with weak to good support, is the grouping of the remaining zeiforms (Zeioidei). Support for the Oreosomatidae varies from weak to very strong among the four analyses. Within the Oreosomatidae, *Pseudocyttus* is the sister group to the remaining genera (*Oreosoma* + *Neocyttus* + *Allocyttus*) in all four of the analyses, but there is little agreement among the trees regarding the relationships of the rest of this family. The Zeniontidae (*Zenion* + (*Capromimus* + *Cyttomimus*)) has moderate to good support in two of the four analyses. The Parazenidae (*Parazen* + (*Cyttopsis* + *Stethopristes*)) has weak to good support among the four analyses. The Grammicolepididae (*Macrurocyttus* + (*Grammicolepis* + *Xenolepidichthys*)) has moderate to strong support among the four analyses. The Zeidae (*Zeus* + *Zenopsis*) has very strong support in all four of the analyses. In three

of the four analyses, Zeidae is the sister group to the Grammicolepididae.

In both of the two unordered analyses (Figures 2, 4), the zeiform families have the following phylogenetic sequence: Cyttidae, Oreosomatidae, Parazenidae, Zeniontidae, Grammicolepididae, and Zeidae. Familial relationships are mostly unresolved in the ordered analysis of the reduced data set (Figure 3) and are partially unresolved in that of the full data set (Figure 1), with the latter having a different sequence of families than in the two unordered analyses (Figures 2, 4).

SYSTEMATICS

Revised Familial Classification of Zeiformes

Of the five traditional zeiform families, only the Oreosomatidae is recognized herein as a monophyletic clade with the usual grouping of genera: *Alloctytus*, *Neocyttus*, *Oreosoma*, and *Pseudocyttus*. Two subfamilies are established for the Oreosomatidae, with *Pseudocyttus* as the sister group of the other three genera. The family-level concepts for the arrangement of all of the other genera must be moderately to radically changed on the basis of the present study. The Grammicolepididae requires the least change: the inclusion for the first time of *Macrurocyttus* along with *Grammicolepis* and *Xenolepidichthys*; two subfamilies are established, with *Macrurocyttus* as the sister group of the other two genera. The formerly monotypic Zeniontidae becomes much expanded with the association for the first time of *Zenion* with *Capromimus* and *Cyttomimus*. The formerly monotypic Parazenidae becomes much expanded with the association for the first time of *Parazen* with *Cyttopsis* and *Stethopristes*; two subfamilies are established, with *Parazen* as the sister group of the other two genera. The Zeidae, formerly a large catch-all category, becomes restricted to only *Zeus* and *Zenopsis*. A new monophyletic group, the Cyttidae, is recognized for the three species of *Cyttus*, as the sister group (Cyttoidei) of all other zeiforms (Zeioidei).

In the recognition of subfamilies, we take into account three factors, listed in decreasing order of importance: the Bremer support values for the monophyly of clades within a family, based mostly on the analysis of the unordered reduced data set (Figure 4) but with secondary consideration to the values in the other three analyses (Figures 1–3); the degree of external and internal morphological distinctiveness between these clades; and the number of species within the clades. For example, with a Bremer value of eight (very strong) in Figure 4 (and with values of 5, 8, and 12 in Figures 1–3) distinguishing the *Xenolepidichthys* + *Grammicolepis* clade from *Macrurocyttus* within the Grammicolepididae, and with substantial morphological differences between the two groups, there is good reason to recognize subfamilies therein, even though there are only three species involved. Similarly, a Bremer value of three (good) in Figure 4 (and values of 3, 5, and 8 in Figures 1–3) distinguishes the *Cyttopsis* + *Stethopristes* clade from *Parazen* within the Parazenidae, and there are substantial morphological

differences between the two groups (supportive of subfamilial recognition even though only three species are involved). More subjective is the recognition of the *Oreosoma* + *Neocyttus* + *Alloctytus* clade as a subfamily distinct from *Pseudocyttus* within the Oreosomatidae, because the Bremer value of this clade of three genera is only two (moderate) in Figure 4 (and with values of 1, 2, and 4 in Figures 1–3). Nevertheless, we do so because there are four species within the *Oreosoma* + *Neocyttus* + *Alloctytus* clade, and we presume that the several species of *Neocyttus* not examined in this work will mostly fit the same pattern as *N. rhomboidalis*. Thus, Oreosomatinae is one of the most speciose subfamilies recognized herein, and we deem it useful to distinguish this clade from the more morphologically primitive *Pseudocyttus*. Within the Zeniontidae, we decline to recognize the *Capromimus* + *Cyttomimus* clade as subfamilially distinct from *Zenion* because the Bremer value of two (moderate) in Figure 4 does not receive additional support in the other three analyses. The Bremer value for this clade is only one (weak) in Figure 2 and two in Figures 1 and 3, and in the latter two cases this clade is involved in multifamily polytomies. Within the Zeidae, the Bremer values for the *Zenopsis* clade in the four analyses range from moderate (2) to very strong (5), but the species of this genus differ so little in overall morphology from those of *Zeus* that nothing useful would be gained in recognizing these differences at other than the generic level.

The new information on the phylogenetic relationships of the zeiform fishes presented here leads us to the following revised classification of the group. Family-level names of various vintage are available for most of these categories, although usually with a much different assemblage of genera than originally used.

Order ZEIFORMES (as usually recognized, excluding caproids).—Dories

Suborder CYTTOIDEI (new)

Family CYTTIDAE Günther, 1860 (as *Cyttina* for all zeiforms; newly restricted herein to *Cyttus* only).—Look-down or bigeye dories

Genus *Cyttus*

Suborder ZEIOIDEI (new)

Family OREOSOMATIDAE Bleeker, 1859 (as Oreosomatoidae for *Oreosoma* only; used herein to include all of the genera traditionally placed in that family).—Oreos or warty dories

Subfamily PSEUDOCYTTINAE (new)

Genus *Pseudocyttus*

Subfamily OREOSOMATINAE Bleeker, 1859 (newly recognized at the subfamilial level)

Genera *Oreosoma*, *Neocyttus*, and *Alloctytus*

Family PARAZENIDAE Greenwood et al., 1966 (originally for *Parazen* only; used herein in a newly expanded sense).—Slender dory and smooth dories

Subfamily PARAZENINAE Greenwood et al., 1966 (originally at the family level).—Slender dory

Genus *Parazen*

Subfamily CYTTOPSINAE Greenwood et al., 1966 (originally Cyttopsidae, as a family-level synonym of Zeidae).—Smooth dories

Genera *Cyttopsis* and *Stethopristes*

Family ZENIONTIDAE Myers, 1960 (originally for *Zenion* and its synonymous *Cyttula*; used herein in a newly expanded sense).—Armorye or elongate dories (*Zenion*) and rough-head or capro dories (*Capromimus* and *Cyttomimus*)

Genera *Zenion*, *Capromimus*, and *Cyttomimus*

Family GRAMMICOLEPIDIDAE Poey, 1873 (originally for *Grammicolepis* only; used herein in a newly expanded sense).—Tinsselfishes or scaly dories, and dwarf dory

Subfamily MACRURACYTTINAE Myers, 1960 (originally at the family level; used herein at the subfamilial level).—Dwarf dory

Genus *Macrurocyttus*

Subfamily GRAMMICOLEPIDINAE Poey, 1873 (newly recognized at the subfamilial level).—Tinsselfishes or scaly dories

Genera *Xenolepidichthys* and *Grammicolepis*

Family ZEIDAE Latreille, 1825 (as the family Zeides, a broad category for *Zeus* as well as *Capros* and several other non-zeiform genera; used herein in a much restricted sense both from that and from present usage).—Buckler dories, John dory, St. Peter fish

Genera *Zeus* and *Zenopsis*

Because the diagnostic characters that indicate the monophyly of the families and subfamilies of zeiforms are mostly internal osteological features, we include below characterizations of each of these categories based mostly on external features for use in systematic accounts, even though there is overlap in many of these features between some of the families. We also include a key to the families and subfamilies and a compilation (Table 2) of meristic features for all of the taxa studied as an aid to future studies on the systematics and phylogeny of zeiforms.

Characterizations of the Families and Subfamilies of Zeiformes

CYTTIDAE (Figures 6–15).—Contained genus: *Cyttus*.

External: Dorsal-fin spines 8 or 9, rarely 10; dorsal-fin rays 28–36; no locking mechanism between dorsal-fin spines. Anal-fin spines 2, first spine sometimes immovable and fully fused to distal end of pterygiophore, appearing as a broad-based, ventrally directed process from pterygiophore and tapering to a point distally; anal-fin rays 28–38; no locking mechanism between anal-fin spines. Pelvic fin I,6; positioned under pectoral-fin base. Pectoral-fin rays 11–18. Principal caudal-fin rays 13; 2 or 3 procurvent rays above and below.

Scales on most of body small (1%–2% SL), rounded to squarish, irregularly spinoid (*C. australis*, *C. traversi*) or relatively cycloid (*C. novaezelandiae*), sometimes deciduous (*C.*

traversi); low sheath of scales along soft dorsal- and anal-fin bases, none of these enlarged or much different in morphology than surrounding scales. Scales along either side of ventral surface of isthmus slightly enlarged as scutes, strongly curved or bent almost at 90° along middle of their width, forming a somewhat flattened surface along much of distance between ventral ends of cleithra to bases of pelvic-fin spines, many scutes from right and left sides of isthmus meeting and slightly overlapping along midline in a zipper-like alternation, with additional smaller spinoid scales often interspersed along area of midline overlap; spiny processes at angle of curvature of right and left zipper-like series of scutes sometimes (especially in *C. traversi*) relatively regularly arranged one after the other to form spiny, parallel lateral edges of the flat isthmus; in *C. traversi* the angular scutes right and left of bases of pelvic-fin spines continue posteriorly, forming two scale rows separated by a naked area enclosing anus, with the two rows converging in front of anal-fin origin; small scute-like scales sometimes (*C. traversi*) present on dorsal profile from supraoccipital to dorsal-fin origin. No buckler scales.

Mouth large, upper-jaw length (from midline front border of premaxilla to ventral end of maxilla) somewhat greater than orbit diameter, and about equal to or slightly longer than snout length. Ascending premaxillary process long, reaching behind front border of orbit about one-half into orbit.

Body moderately deep to deep, about 1.2–2.0 times in SL.

No extended prejuvenile stage in early life history of taxa.

Internal: Total vertebrae 30–42 (usually 31 in *C. australis*, 32 in *C. novaezelandiae*, 41 in *C. traversi*); abdominal vertebrae 11; caudal peduncle vertebrae 4–7 (usually 4 or 5 in *C. australis* and *C. novaezelandiae*, 6 or 7 in *C. traversi*). One or 2 vacant interneural spaces between space 6 and space 10; when 2 spaces vacant, vacancies separated by an occupied space (i.e., spaces are in 2 groups). Infraorbitals slender, 6–9 excluding deep lachrymal. Epurals 2. Supraneural 1.

OREOSOMATIDAE (Figures 16–23).—Contained genera: *Pseudocyttus*, *Oreosoma*, *Neocyttus*, *Allocyttus*.

External: Dorsal-fin spines 5–7, rarely 8; dorsal-fin rays 29–36; locking mechanism between first three dorsal-fin spines in all genera except *Pseudocyttus*. Anal-fin spines 2 or 3, rarely 4; anal-fin rays 27–34; locking mechanism between first two anal-fin spines. Pelvic fin usually I,6 in all genera except I,5 in *Pseudocyttus* (rarely I,7 in *Oreosoma*, sometimes I,5 in *Neocyttus*); positioned under pectoral-fin base. Pectoral-fin rays 18–21, usually 19–21. Principal caudal-fin rays 13; 2 or 3 procurvent rays above and below.

Scales on most of body small (1%–2% SL), rounded to squarish, usually spinoid, surface of many roughened with upright spinules (scales on sides of body in *Oreosoma* and *Pseudocyttus* may be more cycloid and deciduous at some stages (see Karrer, 1986), but all non-prejuvenile specimens examined herein with many spinoid scales, especially toward median-fin bases); low sheath of scales along soft dorsal- and anal-fin bases, scales similar in morphology to and only

TABLE 2.—Some of the meristic characters of all of the zeiform species examined. Several of these species (denoted with “*”) are not included in the analysis because they were examined only as radiographs or limited dry skeletal material, and most of the characters used in the analyses are not available for them. Most of the data are based on the materials examined for this work, but for some characters, especially the number of dorsal- and anal-fin rays, we have incorporated data from the literature cited in the text. In all cases, however, the most common condition(s) (underlined) is based on our materials. (“-” = not applicable; “?” = unknown.)

Species	Dorsal-fin spines	Dorsal-fin rays	Anal-fin spines	Anal-fin rays	Pelvic-fin spines	Pelvic-fin rays	Pectoral-fin rays	Caudal-fin principal rays	Caudal-fin procurent rays	Total vertebrae	Abdominal vertebrae	Caudal peduncle vertebrae	Total vacant interneural spaces	Position(s) of vacant interneural spaces	Groups of vacant interneural spaces	Infraorbitals	Epurals	Supraneurals
<i>Cyttus novaezelandiae</i>	8-9	28-30	² 1	28-30	1	6	11-12	13	2	30-33(<u>32</u>)	11	4-5	1	6	-	8-9	2	1
<i>Cyttus australis</i>	<u>8</u> -9	28-31	2	29-31	1	6	11-12	13	2	30-32(<u>31</u>)	11	<u>4</u> -5	1	6-8	-	6-7	2	1
<i>Cyttus traversi</i>	9-10	34-36	² 2	35-38	1	6	16-18(<u>17</u>)	13	2-3	40-42(<u>41</u>)	11	6-7	2	7-8, 9-10	1-2	7	2	1
<i>Pseudocyttus maculatus</i>	<u>5</u> -6	34-36	<u>2</u> -3	31-34	1	5	19-21(<u>20</u>)	13	2-3	42	14-15	6	7	2, 4-9	2	4	2	1
<i>Oreosoma atlanticum</i>	6-8(<u>7</u>)	29-31	2-3	28-30	1	6-7	19-21(<u>20</u>)	13	2	38	13-14	7	8	2, 4-9, 8-11, 12	3-4	3	2	1
<i>Neocyttus rhomboidalis</i>	7	32-35	3-4	30-33	1	<u>5</u> -6	19-21(<u>20</u>)	13	2-3	38-41(<u>40</u>)	<u>14</u> -15	6-7	7-9(<u>9</u>)	2, 4-11, 11-12	<u>2</u> -3	4	2	1
<i>Alloctytus verrucosus</i>	<u>6</u> -7	29-33	<u>2</u> -3	27-31	1	6	18- <u>20</u>	13	2	36-38(<u>37</u>)	<u>13</u> -14	5-7(<u>6</u>)	6-9(<u>7</u> -8)	2-12, extremely variable	2-4(<u>2</u> -3)	4	2	1
<i>Alloctytus niger</i>	<u>7</u> -8	32-34	3	30-31	1	6	19-20	13	<u>2</u> -3	40	14	7	8	2, 4-9, 10-11(<u>2, 4-9, 11</u>)	3	4	2	1
<i>Alloctytus folletti</i> *	5-7(<u>6</u> -7)	30-33	3	30-32	1	6	19- <u>21</u>	13	2	40	13	7	7	2, 4-6, 8, 10-11	4	?	2	1
<i>Parazen pacificus</i>	8	27-36	1	32-33	0	7	15- <u>16</u>	13	7-8	34	12	7	1	7	-	4	2	0
		(<u>30</u> -32)																
<i>Cyttopsis roseus</i>	<u>7</u> -8	27-30	<u>1</u> ² -2	28-30	0	9	13-15(<u>14</u>)	13	3-4	32	11	6	<u>3</u> -4	3, 6-7, 8-9	<u>2</u> -3	3	2	1
<i>Stethopristes eos</i>	6-7	27-28	1	27-28	0	9	<u>13</u> -14	13	4	<u>32</u> -33	11	5- <u>6</u>	3	6-7, 8-9, 10 (<u>6</u> -7, <u>9</u>)	<u>2</u> -3	3	1	1
<i>Zenion hololepis</i>	6-7	26-31	2	23-29	1	6	<u>16</u> -18	13	2-3	27	11	5	1- <u>2</u>	5-6, 7-8 (<u>6</u> , <u>8</u>)	1-2	<u>6</u> -7	2	1
<i>Zenion leptolepis</i> *	6-7	27-31	2	22-31	1	6	<u>16</u> -18	13	2-3	27	11	5	2	6-7, 8 (<u>6</u> , <u>8</u>)	1- <u>2</u>	?	2	1
<i>Capromimus abbreviatus</i>	7	25-27	2	26-28	1	6	<u>16</u> -17	13	3-4	32	11	7	2	5-6, 8	2	4	1	1
<i>Cyttomimus stelgis</i>	7-8	22-24	2	22-26	1	6	14- <u>15</u>	13	3	28-30(<u>29</u>)	11	6-7	1	7	-	3	1	1
<i>Macrurocyttus acanthopodus</i>	5- <u>7</u>	26-29	0	22-28	1	<u>2</u> - <u>3</u>	12-15(<u>13</u>)	12-16(<u>13</u>)	0	34- <u>36</u>	13	4	4- <u>5</u>	3-5, 6-9, 9-10	2- <u>3</u>	0	1	1
<i>Xenolepidichthys dalgleishi</i>	5- <u>6</u>	27-30	2	27-29	1	6	<u>14</u> -15	15	1	36-38(<u>37</u>)	10	8	4	2-6, 4-7 (<u>3</u> - <u>5</u> , <u>7</u>)	1- <u>2</u>	3-5(<u>3</u> - <u>4</u>)	2	1
<i>Grammicolepis brachiusculus</i>	6- <u>7</u>	32-34	2	33-35	1	6-7	<u>14</u> - <u>15</u>	15	1	43-46(<u>44</u>)	11	8- <u>10</u>	4	3-6, 6-7, 8 (<u>3</u> - <u>5</u> , <u>7</u>)	1-3 (<u>2</u>)	5	2	1
<i>Zeus faber</i>	9- <u>10</u>	22-24	<u>4</u> -5	20-24	1	6- <u>7</u>	12-15 (<u>13</u> - <u>14</u>)	13	1	30-32(<u>31</u>)	13-15(<u>14</u>)	4-5	5	4-5, 6-8, 8-10, 11-12 (<u>4</u> , <u>6</u> - <u>7</u> , <u>8</u> - <u>10</u> , <u>11</u>)	3-4	5-8	1	0
<i>Zeus capensis</i> *	9- <u>10</u>	22-24	4	19-21	1	6	13-14	13	1	30	14	5	5	4, 6-7, 8-10, 11	3-4	?	1	0
<i>Zenopsis conchifer</i>	8-10	24-27	3	24-26	0	6	<u>12</u> -13	13	1	34-36(<u>35</u>)	<u>14</u> -15	4-5	4- <u>5</u>	4-5, 6-8, 9-10, 11 (<u>4</u> - <u>5</u> , <u>7</u> - <u>8</u> , <u>10</u>)	2-4 (<u>3</u>)	8-12 (<u>9</u> - <u>10</u>)	1	0
<i>Zenopsis nebulosus</i>	8-9	25-27	3	24-26	0	6	11- <u>12</u>	13	1	34-36(<u>35</u>)	14- <u>15</u>	4	5	4-5, 7-8, 10	3	11-12	1	0
<i>Zenopsis oblongus</i> *	8-9	27-29	3	25-27	0	6	11-13(<u>12</u>)	13	1	36	14	5	5	3, 5-6, 8, 10	4	?	1	0

¹First anal-fin spine always fused to pterygiophore.

²First anal-fin spine sometimes fused to pterygiophore.

slightly if at all larger than surrounding scales. No specialized bucklers or scutes.

Mouth large, upper-jaw length more or less equaling orbit diameter and much longer than snout length. Ascending premaxillary process moderate, reaching from front border of orbit to behind front border and one-fifth into orbit.

Body moderately deep to deep, about 1.3–1.9 times in SL.

Extended pelagic prejuvenile stage to 100 mm or more SL, with weak ossification, expanded abdominal region, much connective tissue in thick skin, and large conical protuberances (hillocks) of transformed scales.

Internal: Total vertebrae 36–42; abdominal vertebrae 13–15; caudal peduncle vertebrae 6 or 7, rarely 5. Seven to 9, rarely 6, vacant interneural spaces between spaces 2 and 12; vacancies in 2–4 groups. Infraorbitals deep (with large pores, bridges, or open lacunae between upper and lower edges), 3 or 4 excluding deep lachrymal. Epurals 2. Supraneural 1.

PSEUDOCYTTINAE.—Contained genus: *Pseudocyttus*. Pelvic fin I,5; dorsal-fin spines usually 5, sometimes 6; first dorsal-fin spine long, about as long as or longer than second spine; no locking mechanism between dorsal-fin spines; lower border of dentary relatively smooth, without prominent serrations; no serrations along posterior border of supracleithrum; hypurals 1–4 fused and fused to centrum; total vertebrae 42; opercles with delicate and relatively smooth scales, without strong spiny ridges.

OREOSOMATINAE.—Contained genera: *Oreosoma*, *Neocyttus*, and *Alloctytus*. Pelvic fin usually I,6 but sometimes I,5 or I,7 (see family account, above); dorsal-fin spines usually 6 or 7, sometimes 5 or 8; first dorsal-fin spine short, much shorter than second spine; locking mechanism between first three dorsal-fin spines; lower border of dentary with multiple serrations behind symphysis; serrations along posterior border of supracleithrum; hypurals 1 and 2 fused and fused to centrum, but hypurals 3 and 4, although fused, usually not fused to centrum; total vertebrae 36–41, usually 37–40; opercles armed with spiny scales along prominent radiating ridges.

PARAZENINAE (Figures 24–38).—Contained genera: *Parazen*, *Cyttopsis*, *Stethopristes*.

External: Dorsal-fin spines 6–8; dorsal-fin rays 27–36 (usually 27–32); locking mechanism weakly developed between first two dorsal-fin spines in *Parazen* but absent in *Cyttopsis* and *Stethopristes*. One anal-fin spine, this sometimes fused to pterygiophore in *Cyttopsis*; anal-fin rays 27–33 (first anal-fin ray in *Cyttopsis* (second sequential element of anal fin) loses its segmentation at about 100 mm SL and becomes more ossified and spine-like in large specimens, and anal fin could be considered to have two spines); no locking mechanism between anal-fin spine and second element when latter becomes spine-like. Pelvic fin with no spine, rays 7 (*Parazen*) or 9 (*Cyttopsis*, *Stethopristes*; *Cyttopsis* sometimes with 10 rays fide Heemstra, 1980); positioned either under or slightly in front of pectoral-fin base (*Cyttopsis*, *Stethopristes*) or about midway between

anus and pectoral-fin base (*Parazen*). Pectoral-fin rays 13–16. Principal caudal-fin rays 13; procurrent rays either 3 or 4 (*Cyttopsis*, *Stethopristes*) or 7 or 8 (*Parazen*) above and below.

Scales on most of body small (1%–2% SL), more or less rounded, deciduous, either weakly spinoid (*Parazen*) or cycloid (*Cyttopsis*, *Stethopristes*); low sheath of scales along soft dorsal- and anal-fin bases in *Parazen*, but scales absent along these bases in *Cyttopsis* and *Stethopristes* (last two genera with a firm, bony discontinuous ridge produced just below skin along each side of soft dorsal- and anal-fin bases by strong lateral expansions at distal ends of pterygiophores, but this ridge scaleless and not spiny). Large buckler scales (4%–7% SL) present in *Cyttopsis* and *Stethopristes* (absent in *Parazen*) along ventral midline of isthmus in front of bases of pelvic fins and from pelvic fins to anus, many bucklers with a posteriorly directed spiny process (sometimes also accessory smaller spiny processes); bucklers continuous in a median keeled series in *Stethopristes* but partially separated in *Cyttopsis*; about 7–12 bucklers in median series and sometimes fewer, less regularly arranged additional smaller bucklers.

Mouth large, upper-jaw length slightly to much greater than orbit diameter and snout length. Ascending premaxillary process moderate, reaching behind front border of orbit one-fifth (*Cyttopsis*, *Stethopristes*) to one-third (*Parazen*) into orbit.

Body moderately deep to slender, about 1.3–2.5 (*Cyttopsis*, *Stethopristes*) to 2.2–3.0 (*Parazen*) times in SL.

No extended prejuvenile stage in early life history of taxa.

Internal: Total vertebrae 32–34; abdominal vertebrae 11 or 12; caudal peduncle vertebrae 5–7 (usually 6 or 7). Vacant interneural spaces 1 (*Parazen*) or 3 or 4 (usually 3, *Cyttopsis*, *Stethopristes*), located between spaces 3 and 10 (usually 6 to 9); when 3 or 4 spaces vacant, vacancies usually in 2 groups, sometimes 3. Infraorbitals slender, 3 or 4 excluding deep lachrymal. Epurals 2 (*Parazen*, *Cyttopsis*) or 1 (*Stethopristes*). Supraneural 1 (*Cyttopsis*, *Stethopristes*) or 0 (*Parazen*).

PARAZENINAE.—Contained genus: *Parazen*. Dorsal-fin spines 8; pelvic-fin rays 7; pelvic fin positioned about midway between pectoral-fin base and anus; pectoral-fin rays usually 16; procurrent caudal-fin rays 7 or 8; scales spinoid; no buckler scales; low sheath of scales along soft dorsal- and anal-fin bases; total vertebrae 34; abdominal vertebrae 12; caudal peduncle vertebrae 7; neural spines all oriented posterodorsally; no supraneural; 1 vacant interneural space; ventral shaft of first dorsal-fin pterygiophore in middle of first interneural space, not contacting first vertebra; distal ends of dorsal- and anal-fin pterygiophores not much expanded (but prongs present at upper end of thin lateral flanges along pterygiophore); no lateral flange on lowermost pectoral-fin radial; medial processes of basipterygia broadly overlapping near pelvic-fin bases; 1 anal-fin pterygiophore anterior to first haemal spine; 6 anal-fin pterygiophores anterior to third haemal spine; ossified epineurals on most abdominal vertebrae; beryciform foramen represented by a groove along ceratohyal; hypurapophysis present. For additional differential con-

ditions between two subfamilies, see characters 15, 21, 29, 39, 53, 57, and 71 in text, Appendix, Table 1, and Figures 4, 5.

CYTTOPSINAE.—Contained genera: *Cyttopsis*, *Stethopristes*. Dorsal-fin spines usually 6 (rarely 7) or 7 (rarely 8); pelvic-fin rays 9; pelvic-fin positioned under or slightly in front of pectoral-fin base; pectoral-fin rays usually 13 or 14 (rarely 15); procurent caudal-fin rays 3 or 4; scales cycloid; large buckler scales along ventral midline; no sheath of scales along soft dorsal- and anal-fin bases; total vertebrae usually 32; abdominal vertebrae 11; caudal peduncle vertebrae usually 6; some neural spines oriented anterodorsally or at least vertically; 1 supraneural; usually 3 vacant interneural spaces; ventral shaft of first dorsal-fin pterygiophore at front of first interneural space, contacting neural arch and spine of first vertebra; distal ends of dorsal- and anal-fin pterygiophores much expanded laterally; lateral flange on lowermost pectoral-fin radial; no overlapping medial processes of basipterygia, halves of pelvis not in close contact along midline near pelvic-fin bases; 2 anal-fin pterygiophores anterior to first haemal spine; 4 anal-fin pterygiophores anterior to third haemal spine; ossified epineurals absent, or present on a few middle abdominal vertebrae; beryciform foramen present; hypurapophysis absent. For additional differential conditions between subfamilies, see character numbers given above under Parazeninae.

ZENIONTIDAE (Figures 39–59).—Contained genera: *Zenion*, *Capromimus*, *Cyttomimus*.

External: Dorsal-fin spines 6–8; dorsal-fin rays 22–31; locking mechanism between first three dorsal-fin spines (*Zenion*) or between second and third spines (*Capromimus*, *Cyttomimus*). Anal-fin spines 2 (second spine very short and not externally visible in *Zenion*); anal-fin rays 22–31; locking mechanism between anal-fin spines. Pelvic fin I,6; positioned under pectoral-fin base (*Capromimus*, *Cyttomimus*) or slightly behind base (*Zenion*). Pectoral-fin rays 14–18 (usually 15 or 16). Principal caudal-fin rays 13; 2–4 procurent rays above and below.

Scales on most of body of moderate size (2%–4% SL), rounded to squarish, spinoid; no sheath of scales along soft dorsal- and anal-fin bases, but spiny processes present at angle of scales bent around lateral expansions of distal ends of dorsal- and anal-fin pterygiophores, forming a spiny ridge along each side of these fin bases. No specialized bucklers or scutes.

Mouth of moderate size to large, upper-jaw length greater than snout length but either less than orbit diameter (*Zenion*) or much greater than orbit diameter (*Capromimus*, *Cyttomimus*). Ascending premaxillary process moderate, reaching behind front border of orbit about one-fifth (*Zenion*) or about one-third (*Capromimus*, *Cyttomimus*) into orbit.

Body moderately deep to relatively slender, about 2.0–3.0 times in SL.

No extended prejuvenile stage in early life history of taxa.

Internal: Total vertebrae 27–32; abdominal vertebrae 11; caudal peduncle vertebrae 5–7. One or 2 vacant interneural

spaces between spaces 5 and 8; when 2 spaces vacant, vacancies usually separated by an occupied space. Infraorbitals deep (with serrate vertical strengthening flanges, *Zenion*) or slender (*Capromimus*, *Cyttomimus*), 3 or 4 (*Capromimus*, *Cyttomimus*) or 6 or 7 (*Zenion*) excluding deep lachrymal. Epurals 1 (*Capromimus*, *Cyttomimus*) or 2 (*Zenion*). Supraneural 1.

GRAMMICOLEPIDIDAE (Figures 60–72).—Contained genera: *Macrurocyttus*, *Xenolepidichthys*, *Grammicolepis*.

External: Dorsal-fin spines 5–7, usually 6 or 7; dorsal-fin rays 26–34; locking mechanism between second and third dorsal-fin spines. Anal-fin spines 2 (*Xenolepidichthys*, *Grammicolepis*) or absent (*Macrurocyttus*); anal-fin rays 22–35; locking mechanism between anal-fin spines only in *Xenolepidichthys*. Pelvic fin either I,6 or I,7 (usually I,6, *Xenolepidichthys*, *Grammicolepis*) or I,2 or I,3 (usually I,3, *Macrurocyttus*); positioned under or slightly in front of pectoral-fin base. Pectoral-fin rays 12–15, usually 13–15. Principal caudal-fin rays 15 (*Xenolepidichthys*, *Grammicolepis*) or 13 (*Macrurocyttus*, but highly variable, 12–16); procurent rays above and below 1 (*Xenolepidichthys*, *Grammicolepis*) or 0 (*Macrurocyttus*).

Scales absent (*Macrurocyttus*, or highly deciduous and unknown) or narrow and greatly elongate vertically (to more than 25% SL) (*Xenolepidichthys*, *Grammicolepis*), with thin lateral laminae curved posteriorly, relatively smooth edged (*Xenolepidichthys*) or with spinoid serrations (*Grammicolepis*); no sheath of scales along soft dorsal- and anal-fin bases, but spiny processes present (*Xenolepidichthys*, *Grammicolepis*) at angle of scales bent around lateral expansions of distal ends of dorsal- and anal-fin pterygiophores, forming a spiny ridge along each side of these fin bases. No specialized bucklers or scutes.

Mouth of moderate size, about equal to or slightly shorter than orbit diameter and much longer than snout (*Macrurocyttus*), or small, about one-half or less of orbit diameter and much shorter than snout (*Xenolepidichthys*, *Grammicolepis*). Ascending premaxillary process moderate, reaching from front border of orbit to behind front border about one-fifth into orbit.

Body moderately deep to deep, about 1.1–2.6 times in SL.

No extended prejuvenile stage in early life history of taxa (but *Macrurocyttus* bathypelagic and perhaps paedomorphic).

Internal: Total vertebrae 34–46; abdominal vertebrae 10–13; caudal peduncle vertebrae 4–10. Four or 5 vacant interneural spaces between spaces 2 and 10; vacancies in 1–3 (usually 2 or 3) groups. Infraorbitals absent (*Macrurocyttus*) or slender, 3–5 excluding moderate lachrymal (*Xenolepidichthys*, *Grammicolepis*). Epurals 1 or 2. Supraneural 1.

MACRUROCYTTINAE.—Contained genus: *Macrurocyttus*.

Scales absent or highly deciduous and unknown; mouth moderate in size, upper jaw much longer than snout, length about equal to orbit diameter; principal caudal-fin rays usually 13; no procurent caudal-fin rays; pelvic fin I, usually 3; no pelvic-fin-ray serrations; no anal-fin spines; branchiostegal rays usually 2 + 4 = 6; postmaxillary process present (short and broad); basisphenoid absent; total vertebrae usually 36; abdominal vertebrae 13; caudal peduncle vertebrae

4; all hypurals fused to centrum, hypural 5 not free; hypurapophysis absent; anterior end of parhypural simple, not in contact with centrum; epural 1; symplectic without ventral flange; medial processes of basipterygia broadly overlapping near pelvic-fin bases; parietal absent; infraorbitals absent; metapterygoid absent; ossified ribs absent; ossified epineurals absent; beryciform foramen represented by groove along ceratohyal. For additional differential conditions between two subfamilies, see characters 21, 37, 39, 58, 59, 69, and 99 in text, Appendix, Table 1, and Figures 4, 5.

GRAMMICOLEPIDINAE.—Contained genera: *Xenolepidichthys*, *Grammicolepis*. Scales greatly elongate vertically; mouth small, upper-jaw length less than snout length and orbit diameter; principal caudal-fin rays 15; 1 procurrent caudal-fin ray above and below; pelvic fin I, usually 6; serrations on crests of several pelvic-fin rays; 2 anal-fin spines (first spine greatly elongate in juveniles); branchiostegal rays $3 + 4 = 7$; postmaxillary process absent; basisphenoid a short shaft at front of roof of posterior myodome; total vertebrae usually 37 or 44; abdominal vertebrae 10 or 11; caudal peduncle vertebrae 8–10; hypurals 1 through 4 fused to centrum but hypural 5 free; hypurapophysis present; anterior end of parhypural with peg-and-socket-joint articulation with centrum; epurals 2; symplectic with ventral flange; no overlapping medial processes of basipterygia, halves of pelvis not in close contact along midline near pelvic-fin bases; parietal present; infraorbitals present; metapterygoid present; 1 to many ossified ribs present; many ossified epineurals present; beryciform foramen present. For additional differential conditions between subfamilies, see character numbers given above under Macrurocyttinae.

ZEIDAE (Figures 73–88).—Contained genera: *Zeus*, *Zenopsis*).

External: Dorsal-fin spines 8–10; dorsal-fin rays 22–29; locking mechanism between first three dorsal-fin spines. Anal-fin spines usually 3 (*Zenopsis*) or 4 (*Zeus*), rarely 5 (*Zeus*);

anal-fin rays 19–27; locking mechanism between first two anal-fin spines. Pelvic fin I, 6 or I, 7 (*Zeus*) or with no spine and 6 rays (*Zenopsis*, with first element in bilateral halves but unsegmented and thicker than other 5 rays); positioned slightly to distinctly (especially in *Zenopsis*) in front of pectoral-fin base. Pectoral-fin rays 11–15 (usually 12–14). Principal caudal-fin rays 13; 1 procurrent ray above and below.

Scales on most of body small (1%–2% SL), cycloid, and embedded (*Zeus*) or absent entirely except for small lateral-line scales (*Zenopsis*), but greatly enlarged buckler scales (up to 5%–11% SL, and many times larger than any normal scales on body) present along bases of soft dorsal and anal fins, dorsal series of bucklers extending anteriorly along much of base of spinous dorsal fin in *Zenopsis*; these bucklers with a prominent, posteriorly curved spiny process, sometimes bifurcate distally in some species (a smaller accessory spine present near base of main spine in *Zeus faber*); bucklers along dorsal-fin base about 4–14 and along anal-fin base about 4–11; other bucklers present along ventral midline of isthmus in front of bases of pelvic fins and from pelvic fins to anus, these series usually a combination of single median bucklers and strongly keeled (bent about 90°), paired bucklers from right and left sides that slightly overlap along midline and often bear spiny processes.

Mouth large, upper-jaw length much greater than orbit diameter and about equal to or slightly longer than snout length. Ascending premaxillary process moderate, reaching to about front of orbit.

Body moderately deep to deep, about 1.3–2.2 times in SL.

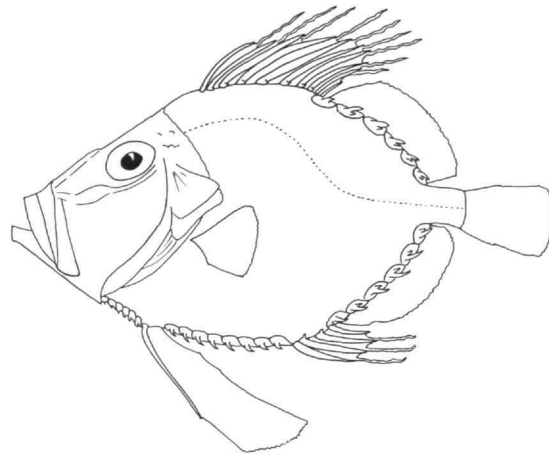
No extended prejuvenile stage in early life history of taxa.

Internal: Total vertebrae 30–36; abdominal vertebrae 13–15 (usually 14 or 15); caudal peduncle vertebrae 4 or 5. Four or 5 (usually 5) vacant interneural spaces between spaces 3 and 12; vacancies in 2–4 (usually 3 or 4) groups. Infraorbitals slender, 5–12 excluding moderate (*Zeus*) to slender (*Zenopsis*) lachrymal. Epural 1. No supraneural.

Key to the Families and Subfamilies of Zeiformes

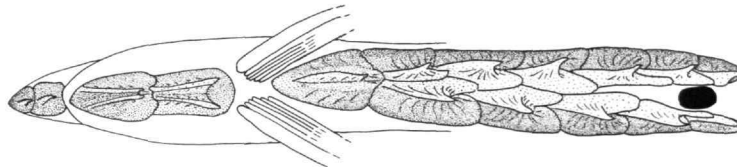
When two or more genera are included in a family or subfamily, keys are also provided to the genera, with the exception of the three genera of Oreosomatinae. Although the monophyly of the oreosomatins has substantial support, the phylogeny within the subfamily is only weakly supported, and the differences between *Oreosoma* and, especially, *Neocyttus* and *Alloctytus* are mostly either morphologically minor and internal or involve differences in scale patterns, allometrically variable proportions, and dorsal profile shapes not thoroughly studied herein. The reader is referred to Heemstra (1980) and Karrer (1986) for the best keys available to the genera of oreosomatids, and to Yearsley and Last (1998) for the species of *Neocyttus*.

- A. Large buckler scales with posteriorly directed, spiny (thorn-like) processes present along bases of dorsal (4–14 scales) and anal (4–11 scales) fins; bucklers present or absent along spinous dorsal-fin base; basal-plate length of larger bucklers ranging from four times in orbit diameter to slightly longer than orbit diameter; bucklers also along ventral midline from isthmus to anus ZEIDAE (B)



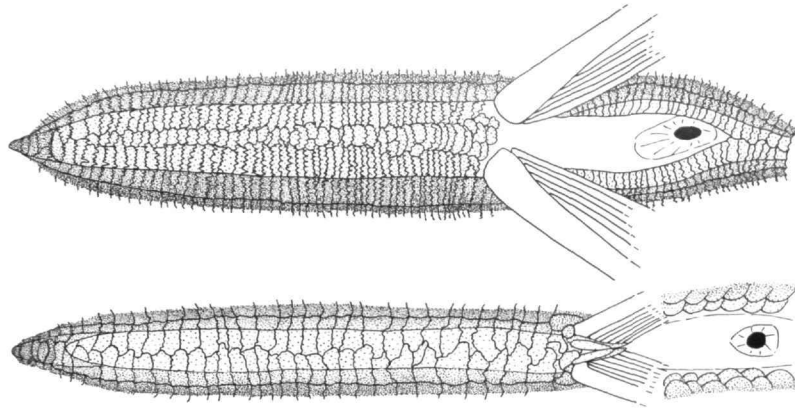
Zeus faber

- B. Large buckler scales along dorsal-fin base not extending forward beyond last dorsal-fin spine; anal-fin spines usually 4, rarely 5; anal-fin rays usually 19–24; dorsal-fin rays usually 22–24; first pelvic-fin element unbranched but stiff and spine-like, followed by 6 or 7 branched rays (total pelvic-fin elements 7 or 8); pectoral-fin rays usually 13 or 14, sometimes 12 or 15; scales on most of body small, cycloid, embedded. **Zeus**
- BB. Large buckler scales along dorsal-fin base extending forward under spinous dorsal fin to about bases of third or fourth spines; anal-fin spines 3; anal-fin rays usually 24–27; dorsal-fin rays usually 24–29; first pelvic-fin element unbranched but flexible and ray-like, followed by 5 branched rays (total pelvic-fin elements 6); pectoral-fin rays usually 12, sometimes 11 or 13; scales absent on most of body, except for those in lateral line **Zenopsis**

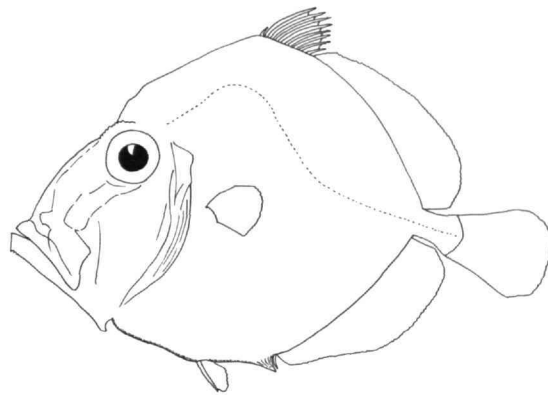


Zenopsis conchifer
ventral view of isthmus to anus

- AA. No large buckler scales present along bases of dorsal and anal fins; bucklers present or absent along ventral midline from isthmus to anus C
- C. Scales along either side of ventral surface of isthmus slightly enlarged as scutes, curved or bent almost 90° along middle of their width, forming a somewhat flattened surface along much of distance between ventral ends of cleithra to bases of pelvic-fin spines, many scutes from right and left sides of isthmus meeting and slightly overlapping along midline in a zipper-like alternation, with additional smaller spinoid scales often interspersed along area of midline overlap; single row of scutes on either side of a naked midline region between pelvic-fin bases and anus or scutes absent; no buckler scales along ventral midline **CYTTIDAE, *Cyttus***
- CC. No slightly enlarged scutes in a zipper-like arrangement along ventral surface of isthmus (but large buckler scales present or absent along ventral midline from isthmus to anus D
- D. Pelvic fin with no spine, rays 7 or 9 **PARAZENIDAE (E)**

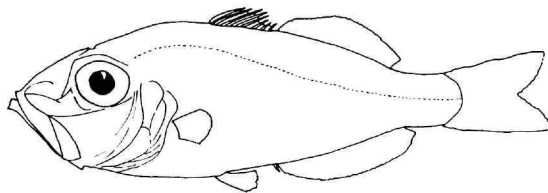


Cyttus traversi above *C. novaezelandiae*
ventral view of isthmus to anus



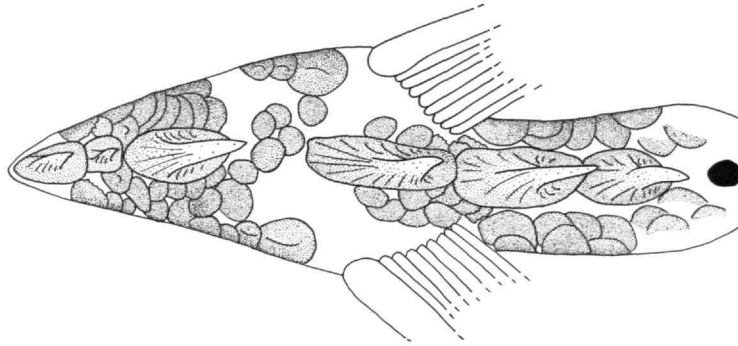
Cyttus traversi

- E. Dorsal-fin spines 8; pelvic-fin rays 7; pelvic-fin positioned about midway between pectoral-fin base and anus; pectoral-fin rays usually 16, rarely 15; procurrent caudal-fin rays 7 or 8; scales spinoid; no large buckler scales along ventral midline; low sheath of scales along soft dorsal- and anal-fin bases **PARAZENINAE, *Parazen***

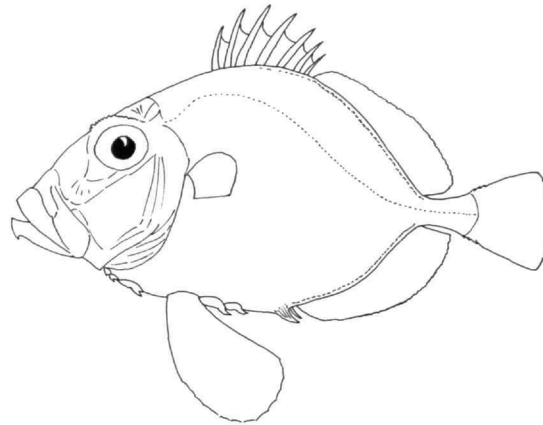


Parazen pacificus

- EE. Dorsal-fin spines usually 6 or 7, rarely 8; pelvic-fin rays 9; pelvic-fin positioned under or slightly in front of pectoral-fin base; pectoral-fin rays usually 13 or 14, rarely 15; procurrent caudal-fin rays 3 or 4; scales cycloid; large buckler scales along ventral midline; no sheath of scales along soft dorsal- and anal-fin bases **CYTTOPSINAE (F)**



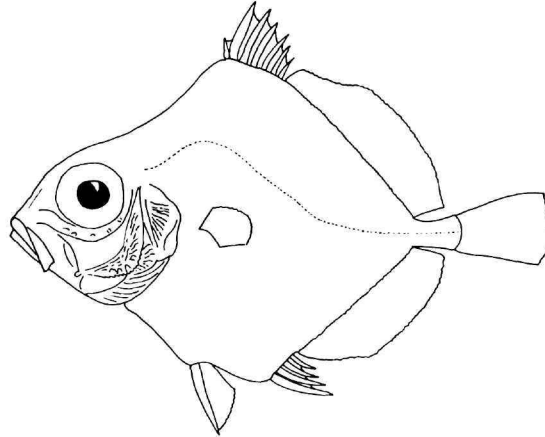
Cyttopsis roseus
ventral view of isthmus to anus



Cyttopsis roseus

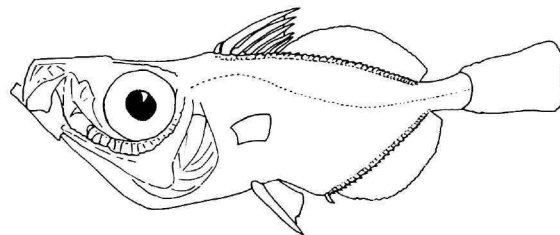
- F. Dorsal-fin spines usually 7, sometimes 8; pectoral-fin rays usually 14, sometimes 13 or 15; large buckler scales along ventral midline of isthmus forming a partially separated spiny keel (a few bucklers not overlapping, especially first, on isthmus, and second, between pelvic-fin bases); no honeycomb pattern on bones on top of head, opercles, and lachrymal-infraorbitals, only long ridges. *Cyttopsis*
- FF. Dorsal-fin spines usually 6, sometimes 7; pectoral-fin rays usually 13, sometimes 14; large buckler scales along ventral midline of isthmus forming a continuous, sharp-edged median spiny keel (nearly all buckler scales strongly overlapping); honeycomb pattern on bones on top of head visible externally. *Stethopristes*
- DD. Pelvic fin with a spine, rays usually 6 or fewer (rarely 7). G
- G. Pectoral-fin rays 18–21, usually 19–21; low sheath of scales along soft dorsal- and anal-fin bases, scales only slightly if at all larger than surrounding scales and of similar morphology; extended prejuvenile stage to 100 mm or more SL, with weak ossification, expanded abdomen, thick skin, and large conical protuberances of transformed scales **OREOSOMATIDAE (H)**
- H. Pelvic fin 1,5; dorsal-fin spines usually 5, sometimes 6; first dorsal-fin spine long, about as long as or longer than second spine; no locking mechanism between dorsal-fin spines **PSEUDOCYTTINAE, *Pseudocyttus***

- HH. Pelvic fin usually 1,6 but sometimes 1,5 or 1,7; dorsal-fin spines usually 6 or 7, sometimes 5 or 8; first dorsal-fin spine short, much shorter than second spine; locking mechanism between first three dorsal-fin spines **OREOSOMATINAE, *Oreosoma, Neocyttus, Allocyttus***



Neocyttus rhomboidalis

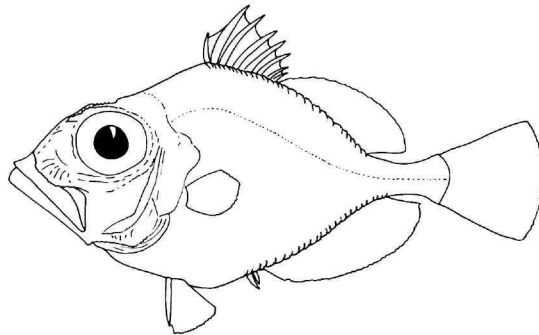
- GG. Pectoral-fin rays 12–18, usually 13–16; no sheath of scales along soft dorsal- and anal-fin bases, but, except one species in which scales are absent, spiny processes present at angle of scales bent around lateral expansions of distal ends of dorsal- and anal-fin pterygiophores, these processes forming spiny ridge along each side of fin bases; no extended prejuvenile stage I
- I. Scales on most of body of moderate size (2%–4% SL), rounded to squarish, spinoid; procurent caudal-fin rays 2–4. **ZENIONTIDAE (J)**
- J. Dorsal-fin spines usually 6, sometimes 7; locking mechanism between first, second, and third dorsal-fin spines; second anal-fin spine below surface of skin and not visible externally; pelvic fin positioned slightly behind pectoral-fin base; upper-jaw length less than orbit diameter; infraorbital bones very deep, covering most of cheek below orbit, with serrate vertical strengthening flanges; no anteromedial processes on medial (lower) surfaces of pelvic-fin rays ***Zenion***



Zenion hololepis

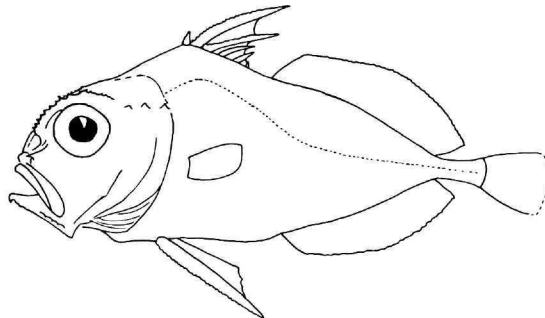
- JJ. Dorsal-fin spines usually 7 or 8; locking mechanism between only second and third dorsal-fin spines; second anal-fin spine short, about equal to length of first spine or slightly less than one-half its length, but visible externally; pelvic fin positioned under pectoral-fin base; upper-jaw length greater than orbit diameter; infraorbital bones slender and tubular, not covering most of cheek below or-

- bit; anteromedial processes present as broad flanges along basal regions of pelvic-fin rays K
- K. Dorsal-fin spines usually 7; dorsal-fin rays usually 25–27; anal-fin rays 26–28; pectoral-fin rays usually 16, sometimes 17; no prominent posterior flange at upper end of postcleithrum; no ectopterygoid teeth; serrations present on pelvic-fin-ray flanges **Capromimus**
- KK. Dorsal-fin spines usually 8, sometimes 7; dorsal-fin rays usually 22–24; anal-fin rays 22–26; pectoral-fin rays usually 15, sometimes 14; prominent posterior flange at upper end of postcleithrum, flared posterolaterally just behind posterior border of opercular flap; ectopterygoid teeth present; no serrations on pelvic-fin-ray flanges **Cyttomimus**



Cyttomimus stelgis

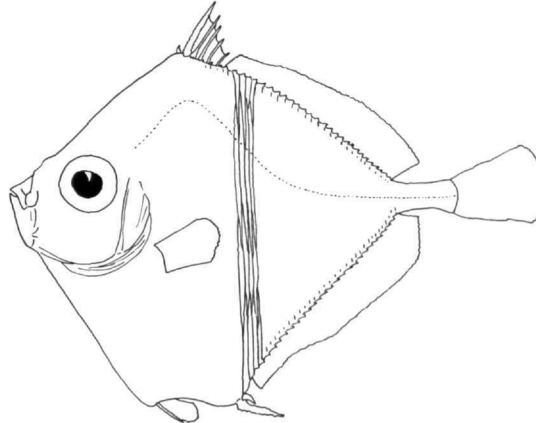
- II. Scales narrow and greatly elongate vertically (to more than 25% SL) on most of body or absent; procurrent caudal-fin rays 1 or 0 **GRAMMICOLEPIDIDAE (L)**
- L. Scales absent (or highly deciduous and unknown); mouth moderate in size, upper jaw much longer than snout and length about equal to orbit diameter; principal caudal-fin rays usually 13; procurrent caudal-fin rays 0; pelvic fin with spine and usually 3 rays; anal-fin spines 0; branchiostegal rays usually 2 + 4 = 6 **MACRUROCYTTINAE, *Macrurocyttus***



Macrurocyttus acanthopodus

- LL. Scales greatly elongate vertically; mouth small, upper-jaw length less than snout length and orbit diameter; principal caudal-fin rays 15; 1 procurrent caudal-fin ray above and below; pelvic fin with spine and usually 6 rays; anal-fin spines 2; branchiostegal rays 3 + 4 = 7 **GRAMMICOLEPIDINAE (M)**

- M. Dorsal-fin spines usually 6, sometimes 5; dorsal-fin rays usually 27–30; anal-fin rays usually 27–29; pectoral-fin rays usually 14, sometimes 15; locking mechanism between anal-fin spines; second anal-fin spine short, less than one-half length of first spine in adults (first spine greatly elongate in juveniles); elongate vertical scales with relatively smooth edges; no prominent horizontal crests on elongate scales and protruding laterally from body at any size *Xenolepidichthys*



Xenolepidichthys dalgleishi

- MM. Dorsal-fin spines usually 7, sometimes 6; dorsal-fin rays 32–34; anal-fin rays usually 33–35; pectoral-fin rays usually 15, sometimes 14; no locking mechanism between anal-fin spines; second anal-fin spine long, more than one-half length of first spine in adults (first spine greatly elongate in juveniles); elongate vertical scales with serrations; in juveniles and young adults up to about 10 horizontal scale crests protrude prominently from lateral surface of body, crests formed from lateral projections along middle regions of 2 to 5 adjacent scales, diminishing in size in large adults (faint remnants of these crests still present as thickened, low emarginations in a 285 mm SL specimen).
 *Grammicolepis*

Conclusion

The present study elucidates the phylogeny of the zeiform fishes and leads to a much revised systematic arrangement of the genera into newly recognized monophyletic families and subfamilies. However, this is but a first effort at understanding zeiform phylogeny, and refinements can be expected when the

several species not included herein are taken into consideration and, especially, when data sets based on molecular genetics, soft anatomy (e.g., muscles and nerves), and other non-osteological features are used. We hope that the present study, based mostly on bony structures, will be an encouragement to such further analyses.

Appendix: Character-State Transformations for the Unordered Reduced Data Set Consensus Tree

(Letters correspond to branches in Figure 4; numbers correspond to the characters and their states used herein. The meristic characters not included in the analysis (93–103) resulting in Figure 4 were optimized onto the tree and are shown in Figure 5.)

- A: 2-2, 6-1, 13-1, 16-1, 20-1, 27-1, 43-1, 53-4, 54-1, 59-0, 63-0, 65-0, 70-1, 71-0, 72-1, 75-0, 87-1
- B: 5-1, 10-2, 13-1, 21-0, 22-2, 25-2, 46-0, 48-3, 54-1, 59-0, 64-1, 65-0, 69-0, 70-3, 71-0, 76-0, 80-4, 82-1, 84-1, 85-2, 90-1
- C: 10-2, 25-1, 31-1, 41-1, 43-3, 46-0, 48-1, 63-0, 64-2, 70-3, 72-6, 83-2, 84-2, 88-4
- D: 3-0, 13-1, 25-1, 35-0, 38-1, 59-1, 63-0, 72-3, 75-0, 77-1
- E: 3-0, 4-1, 6-1, 10-0, 27-1, 33-3, 36-2, 38-1, 59-1, 63-0, 69-2, 71-2, 72-2, 75-0, 80-1, 81-1
- F: 3-0, 8-1, 25-2, 33-1, 35-0, 63-0, 64-2, 70-0, 71-0, 72-0, 75-0, 81-1
- G: 22-2, 77-1
- H: 6-1, 10-0, 17-0, 20-1, 38-1, 60-1, 61-0
- I: 3-0, 4-1, 11-1, 15-3, 21-3, 22-2, 33-3, 34-1, 37-1, 38-1, 40-1, 47-4, 60-1, 64-0, 69-2, 70-4, 71-2, 72-5, 77-1, 80-2, 84-1
- J: 4-1, 9-2, 10-0, 12-1, 16-1, 27-1, 36-2, 37-1, 38-1, 40-1, 44-1, 60-1, 64-2, 69-2, 70-5, 71-3, 72-7, 77-1, 80-1, 81-1, 84-1
- K: 1-1, 2-2, 4-1, 6-1, 9-0, 11-2, 12-1, 13-1, 16-1, 25-1, 27-1, 33-2, 34-1, 37-1, 39-0, 40-1, 47-3, 49-0, 50-1, 51-2, 55-1, 59-1, 60-1, 62-1, 64-0, 69-3, 70-1, 72-0, 75-0, 80-3, 85-3, 86-2
- L: 3-0, 10-0, 16-1, 18-1, 19-1, 21-1, 23-1, 24-1, 25-2, 26-0, 31-1, 35-0, 37-1, 40-1, 41-1, 43-1, 44-1, 49-0, 50-1, 51-1, 52-1, 53-2, 54-1, 55-1, 60-1, 62-1, 64-1, 73-1 (monophyly of Zeiformes)
- M: 9-3, 15-2, 22-2, 30-1, 45-1, 46-0, 47-3, 48-1, 74-1, 83-1, 89-1 (monophyly of *Cyttus*, Cyttidae, Cytoidei)
- N: 22-1, 67-1, 87-1 (autapomorphies of *Cyttus novaezelandiae*)
- O: 77-1 (monophyly of *Cyttus australis* + *C. traversi*)
- P: 36-1, 91-1 (autapomorphies of *Cyttus australis*)
- Q: 50-0, 67-2, 72-2 (autapomorphies of *Cyttus traversi*)
- R: 28-2, 29-1, 47-1, 66-1 (monophyly of Zeioidei)
- S: 10-1, 28-1, 59-1, 92-1 (monophyly of Oreosomatidae)
- T: 3-1 (autapomorphy of *Pseudocyttus maculatus*)
- U: 22-2, 36-1, 53-1, 57-3, 77-1 (monophyly of Oreosomatinae)
- V: 3-1, 28-0, 29-0, 36-0, 48-1, 65-0, 71-0 (autapomorphies of *Oreosoma atlanticum*)
- W: (no autapomorphies for *Neocyttus rhomboidalis*)
- X: 33-1, 58-2, 72-2 (monophyly of *Allocoyttus verrucosus* + *A. niger*)
- Y: (no autapomorphies for *Allocoyttus verrucosus*)
- Z: 28-2, 29-2, 53-2 (autapomorphies of *Allocoyttus niger*)
- A': 46-0, 72-3, 85-2 (monophyly of unnamed clade encompassing taxa *Parazen* through *Zenopsis* in Figure 4)
- B': 45-2, 75-0, 82-1, 83-2 (monophyly of Parazenidae)
- C': 15-1, 21-2, 29-2, 33-1, 39-0, 44-0, 50-0, 53-1, 57-1, 61-0, 64-0, 69-2, 71-2, 81-0, 85-0 (autapomorphies of *Parazen pacificus*)
- D': 48-3, 72-1, 74-1, 87-1, 88-1, 90-1 (monophyly of Cyttopsiinae)
- E': 22-1, 28-1, 48-2, 67-1 (autapomorphies of *Cyttopsis roseus*)
- F': 5-1, 37-0, 51-2, 70-1 (autapomorphies of *Stethopristes eos*)
- G': 51-2, 57-3, 76-0, 90-2 (monophyly of unnamed clade encompassing taxa *Zenion* through *Zenopsis* in Figure 4)
- H': 14-1, 22-2, 33-2, 37-0, 68-1, 77-1, 85-0 (monophyly of Zeniontidae)
- I': 9-2, 10-2, 20-1, 21-2, 38-1, 42-1, 44-0, 51-1, 81-1 (autapomorphies of *Zenion hololepis*)
- J': 15-1, 47-3, 57-2, 71-2, 72-4, 83-2 (monophyly of *Capromimus* + *Cyttomimus*)
- K': 47-2, 84-2 (autapomorphies of *Capromimus abbreviatus*)
- L': 14-0, 17-0, 50-0, 68-0, 76-1 (autapomorphies of *Cyttomimus stelgis*)
- M': 2-2, 8-1, 58-2, 87-3 (monophyly of unnamed clade encompassing taxa *Macrurocoyttus* through *Zenopsis* in Figure 4)
- N': 3-1, 28-0, 29-0, 32-1, 35-1, 42-1, 46-1, 57-2 (monophyly of Grammicolepididae)
- O': 1-1, 9-0, 19-2, 33-1, 37-0, 39-0, 47-3, 48-3, 53-5, 69-2, 72-2, 85-0 (autapomorphies of *Macrurocoyttus acanthopodus*)
- P': 2-1, 12-1, 13-1, 20-1, 21-0, 30-1, 50-0, 51-1, 52-2, 58-1, 59-1, 84-1, 87-2 (monophyly of Grammicolepidinae)
- Q': 46-0, 65-0, 68-1 (autapomorphies of *Xenolepidichthys dalgleishi*)
- R': 9-2, 22-2, 47-5, 66-0 (autapomorphies of *Grammicolepis brachiusculus*)
- S': 6-1, 7-1, 9-5, 11-1, 14-2, 36-2, 43-2, 47-0, 48-1, 56-1, 59-3, 64-0, 78-1, 79-1, 80-1, 83-1, 86-1, 88-3, 90-1 (monophyly of Zeidae)
- T': 2-1, 36-1, 58-3, 87-1, 88-2 (autapomorphies of *Zeus faber*)
- U': 8-2, 39-0, 82-1 (monophyly of *Zenopsis conchifer* + *Z. nebulosus*)
- V': 9-4, 48-0, 91-2 (autapomorphies of *Zenopsis conchifer*)
- W': 72-4 (autapomorphy of *Zenopsis nebulosus*)

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Figures

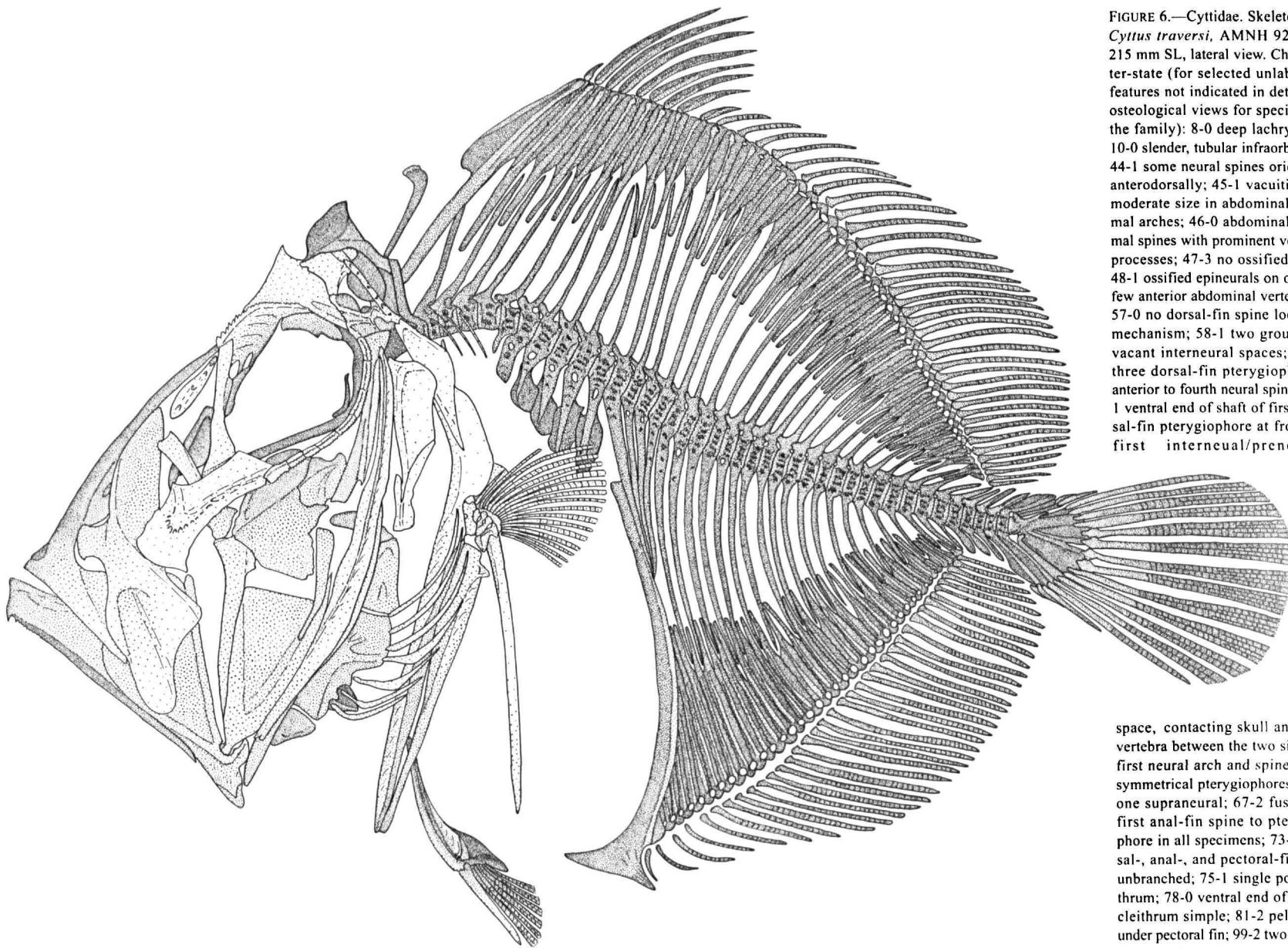


FIGURE 6.—Cyttidae. Skeleton of *Cyttus traversi*, AMNH 92052, 215 mm SL, lateral view. Character-state (for selected unlabeled features not indicated in detailed osteological views for species of the family): 8-0 deep lachrymal; 10-0 slender, tubular infraorbitals; 44-1 some neural spines oriented anterodorsally; 45-1 vacuities of moderate size in abdominal haemal arches; 46-0 abdominal haemal spines with prominent ventral processes; 47-3 no ossified ribs; 48-1 ossified epineurals on only a few anterior abdominal vertebrae; 57-0 no dorsal-fin spine locking mechanism; 58-1 two groups of vacant interneural spaces; 59-2 three dorsal-fin pterygiophores anterior to fourth neural spine; 61-1 ventral end of shaft of first dorsal-fin pterygiophore at front of first interneural/preneural

space, contacting skull and first vertebra between the two sides of first neural arch and spine; 63-1 symmetrical pterygiophores; 64-1 one supraneural; 67-2 fusion of first anal-fin spine to pterygiophore in all specimens; 73-1 dorsal-, anal-, and pectoral-fin rays unbranched; 75-1 single postcleithrum; 78-0 ventral end of supraclithrum simple; 81-2 pelvic fin under pectoral fin; 99-2 two vacant interneural spaces.

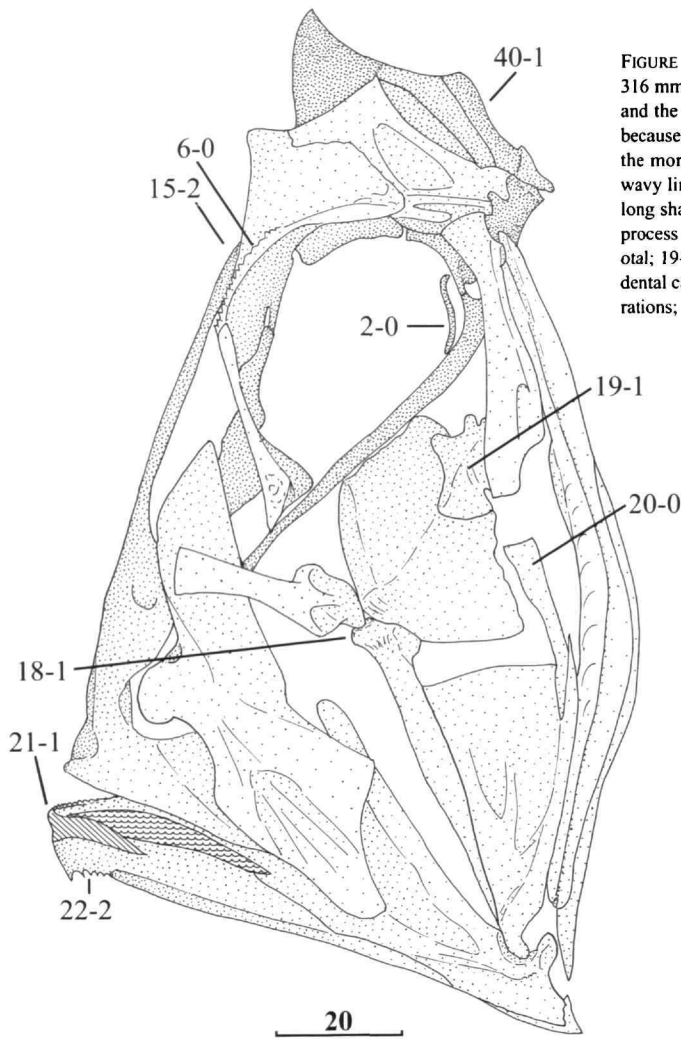
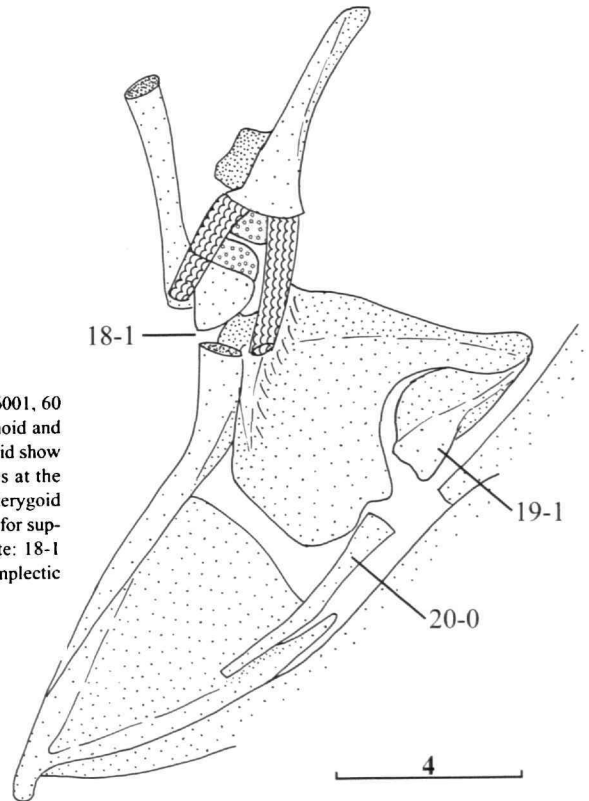


FIGURE 7.—Cyttidae. Skull and first vertebra of *Cyttus traversi*, AMNH 92029, 316 mm SL, lateral view. The lachrymal, infraorbitals, and nasal are removed, and the articulations between some of the otic-occipital bones are not shown because they are unclear in this dry skeleton. On the dentary, parallel lines show the more anterior and shorter of the two dentary cartilages, overlapping the wavy lines of the more posterior cartilage. Character-state: 2-0 basisphenoid a long shaft; 6-0 supraocular serrations on frontal; 15-2 ascending premaxillary process reaching back about one-half into orbit; 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-0 no symplectic ventral flange; 21-1 two dental cartilages of moderate length, the first shorter; 22-2 multiple dentary serrations; 40-1 first neural arch and spine closely applied to skull.

FIGURE 8.—Cyttidae. Suspensorium of *Cyttus australis*, AMS I.32386001, 60 mm SL, lateral view. Wavy lines between the base of the lateral ethmoid and the base of the palatine and the anterodorsal region of the mesopterygoid show ligaments; small circles in mechanical stippling show the cartilages at the bases of the palatine and lateral ethmoid. The dorsal end of the ectopterygoid and the anterodorsal region of the mesopterygoid are especially sturdy for support of the joint with the ventral end of the palatine. Character-state: 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-0 no symplectic ventral flange.



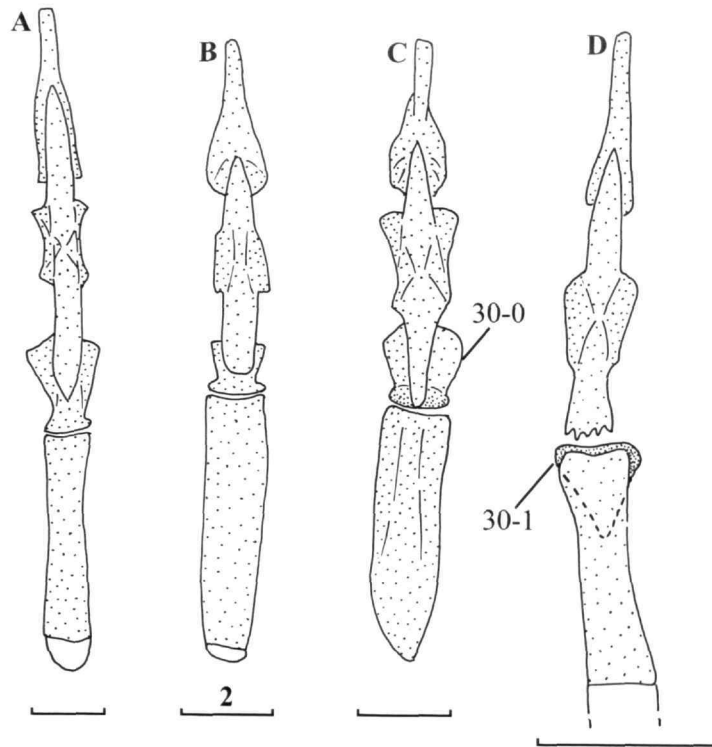


FIGURE 9.—Cyttidae and other families. Basihyal and the three basibranchials (anterior ends downward), dorsal view: A, *Zeus faber* (Zeidae), USNM 320014, 89 mm SL; B, *Cyttopsis roseus* (Parazenidae), AMNH 29460, 75 mm SL; C, *Stethopristes eos* (Parazenidae), USNM 226570, 91 mm SL; D, *Cyttus australis* (Cyttidae), AMS I.32386001, 60 mm SL. From bottom to top, the four elements in the series are the basihyal and the first, second, and third basibranchials. Character-state: 30-0 first basibranchial not depressed below surface of basihyal (A–C); 30-1 first basibranchial depressed below surface of basihyal. (All scale bars=2 mm.)

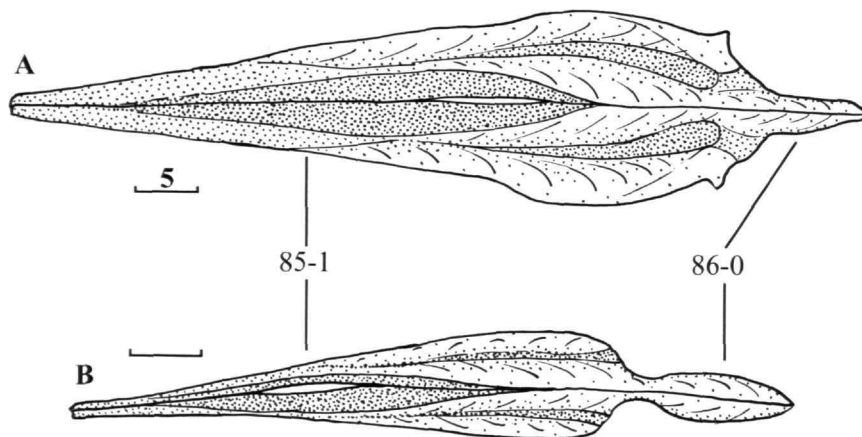


FIGURE 10.—Cyttidae. Pelvis, dorsal view (anterior to left): A, *Cyttus traversi*, AMNH 99777, 455 mm SL; B, *Cyttus australis*, AMNH 91908, 302 mm SL. Character-state: 85-1 basiptyrgia in contact in midline but not overlapped; 86-0 short posterior process of pelvis. (Scale bars=5 mm.)

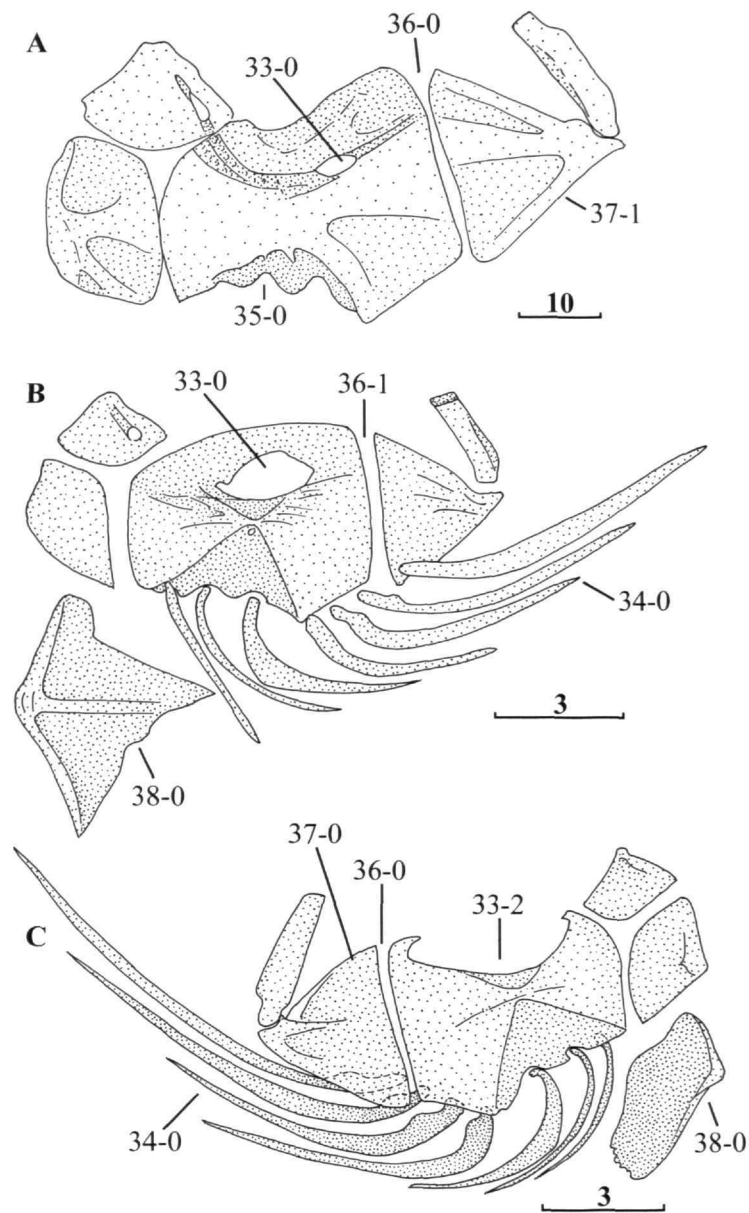


FIGURE 11.—Cyttidae and Zeniontidae. Hyoid arch, lateral (A, B) and medial (C) views: A, *Cyttus traversi* (Cyttidae), AMNH 92029, 316 mm SL; B, *Cyttus australis*, AMS I.32386001, 60 mm SL; C, *Capromimus abbreviatus* (Zeniontidae), AMS I.23650001, 61 mm SL. Character-state: 33-0 beryciform foramen present; 33-2 beryciform foramen represented by deep concavity on dorsal surface of ceratohyal; 34-0 branchiostegals spread over/along both epihyal and ceratohyal (B, C; would apply to A if branchiostegals were shown); 35-0 ceratohyal notches present (A–C); 36-0 ceratohyal-epihyal articulation through cartilage only; 36-1 ceratohyal-epihyal articulation either through cartilage (this specimen) or becoming interdigitated in larger specimens; 37-0 epihyal about same depth as rear of ceratohyal; 37-1 epihyal less deep than rear of ceratohyal (A, B); 38-0 urohyal no longer than ceratohyal (B, C; would apply to A if urohyal were shown).

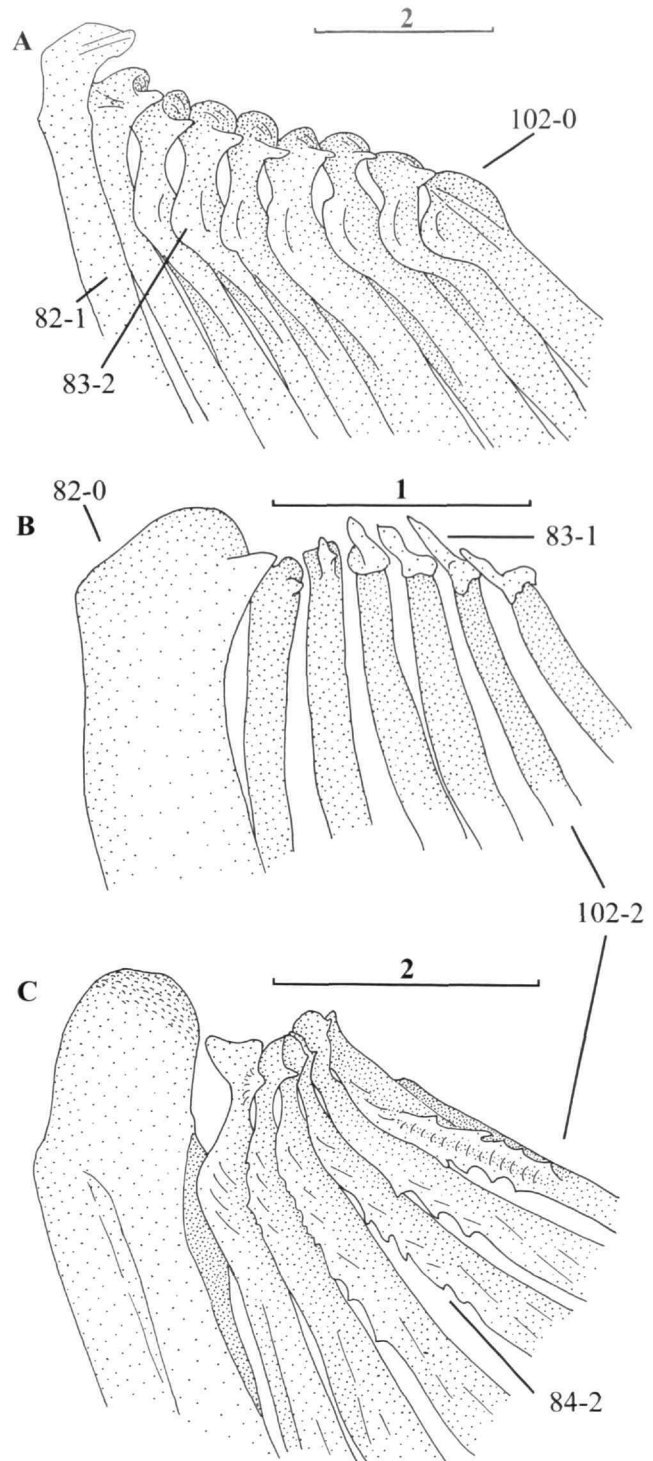


FIGURE 12.—Cyttidae and other families. Basal region of the right pelvic fin, ventral view: A, *Stethopristes eos* (Parazenidae), USNM 226570, 91 mm SL; B, *Cyttus australis* (Cyttidae), AMS I.32386001, 60 mm SL; C, *Capromimus abbreviatus* (Zeniontidae), AMS I.23650001, 61 mm SL. Character-state: 82-0 pelvic-fin spine present (B, C); 82-1 no pelvic-fin spine; 83-1 anterolateral processes as prongs from bases of rays; 83-2 anterolateral processes as broad flanges along basal region of rays (A, C); 84-2 serrations on broad flanges (C); 102-0 total of nine pelvic-fin elements; 102-2 total of seven pelvic-fin elements.

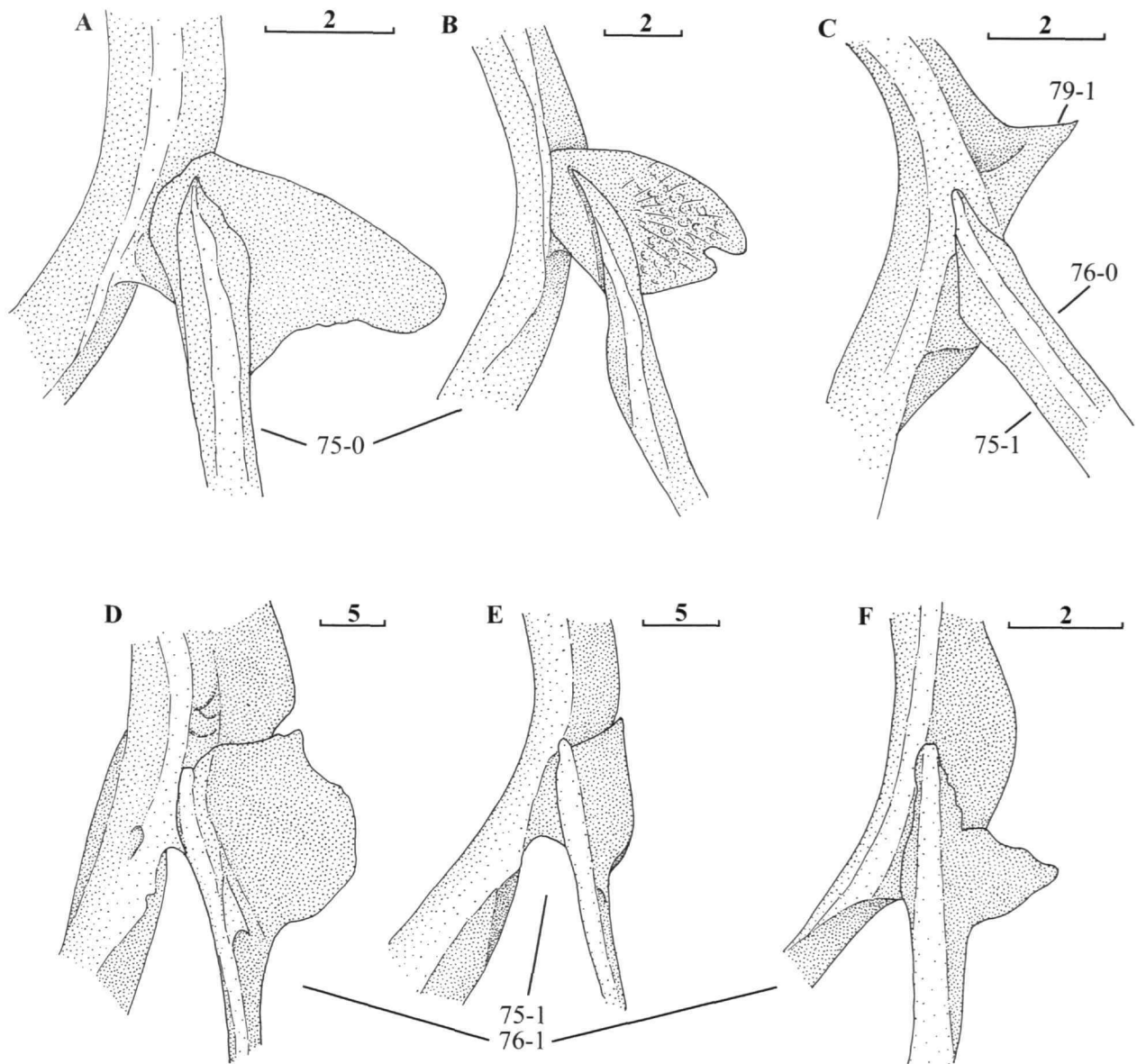


FIGURE 13.—Cyttidae and other families. Right postcleithrum and adjacent region of the cleithrum, medial view: A, *Cyttopsis roseus* (Parazenidae), USNM 187873, 72 mm SL; B, *Stethopristes eos* (Parazenidae), USNM 226570, 91 mm SL; C, *Zenopsis conchifer* (Zeidae), FMNH 67090, 58 mm SL; D, *Cyttus traversi* (Cyttidae), AMNH 92029, 316 mm SL; E, *Cyttus australis*, AMNH 91932, 250 mm SL; F, *Cyttomimus stelgis* (Zeniontidae), USNM 306156, 76 mm SL. Character-state: 75-0 postcleithrum in two pieces; 75-1 single postcleithrum (C-F); 76-0 no flange on single postcleithrum (C); 76-1 flange on single postcleithrum (D-F); 79-1 cleithral process present (C).

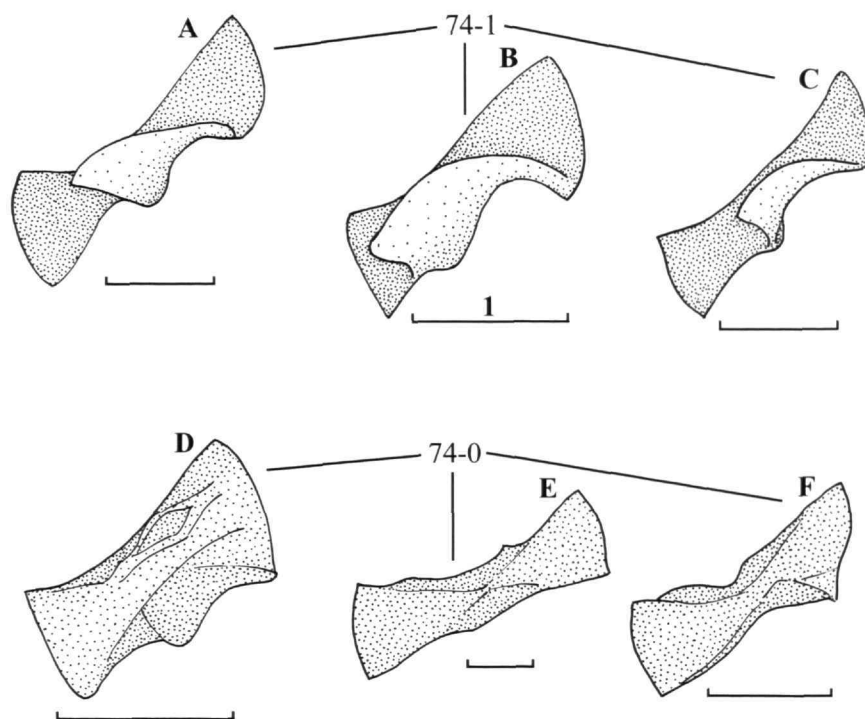


FIGURE 14.—Cyttidae and other families. Lowermost pectoral-fin radial, lateral view: A, *Stethopristes eos* (Parazenidae), USNM 226570, 91 mm SL; B, *Cyttus australis* (Cyttidae), AMS I.32386001, 60 mm SL; C, *Cyttopsis roseus* (Parazenidae), AMNH 29460, 74 mm SL; D, *Zenopsis conchifer* (Zeidae), CAS 47401, 54 mm SL; E, *Zeus faber* (Zeidae), USNM 320014, 89 mm SL; F, *Capromimus abbreviatus* (Zeniontidae), AMS 1.23650001, 61 mm SL. Character-state: 74-0 no lateral flange; 74-1 lateral flange present. (All scale bars=1 mm.)

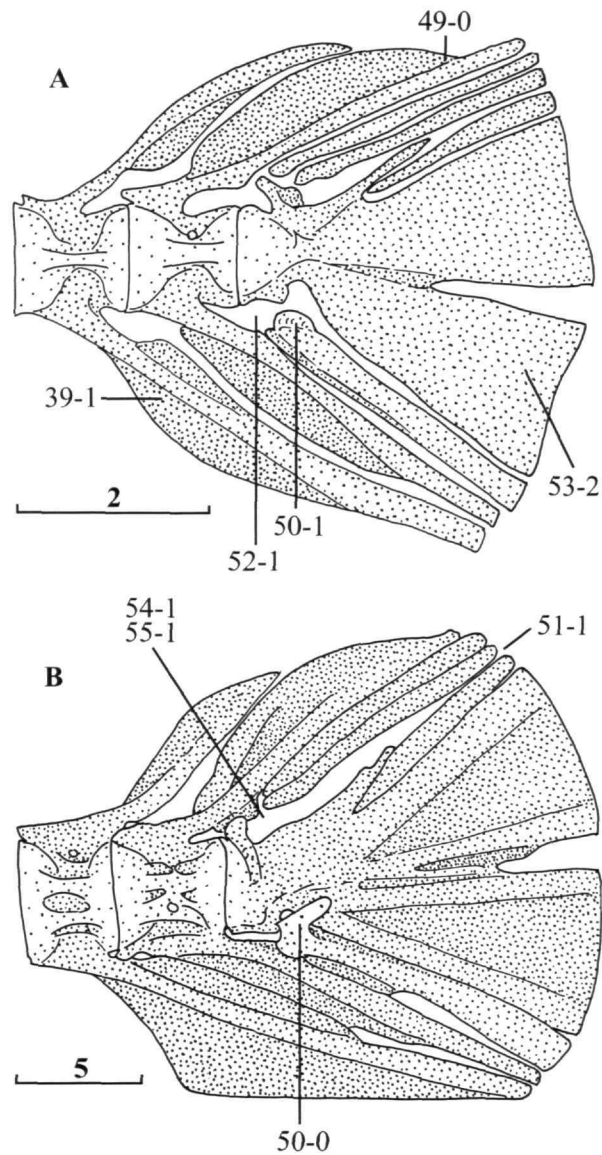


FIGURE 15.—Cyttidae. Caudal skeleton, lateral view: A, *Cyttus australis*, AMS I.32386001, 60 mm SL; B, *Cyttus traversi*, AMNH 99778, 445 mm SL. Character-state: 39-1 PU3 first modified vertebra in caudal peduncle (A, B); 49-0 NPU2 long (A, B); 50-0 hypurapophysis present; 50-1 no hypurapophysis; 51-1 two epurals (A, B); 52-1 anterior end of parhypural slightly removed from and not embracing centrum (A, B); 53-2 hypurals 1 + 2 + 3 + 4 fused and fused to centrum (A, B); 54-1 no uroneural (A, B); 55-1 no stegural (A, B).

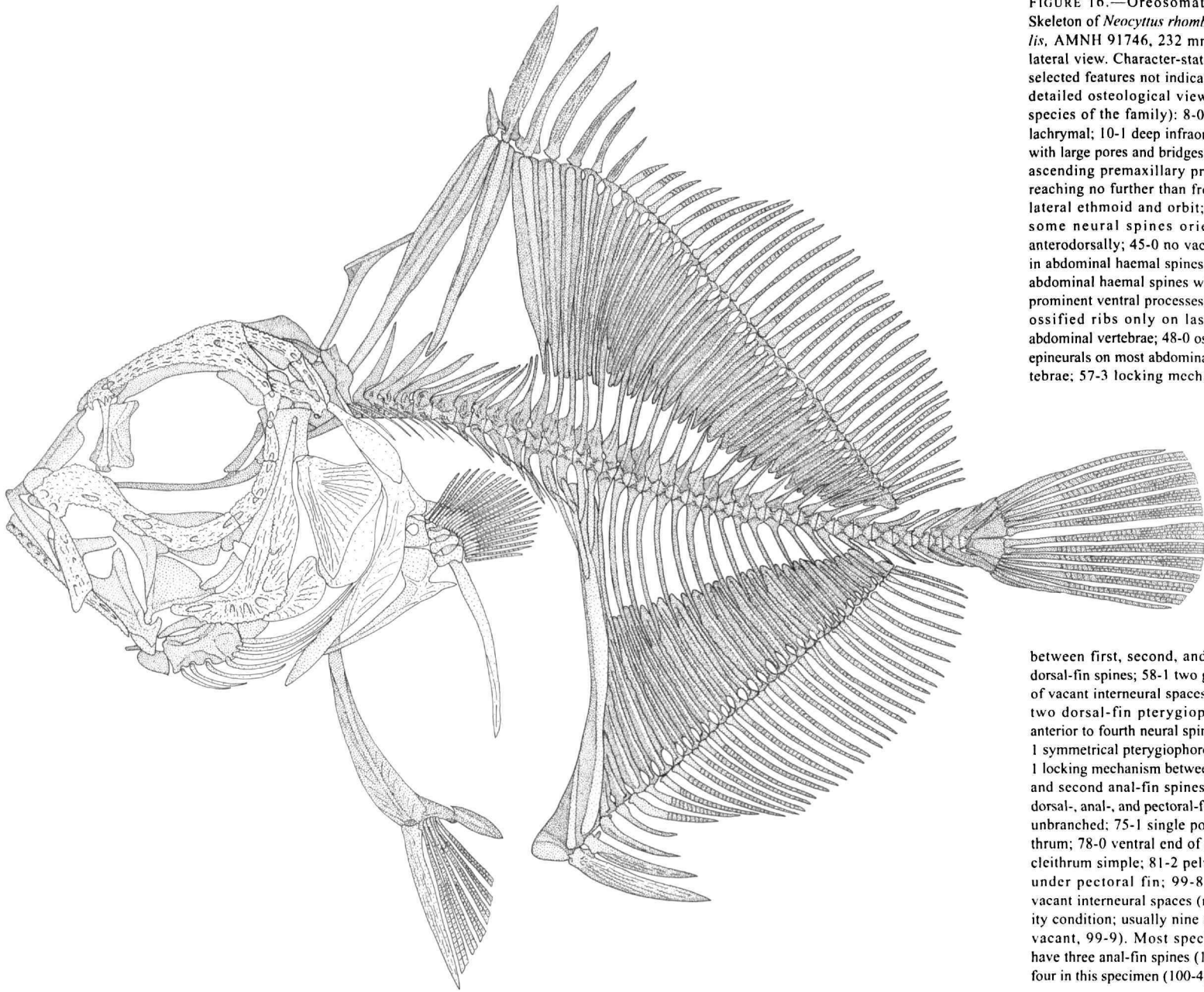


FIGURE 16.—Oreosomatidae. Skeleton of *Neocyttus rhomboidalis*, AMNH 91746, 232 mm SL, lateral view. Character-state (for selected features not indicated in detailed osteological views for species of the family): 8-0 deep lachrymal; 10-1 deep infraorbitals with large pores and bridges; 15-0 ascending premaxillary process reaching no further than front of lateral ethmoid and orbit; 44-1 some neural spines oriented anterodorsally; 45-0 no vacuities in abdominal haemal spines; 46-1 abdominal haemal spines without prominent ventral processes; 47-1 ossified ribs only on last few abdominal vertebrae; 48-0 ossified epineurals on most abdominal vertebrae; 57-3 locking mechanism

between first, second, and third dorsal-fin spines; 58-1 two groups of vacant interneural spaces; 59-1 two dorsal-fin pterygiophores anterior to fourth neural spine; 63-1 symmetrical pterygiophores; 66-1 locking mechanism between first and second anal-fin spines; 73-1 dorsal-, anal-, and pectoral-fin rays unbranched; 75-1 single postcleithrum; 78-0 ventral end of supraclithrum simple; 81-2 pelvic fin under pectoral fin; 99-8 eight vacant interneural spaces (minority condition; usually nine spaces vacant, 99-9). Most specimens have three anal-fin spines (100-3); four in this specimen (100-4).

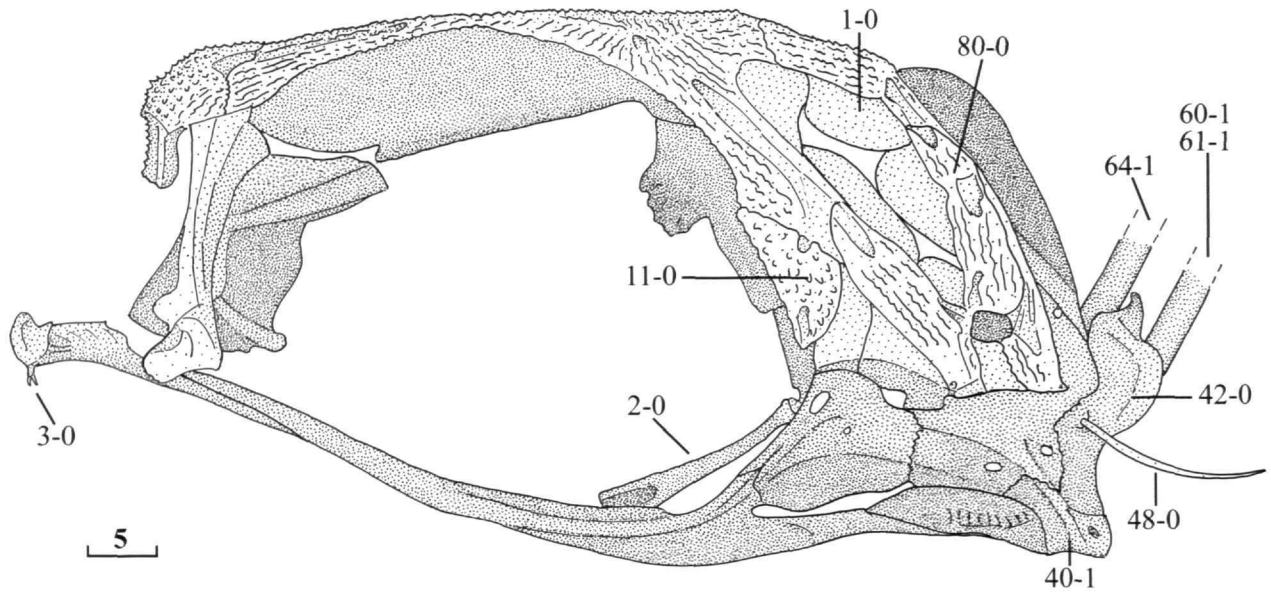


FIGURE 17.—Oreosomatidae. Skull and first vertebra of *Neocyttus rhomboidalis*, AMNH 91743, 295 mm SL, lateral view (some details, especially of the first vertebra, from AMNH 93612, 243 mm SL). Two obliquely oriented shafts have only their basal regions indicated: the anterior shaft is the base of the supraneural and the posterior shaft is the base of the first dorsal-fin pterygiophore. Character-state: 1-0 parietal present; 2-0 basisphenoid a long shaft; 3-0 vomerine teeth present; 11-0 dermosphenotic a distinctly separate ossification; 40-1 first neural arch and spine closely applied to skull; 42-0 no long dorsal extension of first neural spine above attachment to skull; 48-0 ossified epineurals on most abdominal vertebrae (only the first of the long series, on the first vertebra, shown); 60-1 ventral end of shaft of first dorsal-fin pterygiophore in first interneural/preneural space; 61-1 ventral end of shaft of first dorsal-fin pterygiophore at front of first interneural/preneural space, contacting skull and first vertebra between the two sides of first neural arch and spine; 64-1 one supraneural; 80-0 one long extrascapular.

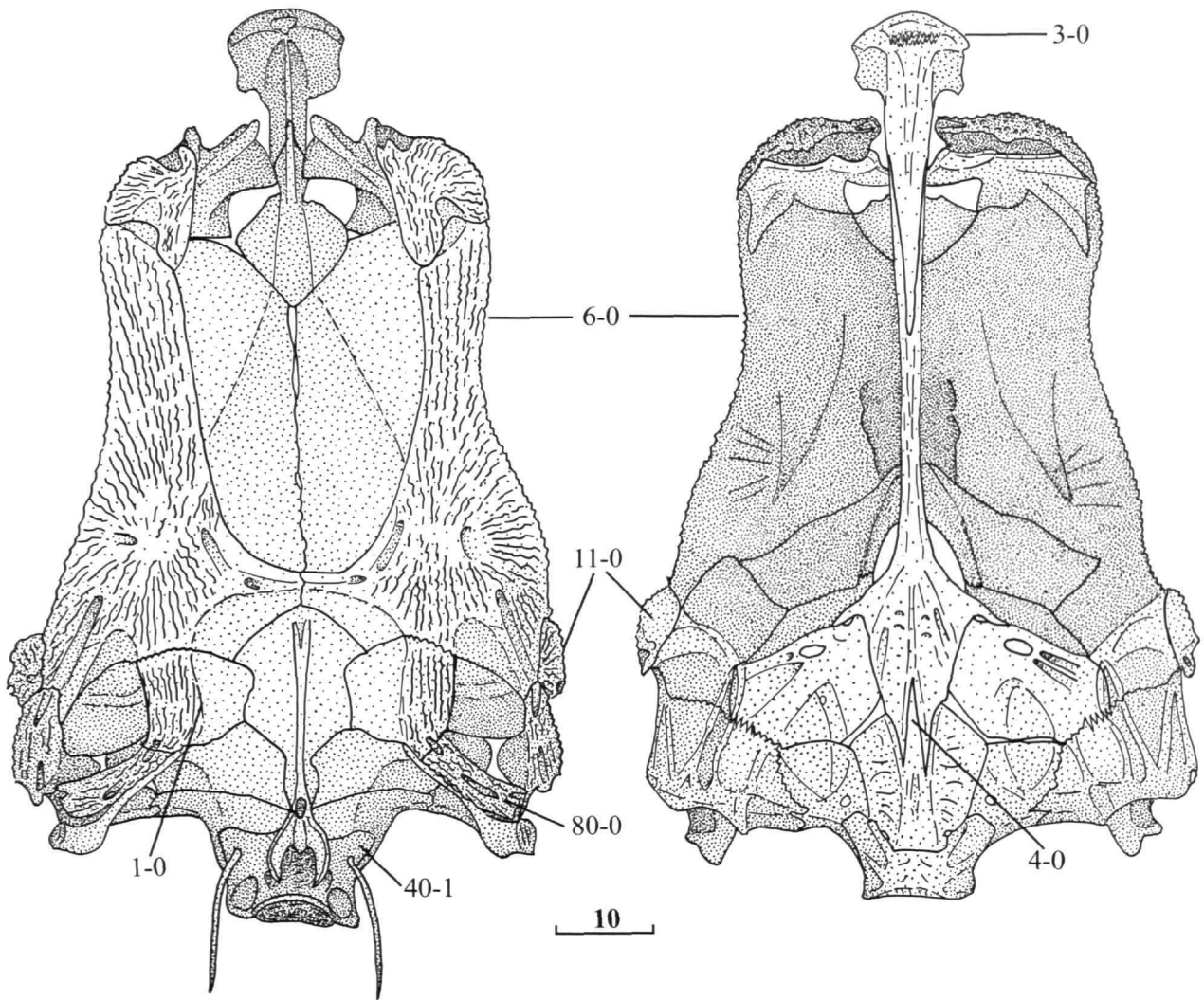


FIGURE 18.—Oreosomatidae. Skull and first vertebra of *Neocyttus rhomboidalis*, AMNH 91743, 295 mm SL, dorsal (left) and ventral views (some details, especially of the first vertebra, from AMNH 93612, 243 mm SL). Character-state: 1-0 parietal present; 3-0 vomerine teeth present; 4-0 no parasphenoid opening into posterior myodome; 6-0 supraocular serrations on frontal; 11-0 dermosphenotic a distinctly separate ossification; 40-1 first neural arch and spine closely applied to skull; 80-0 one long extrascapular.

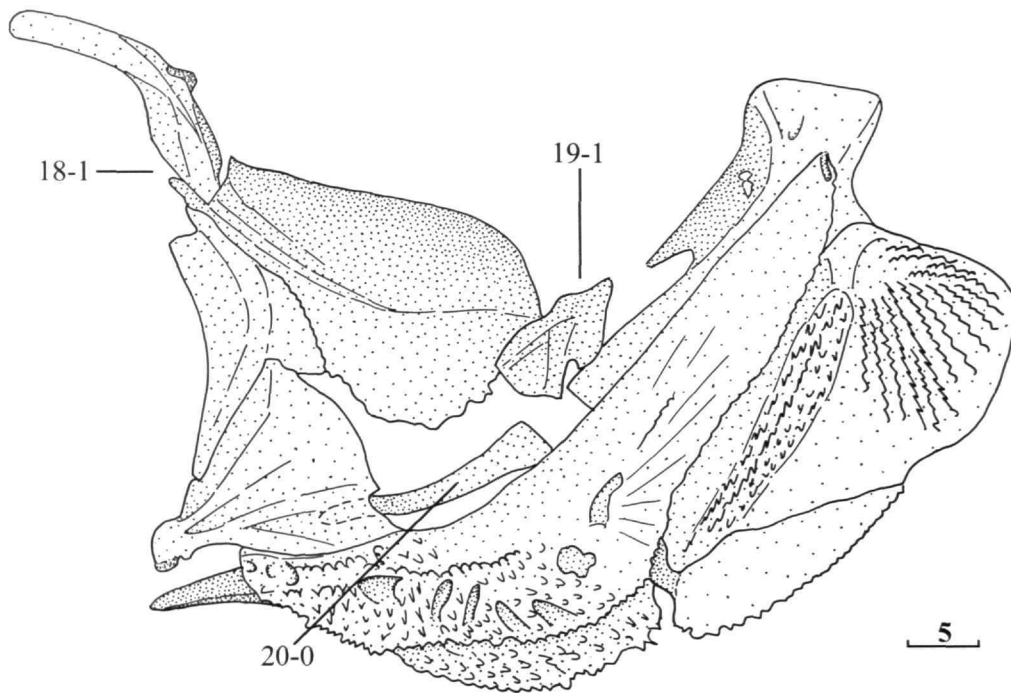


FIGURE 19.—Oreosomatidae. Suspensorium and opercular bones of *Neocyttus rhomboidalis*, AMNH 93612, 243 mm SL, lateral view. The adherent spiny scales on the subopercle and the lower region of the opercle are not shown. Character-state: 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-0 no symplectic ventral flange.

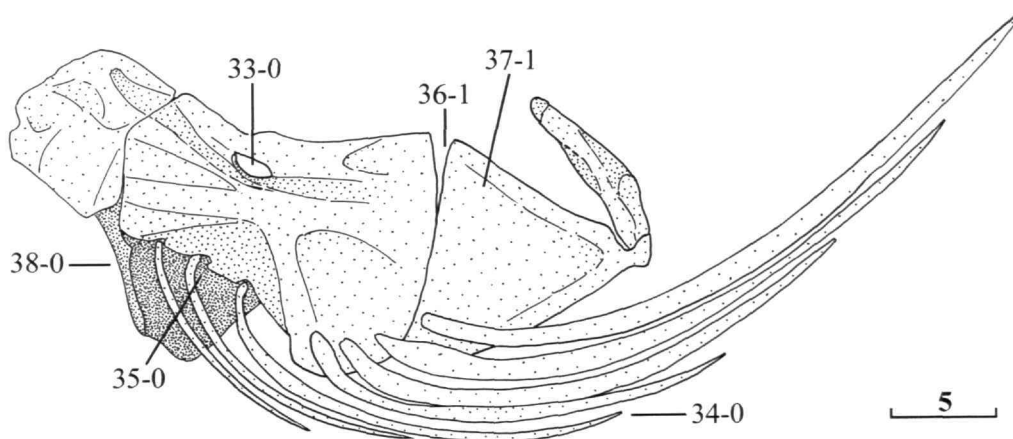


FIGURE 20.—Oreosomatidae. Hyoid arch and branchiostegal rays of *Neocyttus rhomboidalis*, AMNH 93613, 255 mm SL, lateral view. Character-state: 33-0 beryciform foramen present; 34-0 branchiostegals spread over/along both epihyal and ceratohyal; 35-0 ceratohyal notches present; 36-1 ceratohyal-epihyal articulation either through cartilage (this specimen) or becoming interdigitated in larger specimens; 37-1 epihyal less deep than rear of ceratohyal; 38-0 urohyal no longer than ceratohyal.

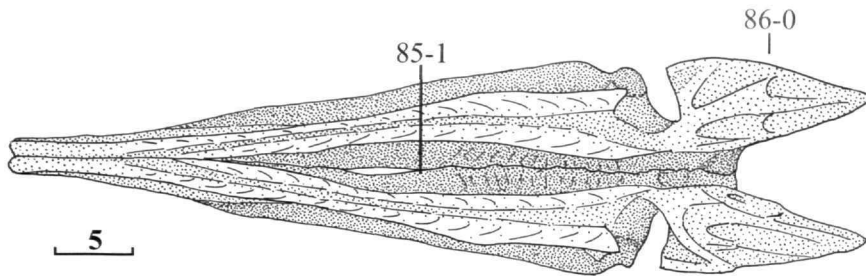
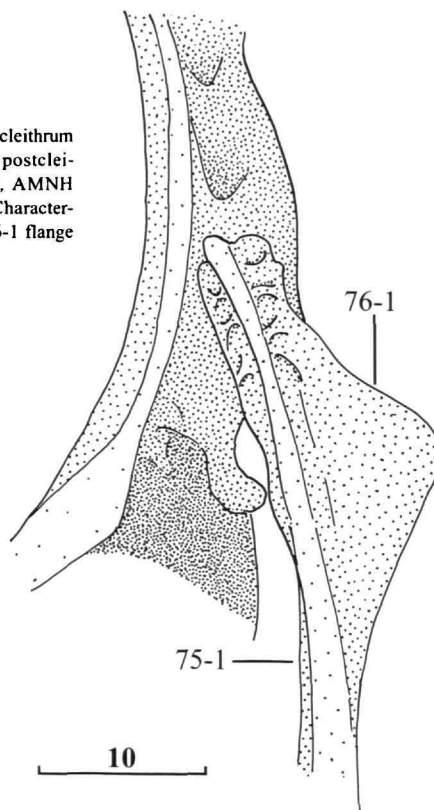


FIGURE 21.—Oreosomatidae. Pelvis of *Neocyttus rhomboidalis*, AMNH 93612, 243 mm SL, dorsal view. Character-state: 85-1 basipterygia in contact in midline but not overlapped; 86-0 short posterior process of pelvis.

FIGURE 22.—Oreosomatidae. Right cleithrum and adjacent region of the single postcleithrum of *Neocyttus rhomboidalis*, AMNH 91743, 295 mm SL, medial view. Character-state: 75-1 single postcleithrum; 76-1 flange on single postcleithrum.



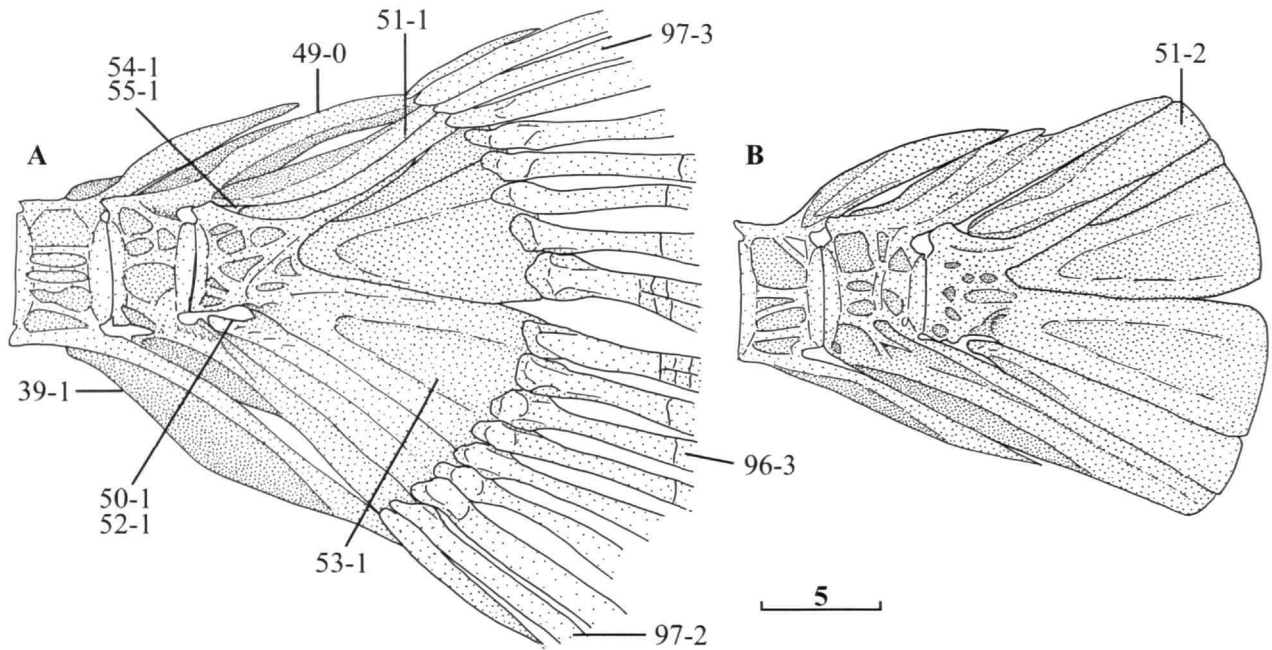


FIGURE 23.—Oreosomatidae. Caudal skeleton of *Neocyttus rhomboidalis*, lateral view: A, AMNH 93613, 255 mm SL; B, AMNH 91746, 232 mm SL. The lengths of HPU3 are different in the two specimens; A has the more normal configuration; in B, POU2 may be a compound vertebra, as indicated by deep grooves along the lengths of the neural and haemal spines. Character-state: 39-1 PU3 first modified vertebra in caudal peduncle; 49-0 NPU2 long; 50-1 no hypurapophysis; 51-1 two epurals; 51-2 one epural (minority condition); 52-1 anterior end of parhypural slightly removed from and not embracing centrum; 53-1 hypurals 1 + 2 fused and fused to centrum, and hypurals 3 + 4 fused and free from centrum; 54-1 no uroneural; 55-1 no stegural; 96-3 13 principal caudal-fin rays; 97-2,3 two (in lower lobe) or three (in upper lobe) procurent caudal-fin rays.

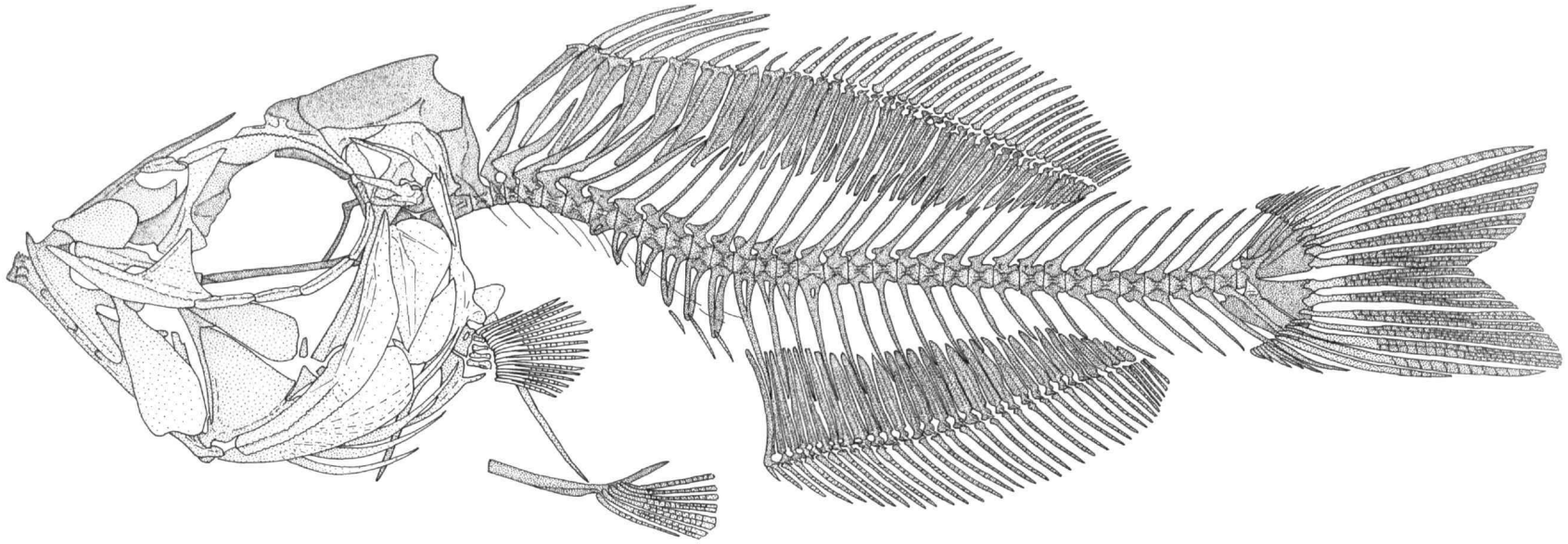


FIGURE 24.—Parazenidae. Skeleton of *Parazen pacificus*, CAS 38404, 96 mm SL, lateral view. Character-state (for selected unlabeled features not indicated in detailed osteological views for species of the family): 8-0 deep lachrymal; 10-0 slender, tubular infraorbitals; 15-1 ascending premaxillary process reaching about one-third into orbit; 44-0 neural spines oriented posterodorsally; 45-2 large vacuities in abdominal haemal spines; 46-0 abdominal haemal spines with prominent ventral processes; 47-1 ossified ribs only on last few abdominal vertebrae; 48-0 ossified epineurals on most abdominal vertebrae; 59-2 three dorsal-fin pterygiophores anterior to fourth neural spine; 61-0 ventral end of shaft of first dorsal-fin pterygiophore in middle of first interneural space, not contacting first neural arch and spine; 63-1 symmetrical pterygiophores; 64-0 no supraneural; 73-1 dorsal-, anal-, and pectoral-fin rays unbranched; 78-0 ventral end of supracleithrum simple; 81-0 pelvic fin about midway between anus and pectoral fin; 99-1 one vacant interneural space.

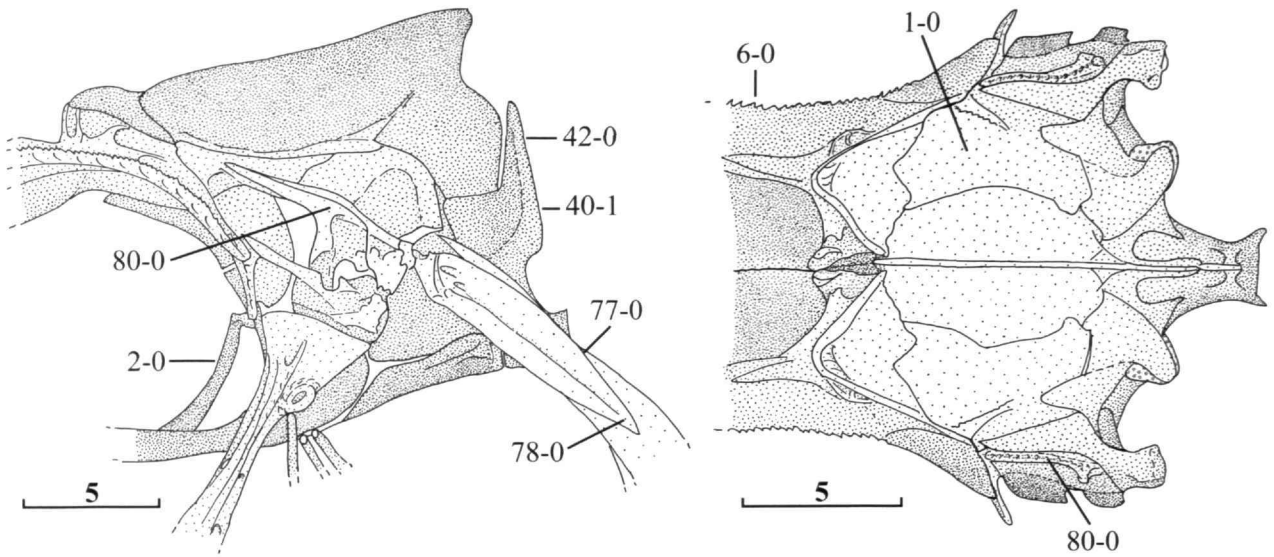


FIGURE 25.—Parazenidae. Rear half of the skull and first vertebra of *Parazen pacificus*, USNM 187892, 110 mm SL, lateral (left) and dorsal views. In the lateral view, the dermosphenotic and infraorbitals are removed, and the upper regions of the suspensory shafts of the three pharyngobranchials are shown in their place of articulation to the prootic (first pharyngobranchial) and to the cartilaginous area between the anterior end of the basioccipital, posterior end of the parasphenoid, and lower border of the prootic (second and third pharyngobranchials). The ossified epineural present on the first vertebra is not shown here or in Figure 26. Character-state: 1-0 parietal present; 2-0 basisphenoid a long shaft; 6-0 supraocular serrations on frontal; 40-1 first neural arch and spine closely applied to skull; 42-0 no long dorsal extension of first neural spine above attachment to skull; 77-0 no supraclithral serrations; 78-0 ventral end of supraclithrum simple; 80-0 one long extrascapular.

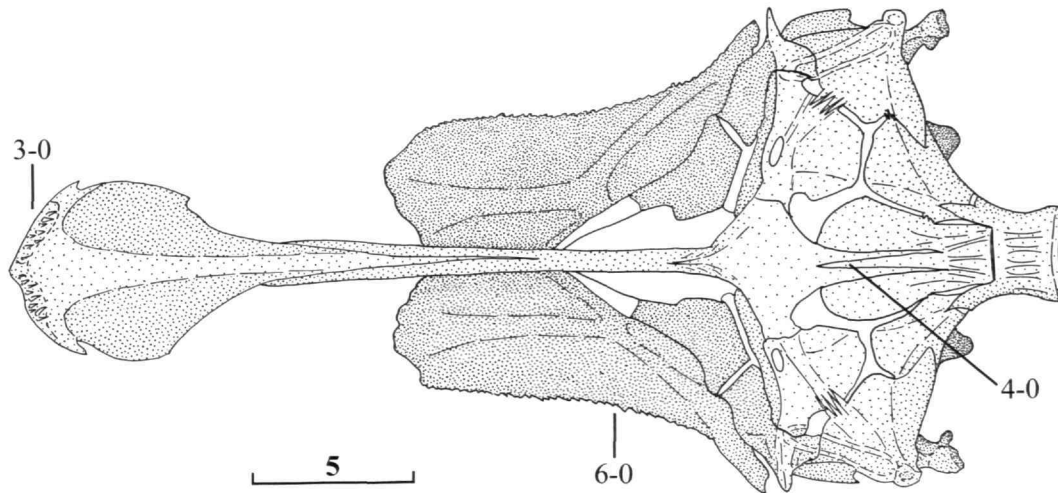


FIGURE 26.—Parazenidae. Skull and first vertebra of *Parazen pacificus*, USNM 187892, 110 mm SL, ventral view. The lateral ethmoids and nasals are removed. Character-state: 3-0 vomerine teeth present; 4-0 no parasphenoid opening into posterior myodome; 6-0 supraocular serrations on frontal.

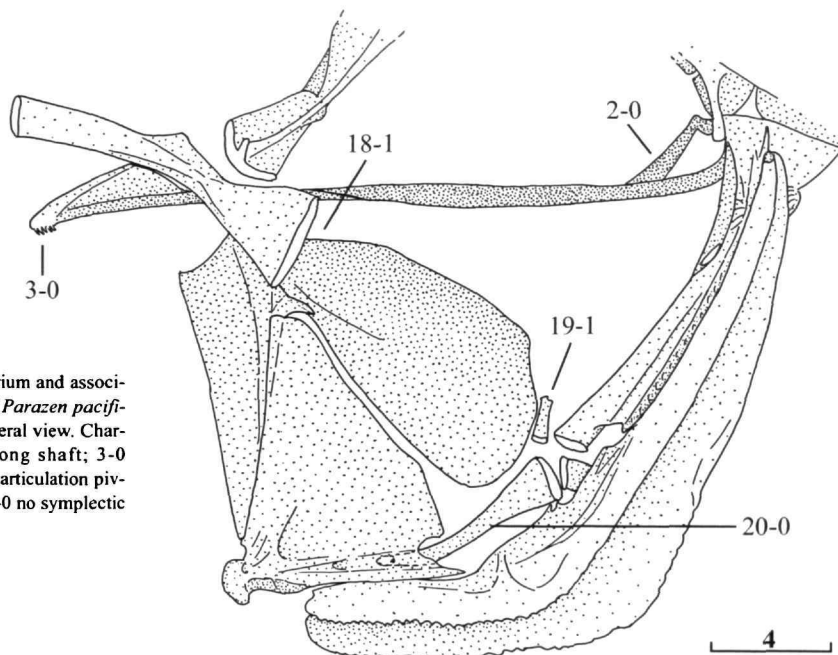


FIGURE 27.—Parazenidae. Suspensorium and associated cranial bones and preopercle of *Parazen pacificus*, USNM 187892, 110 mm SL, lateral view. Character-state: 2-0 basisphenoid a long shaft; 3-0 vomerine teeth present; 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-0 no symplectic ventral flange.

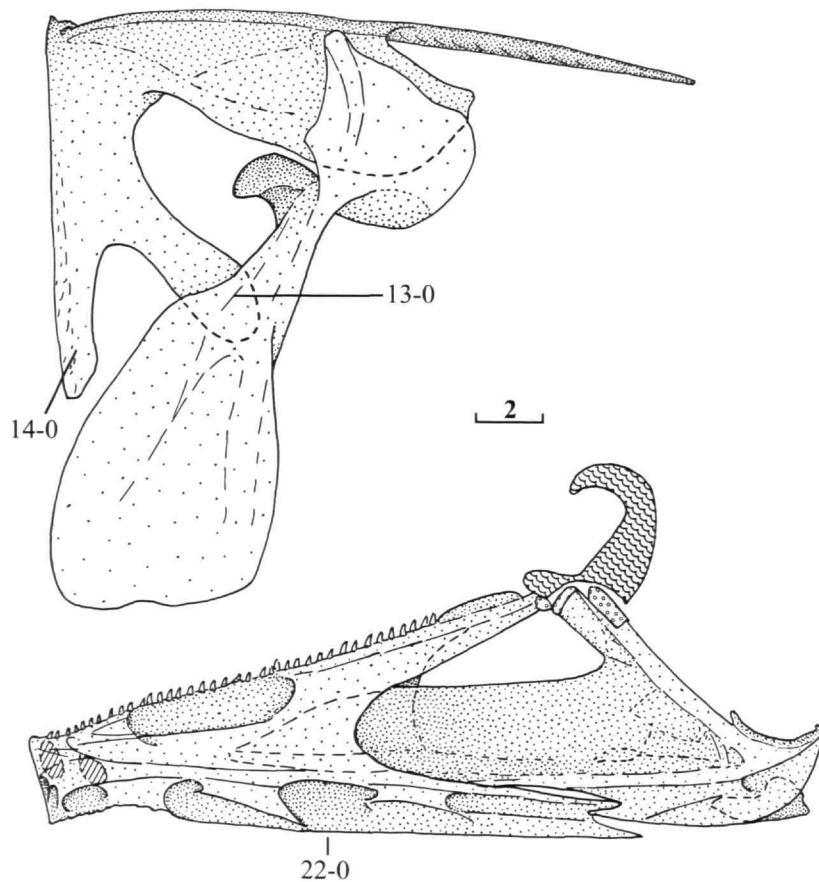


FIGURE 28.—Parazenidae. Upper (above) and lower jaws of *Parazen pacificus*, USNM 187892, 110 mm SL, lateral views. At the front of the dentary, parallel lines show the basal regions of attachment of the two dentary cartilages, which are removed; the wavy lines and small circles in mechanical stippling show cartilages that attach to the inner surface of the maxilla. The bands of teeth on the inner surface along the anterior border of the premaxilla cannot be seen in lateral view. Character-state: 13-0 post-maxillary process present; 14-0 alveolar process of premaxilla simple; 22-0 no dentary serrations (edge may be irregular but not serrate).

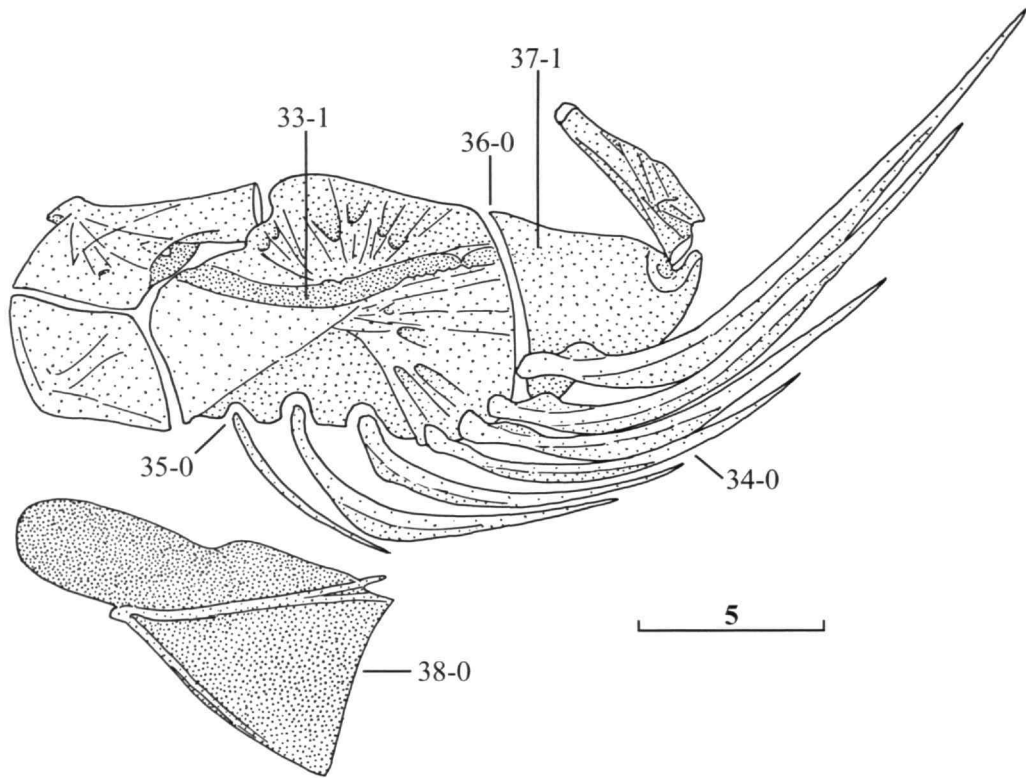


FIGURE 29.—Parazenidae. Hyoid arch, branchiostegal rays, and, illustrated lowered from its natural position, urohyal of *Parazen pacificus*, AMNH 29459, 105 mm SL, lateral view. Character-state: 33-1 beryciform foramen represented by deep groove on ceratohyal; 34-0 branchiostegals spread over/along both epihyal and ceratohyal; 35-0 ceratohyal notches present; 36-0 ceratohyal-epihyal articulation through cartilage only; 37-1 epihyal less deep than rear of ceratohyal; 38-0 urohyal no longer than ceratohyal.

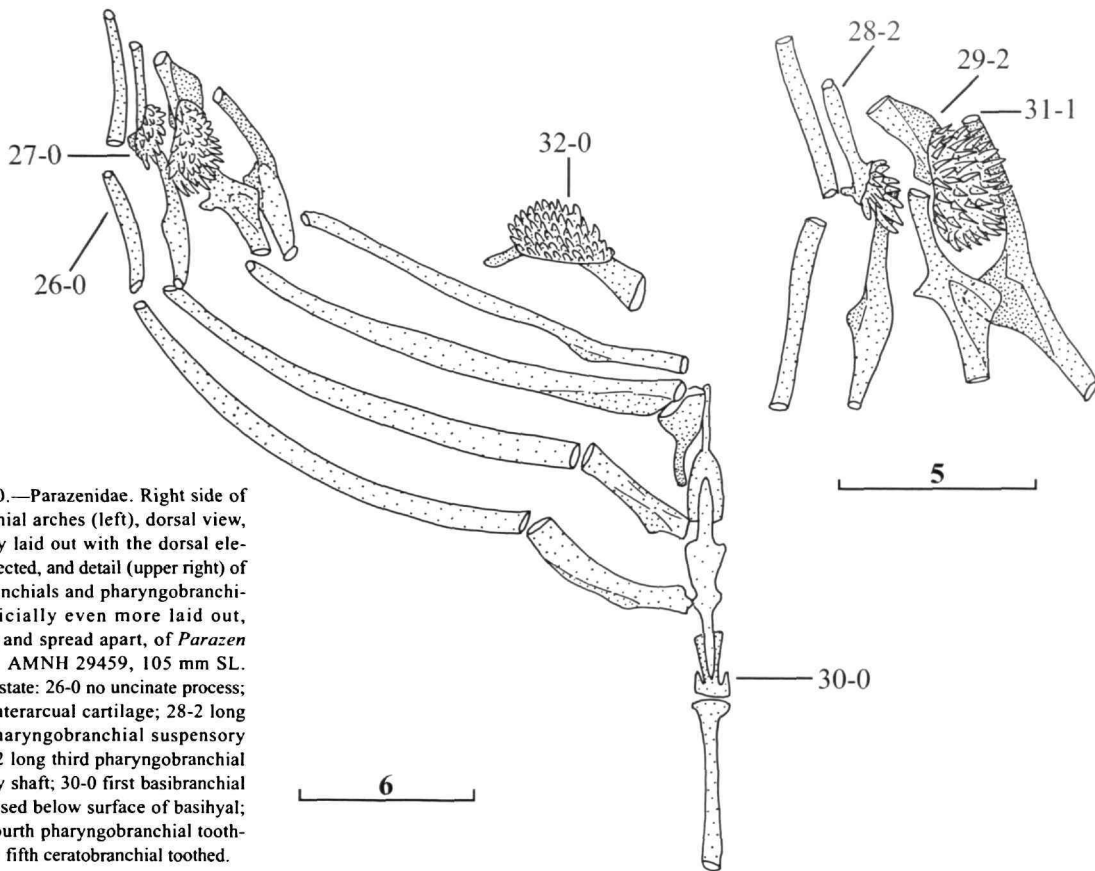
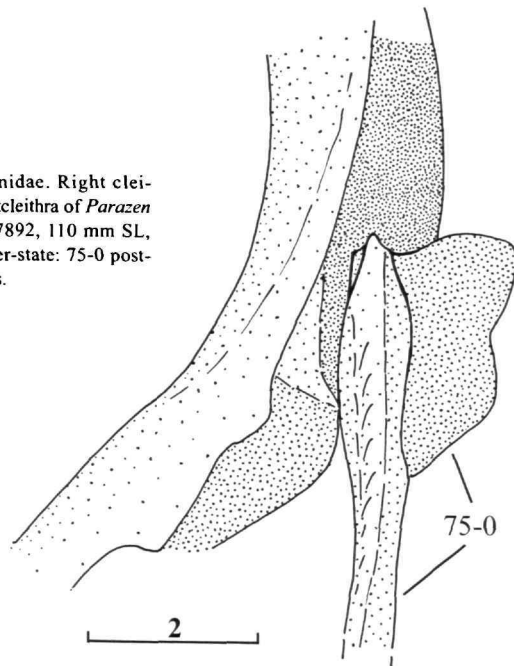


FIGURE 30.—Parazenidae. Right side of the branchial arches (left), dorsal view, artificially laid out with the dorsal elements reflected, and detail (upper right) of the epibranchials and pharyngobranchials, artificially even more laid out, reflected, and spread apart, of *Parazen pacificus*, AMNH 29459, 105 mm SL. Character-state: 26-0 no uncinatous process; 27-0 no interarcual cartilage; 28-2 long second pharyngobranchial suspensory shaft; 29-2 long third pharyngobranchial suspensory shaft; 30-0 first basibranchial not depressed below surface of basihyal; 31-1 no fourth pharyngobranchial tooth-plate; 32-0 fifth ceratobranchial toothed.

FIGURE 31.—Parazenidae. Right cleithrum and the two postcleithra of *Parazen pacificus*, USNM 187892, 110 mm SL, medial view. Character-state: 75-0 postcleithrum in two pieces.



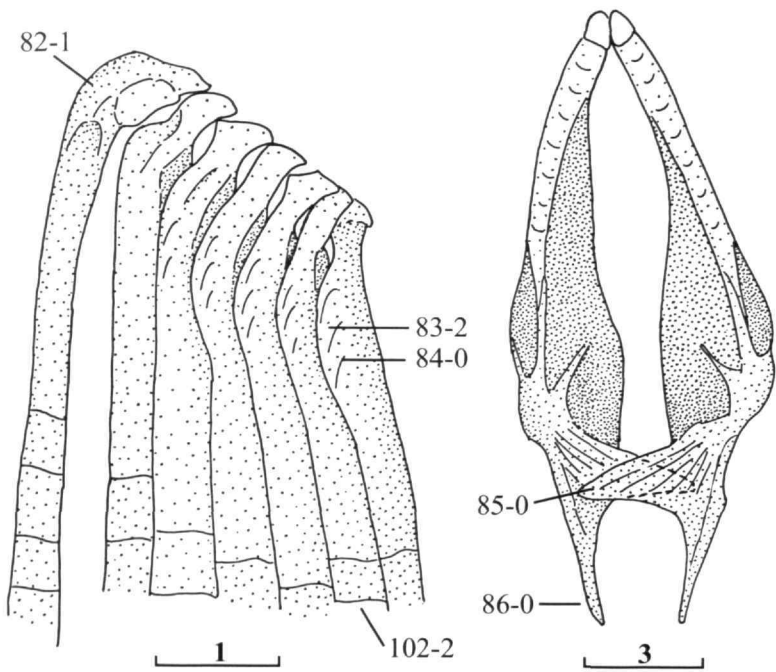


FIGURE 32.—Parazenidae. Basal region of the right pelvic fin (left), ventral view, and pelvis, dorsal view, of *Parazen pacificus*, USNM 187892, 110 mm SL. Character-state: 82-1 no pelvic-fin spine; 83-2 anterolateral processes as broad flanges along basal region of rays; 84-0 no serrations on rays; 85-0 broadly overlapping medial processes of basipterygia; 86-0 short posterior process of pelvis; 102-2 total of seven pelvic-fin elements.

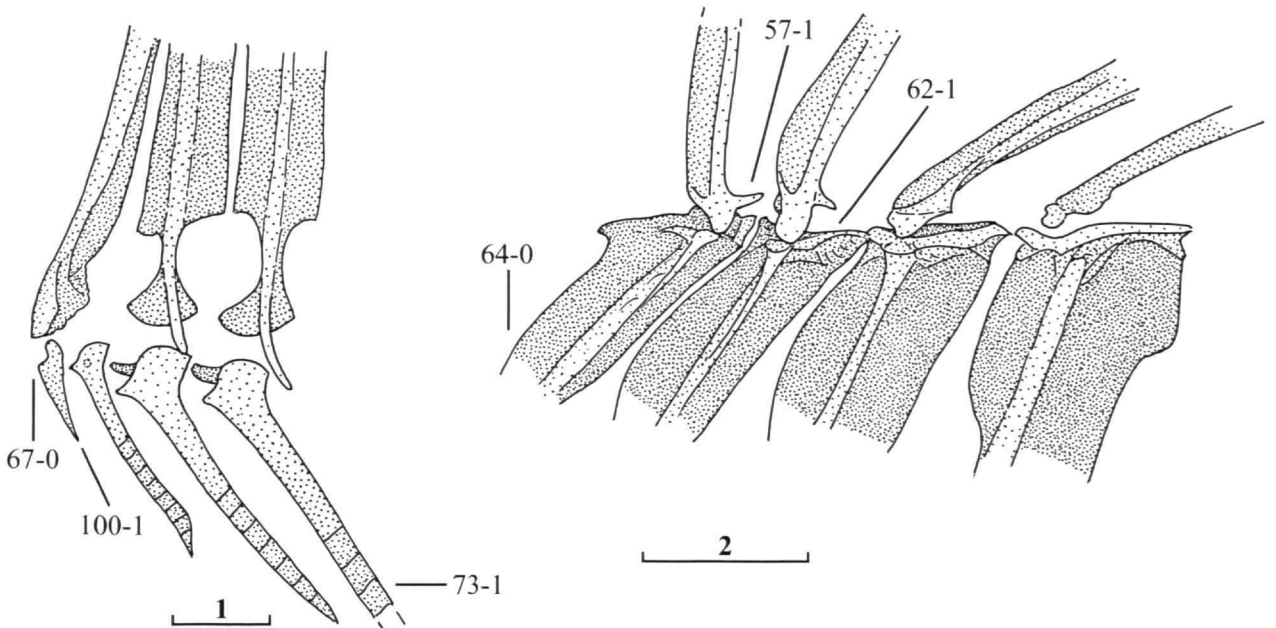


FIGURE 33.—Parazenidae. Lower region of the first three anal-fin pterygiophores, single anal-fin spine, and first three anal-fin rays (left) and the upper region of the first four dorsal-fin pterygiophores and first four dorsal-fin spines of *Parazen pacificus*, CAS 38404, 96 mm SL, lateral views. The anteriorly protruding structure at the base of the second and third anal-fin rays is the paired distal pterygiophore (a tiny pair of distal pterygiophores is also between the two halves of the base of the first anal-fin ray but does not pro-

trude). Character-state: 57-1 locking mechanism between first and second dorsal-fin spines; 62-1 no ossified spinous dorsal-fin distal radial; 64-0 no supraneural; 67-0 no fusion of first anal-fin spine to pterygiophore; 73-1 anal-fin rays unbranched; 100-1 one anal-fin spine. Unnumbered here and in all of the other illustrations showing dorsal-fin spines is a synapomorphy of all zeiforms: a single supernumerary spine on the first dorsal-fin pterygiophore.

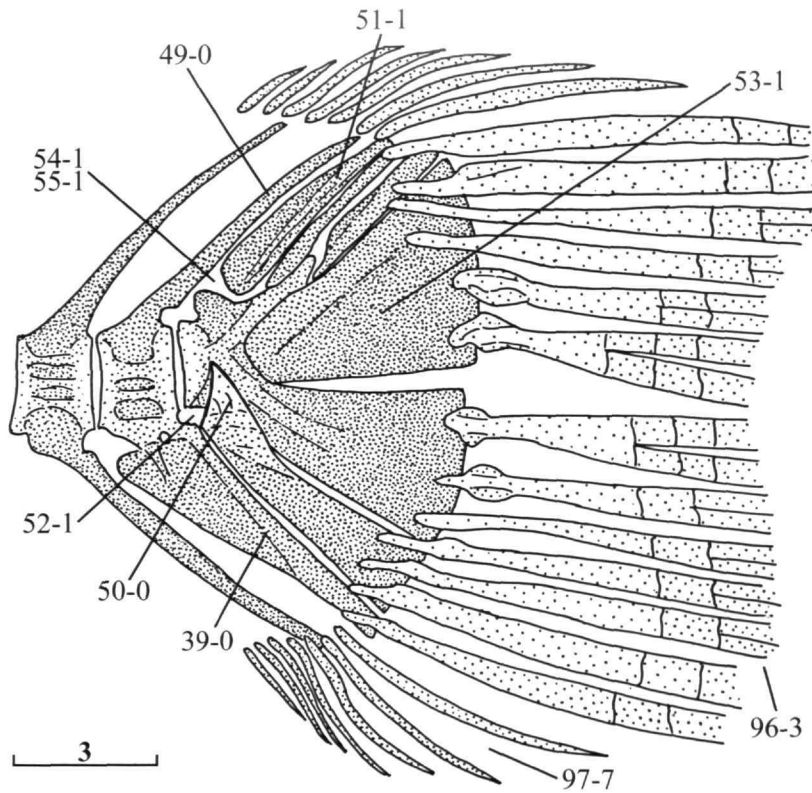


FIGURE 34.—Parazenidae. Caudal skeleton of *Parazen pacificus*, USNM 187892, 110 mm SL, lateral view. Character-state: 39-0 PU2 first modified vertebra in caudal peduncle; 49-0 NPU2 long; 50-0 hypurapophysis present; 51-1 two epurals; 52-1 anterior end of parhypural slightly removed from and not embracing centrum; 53-1 hypurals 1 + 2 fused and fused to centrum, and hypurals 3 + 4 fused and free from centrum; 54-1 no uroneural; 55-1 no stegural; 96-3 13 principal caudal-fin rays; 97-7 seven procurent caudal-fin rays both above and below (polymorphic; about as often eight procurcents, 97-8).

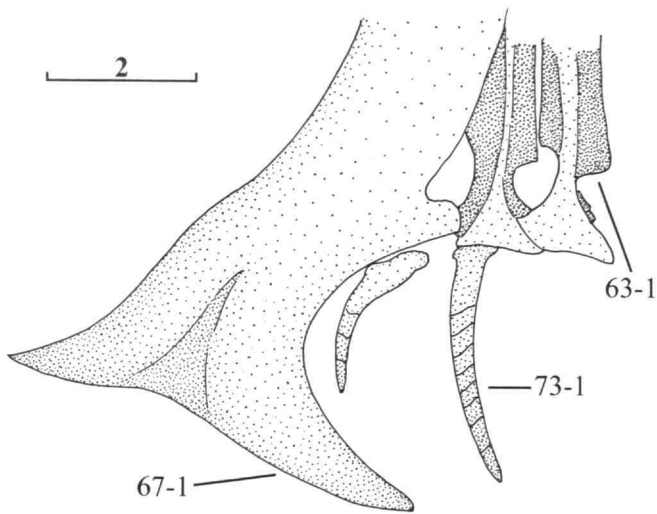


FIGURE 35.—Parazenidae. Lower region of the first three anal-fin basal pterygiophores and the anal-fin spine and first two anal-fin rays of *Cyttopsis roseus*, AMNH 29460, 74 mm SL, lateral view. The anal-fin spine is fused to the first pterygiophore in this specimen, and the first anal-fin ray, also borne on the first pterygiophore, loses its segmentation in large specimens and becomes spine-like. Character-state: 63-1 symmetrical pterygiophores; 67-1 fusion of first anal-fin spine to pterygiophore only in some specimens (as here); 73-1 anal-fin rays unbranched.

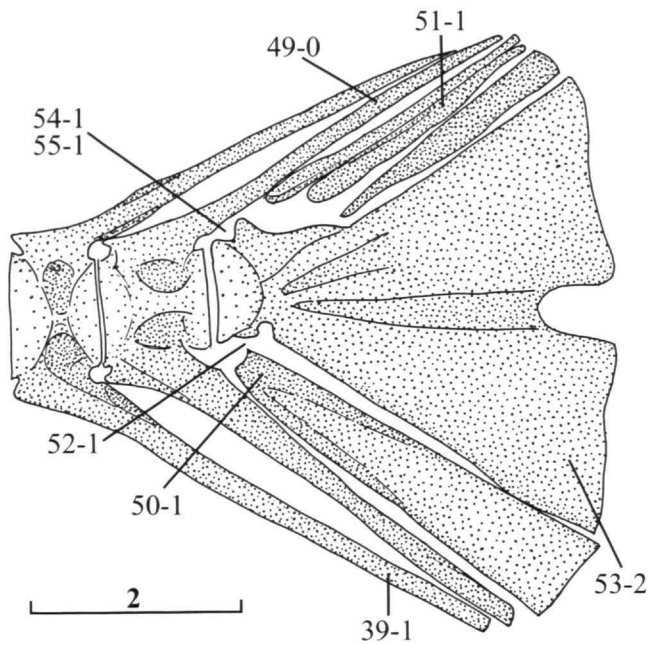


FIGURE 36.—Parazenidae. Caudal skeleton of *Cyttopsis roseus*, USNM 187873, 72 mm SL, lateral view. Character-state: 39-1 PU3 first modified vertebra in caudal peduncle; 49-0 NPU2 long; 50-1 no hypurapophysis; 51-1 two epurals; 52-1 anterior end of parhypural slightly removed from and not embracing centrum; 53-2 hypurals 1 + 2 + 3 + 4 fused and fused to centrum; 54-1 no uroneural; 55-1 no stegural.

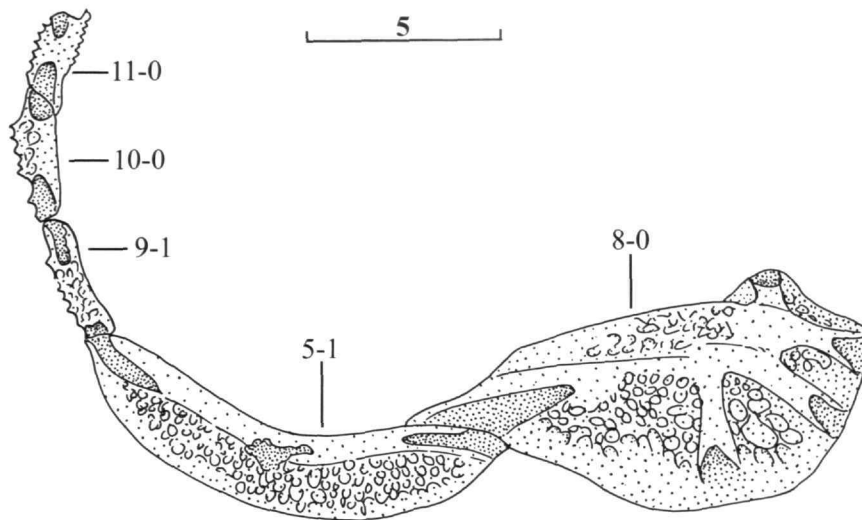


FIGURE 37.—Parazenidae. Right lachrymal, infraorbitals, and (detached from skull) dermosphenotic of *Stethopristes eos*, USNM 226570, 91 mm SL, lateral view. Character-state: 5-1 honeycomb bone sculpturing; 8-0 deep lachrymal; 9-1 three infraorbitals; 10-0 slender, tubular infraorbitals; 11-0 dermosphenotic a distinctly separate ossification.

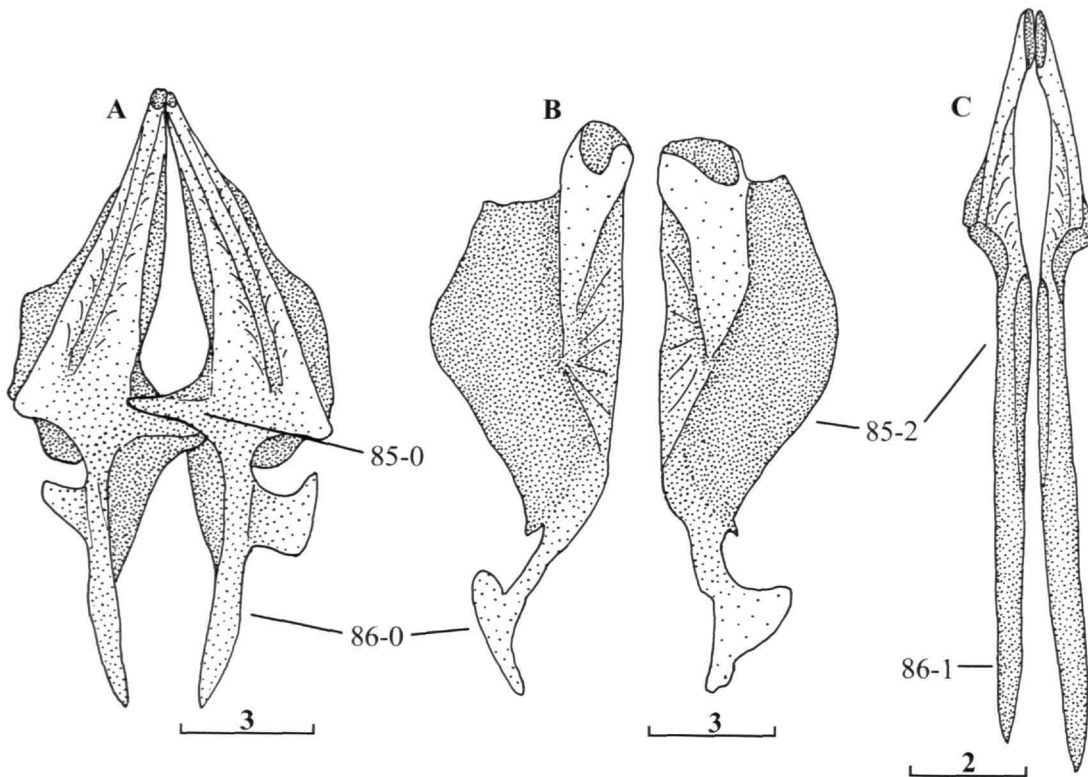


FIGURE 38.—Parazenidae and other families. Pelvis, dorsal view: A, *Capromimus abbreviatus* (Zeniontidae), AMS I.23650001, 61 mm SL; B, *Stethopristes eos* (Parazenidae), USNM 226570, 91 mm SL; C, *Zenopsis conchifer* (Zeidae), USNM 117280, 51 mm SL. Character-state: 85-0 broadly overlapping medial processes of basipterygia; 85-2 basipterygia not in close contact in middle region; 86-0 short posterior process of pelvis; 86-1 long, rod-like posterior process of pelvis.

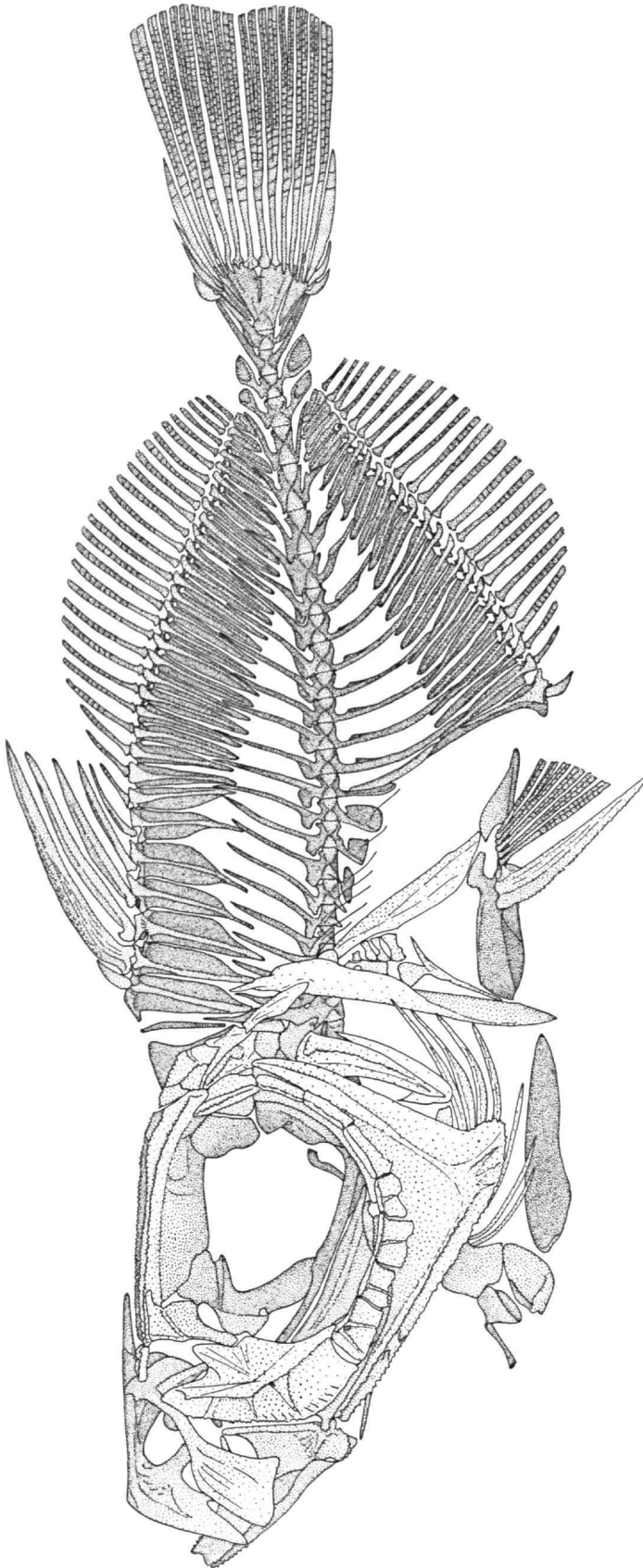


FIGURE 39.—Zeniontidae. Skeleton of *Zenion hololepis*, CAS 38409, 70 mm SL, lateral view. The pectoral fin has been removed so as not to obscure underlying features. Character-state for selected unlabeled features not indicated in detailed osteological views for species of the family: 15-0 ascending premaxillary process reaching no further than front of lateral ethmoid and orbit; 44-0 all neural spines oriented posterodorsally; 45-0 no vacuities in abdominal haemal spines; 46-0 abdominal haemal spines with prominent ventral processes; 47-1 ossified ribs only on last abdominal vertebra; 48-0 ossified epineurals on most abdominal vertebrae; 58-1 two groups of vacant interneural spaces; 59-2 three dorsal-fin pterygiophores anterior to fourth neural spine; 63-1 symmetrical pterygiophores; 73-1 dorsal- and anal-fin rays unbranched (also pectoral-fin rays, not shown); 78-0 ventral end of supracleithrum simple; 81-1 pelvic fin slightly behind pectoral fin; 99-2 two vacant interneural spaces.

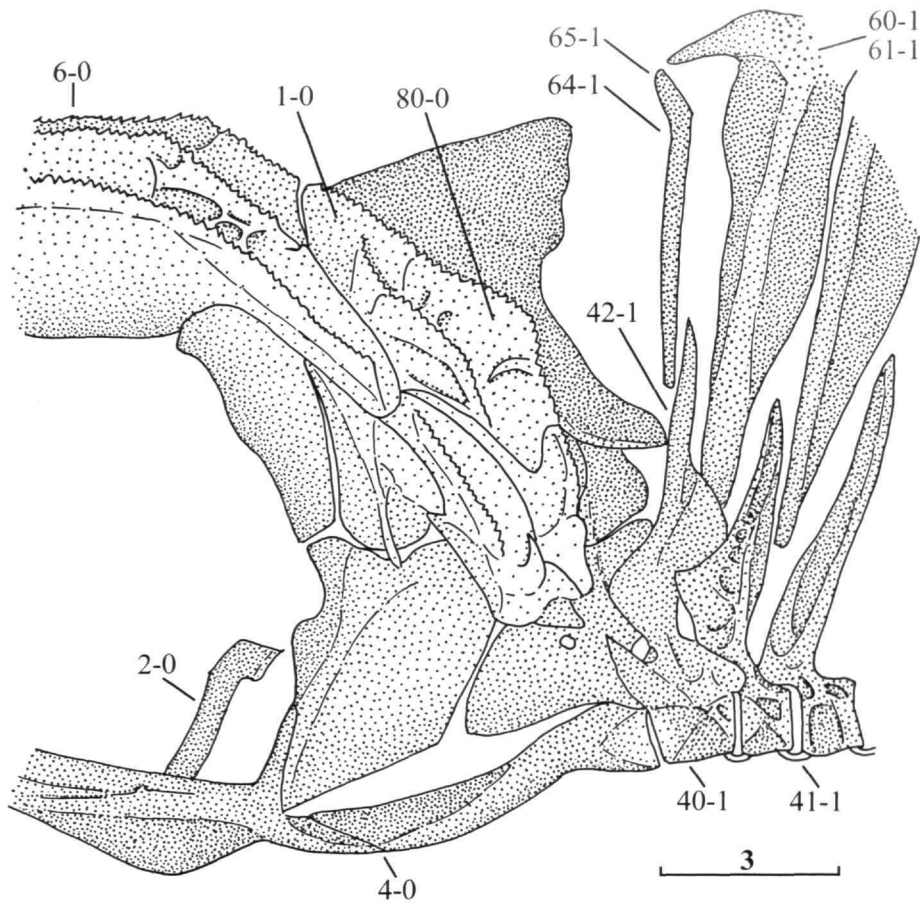


FIGURE 40.—*Zeniontidae*. Rear half of the skull, first three vertebrae, supraneural, and first two dorsal-fin pterygiophores of *Zenion hololepis*, CAS 38409, 70 mm SL, lateral view. The dermosphenotic is removed, and the ossified epineurals on the first and more posterior vertebrae are not shown. Character-state: 1-0 parietal present; 2-0 basisphenoid a long shaft; 4-0 no parasphenoid opening into posterior myodome; 6-0 supraocular serrations on frontal; 40-1 first neural arch and spine closely applied to skull; 41-1 flexible articulation of second and next few anterior abdominal vertebrae with skull-first vertebra, these vertebrae linked laterally and ventrally by ligamentous bands; 42-1 long dorsal extension of first neural spine above attachment to skull; 60-1 ventral end of shaft of first dorsal-fin pterygiophore in first interneural/preneural space; 61-1 ventral end of shaft of first dorsal-fin pterygiophore at front of first interneural/preneural space, contacting skull and first vertebra between the two sides of first neural arch and spine; 64-1 one supraneural; 65-1 no cartilage at distal end of supraneural; 80-0 one long extrascapular.

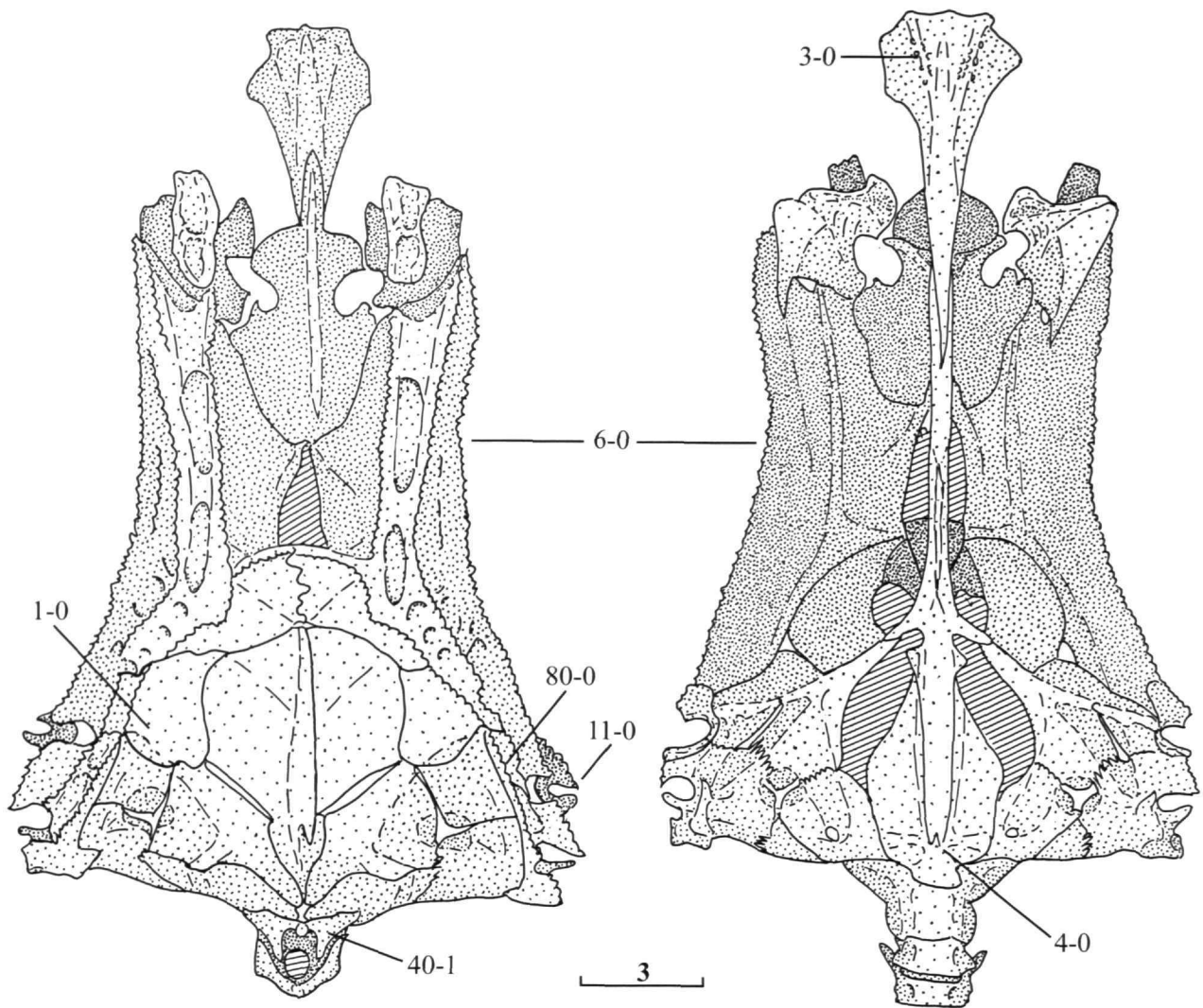


FIGURE 41.—Zeniontidae. Skull, dorsal (left) and ventral views, first two vertebrae, dorsal view, and first three vertebrae, ventral view, of *Zenion hololepis*, CAS 38409, 70 mm SL. The supraneural is removed, and the ossified epineurals on the first and more posterior vertebrae are not shown. In the dorsal view, the parallel lines between the first two vertebrae show where the ventral end of the shaft of the first dorsal-fin pterygiophore (which is removed) is articulated; the parallel lines medially behind the ethmoid and between the frontals are cartilage. In the ventral view, parallel lines between the frontals and the pterosphenoids, and between the basisphenoid, exoccipitals, and prootics, are cartilage. Character-state: 1-0 parietal present; 3-0 vomerine teeth present (teeth tiny; row of foramina lateral to each patch of teeth); 4-0 no parasphenoid opening into posterior myodome; 6-0 supraocular serrations on frontal; 11-0 dermosphenotic a distinctly separate ossification; 40-1 first neural arch and spine closely applied to skull; 80-0 one long extrascapular.

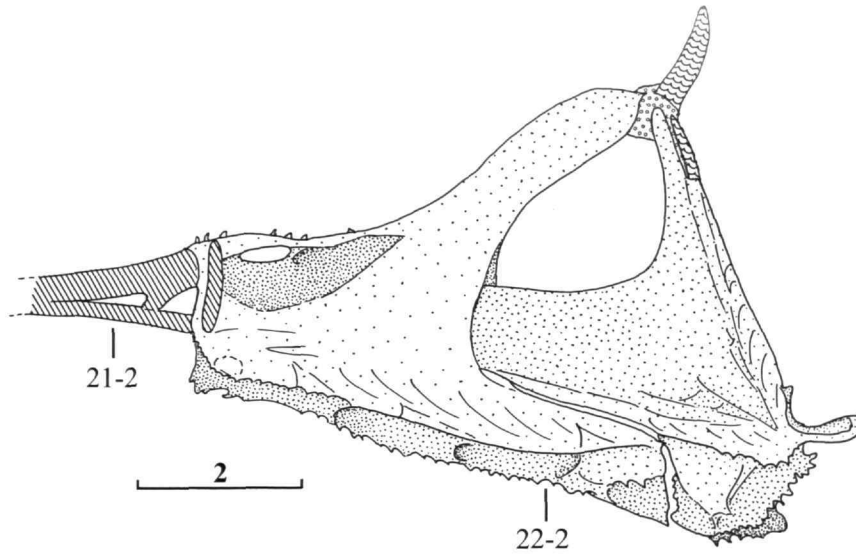


FIGURE 42.—Zeniontidae. Lower jaw and associated cartilages of *Zenion hololepis*, USNM 307305, 48 mm SL, lateral view. Parallel lines in front of the dentary show the proximal half of the more anterior of the two dentary cartilages, rotated forward, and just behind it the proximal region of attachment of the more posterior dentary cartilage, which has been removed (like the anterior cartilage, the posterior cartilage has a divided base). The wavy lines and small circles in mechanical stippling at the top of the dentary and articular show cartilages and ligaments that attach through a broad band of connective tissue along much of the posterior border of the maxilla. Character-state: 21-2 two dental cartilages of moderate length, about equal or the first slightly shorter; 22-2 multiple dentary serrations.

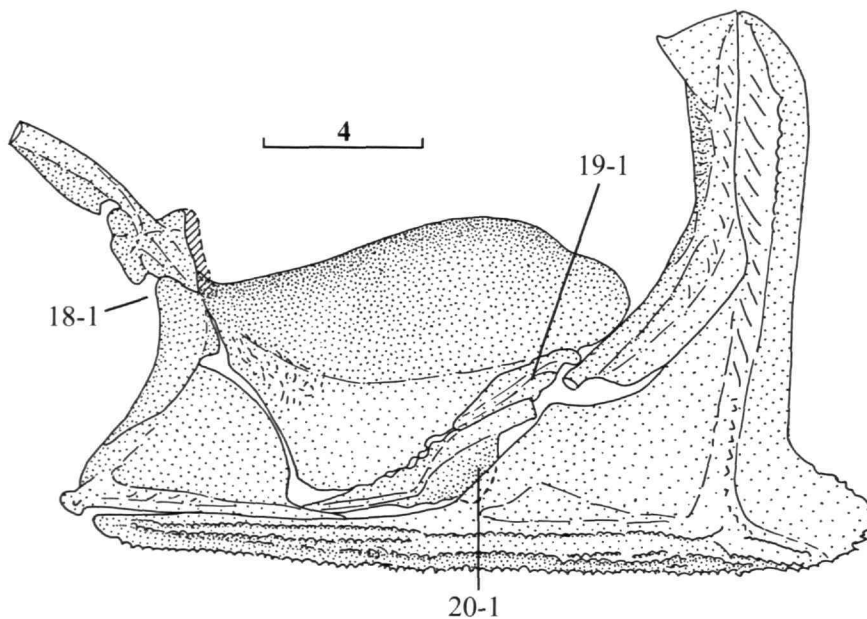


FIGURE 43.—Zeniontidae. Suspensorium and preopercle of *Zenion hololepis*, CAS 38409, 70 mm SL, lateral view, somewhat flattened out from its slightly oblique natural position to better expose the metapterygoid. Parallel lines at the posterior border of the palatine show its cartilaginous core. The extent of the ventral flange of the symplectic below the upper border of the preopercle is indicated by a dashed line. Character-state: 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-1 symplectic ventral flange.

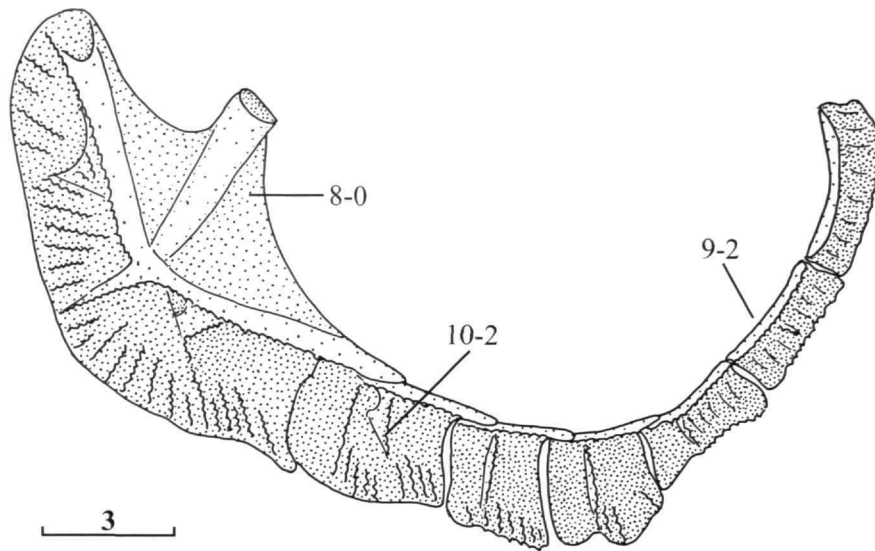


FIGURE 44.—Zeniontidae. Lachrymal and infraorbitals (excluding dermosphenotic) of *Zenion hololepis*, CAS 76856, 73 mm SL, lateral view. Specimens sometimes have one less infraorbital than illustrated, and the sixth and seventh are sometimes consolidated. Character-state: 8-0 deep lachrymal; 9-2 six infraorbitals; 10-2 deep infraorbitals with serrate vertical supporting flanges.

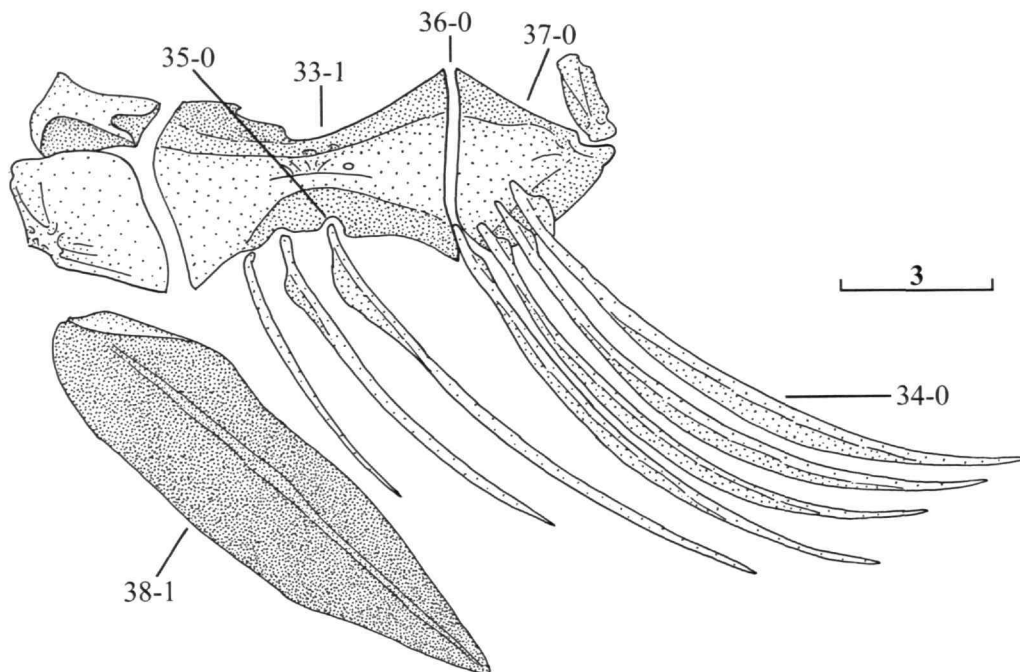


FIGURE 45.—Zeniontidae. Hyoid arch, branchiostegal rays, and urohyal of *Zenion hololepis*, CAS 38409, 70 mm SL, lateral view. Because the branchial apparatus is excessively flared in preserved specimens, the urohyal is illustrated lower than its natural position. Character-state: 33-1 beryciform foramen represented by deep groove on ceratohyal (ontogenetically polymorphic; beryciform foramen present at smaller sizes, 33-0); 34-0 branchiostegals spread over/along both epihyal and ceratohyal; 35-0 ceratohyal notches present; 36-0 ceratohyal-epihyal articulation through cartilage only; 37-0 epihyal about same depth as rear of ceratohyal; 38-1 urohyal large, longer than ceratohyal.

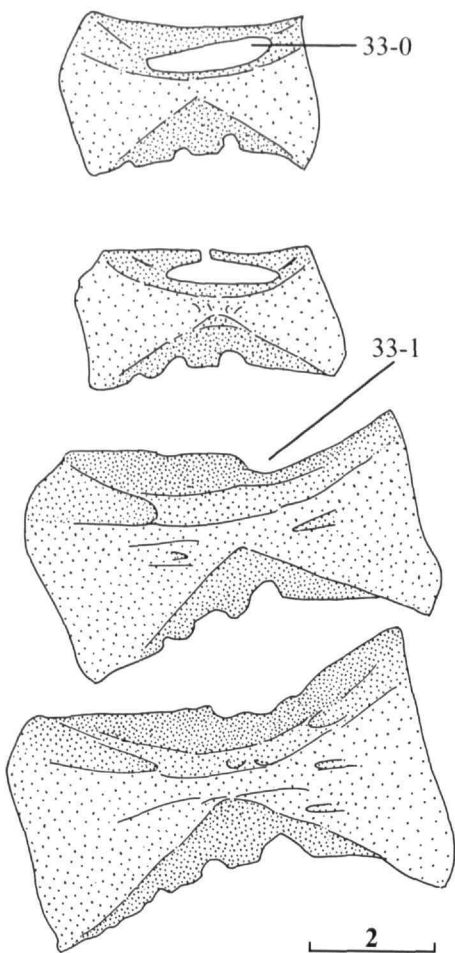


FIGURE 46.—Zeniontidae. Ontogenetic reduction of the beryciform foramen in the ceratohyal of *Zenion hololepis*, lateral views. It is represented in large specimens by a deep groove along the surface of the bone: from top to bottom, USNM 187864, 50 mm SL; USNM 307305, 48 mm SL; USNM 187864, 65 mm SL; USNM 187864, 73 mm SL. Character-state: 33-0 beryciform foramen present; 33-1 beryciform foramen represented by deep groove on ceratohyal.

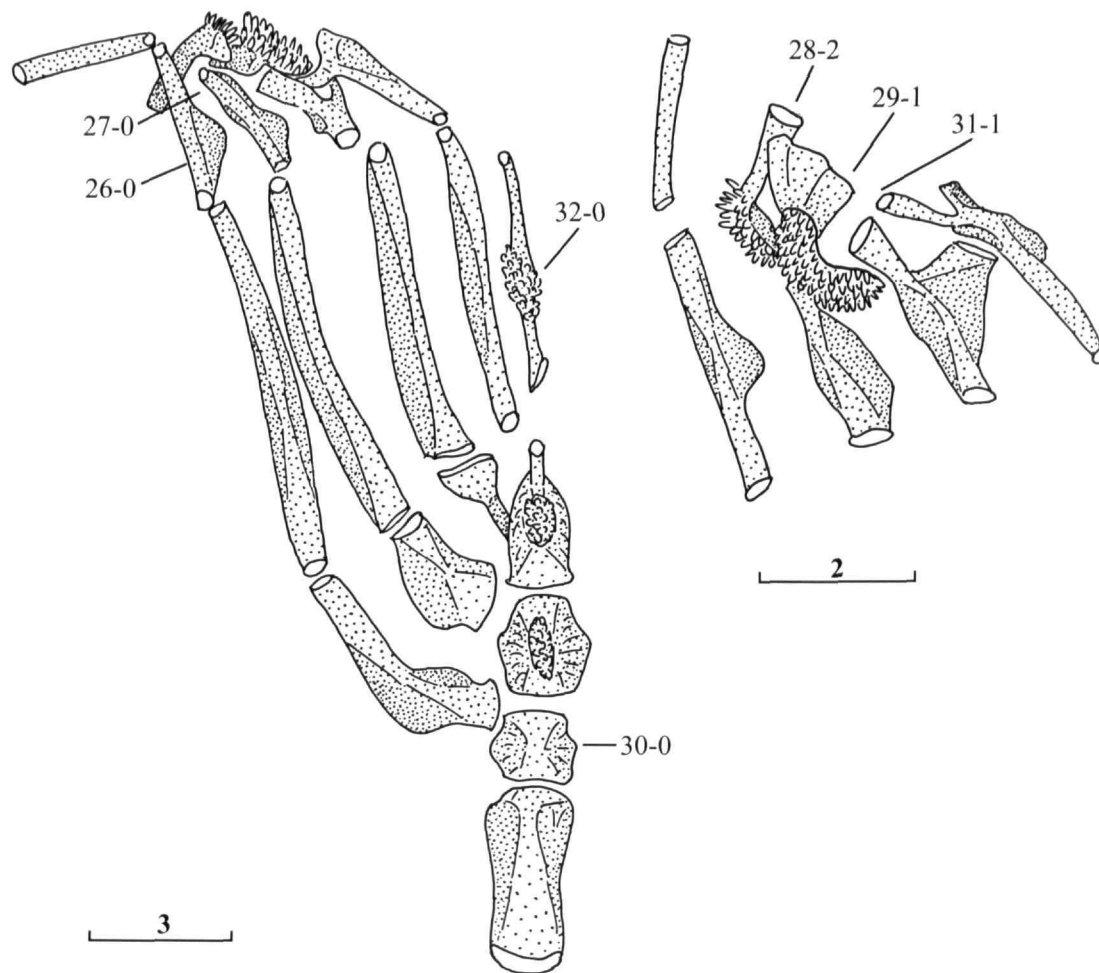


FIGURE 47.—Zeniontidae. Dorsal view of the right side of the branchial arches (left), artificially laid out with the dorsal elements reflected, and detail (upper right) of the epibranchials and pharyngobranchials, artificially even more laid out, reflected, and spread apart, of *Zenion hololepis*, CAS 38409, 70 mm SL. Character-state: 26-0 no unciniate process; 27-0 no interarcual cartilage; 28-2 long second pharyngobranchial suspensory shaft; 29-1 moderately long third pharyngobranchial suspensory shaft; 30-0 first basibranchial not depressed below surface of basihyal; 31-1 no fourth pharyngobranchial toothplate; 32-0 fifth ceratobranchial toothed.

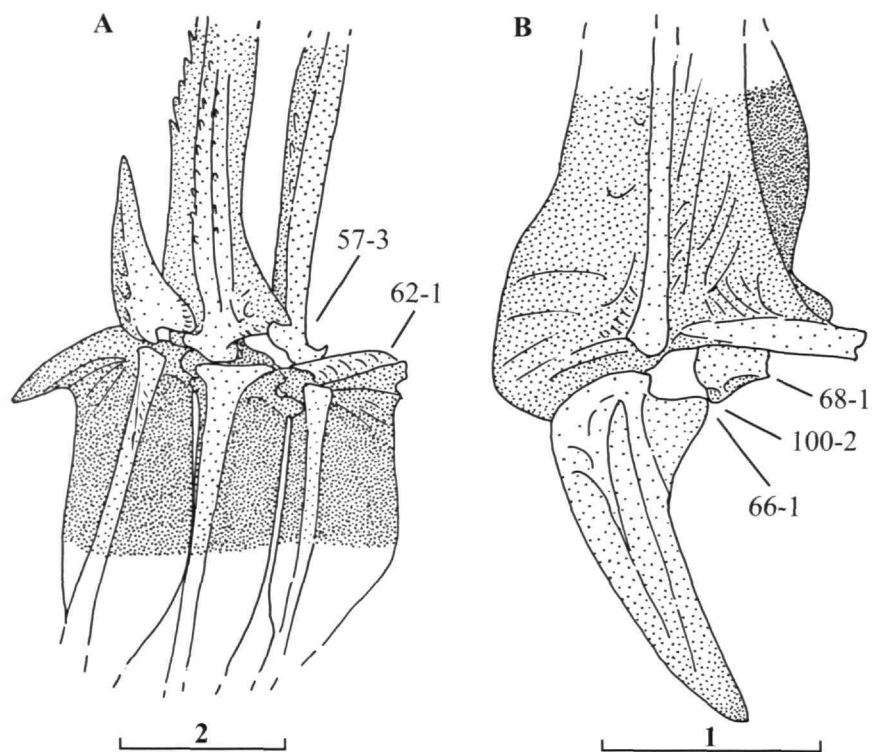


FIGURE 48.—Zeniontidae. *Zenion hololepis*, USNM 187864, 50 mm SL, lateral views: A, first three dorsal-fin spines and pterygiophores; B, the two anal-fin spines and first anal-fin pterygiophore. Character-state: 57-3 locking mechanism between first, second, and third dorsal-fin spines; 62-1 no ossified spinous dorsal-fin distal radial; 66-1 locking mechanism between first and second anal-fin spines; 68-1 second anal-fin spine less than one-half length of first spine; 100-2 two anal-fin spines.

FIGURE 49.—Zeniontidae. Pelvis of *Zenion hololepis*, USNM 187864, 65 mm SL, dorsal view. The lateral extent of the overlapping medial flanges is indicated by dashed lines. Character-state: 85-0 broadly overlapping medial processes of basipterygia; 86-0 short posterior process of pelvis.

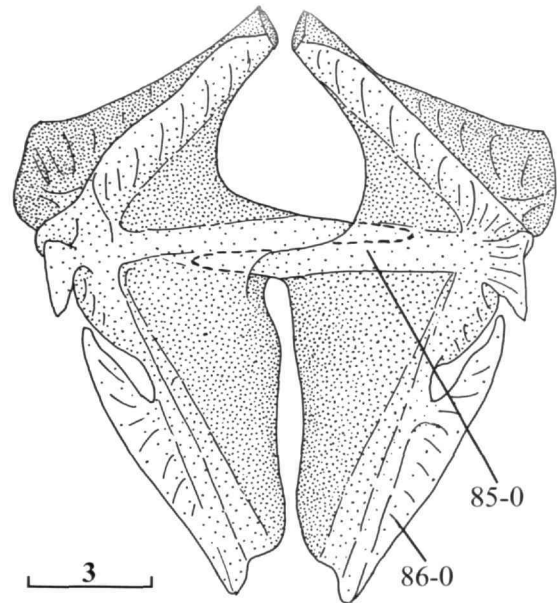
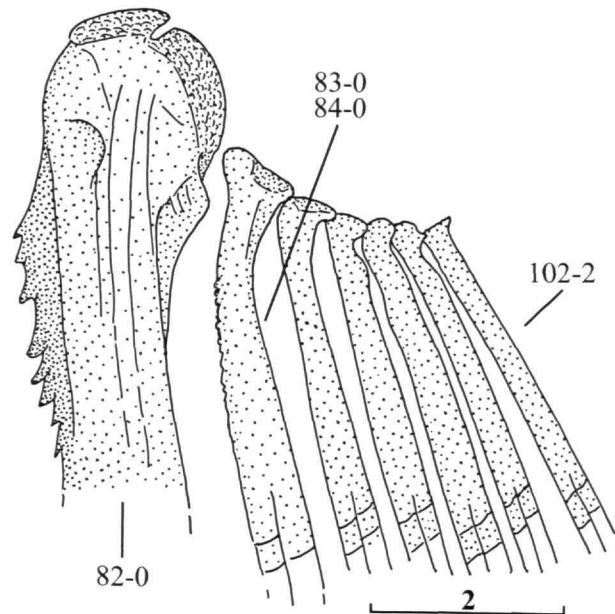


FIGURE 50.—Zeniontidae. Basal region of the right pelvic fin of *Zenion hololepis*, USNM 187864, 73 mm SL, ventral view. See Figure 51 for details of the locking mechanism of the pelvic-fin spine against the pelvis. Character-state: 82-0 pelvic-fin spine present; 83-0 no anterolateral processes from bases of rays; 84-0 no serrations on rays; 102-2 total of seven pelvic-fin elements.



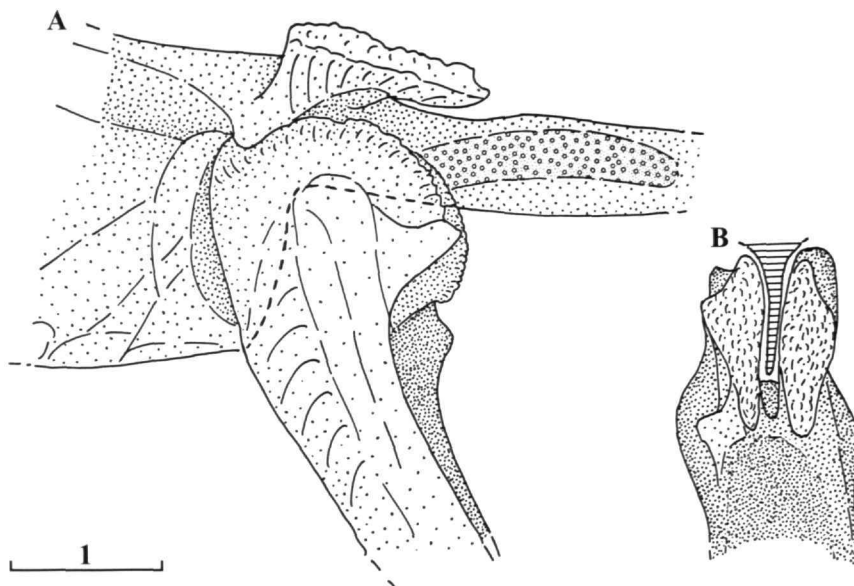


FIGURE 51.—Zeniontidae. *Zenion hololepis*, USNM 187864, 50 mm SL, lateral (A) and posterior (slightly oblique) (B) views: A, locking articulation between the roughened surface of the pelvic-fin spine and the pelvis; B, detail of the deep indentation in the base of the pelvic-fin spine that rotates around a strong flange from the anterior region of the articular facet on the pelvis. Small circles in mechanical stippling on the side of the pelvis behind the pelvic-fin spine show the band of cartilage against which the pelvic-fin rays articulate. Character-states are as in Figure 50.

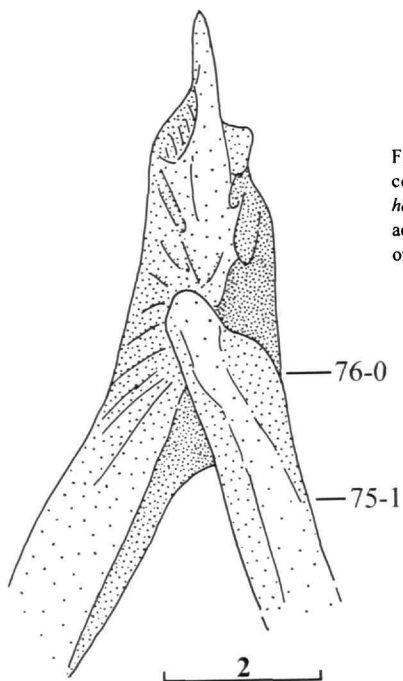


FIGURE 52.—Zeniontidae. Right cleithrum and adjacent region of the single postcleithrum of *Zenion hololepis*, CAS 38409, 70 mm SL, medial view. Character-state: 75-1 single postcleithrum; 76-0 no flange on single postcleithrum.

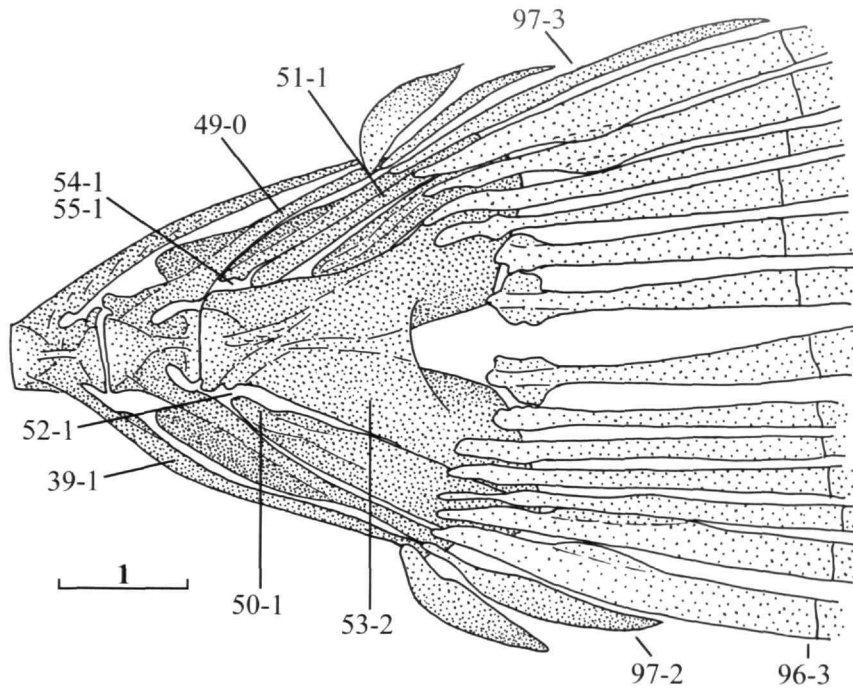


FIGURE 53.—Zeniontidae. Caudal skeleton of *Zenion hololepis*. USNM 307305, 48 mm SL, lateral view. Character-state: 39-1 PU3 first modified vertebra in caudal peduncle; 49-0 NPU2 long; 50-1 no hypurapophysis; 51-1 two epurals; 52-1 anterior end of parhypural slightly removed from and not embracing centrum; 53-2 hypurals 1 + 2 + 3 + 4 fused and fused to centrum; 54-1 no uroneural; 55-1 no stegural; 96-3 13 principal caudal-fin rays; 97-2,3 two (in lower lobe) or three (in upper lobe) procurent caudal-fin rays.

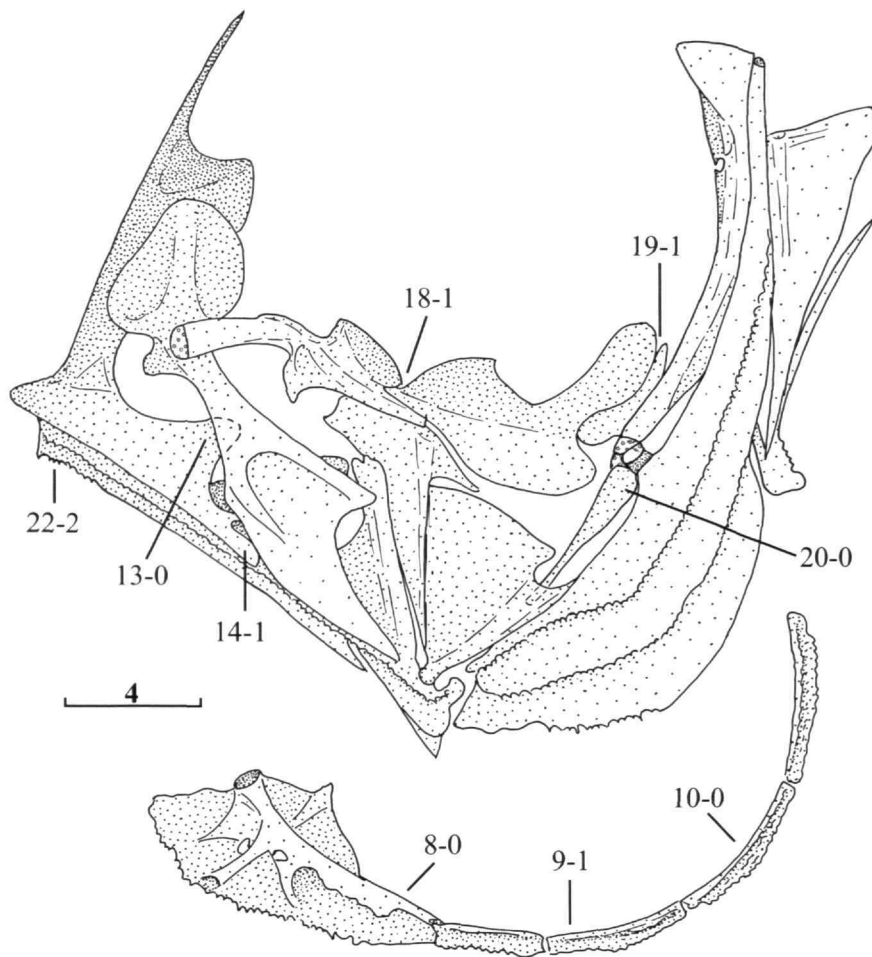


FIGURE 54.—Zeniontidae. Jaws, suspensorium, and opercular bones (above) and lachrymal and infraorbitals (excluding dermosphenotic) of *Capromimus abbreviatus*, AMS I.23650001, 61 mm SL, lateral views. Character-state: 8-0 deep lachrymal; 9-1 four infraorbitals; 10-0 slender, tubular infraorbitals; 13-0 postmaxillary process present; 14-1 alveolar process of premaxilla ventrally indented into two blunt lobes; 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-0 no symplectic ventral flange; 22-2 multiple dentary serrations.

FIGURE 55.—Zeniontidae. Dentary of *Capromimus abbreviatus*, AMS I.23650001, 61 mm SL, lateral view. Parallel lines and wavy lines show, respectively, the more anterior and more posterior dental cartilages in their natural position. The distal end of the posterior dental cartilage attaches to the inner surface of the lower end of the maxilla. Small circles in mechanical stippling show the lower region of the ligament from the upper ends of the dentary and articular that attaches to the inner surface of the middle of the maxilla. Character-state: 21-1 two dental cartilages of moderate length, the first shorter; 22-2 multiple dentary serrations.

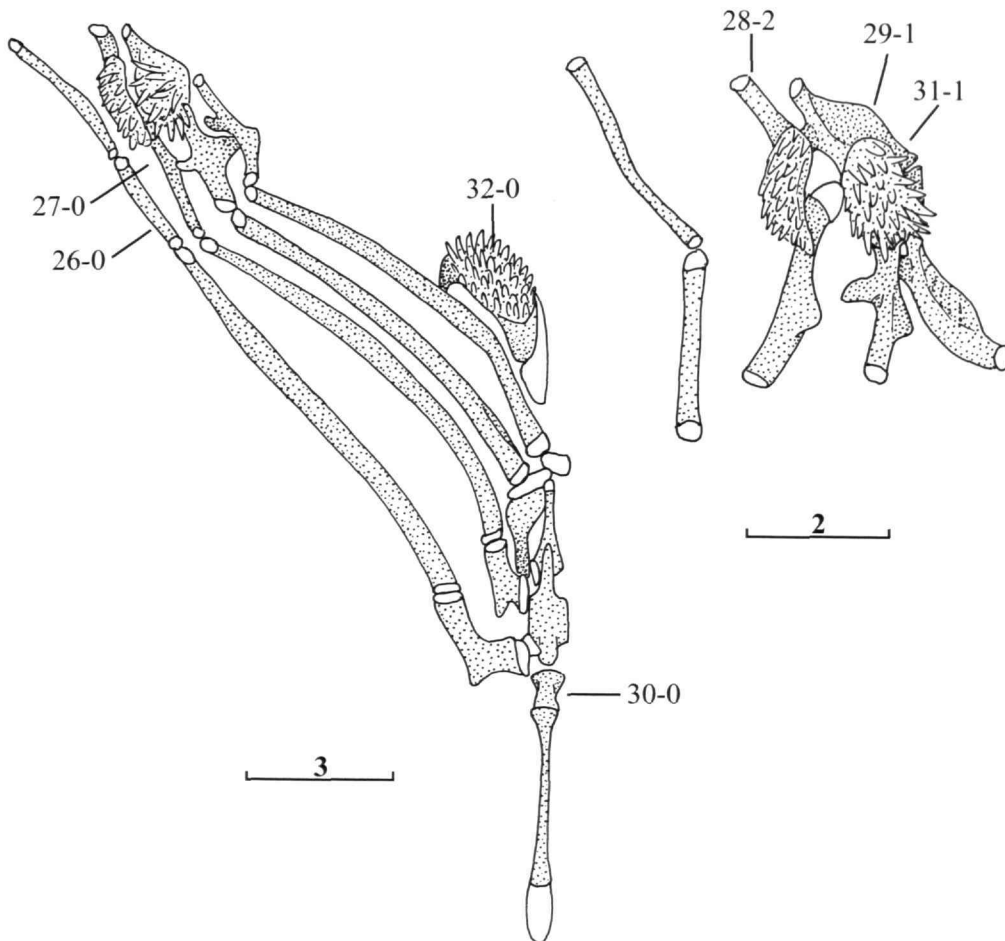
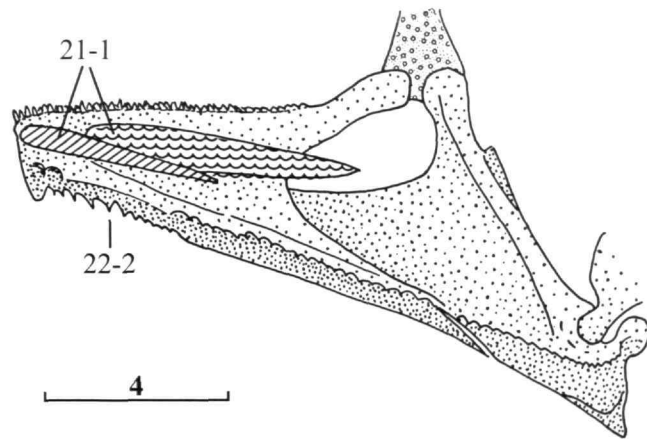


FIGURE 56.—Zeniontidae. Right side of the branchial arches (left), artificially laid out with the dorsal elements reflected, and detail (upper right) of the epibranchials and pharyngobranchials, artificially even more laid out, reflected, and spread apart, of *Capromimus abbreviatus*, AMS I.23650001, 61 mm SL, dorsal view. Character-state: 26-0 no uncinat process; 27-0 no interarcual cartilage; 28-2 long second pharyngobranchial suspensory shaft; 29-1 moderately long third pharyngobranchial suspensory shaft; 30-0 first basibranchial not depressed below surface of basihyal; 31-1 no fourth pharyngobranchial toothplate; 32-0 fifth ceratobranchial toothed.

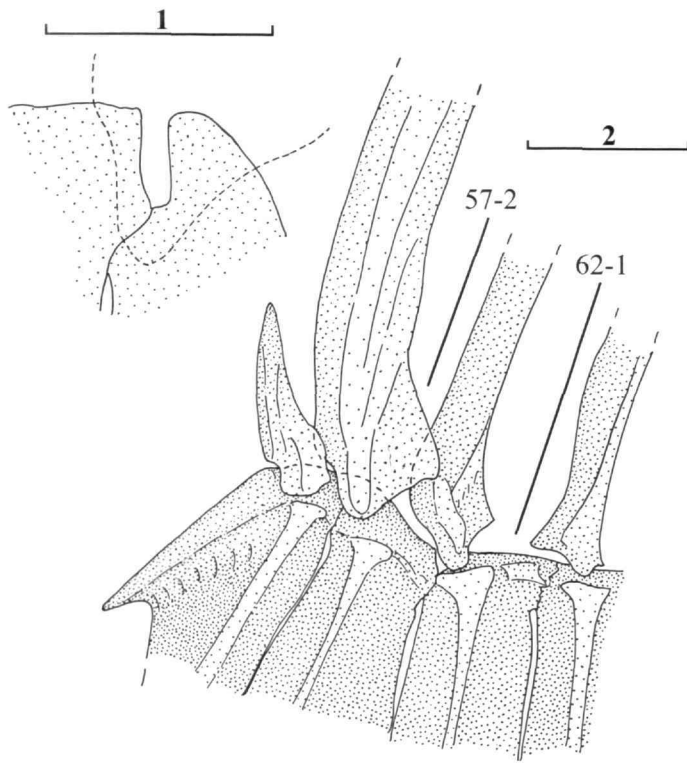


FIGURE 57.—Zeniontidae. First four dorsal-fin spines and first four dorsal-fin pterygiophores, with an inset (top left) of the median flange on the distal ends of the first two pterygiophores around which the second dorsal-fin spine articulates (base of second dorsal spine outlined by dashed line), of *Capromimus abbreviatus*, AMS I.23650001, 61 mm SL, lateral view. Character-state: 57-2 locking mechanism between second and third dorsal-fin spines; 62-1 no ossified spinous dorsal-fin distal radial.

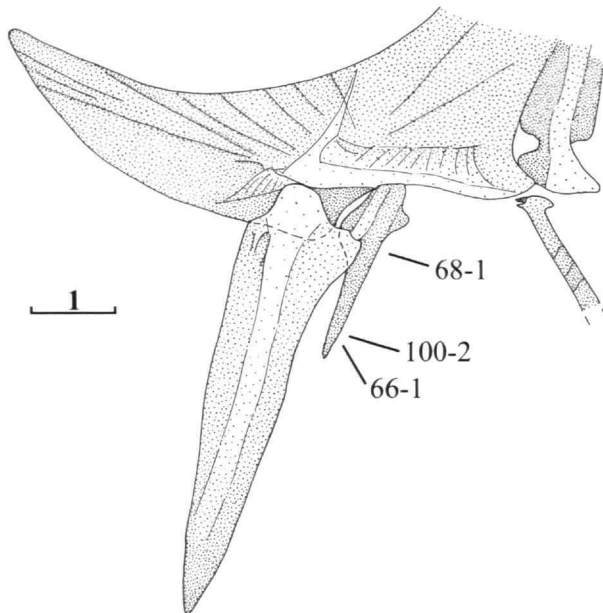


FIGURE 58.—Zeniontidae. The two anal-fin spines, first anal-fin ray, and lower region of the first two anal-fin pterygiophores of *Capromimus abbreviatus*, AMS I.23650001, 61 mm SL, lateral view. At the base of the anal-fin ray, the anteriorly protruding structure is the paired distal pterygiophore. The region of the second anal-fin spine overlapped by the locking flange of the first anal-fin spine is indicated by a dashed line. Character-state: 66-1 locking mechanism between first and second anal-fin spines; 68-1 second anal-fin spine less than one-half length of first spine; 100-2 two anal-fin spines.

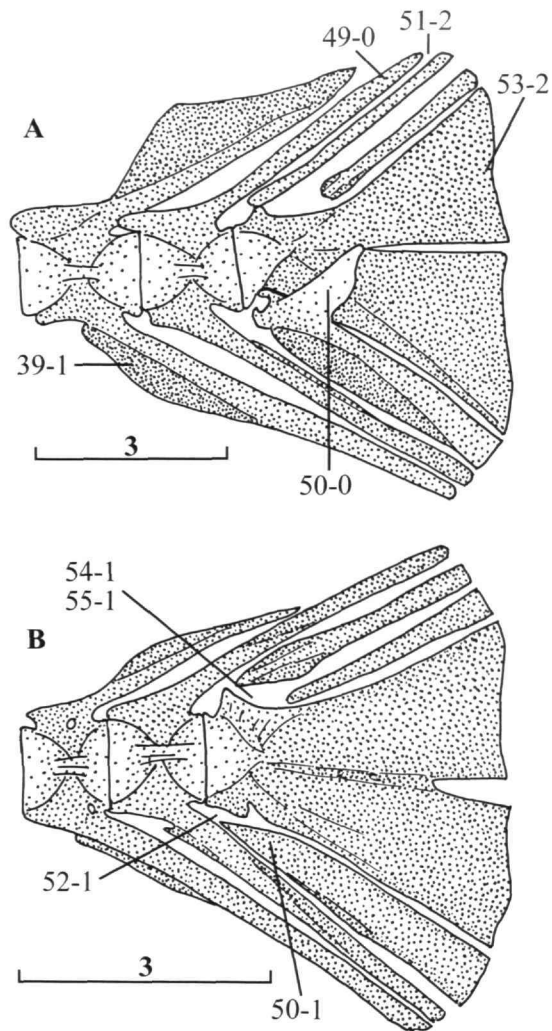


FIGURE 59.—Zeniontidae. Caudal skeleton, lateral view: A, *Cyttomimus stelgis*, USNM 306156, 76 mm SL; B, *Capromimus abbreviatus*, AMS I.23650001, 61 mm SL. Character-state: 39-1 PU3 first modified vertebra in caudal peduncle (A, B); 49-0 NPU2 long (A, B); 50-0 hypurapophysis present; 50-1 no hypurapophysis; 51-2 one epural (A, B); 52-1 anterior end of parhypural slightly removed from and not embracing centrum (A, B); 53-2 hypurals 1 + 2 + 3 + 4 fused and fused to centrum (A, B); 54-1 no uroneural (A, B); 55-1 no stegural (A, B).

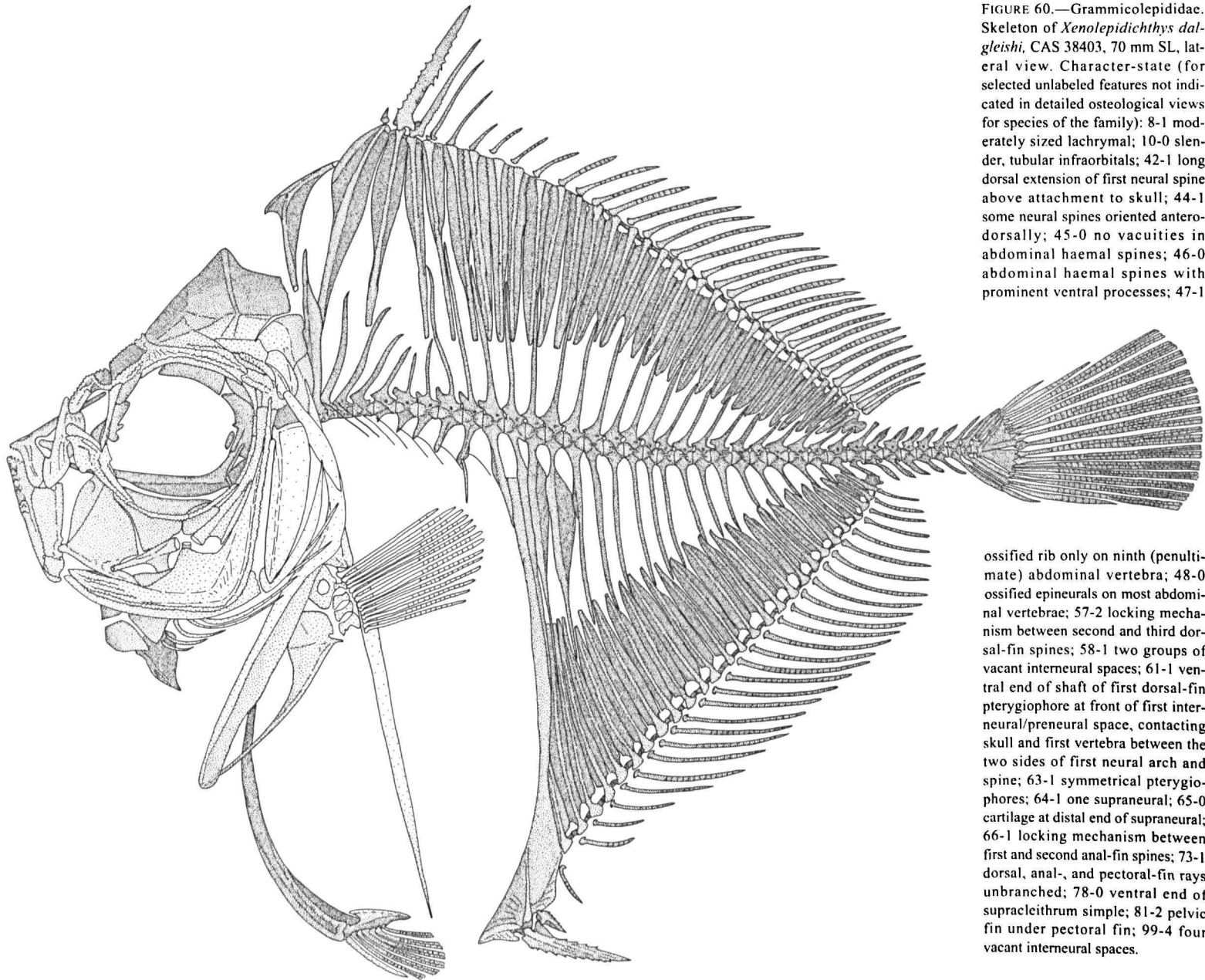


FIGURE 60.—Grammicolepididae. Skeleton of *Xenolepidichthys dalgleishi*, CAS 38403, 70 mm SL, lateral view. Character-state (for selected unlabeled features not indicated in detailed osteological views for species of the family): 8-1 moderately sized lachrymal; 10-0 slender, tubular infraorbitals; 42-1 long dorsal extension of first neural spine above attachment to skull; 44-1 some neural spines oriented anterodorsally; 45-0 no vacuities in abdominal haemal spines; 46-0 abdominal haemal spines with prominent ventral processes; 47-1

ossified rib only on ninth (penultimate) abdominal vertebra; 48-0 ossified epineurals on most abdominal vertebrae; 57-2 locking mechanism between second and third dorsal-fin spines; 58-1 two groups of vacant interneural spaces; 61-1 ventral end of shaft of first dorsal-fin pterygiophore at front of first interneural/preneural space, contacting skull and first vertebra between the two sides of first neural arch and spine; 63-1 symmetrical pterygiophores; 64-1 one supraneural; 65-0 cartilage at distal end of supraneural; 66-1 locking mechanism between first and second anal-fin spines; 73-1 dorsal, anal-, and pectoral-fin rays unbranched; 78-0 ventral end of supracleithrum simple; 81-2 pelvic fin under pectoral fin; 99-4 four vacant interneural spaces.

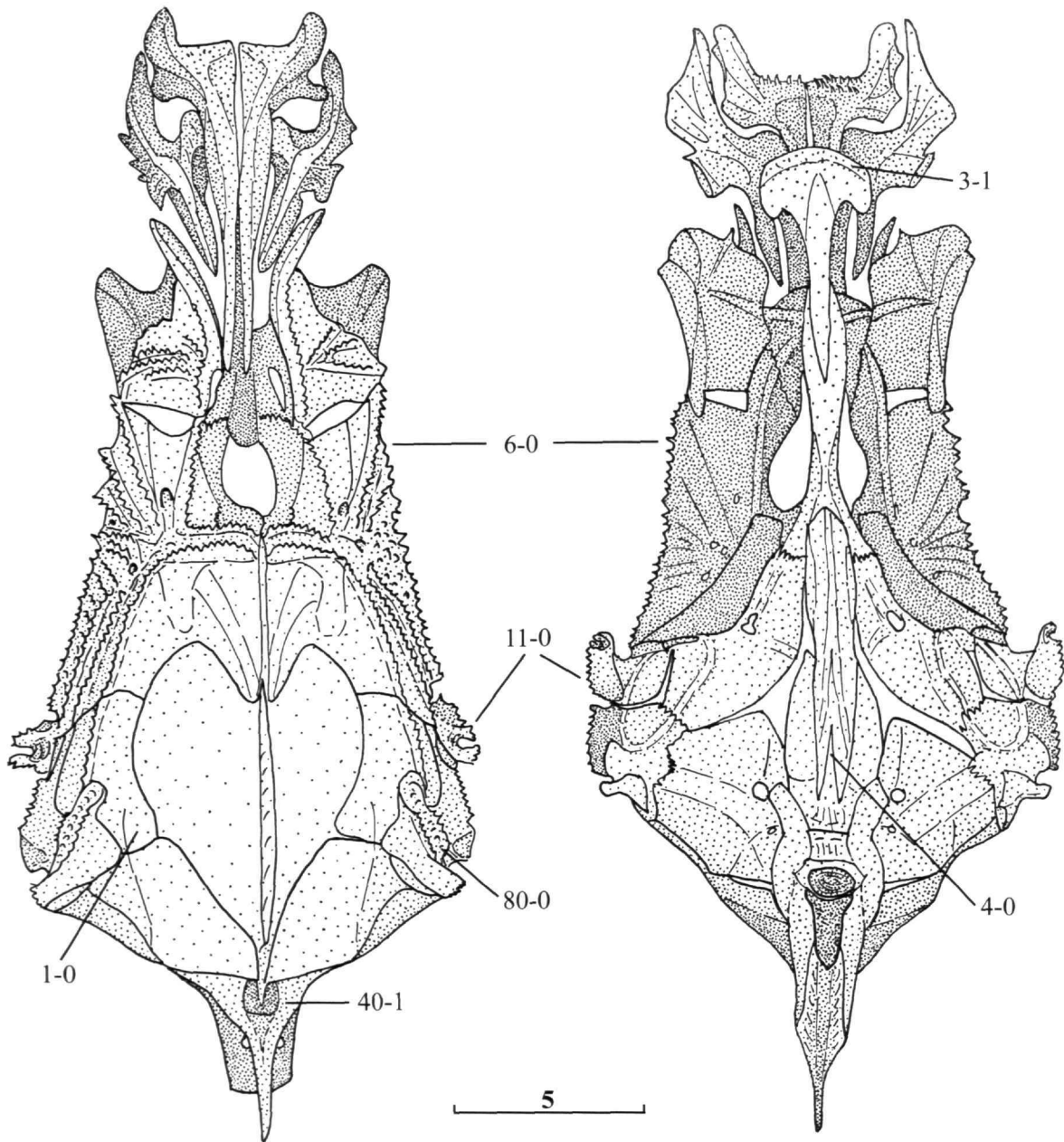


FIGURE 61.—Grammicolepididae. Skull and first vertebra of *Xenolepidichthys dalgleishi*, CAS 38406, 75 mm SL, dorsal (left) and ventral views. Character-state: 1-0 parietal present; 3-1 no vomerine teeth; 4-0 no parasphenoid opening into posterior myodome; 6-0 supraocular serrations on frontal; 11-0 dermosphenotic a distinctly separate ossification; 40-1 first neural arch and spine closely applied to skull; 80-0 one long extrascapular.

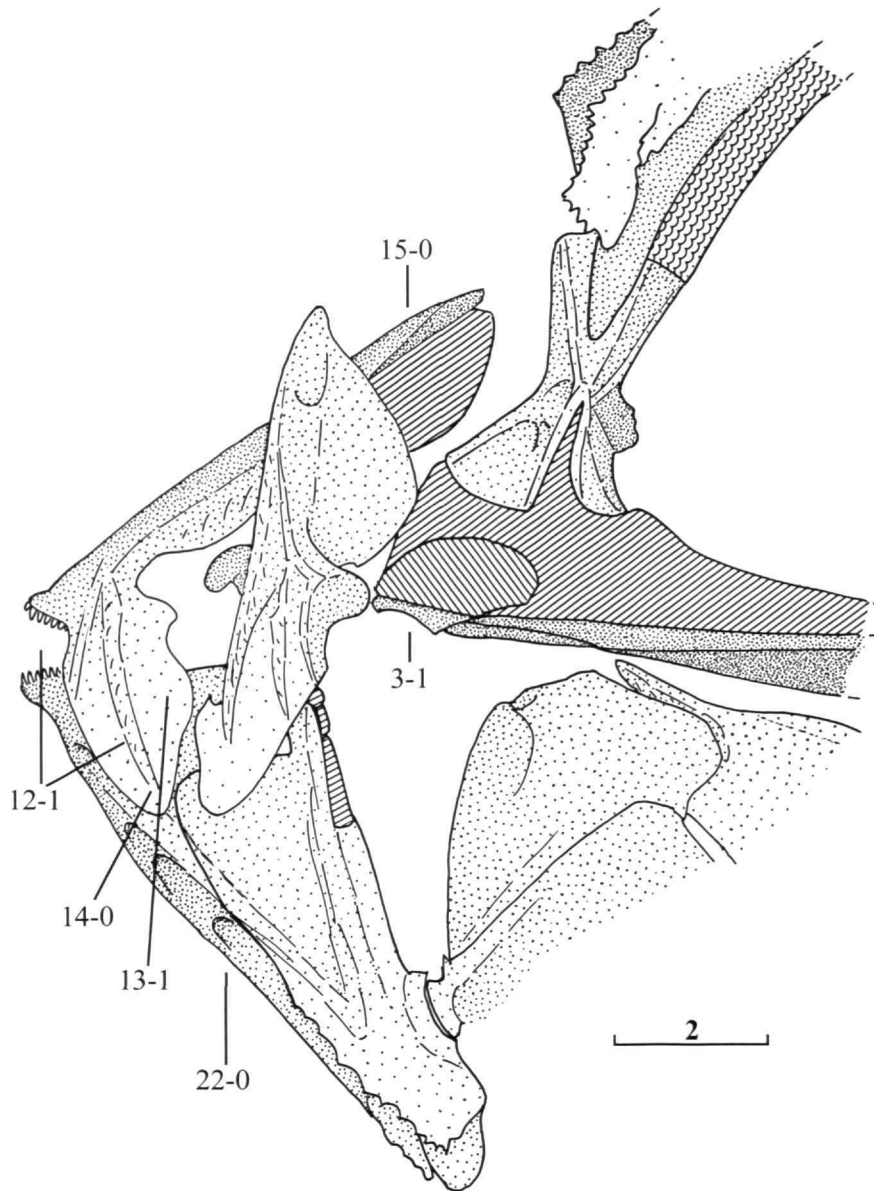


FIGURE 62.—Grammicolepididae. Jaws and cartilages in the ethmoid region of *Xenolepidichthys dalgleishi*, USNM 320016, 64 mm SL, lateral view. Parallel lines show the cartilages below the rear end of the ascending premaxillary process, between the lateral ethmoid and the vomer and parasphenoid, and along the upper rear border of the articular. Wavy lines show the cartilage that continues posteriorly to the rear of the orbit and contacts the pterosphenoids, a probable synapomorphy of zeiforms not enumerated herein because the condition is unknown in many taxa (for our documentation of this, see character VI of Johnson and Patterson, 1993, in "Previous Phylogenetic Analyses of Zeiforms"). Character state: 3-1 no vomerine teeth; 12-1 small mouth, alveolar process less deep than lateral ethmoid; 13-1 no postmaxillary process; 14-0 alveolar process of premaxilla simple; 15-0 ascending premaxillary process reaching no further than front of lateral ethmoid and orbit; 22-0 no dentary serrations.

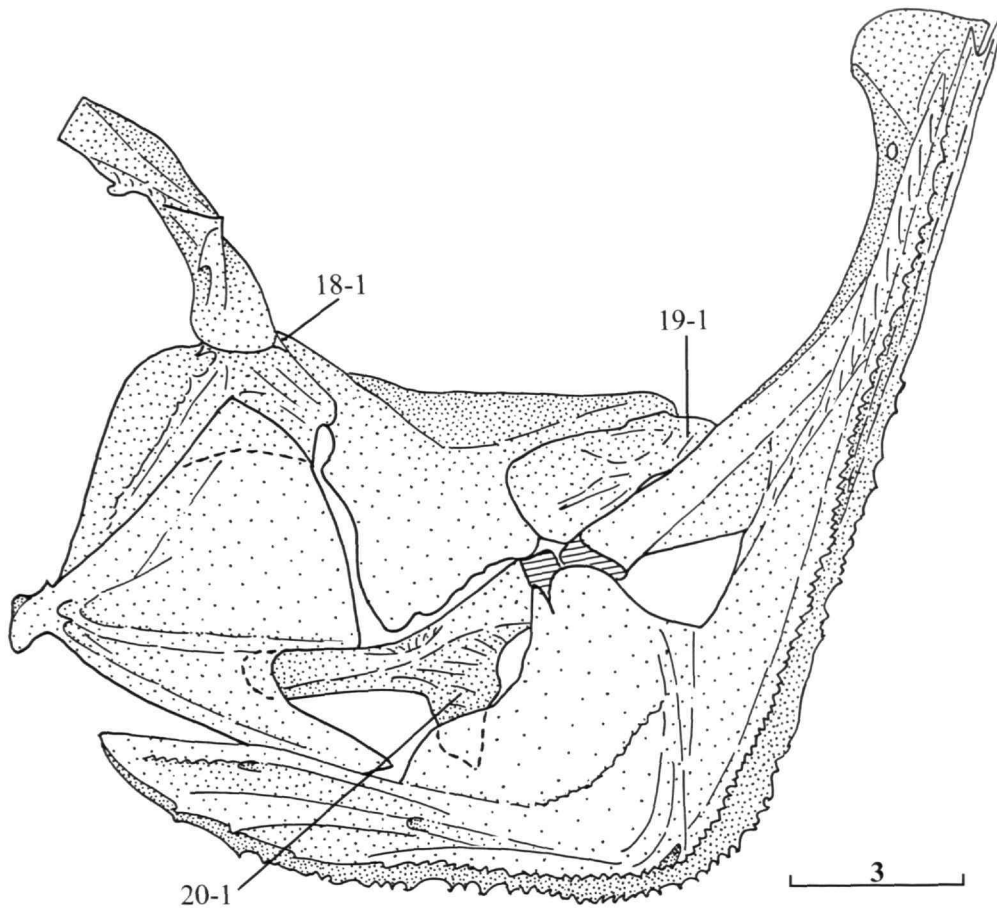


FIGURE 63.—Grammicolepididae. Suspensorium and preopercle of *Xenolepidichthys dalgleishi*, CAS 38406, 75 mm SL, lateral view. The extent of the ventral flange of the symplectic below the upper border of the preopercle is indicated by a dashed line, as is its anterior end under the quadrate. Character-state: 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-1 symplectic ventral flange.

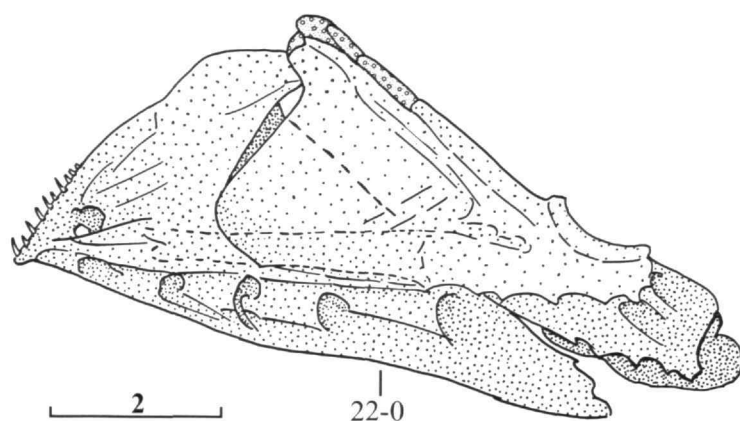


FIGURE 64.—Grammicolepididae. Lower jaw of *Xenolepidichthys dalgleishi*, USNM 320016, 59 mm SL, lateral view. The illustration is at a right angle to the lower jaw, whereas the view of the lower jaw in Figure 62 is somewhat oblique because of the considerable inward slant of the lower border in its natural position. Small circles in mechanical stippling show cartilages along the upper border of the articular. Character-state: 22-0 no dentary serrations.

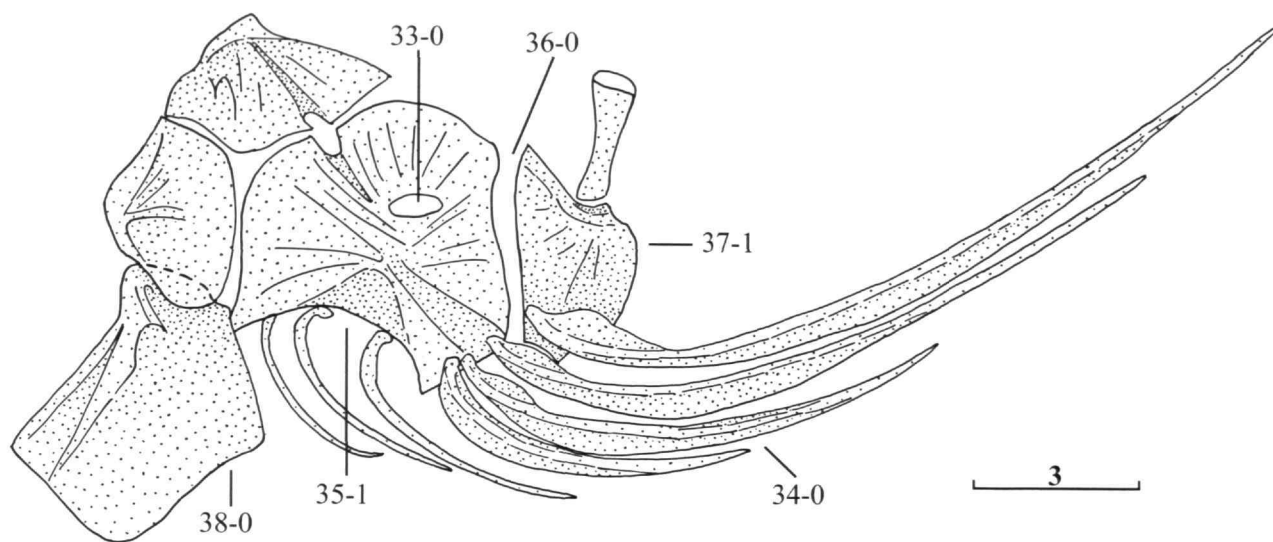


FIGURE 65.—Grammicolepididae. Hyoid arch, branchiostegal rays, and urohyal of *Xenolepidichthys dalgleishi*, CAS 38406, 75 mm SL, lateral view. Character-state: 33-0 beryciform foramen present; 34-0 branchiostegals spread over/along both epihyal and ceratohyal; 35-1 no ceratohyal notches; 36-0 ceratohyal-epihyal articulation through cartilage only; 37-1 epihyal less deep than rear of ceratohyal; 38-0 urohyal no longer than ceratohyal.

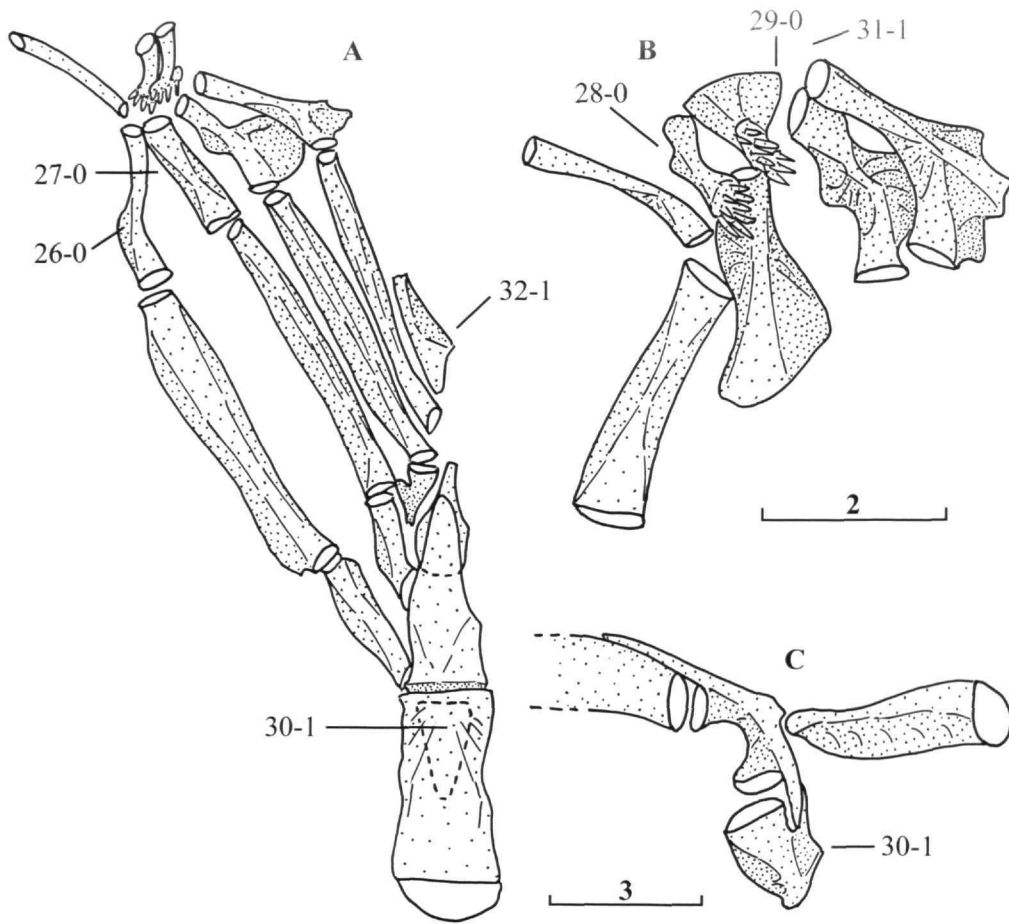


FIGURE 66.—Grammicolepididae. *Xenolepidichthys dalgleishi*, CAS 38406, 75 mm SL, dorsal (A, B) and lateral (C) views: A, right side of the branchial arches, artificially laid out with the dorsal elements reflected; B, detail of the epibranchials and pharyngobranchials, artificially even more laid out, reflected, and spread apart; C, basihyal (right) and the three basibranchials (first to third, from front (below) to rear (above)). (Scale bar the same for A and C.) Character-state: 26-0 no uncinat process; 27-0 no interarcual cartilage; 28-0 short second pharyngobranchial suspensory shaft; 29-0 short third pharyngobranchial suspensory shaft; 30-1 first basibranchial depressed below surface of basihyal; 31-1 no fourth pharyngobranchial toothplate; 32-1 no fifth ceratobranchial teeth.

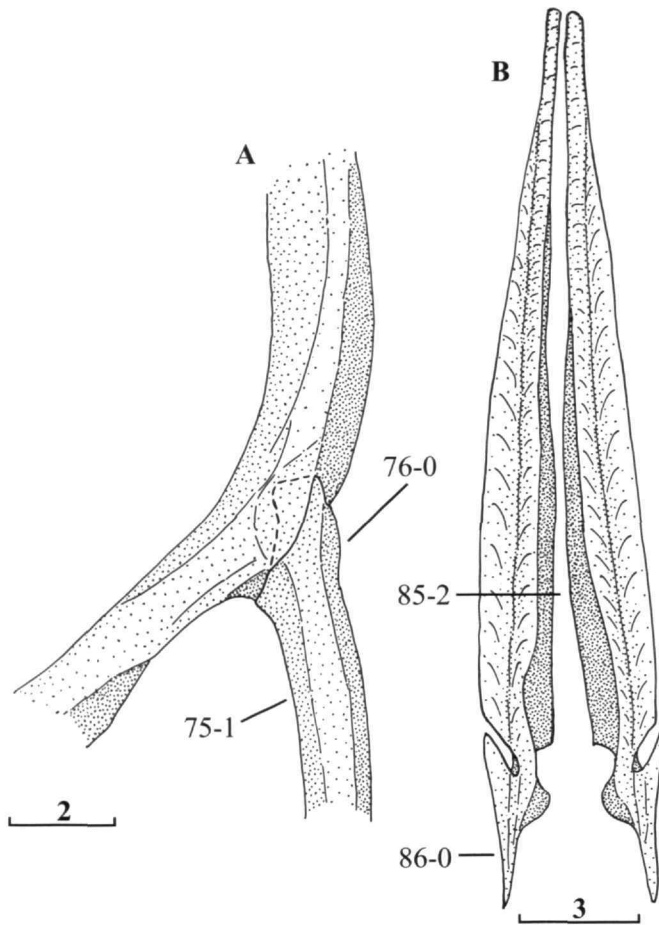


FIGURE 67.—Grammicolepididae. *Xenolepidichthys dalgleishi*, CAS 38406, 75 mm SL: A, right cleithrum and adjacent region of the single postcleithrum, medial view; B, pelvis, dorsal view. Character-state: 75-1 single postcleithrum; 76-0 no flange on single postcleithrum; 85-2 basiptyrgia not in close contact in middle region; 86-0 short posterior process of pelvis.

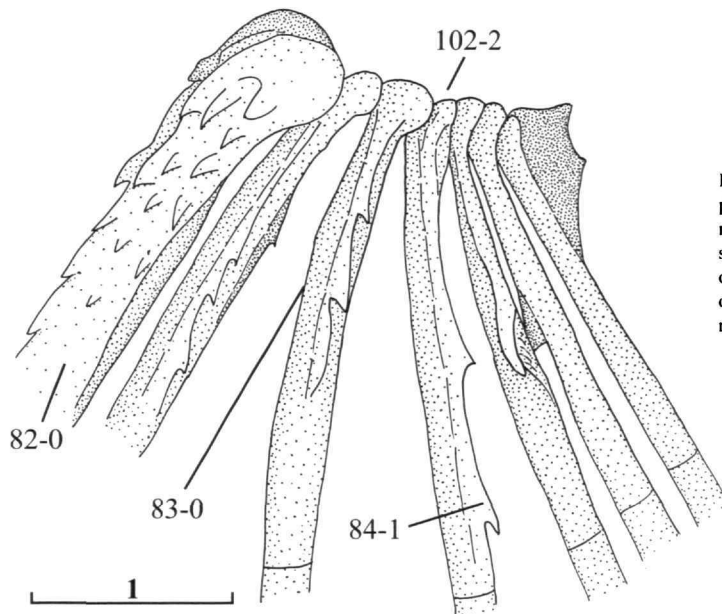


FIGURE 68.—Grammicolepididae. Basal region of the right pelvic fin of *Xenolepidichthys dalgleishi*, CAS 38406, 75 mm SL, ventral view. Character-state: 82-0 pelvic-fin spine present; 83-0 no anterolateral processes from bases of rays; 84-1 serrations present on low crests along posteroventral edges of rays; 102-2 total of seven pelvic-fin elements.

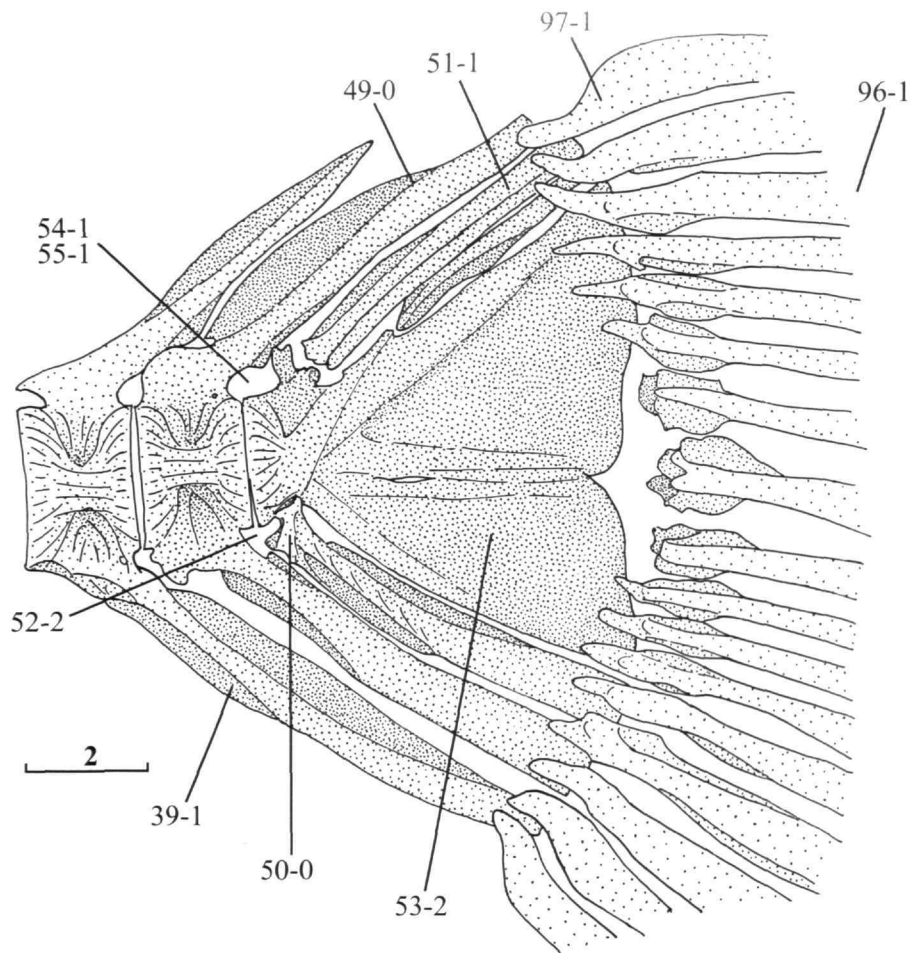


FIGURE 69.—Grammicolepididae. Caudal skeleton of *Xenolepidichthys dalgleishi*, CAS 38406, 75 mm SL, lateral view. Character-state: 39-1 PU3 first modified vertebra in caudal peduncle; 49-0 NPU2 long; 50-0 hypurapophysis present (relatively low and short); 51-1 two epurals; 52-2 peg and socket joint; 53-2 hypurals 1 + 2 + 3 + 4 fused and fused to centrum; 54-1 no uroneural; 55-1 no stegural; 96-1 15 principal caudal-fin rays; 97-1 one procurvent caudal-fin ray, both above and below.

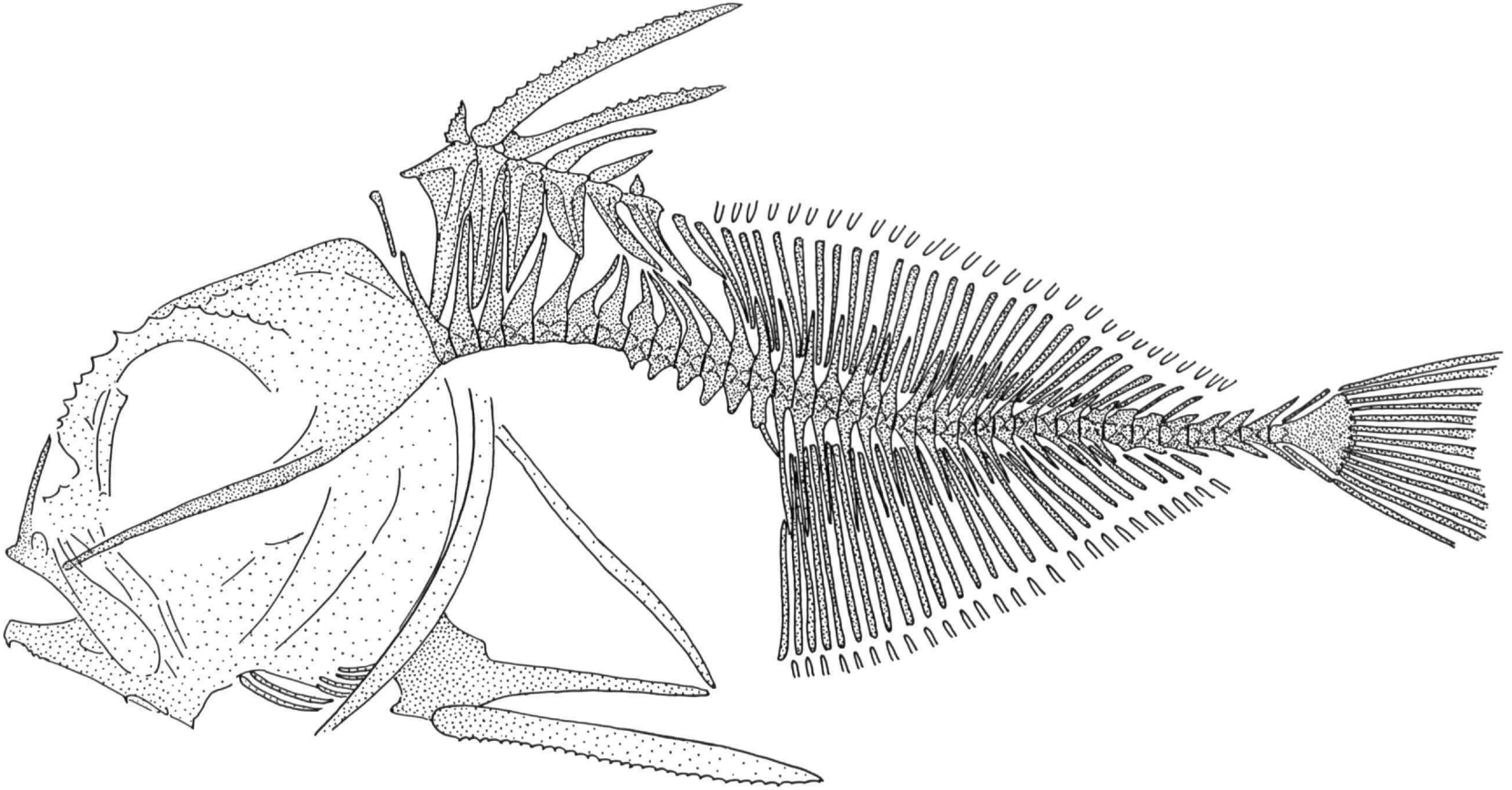


FIGURE 70.—Grammicolepididae. Skeleton of *Macrurocyttus acanthopodus*, MNHN 1994-1073, 45 mm SL, lateral view, based on a radiograph. The neural spine of the ninth caudal vertebra is abnormally bifurcate. Character-state (for selected unlabeled features not indicated in detailed osteological views for this species): 15-0 ascending premaxillary process reaching no further than front of lateral ethmoid and orbit; 44-1 some neural spines oriented anterodorsally; 45-0 no vacuities in abdominal haemal spines; 46-1 abdominal haemal spines without prominent ventral processes; 47-1 ossified rib only on thirteenth (last) abdominal vertebra (minority condition, in two of seven specimens; usually no ossified ribs, 47-3); 48-3 no ossified epineurals; 58-1 two groups of vacant interneural spaces (minority condition; usually three groups, 58-2); 59-2 three dorsal-fin pterygiophores anterior to fourth neural spine; 61-1 ventral end of shaft of first dorsal-fin pterygiophore at front of first interneural/preneural space, contacting skull and first vertebra between the two sides of first neural arch and spine; 63-1 symmetrical pterygiophores; 64-1 one supraneural; 81-2 pelvic fin somewhat anterior to pectoral fin; 99-5 five vacant interneural spaces; 100-0 no anal-fin spine.

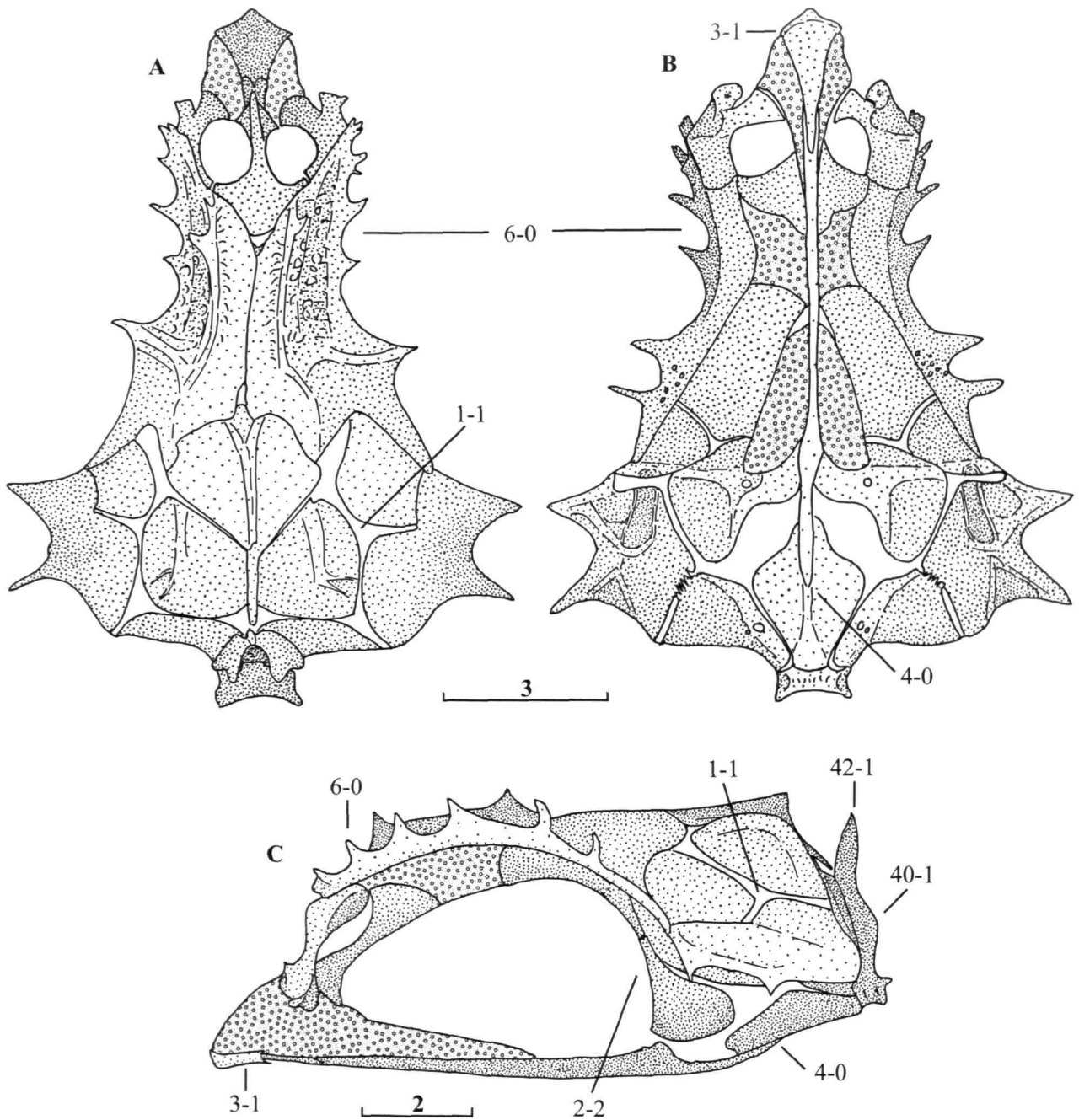


FIGURE 71.—Grammicolepididae. Skull and first vertebra of *Macrurocyttus acanthopodus*, USNM 93144, disarticulated specimen of unknown SL (see "Material"), dorsal (A), ventral (B), and lateral (C) views. Small circles in mechanical stippling show some of the major cartilages, with open spaces between the bones of the rear of the skull also cartilaginous. Character-state: 1-1 no parietal; 2-2 no basisphenoid; 3-1 no vomerine teeth; 4-0 no parasphenoid opening into posterior myodome; 6-0 supraocular serrations on frontal; 40-1 first neural arch and spine closely applied to skull; 42-1 long dorsal extension of first neural spine above attachment to skull.

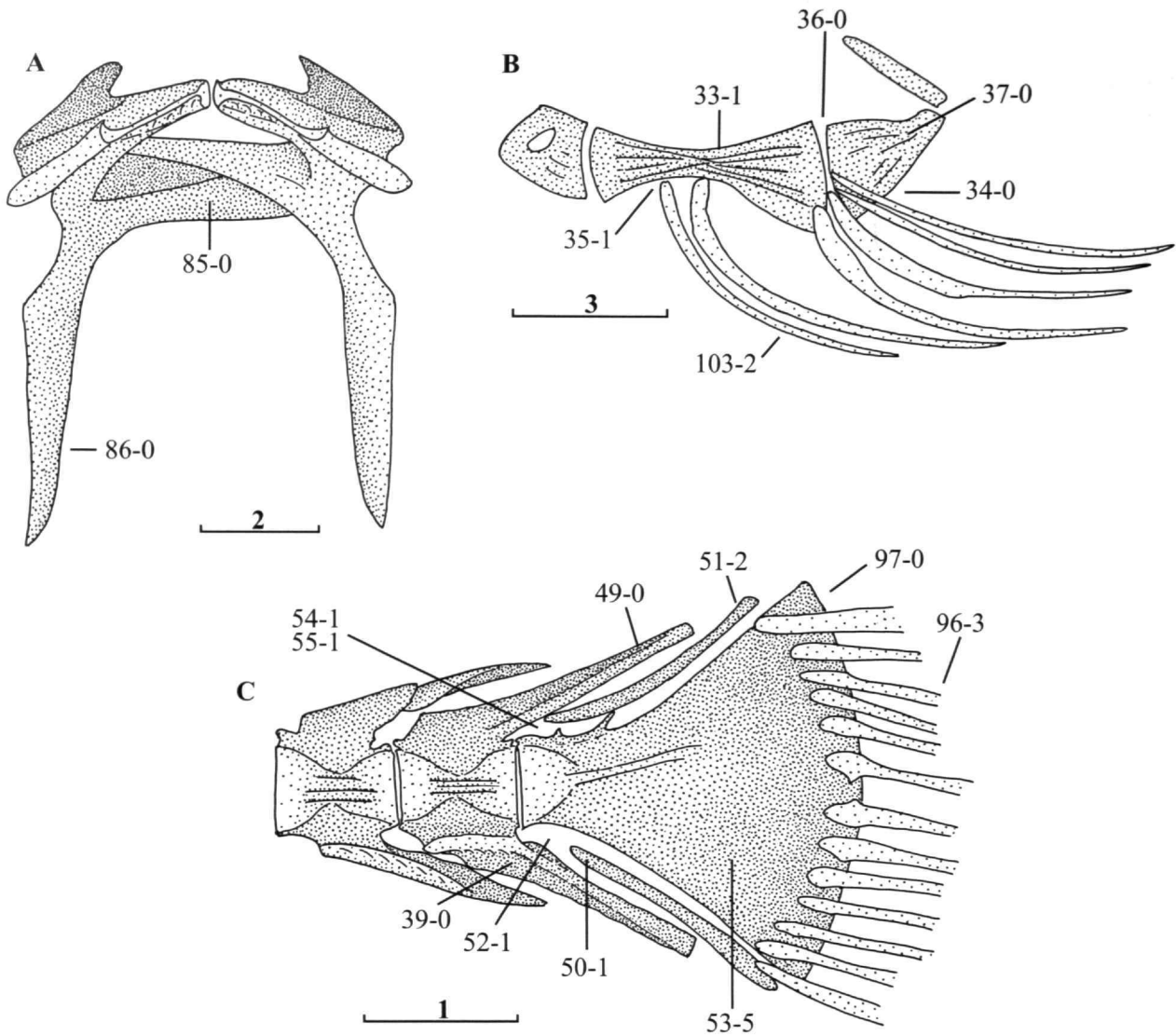


FIGURE 72.—Grammicolepididae. *Macrurocyttus acanthopodus*: A, USNM 93144, pelvis of disarticulated specimen of unknown SL (see "Material"), dorsal view. B, C, MNHN 1994-1072, 43 mm SL, lateral view: B, hyoid arch and branchiostegals; C, caudal skeleton. Character-state: 33-1 beryciform foramen represented by deep groove on ceratohyal; 34-0 branchiostegals spread over/along both epihyal and ceratohyal; 35-1 no ceratohyal notches; 36-0 ceratohyal-epihyal articulation through cartilage only; 37-0 epihyal about same depth as rear of ceratohyal; 39-0 PU2 first modified vertebra in caudal peduncle; 49-0 NPU2 long; 50-1 no hypurapophysis; 51-2 one epural; 52-1 anterior end of parhypural slightly removed from and not embracing centrum; 53-5 all hypurals fused to centrum (fifth hypural indistinguishably fused to the others or absent, in either case a condition unique among zeiforms, although fifth hypural with partial fusion in some zeids); 54-1 no uroneural; 55-1 no stegural; 85-0 broadly overlapping medial processes of basipterygia; 86-0 moderately long posterior process of pelvis; 96-3 13 principal caudal-fin rays; 97-0 no procurrent caudal-fin rays above or below; 103-2 six branchiostegals (2+4). There is only one hypohyal, a condition unique among zeiforms, but the foramen in the largely cartilaginous element may indicate a compound origin of the single piece.

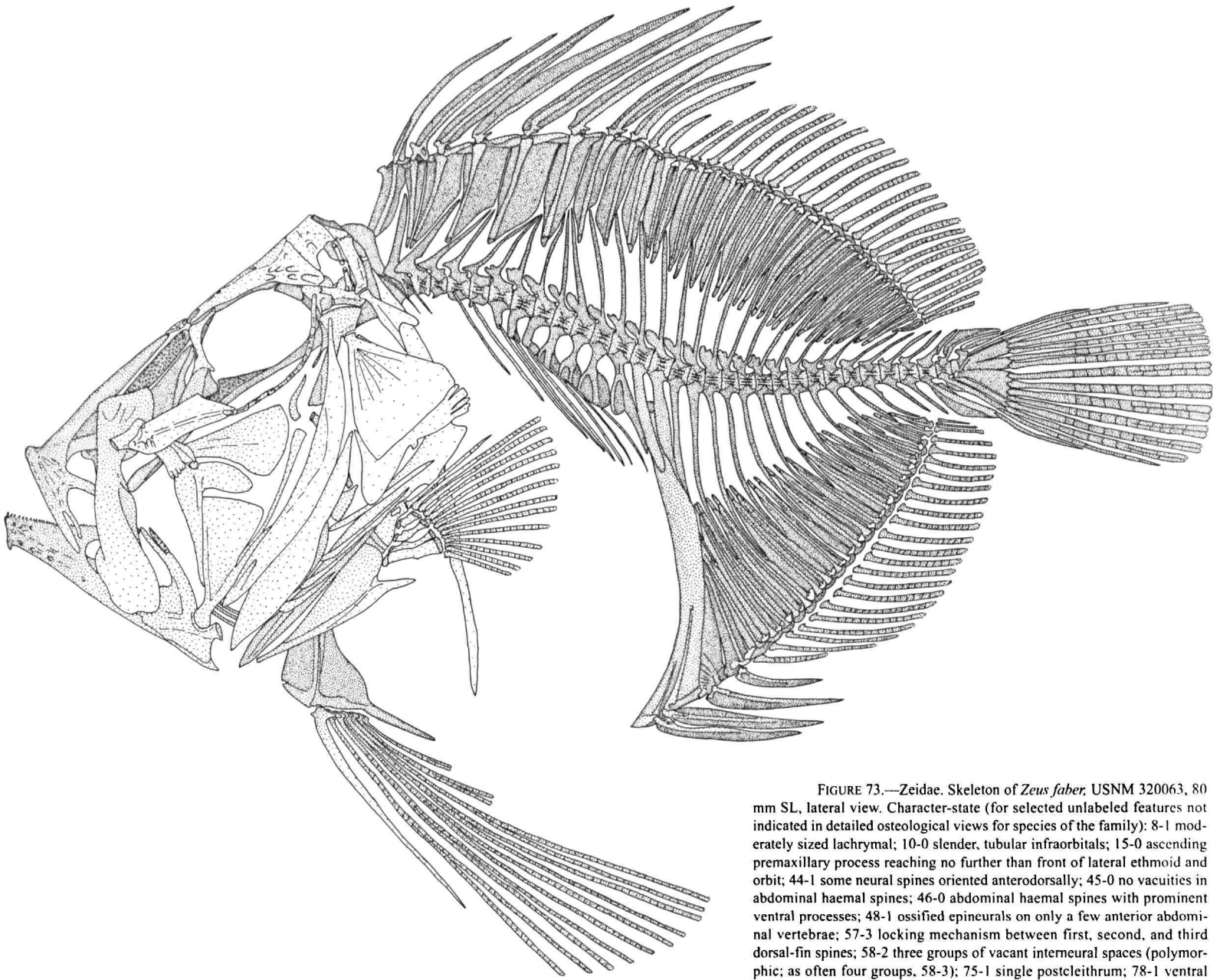


FIGURE 73.—Zeidae. Skeleton of *Zeus faber*, USNM 320063, 80 mm SL, lateral view. Character-state (for selected unlabeled features not indicated in detailed osteological views for species of the family): 8-1 moderately sized lachrymal; 10-0 slender, tubular infraorbitals; 15-0 ascending premaxillary process reaching no further than front of lateral ethmoid and orbit; 44-1 some neural spines oriented anterodorsally; 45-0 no vacuities in abdominal haemal spines; 46-0 abdominal haemal spines with prominent ventral processes; 48-1 ossified epineurals on only a few anterior abdominal vertebrae; 57-3 locking mechanism between first, second, and third dorsal-fin spines; 58-2 three groups of vacant interneural spaces (polymorphic; as often four groups, 58-3); 75-1 single postcleithrum; 78-1 ventral end of supracleithrum deeply bifurcate; 81-2 pelvic fin anterior to pectoral fin; 99-5 five vacant interneural spaces.

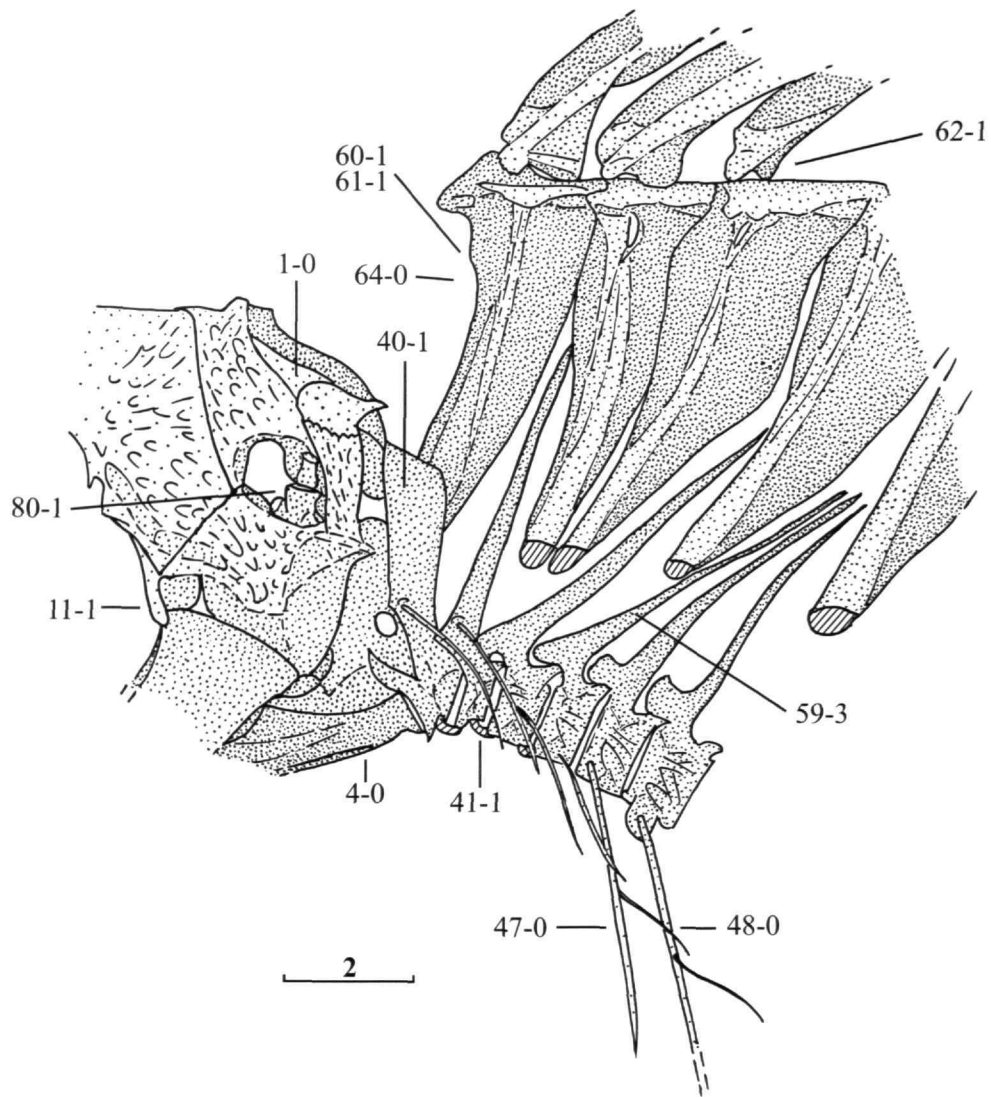


FIGURE 74.—Zeidae. Rear of the skull and the first six vertebrae and the more anterior dorsal-fin pterygiophores and dorsal-fin spines of *Zenopsis conchifer*, CAS 47401, 54 mm SL, lateral view. Parallel lines show the cartilaginous ventral ends of the pterygiophores and the bands of connective tissue between the anterior few vertebrae (which appear as ventral straps in lateral view under transmitted light but are actually much broader bands). Character-state: 1-0 parietal present; 4-0 no parasphenoid opening into posterior myodome; 11-1 dermosphenotic consolidated with sphenotic; 40-1 first neural arch and spine closely applied to skull; 41-1 flexible articulation of second and next few anterior abdominal vertebrae with skull-first vertebra, these vertebrae linked laterally and ventrally by ligamentous bands; 47-0 ossified ribs on most abdominal vertebrae behind fourth; 48-0 ossified epineurals on most abdominal vertebrae; 59-3 four dorsal-fin pterygiophores anterior to fourth neural spine; 60-1 ventral end of shaft of first dorsal-fin pterygiophore in first interneural/preneural space; 61-1 ventral end of shaft of first dorsal-fin pterygiophore at front of first interneural/preneural space, contacting skull and first vertebra between the two sides of first neural arch and spine; 62-1 no ossified spinous dorsal-fin distal radial; 64-0 no supraneural; 80-1 two tubular extrascapulars, not closely held to skull.

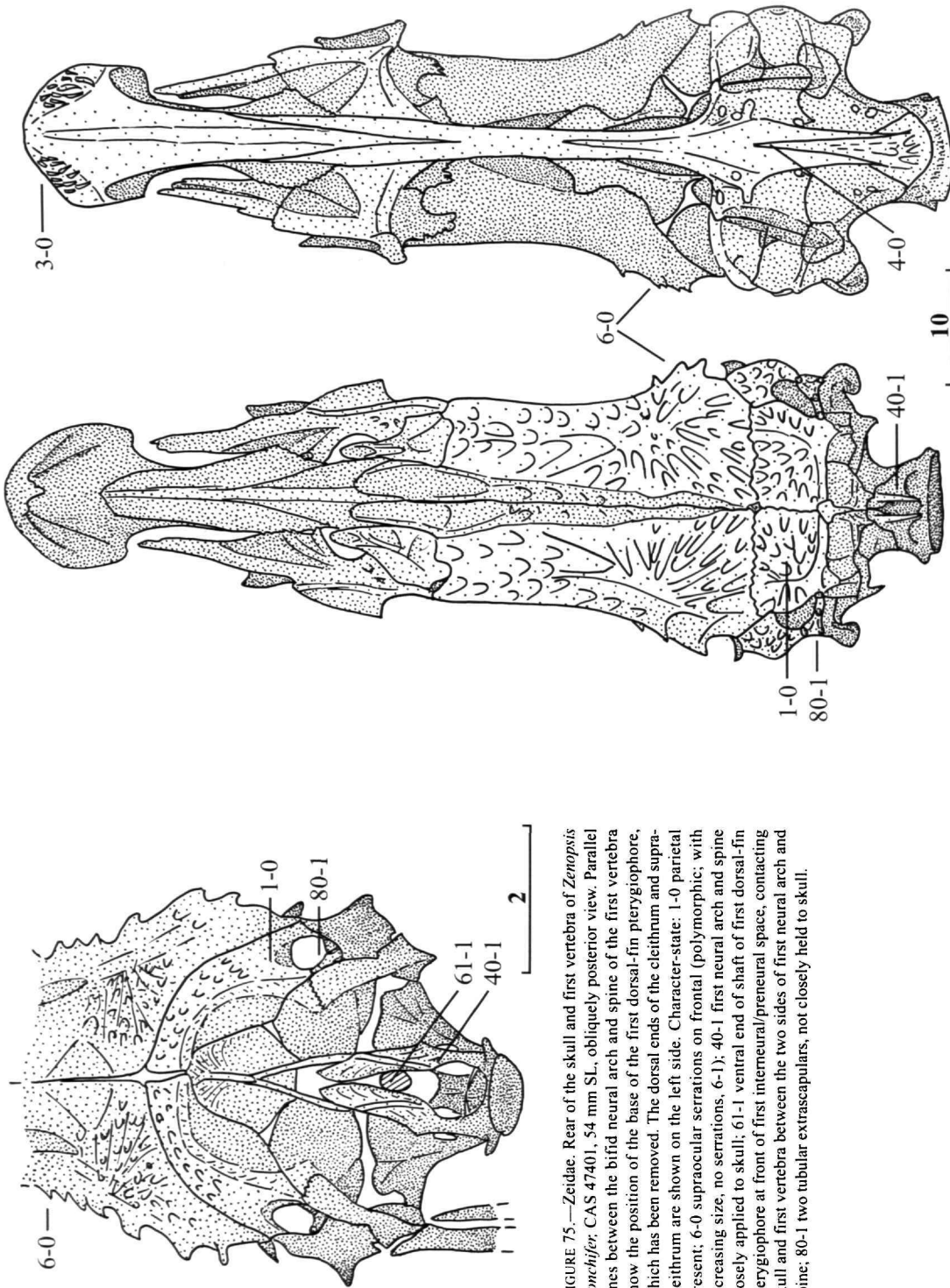


FIGURE 75.—Zeidae. Rear of the skull and first vertebra of *Zenopsis conchifer*; CAS 47401, 54 mm SL, obliquely posterior view. Parallel lines between the bifid neural arch and spine of the first vertebra show the position of the base of the first dorsal-fin pterygiophore, which has been removed. The dorsal ends of the cleithrum and supra-cleithrum are shown on the left side. Character-state: 1-0 parietal present; 6-0 supraocular serrations on frontal (polymorphic; with increasing size, no serrations, 6-1); 40-1 first neural arch and spine closely applied to skull; 61-1 ventral end of shaft of first dorsal-fin pterygiophore at front of first interneural/preneural space, contacting skull and first vertebra between the two sides of first neural arch and spine; 80-1 two tubular extrascapulars, not closely held to skull.

FIGURE 76.—Zeidae. Skull of *Zenopsis nebulosus*, AMNH 92291, 325 mm SL, dorsal (left) and ventral views. Character-state: 1-0 parietal present; 3-0 vomerrine teeth present; 4-0 no parasphenoid opening into posterior myodome; 6-0 supraocular serrations on frontal (many more serrations at smaller sizes, but polymorphic; serrations lost at largest sizes, 6-1); 40-1 first neural arch and spine closely applied to skull; 80-1 two tubular extrascapulars, not closely held to skull.

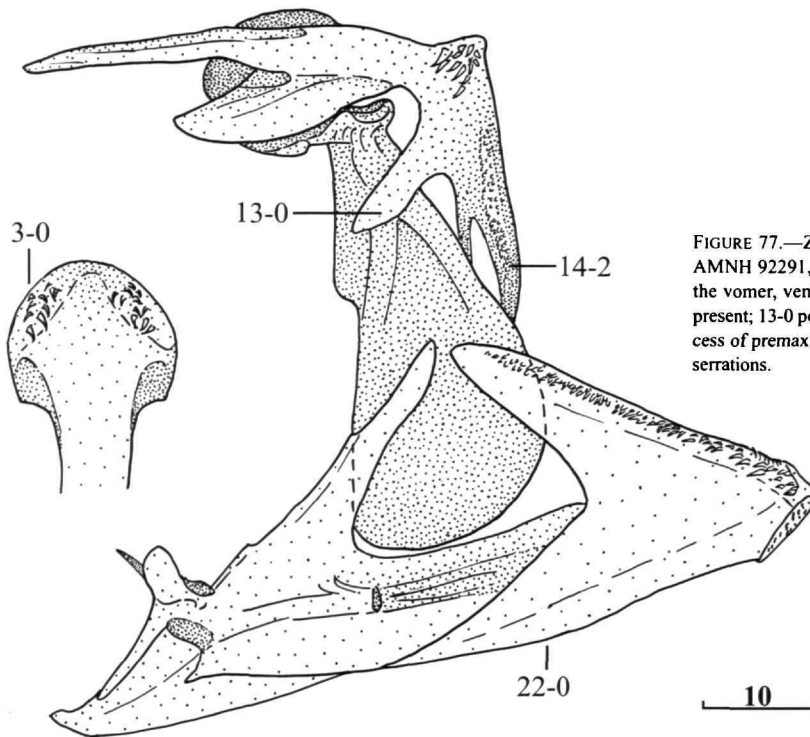


FIGURE 77.—Zeidae. Left-side jaws of *Zenopsis nebulosus*, AMNH 92291, 325 mm SL, medial view, and detail (left) of the vomer, ventral view. Character-state: 3-0 vomerine teeth present; 13-0 postmaxillary process present; 14-2 alveolar process of premaxilla deeply bifurcate ventrally; 22-0 no dentary serrations.

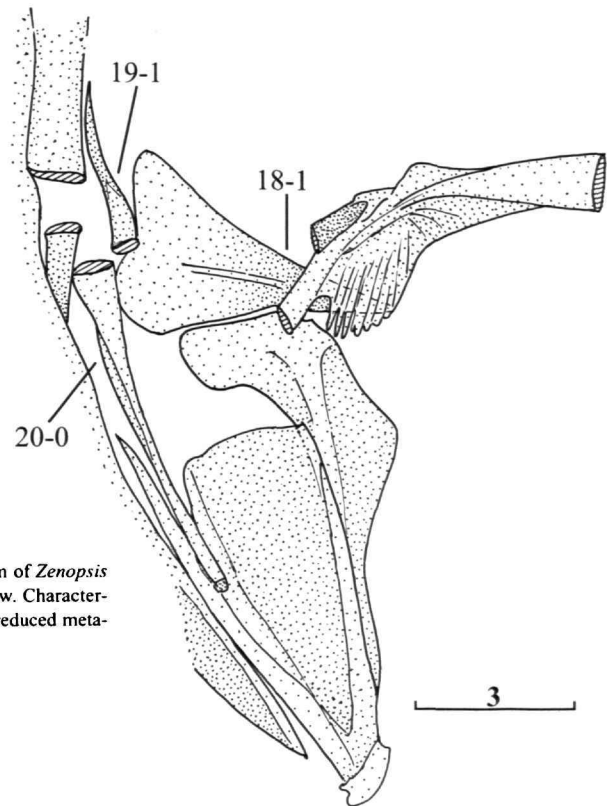


FIGURE 78.—Zeidae. Right-side suspensorium of *Zenopsis conchifer*, CAS 47401, 54 mm SL, lateral view. Character-state: 18-1 palatine articulation pivotal; 19-1 reduced metapterygoid; 20-0 no symplectic ventral flange.

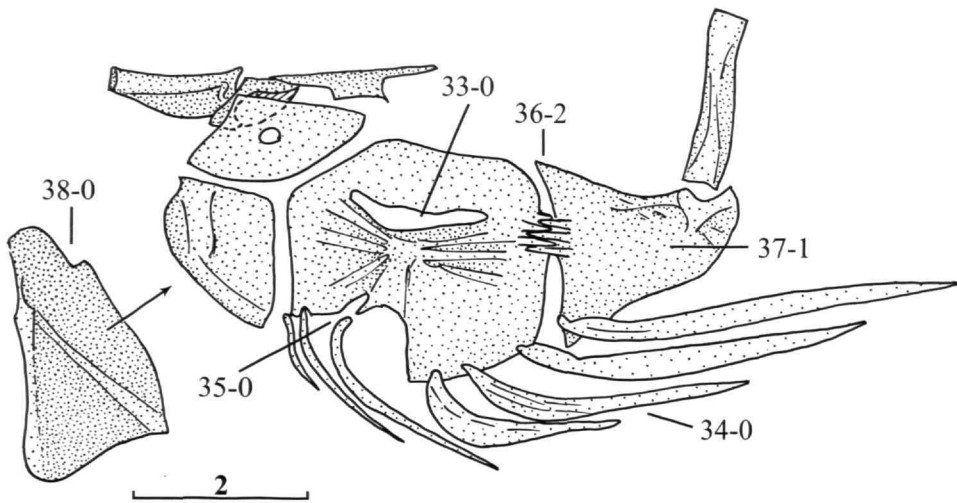


FIGURE 79.—Zeidae. Hyoid arch, branchiostegal rays, basihyal, and first two basibranchials of *Zenopsis conchifer*, CAS 47401, 54 mm SL, lateral view. The urohyal is illustrated lower and forward of its natural position internal to the hypohyals and anterior end of the ceratohyal. Character-state: 33-0 beryciform foramen present; 34-0 branchiostegals spread over/along both epihyal and ceratohyal; 35-0 ceratohyal notches present; 36-2 ceratohyal-epihyal articulation with bony interdigitations at all sizes; 37-1 epihyal less deep than rear of ceratohyal; 38-0 urohyal no longer than ceratohyal.

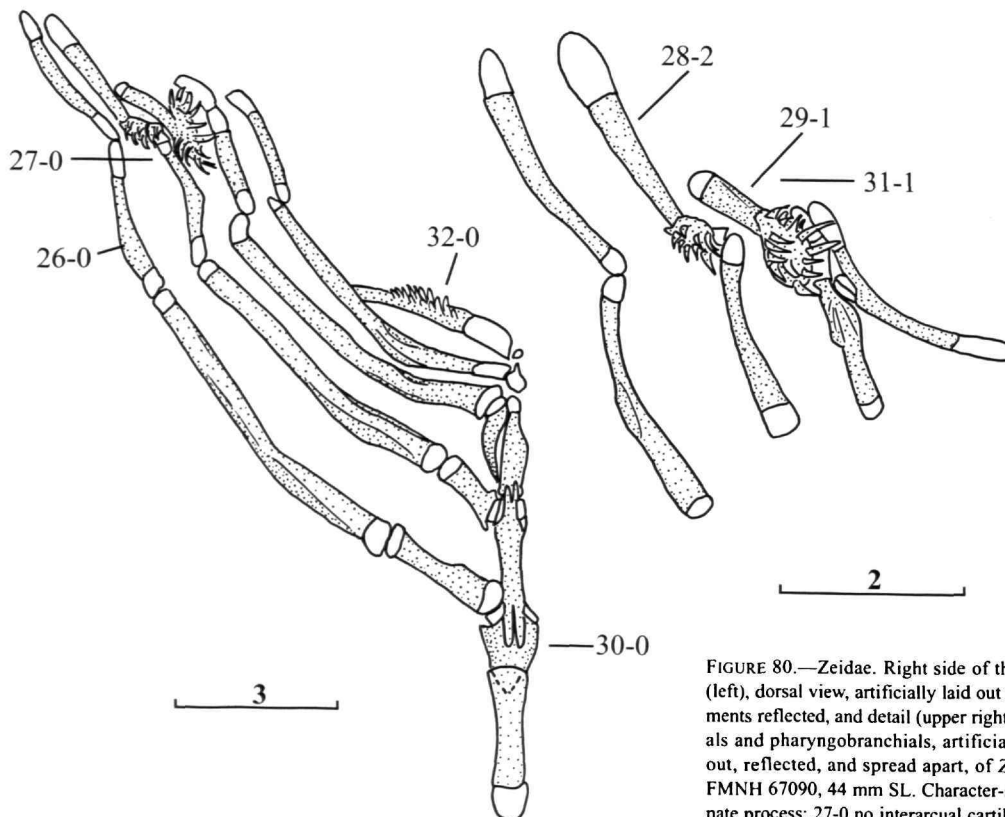


FIGURE 80.—Zeidae. Right side of the branchial arches (left), dorsal view, artificially laid out with the dorsal elements reflected, and detail (upper right) of the epibranchials and pharyngobranchials, artificially even more laid out, reflected, and spread apart, of *Zenopsis conchifer*, FMNH 67090, 44 mm SL. Character-state: 26-0 no uncinate process; 27-0 no interarcual cartilage; 28-2 long second pharyngobranchial suspensory shaft; 29-1 moderately long third pharyngobranchial suspensory shaft; 30-0 first basibranchial not depressed below surface of basihyal; 31-1 no fourth pharyngobranchial toothplate; 32-0 fifth ceratobranchial toothed.

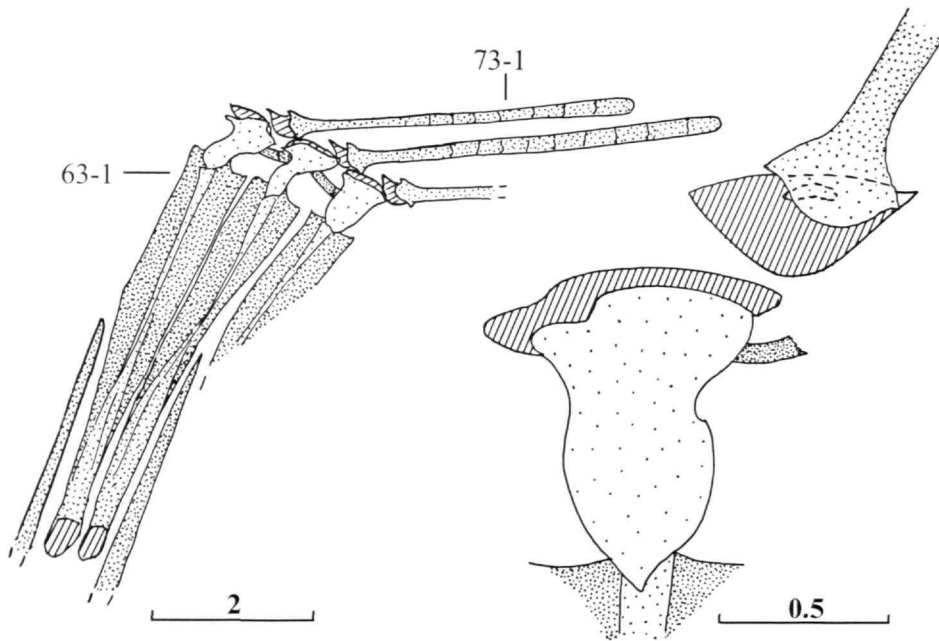


FIGURE 81.—Zeidae. Typical soft dorsal-fin pterygiophores (between neural spines of third and fourth abdominal vertebrae) (left), and detail of the articulation of the base of a dorsal-fin ray with the distal end of the pterygiophore in *Zenopsis conchifer*, FMNH 67090, 44 mm SL, lateral views. Parallel lines are cartilages. The dashed line at the base of the dorsal-fin ray in the detail is the ossified distal pterygiophore. Character-state: 63-1 symmetrical pterygiophores; 73-1 dorsal-fin rays unbranched.

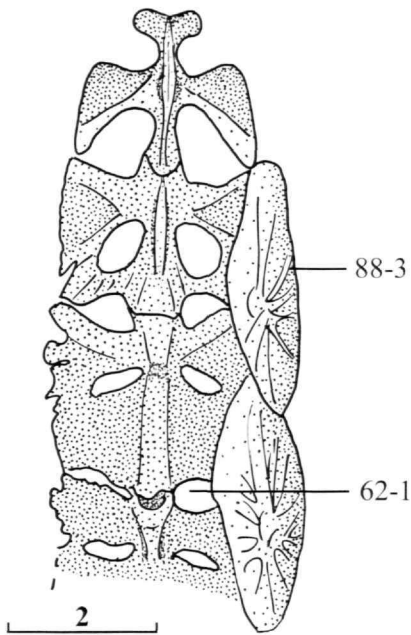


FIGURE 82.—Zeidae. First three spinous dorsal-fin pterygiophores (fourth incomplete), with the first two buckler plates in place on the right side, of *Zenopsis conchifer*, CAS 47401, 54 mm SL, dorsal view. The first three dorsal-fin spines articulate around the median crests on each pterygiophore (toward middle of first pterygiophore and front of second and third pterygiophores). Character-state: 62-1 no ossified spinous dorsal-fin distal radial; 88-3 large buckler plates along base of anterior dorsal-fin spines.

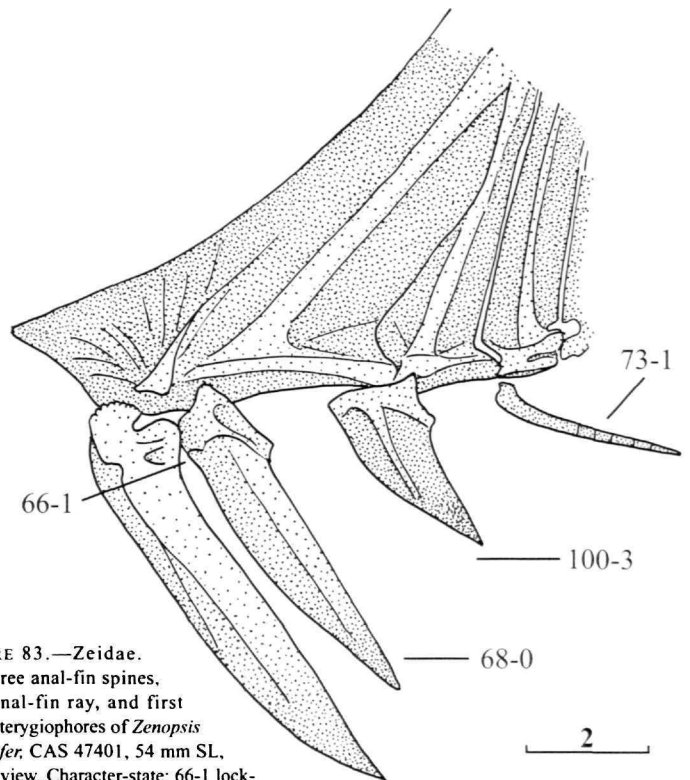


FIGURE 83.—Zeidae. The three anal-fin spines, first anal-fin ray, and first three pterygiophores of *Zenopsis conchifer*, CAS 47401, 54 mm SL, lateral view. Character-state: 66-1 locking mechanism between first and second anal-fin spines; 68-0 second anal-fin spine more than one-half length of first spine; 73-1 anal-fin rays unbranched; 100-3 three anal-fin spines.

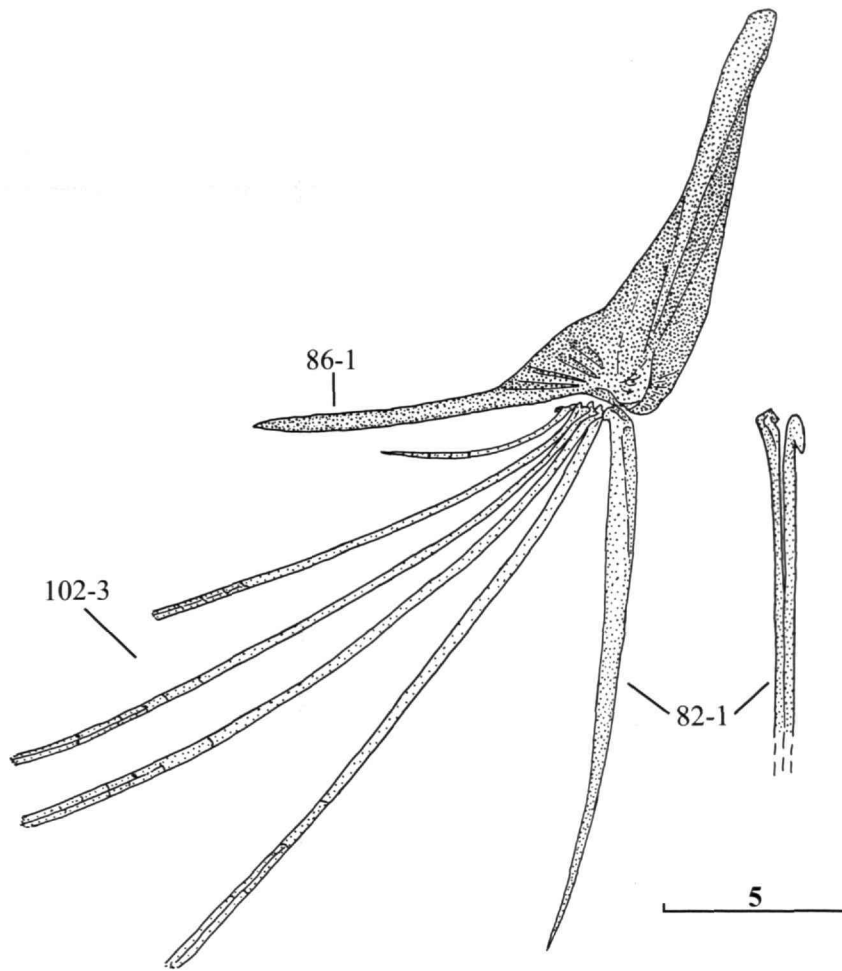


FIGURE 84.—Zeidae. Left-side pelvis and pelvic fin (anterior to right) of *Zenopsis conchifer*, CAS 47401, 54 mm SL, medial view, with detail (right) of the ray-like first element of the pelvic-fin (lateral and medial halves separate throughout their lengths and unbranched, but unsegmented), anterior view. Character-state: 82-1 no pelvic-fin spine; 86-1 long, rod-like posterior process of pelvis; 102-3 total of six pelvic-fin elements.

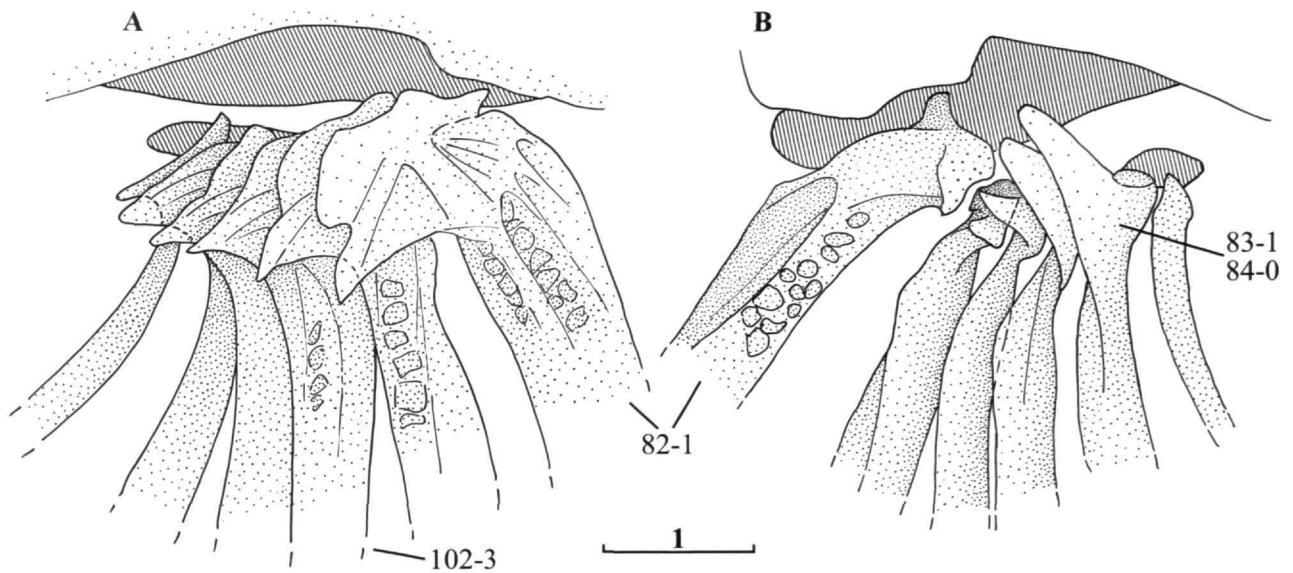


FIGURE 85.—Zeidae. Basal region of the right pelvic fin of *Zenopsis conchifer*, USNM 117280, 81 mm SL, lateral (A) and medial (B) views. Parallel lines show cartilage. (Anterior to right in A, to left in B.) Character-state: 82-1 no pelvic-fin spine; 83-1 anterolateral processes as prongs from bases of rays; 84-0 no serrations on rays; 102-3 total of six pelvic-fin elements.

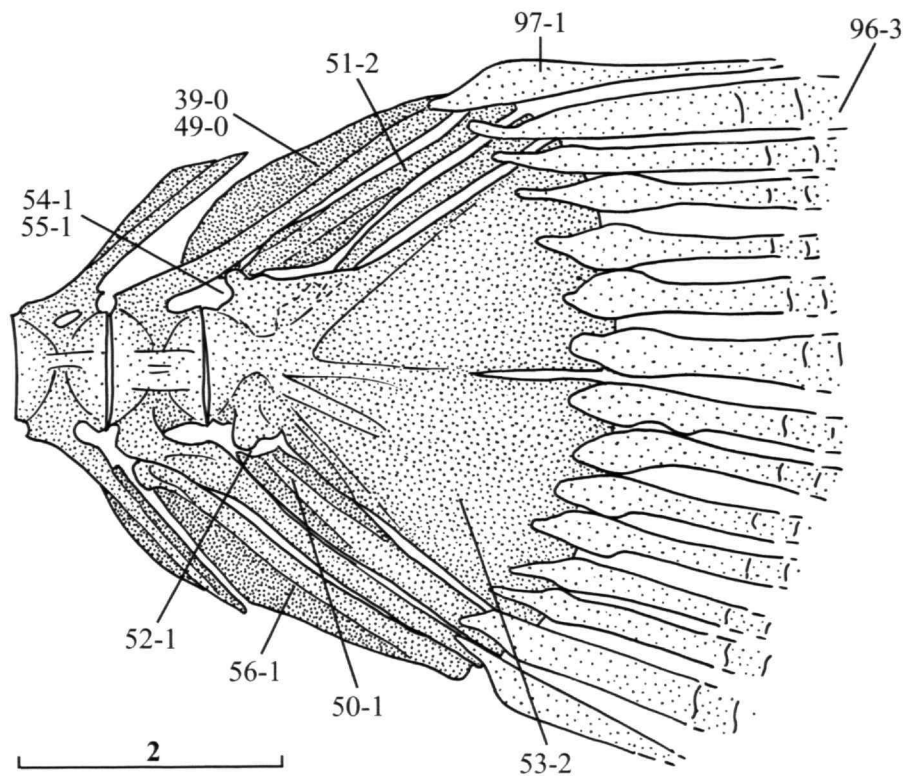


FIGURE 86.—Zeidae. Caudal skeleton of *Zenopsis conchifer*, CAS 47401, 54 mm SL, lateral view. Character-state: 39-0 PU2 first modified vertebra in caudal peduncle; 49-0 NPU2 long; 50-1 no hypurapophysis; 51-2 one epural; 52-1 anterior end of parhypural slightly removed from and not embracing centrum; 53-2 hypurals 1 + 2 + 3 + 4 fused and fused to centrum; 54-1 no uro-neural; 55-1 no stegural; 56-1 extra-caudal ossicle present; 96-3 13 principal caudal-fin rays; 97-1 one procurcent caudal-fin ray above and below.

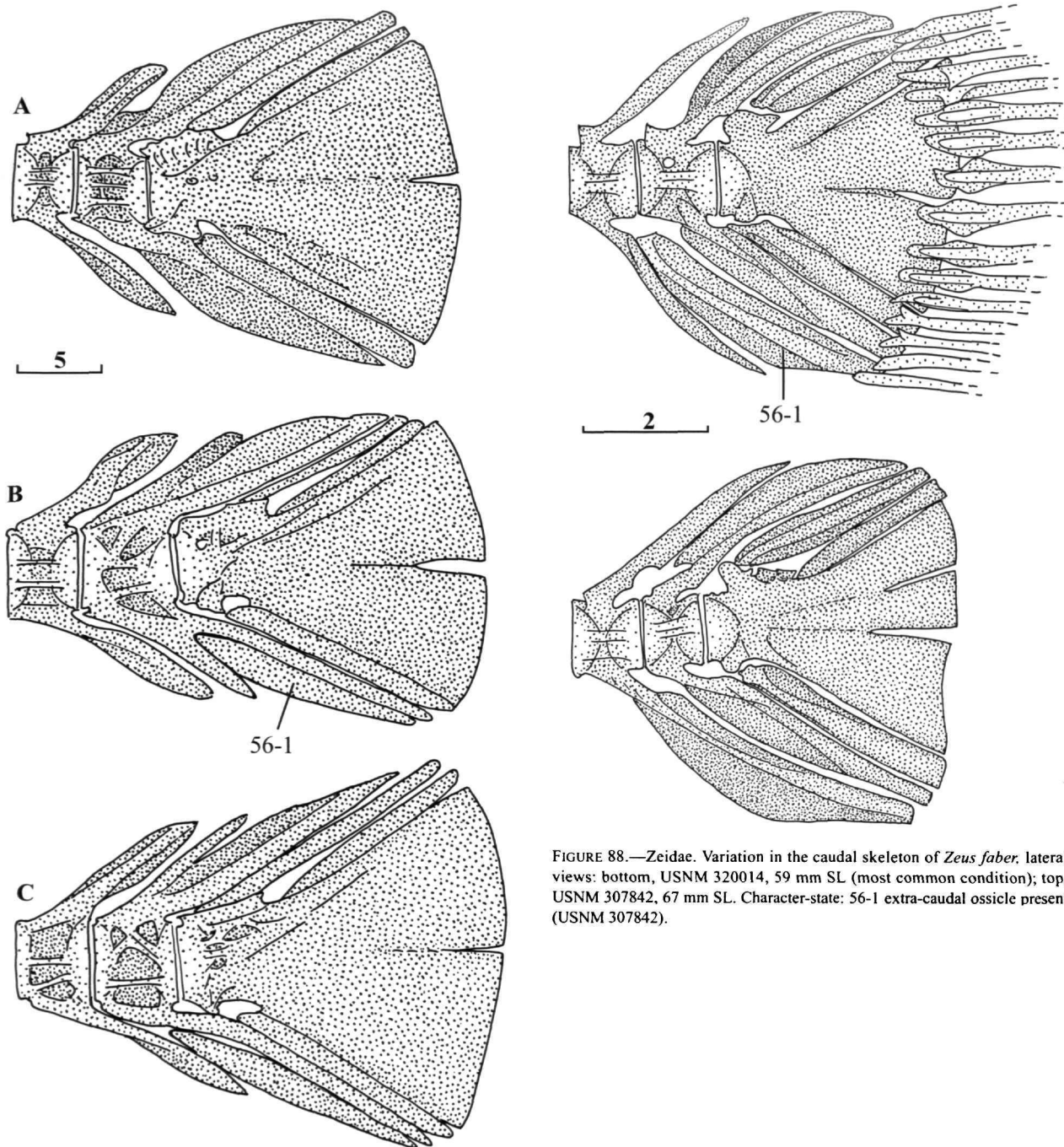


FIGURE 87.—Zeidae. Variation in the caudal skeleton of *Zenopsis nebulosus*, lateral views: A, AMNH 92291, 325 mm SL (most common condition); B, AMNH 95024, 335 mm SL; C, AMNH 95028, 340 mm SL. Character-state: 56-1 extra-caudal ossicle present (B, C).

FIGURE 88.—Zeidae. Variation in the caudal skeleton of *Zeus faber*, lateral views: bottom, USNM 320014, 59 mm SL (most common condition); top, USNM 307842, 67 mm SL. Character-state: 56-1 extra-caudal ossicle present (USNM 307842).



FIGURE 89.—Fossil Zeiformes. Skeleton of *Cretezeus rinaldi* Tyler et al. (2001), holotype, Collezione della Città di Nardò, CCN 6659C, 53 mm SL, lateral view. This is the earliest known zeiform, from the Upper Cretaceous of Nardò, Italy (about 72 m.y.a.), and, like the two morphologically primitive taxa of early zeiforms from the upper Paleocene, it cannot be placed in any of the extant families. *Cretezeus* already exhibits such derived zeiform features as 18-1 palatine articulation pivot; 19-1 reduced metapterygoid; 40-1 first neural arch and spine closely applied to skull (better seen in other specimens); 44-1 some neural spines oriented anterodorsally; 49-0 NPU2 long; 52-1 anterior end of parhypural slightly removed from and not embracing centrum; 53-2 hypurals 1 + 2 + 3 + 4 fused and fused to centrum; 54-1 no uroneural; 58-0, one group of vacant interneural spaces (variable between the five type specimens, two vacancies in one group in this specimen); 60-1 first dorsal-fin pterygiophore attached to skull at first neural arch and spine; 63-1 symmetrical pterygiophores; 64-1 one supraneural; 73-1 unbranched dorsal-, anal-, and pectoral-fin rays; 88-4 large buckler plates mid-abdominally from pelvic fin to anus (independent of *Hopllostethus*); 11 principal caudal-fin rays, even fewer than the 13 of nearly all extant zeiforms (96-3). The total number of vertebrae in this species is 28 or (this specimen) 29; single supernumerary dorsal-fin spine on first pterygiophore (not enumerated).

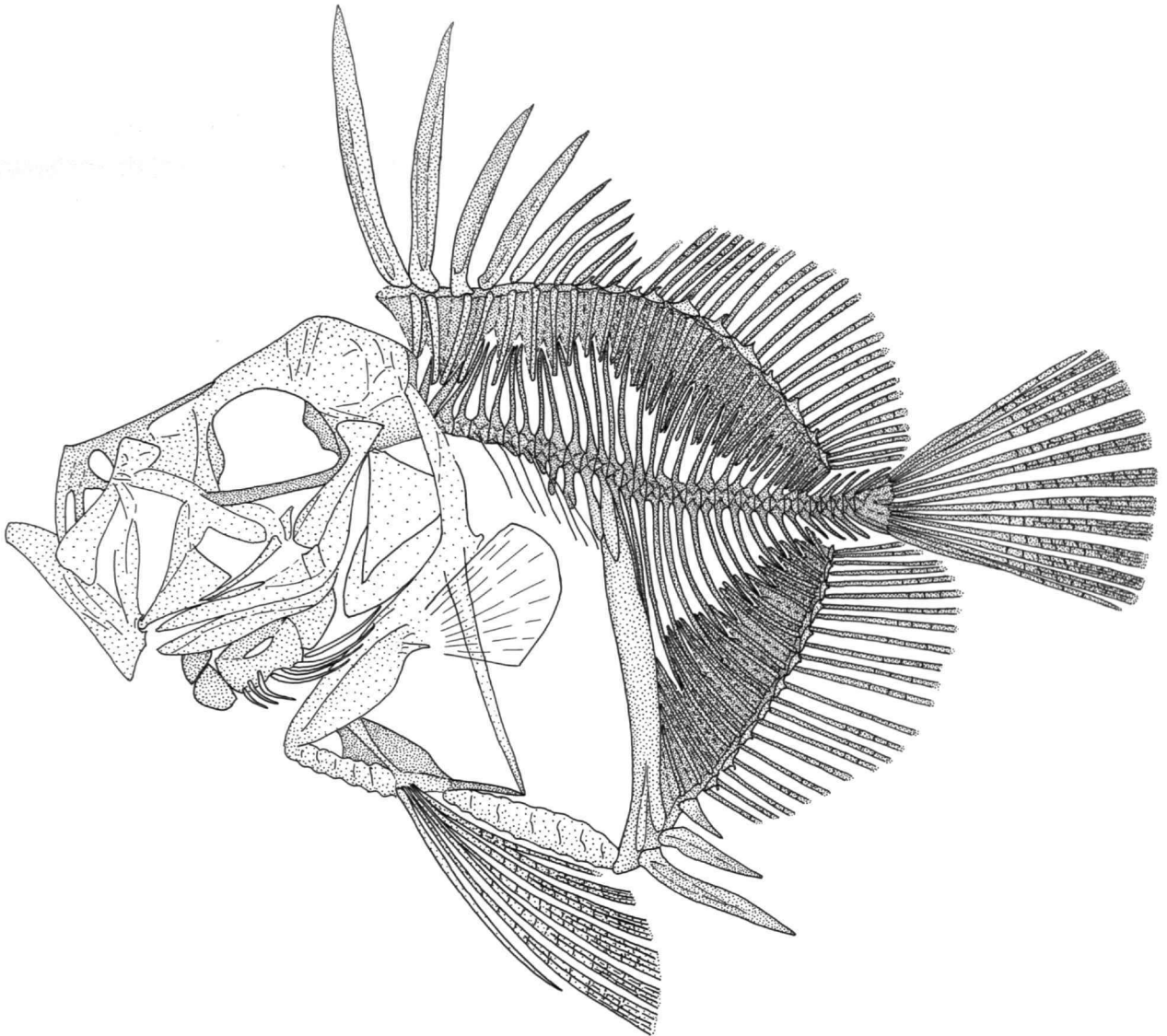


FIGURE 90.—Fossil Zeiformes. Skeleton of *Zenopsis clarus* Danilchenko (1960), holotype, Paleontological Institute, Moscow, PIN 1413-22, 25 mm SL, lateral view. This is one of the several taxa of zeiforms from the Oligocene (in this case from the Caucasus, Russia), all of which clearly are members of the Zeidae and can be assigned to either *Zenopsis* or *Zeus* (Baciu, Bannikov, and Tyler, in prep.). In addition to most of the characters given in the legend for Figure 89 of the Upper Cretaceous *Cretazeus* (except supraneural absent, different buckler arrangement, 34 or 35 vertebrae, and 13 caudal-fin rays), the Oligocene taxa of *Zenopsis* have the following zeid features: 14-2 alveolar process of premaxilla deeply bifurcate ventrally; 47-0 ossified ribs on most abdominal vertebrae behind fourth; 59-3 four dorsal-fin pterygiophores anterior to fourth neural spine; 79-1 cleithral process present; 86-1 long, rod-like posterior process of pelvis; 88-3 large buckler plates along dorsal- and anal-fin bases and mid-abdominally; 94-5 14 abdominal vertebrae; 98-6 10 dorsal-fin spines; 102-3 total of six pelvic-fin elements.

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