Interrelationships of Aulopiformes

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I. Introduction

In 1973, Rosen erected the order Aulopiformes for all non-ctenosquamate eurypterygians, that is, the Iniomi of Gosline *et al.* (1966) minus the Myctophiformes (Myctophidae and Neoscopelidae). Rosen's aulopiforms included 15 families (Alepisauridae, Anotopteridae, Aulopidae, Bathysauridae, Bathypteroidae, Chlorophthalmidae, Evermannellidae, Giganturidae, Harpadontidae, Ipnopidae, Omosudidae, Paralepididae, Scopelarchidae, Scopelosauridae, and Synodontidae) and 17 fossil genera, a morphologically diverse group of benthic and pelagic fishes that range in habitat from estuaries to the abyss.

Rosen (1973) diagnosed the Aulopiformes by the presence of an elongate uncinate process on the second epibranchial (EB2) bridging the gap between a posterolaterally displaced second pharyngobranchial (PB2) and the third pharyngobranchial (PB3). He noted that paralepidid fishes lack this distinctive configuration of EB2 and thus questioned their placement in the order. Subsequently, R. K. Johnson (1982) recognized that certain paralepidids (*Paralepis*, and *Notolepis*) have an enlarged EB2 uncinate process but questioned Rosen's use of this feature to diagnose aulopiforms because he believed the same condition occurs in neoscopelids. Instead he suggested that the modification is a primitive iniome condition and that the small EB2 uncinate process of myctophids is secondarily derived. R. K. Johnson (1982) resurrected a more traditional view of iniome

relationships in which Rosen's (1973) aulopiforms and myctophiforms are united in the order Myctophiformes.

In 1985, Rosen altered his concept of a monophyletic Aulopiformes, noting that *Aulopus* shares several derived features with ctenosquamates, most notably a median rostral cartilage. Hartel and Stiassny (1986) considered a true median rostral cartilage a character of acanthomorphs and concluded that the morphology of the rostral cartilage is highly variable below that level. Nevertheless, Stiassny (1986) supported Rosen's (1985) view of a paraphyletic Aulopiformes, proposing that *Chlorophthalmus*, *Parasudis* and *Aulopus* form the sister group of ctenosquamates based on an elevated, reoriented cranial condyle on the maxilla and concurrent exposure of a "maxillary saddle" for reception of the palatine prong. G.D. Johnson (1992) discussed the shortcomings of Rosen's (1985) analysis and observed that neither Rosen nor Stiassny (1986) mentioned the distinctive gill-arch configuration originally described by Rosen (1973) as unique to aulopiforms. He added an additional gill-arch character to Rosen's (1973) complex, the absence of a cartilaginous condyle on PB3 for articulation of EB2, and concluded that a suite of gill-arch modifications constitutes a complex specialization supporting the monophyly of Rosen's (1973) Aulopiformes. In addition, Johnson (1992) offered further evidence (absence of the fifth upper pharyngeal toothplate and associated third internal levator muscle) for the monophyly of Rosen's (1973) Ctenosquamata, which include myctophids, neoscopelids and acanthomorphs, but not aulopi-

Gosline et al. (1966):
Order Iniomi
  Myctophoidea
    Aulopidae
    Bathysauridae
    Synodontidae
    Harpadontidae
    Bathypteroidae
    Ipnopidae
    Chlorophthalmidae
    Notosudidae (=Scopelosauridae)
    Myctophidae
    Neoscopelidae
  Alepisauroidea
    Paralepididae
    Omosudidae
    Alepisauridae
    Anotopteridae
    Evermannellidae
    Scopelarchidae

Rosen (1973):
Order Aulopiformes, new name
  Suborder Aulopoidei, new name
    Aulopidae
    Bathysauridae
    Bathypteroidae
    Ipnopidae
    Chlorophthalmidae
    Notosudidae (=Scopelosauridae)
  Suborder Alepisauroidei
    [15 fossil genera]
    Superfamily Synodontoidea, new usage
      [2 fossil genera]
      Synodontidae
      Harpadontidae
      Giganturidae (? + Rosauridae)
    Superfamily Alepisauroidea
      Paralepididae
      Omosudidae
      Alepisauridae
      Anotopteridae
      Evermannellidae
      Scopelarchidae

Sulak (1977):
Benthic Myctophiformes:
  Aulopidae
    Aulopus (including *Hime, Latropiscus*)
  Synodontidae
    Subfamily Harpadontinae
      Harpadon (incl. *Peltharpadon*)
      Saurida
    Subfamily Bathysaurinae
      Bathysaurus (incl. *Macristium*)
    Subfamily Synodontinae
      Synodus (incl. *Xystodus*)
      Trachinocephalus
  Chlorophthalmidae
    Subfamily Chlorophthalminae
      Chlorophthalmus
      Parasudis
      Bathysauropsis (incl. *Bathysaurops*)
    Subfamily Ipnopinae
      Tribe Ipnopini
        Ipnops (incl. *Ipnoceps*)
      Tribe Bathypteroini
        Bathypterois (incl. *Benthosaurus*)
      Tribe Bathymicropini
        Bathymicrops
        Bathytyphlops (incl. *Macristiella*)

R. K. Johnson (1982):
Myctophiformes:
  Aulopoids
    Aulopidae
  Myctophoids + Chlorophthalmoids
    Myctophoids
      Myctophidae
      Neoscopelidae
    Chlorophthalmoids
      Notosudidae
      Scopelarchidae
      Chlorophthalmidae
      Ipnopidae
  Synodontoids + Alepisauroids
    Synodontoids
      Synodontidae
      Harpadontidae
      Bathysauridae
    Alepisauroids
      Paralepididae
      Anotopteridae
      Evermannellidae
      Omosudidae
      Alepisauridae

FIGURE 1 Four previously hypothesized classifications of aulopiform or myctophiform fishes.

forms (see also Stiassny, this volume). Johnson *et al.* (1996) argued that *Aulopus* is not closely related to ctenosquamates but is the cladistically primitive member of their Synodontoidei, a lineage that also includes *Pseudotrichonotus, Synodus, Trachinocephalus, Saurida,* and *Harpadon.* Finally, Patterson and Johnson (1995) provided corroborative evidence from the intermuscular bones and ligaments for Rosen's (1973) Aulopiformes, in the extension of the epipleural series anteriorly to the first or second vertebra.

Various schemes of relationships among iniomous fishes have accompanied confusion about the recognition of a monophyletic Aulopiformes (Fig. 1). Gosline

et al. (1966) recognized two "suborders": myctophoids (Aulopidae, Bathysauridae, Synodontidae, Harpadontidae, Bathypteroidae, Ipnopidae, Chlorophthalmidae, Notosudidae [= scopelosaurids of Marshall, 1966—see Paxton, 1972; Bertelsen *et al.,* 1976], Myctophidae, and Neoscopelidae); and alepisauroids (Paralepididae, Omosudidae, Alepisauridae, Anotopteridae, Evermannellidae, and Scopelarchidae). Rosen (1973) added synodontids and harpadontids (his synodontoids) and 17 fossil genera to the Alepisauroidei, described a new suborder, the Aulopoidei, for Aulopidae, Bathysauridae, Bathypteroidae, Ipnopidae, Chlorophthalmidae, and Notosudidae and, as noted,

restricted the Myctophiformes to myctophids and neoscopelids.

Sulak (1977) examined aspects of the osteology of the benthic "myctophiforms" and envisioned them forming two divergent lineages exhibiting progressively greater differentiation from the basal aulopid body plan, an expanded Synodontidae that included bathysaurids, synodontids, and harpadontids, and an expanded Chlorophthalmidae for chlorophthalmids (including *Bathysauropsis*) and ipnopids (including bathypteroids).

To examine a previously proposed relationship between the Evermannellidae and Scopelarchidae (e.g., Marshall, 1955; Gosline et al., 1966), R. K. Johnson (1982) studied the distribution of selected characters among iniomes. He did not present a formal classification but described three perceived iniomous clades. One comprised only aulopids, a second was equivalent to Rosen's (1973) alepisauroids minus scopelarchids, and the third included myctophids, neoscopelids, chlorophthalmids, ipnopids, notosudids, and scopelarchids. R. K. Johnson's (1982) phylogeny corroborated Sulak's (1977) placement of bathysaurids in the synodontid + harpadontid lineage, but he noted that only two clades resulting from his analysis, the myctophoids (Myctophidae, and Neoscopelidae) and the alepisauroids (Paralepididae, Anotopteridae, Evermannellidae, Omosudidae, and Alepisauridae) were well supported.

Okiyama (1984b) examined R. K. Johnson's (1982) hypothesis in light of evidence from aulopiform larvae. He did not produce an independent hypothesis of relationships but noted that his data offer little support for a notosudid + scopelarchid + chlorophthalmid + ipnopid lineage; rather, in his similarity matrix, scopelarchids share the most derived features (two) with evermannellids. Larval morphology also does not support a close association between bathysaurids and the synodontid + harpadontid lineage, but, as Okiyama (1984a) noted, *Bathysaurus* larvae are highly specialized.

To demonstrate the potential systematic value of the intermuscular ligaments and bones in teleostean fishes, Patterson and Johnson (1995) investigated aulopiform interrelationships based on this skeletal system. Their data provided support for a monophyletic Synodontoidei (*sensu* Johnson et al., 1996) and a sister-group relationship between evermannellids and scopelarchids. Novel relationships depicted in their strict consensus of 24 equally parsimonious trees include the following: a clade comprising all aulopiform taxa except ipnopids (represented by *Bathypterois* in their analysis) and *Parasudis*; sister-group relationships between *Chlorophthalmus* and synodontoids,

notosudids and the evermannellid–scopelarchid lineage, and bathysaurids and giganturids; and a paraphyletic Paralepididae, with *Paralepis* forming the sister group of a monophyletic clade comprising *Omosudis* and *Alepisaurus*. Patterson and Johnson (1995) noted that the paraphyly of the Paralepididae suggested by their data may be artificial, a result of the greatly reduced number of intermuscular elements in *Macroparalepis*.

No other comprehensive studies of aulopiform relationships have been undertaken, and thus considerable conflict about the evolutionary history of aulopiform fishes existed when we initiated this study, the goal of which was to hypothesize a phylogeny of extant aulopiform genera based on cladistic analysis of a wide range of morphological data. R. K. Johnsons's (1982) cladistic analysis of iniome relationships used commonality rather than outgroup comparison to assess character polarity, and we thus found that many of his polarity decisions were reversed in our analysis. Patterson and Johnson's (1995) phylogeny is of limited value because it was constructed on the basis of a single complex. Despite their shortcomings these publications, as well as those of Rosen (1973), Sulak (1977) and Okiyama (1984b), proved useful in this study, and we derived many informative characters from them.

II. Methods

Osteological abbreviations are listed in Appendix 1, and a full list of materials examined is given in Appendix 2. Terminology for bones of the pelvic girdle follows Stiassny and Moore (1992), and that for the intermuscular bones and ligaments follows Patterson and Johnson (1995). In all line drawings, scale bars represent 1 mm, and open circles indicate cartilage.

A. Data Analysis

Character data were analyzed using heuristic methods in Swofford's (1991) PAUP Version 3.0, and character distributions were explored using MacClade Version 3.04 of Maddison and Maddison (1992). Ctenosquamates, represented by the cladistically primitive Myctophidae, Neoscopelidae, *Metavelifer*, and *Polymixia* (Stiassny, 1986; G. D. Johnson, 1992; Johnson and Patterson, 1993), were considered the first outgroup, and stomiiforms, represented by the cladistically primitive *Diplophos* (Fink and Weitzman, 1982), the second. The analysis included all aulopiform genera except the notosudid *Luciosudis*; the recently described ipnopid, *Discoverichthys* (Merrett and

Nielsen, 1987); and the paralepidids *Dolichosudis, Magnisudis,* and *Notolepis.*

All characters were weighted equally, and all multistate characters were treated as unordered unless otherwise noted. Steps in the transformation of a single character are denoted by subscripts following the character number (e.g., 1_2 is state 2 of character 1). Many characters have more than one equally parsimonious reconstruction, and we optimized ambiguous characters on the tree using ACCTRAN, a method that favors reversals over parallel acquisitions when the choice is equally parsimonious (Farris, 1970; Swofford and Maddison, 1987). Ambiguous character states resolved using ACCTRAN are denoted in Discussion (Section VI) with an asterisk, e.g., (34_1^*).

Character data also were analyzed using Hennig86 (Farris, 1988) and the results exported to Clados Version 1.2 (Nixon, 1992) for construction of a tree on which characters and states are indicated (Fig. 6). There are some discrepancies in the distribution of character states between PAUP–MacClade and Hennig86–Clados, primarily because (1) for ambiguous characters optimized with e.g., ACCTRAN, MacClade recognizes that ambiguity may still exist at certain nodes, whereas Clados forces a resolution at all nodes; and (2) PAUP–MacClade allows polymorphisms in terminal taxa, whereas Hennig86–Clados does not. Character states on the tree (Fig. 6) that appear as synapomorphies in Clados but not MacClade are marked with a large dot; they are not discussed in the text, which is based on the PAUP–MacClade results.

B. Taxonomy

Parin and Kotlyar (1989) resurrected the aulopid genus *Hime* Starks (type species *A. japonicus* Günther) for Pacific aulopids based on a difference in the length of the dorsal-fin base between Atlantic and Pacific species but used length of the anal-fin base as a taxonomic feature within *Hime.* We find the evidence for generic distinction unconvincing and thus follow Mead (1966a) in recognizing a single genus, *Aulopus,* for all aulopid species.

We place *Harpadon* and *Saurida* in the Synodontidae as did Sulak (1977), *Omosudis* in the Alepisauridae, and *Anotopterus* in the Paralepididae (see Discussion). "*Scopelarchoides*" herein refers to *S. signifer* which, according to R. K. Johnson (1974a), may be an incorrect generic assignment for that species. He hypothesized that *S. nicholsi* (the type species of *Scopelarchoides*) and *S. danae* are more closely related to *Scopelarchus* than to other species of *Scopelarchoides* but retained *Scopelarchoides* for *S. signifer* pending further investigation.

Early in our study it became apparent that *Bathysauropsis gigas* (Kamohara) is not closely related to *B. gracilis* Regan and *B. malayanus* (Fowler). *Bathysauropsis gracilis* is the type species of *Bathysauropsis* Regan, and thus all reference to *Bathysauropsis* is to *B. gracilis* and *B. malayanus.* A new genus, *Bathysauroides,* is erected for *Bathysauropsis gigas.*

III. *Bathysauroides* Gen. Nov.

Diagnosis—An aulopiform distinguished from all other genera by the following combination of characters: a low number of caudal vertebrae (5–7, or ca. 11–15% of total vertebrae in *Bathysauroides gigas*), slightly elliptical eyes with an anterior aphakic space and gill rakers present as toothplates.

Type species—*Bathysaurops gigas* Kamohara 1952.

Etymology—From the Greek *bathys,* deep, and *sauros,* lizard, in reference to the deep habitat and superficial resemblance to lizardfishes.

Gender—Masculine.

Justification—Our hypothesis of cladistic relationships among aulopiform genera (Fig. 2) is best reflected by removing *Bathysauropsis gigas* from *Bathysauropsis* Regan and placing it in a distinct genus. In addition to the diagnostic characters listed above, *Bathysauroides gigas* can be distinguished from its former congeners based on the following features identified in this study or taken from the original description of *Bathysaurops gigas* (Kamohara, 1952): palatine with more prominent teeth than premaxilla; epipleurals extending anteriorly to the 1st vertebra (vs 2nd); epineurals on about the 3rd through 17th vertebrae originating on centrum (vs neural arch); 16–17 pectoral-fin rays (vs 22–24); basihyal with two rows of large teeth (vs no basihyal teeth); pectoral fin extending to vertical through middle of dorsal-fin base (vs beyond base of dorsal); anus much closer to pelvic fins than to anal fin (vs closer to anal fin); and adipose fin inserting above anterior part of anal-fin base (vs well behind anal base)

IV. Monophyly of Aulopiformes

We agree with Rosen (1973) that a lateral displacement of the proximal end of PB2 and a concomitant elongation of the uncinate process on EB2 to bridge the large gap between EB2 and PB3 are derived for aulopiforms (Character 1, Fig. 3). We disagree with R. K. Johnson's (1982) assessment of an elongate EB2 uncinate process as a primitive iniome condition because the first and second outgroups for iniomes are
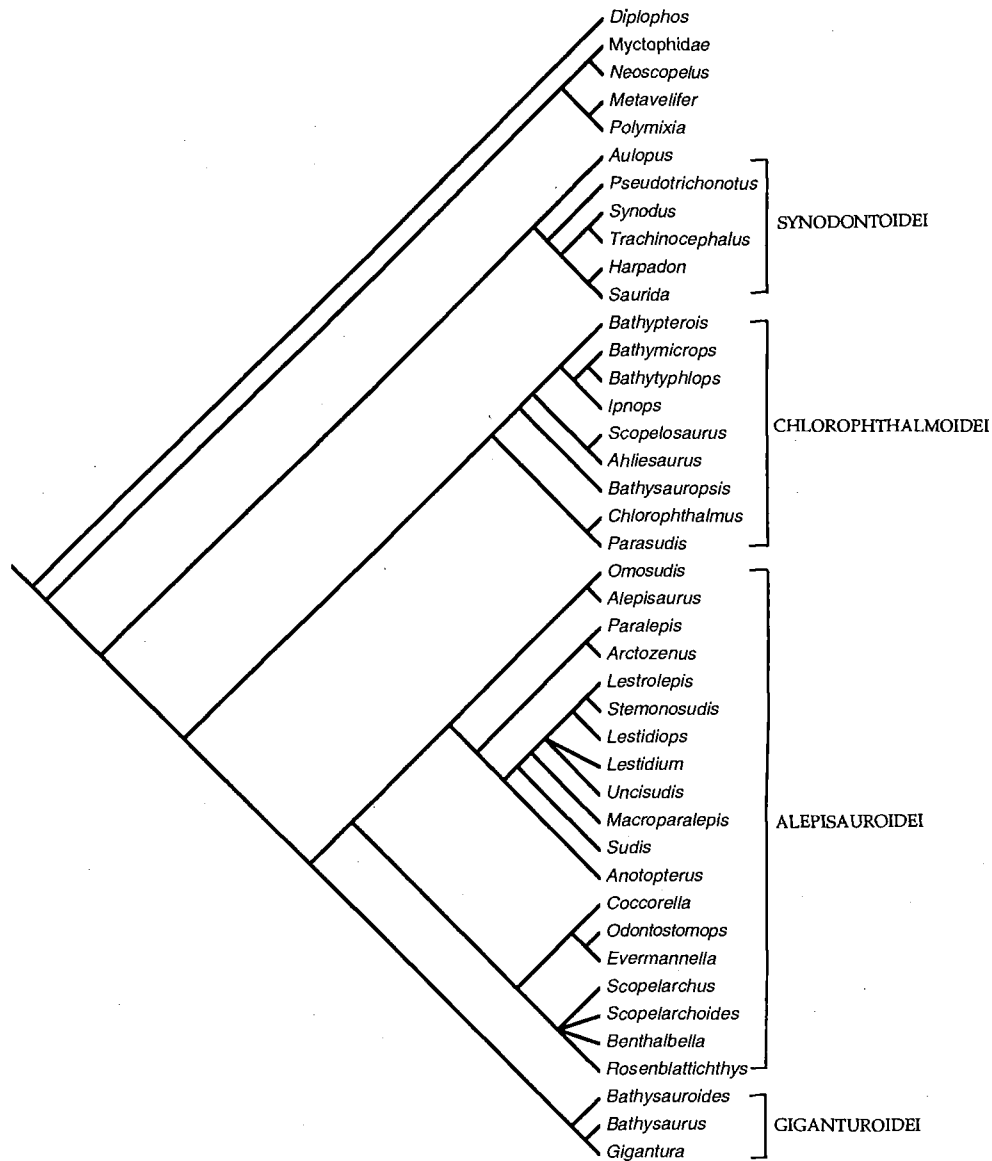
FIGURE 2 Proposed phylogenetic relationships among aulopiform genera based on strict consensus of nine equally parsimonious trees (length = 364, CI = 0.55, RI = 0.80).

acanthomorphs and stomiiforms, neither of which has an EB2 uncinate process. We also disagree with his interpretation of the unbranched anterior portion of the EB2 of *Neoscopelus* as an elongate uncinate process. There is nothing in the EB2 morphology of *Neoscopelus* (Rosen, 1973, fig. 71) to suggest that it is configured differently from that of myctophids and stomiiforms—that is, the cartilaginous tip is somewhat expanded such that it articulates with both PB2 and PB3 (Rosen, 1973, figs. 18–22 and 69–70). Furthermore, like those two groups, the EB2 of *Neoscopelus* articulates with a cartilaginous condyle on PB3,

the absence of which is another aulopiform synapomorphy (Character 2; Johnson, 1992).

Rosen (1973, figs. 14–16) questioned an aulopiform affinity for paralepidids because of (1) the primitive, salmoniform-like appearance of the dorsal gill arches of juvenile *Paralepis speciosa* and (2) the absence in adult *Paralepis* and *Lestrolepis* of the long EB2 uncinate process and laterally displaced PB2 characteristic of other aulopiforms. The first is invalid because Rosen's (1973, fig. 16) "juvenile *Paralepis*" is not a paralepidid. We examined the specimen upon which his description and illustration were based (AMNH 17232) and
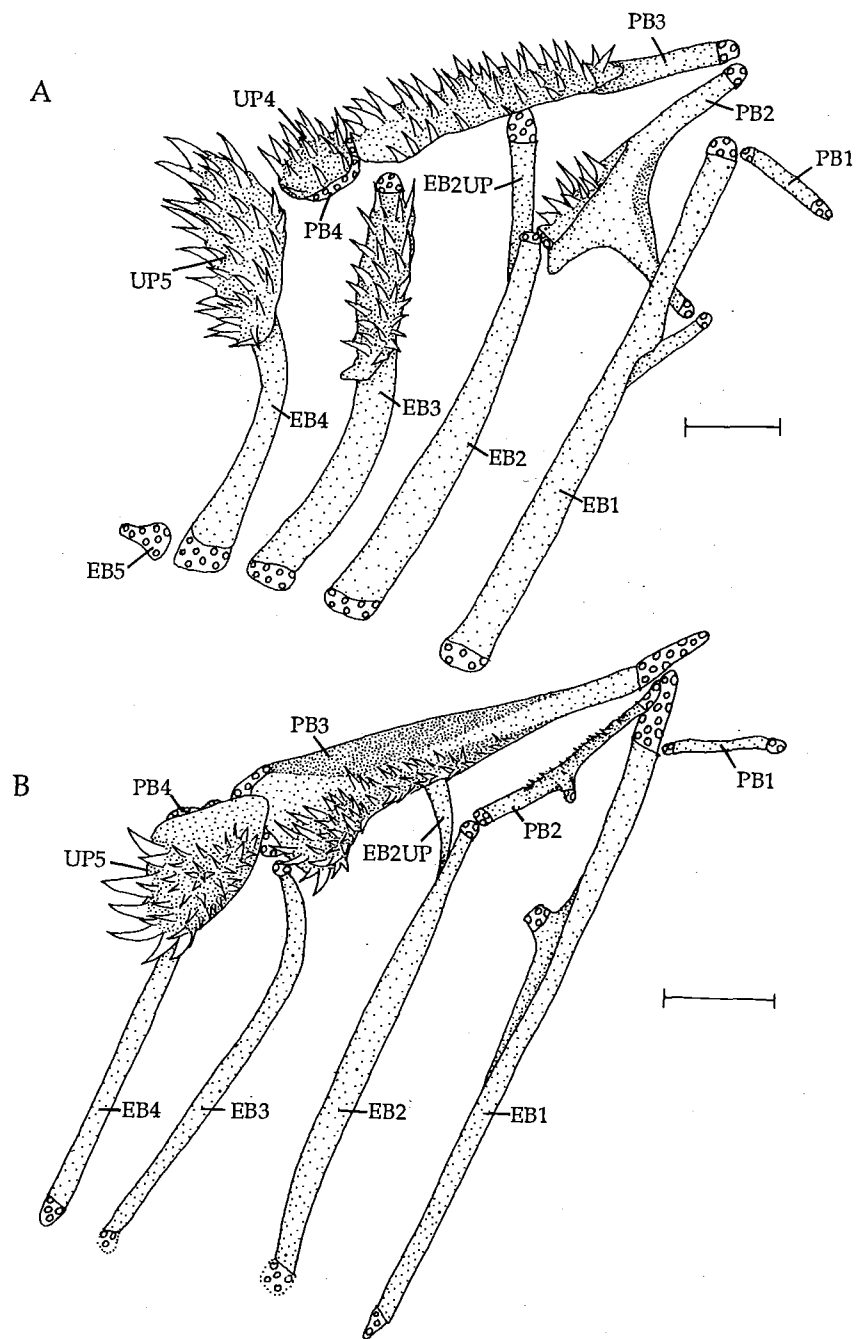
FIGURE 3   Ventral view of dorsal gill arches from left side of (A) *Chlorophthalmus atlanticus*, USNM 339774 and (B) *Synodus variegatus*, USNM 339776.

concluded on the basis of meristic and other features that it is an argentinoid, probably *Bathylagus*. Several features characteristic of bathylagid (and not aulopiform) gill arches are evident in Rosen's fig. 16: PB2 is broad anteriorly rather than tapered, UP4 is absent, UP5 (labelled UP4 or UP5 by Rosen) is extremely reduced to a small ovoid plate, and there is a long levator process on EB4. Note also that the muscle labelled "RAB" by Rosen inserts on EB4 rather than the pha-

ryngobranchials, indicating that it is the oesophageal sphincter, not the retractor dorsalis. Rosen's (1973) "juvenile *Paralepis*" also has an uncinate process on PB3 for articulation with the uncinate process of EB2, a primitive teleostean feature lacking in aulopiforms (Johnson, 1992).

Rosen's (1973) second claim, that paralepidids lack a laterally displaced PB2 and concomitant elongation of the EB2 uncinate process is not true of *Paralepis*,

Arctozenus, Anotopterus, or *Sudis.* In those taxa, as in other aulopiforms, the uncinate process of EB2 (which is cartilaginous in *Paralepis* and *Arctozenus*) spans the gap between PB3 and the posterolaterally displaced PB2. In other paralepidids examined (*Macroparalepis, Uncisudis, Lestidium, Lestidiops, Stemonosudis, and Lestrolepis*), the uncinate process of EB2 is parallel and closely applied to the main arm of EB2, which undoubtedly explains why Rosen overlooked it. The configuration of the dorsal gill arches of those paralepidids involves several diagnostic modifications that we discuss in more detail in a later section (see character 9).

Additional evidence corroborating the monophyly of Rosen's (1973) Aulopiformes is found in the pattern of the intermuscular bones (Patterson and Johnson, 1995). The group is uniquely characterized by having attached epipleural bones extending forward to at least the second, and frequently the first, vertebra (character 54). Epipleurals are most commonly restricted to midbody as they are in stomiiforms, myctophiforms, and *Polymixia* (the only acanthomorph with epipleural bones). Our analysis also indicates that another feature of the intermuscularis, the displacement of one or more of the anterior epipleurals dorsally into the horizontal septum (character 55), a feature used by Patterson and Johnson (1995) to indicate relationships within the Aulopiformes, is best interpreted as a synapomorphy of the group.

Another aulopiform character is their lack of a swimbladder (character 112; see Marshall, 1954, 1960; Marshall and Staiger, 1975). Many deep-sea fishes lack a swimbladder, but the presence of a swimbladder primitively in stomiiforms (including *Diplophos*) and ctenosquamates (most myctophids and neoscopelids, lampridiforms, and polymixiids)—see Marshall (1960), Woods and Sonoda (1973)—suggests that loss of the swimbladder in aulopiforms is independent of losses in other teleosts. R. K. Johnson (1982) hypothesized three losses of the swimbladder among iniomes: in aulopids, in the chlorophthalmoid lineage of his myctophoid + chlorophthalmoid clade, and in the ancestor of his alepisauroid + synodontoid lineage. Rosen's (1973) hypothesis of a monophyletic Aulopiformes requires a single loss in the ancestral aulopiform.

We agree with R. K. Johnson's suggestion that peritoneal pigment in larvae may be diagnostic of Rosen's (1973) aulopiforms (character 116). Larvae of *Diplophos*, myctophiforms, and primitive acanthomorphs lack peritoneal pigment, as do several aulopiforms (notosudids, some ipnopids, and the scopelarchid *Benthalbella*), presumably secondarily. Larvae of *Bathysauropsis* and *Bathysauroides* are unknown.

Finally, we have found new evidence for aulopiform monophyly in the morphology of the pelvic gir-

dle. Primitively in euteleosts, the pelvic plates often approach one another or abut medially in the region of the medial processes (Stiassny and Moore, 1992), as in *Diplophos* and myctophiforms (Fig. 4A), but the medial processes are never fused. Uniquely in aulopiforms, the medial processes of the pelvic girdle are long broad plates that are joined medially by cartilage (character 87, Figs. 4B–4D, and 5).

Stiassny (1986) rejected Rosen's concept of Aulopiformes, arguing that three genera of that group (*Aulopus, Chlorophthalmus,* and *Parasudis*) form the sister group of ctenosquamates based on a particular type of association between the maxilla and the palatine (her fig. 5). This single feature (character 44) does not outweigh the branchial, intermuscular, swimbladder, larval pigmentation, and pelvic girdle evidence that unites aulopiforms. Furthermore, placement by Johnson *et al.* (1996) of the Aulopidae as the sister-group of other synodontoids and our placement of the Chlorophthalmidae as the sister group of other chlorophthalmoids are in direct conflict with Stiassny's (1986) hypothesis.

V. Character Analysis

Our hypothesis of the relationships among aulopiform genera (Fig. 2) was derived from the data matrix in Table 1. The tree represents a strict consensus of nine fully resolved trees (each 364 steps in length, CI=0.55, RI=0.80 in the PAUP analysis), all of the ambiguity occurring within the Paralepididae and Scopelarchidae. The Hennig86 analysis yielded the same trees, although there were small differences in tree statistics.

Based on our analysis, we divide aulopiform genera into four clades: Synodontoidei (Aulopidae, Pseudotrichonotidae, and Synodontidae), Chlorophthalmoidei (Chlorophthalmidae, *Bathysauropsis*, Notosudidae, and Ipnopidae), Alepisauroidei (Alepisauridae, Paralepididae, Evermannellidae, and Scopelarchidae), and Giganturoidei (*Bathysauroides*, Bathysauridae, and Giganturidae). In the following comparison of phylogenetically informative characters among aulopiforms, character numbers refer to those in the matrix (Table 1) and on the Clados-derived tree (Fig. 6).

A. Gill Arches

1. *Second Epibranchial Uncinate Process (Fig. 3)*—As discussed above (in Monophyly of Aulopiformes) the presence of an uncinate process on EB2 articulating with PB3 characterizes all aulopiforms except *Bathypterois* and some paralepidids. In *Bathypterois* (Fig. 7B),
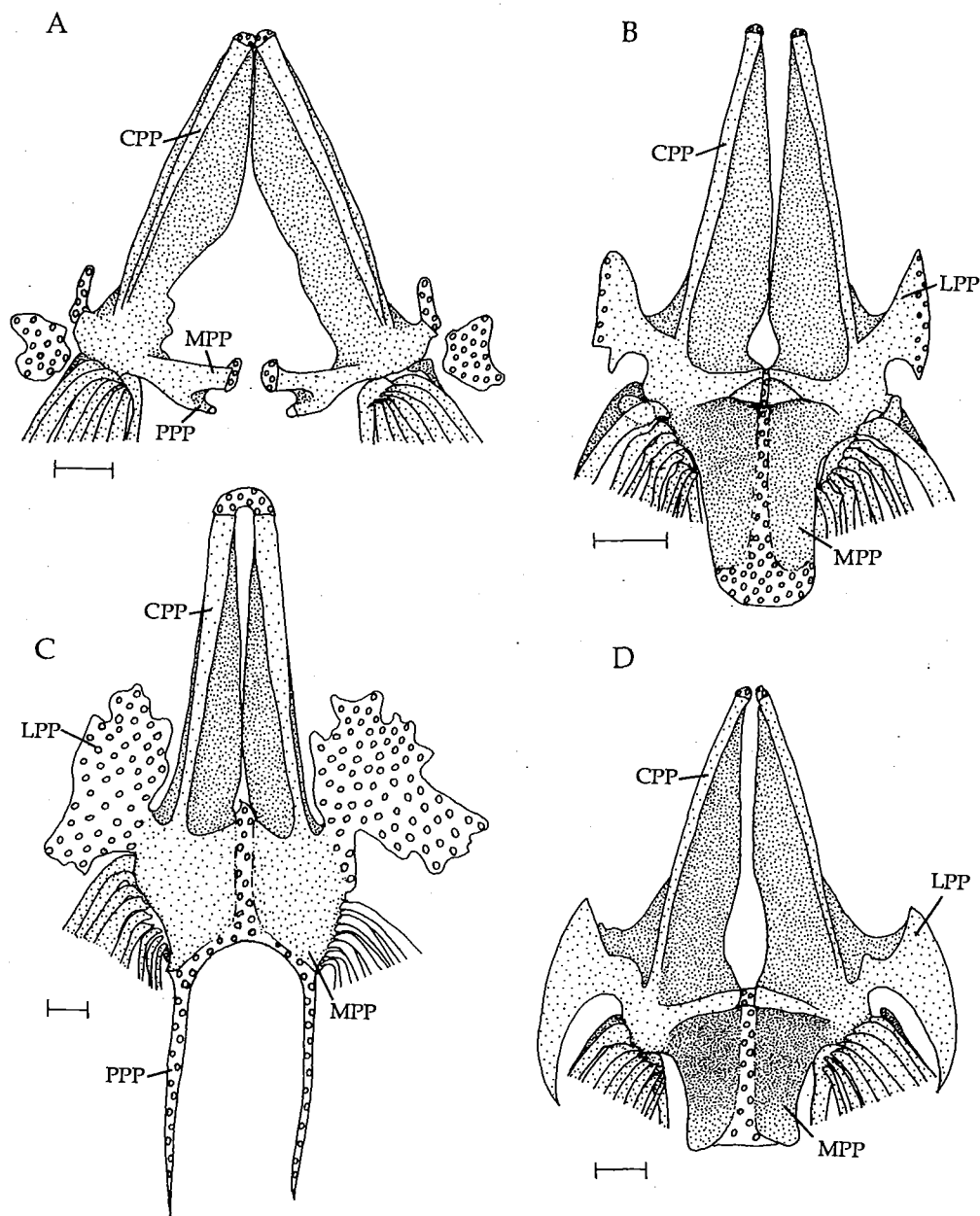
FIGURE 4 Ventral view of pelvic girdle of (A) *Myctophum obtusirostre*, AMNH 29140SW, (B) *Chlorophthalmus agassizi*, USNM 159385, (C) *Bathypterois pectinatus*, FMNH 88982, and (D) *Scopelosaurus hoedti*, USNM 264256.

the EB2 uncinate process falls well short of PB3, but PB2 is posterolaterally displaced as it is in other aulopiforms. In certain paralepidids (*Macroparalepis, Uncisudis, Lestidium, Lestidiops, Stemonosudis, and Lestrolepis* [Fig. 8B]), PB2 is reoriented and the resulting configuration of EB2 and its uncinate process is very different from that of other aulopiforms. We describe this condition more fully in Character 9 below and, to avoid duplicating what we interpret as a unique specializa-

tion of paralepidids, we do not assign a different state to that condition here. Other features clearly place *Bathypterois* and all paralepidids deep within the Aulopiformes, and thus the variation in the EB2 uncinate process in those taxa is derived relative to the primitive aulopiform condition.

(1_0) = EB2 uncinate process absent
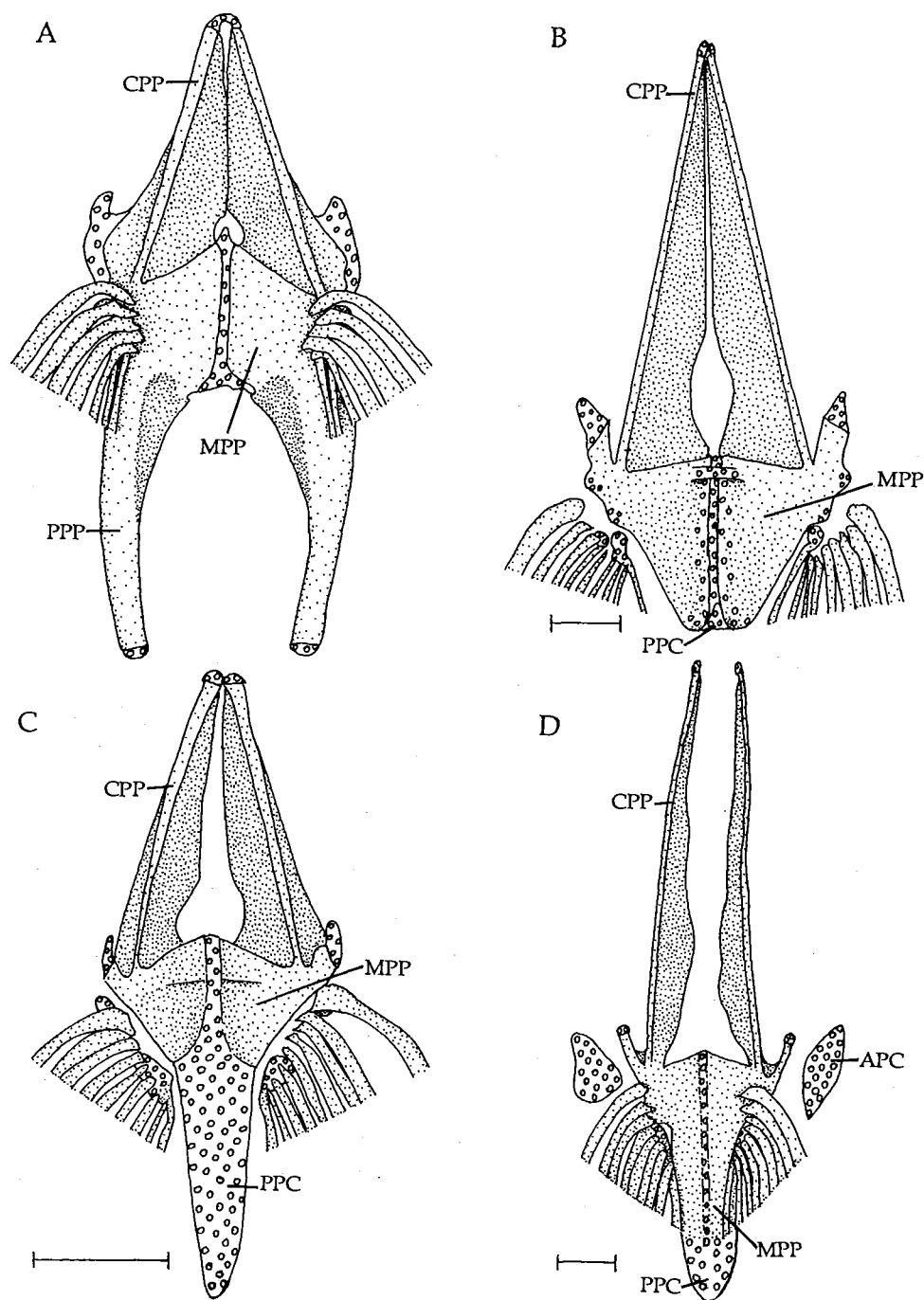(1_1) = EB2 uncinate process present and enlarged;

FIGURE 5 Ventral view of pelvic girdle of (A) *Pseudotrichonotus altivelis* ZUMT 59882 (redrawn from Johnson *et al.*, 1996), (B) *Scopelarchoides signifer*, USNM 274385, (C) *Evermannella indica*, USNM 235141, and (D) *Lestrolepis intermedia*, USNM 290253. The dorsally projecting autogenous pelvic cartilages in *Evermannella* are not shown because they are obscured by the pelvic girdle; in *Lestrolepis*, these cartilages have been manually displaced from their dorsally directed orientation for illustration.

PB2 displaced posterolaterally (except in some paralepidids)

(1₂) = EB2 uncinate process present, but not enlarged; PB2 displaced posterolaterally

2. *Cartilaginous Condyle on Dorsal Surface of Third Pharyngobranchial*—Aulopiforms lack a condyle on PB3 articulating with EB2 (Johnson, 1992). This condyle is a primitive euteleostean condition and is pres-

TABLE 1   Matrix for 118 Characters in 37 Aulopiform Genera, the Stomiiform *Diplophos*, the Myctophiforms Myctophidae (*Myctophum, Lampanyctus*) and *Neoscopelus*, and the acanthomorphs *Metavelifer* and *Polymixia*.

	Character																							
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	101–105	106–110	111–115	116–118
Diplophos	00100	01000	00010	00000	00000	00000	00110	00000	00000	00000	00000	00000	00020	00011	00100	00000	00000	00000	00011	20100	00000	0001?	00000	000
Myctophidae	00000	00000	00000	01000	?1100	00000	00200	00000	00020	00000	00000	00000	00100	00010	02000	000?0	00000	00000	10000	00000	00000	00000	0?0?0	000
Neoscopelus	00000	00000	00000	01000	01000	00000	00000	00000	00020	00000	00000	00000	00100	00010	02000	00021	0000?	00000	00000	00000	00000	00000	0?000	000
Metavelifer	0000?	00000	00000	00000	01000	10001	00000	00001	00010	50000	003??	?????	00000	00210	02012	00030	0003?0	00000	00000	10100	00000	0021?	00000	000
Polymixia	00000	00000	00000	01000	01000	00001	00000	00001	00020	00000	00000	00000	10000	00010	02000	00030	00000	00000	00000	00000	00000	00110	00000	000
Aulopus	11000	00000	00020	02000	01000	00120	00000	00000	00020	00000	00011	00000	01000	00011	00020	0103?	20000	01100	00000	30000	00000	00000	01000	100
Pseudotrichonotus	11100	01000	00020	00000	01000	00100	00000	00010	00020	00000	00011	10000	01000	00110	00120	01030	21200	01100	00000	00000	00000	00000	01000	200
Synodus	11111	00000	00000	22000	00000	10120	00000	01111	10000	00000	10011	10000	01000	00001	10220	01030	21200	01100	00000	00000	00000	00010	01000	200
Trachinocephalus	11111	00000	00010	22000	00001	10120	00000	01111	10000	00000	10011	10000	01000	00001	10220	01030	21200	01100	00000	00000	00000	00000	01000	200
Harpadon	11101	00001	11010	22100	00001	10120	00100	01000	10000	00000	20011	00000	00030	00001	00320	11030	01100	01100	00000	20000	00000	00000	01000	200
Saurida	11101	00000	11010	22100	00001	10120	00100	01000	10000	00000	10011	00000	00030	00001	00120	11030	20100	01100	00000	10000	00000	00000	01000	200
Bathypterois	21000	21000	00020	00000	01100	00010	00010	01001	01001	00000	01110	00000	00000	00210	01310	00020	00000	01011	00000	10000	00000	?2101	01100	?00
Bathymicrops	11100	20000	00020	00010	11110	00000	00010	01101	01101	50000	01110	00000	00000	00220	01550	10130	04200	01021	00000	20010	00000	?2211	01100	000
Bathytyphlops	11002	21000	00020	00000	11110	00000	00010	01101	01101	30000	01111	00000	00000	00120	01310	00030	00100	01011	00000	00010	00000	?2111	01100	100
Ipnops	11000	21000	00020	00010	01100	00000	00010	01001	01001	30000	0?11?	?0000	01000	00220	02310	00130	02100	01011	00000	20000	00000	?5111	01100	000
Scopelosaurus	11000	20000	00010	00001	11100	00000	00100	00001	00001	10000	00011	01000	10000	00210	01010	00020	00000	01021	00000	00000	00000	11101	01010	000
Ahliesaurus	11000	20000	00010	00001	11100	00000	00100	00001	00001	10000	00011	01000	10000	00210	01010	00020	00000	01021	00000	00000	00000	11?01	01010	000
Chlorophthalmus	11000	10000	00020	00000	00001	00001	00000	00021	00021	00000	00011	00000	01100	00120	01010	0000?	00000	01021	00000	30000	00001	10001	01000	100
Parasudis	11000	10000	00020	00000	01000	00001	00000	00021	00021	00000	00010	00000	00100	10210	01010	00000	00000	01021	00000	00000	00001	10001	01000	101
Bathysauropsis	11000	10000	00020	00000	01100	00000	00010	00001	00001	20000	00011	00000	00000	00010	01010	00000	00000	01022	00000	30000	00000	11001	01???	?20
Omosudis	11001	01101	11002	00100	00000	?0000	?0000	20000	00000	20000	00021	00110	00021	10210	01421	00070	01010	01020	10010	00100	12100	00001	11001	101

Alepisaurus	11001	01001	11002	00100	00000	00001	00020	20000	00000	20000	00021	00100	00021	10310	01421	00000	01010	01020	10010	20100	12100	00001	11001	101
Coccorella	11001	01101	11003	10000	10000	00001	00020	20000	00000	20000	00021	00000	10000	31120	01010	00000	00201	01020	10110	30101	11000	03001	01020	100
Odontostomops	11001	01100	11002	10000	10000	01001	10020	20000	00000	20000	00021	0?000	??0??	31120	01010	00000	00201	11020	10110	30101	11000	00001	01020	100
Evermannella	11001	01100	11002	10000	10000	01001	10020	20000	00000	20000	00021	00000	10000	31120	01010	00000	00201	11020	10110	30101	11000	03001	01020	100
Scopelarchus	11001	01000	11002	00000	00000	00001	00001	20000	00000	00000	00021	00000	10000	01020	01340	00000	00000	01021	01010	00101	10000	03001	01020	100
Scopelarchoides	11001	01000	11001	00000	00000	00001	00001	20000	00000	00000	00021	00000	10000	01020	01040	00000	00000	21020	01010	00101	10000	03001	01020	100
Benthalbella	11001	00000	11001	00000	00000	00001	00001	20000	00000	00000	00021	00000	10000	01020	01040	00?00	00000	01020	01010	00101	10000	03001	01020	100
Rosenblattichthys	11001	01000	11001	00000	00000	00001	00001	20000	00000	00000	0002?	00?00	10040	07020	01040	00000	00000	01020	01010	00101	10000	03001	01020	000
Paralepis	11001	01000	11002	00002	01000	00001	21000	20000	00000	21111	00021	00120	00213	20110	01421	00?00	00000	01020	10010	30100	10000	00001	01000	100
Arctozenus	11001	01000	11002	00002	01000	01001	21000	20000	00000	21111	00021	00020	00203	20110	01021	02000	02000	01020	10010	00100	10000	00001	01000	100
Lestrolepis	11001	01010	2?002	00002	00000	00001	21000	20000	00000	21111	00021	00001	00000	20120	01121	00020	00?00	01020	10011	01100	11010	00001	01000	101
Lestidium	11001	01010	2?002	00002	00000	00001	21000	20000	00000	21111	00021	00001	00000	20110	01021	00010	00?00	01020	10011	01100	11010	00001	01000	100
Stemonosudis	11001	01010	2?002	00002	00000	00001	21000	20000	00000	21111	00021	00001	00000	20110	01121	00020	00000	01021	10011	01100	11010	00001	01000	101
Uncisudis	11001	01010	2?002	00002	00000	00001	21000	20000	00000	21111	0002?	?0???	?????	??110	?12??	?0010	00020	01020	10011	01100	11010	00001	01000	100
Macroparalepis	11001	01010	27002	00002	00000	00001	21000	20000	00000	21111	00021	00001	00010	20110	01221	00000	00000	01020	10011	01100	11010	00001	01000	100
Lestidiops	11001	01010	27002	00002	00000	00001	21000	20000	00000	21111	0002?	?0??	00?00	??110	01120	00010	00?00	01020	10011	00100	11010	00001	01000	101
Sudis	11001	01000	27002	00002	00000	00001	20000	20000	00000	?111?	00021	00001	??000	20110	0112?	00000	00000	01020	10011	20100	11010	00001	01101	100
Anotopterus	11101	01001	27002	00002	00000	00001	00000	20000	00000	01111	10021	00000	00002	20?10	01371	0000?	0$^?_2$0?	01020	0?00?	11100	01200	00001	01000	100
Bathysauroides	11001	00000	01110	00000	01000	00001	00000	20000	00000	00000	00021	00000	11000	00000	01010	00001	20000	01020	00000	30000	00000	11001	01???	?00
Bathysaurus	11001	00000	01110	00000	01101	00001	00000	10000	00000	00000	30021	00000	20040	20000	00310	00001	00000	01020	00000	30000	00000	010$^?_1$	01100	110
Gigantura	1100?	0?000	01???	?0???	????0	??00?	0?000	20000	00000	6000?	20021	00000	20300	20?00	0053?	20220	10200	07020	00010	20200	02000	04001	01000	110

Note. "?" indicates a missing data point. Polymorphisms are represented by a superscript over a subscript, e.g., $^0_1$.
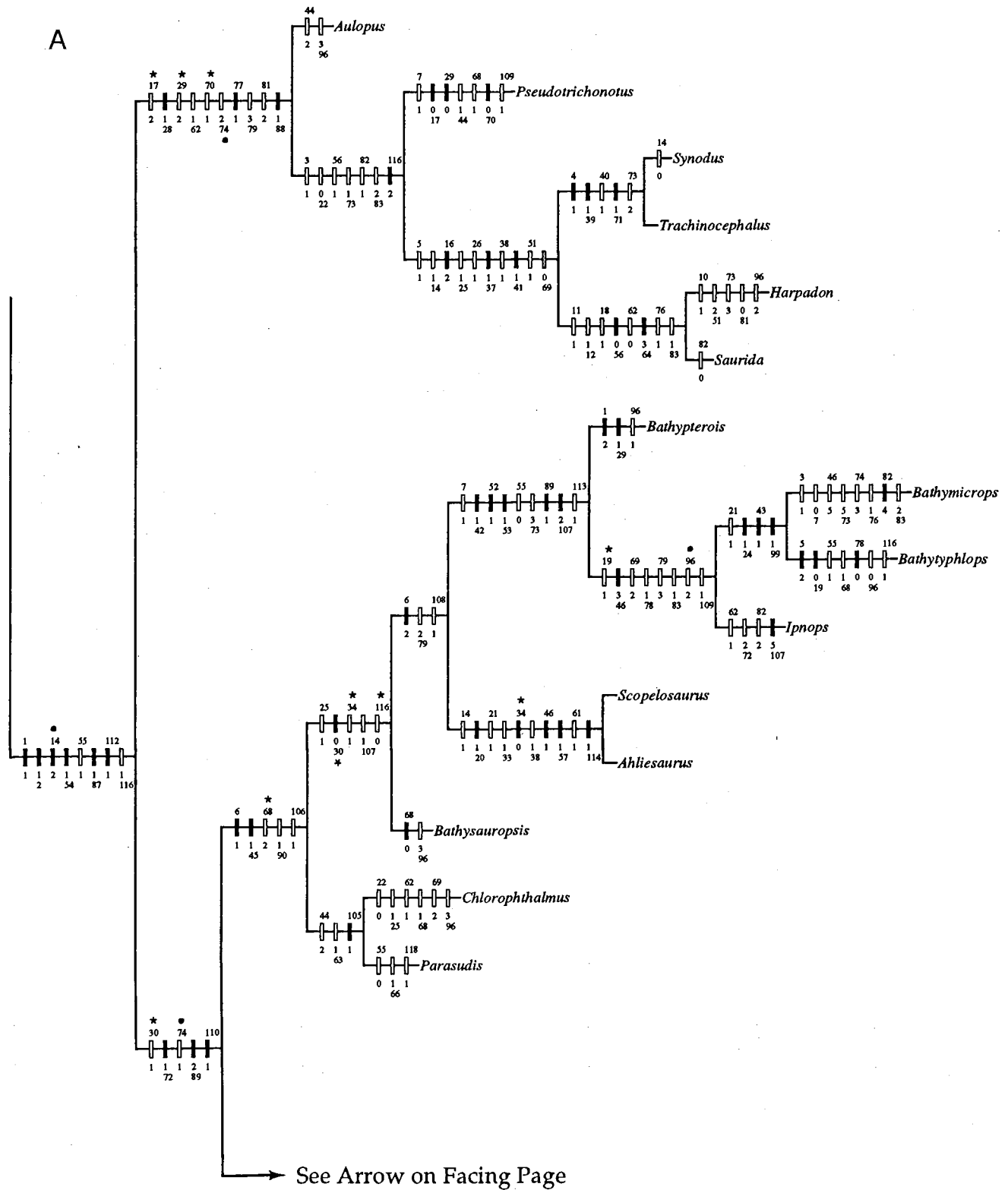
A

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FIGURE 6 Distribution of derived character states among aulopiform genera. (A) Synodontoidei and Chlorophthalmoidei; (B) Alepisauroidei and Giganturoidei. Black bars denote non-homoplasious forward changes; open bars indicate homoplasious forward changes. Character state numbers are directly below bars; character numbers are alternated above and below bars. Ambiguous character states resolved using ACCTRAN are marked with an asterisk. Derived character states that appear in the Hennig86–Clados analysis but not in PAUP–MacClade are marked with a black dot.

FIGURE 6 (continued)

ent in *Diplophos*, myctophiforms, and ctenosquamates in general.

(2_0) = PB3 with cartilaginous condyle articulating with EB2

(2_1) = PB3 without cartilaginous condyle articulating with EB2

3. *Fourth Pharyngobranchial Toothplate (Fig. 3)*—Johnson et al. (1996) described the distribution of the fourth pharyngobranchial toothplate (UP4) among aulopiforms and outgroups and concluded that although polarity for Aulopiformes is equivocal (absent in *Diplophos*, present in ctenosquamates), loss of UP4 is a synapomorphy of Pseudotrichonotidae, Synodontidae, and Harpadontidae. Our analysis corroborates this hypothesis. Independent losses of UP4 occur in *Bathymicrops* and *Anotopterus*.

(3_0) = UP4 present
(3_1) = UP4 absent

4. *Articulation of First Pharyngobranchial (Fig. 3B)*—In *Synodus* and *Trachinocephalus* the first pharyngobranchial (PB1) articulates with the proximal base of the elongate cartilaginous tip of EB1. In all other aulopiforms and outgroups, PB1 (if present) articulates at the distal end of the cartilaginous tip of EB1.

(4_0) = PB1 articulates at distal tip of EB1
(4_1) = PB1 articulates at proximal base of cartilaginous tip of EB1

5. *Gill Rakers or Toothplates*—R. K. Johnson (1982) hypothesized independent replacement of gill rakers by toothplates in scopelarchids and the ancestor of his synodontoids + alepisauroids. Our analysis suggests that scopelarchids are closely related to alepisauroids but synodontids are not, and thus the presence of toothplates is both a synapomorphy of alepisauroids plus giganturoids and of synodontids. Gill rakers are lathlike in most chlorophthalmoids, pseudotrichonotids, aulopids and the outgroups. *Bathytyphlops* has all rakers present as toothplates except for a single elongate raker on EB1. *Metavelifer* has normal rakers on the first arch but reduced rakers on the others. Gill rakers and toothplates are lacking in *Gigantura*.

(5_0) = Gill rakers long, lathlike
(5_1) = Gill rakers present as toothplates
(5_2) = Single elongate gill raker on EB1

6. *Second Pharyngobranchial with Extra Uncinate Process (Figs. 7, and 8)*—The typical aulopiform PB2 is tipped with cartilage at the proximal and distal ends and has an uncinate process for articulation with the uncinate process of EB1 (Fig. 3, and 8B). Ipnopids (Fig. 7B) and notosudids (Fig. 7A) have an extra PB2

uncinate process proximally that extends along the lateral surface of the distal portion of EB2. It is best developed in *Bathypterois*. In other chlorophthalmoids, there is no extra uncinate process, but the proximal cartilaginous head of PB2 is expanded laterally so that it extends slightly along the lateral aspect of EB2 (Fig. 8A). This appears to be intermediate between the condition in ipnopids and notosudids, in which there is a clear separation of the proximal cartilaginous head of PB2 into two cartilage-tipped processes, and that of other aulopiforms and the outgroups in which the proximal head of PB2 is not expanded or divided and contacts EB2 squarely. An expanded proximal PB2 base is a synapomorphy of chlorophthalmoids, the extra uncinate process appearing in the ancestor of ipnopids and notosudids.

(6_0) = PB2 without extra uncinate process
(6_1) = PB2 without extra uncinate process but with an expanded proximal base
(6_2) = PB2 with extra uncinate process

7. *Second Pharyngobranchial Toothplate (Fig. 3)*—A toothplate fused to PB2 (UP2) is present in synodontoids (except *Pseudotrichonotus*), chlorophthalmids, *Bathysauropsis*, *Bathymicrops*, notosudids, *Bathysauroides*, and *Bathysaurus*. It is lacking in other aulopiforms, including all alepisauroids except the scopelarchid *Benthalbella*, which has a very small toothplate proximally. R. K. Johnson (1982) noted that *Scopelarchoides signifer* also has UP2, but he did not illustrate it as such (R. K. Johnson, 1974a, fig. 10), and UP2 is lacking in our specimen of *S. signifer*. Presence of UP2 in ctenosquamates and absence in primitive stomiiforms suggests that polarity for aulopiforms is equivocal. Nevertheless, all reconstructions of aulopiform phylogeny produced in this study indicate that UP2 is primitively present in aulopiforms, and thus its absence in alepisauroids is derived. UP2 is lost in the ancestor of the Ipnopidae (R. K. Johnson, 1982) and independently in *Pseudotrichonotus*. It is reacquired in *Bathymicrops* and *Benthalbella*. PB2 is lacking in adults of the highly specialized *Gigantura*.

(7_0) = UP2 present
(7_1) = UP2 absent

8. *Second Pharyngobranchial Uncinate Process (Fig. 9B)*—Evermannellids and *Omosudis* have a long, laterally directed uncinate process on PB2 that articulates with a laterally directed uncinate process on the first epibranchial (EB1). The EB1 uncinate process is more medially directed in other aulopiforms (e.g., Figs. 3, 7, and 8) and the outgroups, and thus a much shorter PB2 uncinate process bridges the gap between the two bones. The EB1 uncinate process is also medially
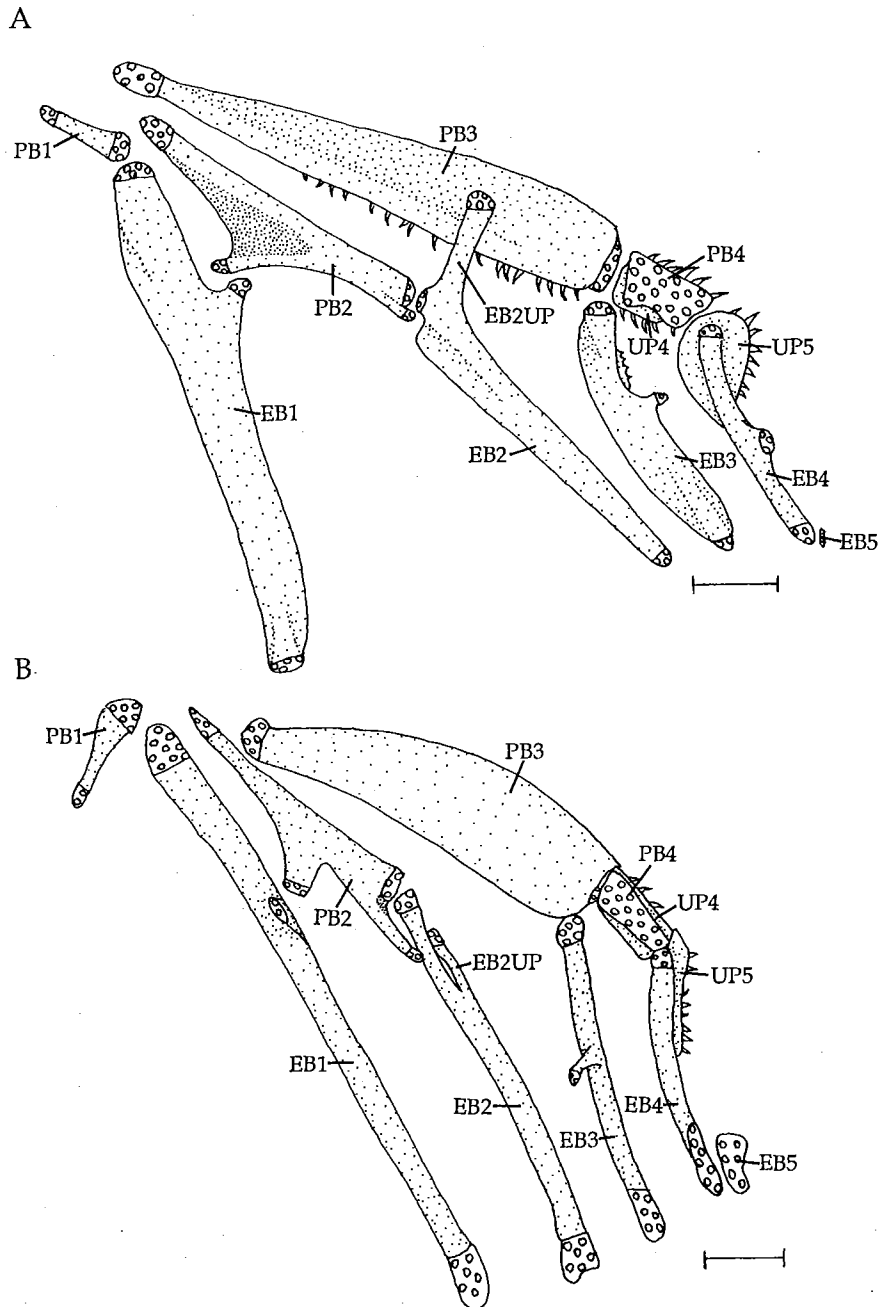
FIGURE 7 Dorsal view of dorsal gill arches from left side of (A) *Scopelosaurus hoedti*, USNM 264256 and (B) *Bathypterois pectinatus*, FMNH 88982.

directed and the uncinate process of PB2 is short in *Alepisaurus*, paralepidids, and scopelarchids, and thus it is most parsimonious to hypothesize independent origins of the long uncinate process in *Omosudis* and the ancestral evermannellid.

(8_0) = PB2 with short uncinate process
(8_1) = PB2 with long uncinate process

9. *Uncinate Process of Second Epibranchial Adjacent to*

Second Epibranchial (Fig. 8B)—The dorsal gill arches of the paralepidid genera *Macroparalepis, Uncisudis, Lestidium, Lestrolepis, Stemonosudis,* and *Lestidiops* ("*Macroparalepis* and above" for short) are distinctive among aulopiforms in that both EB2 and its uncinate process terminate distally at or near PB3. This arrangement is the result of a shift in the position of PB2, which primitively runs anteromedial to posterolateral in aulopiforms and outgroups but extends almost an-
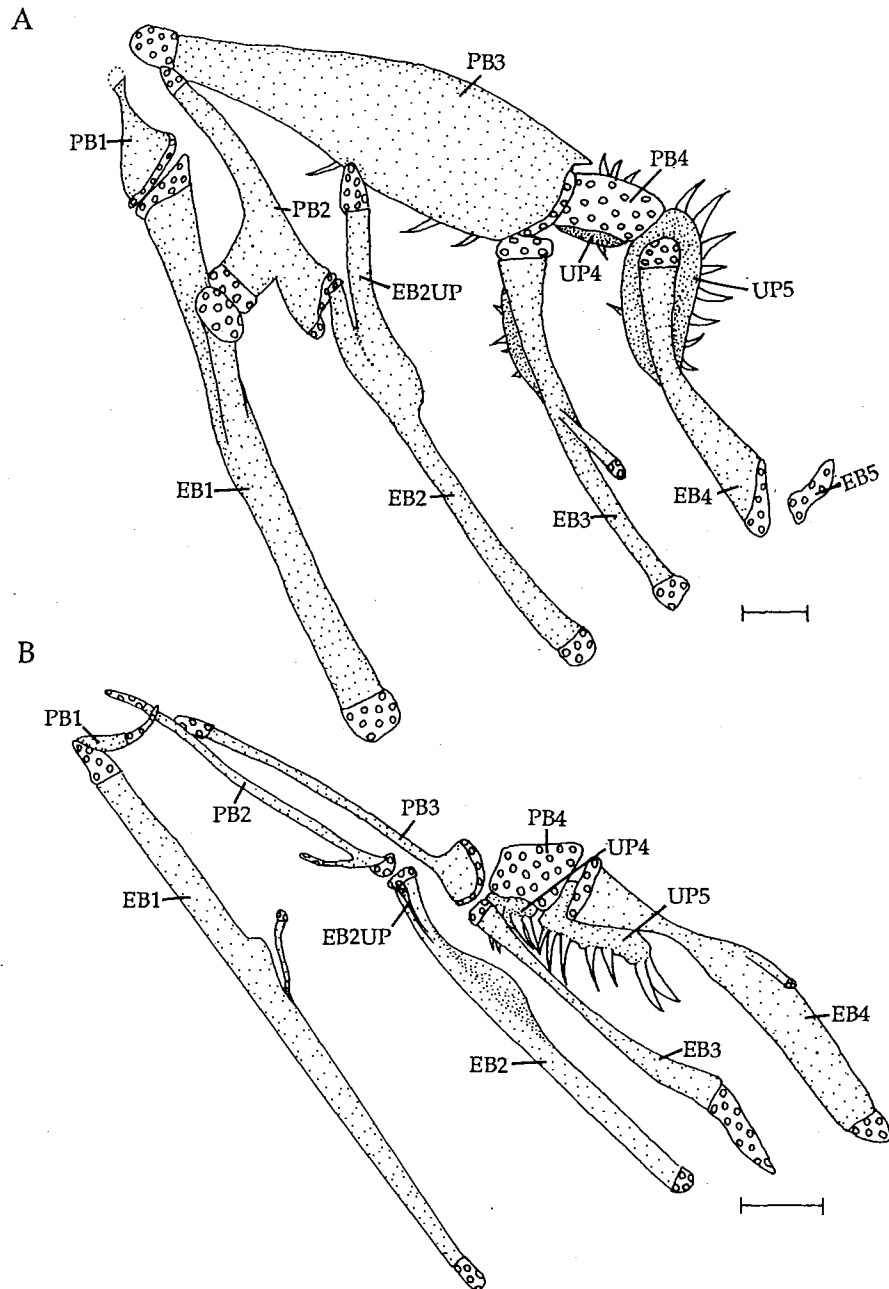
FIGURE 8　Dorsal view of dorsal gill arches from left side of (A) *Bathysauropsis gracilis*, AMS IA6934 and (B) *Lestrolepis intermedia*, USNM 290253.

terior to posterior in *Macroparalepis* and above, lying directly or nearly so against PB3. This modification brings the proximal end of PB2 close to PB3, and thus EB2 approaches PB3 at its articulation with PB2. The main arm of the second epibranchial and its uncinate process therefore are adjacent as they approach PB3 and PB2, respectively. The uncinate process of EB2 is in such close proximity to EB2 in some paralepidids

as to be easily overlooked (e.g., Rosen, 1973, fig. 15), and in *Lestrolepis*, it is a small strut that falls well short of PB3. Those conditions are not found elsewhere among aulopiforms or outgroups.

(9_0) = EB2 uncinate process diverges from EB2 as it approaches PB3; PB2 oriented anteromedial to posterolateral
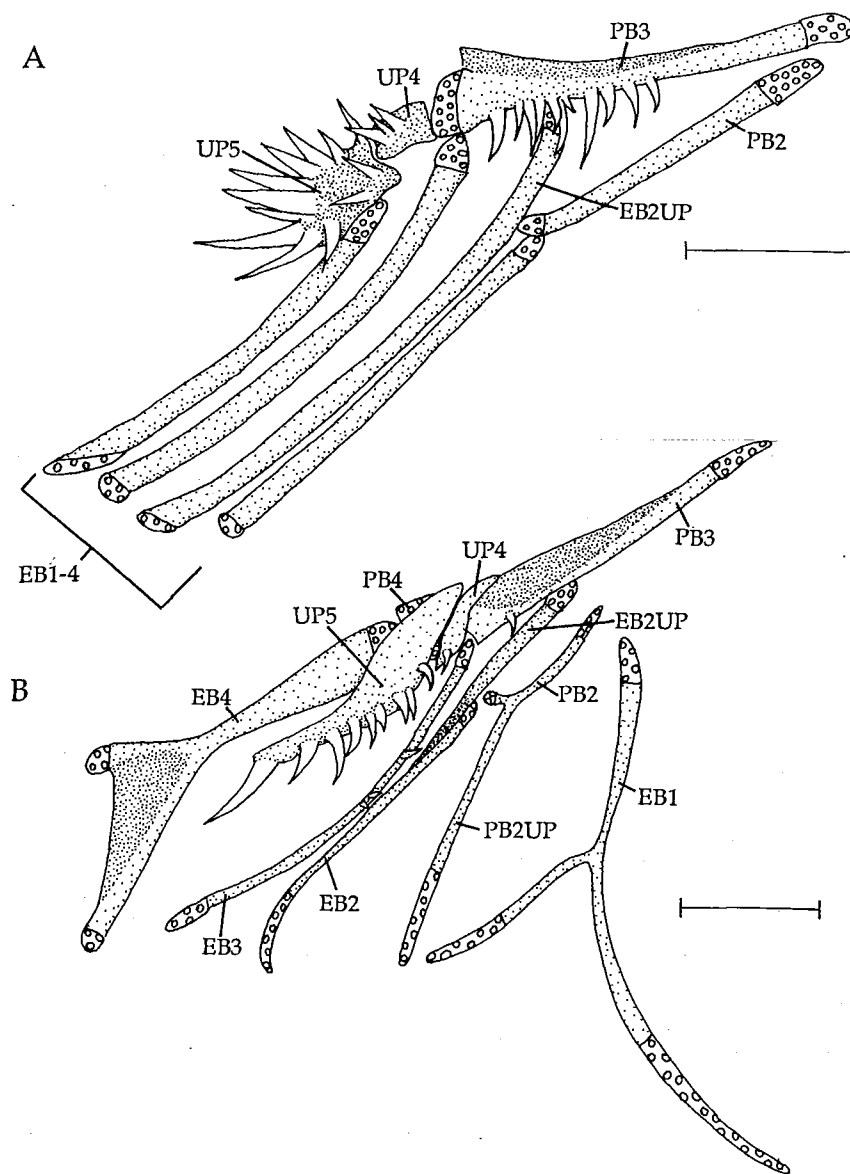
FIGURE 9 Ventral view of dorsal gill arches from left side of (A) *Scopelarchus analis*, USNM 234988 and (B) *Coccorella atlantica*, USNM 235189.

(9_1) = EB2 uncinate process adjacent to EB2 as both approach PB3; PB2 oriented anterior to posterior

10. *Third Pharyngobranchial Produced (Fig. 9B)*—In *Harpadon, Omosudis, Alepisaurus, Anotopterus,* and *Coccorella*, PB3 extends anteriorly well beyond the distal ends of EB1 and PB2. In other aulopiforms and outgroups, PB3 extends to or falls slightly short of the terminal points of those bones. Parsimony indicates convergence in the evolution of a produced PB3—in the ancestor of alepisaurids and independently in *Harpadon, Anotopterus,* and *Coccorella*.

(10_0) = PB3 not extending anteriorly beyond the tips of EB1 and PB2

(10_1) = PB3 extending anteriorly beyond the tips of EB1 and PB2

11. *Distribution of PB3 Teeth (Fig. 9).*—Alepisauroids share a reduced third pharyngobranchial toothplate (UP3), the teeth being reduced in number and restricted to the lateral edge of the ventral surface of PB3. A further reduction occurs in the Paralepididae (including *Anotopterus*), where UP3 is lacking in all members of the family examined except *Paralepis* and

Arctozenus. Primitively in aulopiforms (including *Bathysaurus* and larval *Gigantura*) and outgroups, UP3 is not confined to the lateral edge and sometimes covers most of PB3 (Fig. 3). UP3 is independently reduced in *Harpadon* and *Saurida*, where it resembles that of alepisauroids in being restricted to the lateral edge of PB3.

(11_0) = UP3 covering large area of ventral surface of PB3
(11_1) = UP3 restricted to lateral edge of ventral surface of PB3
(11_2) = UP3 absent

12. Size of PB3 Teeth—Giganturoids share with alepisauroids very large PB3 teeth. We did not measure teeth and thus our analysis of the character is not quantitative, but compare the size of PB3 teeth in *Aulopus* (Rosen, 1973, fig. 4) with that of *Alepisaurus* (Rosen, 1973, fig. 9) and *Gigantura* (Rosen, 1973, fig. 17). *Harpadon* and *Saurida* again are homoplastic in exhibiting large PB3 teeth.

(12_0) = PB3 teeth small
(12_1) = PB3 teeth large

13. First Pharyngobranchial—A suspensory pharyngobranchial is absent in *Pseudotrichonotus, Omosudis, Alepisaurus, Anotopterus, Coccorella, Scopelarchus,* and some *Scopelarchoides,* e.g., *S. danae* and *S. nicholsi* (see R. K. Johnson, 1974a). It is reduced to a small cartilage in *Odontostomops, Evermannella* and *Scopelarchoides signifer.* It is thus a variable feature within the Aulopiformes, especially in alepisauroids among which relationships are uncertain, and we are unable to explain convincingly its pattern of evolution within the group.

In *Bathysauroides* and *Bathysaurus,* the suspensory pharyngobranchial is an unusually long bone, roughly one-third the size of the first epibranchial. PB1 is relatively smaller in other aulopiforms and outgroups, approximately one-fifth the size of the first epibranchial or smaller (as in *Chlorophthalmus, Synodus, Scopelosaurus, Bathypterois, Bathysauropsis,* and *Lestrolepis,* Figs. 3, 7, and 8). Although PB1 is large in larval *Gigantura* (see Fig. 19) it is absent in adults, and we conservatively code this character as "missing data" in *Gigantura.* Regardless, a long PB1 emerges as a synapomorphy of giganturoids.

(13_0) = PB1 normal, reduced, or absent
(13_1) = PB1 very long

14. Fifth Epibranchial (Figs. 3,7, and 8)—A fifth epibranchial (EB5–see Bertmar, 1959; Nelson, 1967) is lacking in all ctenosquamates, and present as a tiny cartilage in *Diplophos.* It is present and large in *Aulopus, Pseudotrichonotus,* chlorophthalmids, *Bathysaur-*

opsis, and ipnopids, and reduced or absent in other synodontoids and chlorophthalmoids. Alepisauroids lack EB5, and giganturoids have it in the form of a small cartilaginous element (except the highly modified *Gigantura* in which it is absent). There are many possible reconstructions of the evolution of this feature, but in all of them a small cartilaginous EB5 is a synapomorphy of notosudids.

(14_0) = EB5 absent
(14_1) = EB5 present as a small cartilage
(14_2) = EB5 present as a large cartilage

15. Dentition of Fifth Ceratobranchial (Fig. 10)—Primitively in aulopiforms and outgroups, small teeth cover the medially expanded anterior surface of CB5 (Fig. 10B). In most alepisauroids (Fig. 10A), teeth are restricted to the medial edge of CB5, although in the scopelarchid genera *Scopelarchoides, Benthalbella,* and *Rosenblattichthys,* most teeth are medial, but one or two are scattered across the center of the dorsal surface. We tentatively interpret the reduction of the tooth-bearing area of CB5 as a synapomorphy of alepisauroids, with one or more modifications in scopelarchids. CB5 teeth are lacking in *Coccorella* (R. K. Johnson, 1982).

(15_0) = CB5 with teeth scattered all over anterodorsal surface
(15_1) = CB5 with most teeth restricted to medial edge of anterodorsal surface
(15_2) = CB5 with all teeth restricted to medial edge of anterodorsal surface
(15_3) = CB5 without teeth

16. Shape of Fifth Ceratobranchial—In aulopiforms and outgroups, CB5 is primitively rod-shaped posteriorly, with a medially expanded tooth-bearing surface anteriorly (Fig. 10B). Synodontids have a somewhat V-shaped CB5 in which the medial expansion is robust (Fig. 10C). Evermannellids also have a somewhat V-shaped CB5, the medial expansion of which is very slender (R. K. Johnson, 1982, figs. 15D, and 15H).

(16_0) = CB5 not V-shaped
(16_1) = CB5 V-shaped, the medial limb slender
(16_2) = CB5 V-shaped, the medial limb robust

17. Gap Between the Fourth Basibranchial Cartilage and Fifth Ceratobranchials (Fig. 10)—In *Diplophos* and most aulopiforms, BB4 extends posteriorly beyond its articulation with the CB4s to articulate with the proximal tips of the CB5s (Fig. 10A). In myctophids, neoscopelids, and *Polymixia,* BB4 is reduced in length, not extending beyond the bases of the CB4s; the CB5s closely approach but do not articulate with BB4. The main body of BB4 is also reduced in *Aulopus* and synodon-
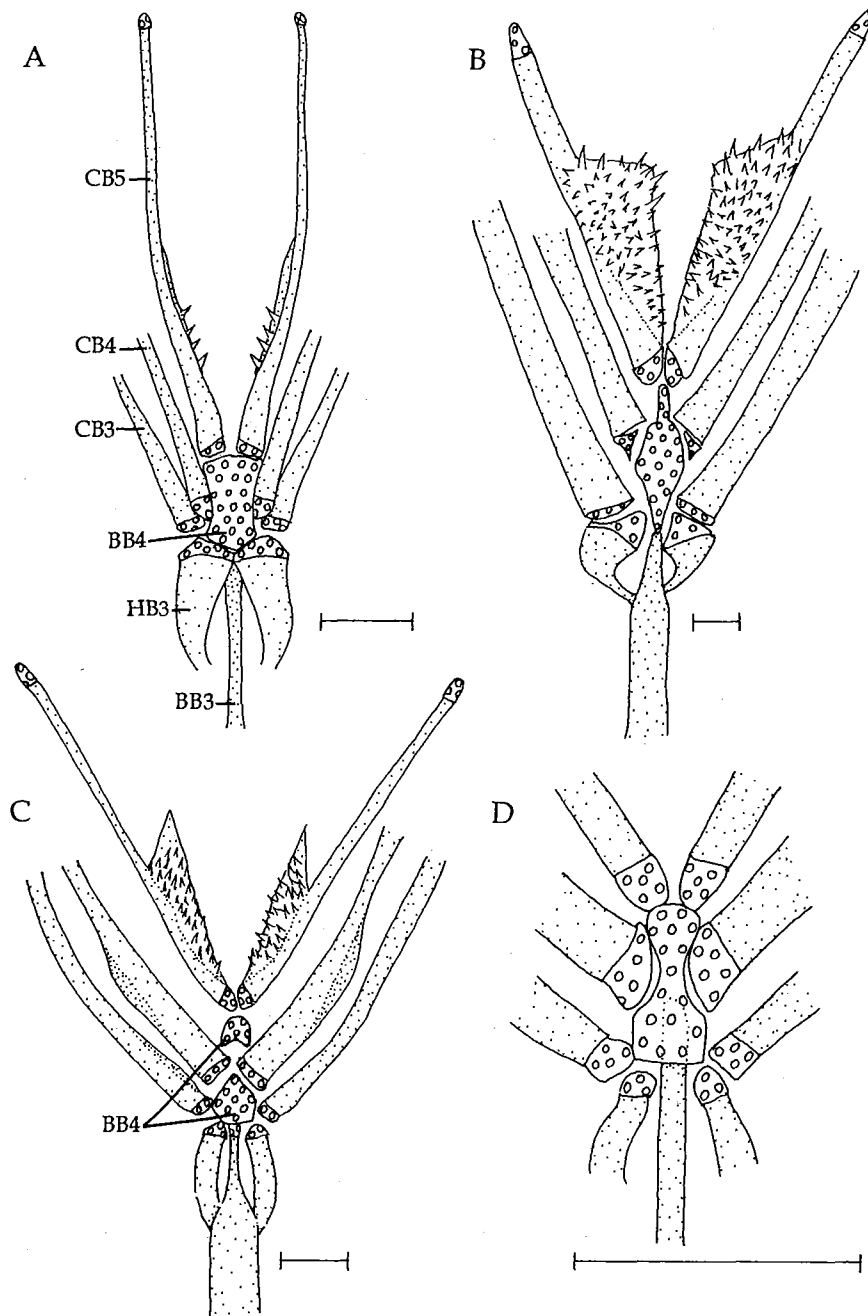
FIGURE 10 Dorsal view of posterior portion of ventral gill arches, posterior toward top of page. (A) *Lestrolepis* sp., USNM 307290, (B) *Aulopus filamentosus*, USNM 292105, (C) *Synodus variegatus*, USNM 339776, and (D) a larval *Synodus variegatus*, USNM 339775.

tids, but in those taxa the CB5s are well separated from the main body of BB4 by a tail of cartilage (aulopids) or one or two small separate cartilages (synodontids) that extend posteriorly from the main body of BB4 (Figs. 10B and 10C). We interpret the conditions in synodontoids and primitive ctenosquamates as distinct.

The absence of the derived synodontoid condition in pseudotrichonotids renders a hypothesis of independent acquisition of the gap in aulopids and the ancestor of synodontids as parsimonious as a single origin in the synodontoid ancestor with reversal in *Pseudotrichonotus*. However, there is some indication that the different configurations of BB4 and CB5s

within synodontoids are homologous: in synodontids, the small posterior cartilages that are separate from BB4 in adults (Fig. 10C) are continuous with that element in larvae (Fig. 10D), a condition very similar to that of *Aulopus* (Fig. 10B) in which a cartilaginous tail extends posteriorly from BB4.

(17_0) = No gap between CB5s and BB4 cartilage
(17_1) = Gap between CB5s and BB4 cartilage, CB5s not articulating with reduced BB4
(17_2) = CB5s separated from main body of BB4 by tail or small nubbins of cartilage extending posteriorly from BB4.

18. Third Basibranchial Extends beyond Fourth Basibranchial Cartilage—In *Harpadon, Saurida,* and alepisaurids, BB3 extends beneath BB4, terminating posteriorly beyond the posterior end of BB4. In other aulopiforms and outgroups, BB3 terminates beneath the anterior end of BB4 (Fig. 10) or slightly more posteriorly in *Macroparalepis* and *Lestrolepis.*

(18_0) = BB3 terminates beneath the anterior end of BB4 cartilage
(18_1) = BB3 terminates beyond the posterior end of BB4 cartilage

19. Fourth Basibranchial Ossified—BB4 is ossified in only two aulopiforms, the ipnopids *Bathymicrops* and *Ipnops.* Because of the proposed sister-group relationship between *Bathymicrops* and *Bathytyphlops,* which has a cartilaginous BB4, we hypothesize ossification of BB4 in the ancestor of *Bathytyphlops* + *Bathymicrops* + *Ipnops* with reversal in *Bathytyphlops.* Alternatively, BB4 ossified independently in *Bathymicrops* and *Ipnops.*

(19_0) = BB4 cartilaginous
(19_1) = BB4 ossified

20. Elongate First Basibranchial—BB1 is typically very small in aulopiforms and outgroups. In notosudids and most paralepidids (including *Anotopterus*), BB1 is elongate, such that the first gill arch is widely separated from the hyoid arch. The condition in notosudids and paralepidids is different, however, in that BB1 is a long ossified element in the former and mostly cartilaginous in the latter. The basibranchials are of approximately equal length in *Paralepis,* but as in other paralepidids, BB1 comprises a short ossified segment anteriorly followed by a long posterior cartilage.

(20_0) = BB1 not elongate
(20_1) = BB1 elongate, ossified
(20_2) = BB1 usually elongate, comprising a short ossified anterior segment followed by a long posterior cartilage

21. Elongate Second Basibranchial—The first and second gill arches are widely separated by an elongate BB2 in notosudids, *Bathytyphlops, Bathymicrops,* and evermannellids. Stiassny (this volume) considered an elongate BB2 a synapomorphy of lampanyctine myctophids, but elongate basibranchials are lacking in other outgroups.

(21_0) = BB2 not elongate
(21_1) = BB2 elongate

22. Gillrakers or Toothplates on Third Hypobranchials—Gillrakers are primitively present on HB3 in aulopiforms and ctenosquamates. Loss of gillrakers on HB3 occurred three times within aulopiforms: once in the ancestor of *Pseudotrichonotus* + synodontids, in *Chlorophthalmus,* and again in the ancestral alepisauroid. The reappearance of HB3 gillrakers is a synapomorphy of *Paralepis* and *Arctozenus.*

(22_0) = Gillrakers or toothplates present on HB3
(22_1) = Gillrakers or toothplates lacking on HB3

23. Gillrakers or Toothplates on Basibranchial(s)—Myctophids have gillrakers extending onto BB2 and BB3, but other outgroups and most aulopiforms lack gillrakers on the basibranchials. *Bathysauropsis,* notosudids, and all ipnopids have gillrakers or toothplates at least on BB2 and sometimes on BB1 and BB3. In those chlorophthalmoids, the basibranchials are deeper than in most other aulopiforms, creating a surface for attachment of the rakers. *Bathysaurus* is the only other aulopiform with gillrakers (present as toothplates in that genus) on BB2. In some paralepidids, the gill filaments and toothplates extend alongside of but do not articulate with BB1 and BB2, which are very thin bones with little surface area laterally for the attachment of rakers.

(23_0) = Gillrakers or toothplates lacking on basibranchials
(23_1) = Gillrakers or toothplates on BB2, sometimes BB1 and BB3

24. Ligament between First Hypobranchial and Ventral Hypohyal—In most aulopiforms and all outgroups, a ligament connects HB1 to the hyoid arch, usually the hypohyal but sometimes the anterior ceratohyal (e.g., *Synodus*). *Bathymicrops* and *Bathytyphlops* are unique among aulopiforms in having this ligament ossified. In *Bathymicrops,* the dorsal and ventral hypohyals are not separate from one another or from the ceratohyal, but the ossified ligament articulates with the hyoid near its junction with the branchial skeleton.

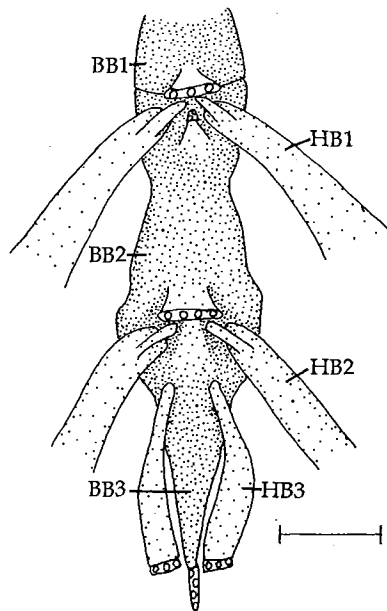(24_0) = Ligament from HB1 to ventral hypohyal not ossified

FIGURE 11 Ventral view of midportion of ventral gill arches of *Synodus variegatus*, USNM 339776, hyoid arch removed.

(24_1) = Ligament from HB1 to ventral hypohyal ossified

25. *First Hypobranchial with Ventrally Directed Process (Fig. 11)*—A small process projects ventrally from HB1 in synodontids, *Chlorophthalmus*, and *Bathysaurus*. Ventral hypobranchial processes on HB1 are lacking in other aulopiform and outgroup taxa.

(25_0) = HB1 without ventrally directed processes
(25_1) = HB1 with a ventrally directed process

26. *Second Hypobranchial with Ventrally Directed Process (Fig. 11)*—Synodontids also have a small process on HB2, a feature that occurs elsewhere among aulopiforms and outgroups only in *Metavelifer*.

(26_0) = HB2 without ventrally directed process
(26_1) = HB2 with ventrally directed process

27. *Third Hypobranchials Fused Ventrally*—In most aulopiforms and all outgroups, the third hypobranchials are variously separated widely from one another or bound closely together ventrally. The third hypobranchials are fused ventrally only in the evermannellids *Evermannella* and *Odontostomops* and the paralepidid *Arctozenus*.

(27_0) = Third hypobranchials not fused ventrally
(27_1) = Third hypobranchials fused ventrally

B. Hyoid Arch

28. *Ventral Ceratohyal Cartilage (Fig. 12)*—An autogenous cartilage extending along part of the ventral margin of the anterior ceratohyal (Fig. 12D) is a derived feature of synodontoids (Johnson *et al.*, 1996). An autogenous cartilage on the ventral surface of the anterior ceratohyal is lacking in other aulopiforms and outgroups (Figs. 12A–12C).

(28_0) = Anterior ceratohyal without autogenous ventral cartilage
(28_1) = Anterior ceratohyal with autogenous cartilage along ventral margin

29. *Number of Branchiostegals on the Posterior Ceratohyal*—McAllister (1968) noted that aulopids, synodontids, and harpadontids differ from other "myctophiforms" in having numerous branchiostegals. Johnson *et al.* (1996) considered six or more branchiostegals on the posterior ceratohyal as a synapomorphy of synodontoids. We concur, as four or fewer is a primitive feature for aulopiforms. *Pseudotrichonotus* has only two, and thus an increase in the number of branchiostegals on the posterior ceratohyal could have been independently acquired in aulopids and in the ancestor of synodontids. Five branchiostegals on the posterior ceratohyal is an autapomorphy of *Bathypterois*.

(29_0) = Four or fewer branchiostegals on posterior ceratohyal
(29_1) = Five branchiostegals on posterior ceratohyal
(29_2) = Six or more branchiostegals on posterior ceratohyal

30. *Number of Branchiostegals on the Anterior Ceratohyal (Fig. 12)*—Synodontoids, most chlorophthalmoids, and most outgroups have five or more branchiostegals on the anterior ceratohyal (Figs. 12B and 12D). *Metavelifer*, *Polymixia*, chlorophthalmids, alepisauroids (Figs. 12A and 12C) and giganturoids have four or fewer (four in all taxa except *Polymixia*, *Coccorella*, and *Alepisaurus* which have three). A reduced number of branchiostegals on the anterior ceratohyal is interpreted in our analysis as a synapomorphy of chlorophthalmoids + alepisauroids + giganturoids with reversal in the ancestor of *Bathysauropsis* + notosudids + ipnopids; it could have evolved independently in the ancestors of the Chlorophthalmidae and Alepisauroidei + Giganturoidei.

(30_0) = Five or more branchiostegals on anterior ceratohyal
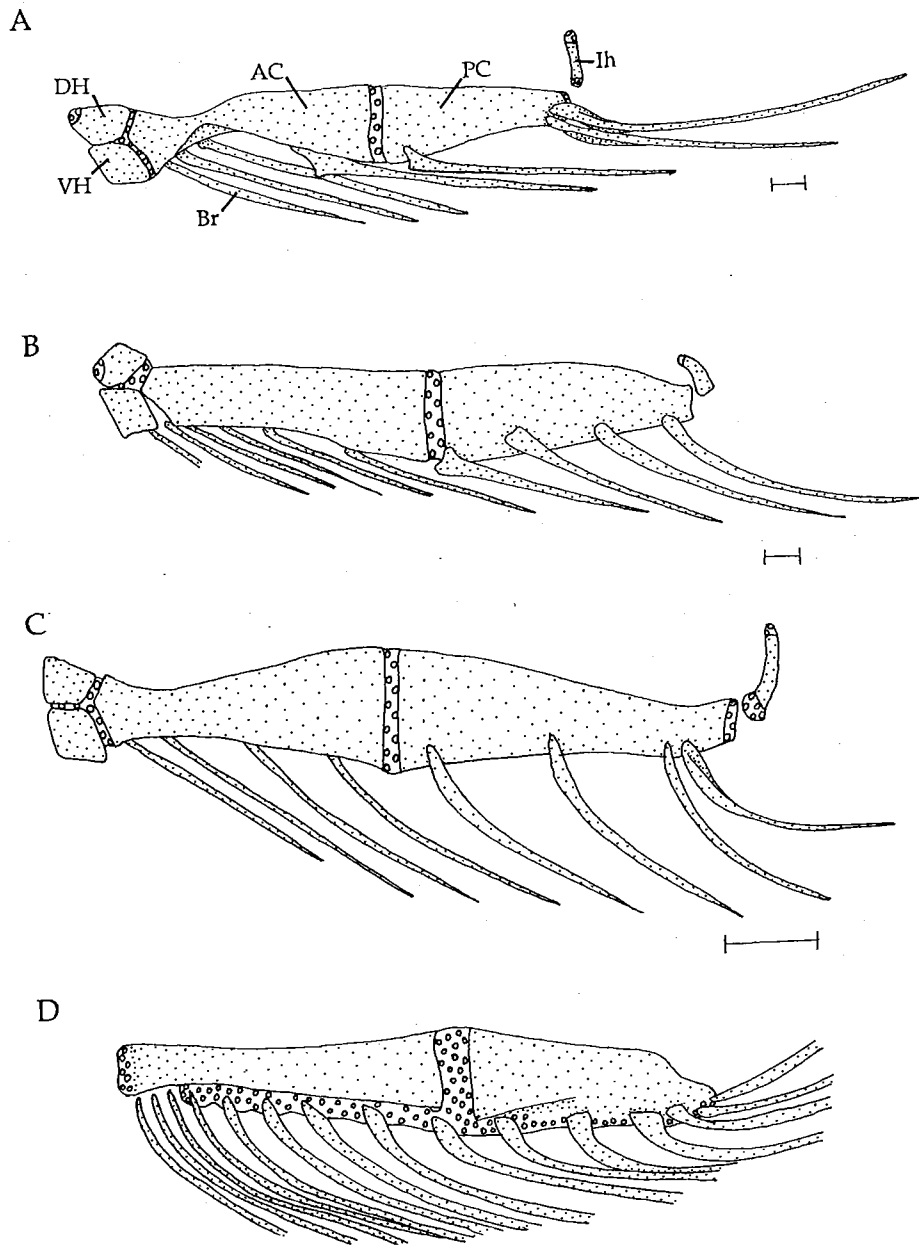(30_1) = Four or fewer branchiostegals on anterior ceratohyal

FIGURE 12   Lateral view of hyoid arch from left side of (A) *Stemonosudis rothschildi*, AMS I.22826001, (B) *Scopelosaurus hoedti*, USNM 264256, (C) *Evermannella indica*, USNM 235141, and (D) *Synodus variegatus*, USNM 31518.

31. *Proximity of Posteriormost Two Branchiostegals (Fig. 12)*—In all paralepidids except *Anotopterus*, the posteriormost two branchiostegals are inserted very close to one another on the posteroventral corner of the posterior ceratohyal (Fig. 12A). Branchiostegals on the posterior ceratohyal in other aulopiforms and the outgroups are well spaced (Figs. 12B and 12D) except in *Evermannella* and *Odontostomops*, in which the posteriormost two are also close but articulate more anteriorly on the posterior ceratohyal than in paralepidids (Fig. 12C).

(31_0) = All branchiostegals on posterior ceratohyal evenly spaced

(31_1) = Two posteriormost branchiostegals close, inserting on ventral margin of posterior ceratohyal

(31_2) = Two posteriormost branchiostegals close, inserting on posteroventral corner of posterior ceratohyal

32. *3 + 1 Arrangement of Branchiostegals on the Anterior Ceratohyal (Fig. 12A)*—In most paralepidids, the ventral margin of the anterior ceratohyal is deeply

indented. Three of the four anterior ceratohyal bran-chiostegals are inserted close to one another on the anterior side of the indentation, and the fourth is inserted posterior to the indentation. McAllister (1968) indicated that the unusual spacing of branchio-stegals may be diagnostic of the Paralepididae, but in *Anotopterus* and *Sudis* (and other aulopiforms with four anterior ceratohyal branchiostegals), the elements are more evenly spaced, although there may be a well-defined indentation in the bone. Parsimony suggests the 3+1 pattern evolved twice: once in the ancestor of *Arctozenus* and *Paralepis* and again in the ancestor of *Macroparalepis*, *Uncisudis*, *Lestidium*, *Lestidiops*, *Stemonosudis*, and *Lestrolepis*.

(32_0) = Branchiostegals on anterior ceratohyal roughly evenly spaced

(32_1) = Branchiostegals on anterior ceratohyal arranged in "3+1" pattern

33. Hypohyal Branchiostegals (Fig. 12B)—*Scopelosaurus* and *Ahliesaurus* have the anteriormost branchiostegal inserting on the ventral hypohyal. In other aulopiforms and most outgroups, all branchiostegals insert on the ceratohyals. *Diplophos* also has a branchiostegal on the ventral hypohyal, and the myctophid *Lampanyctus* has three branchiostegals on the very elongate ventral hypohyal.

(33_0) = No branchiostegals on ventral hypohyal

(33_1) = Anteriormost branchiostegal on ventral hypohyal

(33_2) = Anteriormost three branchiostegals on ventral hypohyal

34. Basihyal Morphology—The morphology of the basihyal is variable among aulopiforms and outgroups, but typically it is horizontal, has a triangular ossification anteriorly (in dorsal view), and is covered by an edentate or strongly toothed dermal plate. A small, obliquely aligned basihyal occurs in ipnopids and *Bathysauropsis* (Hartel and Stiassny, 1986, fig. 7). Notosudids share with most aulopiforms and outgroups a horizontal basihyal, a condition interpreted here as a reversal. An obliquely aligned basihyal is independently present in *Diplophos*.

A more extreme form of the ipnopid condition is found in evermannellids, where the basihyal lies at 90° to the first basibranchial (R. K. Johnson, 1982, fig. 13B). Our phylogeny suggests that the configurations of the basihyal in the two groups are unrelated.

(34_0) = Basihyal oriented horizontally

(34_1) = Basihyal oriented obliquely

(34_2) = Basihyal oriented at 90° angle to BB1

35. Basihyal Teeth—Basihyal teeth are variously present or absent among aulopiforms and outgroups.
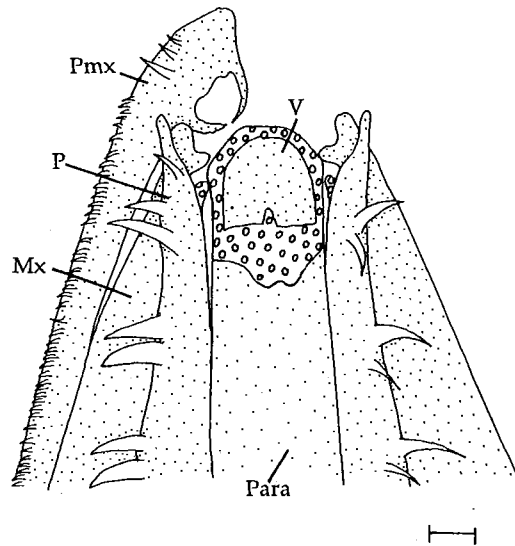

FIGURE 13 Ventral view of palate of *Lestrolepis intermedia*, USNM 290253; premaxilla removed from left side.

They are present in scopelarchids as large, posteriorly curved structures that form a single row down the center of the bone (R. K. Johnson, 1974a, fig. 9).

(35_0) = Basihyal teeth absent or unmodified if present

(35_1) = Basihyal teeth present as large, posteriorly curved structures

C. Jaws, Suspensorium, and Circumorbitals

36. Dominant Tooth-bearing Bone (Fig. 13)—In alepisauroids and *Bathysauroides*, the palatine is the dominant tooth-bearing bone of the upper "jaws." In most of those taxa, the premaxilla also bears teeth, but they are considerably smaller than the palatine teeth. *Bathysaurus* has premaxillary and palatine teeth about equally developed. The large teeth in *Gigantura* are on the premaxilla, but the dermopalatine never develops, and the autopalatine is lost ontogenetically. In all other aulopiforms and outgroups, the palatine may bear teeth, but the premaxilla (and maxilla in stomiiforms) is the dominant tooth-bearing bone of the upper jaw.

(36_0) = Premaxilla (or premaxilla and maxilla) is the dominant tooth-bearing bone of upper jaw

(36_1) = Premaxilla and palatine are the dominant tooth-bearing bones of upper jaw

(36_2) = Palatine is the dominant tooth-bearing bone of "upper jaw"

37. Quadrate with Produced Anterior Limb (Fig. 14)—Johnson *et al.* (1996) described a series of suspensorial
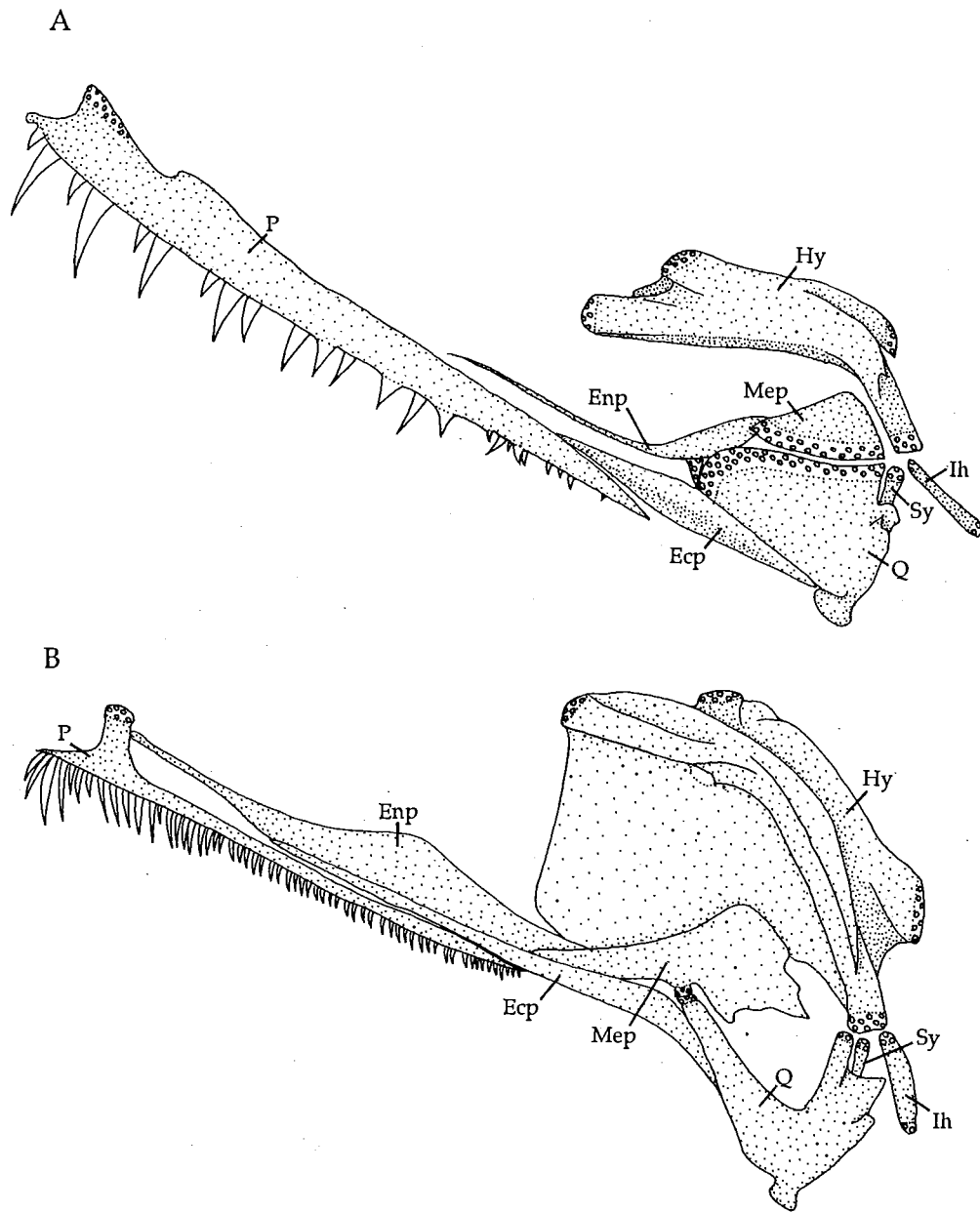
A

B

FIGURE 14 Lateral view of suspensorium from left side of (A) *Bathysaurus mollis*, VIMS 6107 and (B) *Synodus variegatus*, USNM 315318.

modifications that support the monophyly of syno-dontids. Among these is the loss of the typical fan-shaped quadrate due to the presence of a produced anterior limb (Fig. 14B).

(37_0) = Quadrate fan-shaped
(37_1) = Quadrate with produced anterior limb

38. *Quadrate with Two Distinct Cartilaginous Heads (Fig. 14)*—Synodontids have two distinct cartilaginous condyles on the quadrate, one anteriorly and one pos-

teriorly, both anterior to the symplectic incisure (Fig. 14B). In most other aulopiforms and outgroups, a single large cartilage borders the dorsal and anterodorsal margins of the fan-shaped quadrate (Fig. 14A). Separation of the quadrate cartilage into two discrete condyles occurs independently in notosudids.

(38_0) = Quadrate with single large cartilage on dorsal border
(38_1) = Quadrate cartilage separated into two condyles

39. *Large Concavity in Dorsal Margin of Quadrate (Fig. 14)*—Among those aulopiforms having the quadrate cartilage separated into two condyles, *Synodus* and *Trachinocephalus* are unique in having a large concavity between them (Fig. 14B).

(39_0) = No concavity in quadrate (excluding symplectic incisure)

(39_1) = Concavity between anterior and posterior cartilaginous condyles

40. *Posterior Cartilaginous Condyle of Quadrate Articulates with Hyomandibular (Fig. 14)*—In *Synodus* and *Trachinocephalus*, the posterior cartilaginous condyle of the quadrate articulates with the ventral cartilaginous condyle of the hyomandibular (Fig. 14B). In other aulopiforms and outgroups, the posterior portion of the single quadrate cartilage or the posterior of the separate cartilaginous condyles articulates with a ventral cartilaginous condyle on the metapterygoid (e.g., as in *Bathysaurus*, Fig. 14A). In synodontids, the metapterygoid is displaced anteriorly, well forward of the posterior limb of the quadrate, and lacks a ventral cartilaginous condyle.

(40_0) = Posterior portion of quadrate articulates dorsally with metapterygoid

(40_1) = Posterior cartilaginous condyle of quadrate articulates dorsally with hyomandibular.

41. *Metapterygoid Produced Anteriorly (Fig. 14)*— In synodontids, the metapterygoid has an anterior extension that overlies the posterior part of the ectopterygoid (Fig. 14B). In other aulopiforms and outgroups, the metapterygoid overlies the quadrate and does not extend anteriorly over the ectopterygoid (Fig. 14A).

(41_0) = Metapterygoid overlies quadrate

(41_1) = Metapterygoid extends anteriorly over posterior portion of ectopterygoid

42. *Metapteryoid Free of Hyomandibular*—In ipnopids, the posterior end of the metapterygoid overlies the hyomandibular, but the two bones are not tightly bound together and do not articulate with one another through cartilage. In *Bathypterois*, the suspensorium is even less articulated, as the hyomandibular is also free from the symplectic. In other aulopiforms and outgroups, the metapterygoid may overlie the hyomandibular, but it is always tightly bound to it—through a cartilage process on the posterior margin of the metapterygoid, connective tissue, or sometimes a bony strut extending from the dorsal aspect of the metapterygoid posteriorly to the hyomandibular shaft.

(42_0) = Metapterygoid bound to hyomandibular

(42_1) = Metapterygoid free from hyomandibular

43. *Hyomandibular and Opercle Oriented Horizontally*—In *Bathytyphlops* and *Bathymicrops*, the hyomandibular is rotated so that it lies almost parallel to the long axis of the body. The opercle is similarly rotated and lies directly above the hyomandibular (Sulak, 1977, fig. 11). Accompanying those changes are an elongation of the ectopterygoid and reduction of the endopterygoid (Sulak, 1977, fig. 11). In other aulopiforms and outgroups, the orientation of the hyomandibular ranges from slightly oblique, as in *Chlorophthalmus* (Sulak, 1977, fig. 7A), to oblique (ca. 45°), as in *Harpadon* (Sulak, 1977, fig. 6C; Johnson et al., 1996, fig. 27). In none of those taxa does the hyomandibular approach a horizontal orientation, and the opercle is never rotated dorsally to lie above it.

(43_0) = Hyomandibular oriented vertically or subvertically, opercle posterior to suspensorium

(43_1) = Hyomandibular oriented ca. horizontally, opercle rotated dorsally to lie above hyomandibular

44. *Maxillary Saddle (Fig. 15)*—Regan (1911) first noted that iniomous fishes usually differ from isospondylous fishes in having a process on the palatine that projects outward and upward and articulates with a depression (maxillary saddle) in the proximal end of the maxilla. Gosline et al. (1966) referred to the palatine projection as a "palatine prong" and noted that its presence in only some iniomes renders it of questionable value in distinguishing iniomous fishes from those of the Isospondyli. Stiassny (1986) found that, among Rosen's (1973) aulopiforms, only *Aulopus*, *Chlorophthalmus*, and *Parasudis* have a palatine prong system and that the presence of that feature as well as a deeply folded articular head on the maxilla (Rosen, 1973, p. 505) unites those genera with the Ctenosquamata.

We concur with Stiassny (1986) that a palatine prong system is unique among aulopiforms to aulopids and chlorophthalmids, but our analysis supports the monophyly of Rosen's (1973) aulopiforms, and we therefore disagree with Stiassny's interpretation of this feature as evidence of a paraphyletic Aulopiformes. It is most parsimonious to hypothesize independent evolution of the palatine prong system in ctenosquamates, aulopids, and chlorophthalmids, but we note that only one additional step is required for evolution of the system at the level of Eurypterygii with reversals within the Aulopiformes. *Pseudotrichonotus* is unique among aulopiforms in having a well-developed maxillary saddle for attachment of the palato-maxillary ligament; it lacks a palatine prong
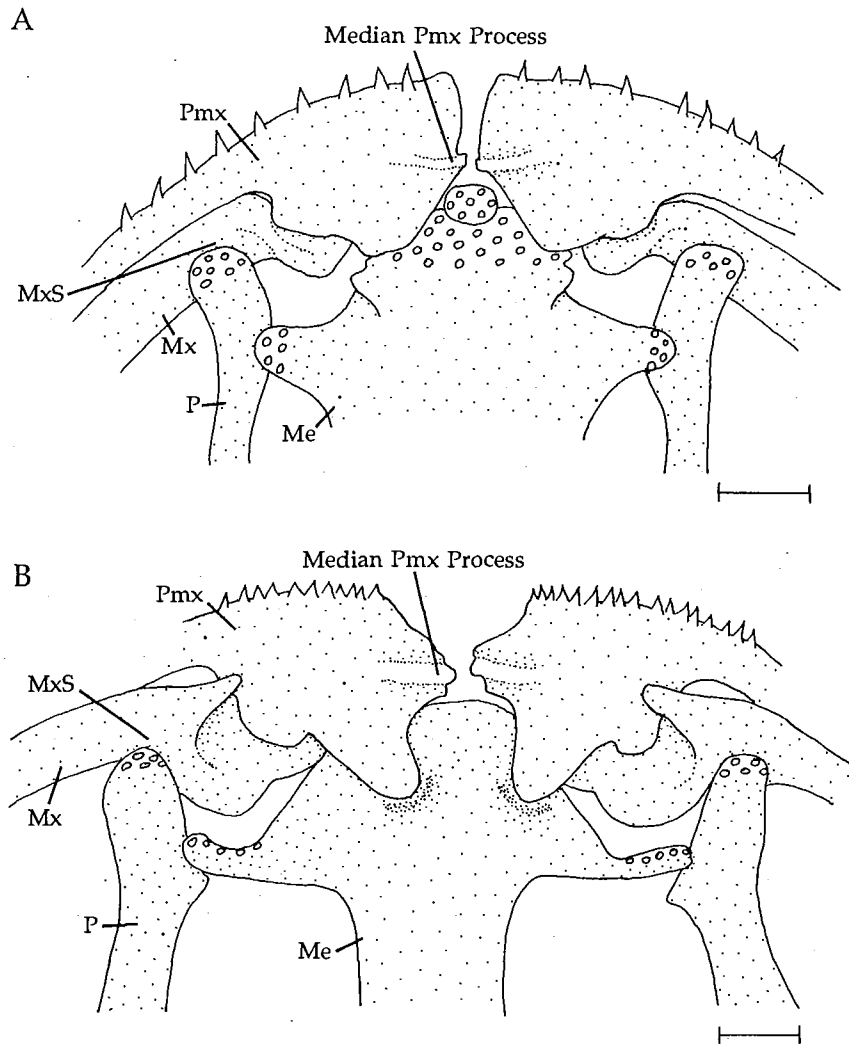
FIGURE 15   Dorsal view of snout region of head in (A) *Parasudis truculentus*, USNM 159850 and (B) *Chlorophthalmus atlanticus*, USNM 339774.

(Johnson et al., 1996). As noted by Olney et al. (1993), *Metavelifer* has lost the connection between the palatine and maxilla, a modification that allows greater protrusibility of the upper jaw.

(44_0) = Palatine prong and maxillary saddle absent
(44_1) = Palatine prong absent, maxillary saddle present
(44_2) = Palatine prong and maxillary saddle present

45. *Dorsomedially Directed Premaxillary Process (Fig. 15)*—In chlorophthalmoids, a dorso-medially directed process arises from near the medial edge of each premaxilla and is ligamentously bound to its contralateral member. We have not observed this process in other aulopiforms or outgroups, which typically have a smooth medial premaxillary margin (as in *Lestrolepis*, Fig. 13).

(45_0) = Premaxilla without dorso-medially directed process on medial edge
(45_1) = Premaxilla with dorso-medially directed process on medial edge

46. *Number of Infraorbitals*—Aulopiforms primitively have six infraorbitals, as do stomiiforms, myctophiforms, and *Polymixia*. *Metavelifer* has three, as does *Bathymicrops*. *Ipnops* and *Bathytyphlops* have five infraorbitals, a synapomorphy of those genera and *Bathymicrops* in our analysis, with further reduction in the latter.

R. K. Johnson (1982) noted that seven infraorbitals is a synapomorphy of notosudids, a hypothesis corroborated by our analysis. Alepisaurids, most paralepidids, and evermannellids have eight infraorbitals, an ambiguous character state interpreted here as a

synapomorphy of alepisauroids, with reversal to six in scopelarchids and *Anotopterus*.

(46_0) = Six infraorbitals
(46_1) = Seven infraorbitals
(46_2) = Eight infraorbitals
(46_3) = Five infraorbitals
(46_4) = Three infraorbitals
(46_5) = No infraorbitals

47. Long Snout—Paralepidids have a long snout ranging from approximately 50% of the head length in *Paralepis, Arctozenus, Macroparalepis, Lestidium, Lestidiops*, and *Lestrolepis* to well over 50% head length in *Anotopterus, Sudis, Uncisudis*, and *Stemonosudis*. In all other aulopiforms and outgroups, the snout is considerably less than 50% head length.

(47_0) = Snout length much < 50% head length
(47_1) = Snout length > 50% head length

48. Premaxillary Fenestra (Fig. 13)—R. K. Johnson (1982) considered the presence of a fenestrated premaxilla as a synapomorphy of paralepidids and *Anotopterus*, noting that although Rosen (1973) viewed the feature as diagnostic of his alepisauroids, it does not appear to be present in alepisaurids, evermannellids, and other iniome fishes. We concur and note that all paralepidids examined have at least a partial fenestra in the anterior end of the premaxilla. The fenestra is usually complete in larger specimens.

(48_0) = No premaxillary fenestra
(48_1) = Anterior premaxilla with fenestra

49. Palatine Articulates with Premaxilla (Fig. 13)—In paralepidids, the palatine terminates anteriorly in a long process that articulates by connective tissue with the medial surface of the premaxilla, just posterior to the premaxillary fenestra. Various associations between the palatine and maxilla (when present) exist among aulopiforms and outgroups, but the palatine typically terminates near the point where it articulates with the maxilla and does not extend anteriorly to meet the premaxilla.

The palatine also articulates with the premaxilla in *Harpadon*, but this condition differs from that in paralepidids in that the premaxilla replaces the maxilla as the site of articulation with the palatine and ethmoid because the maxilla is present only as a small remnant.

(49_0) = Palatine without process for articulation with premaxilla
(49_1) = Palatine with long process for articulation with premaxilla

50. Lacrimal Oriented Horizontally on Snout—The lacrimal typically borders the orbit anteriorly. In para-

lepidids, the second infraorbital is in the position normally occupied by the lacrimal, and the lacrimal is located horizontally on the snout, well rostral to the orbit. Our identification of this bone as the lacrimal rather than the antorbital is based on its relatively large size and association with the upper jaw; as is typical of the lacrimal, this bone extends along a portion of the upper border of the maxilla. In our small specimens of *Sudis*, the position of the lacrimal cannot be determined.

(50_0) = Lacrimal bordering orbit anteriorly
(50_1) = Lacrimal anterior to orbit, oriented horizontally.

51. Maxilla Reduced—Johnson *et al.* (1996) discussed the problems associated with Sulak's (1977) interpretation of a reduced maxilla in *Harpadon* and *Saurida*, especially his assessment of a division of the maxilla into anterior and posterior elements. They concluded that a reduced maxilla is a synapomorphy of synodontids and harpadontids and suggested that the reduced maxilla in *Bathysaurus*, which exists as a remnant anteriorly, is not homologous with the posterior remnant in *Harpadon*. The condition in *Bathysaurus*, however, may be homologous with the posterior maxillary remnant of *Gigantura*, as our phylogeny supports Patterson and Johnson's (1995) hypothesis of a sister-group relationship between *Bathysaurus* and *Gigantura* (see character 117 below and Discussion); nevertheless, we conservatively consider anterior and posterior maxillary remnants as distinct.

The maxilla of most alepisauroids is slender relative to that of other aulopiforms, but usually retains the same shape in that the posterior end is expanded. We do not recognize the alepisauroid condition as a separate state except in *Anotopterus*, in which the maxilla is a very slender, strut-like bone with no posterior expansion.

(51_0) = Maxilla well developed with posterior end expanded
(51_1) = Maxilla intact but slender, posterior end not expanded
(51_2) = Maxilla present as posterior remnant
(51_3) = Maxilla present as anterior remnant

D. Cranium

We did not examine the cranial morphology of aulopiforms in detail but describe certain aspects of the ipnopid cranium below.

52. Frontal Expanded Laterally over Orbit—The skull of ipnopids is dorsoventrally compressed, and the frontals extend laterally over the eyes in *Bathypterois*,

Bathymicrops, and *Bathytyphlops* and beneath the large photosensitive plates in *Ipnops*. In other aulopiforms and outgroups, the frontals lie completely between the orbits.

(52_0) = Frontal not expanded laterally
(52_1) = Frontal expanded laterally

53. *Sphenotic Process*—The sphenotic is modified in all ipnopids such that a process of the bone extends anteriorly beneath the greatly expanded frontal. In its most extreme form, the process extends forward to the lateral ethmoid, as in *Bathytyphlops*. It extends about halfway to the lateral ethmoid in *Bathymicrops*, and only a little forward in *Ipnops*. It is least developed but present as a small rounded extension beneath the frontal in *Bathypterois*. In other aulopiforms and outgroups, the sphenotic abuts the frontal but has no anteriorly directed process.

(53_0) = Sphenotic without anterior process
(53_1) = Sphenotic with anterior process

E. Intermuscular Bones and Ligaments

Unless otherwise noted, all characters described in this section are from Patterson and Johnson (1995). Our survey of aulopiform intermusculars is more extensive than that of Patterson and Johnson, but it is still incomplete (Table 1). Further investigation is needed.

54. *Epipleurals Extend Anteriorly to First or Second Vertebra*—In synodontoids and chlorophthalmoids, epipleurals extend anteriorly to the second vertebra (V2); in alepisauroids and giganturoids, they extend to V1. When present, epipleurals begin on V3 in the outgroups. *Metavelifer* and all acanthomorphs except *Polymixia* lack epipleurals, a condition we code as a separate state for this character but as "missing data" for other epipleural characters in this section to avoid erroneously inflating tree length and modifying other tree statistics. Patterson and Johnson (1995) hypothesized that the anterior extension of epipleurals to V2 is a synapomorphy of Aulopiformes, but their consensus tree indicates that the extension of epipleurals to V1 (from V2) evolved independently in the ancestor of the Evermannellidae + Scopelarchidae and the remaining alepisauroids. Our phylogeny suggests that the extension of epipleurals to V1 occurred once, in the ancestor of alepisauroids + giganturoids.

(54_0) = Epipleurals originate on V3
(54_1) = Epipleurals originate on V2
(54_2) = Epipleurals originate on V1
(54_3) = Epipleurals absent

55. *One or More Epipleurals Displaced Dorsally Into Horizontal Septum*—The presence of one or more anterior epipleurals displaced dorsally into the horizontal septum is a synapomorphy of aulopiforms. *Aulopus* and *Gigantura* have a single epipleural in the horizontal septum, but most other aulopiforms have more than one displaced. *Bathypterois, Bathymicrops,* and *Parasudis* have all epipleurals beneath the horizontal septum, and those taxa fall outside of a clade comprising the remaining aulopiforms in Patterson and Johnson's (1995) tree constructed solely on the basis of intermuscular characters. It is more parsimonious to interpret the absence of dorsally displaced epipleurals in *Bathypterois, Bathymicrops,* and *Parasudis* as reversals. Our small cleared and stained specimen of *Ipnops* lacks ossified epipleurals anteriorly, and we were not able to conclusively identify ligamentous epipleurals anteriorly in that specimen.

(55_0) = All epipleurals beneath the horizontal septum
(55_1) = One or more epipleurals displaced dorsally into horizontal septum

56. *Abrupt Transition of Epipleurals in and beneath the Horizontal Septum*—Two states of the derived condition of dorsally displaced anterior epipleurals occur in aulopiforms. In one, the transition between epipleurals in and beneath the horizontal septum is abrupt, such that the last posterolaterally directed epipleural in the horizontal septum is followed immediately by a ventrolaterally directed epipleural that is completely below the horizontal septum. This occurs only in *Pseudotrichonotus, Synodus,* and *Trachinocephalus*. In other aulopiforms, including *Harpadon* and *Saurida*, the transition is gradual, occurring over a series of vertebrae.

We initially coded this character as having three states (no epipleurals in the horizontal septum, an abrupt transition of epipleurals in and beneath the horizontal septum, and a gradual transition of those epipleurals) to determine the primitive aulopiform state. Parsimony indicates that a gradual transition is primitive for aulopiforms and a synapomorphy of the order. However, it does not seem valid to consider both the presence of one or more dorsally displaced epipleurals (55_1) and a gradual transition of epipleurals in and beneath the horizontal septum as synapomorphies of aulopiforms because the latter is a state of the former. Accordingly, for this character, we group the most common outgroup condition (no dorsally displaced epipleurals) and the primitive ingroup condition (gradual transition of epipleurals) as a single state. This allows us to recognize the abrupt transition of epipleurals in some synodontoids as a derived fea-

ture without creating two synapomorphies of aulopiforms where only one is warranted.

(56_0) = No epipleurals displaced dorsally into the horizontal septum or the transition between epipleurals in and beneath the horizontal septum is gradual.

(56_1) = Abrupt transition between epipleurals in and beneath the horizontal septum

57. One or More Epipleurals Forked Distally—In the region where the epipleurals leave the horizontal septum in notosudids, around V19 (*Ahliesaurus*) or V20–V24 (*Scopelosaurus*), the epipleurals are bifurcate distally. In other aulopiforms and outgroups, epipleurals are not forked distally at the transition in and beneath the horizontal septum (or none are in the septum).

(57_0) = Epipleurals not forked distally

(57_1) = Epipleurals forked distally at transition of epipleurals in and beneath the horizontal septum

58. Epipleural on First and Second Vertebrae Fused to Centrum—In *Omosudis*, *Alepisaurus*, and *Paralepis*, the epipleurals on V1 and V2 are fused to the centrum. Those epipleurals are free in other paralepidids, aulopiforms, and outgroups. Fusion of the epipleurals in *Paralepis* is independent of that in the alepisaurid lineage.

(58_0) = Epipleurals on V1 and V2 autogenous

(58_1) = Epipleurals on V1 and V2 fused to centrum

59. Epipleurals Not Attached to Axial Skeleton—Most epipleurals are not attached to the axial skeleton in *Omosudis*, *Paralepis*, and *Arctozenus*, but most or all are attached in *Alepisaurus*, other aulopiforms, and outgroups. As with the epineurals (see character 63 below), *Paralepis* and *Arctozenus* have the anterior epipleurals forked anteriorly, and the branch that attaches the bone to the axial skeleton disappears posteriorly leaving a large series of unattached epipleurals.

(59_0) = Most or all epipleurals attached to axial skeleton

(59_1) = Most epipleurals not attached to axial skeleton

(59_2) = Most epipleurals are free dorsal branches

60. Reduced Number of Epipleurals—Most aulopiforms have a long series of epipleurals that begin on V1 or V2. Most outgroups also have a well-developed series of epipleurals, although they begin more posteriorly than in aulopiforms (see character 54). In the paralepidids *Lestrolepis*, *Macroparalepis*, and *Sudis*, the epipleural series is confined to the first five or fewer vertebrae. Epipleurals are not evident in our small specimens of *Uncisudis*, *Stemonosudis*, and *Lestidiops*.

(60_0) = Long series of epipleurals

(60_1) = Epipleural series not extending posteriorly beyond V5

61. Origin of Epineurals—In *Scopelosaurus* and *Ahliesaurus*, anterior epineurals originate on the neural arch. The origin of subsequent epineurals descends to the centrum or parapophysis, and then it reascends in posterior epineurals to the neural arch. A similar configuration of ventrally displaced epineurals occurs in evermannellids, scopelarchids, and *Bathysauroides*. In those taxa, the origin of epineurals always returns to the neural arch posteriorly, and usually less than half of the epineurals originate on the centrum. In *Bathysaurus*, the first five epineurals originate on the neural arch, and the origin of the rest descends to the centrum. In *Gigantura*, all epineurals originate on the centrum. In other aulopiforms, *Diplophos*, myctophiforms, and *Metavelifer*, all epineurals originate on the neural arch. In *Polymixia*, epineurals on V3–10 originate on the centrum, those more anterior and posterior originate on the neural arch or spine. The origin of some of the central epineurals on the centrum (with reascension posteriorly) and the origin of most or all epineurals on the centrum (without reascension posteriorly) are derived conditions within the Aulopiformes.

(61_0) = All epineurals originate on neural arch

(61_1) = Some epineurals originate on the centrum or parapophysis; these flanked anteriorly and posteriorly by epineurals originating on the neural arch

(61_2) = Most or all epineurals originate on centrum; epineurals not reascending to neural arch posteriorly

62. First One to Three Epineurals with Distal End Displaced Ventrally—In some aulopiforms, the first one to three epineurals are turned downward such that they extend lower than their successors. The distal end of the epineurals on V1–V3 is so modified in *Aulopus*, *Pseudotrichonotus* (V1–V2), *Synodus* (V1–V2), *Trachinocephalus* (V1), *Chlorophthalmus* (V1–V2), *Ipnops* (V1), and *Bathysauroides* (V1–V2). Patterson and Johnson (1995) suggested that *Chlorophthalmus* may be the sister group of synodontoids based on this feature, but our analysis indicates that having the distal end of the anteriormost one or more epineurals turned downward evolved independently in *Chlorophthalmus*, *Bathysauroides*, and the ancestral synodontoid. The condition is reversed in *Harpadon* and *Saurida*.

(62_0) = Distal end of epineurals not displaced ventrally

(62_1) = Distal end of first one to three epineurals displaced ventrally

63. *Some Epineurals and Epipleurals Forked Proximally*—Beginning on about V12 or V15, the epineurals in *Chlorophthalmus* and *Parasudis* are forked proximally. Posteriorly, the dorsomedial branch, which attaches the epineural to the axial skeleton, disappears, leaving a short series of unattached epineurals. A similar condition occurs primitively in myctophiforms. Patterson and Johnson (1995) did not identify forked epineurals in *Paralepis*, but our examination of additional specimens of that genus indicates that the anteriormost five or six epineurals are forked proximally, the dorsal branch disappearing posteriorly, leaving a long series of unattached epineurals (see character 65). A nearly identical pattern characterizes *Arctozenus*. A unique branching of the epineurals characterizes *Gigantura* (Patterson and Johnson, 1995).

Proximal branching of epipleurals occurs in the same pattern as that of the epineurals among aulopiforms, and we group the branching of the two series of bones as a single character.

(63_0) = No epineurals (or epipleurals) forked proximally
(63_1) = Epineurals (and epipleurals) from about V12–V15 to near end of series forked proximally
(63_2) = Epineurals (and epipleurals) on about V1–V5 forked proximally
(63_3) = "*Gigantura*" pattern of branching

64. *Epineurals Fused to Neural Arch*—Epineurals are fused to the neural arch on V1–V10 in *Harpadon* and *Saurida*. Epineurals typically are not fused to the axial skeleton in aulopiforms and outgroups, although they are fused to the neural arch on V1–V5 in *Diplophos* and *Alepisaurus* and on V1 in *Paralepis* and *Macroparalepis*; most are fused to the centrum in *Rosenblattichthys* and *Bathysaurus*. Fusion of epineurals to the axial skeleton has thus evolved several times within aulopiforms, and our analysis suggests that this condition is phylogenetically significant only as a synapomorphy of *Harpadon* and *Saurida*.

(64_0) = Epineurals not fused to axial skeleton
(64_1) = Epineural fused to neural arch on V1
(64_2) = Epineurals fused to neural arch on V1–V5
(64_3) = Epineurals fused to neural arch on V1–V10
(64_4) = Most epineurals fused to centrum

65. *Epineurals Attached to Axial Skeleton*—In *Alepisaurus* and *Omosudis*, most epineurals are not attached to the axial skeleton, and in *Anotopterus*, all are unattached. *Paralepis* and *Arctozenus* have the anterior epineurals forked and attached to the axial skeleton by

the dorsal branch of the fork; on about V5 or V6, only the ventral branch remains, and the epineurals are thus unattached posteriorly. In other aulopiforms and outgroups, all or most epineurals are attached.

(65_0) = Most or all epineurals attached to axial skeleton
(65_1) = Most epineurals unattached
(65_2) = All epineurals unattached
(65_3) = Unattached epineurals represent only free ventral branches of forked epineurals

66. *Epicentrals*—Paralepidids, *Bathysaurus*, and *Gigantura* lack epicentrals. *Omosudis* and *Alepisaurus* have them ossified and beginning on V3. *Parasudis* has all epicentrals ossified and beginning on V1. All other aulopiforms and outgroups have ligamentous epicentrals, except the anterior epicentrals are cartilaginous in evermannellids (see next character), and the ligamentous epicentrals of *Polymixia* contain a cartilaginous rod distally (Patterson and Johnson, 1995). It is equally parsimonious to consider ligamentous epicentrals, ossified epicentrals, or no epicentrals as the ancestral condition for the clade comprising alepisaurids and paralepidids, but it seems unlikely that ligamentous epicentrals transformed into ossified ones and then were lost or that ligamentous epicentrals were lost and then regained as ossified epicentrals. There is evidence from *Parasudis* that ligamentous epicentrals ossify and from giganturoids that ligamentous epicentrals are lost (the ancestral chlorophthalmoid and giganturoid intermuscular systems are characterized by ligamentous epicentrals), and thus we believe it most likely that the ossification of ligamentous epicentrals is a synapomorphy of alepisaurids, and loss of ligamentous epicentrals is a derived feature of paralepidids. To reflect this, we partially ordered this character such that a single step is required to lose or ossify ligamentous epicentrals, but two steps are required to lose ossified epicentrals or gain ossified epicentrals when none existed ancestrally. Considering this character entirely unordered does not change the phylogeny but eliminates a synapomorphy of alepisaurids and one of paralepidids.

(66_0) = Epicentrals ligamentous
(66_1) = Epicentrals ossified
(66_2) = Epicentrals absent
(66_3) = Epicentrals cartilaginous anteriorly, ligamentous posteriorly

67. *Anterior Epicentrals Closely Applied to Distal End of Epipleurals*—Evermannellids are unique among aulopiforms in having the anterior epicentrals present as small rods of cartilage closely applied to the distal ends of the epipleurals. This is unusual because epi-

centrals are almost always attached to the centrum or parapophyses. A similar condition occurs in scopelarchids except that the anterior epicentrals are in ligament.

(67_0) = All epicentrals attached to centrum or parapophyses

(67_1) = Anterior epicentrals attached to distal end of epipleurals

F. Postcranial Axial Skeleton

68. *Number of Supraneurals*—Presence of three supraneurals preceding the dorsal fin is a synapomorphy of eurypterygians (Johnson and Patterson, this volume), but many aulopiforms have two or fewer, and numerous reconstructions of the reductions are possible. We interpret a single supraneural as a synapomorphy of chlorophthalmoids with reversals in *Chlorophthalmus*, *Bathysauropsis*, and *Bathytyphlops*. Presence of two supraneurals is a synapomorphy of alepisauroids, with further reduction to one (*Omosudis*) or none (*Alepisaurus*) in alepisaurids (or in their common ancestor) and reversal to three in the ancestral scopelarchid.

(68_0) = Three or more supraneurals
(68_1) = Two supraneurals
(68_2) = One supraneural
(68_3) = No supraneurals

69. *Number of Caudal Vertebrae*—Aulopiforms, stomiiforms, and ctenosquamates primitively have about half (40–60%) of the vertebrae as caudal vertebrae. A reduction in the number of caudal vertebrae occurs independently in the synodontid–harpadontid clade (17–19%) and in giganturoids (11–24%). Scopelarchids and evermannellids have 62–70% caudal vertebrae, a condition that we interpret as synapomorphic for those families. A large number of caudal vertebrae occur independently in *Chlorophthalmus* (62%), *Bathymicrops* (68%), and *Arctozenus* (70%). It seems reasonable that both the very low and very high numbers of caudal vertebrae were derived from the primitive aulopiform condition of about 50% (coded as 69_1), and thus we consider the three states to form an ordered transformation series ($69_0 \leftrightarrow 69_1 \leftrightarrow 69_2$).

(69_0) = < 25% caudal vertebrae
(69_1) = 40–60% caudal vertebrae
(69_2) = > 60% caudal vertebrae

70. *Accessory Neural Arch*—An accessory neural arch on V1 is present in *Diplophos*, *Aulopus*, and synodontids. It is absent in all ctenosquamates, *Pseudotricho-* *notus*, chlorophthalmoids, alepisauroids, and giganturoids. Polarity of this character for aulopiforms is equivocal, but in our analysis, an accessory neural arch is a synapomorphy of synodontoids.

(70_0) = Accessory neural arch absent
(70_1) = Accessory neural arch present

71. *First Neural Arch with Brush-like Growth*—There is a unique brush-like posterodorsal outgrowth of bone on the first neural arch of *Synodus* and *Trachinocephalus* (Patterson and Johnson, 1995).

(71_0) = No brush-like growth on first neural arch
(71_1) = Brush-like growth on first neural arch

72. *Number of Open Neural Arches*—In chlorophthalmoids (except *Ipnops*), alepisauroids, and *Bathysauroides*, the neural arch on V1 and sometimes V2–V4 is open dorsally. In ctenosquamates, all neural arches are closed dorsally (see also Stiassny, this volume), whereas many are open in synodontoids, *Bathysaurus*, *Gigantura*, and *Diplophos*. The latter is the primitive aulopiform condition, and thus a reduced number of open neural arches is a synapomorphy of the Chlorophthalmoidei + Alepisauroidei + Giganturoidei. Having many open neural arches is a reversal uniting giganturids and bathysaurids.

(72_0) = Many neural arches open dorsally
(72_1) = Neural arches open on V1 and sometimes V2–V4
(72_2) = All neural arches closed dorsally

73. *Origin of First Rib*—The origin of the first rib varies among aulopiforms from V1 to V5. The first rib originates on V3 primitively in aulopiforms, but its origin changes within all aulopiform suborders. Nearly 75 reconstructions of this character are possible in aulopiforms, the only hypothesis of relationship common to all of them being that a more posterior origin (V4) of the first rib is a synapomorphy of Pseudotrichonotidae + Synodontidae, with the origin shifting to V5 in the ancestor of *Synodus* and *Trachinocephalus* and to V2 in *Harpadon*. Our analysis also suggests that the origin of the first rib moved anteriorly from V3 to V2 in the ancestral ipnopid and from V3 to V1 in the ancestor of the alepisaurid + paralepidid clade.

(73_0) = First rib originates on V3
(73_1) = First rib originates on V4
(73_2) = First rib originates on V5
(73_3) = First rib originates on V2
(73_4) = First rib originates on V1
(73_5) = Ribs absent

74. *Ossification of Ribs*—In synodontoids, alepisaurids, and paralepidids, all ribs ossify in membrane

bone. In most scopelarchids, ribs are ligamentous, but in *Scopelarchoides signifer*, most ribs ossify in membrane bone, and only the last two are ligamentous. In all other aulopiforms except *Bathymicrops* and *Gigantura*, which lack ribs, at least some ribs ossify in membrane bone. In the outgroups, all ribs ossify in cartilage. Having any or all ribs ossify in membrane bone is derived for aulopiforms, but the distribution of the two states is such that the ancestral aulopiform condition could be either. However, ossification of only some ribs in membrane bone is primitive for the clade comprising chlorophthalmoids, alepisauroids, and giganturoids, and thus having all ribs ossify in membrane bone in paralepidids and alepisaurids is derived for that group.

(74_0) = All ribs ossify in cartilage
(74_1) = Some ribs ossify in membrane bone
(74_2) = All ribs ossify in membrane bone
(74_3) = Ribs absent
(74_4) = Some or all ribs ligamentous

75. *Origin of Baudelot's Ligament*—Baudelot's ligament originates on more than one vertebra in most paralepidids (V1 and V2) and alepisaurids (V2–V4). In all other aulopiforms and outgroups, Baudelot's ligament originates on V1 (V1 and the occiput in *Metavelifer*).

(75_0) = Baudelot's ligament originates on V1
(75_1) = Baudelot's ligament originates on more than one vertebra
(75_2) = Baudelot's ligament originates on V1 and the occiput

76. *Ossification of Baudelot's Ligament*—Baudelot's ligament is ossified in *Harpadon* and *Saurida*, a derived condition that occurs independently in *Bathymicrops*. Baudelot's ligament is lacking in *Gigantura*.

(76_0) = Baudelot's ligament is ligamentous
(76_1) = Baudelot's ligament is ossified
(76_2) = Baudelot's ligament is absent

G. Caudal Skeleton

77. *Modified Proximal Segmentation of Caudal-fin Rays*—Johnson et al. (1996, Figs. 20, 23, and 26) described a peculiar proximal segmentation of most principal caudal rays in synodontoids in which a small proximal section is separated from the remainder of the ray by a distinctive joint. The ends of the hemitrichs that meet at this joint are round, whereas those meeting at joints of the normal segmentation of caudal rays are laterally compressed and curved.

(77_0) = Proximal portion of principal caudal-fin rays not modified
(77_1) = Proximal portion of most principal caudal rays with modified segment

78. *Segmentation Begins on Distal Half of Each Caudal Ray*—In most aulopiforms and outgroups, segmentation of caudal rays begins on the proximal half of each ray, sometimes very close to the attachment of the rays to the caudal skeleton. In *Ipnops* and *Bathymicrops*, segmentation of caudal rays begins much farther posteriorly, on the distal half of each ray. Our analysis suggests evolution of posteriorly displaced segmentation in the ancestor of *Ipnops*, *Bathymicrops*, and *Bathytyphlops*, with reversal in the last. *Gigantura* lacks segmentation of caudal-fin rays.

(78_0) = Segmentation begins on proximal half of each caudal ray
(78_1) = Segmentation begins on distal half of each caudal ray
(78_2) = Caudal rays not segmented

79. *Median Caudal Cartilages*—A pair of autogenous median caudal cartilages ("CMCs" of Fujita, 1990) is present primitively in aulopiforms and outgroups except acanthomorphs which have none. CMCs are also absent in synodontoids, *Bathymicrops*, *Bathytyphlops*, and *Ipnops*. The dorsal CMC is absent in *Neoscopelus*, notosudids, *Bathypterois*, *Lestrolepis*, and *Stemonosudis* and reduced in size in *Uncisudis*, *Lestidium*, and *Lestidiops*. *Gigantura* has a single median CMC.

(79_0) = Two CMCs, about equal in size
(79_1) = Two CMCs, the dorsal one minute
(79_2) = One CMC
(79_3) = No CMCs

80. *Urodermal*—Fujita (1990) noted that a small ossified urodermal occurs near the proximal end of a caudal-fin ray of the dorsal caudal-fin lobe in some myctophids, *Neoscopelus*, one species of *Aulopus*, one *Chlorophthalmus*, and *Bathysaurus*. A urodermal is lacking in all other aulopiforms and other outgroups examined except *Bathysauroides*.

(80_0) = No urodermal
(80_1) = Small urodermal in upper caudal lobe

81. *Expanded Neural and Haemal Spines on Posterior Vertebrae*—Synodontoids (except *Harpadon*) have broad laminar expansions on the last three to six preural vertebrae (Johnson et al., 1996, figs. 16, 20, and 21). Neural and haemal spines on PU2 and PU3 are expanded in *Bathysauroides* and on PU2 in *Gigantura*.

(81_0) = Posterior neural and haemal spine not expanded

(81_1) = Neural and haemal spines of PU2 expanded
(81_2) = Neural and haemal spines of PU2 and PU3 (to PU6 in some) expanded

82. *Number of Hypurals*—Presence of six hypurals is primitive for aulopiforms and outgroups. Loss of the sixth hypural occurs in the ancestor of the synodontoid clade Pseudotrichonotidae + Synodontidae (Johnson et al., 1996) and independently in the ancestral alepisaurid. Five hypurals also characterize *Arctozenus*, but the reduction is the result of fusion of the first and second hypurals (or failure of the two bones to differentiate). Other reductions in number of hypurals occur in *Anotopterus* (four or five; one and two sometimes fused, sixth lost) and *Bathymicrops* (two plates in the young specimen we examined, one comprising the parhypural and first two hypurals fused distally, and the other hypurals 3–5 fused distally— the distal portions of the plates are cartilaginous, and further differentiation of hypurals may accompany their ossification).

(82_0) = Six hypurals
(82_1) = Five hypurals; the sixth lost or fused
(82_2) = Five hypurals; the first and second not differentiated
(82_3) = Four hypurals; the first and second not differentiated, the sixth lost or fused
(82_4) = Two hypurals

83. *Number of Epurals*—The presence of three epurals is primitive for aulopiforms and the four aulopiform suborders, but the number is reduced within each. In synodontoids, a single epural is a synapomorphy of pseudotrichonotids and synodontids, with reversal to two in the ancestral harpadontid. Within the Chlorophthalmoidei, two epurals is a derived feature of *Ipnops, Bathytyphlops,* and *Bathymicrops,* with further reduction to one in the last. Among alepisauroids, evermannellids share a single epural, a reduction independently derived in *Anotopterus* and *Gigantura.* Adults of several other aulopiforms, including *Parasudis, Omosudis, Alepisaurus,* and some paralepidids, also have only two epurals, but one of them is split, suggesting that it may represent partial fusion of two epural bones. Where available, ontogenetic evidence supports this hypothesis, and we do not recognize this condition as distinct from that of three epurals here (but see character 118 below). Accordingly, although R. K. Johnson (1982) interpreted the reduction of epurals to one or two as a synapomorphy of evermannellids, omosudids, and alepisaurids, we disagree.

(83_0) = Adults with two or three epurals; if two, one split

(83_1) = Adults with two epurals, neither split
(83_2) = Adults with one epural

H. Median Fins

84. *Fusion of Adjacent Pterygiophores (Figs. 16A, and 16B)*—In *Omosudis* (Fig. 16A), the posterior portion of the proximal–middle element of the penultimate anal-fin pterygiophore is fused to the anterior aspect of the same element of the ultimate pterygiophore. The nine posteriormost pterygiophores are fused in this manner in *Alepisaurus* (Fig. 16B). The only other aulopiform examined with fused pterygiophores is the paralepidid, *Uncisudis,* which has most of the dorsal-fin pterygiophores fused. Among the outgroups, pterygiophores are fused only in *Metavelifer.* The three aulopiforms in which we observed fused pterygiophores are young specimens, and the fused cartilaginous pterygiophores may separate upon ossification. Nevertheless, the cartilaginous pterygiophores of no other young aulopiform specimens examined are fused.

(84_0) = No fusion of pterygiophores of dorsal or anal fin
(84_1) = Adjacent posterior anal-fin pterygiophores fused
(84_2) = Adjacent dorsal-fin pterygiophores fused

85. *Pterygiophores of Dorsal Fin Triangular Proximally (Fig. 16C)*—The proximal end of each dorsal-fin pterygiophore in all evermannellid genera is roughly triangular, the result of an expansion of the small flanges that flank the central axis. No other aulopiforms or outgroups have the proximal ends of the dorsal-fin pterygiophores triangular.

(85_0) = Pterygiophores of dorsal fin not triangular proximally
(85_1) = Pterygiophores of dorsal fin triangular proximally

86. *Pterygiophores of Anal Fin Triangular Proximally*—*Evermannella* and *Odontostomops* have anterior pterygiophores of the anal fin that are triangular proximally. The anal-fin pterygiophores are not modified in *Coccorella* or in other aulopiforms and outgroups except *Scopelarchoides,* in which the posterior pterygiophores of the anal fin are broadened proximally.

(86_0) = Pterygiophores of anal fin not triangular proximally
(86_1) = Anterior pterygiophores of anal fin triangular proximally
(86_2) = Posterior pterygiophores of anal fin triangular proximally

A

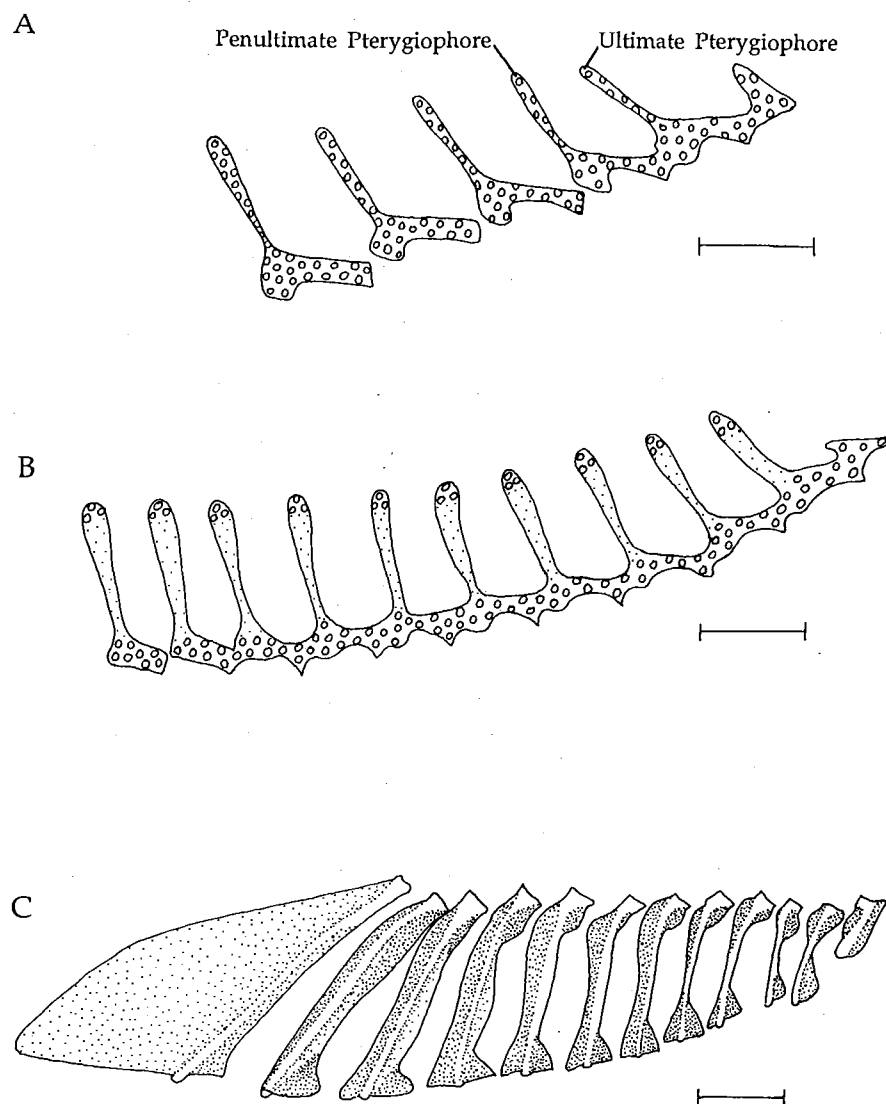Penultimate Pterygiophore   Ultimate Pterygiophore

B

C

FIGURE 16   Proximal–middle pterygiophores of three alepisauroids: (A) and (B), lateral view of posterior anal-fin pterygiophores from left side of *Omosudis lowei*, USNM 219982 and *Alepisaurus* sp., MCZ 60345, respectively; (C) lateral view of dorsal-fin pterygiophores from left side of *Evermannella indica*, USNM 235141.

I. Pelvic and Pectoral Girdles and Fins

87. Medial Processes of Pelvic Girdle Joined Medially by Cartilage (Figs. 4 and 5)—As already noted, aulopiforms have very elongate medial pelvic processes that are joined by cartilage. The medial processes are typically much smaller and do not articulate with one another in stomiiforms and myctophiforms and, although they overlap in some acanthomorphs (Stiassny and Moore, 1992), they are never fused medially as in aulopiforms.

(87_0) = Medial processes not joined medially
(87_1) = Medial processes joined medially by cartilage

88. Posterior Processes of Pelvic Girdle Elongate and Widely Separated (Fig. 5A)—Posterior pelvic processes are lacking in most aulopiforms (character 89), and they are small, usually slender processes of various shape and orientation in the outgroups. In all synodontoids, the posterior processes are very well developed, widely separated, elongate structures that give the pelvic girdle a "bowed" appearance.

(88_0) Posterior pelvic processes small (or absent)
(88_1) Posterior pelvic processes elongate, widely separated

89. Posterior Processes of Pelvic Girdle Absent (Figs. 4B, 4D, and 5B–5D)—Posterior pelvic processes are

primitively present in aulopiforms. In chlorophthalmids, *Bathysauropsis*, notosudids, alepisauroids, and giganturoids, the posterior pelvic processes are absent. In *Bathypterois*, the cartilage joining the medial processes divides posteriorly and forms two slender, widely separated cartilages (Fig. 4C). A similar condition occurs in *Ipnops* and *Bathytyphlops*, but the posterior cartilaginous processes are very short. In some alepisauroids, the cartilage between the medial processes continues posteriorly as a single, median cartilage, and the posterior tip of this cartilage is sometimes bifurcate. We interpret this condition as a terminal bifurcation of a median cartilage, in contrast to the formation of short cartilaginous posterior processes in some ipnopids. It is sometimes difficult to distinguish the two conditions, especially in, e.g., *Bathytyphlops* where the cartilaginous posterior processes are not as widely separated as in *Bathypterois* and *Ipnops*.

It is most parsimonious to hypothesize loss of the posterior processes in the ancestor of chlorophthalmoids + alepisauroids + giganturoids with evolution of cartilaginous posterior processes in the ancestral ipnopid. The small specimens of *Bathymicrops* that we examined appear to lack posterior processes, but investigation of larger material is needed. In young *Paralepis*, the lateral edges of the median cartilaginous plates ossify first, creating the impression of well-separated, ossified posterior processes, but these are not homologous with the posterior processes of synodontoids.

(89_0) = Ossified posterior processes of pelvic girdle present
(89_1) = Posterior processes are cartilaginous
(89_2) = Posterior processes of pelvic girdle absent

90. Lateral Pelvic Processes (Figs. 4B–4D)—Where the central process bends laterally and terminates, it is capped by a very large cartilaginous process in chlorophthalmoids. In *Chlorophthalmus, Parasudis*, and *Scopelosaurus*, the process is partially or entirely ossified, but it is cartilaginous in our small specimens of other chlorophthalmoids. All aulopiforms and outgroups examined have a lateral pelvic-fin process, but it is typically only a small nubbin of cartilage capping the tip of the central process. In young specimens of some alepisauroids, a large cartilage also caps the central process, but in adults, only a small lateral cartilage is present, along with an autogenous cartilage that apparently is pinched off of the large cartilage (character 91). The retention of a large cartilaginous or ossified lateral pelvic process is a synapomorphy of chlorophthalmoids. A similar cartilage is present

in *Scopelarchus analis*, an acquisition independent of that in chlorophthalmoids.

(90_0) = Lateral pelvic processes small
(90_1) = Lateral pelvic processes large, sometimes ossifying in adults

91. Autogenous Pelvic Cartilages (Fig. 5D)—Paralepidids (except *Anotopterus*), *Alepisaurus*, and evermannellids have a well-developed cartilage that extends dorsally into the body musculature from the region where the lateral pelvic-fin rays articulate with the girdle. In some young specimens, this cartilage is attached by a small rod of cartilage to the cartilage capping the central process, suggesting that it originates as part of the lateral cartilage. A similar cartilage is present in myctophids (Fig. 4A) but lacking in other aulopiforms and outgroups.

(91_0) = Autogenous pelvic cartilages absent
(91_1) = Autogenous pelvic cartilages present

92. Ventrally Directed Posterior Cartilage of the Pelvic Fin (Fig. 5B)—In scopelarchids, the cartilage joining the medial processes continues posteriorly beyond the posterior tips of the medial processes as a broad cartilaginous plate. It narrows posteriorly then abruptly curves ventrally, terminating as a small, ventrally directed process that is bound by connective tissue to the abdominal cavity wall (R. K. Johnson, 1974a). In other alepisauroids, the median cartilage may extend posteriorly beyond the medial processes, but it never deviates from the horizontal.

(92_0) = Cartilage between medial processes, if present, not terminating in ventrally directed process
(92_1) = Cartilage between medial processes terminating in ventrally directed process

93. Posterior Pelvic Cartilage Elongate (Fig. 5C)—In evermannellids, the cartilage joining the medial pelvic processes also extends posteriorly as a broad plate, but it is uniquely elongate in this family, extending well beyond the posterior tips of the medial processes, reaching up to two-thirds the length of the bony girdle (R. K. Johnson, 1982).

(93_0) = Cartilage extending posteriorly from between medial processes, if present, not elongate
(93_1) = Cartilage extending posteriorly from between medial processes elongate

94. Position of Pectoral and Pelvic Fins—In alepisauroids, the pectoral fins are positioned low on the body (closer to the ventral midline than to the lateral midline), and the pelvics are abdominal. These are primitive teleostean and neoteleostean features, but they are derived within aulopiforms, which primitively

have high-set pectorals and subthoracic pelvics as in synodontoids, chlorophthalmoids, *Bathysaurus*, and *Bathysauroides*. As noted by Rosen (1973), a more dorsal placement of the pectoral fins and an anterior shift in the pelvic fins appear to be synapomorphies of aulopiforms plus ctenosquamates, i.e., the Eurypterygii.

(94_0) = Pectoral fins set high on body, pelvics subthoracic

(94_1) = Pectoral fins set low on body, pelvics abdominal

95. *Relative Position of Abdominal Pelvic Fins*—Primitively in alepisauroids, the abdominal pelvic fins are inserted beneath or behind a vertical through the origin of the dorsal fin. In *Sudis, Macroparalepis, Uncisudis, Lestidiops, Stemonosudis,* and *Lestrolepis* the dorsal fin originates more posteriorly than in most other alepisauroids (except in *Anotopterus* in which it is lacking), and the abdominal pelvic fins insert anterior to a vertical through the origin of the dorsal. Pelvic fins are absent in juvenile and adult *Gigantura*; in larvae, they are abdominal and insert beneath the origin of the dorsal fin.

(95_0) = Pelvic fins subthoracic or, if abdominal, inserting beneath or behind a vertical through the origin of the dorsal fin

(95_1) = Pelvic fins abdominal, inserting anterior to vertical through dorsal fin

96. *Number of Postcleithra*—Gottfried (1989) considered the presence of two postcleithra (the second and third of primitive teleosts) as a synapomorphy of ctenosquamates and noted that although the number of postcleithra varies among aulopiforms, the presence of three in basal taxa such as *Aulopus* indicates that three is primitive for aulopiforms. However, most synodontoids, chlorophthalmoids, and alepisauroids have two or fewer postcleithra, and our analysis suggests the primitive number for the order is two. Loss of the dorsal postcleithrum may be a synapomorphy of eurypterygians, not ctenosquamates, as proposed by Stiassny (this volume). Further study of the homology of postcleithral elements among aulopiforms and ctenosquamates is needed, but Gottfried (1989) noted the two postcleithra of *Synodus* and *Trachinocephalus* appear to be the same two (the second and third) that characterize ctenosquamates.

Of phylogenetic significance within aulopiforms is the presence of three postcleithra in evermannellids (a synapomorphy of the three included genera), *Bathysauroides,* and *Bathysaurus. Gigantura* lacks postcleithra. The number of postcleithra is reduced in most ipnopids (one in *Bathypterois* and none in *Bathymicrops*

and *Ipnops*), but the primitive state for the family is ambiguous.

(96_0) = Two postcleithra

(96_1) = One postcleithrum

(96_2) = Postcleithra absent

(96_3) = Three postcleithra

97. *Cleithrum with Strut Extending to Dorsal Postcleithrum (Fig. 17)*—In certain paralepidids, there is a distinctive projection extending from the cleithrum to the dorsal postcleithrum. It is very narrow where it arises from the cleithrum and then broadens posteriorly at or near its contact with the postcleithrum, and it is often closely applied to the lateral surface of the scapula. This strut occurs among aulopiforms only in *Anotopterus, Macroparalepis, Uncisudis, Lestidium, Stemonosudis,* and *Lestrolepis* and is absent in the outgroups, but some aulopiforms have a small, blunt posterior cleithral projection in the same region.

(97_0) = Cleithrum with small rounded posterior projection or projection absent

(97_1) = Cleithrum with strut extending posteriorly to postcleithrum

98. *Orientation of Pectoral-Fin Base*—The pectoral-fin base is oriented more horizontally than vertically in alepisauroids, *Diplophos,* and *Metavelifer,* and more vertically in other aulopiforms, myctophiforms, and *Polymixia.* The latter is primitive for aulopiforms. Parr (1928) noted that scopelarchids and evermannellids differ markedly in insertion and development of pectoral fins, but our observations suggest that although the insertion of the pectorals in scopelarchids (and paralepidids) is not as low on the body as in evermannellids and alepisaurids, in all of those taxa the base of the fin is more horizontal than in cladistically primitive aulopiforms. In preserved specimens, this reorientation of the pectoral-fin base is easily identified because rather than lying flat against the body the fin projects ventrolaterally. In the reoriented position, the fin movement is more up and down than front and back as in other aulopiforms.

The very high-set pectoral fins of *Gigantura,* which also have a nearly horizontal base, are autapomorphic.

(98_0) = Pectoral-fin base more vertical than horizontal

(98_1) = Pectoral-fin base more horizontal than vertical, inserted on the ventrolateral surface of the body

(98_2) = Pectoral-fin base horizontal, inserted on dorsolateral surface of body

99. *Greatly Elongated Supracleithrum*—*Bathytyphlops* and *Bathymicrops* have a very long supracleithrum,
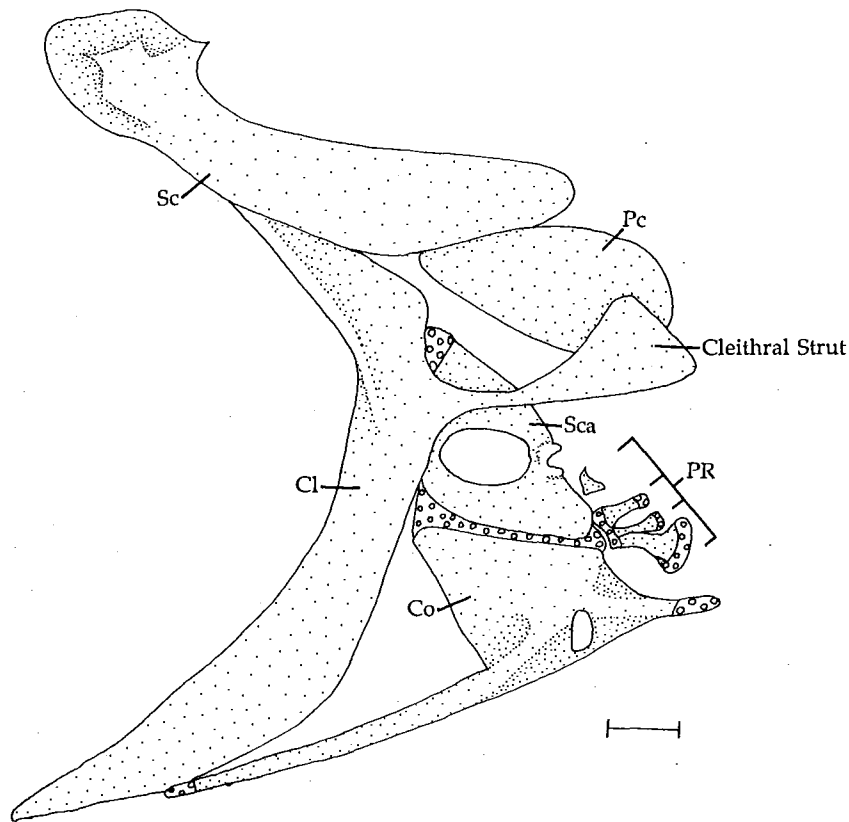
FIGURE 17 Lateral view of pectoral girdle from left side of *Stemonosudis rothschildi*, AMS I. 22826001.

equal to or longer than the cleithrum (Sulak, 1977, fig. 10). In other aulopiforms and outgroups, the supracleithrum is shorter than the cleithrum. Merrett and Nielsen (1987) noted that the supracleithrum in *Discoverichthys praecox* is about equal in length to the cleithrum, suggesting a possible relationship with *Bathymicrops* and *Bathytyphlops*.

(99_0) = Supracleithrum shorter than cleithrum
(99_1) = Supracleithrum equal to or longer than cleithrum

100. *Ventral Limb of Posttemporal Not Ossified*—R. K. Johnson (1982) noted that scopelarchids and evermannellids are unique among iniomes in having an unforked posttemporal. In those families, an ossified dorsal limb articulates with the epiotic, but there is no ossified ventral limb. Instead, a ligament connects the main body of the posttemporal to the intercalar. A forked posttemporal in which both the dorsal and ventral limbs are ossified is present in other aulopiforms and outgroups.

(100_0) = Posttemporal forked, both branches ossified

(100_1) = Posttemporal unforked, the ventral branch ligamentous

J. External Morphology

101. *Margin of Anal Fin Indented*—A derived feature of the Alepisauroidei is the shape of the anal fin, the margin of which is deeply indented near the anterior end. In other aulopiforms and outgroups, the margin of the anal fin may be straight, slightly convex, or concave, but it is usually not deeply indented. Some *Polymixia* (e.g., *P. nobilis*) have the anal fin indented similar to that of alepisauroids. Absence of an indented anal fin in *Anotopterus* is a reversal.

(101_0) = Margin of anal fin not indented
(101_1) = Margin of anal fin indented

102. *Scales*—Ossified scales on the body and lateral line are primitive for aulopiforms. R. K. Johnson (1982) noted that ossified scales or scale-like structures are absent in three families, Evermannellidae, Omosudidae, and Alepisauridae. However, our investigation indicates that ossified lateral-line structures are

present in all evermannellids. Body scales are absent in evermannellids, as they are in alepisaurids and all paralepidids examined except *Paralepis* and *Arctozenus*. Only alepisaurids and giganturids lack ossified body and lateral line scales.

(102_0) = Body and lateral-line scales present and ossified

(102_1) = Body scales absent, lateral-line scales or structures at least partially ossified

(102_2) = Body and lateral-line scales or structures absent

103. *Fleshy Mid-lateral Keel*—R. K. Johnson (1982) considered the presence of a fleshy, mid-lateral keel on each side of the posterior section of the body as a derived feature of alepisaurids (the keel is restricted to the caudal peduncle in *Omosudis* and covers the posterior one-third to one-half of the body in *Alepisaurus*). We agree and note that a fleshy midlateral keel does not occur elsewhere among aulopiforms or outgroups except in *Anotopterus*, which has a pair of fleshy keels on each side of the caudal peduncle (Rofen, 1966c, fig. 182).

(103_0) = Fleshy mid-lateral keel absent

(103_1) = Single fleshy mid-lateral keel on posterior portion of body

(103_2) = Pair of fleshy mid-lateral keels on caudal peduncle

104. *Body Transparent, Glassy in Life*—Rofen (1966b, p. 210) noted that *Sudis* and all other paralepidids except *Paralepis* and *Arctozenus* are "transparent or nearly so, glassy in life, the surface of the skin iridescent in a kaleidoscope of colors." Our review of the literature indicates that other paralepidids, aulopiforms, and outgroups may be iridescent, but if so they are silvery and not transparent. We have not examined any living or fresh specimens of Paralepididae, but we tentatively consider the glassy appearance described by Rofen (1966a) as a synapomorphy of *Sudis, Macroparalepis, Uncisudis, Lestidium, Lestidiops, Stemonosudis,* and *Lestrolepis*.

(104_0) = Appearance in life not transparent or glassy

(104_1) = Appearance in life transparent, glassy

105. *Scale Pockets in Continuous Flap of Skin*—Hartel and Stiassny (1986) hypothesized a sister-group relationship between *Parasudis* and *Chlorophthalmus*, citing as evidence the presence of scale pockets in a continuous flap of skin. The skin flap is pigmented distally, and thus the overall appearance of pigmentation in those genera is a zig-zag or herringbone pattern (Hartel and Stiassny, 1986; Mead, 1966d). Other au-

lopiforms, including other chlorophthalmoids, do not have scales implanted in pockets along a continuous flap of pigmented skin.

(105_0) = Scale pockets not in continuous flap of skin

(105_1) = Scale pockets in a continuous flap of marginally pigmented skin

106. *Elliptical or Keyhole Aphakic Space*—Mead (1966d) noted that *Chlorophthalmus* and *Parasudis* have a keyhole-shaped pupil, created by a conspicuous aphakic (i.e., lensless) space anteriorly. Marshall (1966) and Bertelsen et al. (1976) described a similar, but elliptical, lensless space in notosudids, and we have observed the same condition in *Bathysauropsis malayanus, B. gracilis,* and *Bathysauroides*. An aphakic space is lacking in other aulopiforms and outgroups. If the two forms of aphakic space are considered as separate states, the character is ambiguous, and neither state is phylogenetically informative. If we accept the two conditions as primary homologues, the presence of an aphakic space is a synapomorphy of chlorophthalmoids. We code this character as "missing" in ipnopids, which have greatly reduced or modified eyes. The aphakic space of *Bathysauroides* is best interpreted as independently derived; a modification of the iris of that species (incomplete or divided anteriorly at least in subadults) may be further evidence that the eye morphology of *Bathysauroides* is unique.

(106_0) = No aphakic space

(106_1) = Elliptical or keyhole shaped aphakic space

107. *Eye Morphology*—A laterally directed round eye characterizes synodontoids, chlorophthalmids, alepisaurids, paralepidids, and *Odontostomops*. Within the Chlorophthalmoidei, there is a trend toward reduction in eye size, from slightly flattened or elliptical in *Bathysauropsis* and notosudids, to minute in most ipnopids. *Ipnops* lacks recognizable eyes but has broad, lensless light-sensitive organs on the surface of the head (see Mead, 1966c). It is most parsimonious to hypothesize a reduction in eye size in the ancestor of *Bathysauropsis*, notosudids, and ipnopids with further reduction in the last. An elliptical eye also characterizes *Bathysauroides* and *Bathysaurus*. Giganturids are unique among aulopiforms in having anteriorly directed telescopic eyes.

Scopelarchids and most evermannellids have dorsally directed semitubular or tubular eyes. The laterally directed round eyes in *Odontostomops*, which is the sister group of *Evermannella*, are best interpreted as a reversal. Lending support to the interpretation of tubular eyes as a synapomorphy of the Evermannellidae and Scopelarchidae is the fact that larvae of both families have dorsoventrally elongate eyes (R. K.

Johnson, 1974a, 1982), implying a similar ontogeny of the adult condition (Character 114).

(107_0) = Eyes laterally directed, round
(107_1) = Eyes slightly flattened to elliptical
(107_2) = Eyes minute or absent
(107_3) = Eyes dorsally directed, semitubular or tubular
(107_4) = Eyes anteriorly directed, telescopic
(107_5) = Eyes are broad, lensless plates on dorsal surface of head

108. Gular Fold—Mead (1966b) noted that *Bathypterois* has a thick gular fold that covers the ventral surface of the branchiostegal membranes where they overlap anteriorly. Hartel and Stiassny (1986) noted that a well-developed gular fold is characteristic of all ipnopids as well as *Bathysauropsis*, and they considered this feature as further evidence that *Bathysauropsis* is an ipnopid.

We examined the gular region of all aulopiforms and found that the thickness of the gular fold varies with size. Nevertheless, the gular fold of ipnopids is different from the typical aulopiform condition in that the posterior edge of the fold is crescent-shaped and is not tightly bound to the branchiostegal membranes except along the lateral edges. In most other aulopiforms, the posterior margin of the gular fold is tent-shaped and tightly bound to the branchiostegal membranes. Thus in ipnopids, a probe inserted beneath the fold can be extended to near the symphysis of the dentary bones, whereas in other aulopiforms and most outgroups, extension of a probe beneath the fold anteriorly is impossible because of the attachment of the fold to the branchiostegal membranes.

Notosudids, but not *Bathysauropsis*, also have a crescent-shaped gular fold that is loosely bound to the branchiostegal membranes, a derived feature that we consider further evidence of a sister-group relationship between notosudids and ipnopids. A crescent-shaped gular fold is independently derived in *Polymixia*.

(108_0) = Gular fold tent-shaped
(108_1) = Gular fold crescent-shaped

109. Adipose Fin—Presence of a dorsal adipose fin is primitive for aulopiforms, although several outgroups (*Diplophos* and acanthomorphs) lack an adipose fin. Among aulopiforms, an adipose fin is lacking in *Pseudotrichonotus*, *Bathysaurus*, and the ipnopids *Bathymicrops*, *Bathytyphlops*, and *Ipnops*.

(109_0) = Adipose fin present
(109_1) = Adipose fin absent

K. Internal Soft Anatomy

110. Mode of Reproduction—R. K. Johnson (1982) hypothesized that synchronous hermaphroditism evolved three times among iniome fishes—once in the ancestor of his chlorophthalmid + ipnopid + notosudid + scopelarchid lineage, once in bathysaurids, and again in the ancestor of his alepisauroid clade. Our phylogeny suggests that all of those taxa form a monophyletic group, and thus we hypothesize a single origin of hermaphroditism, in the ancestor of our chlorophthalmoid + alepisauroid + giganturoid lineage. Synodontoids, myctophiforms, and *Polymixia* have separate sexes (see R. K. Johnson, 1982, for references) and, although the mode of reproduction in many stomiiforms is unknown, gonochorism also appears to be the primitive aulopiform strategy.

(110_0) = Separate sexes
(110_1) = Synchronous hermaphrodites

111. Thin-Walled, Heavily Pigmented Stomach—R. K. Johnson (1982) considered the presence of a highly distensible black stomach as a derived feature of alepisaurids. He noted that other iniomes examined by him have a heavily muscularized, unpigmented stomach.

(111_0) = Stomach not highly distensible, with thick unpigmented walls
(111_1) = Stomach highly distensible, with thin heavily pigmented walls

112. Swimbladder—Aulopiforms lack a swimbladder, but ctenosquamates primitively have one (absent in some myctophiforms) as do most stomiiforms (e.g., gonostomatids, sternoptychids, photichthyids, some astronesthids, and stomiids) (Marshall, 1954, 1960; Marshall and Staiger, 1975; R. K. Johnson, 1982).

(112_0) = Swimbladder present
(112_1) = Swimbladder absent

L. Larval Morphology

113. Enlarged Pectoral Fins—Okiyama (1984b) noted that ipnopid larvae share the derived condition of greatly enlarged, fanlike pectoral fins. Larvae of *Sudis hyalina* also have elaborate pectorals (Okiyama, 1984a, fig. 113F), and larvae of *Bathysaurus* have all fins except the caudal greatly enlarged (Okiyama, 1984a, fig. 111C). The pectoral fins of larval *Rosenblattichthys* are well developed relative to other scopelarchids (see R. K. Johnson, 1984a, fig. 127A,B) but not nearly as much as in ipnopids. Okiyama (1984b, p. 256) indicated in his character matrix that alepisaurids have elongate pectoral fins, but the illustrations of *A. brevirostris* and *A. ferox* (Okiyama, 1984a, fig. 112A,B) do

not reflect this condition. Pectoral fins are enlarged in certain myctophiforms (e.g., some *Lampanyctus*, Moser et al., 1984, Fig. 124F) but not in other outgroups.

(113_0) = Pectoral fins not enlarged in larvae
(113_1) = Pectoral fins enlarged in larvae

114. Elongate Eyes—The eyes are dorsoventrally elongate in larval scopelarchids and evermannellids. R. K. Johnson (1984b) noted that the eyes are not elongate in larvae of *Odontostomops*, and thus evermannellids and scopelarchids may have independently acquired them. We have not examined larval *Odontostomops*, but in illustrations of *O. normalops* (R. K. Johnson, 1982, Figs. 5D and 6D) the eye appears to be slightly wider than in other evermannellids, but it is dorsoventrally elongate rather than round.

Notosudid larvae also have narrow eyes, but they differ from evermannellid eyes in being elongate in the anteroposterior plane (Bertelsen et al., 1976; Okiyama, 1984a, fig. 111A). Some myctophids have dorsoventrally elongate eyes, but round eyes are primitive for aulopiforms.

(114_0) = Eyes in larvae round
(114_1) = Eyes in larvae elongate; the horizontal axis longer than the vertical
(114_2) = Eyes in larvae elongate; the vertical axis longer than the horizontal

115. Head Spination—Head spines are uncommon in larvae of non-acanthomorph teleosts, but serrate cranial ridges and preopercular spines are present in a strikingly similar configuration in *Alepisaurus ferox* and *Omosudis* (Okiyama, 1984a, figs. 112B, 112E, and 112F). Larvae of *A. brevirostris* apparently lack head spines (Rofen, 1966b, fig. 171; Okiyama, 1984a, fig. 112A), and thus ornamentation in the two genera could be nonhomologous. However, the presence of two nearly identical patterns of head spines among a group of teleosts that are not known for elaborate head ornamentation leads us to believe that the conditions in *A. ferox* and *Omosudis* are homologous.

The paralepidid *Sudis* also has head ornamentation, in the form of serrate cranial ridges and a large, strongly serrate spine at the angle of the preopercle. Other paralepidids lack head spines, and it is thus most parsimonious to hypothesize independent acquisition of head ornamentation in *Sudis* and the Alepisauridae.

(115_0) = Head spines lacking in larvae
(115_1) = Head spines present in larvae

116. Peritoneal Pigment—As noted, R. K. Johnson (1982) suggested that peritoneal pigment in larvae

may be diagnostic of Rosen's (1973) Aulopiformes, a notion supported in our analysis, despite the absence of peritoneal pigment in larvae of some chlorophthalmoids (notosudids, *Ipnops*, *Bathymicrops*, and some *Bathypterois*). Okiyama (1984b) and R. K. Johnson (1982) described several states of this character: a single, unpaired peritoneal pigment "section"; multiple, unpaired pigment sections; a single unpaired section changing ontogenetically to several unpaired sections; multiple paired pigment spots; and absence of peritoneal pigment. Johnson et al. (1996) considered the presence of paired peritoneal pigment spots in larvae and juveniles a synapomorphy of *Pseudotrichonotus* and synodontids. These spots are retained in the abdominal wall of adults as tiny dense discs of pigment. Our investigation suggests that the presence of one or more unpaired peritoneal pigment sections is primitive for aulopiforms, and thus we concur with Johnson et al. (1996) that the presence of paired peritoneal pigment sections in some larval synodontoids is derived.

(116_0) = Peritoneal pigment absent in larvae
(116_1) = Single or multiple unpaired peritoneal pigment sections in larvae
(116_2) = Multiple paired peritoneal pigment sections in larvae

117. Ontogenetic Reduction of Large Maxilla (Fig. 18)—Adults of *Gigantura* have only a small maxillary remnant posteriorly, but in larval giganturids ("*Rosaura*") the maxilla is a very large, leaf-shaped bone that tapers abruptly anteriorly near its articulation with the premaxilla (Fig. 18B). Rosen (1971) discussed the relationships of Regan's (1903) Macristiidae, a "myctophoid" family described on the basis of a single specimen of *Macristium chavesi* that is now lost. He described a new *Macristium*-like larval fish (the "Chain" larva) and concluded that it is probably the young stage of *Bathysaurus*, a notion corroborated by R. K. Johnson (1974b). In his paper, Rosen (1971) illustrated a lateral view of the skull bones of the "Chain larva" (Fig. 18A). Adult *Bathysaurus* have only a small, anterior remnant of the maxilla (e.g., Sulak, 1977, fig. 5A), but Rosen's illustration shows a very large maxilla in the larva that bears a striking resemblance to that of larval *Gigantura*. It is large and leaf-shaped and tapers abruptly anteriorly (Fig. 18).

Dramatic ontogenetic reduction of a large maxilla is thus shared by *Bathysaurus* and *Gigantura*, and we have not observed it elsewhere in the Aulopiformes, including synodontids in which the maxilla is reduced in adults (see e.g., Okiyama, 1984a, figs. 111D–111G). Larval *Bathysauroides* are undescribed, but adults have a well-developed maxilla; we thus predict that the
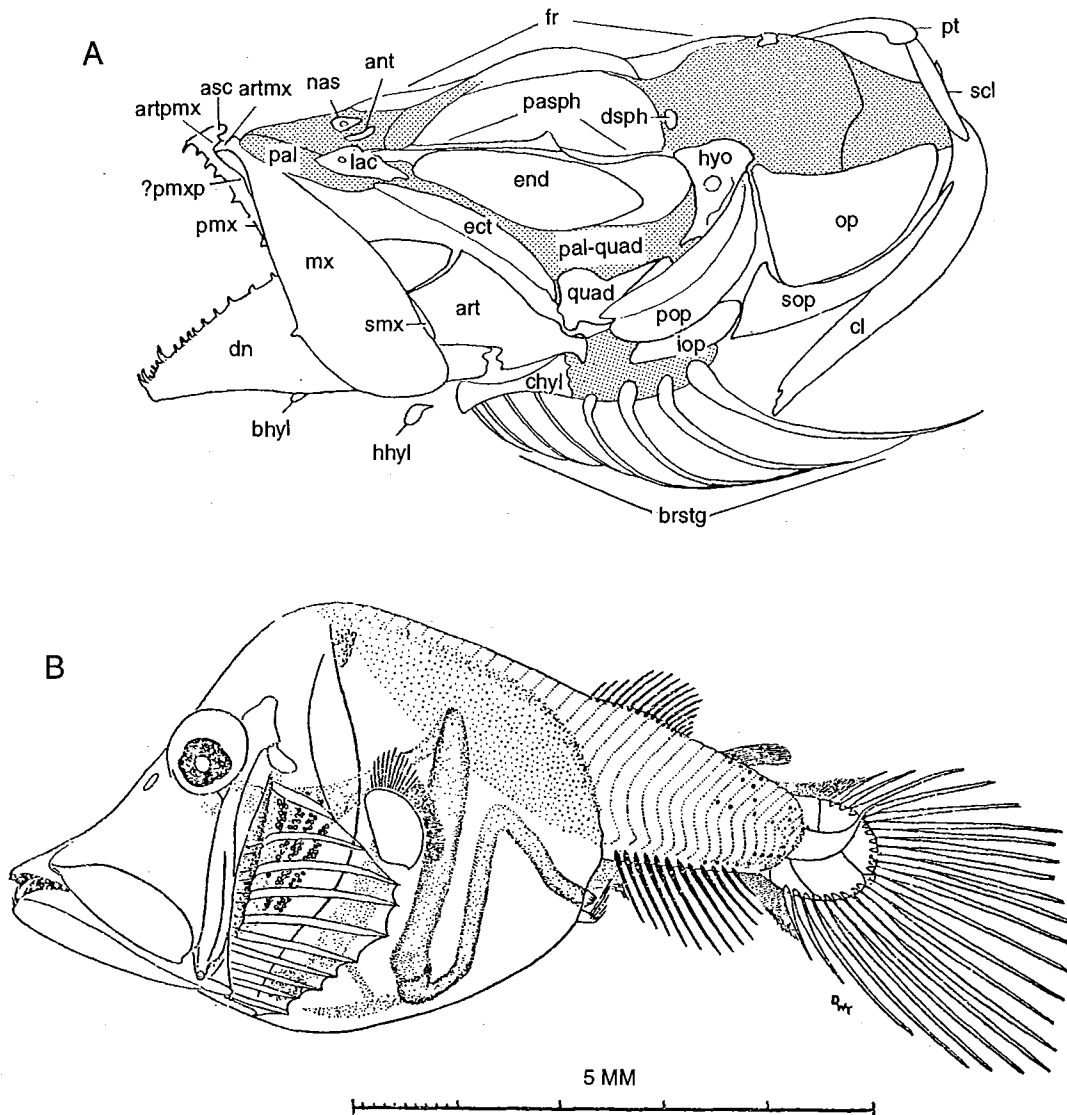
FIGURE 18 Larvae of (A) *Bathysaurus* (from Rosen, 1971, fig. 5, depicting the syncranium of the "Chain" larva) and (B) *Gigantura* (from Tucker, 1954, fig. 1).

maxilla in larval *Bathysauroides* is not enlarged or reduced ontogenetically.

(117_0) = Maxilla not enlarged in larva, not greatly reduced ontogenetically

(117_1) = Maxilla enlarged in larva, greatly reduced ontogenetically

118. Ontogenetic Fusion of Epurals—Adult *Parasudis* have two epurals, but the anterior is split distally. Larval *Parasudis* have three epurals, suggesting the adult condition is the result of partial ontogenetic fusion of the first and second epurals. Partial fusion of two epurals also apparently occurs in *Omosudis*, *Alepisaurus*, *Lestrolepis*, *Lestidiops*, and *Stemonosudis*,

which have two epurals in adults, one of which is split proximally. As in larval *Parasudis*, larval *Stemonosudis* have three cartilaginous epurals. We have not examined this feature in larvae of other paralepidids and alepisaurids listed above, but it is reasonable to assume that the divided epurals in adults of those taxa are also the result of ontogenetic fusion. Our analysis indicates that such ontogenetic fusion occurred three times within aulopiforms: in *Parasudis*, in the ancestral alepisaurid, and in the ancestor of the paralepidid clade comprising *Lestidiops*, *Stemonosudis*, and *Lestrolepis*.

(118_0) = No ontogenetic fusion of epurals

(118_1) = Partial ontogenetic fusion of two epurals

VI. Discussion

Monophyly of Rosen's (1973) Aulopiformes is supported by seven derived features. Four characters were previously recognized as synapomorphies of the order: (1_1) an enlarged EB2 uncinate process (Rosen, 1973); (2_1) absence of a cartilaginous condyle on PB3 for articulation of EB2 (Johnson, 1992); (54_1) anterior extension of the epipleural series to at least V2 (Patterson and Johnson, 1995); and (116_1) peritoneal pigment in larvae (R. K. Johnson, 1982). Two previously described characters were not recognized as aulopiform synapomorphies: (55_1) displacement of one or more of the anterior epipleurals dorsally into the horizontal septum (Patterson and Johnson, 1995) and (112_1) absence of a swimbladder (e.g., R. K. Johnson, 1982). We identified a seventh diagnostic feature of aulopiforms, (87_1) fusion of the medial processes of the pelvic girdle. Additionally, although not recognized formally in our analysis, a benthic existence may be a synapomorphy of aulopiforms. Because stomiiforms and primitive ctenosquamates are pelagic (polymixiids and *Metavelifer* are benthopelagic), and adults of most aulopiforms are benthic, a transition from a pelagic to a benthic environment may have characterized the ancestral aulopiform. Several aulopiforms have reinvaded the pelagic realm.

Aulopiform genera comprise four major clades that we designate the suborders Synodontoidei, Chlorophthalmoidei, Alepisauroidei, and Giganturoidei. Below we summarize the evidence supporting the monophyly of those clades and relationships among them. Within suborders, we emphasize characters supporting newly proposed clades as well as those previously undescribed or recognized as synapomorphies at different taxonomic levels.

Limits and relationships of the Synodontoidei of Johnson *et al.* (1996) are well supported in this study, with each clade being diagnosed by five or more unambiguous derived features (Fig. 6). *Aulopus* is cladistically the most primitive synodontoid, a hypothesis that conflicts with previous proposals (e.g., Rosen, 1985; Hartel and Stiassny, 1986) in which aulopids and sometimes chlorophthalmids were considered more closely related to ctenosquamates than to other aulopiforms. Synodontoids share eight derived features (Fig. 6), including two not recognized by Johnson *et al.* (1996): (172^*) gap between BB4 and CB5s and (88_1) elongate, widely separated posterior pelvic processes. Most of the homoplasy within the group occurs in the highly modified *Pseudotrichonotus* and the secondarily free-swimming *Harpadon*.

Sulak (1977) considered *Bathysaurus* as a subfamily of his expanded Synodontidae, but our data reject that notion. *Bathysaurus* lacks all synapomorphies of synodontoids and the clade comprising *Pseudotrichonotus* + synodontids and has only 2 of the 10 derived features uniting synodontids (Fig. 6): (5_1) gill rakers reduced to toothplates and (69_0) reduced number of caudal vertebrae.

Rosen (1973) argued that synodontids and harpadontids are closely related to alepisauroids and included the superfamily Synodontoidea in his suborder Alepisauroidei. He appears to have based this on three characters, a single upper pharyngeal toothplate (UP4 or UP5), enlarged orobranchial teeth, and gill rakers present as toothplates. Johnson (1992) noted that all alepisauroids except *Anotopterus* have both UP4 and UP5. UP4 is absent (3_1) only in *Pseudotrichonotus* and synodontids (Fig. 3B), a derived feature of that clade. Enlarged orobranchial teeth also fails as a synapomorphy of synodontids and alepisauroids because the enlarged teeth are premaxillary in synodontids and their relatives, whereas in alepisauroids, premaxillary teeth are often minute, and the enlarged teeth are on the palatine (36_2). Rosen's third character, (5_1) gill rakers present as toothplates, is apparently independently derived in synodontoids and alepisauroids.

The remaining aulopiforms—chlorophthalmoids, alepisauroids, and giganturoids—form a novel clade diagnosed on the basis of four derived features: (30_1^*) anterior ceratohyal bearing four or fewer branchiostegals, (72_1) neural arches open dorsally only on the anteriormost four or fewer vertebrae, (89_2) ossified posterior pelvic processes absent, and (110_1) sexual reproduction by synchronous hermaphroditism. Most of these fishes inhabit depths of 1000 to 6000 m, and the evolution of synchronous hermaphroditism may have contributed to their successful radiation into the deep. Synodontoids have separate sexes and are primarily shallow-water fishes.

The Chlorophthalmoidei include the Chlorophthalmidae, *Bathysauropsis* (c.f. *B. gracilis* and *B. malayanus*), Notosudidae, and Ipnopidae. Monophyly of chlorophthalmoids is supported by the following: (6_1) proximal end of PB2 expanded laterally; (45_1) medial edge of premaxilla with a dorsomedially directed process; (68_2^*) one supraneural; (90_1) central process of pelvic girdle capped laterally by a very large winglike process, ossified in some taxa; and (106_1) pupil elliptical or keyhole-shaped, with a prominent aphakic space anteriorly (except in ipnopids where eyes are minute or greatly modified).

The Chlorophthalmidae (*Chlorophthalmus* and *Parasudis*) share three previously described derived fea-

tures (44_2, 63_1, and 105_1) relating to squamation, intermusculars, and jaw morphology (Hartel and Stiassny, 1986; Stiassny, 1986; Patterson and Johnson, 1995). Ipnopids have a small, obliquely aligned basihyal, and its presence in *Bathysauropsis gracilis* led Hartel and Stiassny (1986, fig. 7) to reassign *Bathysauropsis* to the Ipnopidae (from the Chlorophthalmidae). Our phylogeny indicates that *Bathysauropsis* is the sister group of ipnopids + notosudids, and thus we interpret (34_1^*) an obliquely aligned basihyal as a synapomorphy of *Bathysauropsis*, notosudids, and ipnopids, with reversal in notosudids. The *Bathysauropsis* clade also shares (23_1) gill rakers extending onto lateral surfaces of deep basibranchials, (30_0^*) five or more branchiostegals on anterior ceratohyal, and (107_1) reduced or modified eyes relative to the very large, round eyes of chlorophthalmids.

A sister-group relationship between notosudids and ipnopids has not been proposed previously. Bertelsen *et al.* (1976) suggested that notosudids are most closely related to chlorophthalmids, R. K. Johnson (1982) placed notosudids as the sister group of his scopelarchid + chlorophthalmid + ipnopid clade, and Patterson and Johnson (1995) considered notosudids as the sister group of the Scopelarchidae + Evermannellidae. R. K. Johnson (1982) based his hypothesis on two derived features, absence of a swimbladder and presence of synchronous hermaphroditism, but we consider those features as synapomorphies of aulopiforms and the chlorophthalmoid + alepisauroid + giganturoid clade, respectively. Patterson and Johnson (1995) cited the origin of epineurals on the centrum or parapophysis on about vertebrae 5–15 as evidence for their placement of notosudids, but our analysis suggests independent evolution of ventrally displaced epineurals in notosudids and alepisauroids. Our hypothesis of a sister-group relationship between notosudids and ipnopids is supported by (6_2) an unusual modification of PB2 in which the proximal end has an extra uncinate process, (79_2) absence of at least one CMC, and (108_1) a thick, crescent-shaped gular fold.

The notosudid genera *Scopelosaurus* and *Ahliesaurus* share 10 derived features (Fig. 6), including (20_1) elongate BB1, (33_1) anteriormost branchiostegal on ventral hypohyal, (38_1) quadrate with two cartilaginous heads, and (57_1) epipleurals forked distally at transition of epipleurals in and beneath horizontal septum. Although we did not examine the monotypic *Luciosudis*, information from Bertelsen *et al.* (1976) suggests that *L. normani* has at least two synapomorphies of *Scopelosaurus* and *Ahliesaurus*, (46_1) seven infraorbitals and (114_1) horizontally elongate eyes in larvae. We conclude that the Notosudidae are monophyletic, but

further study is needed to elucidate relationships among the three genera.

Ipnopids (*Bathypterois*, *Bathymicrops*, *Bathytyphlops*, and *Ipnops*) share nine derived features (Fig. 6), including (113_1) an enlarged pectoral fin in larvae, a condition that occurs elsewhere among aulopiforms and the outgroups only in *Sudis*, *Rosenblattichthys*, and *Bathysaurus*. Ipnopids also share the following: (7_1) UP2 usually absent, (42_1) metapterygoid free from hyomandibular, (52_1) frontal expanded laterally over orbit, (53_1) sphenotic with an anteriorly directed process extending beneath frontal, (73_3) ribs, when present, beginning on V2, and (89_1) posterior processes of pelvic girdle cartilaginous; most have (107_2) minute eyes. Some of these features are reversed in *Bathymicrops*, which lacks ribs, has UP2, and apparently lacks posterior pelvic processes. Nevertheless, our analysis places *Bathymicrops* as the sister group of *Bathytyphlops*, as proposed by Sulak (1977). The two share (43_1) a horizontally oriented hyomandibular and opercle, (99_1) a long supracleithrum, (21_1) an elongate BB2, and (24_1) ossification of the ligament between HB1 and the hyoid.

Bathypterois, formerly placed in a separate family (Bathypteroidae; see, e.g., Mead (1966b)), is the sister group of the other ipnopid genera, which are united on the basis of several, mostly reductive, derived features: (46_3) five (or fewer) infraorbitals, (79_3) loss of CMCs, (83_2) two (or one) epurals, and (109_1) absence of an adipose fin. They also share (69_2) a high percentage of caudal vertebrae. *Ipnops* and *Bathymicrops* have (19_1) ossified BB4 and (78_1) segmentation of caudal rays beginning on distal half of each ray, additional features treated as synapomorphies of *Ipnops* + *Bathymicrops* + *Bathytyphlops* in our analysis, with reversal in *Bathytyphlops*.

We did not examine the single known specimen of the ipnopid *Discoverichthys praecox*, but we used data from Merrett and Nielsen (1987) to explore its relationships. Although the configuration of the gill arches, pelvic girdle, and intermusculars are unknown, *Discoverichthys* lacks a swimbladder and is hermaphroditic, suggesting that it belongs in the chlorophthalmoid + alepisauroid + giganturoid clade of aulopiforms. Because the premaxilla is the dominant tooth-bearing bone of the upper jaw, and the gillrakers are lathlike, *Discoverichthys* is best placed in the chlorophthalmoid lineage. It has the well-developed gular fold of notosudids, *Bathysauropsis*, and ipnopids, the small oblique basihyal of *Bathysauropsis* and ipnopids, the minute eye of most ipnopids, and, like *Bathymicrops*, *Bathytyphlops*, and *Ipnops*, it lacks an adipose fin. *Discoverichthys* does not have the opercle and hyomandibular reoriented as in *Bathymicrops* and *Bathytyphlops*,

nor does it share with those genera a greatly elongated supracleithrum. We tentatively conclude that *Discoverichthys* is most closely related to the clade comprising *Bathymicrops*, *Bathytyphlops*, and *Ipnops*, but it does not appear to belong to the *Bathymicrops* + *Bathytyphlops* group.

Alepisauroids and giganturoids form another new clade in our tree and share several derived features, most notably the following: (5_1) gill rakers present as toothplates, (36_2) palatine the dominant tooth-bearing bone of the "upper jaw", (54_2) epipleurals extending to V1, and $(61_1{}^*)$ origin of some (or all) epineurals on centrum. Adults of *Gigantura* lack a dermopalatine and most elements of the branchial skeleton but share with alepisauroids, *Bathysaurus*, and *Bathysauroides* the anterior extension of epipleurals to V1 (see discussion of *Gigantura* below).

Our Alepisauroidei comprise the Alepisauridae (including *Omosudis*), Paralepididae (including *Anotopterus*), Evermannellidae, and Scopelarchidae. Rosen's (1973) alepisauroids were characterized by gill-arch morphology, especially attenuation of epibranchial and pharyngobranchial elements, absence of UP2, UP5, and a toothplate on EB3 (ET3), and large pharyngobranchial teeth. UP4 and UP5 are present in most alepisauroids, and large pharyngobranchial teeth also characterize giganturoids. Aulopiforms vary considerably in length of epibranchial and pharyngobranchial elements and the presence of ET3, and neither convincingly diagnoses alepisauroids. However, alepisauroids do have distinctive gill arches, characterized in part by (7_1) absence of UP2. Other diagnostic features of alepisauroid gill arches include: (11_1) teeth on UP3 (when present) restricted to lateral edge, (15_2) teeth on CB5 restricted to medial edge, and (22_0) gillrakers (present as toothplates) not extending onto HB3. Alepisauroids also share the following: $(46_2{}^*)$ eight infraorbitals, $(68_1{}^*)$ two supraneurals, $(91_1{}^*)$ autogenous lateral pelvic cartilages, (94_1) abdominal pelvic fins, (98_1) a nearly horizontal (or more horizontal than vertical) pectoral-fin base, and (101_1) an indented anal fin. Furthermore, the pelagic lifestyle of alepisauroids may represent a single evolutionary transition from the benthic existence of primitive aulopiforms.

We agree with R. K. Johnson (1982) that *Omosudis* and *Alepisaurus* are sister taxa. They share 12 unambiguous derived characters, including features of the gill arches, intermuscular system, caudal skeleton, external morphology, internal soft anatomy, and head spination in larvae (Fig. 6), the following several of which are previously unrecognized alepisaurid synapomorphies: (10_1) PB3 extending anteriorly beyond EB1 and PB2, (18_1) BB3 extending beneath BB4, (58_1) epipleurals on V1 and V2 fused to centrum, (65_1) most epineur-

als unattached, and (84_1) adjacent posterior anal-fin pterygiophores fused. The close relationship between *Omosudis* and *Alepisaurus* is best represented by referring *Omosudis* to the Alepisauridae.

Patterson and Johnson (1995) hypothesized a sister-group relationship between the *Omosudis* + *Alepisaurus* clade and paralepidids. They based this on three derived features: (74_2) all ribs ossified in membrane bone, (76_1) Baudelot's ligament originating on more than one vertebra, and epineurals on the first five or fewer vertebrae fused to the neural arch. Examination of additional taxa indicates that epineurals are free from the axial skeleton except in the two genera, *Paralepis* and *Macroparalepis*, examined by Patterson and Johnson (1995). An additional but ambiguous synapomorphy of alepisaurids and paralepidids is (73_4) ribs originating on V1. Further study of this group is clearly needed.

We concur with R. K. Johnson (1982) that paralepidids and *Anotopterus* form a monophyletic lineage. In addition to his character, (48_1) a fenestrate premaxilla, they share (20_2) an elongate BB1, (47_1) a prolonged snout, (49_1) an anterior extension of the palatine to meet the premaxilla, (50_1) a long horizontally oriented lacrimal on the elongate snout, and (66_2) absence of epicentrals. Relationships among the speciose paralepidids are poorly understood, and we have contributed little toward their resolution. Our preliminary data do not corroborate all aspects of the classifications of Rofen (1966a) and Post (1987), wherein *Sudis* is given subfamilial or familial status, respectively, and the remaining genera are divided between two tribes or subfamilies. Post (1987) included *Arctozenus*, *Magnisudis*, *Notolepis*, and *Paralepis* in his subfamily Paralepidinae based on apparently primitive aulopiform features (e.g., cycloid body scales, no luminous organs, and no ventral adipose fin). We examined two genera of Post's Paralepidinae, *Paralepis* and *Arctozenus*, and found that they share three intermuscular characters $(59_2, 63_2,$ and $65_2)$ as well as (22_1) gill rakers (present as toothplates) on HB3 and (32_1) branchiostegals on anterior ceratohyal in 3+1 pattern. They lack the diagnostic features of the lineage comprising *Anotopterus* and all other paralepidid genera, including *Sudis*: (11_2) UP3 absent, (97_1) cleithral strut present; and (102_1) body scales absent but ossified lateral-line scales present. A toothplate fused to PB3 is a conservative feature among euteleosts, and its absence is strong evidence of the phylogenetic integrity of this paralepidid group. Placement of *Anotopterus* as the sister group of one paralepidid clade requires its inclusion in the Paralepididae.

Sudis shares with *Lestidiops*, *Lestidium*, *Lestrolepis*, *Macroparalepis*, *Stemonosudis*, and *Uncisudis* (60_1) a re-

duced number of epipleurals and (104_1) a transparent, "glassy" body. A close association between the main branch of EB2 and its uncinate process (9_1) and (32_1) a 3 + 1 pattern of branchiostegals on the anterior ceratohyal unite all of those genera, excluding Sudis, as a monophyletic assemblage. Uncisudis, Lestidium, Lestidiops, Stemonosudis, and Lestrolepis have (79_1) the dorsal CMC reduced to a tiny nubbin (or absent). Lestidiops, Stemonosudis, and Lestrolepis exhibit (118_1) partial ontogenetic fusion of two epurals. Finally, Lestrolepis and Stemonosudis share (79_2) absence of the dorsal CMC. No further resolution of relationships among paralepidid genera is evident from our data, and further study is needed.

We agree with R. K. Johnson (1982) that Coccorella, Evermannella, and Odontostomops constitute a monophyletic Evermannellidae but diagnose the family based on 10 additional derived features (Fig. 6). Most striking among these are (34_2) basihyal oriented at about a 90° angle to first basibranchial, (66_3) anterior epicentrals cartilaginous, (85_1) pterygiophores of dorsal fin triangular proximally, and (93_1) a long tail of cartilage extending posteriorly from the pelvic girdle. Our data do not corroborate R. K. Johnson's (1982) hypothesis of a sister-group relationship between Coccorella and Evermannella. Rather, three derived features indicate that Evermannella and Odontostomops are sister taxa: (27_1) third hypobranchials fused ventrally, (31_1) posteriormost two branchiostegals close, and (86_1) proximal ends of anal-fin pterygiophores expanded.

The Scopelarchidae are monophyletic, as proposed by R. K. Johnson (1974a, 1982), the four genera (Benthalbella, Scopelarchus, Scopelarchoides, and Rosenblattichthys) sharing reversals of several derived alepisauroid conditions (46_0*, 68_0*, and 91_0) as well as three novel derived features: (35_1) large, posteriorly curved basihyal teeth; (74_4) some or all ribs in ligament; and (92_1) a median cartilage extending posteriorly from the pelvic girdle that bends down to terminate as a small, ventrally directed process. Our data do not elucidate relationships within the Scopelarchidae.

Although scopelarchids were traditionally placed near evermannellids (e.g., Marshall, 1955; Gosline et al., 1966), R. K. Johnson (1982) suggested that resemblances between the two families may be superficial. Five unambiguous synapomorphies support a sister-group relationship between the Scopelarchidae and Evermannellidae: (67_1) attachment of anterior epicentrals to distal ends of epipleurals, (69_2) high percentage (>60%) of caudal vertebrae, (100_1) unossified ventral posttemporal limb, (114_2) dorsoventrally elongate eyes in larvae, and (107_3) dorsally directed, semitubular or tubular eyes in adults. Eyes are lateral and not

tubular in Odontostomops, and R. K. Johnson (1982) hypothesized that tubular eyes are a synapomorphy of Coccorella and Evermannella. Our hypothesis of a sister-group relationship between Evermannella and Odontostomops indicates that the absence of tubular eyes in Odontostomops is best interpreted as a reversal of the primitive evermannellid + scopelarchid condition.

R. K. Johnson (1982) hypothesized that evermannellids, not paralepidids, are the sister group of the alepisaurid clade and that scopelarchids are part of a clade comprising notosudids, chlorophthalmids, and ipnopids. His arrangement of evermannellids and alepisaurids is five steps longer than ours, and inclusion of scopelarchids in our Chlorophthalmoidei requires at least 18 additional steps. Patterson and Johnson's (1995) placement of the Evermannellidae + Scopelarchidae clade as the sister group of notosudids, which was based on a single feature of the intermusculars, is 19 steps longer than our hypothesis.

Our giganturoids include Bathysauroides, Bathysaurus, and Gigantura, but historically relationships of these fishes have been perceived differently: Bathysauroides (along with Bathysauropsis gracilis and B. malayanus) was considered a chlorophthalmid (Sulak, 1977) or ipnopid (Hartel and Stiassny, 1986); Bathysaurus was considered a synodontid by Sulak (1977) and a close relative of aulopids and chlorophthalmids by Rosen (1973); and Gigantura, which has only sometimes been included in the aulopiforms (see discussion below), was considered closely related to synodontids by Rosen (1973). Support for the Giganturoidei is not strong because most derived features shared by Bathysauroides and Bathysaurus are absent in the highly modified Gigantura, but our analysis suggests they are united on the basis of five derived features: (13_1) elongate PB1 (PB1 absent in adult Gigantura); (69_0) reduced number (<25%) of caudal vertebrae; (80_1*) small urodermal in upper caudal lobe (absent in Gigantura); (96_3) three postcleithra (none in Gigantura); and (107_1) elliptical eyes (eyes greatly modified in Gigantura).

Gigantura has usually been placed in a separate order (e.g., Regan, 1925; Berg, 1940; Walters, 1961). Regan (1925) suggested that giganturids might be related to synodontids, and Rosen (1973) concluded that giganturids are alepisauroid aulopiforms, most closely related to synodontids and harpadontids. Rosen's hypothesis was not based on explicit evidence, and, as he noted, the gill arches of adult Gigantura are much reduced and do not exhibit the distinctive EB2 uncinate process diagnostic of aulopiforms. The gill arches of larval Gigantura, however, are more complete, and our examination of them indicates the pres-
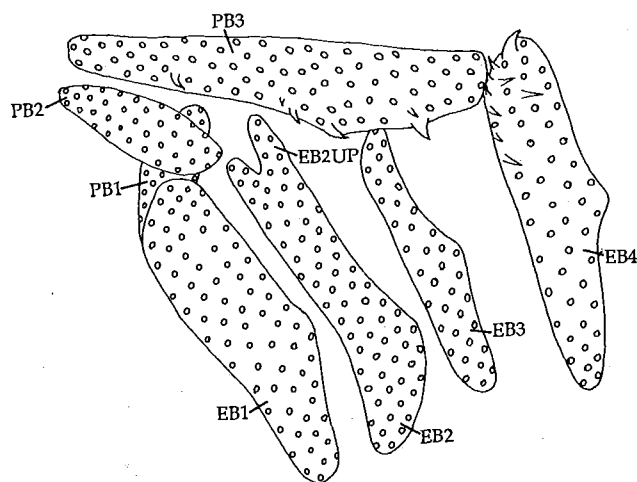
FIGURE 19 Ventral view of dorsal gill arches from right side of larval *Gigantura chuni*, MCZ 60324.

ence of the characteristic EB2 uncinate process (Fig. 19). Furthermore, Patterson and Johnson (1995) noted that intermuscular data, particularly $(54_{1,2})$ the anterior extension of epipleurals, support inclusion of giganturids in the Aulopiformes. *Gigantura* also has three additional aulopiform synapomorphies: (55_1) first epipleural in horizontal septum (Patterson and Johnson, 1995), (112_1) swimbladder absent, and (116_1) peritoneal pigment in larvae. We believe the evidence convincingly places the bizarre giganturids in the Aulopiformes.

Giganturids are aligned with chlorophthalmoids, alepisauroids, and other giganturoids based on (110_1) reproduction by synchronous hermaphroditism (Johnson and Bertelsen, 1991), and they share with alepisauroids and other giganturoids (54_2) anterior extension of epipleurals to V1 and (12_1) large pharyngobranchial teeth.

Patterson and Johnson (1995) suggested a sister-group relationship between *Bathysaurus* and *Gigantura* based on two derived features: (69_0) reduction in number of caudal vertebrae and (61_2^*) origin of most or all epineurals on centra rather than neural arches. A reduced number of caudal vertebrae is a synapomorphy of giganturoids, and the latter character is ambiguous (it could be a synapomorphy of giganturoids with reversal in *Bathysauroides gigas*), but our analysis supports Patterson and Johnson's (1995) interpretation. *Bathysaurus* and *Gigantura* also share (66_2) epicentral series absent (this occurs elsewhere among aulopiforms only in paralepidids); (72_0) most neural arches open dorsally (a reversal of the primitive chlorophthalmoid + alepisauroid + giganturoid condition); and (117_1) maxilla reduced ontogenetically from a very

large broad bone in larvae to a small anterior (*Bathysaurus*) or posterior (*Gigantura*) remnant in adults.

In summary, Aulopiformes are monophyletic and comprise four monophyletic suborders. Our suborder Synodontoidei is the same as that of Johnson et al. (1996). Our suborder Chlorophthalmoidei is similar to R. K. Johnson's (1982) chlorophthalmoid clade except that we exclude the Scopelarchidae. Our suborder Alepisauroidei comprises the same recent genera as Rosen's (1973) superfamily Alepisauroidea, and our suborder Giganturoidei combines the new genus *Bathysauroides* with the giganturid–bathysaurid lineage proposed by Patterson and Johnson (1995). Among the most significant aspects of our phylogeny are the following: *Aulopus* is a synodontoid and thus not closely related to ctenosquamates. Synodontoids are not alepisauroids but the primitive sister group of all other aulopiforms. *Bathysaurus* is not a synodontid but a giganturoid. *Bathysauropsis* is polyphyletic, *B. gracilis* and *B. malayanus* being more closely related to notosudids and ipnopids than to *B. gigas*. *Bathysaurops gigas* Kamohara (= *Bathysauropsis gigas*) is the type species of a new genus, *Bathysauroides*, which is related to bathysaurids and giganturids. *Omosudis* is reassigned to the Alepisauridae, and *Anotopterus* is reassigned to the Paralepididae. Scopelarchids are alepisauroids and the sister group of evermannellids. And finally, *Gigantura* is an aulopiform and may be the sister group of *Bathysaurus*. Further study is needed to elucidate relationships within the Paralepididae and Scopelarchidae and to test all poorly supported relationships hypothesized herein. We have examined certain aspects of aulopiform morphology in detail, but there is much yet to be studied; we view this work as a foundation for further study of this diverse order of fishes.

VII. CLASSIFICATION

As diagnosed here, the extant aulopiforms comprise 43 genera. *Bathysauropsis* and *Bathysauroides* have no familial assignment in our phylogeny, but we assign the remaining 41 genera to 12 families. A new classification of aulopiform genera reflecting phylogenetic relationships as perceived herein follows (suborders are listed in phyletic sequence):

Order Aulopiformes
    Suborder Synodontoidei
        Family Aulopidae (*Aulopus*)
        Family Pseudotrichonotidae (*Pseudotrichonotus*)
        Family Synodontidae (*Harpadon, Saurida, Synodus, Trachinocephalus*)

Suborder Chlorophthalmoidei
  Family Chlorophthalmidae (*Chlorophthalmus, Parasudis*)
  Bathysauropsis (*B. gracilis, B. malayanus*)
  Family Notosudidae (*Ahliesaurus, Luciosudis, Scopelosaurus*)
  Family Ipnopidae (*Bathymicrops, Bathypterois, Bathytyphlops, Discoverichthys, Ipnops*)
Suborder Alepisauroidei
  Family Alepisauridae (*Alepisaurus, Omosudis*)
  Family Paralepididae (*Anotopterus, Arctozenus, Dolichosudis, Lestidiops, Lestidium, Lestrolepis, Macroparalepis, Magnisudis, Notolepis, Paralepis, Stemonosudis, Sudis, Uncisudis*)
  Family Evermannellidae (*Coccorella, Evermannella, Odontostomops*)
  Family Scopelarchidae (*Benthalbella, Rosenblattichthys, Scopelarchoides, Scopelarchus*)
Suborder Giganturoidei
  Bathysauroides gigas (new genus)
  Family Bathysauridae (*Bathysaurus*)
  Family Giganturidae (*Gigantura*)

VIII. Summary

Relationships among aulopiform genera are investigated based on cladistic analysis of 118 morphological characters. Monophyly of Rosen's (1973) Aulopiformes, which he diagnosed on the basis of unique modifications in the dorsal gill arches, is corroborated by features of the intermuscular system, internal soft anatomy, and larval pigmentation as well as new evidence from the morphology of the pelvic girdle. Our analysis suggests four aulopiform clades, listed below in phyletic sequence: (1) Synodontoidei (Aulopidae, Pseudotrichonotidae, and Synodontidae—including *Harpadon* and *Saurida*); (2) Chlorophthalmoidei (Chlorophthalmidae, *Bathysauropsis*, Notosudidae, and Ipnopidae); (3) Alepisauroidei (Alepisauridae—including *Omosudis*, Evermannellidae, Scopelarchidae, and Paralepididae—including *Anotopterus*); and (4) Giganturoidei (Bathysauridae, Giganturidae, and *Bathysauroides*, a new genus erected for *Bathysauropsis gigas* [Kamohara]).

Acknowledgments

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Appendix 1

Abbreviations Used in Text Figures

AC	Anterior Ceratohyal
APC	Autogenous Pelvic Cartilage
BBn	nth Basibranchial
Br	Branchiostegal
CBn	nth Ceratobranchial
Cl	Cleithrum
Co	Coracoid
CPP	Central Pelvic Process
DH	Dorsal Hypohyal
Ecp	Ectopterygoid
EBn	nth Epibranchial
Enp	Endopterygoid
HBn	nth Hypobranchial
Hy	Hyomandibular
Ih	Interhyal
LPP	Lateral Pelvic Process
Me	Mesethmoid
Mep	Metapterygoid
MPP	Medial Pelvic Process
Mx	Maxilla
MxS	Maxillary Saddle
P	Palatine
Para	Parasphenoid
PBn	nth Pharyngobranchial
Pc	Postcleithrum
PC	Posterior Ceratohyal
Pmx	Premaxilla
PPC	Posterior Pelvic Cartilage
PPP	Posterior Pelvic Process
PR	Pectoral-fin Radial
Q	Quadrate
Sca	Scapula
Sc	Supracleithrum
Sy	Symplectic
UP	Uncinate Process
UPn	nth Upper Pharyngeal Toothplate
V	Vomer
VH	Ventral Hypohyal

Appendix 2

Material Examined

Our analysis included examination of representatives of more than 40 neoteleostean genera listed below using institutional abbreviations specified by Leviton *et al.* (1985). Whole and cleared and stained specimens or parts of specimens (e.g., gill arches and paired fins) dissected from very large specimens were examined for most taxa. Cleared and stained lots are indicated by "cs."

Aulopiformes—*Ahliesaurus berryi*: USNM 240503, 240505 (cs). *Alepisaurus brevirostris* USNM 200817 (gill arches, pelvic fin cs), 201275. *Alepisaurus* sp.: MCZ 60345 (cs). *Anotopterus pharao*: CAS 164180 (cs); SIO 5553 (cs); USNM 140825 (cs), 201286, 221035, 221035 (cs), 206844; SIO 62-775 (cs). *Arctozenus rissoi* USNM 302410 (1 cs), 283485 (cs). *Aulopus filamentosus*: USNM 292105 (cs), 301018. *Aulopus japonicus*: AMNH 28635SW (cs); FMNH 71831 (cs). *Aulopus* sp.: AMNH 28635 (cs). *Bathymicrops regis*: BMNH 1989.7.25.56.61 (cs). *Bathypterois longipes* USNM 35635. *Bathypterois pectinatus*: FMNH 88982 (cs). *Bathypterois* sp. MCZ 40567 (cs). *Bathypterois viridensis* USNM 117215. *Bathysauropsis gracilis* AMS IA6934 (cs): NMV A6932. *Bathysauropsis malayanus* USNM 098888 (holotype of *Bathysaurops malayanus*). *Bathysaurus ferox* AMS I.29591001; MCZ 62409 (cs); USNM 316825. *Bathysaurus mollis*: VIMS 6107 (cs). *Bathysauroides gigas*: AMS I, 22822001 (cs); NMV A5770, A4438, A4440 (cs). *Bathytyphlops marionae* USNM 336666 (cs), 336713 (formerly VIMS 06104); 341861 (gill arches cs). *Benthalbella dentata*: SIO 63-379 (cs). *Benthalbella elongata* USNM 207279. *Benthalbella macropinna* USC E1671. *Chlorophthalmus agassizi*: AMNH 40829SW (cs); USNM 159385 (cs), 302386. *Chlorophthalmus atlanticus* USNM 339774 (1 cs). *Coccorella atlantica*: USNM 235170, 235189 (cs), 235199 (cs). *Evermannella balbo* USNM 301265. *Evermannella indica*: U.H. 71-3-9 (cs); USNM 235141. *Gigantura chuni* AMNH 55345SW (cs); MCZ 60324 (cs). *Gigantura indica* MCZ 54133 (cs): SIO 76-9; USNM 215407. *Harpadon nehereus*: AMNH 17563 (cs); FMNH 179018 (cs); USNM 308838. *Harpadon squamosus*: FMNH 80823 (cs). *Ipnops agassizi*: USNM 54618 (gill arches cs). *Ipnops meadi* SIO 61-175 (cs). *Ipnops murrayi* USNM 101371, 336711 (formerly VIMS 6736), 336712 (formerly VIMS 6737). *Lestidiops affinis* MCZ 60632 (cs). *Lestidiops* sp.: USNM 307290 (cs). *Lestidium atlanticum*: USNM 201183 (cs), uncat. (cs). *Lestidium* sp.: USNM 341877 (1 cs). *Lestrolepis intermedia* USNM 290253 (2 cs). *Lestrolepis* sp. USNM 307290 (1 cs). *Macroparalepis affine*: USNM 302410 (cs); 201184 (cs). *Macroparalepis* sp.: FMNH

49988 (cs); USNM 201186 (cs). *Odontostomops normalops*: USNM 235029 (cs), 274377 (1 cs). *Omosudis lowei* USNM 219982 (cs), 206838, 287310. *Paralepis brevirostris*: USNM 196109 (cs). *Paralepis coregonoides*: USNM 196098, 290253 (cs). *Parasudis truculentus*: FMNH 67150 (cs); MCZ 62398 (cs); USNM 159096 (1 cs), 159407 (cs), 159850 (cs). *Pseudotrichonotus altivelis*: USNM 280366 (cs); ZUMT 55678 (cs), 59882 (cs). *Rosenblattichthys hubbsi* MCZ 52821 (cs). *Saurida brasiliensis*: USNM 185852 (cs); 187994 (cs). *Saurida gracilis*: USNM 256409 (cs). *Saurida normani*: USNM 341878 (cs). *Saurida parri*: USNM 193763 (cs), 340398 *Saurida undosquamous*: USNM 325180 (cs). *Scopelarchus analis*: MCZ 62599 (cs); USNM 234988 (cs). *Scopelarchoides nicholsi*: USNM 201154 (cs), 207295. *Scopelarchoides signifer*: USNM 274385 (cs). *Scopelosaurus argenteus* MCZ 63321 (cs), 62105 (cs), 62405 (cs). *Scopelosaurus fedorovi* SIO 60-251 (cs). *Scopelosaurus hoedti*: USNM 264256 (2 cs). Syno-dontidae: USNM 309851 (cs). *Stemonosudis rothschildi* AMS I. 22826001 (cs). *Stemonosudis* sp. USNM 330273 (cs). *Sudis atrox* MCZ 60336 (cs); USNM 330285 (cs). *Sudis hyalina* USNM 340399 *Synodus jenkensi*: USNM 321745 (1 cs). *Synodus synodus*: USNM 318960 (1 cs). *Synodus variegatus*: USNM 140825 (cs); 315318 (cs). *Trachinocephalus myops*: FMNH 45392 (cs); MCZ 62106 (cs); USNM 305292, 185861 (cs); 339775 (larva, cs); 339776 (cs). *Uncisudis advena* MCZ 68531 (cs). Stomiiformes—*Diplophos taenia*: MCZ 55469 (cs); USNM 206614 (cs), 274404. Myctophiformes—*Lampanyctus cuprarius* USNM 300490 (cs). *Myctophum obtusirostre*: AMNH 29140SW (cs). *Neoscopelus macrolepidotus*: USNM 188056 (cs); 317160 (cs). *Neoscopelus* sp. USNM 159417 (cs). *Notoscopelus resplendens*: AMNH 25928SW (cs). Lampridiformes—*Metavelifer*: BPBM 23953 (cs). Polymixiiformes—*Polymixia lowei* USNM 137750, 185204 (cs), 308378 (cs).