C H A P T E R

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Relationships of Lower Euteleostean Fishes

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We all make mistakes; then we're sorry.

Popular song

I. Introduction

In the first *Interrelationships of Fishes* lower euteleosts, or "protacanthopterygians" as they were then called, were omitted, with only a comment in the Preface citing Weitzman (1967, on osmeroids and stomiatoids), McDowall (1969, on osmeroids and galaxioids), Rosen and Greenwood (1970, on gonorynchiforms and ostariophysans), Greenwood and Rosen (1971, on argentinoids and alepocephaloids), and Nelson (1970b, on salangids and argentinids; 1972, on esocoids and galaxioids).

Ten years later, in *Ontogeny and Systematics of Fishes*, Fink (1984a) summarized the history of protacanthopterygians as "erosion" and "attrition, most notably at the hands of Rosen (1973)" [in the first *Interrelationships of Fishes*]. Fink then saw the problems as these: (1) What are the relationships of the Esocoidei? (2) What are the relationships of the Ostariophysi? Do these fishes lie above or below the Esocoidei? (3) What is the pattern of relationships among the traditional "salmoniform" taxa, exclusive of Esocoidei and Ostariophysi? (4) What are the relationships of and within the Argentinoidei (sensu Greenwood and Rosen, 1971, i.e., argentinoids plus alepocephaloids)? (5) What are the relationships of and within the Osmeroidei? (6) What are the relationships of and within Salmonidae? (7) Where does *Lepidogalaxias* belong? (8) What are the relationships within stomiiform fishes? (9) What of the Myctophoidei, as recognized by Greenwood *et al.* (1966, i.e., Aulopiformes and Myctophiformes in current terminology)? In that agenda, items (8) and (9) are treated elsewhere in this volume and do not concern us, but items (1) through (7) do.

Some classifications and/or cladograms of lower euteleosts, dating back to the first application of cladistic method, are summarized in Fig. 1. As is obvious from incongruence between all the patterns in Fig. 1, there has been protracted argument on how lower euteleostean groups are interrelated, how they are related to neoteleosts (stomiiforms and eurypterygians, Johnson, 1992), and what group is basal to other euteleosts. The most substantial treatment of these problems is in Begle's (1991, 1992) cladistic analyses of Osmeroidei (1991) and Argentinoidei (1992) (Fig. 1G). Begle's two papers resulted in the cladogram in Fig. 2, in which the terminals are the genera or higher taxa sampled in his matrix. His classification (Begle, 1991, fig.1; 1992, table 2) to family level, without ranks above the superfamily and sequenced according to the conventions of Wiley (1981), was as follows:

Euteleostei
  Esocae
    Ostariophysi *sedis mutabilis*

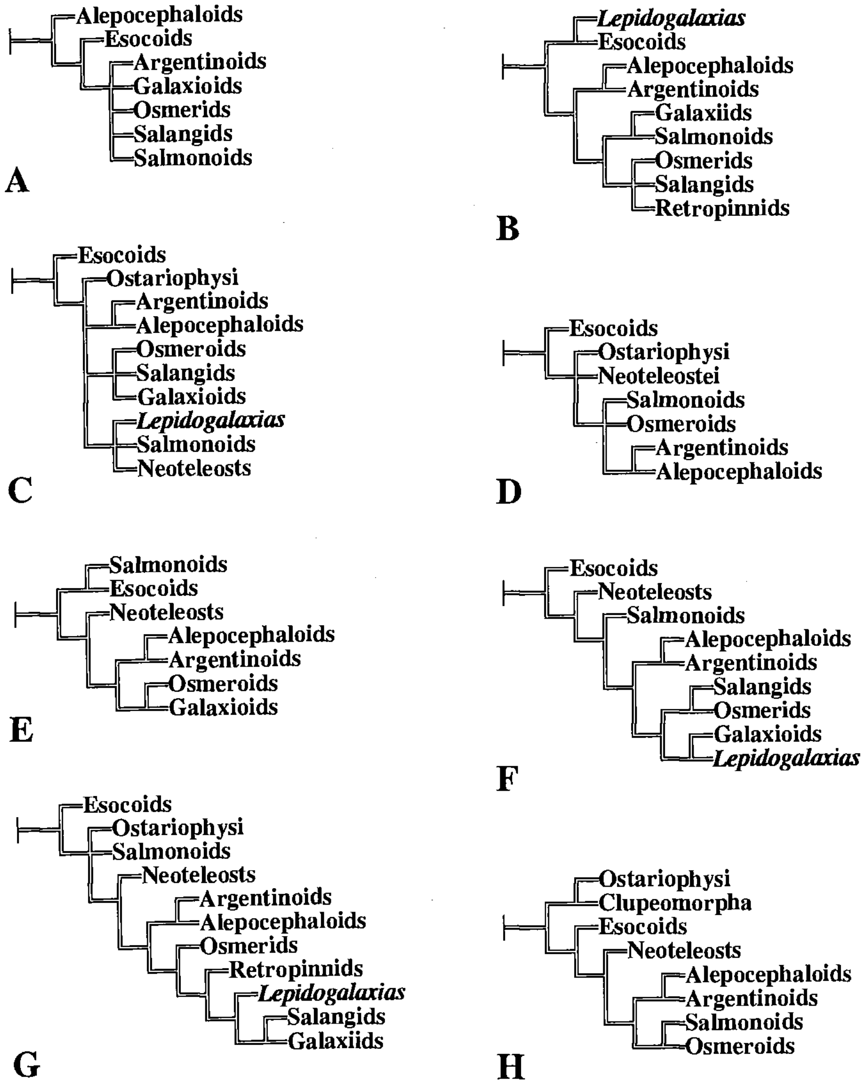

FIGURE 1 Cladograms or classifications of lower euteleostean fishes summarized as branching diagrams. Common names (e.g., alepocephaloids and esocoids) are used instead of formal taxon names to emphasize the equivalence of groups that may be given different ranks, and so names with different terminations, in classifications. (A) G. J. Nelson (1970b). (B) Rosen (1974). (C) Fink (1984b). (D) Sanford (1990). (E) Williams (1987; summarized in J. S. Nelson, 1994, p. 175). (F) J. S. Nelson (1994). (G) Begle (1991, 1992). (H) Patterson (1994).

- Salmonoidei *sedis mutabilis*
- (Neoteleostei + Osmerae) *sedis mutabilis*
  - Neoteleostei
  - Osmerae
    - Argentinoidei
      - Argentinoidea
        - Argentinidae
        - Microstomatidae
        - Bathylagidae
        - Opisthoproctidae
      - Alepocephaloidea
        - Alepocephalidae (including Bathylaconidae, Bathyprionidae, Leptochilichthyidae, Platytroctidae)
    - Osmeroidei
      - Osmeroidea
        - Osmeridae (including Plecoglossidae)
      - Galaxioidea
        - Retropinnidae (including Prototroctidae)
        - Lepidogalaxiidae

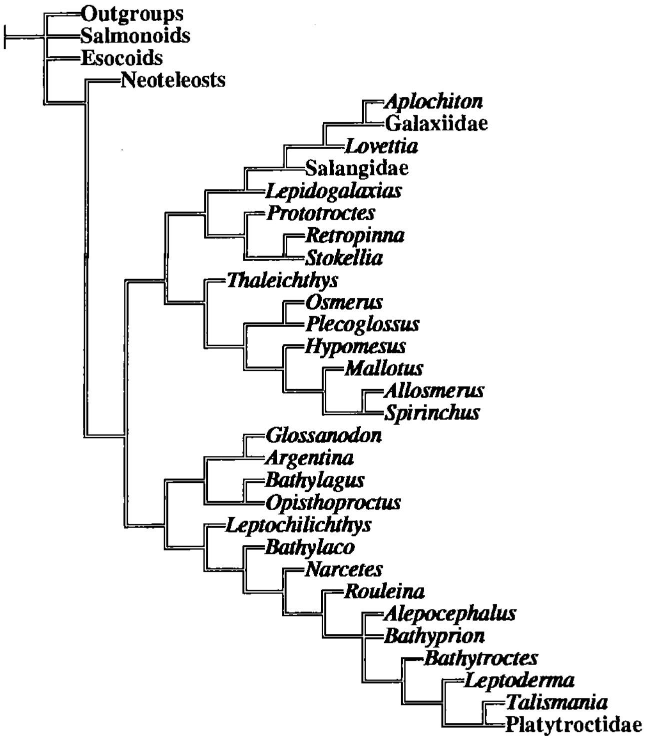

FIGURE 2 Result of Begle's (1991, 1992) cladistic analyses of a sample of lower euteleosts.

Salangidae (including Sundasalangidae)
Galaxiidae (including Aplochitonidae)

The original plan for this volume was that Douglas P. Begle should write about lower euteleosts since he had covered the ground in his two papers (Begle, 1991, 1992). However, in 1993 Begle left ichthyology to move into computer programming. To fill the gap, we agreed to take on lower euteleosts, believing that we had a new angle on them from our work on intermusculars (Patterson and Johnson, 1995). In particular, the discovery of cartilaginous epicentrals in salmonoids and osmeroids, together with the absence of ossified epipleurals in both, implied that they might be sister-groups (Patterson and Johnson, 1995, p. 26, fig. 9). In arguing for that proposal, we criticized the characters supporting some of the higher-level relationships in Begle's cladogram, but we anticipated that his conclusions at lower levels (e.g., within osmerids or within galaxioids) would withstand criticism. However, when we began checking Begle's character descriptions and coding, we found many errors. Because Begle's work resulted in the only fully resolved phylogeny of lower euteleosts, and because the characters that he used included the great majority of those previously used in systematic studies of those fishes, we decided that we must check each character against specimens. At the same time, we found that our own survey of lower euteleostean intermusculars (Patterson and Johnson, 1995) was deficient both in sampling and in the quality of our material, casting doubt on the pairing of salmonoids and osmeroids that we proposed. Given this disquiet about both recent sources of published information, Begle's and our own, we were thrown into a detailed survey of lower euteleosts, limited only by time and by the availability of specimens. On sampling, we limited ourselves principally to the 33 taxa in Begle's sample (Fig. 2), but we excluded the alepocephaloid *Bathyprion* (unavailable) and added more argentinoids (bathylagids, opisthoproctids, and microstomatids, which Begle did not sample) and more platytroctid alepocephaloids. On characters, we concentrated on the 108 used by Begle (1992), the majority of them taken from the literature [e.g., nos. 1–28, 54, 55, from Fink (1984b); nos. 30–38, 51, 63, from Howes and Sanford (1987b)], because we were driven to discover every detail of his miscoding or misconduct. But during our survey almost 100 other characters came to light.

In presenting our data, we originally had a section criticizing our own work on the intermusculars, a longer critique of Begle's 108 characters, and a section describing new characters. Referees and others pointed out that this sequence gave too much attention to our critique of Begle's work and artificially separated characters into three different sets. We have therefore organized the primary data into a single survey of characters structured by anatomical region. We then discuss in sequence the outgroup and ingroup relationships of osmerids [Osmeridae and Salangidae of Begle (1991)], osmeroids [= Osmerae of Begle (1991)], argentinoids and alepocephaloids [= Argentinoidei of Greenwood and Rosen (1971)], salmonoids, esocoids, and euteleosteans as a whole. We do not include the "salangid" *Sundasalanx*, only member of the Sundasalangidae (Roberts, 1984), in our study because it is not euteleostean (Darrell Siebert, 1996, and personal communication).

We dedicate this work to two absent friends, Humphry Greenwood (1927–1995), senior editor of the first *Interrelationships*, and Donn Rosen (1929–1986), the length of whose chapter in that book was justified by the information it contained. May we be so excused.

II. Character Survey

The following survey of 200 characters is organized by anatomical region or system, beginning with the braincase and ending with reproductive and soft anatomical features. One purpose of this survey is to check and correct the character coding in Begle (1991, 1992), who based his cladistic analyses on matrices of 84 (1991) or 108 (1992) characters, each coded in 20 (1991) or 33 (1992) terminal taxa. We take Begle's more complete, 1992 matrix as definitive but mention significant differences in character description or coding between the data sets in Begle (1991) and (1992). Twenty-six of the 33 terminals in Begle's 1992 paper are genera, and 7 are collective at higher levels: "outgroups" (a hypothetical ancestor comprising a row of zeros), salmonoids, esocoids, neoteleosts, Platytroctidae, Salangidae, and Galaxiidae. Begle organized his character sequence partly by source [nos. 1–28 were from Fink (1984b), and nos. 29–38 from Howes and Sanford (1987b)] and partly according to his two publications [nos. 85–108 are only in Begle (1992), not Begle (1991)]. Where a character in our survey is in Begle (1992), we give his number (Table 1) and his character description and coding in square brackets, followed by comments on that coding. Our own character coding is in Appendices 1–4. This survey is based on cleared-and-stained specimens, but we include references to published illustrations, where they exist, so that workers without ready access to specimens may check our observations.

Our characters are distributed as follows:

A. Braincase: numbers 1–26
B. Suspensorium: numbers 27–48
C. Jaws: numbers 49–64
D. Circumorbital bones: numbers 65–68
E. Hyoid bar, branchiostegals, and operculum: numbers 69–79
F. Gill arches: numbers 80–112
G. Axial skeleton (including caudal skeleton and fin): numbers 113–147
H. Pectoral girdle and fin: numbers 148–159
I. Pelvic girdle and fin: numbers 160–165
J. Median fins: numbers 166–170
K. Squamation: numbers 171–173
L. Sensory canals and bones carrying them: numbers 174–181
M. Reproductive structures: numbers 182–187
N. Other soft anatomical features: numbers 188–198
O. Life cycle: numbers 199 and 200

A. Braincase

1. Dermethmoid. Paired dermal ethmoid bones (proethmoids; lateral dermethmoids of Fink and Weitzman, 1982, p. 36) occur in esocoids, some stomiiforms, and all osmerids except *Hypomesus, Plecoglossus*, and *Mallotus*, which, like salangids, have a median dermethmoid (we observed paired proethmoids in one specimen of *Hypomesus transpacificus*). As argued by Patterson (1975) and Fink and Weitzman (1982), paired dermethmoids are a derived feature. The proethmoids of esocoids are elongate, unlike the small, platelike bones in osmerids. Other osmeroids (retropinnids, *Aplochiton, Lovettia, Lepidogalaxias*, and galaxiids) lack the dermethmoid (no. 2 below).

2. Ethmoid endoskeleton. The ethmoid endoskeleton in elopocephalans and clupeocephalans is primitively well ossified, with paired lateral ethmoids, a median mesethmoid that incorporates the supraethmoid and rostrodermethmoid, and a median ventral ethmoid that is usually fused with the vomer (Patterson, 1975). In lower euteleosts the most completely ossified ethmoid endoskeleton is in argentinids (Kobyliansky, 1990, fig. 10); elsewhere, ethmoid ossification is generally reduced. Apart from lateral ethmoids, there is no endoskeletal ethmoid ossification in opisthoproctids, retropinnids (McDowall, 1969), salangids (Roberts, 1984), and most salmonids (Stearley and Smith, 1993). Coregonids and osmerids are unusual in having the supraethmoid and dermethmoid separate, not fused. That condition has been reported elsewhere only in a Cretaceous euteleost of unknown relationships (Patterson, 1970, fig. 2) and in some stomiiforms (Weitzman, 1967; Fink and Weitzman, 1982); in other stomiiforms the two components are thought to be fused (Fink, 1985, p. 13). In esocoids the proethmoids fuse with paired endoskeletal ossifications (Jollie, 1975; Wilson and Veilleux, 1982; Reist, 1987). In *Aplochiton, Lovettia, Lepidogalaxias*, and galaxiids there is an endoskeletal mesethmoid that appears to lack any dermethmoid component.

The ethmoid endoskeleton in *Mallotus* differs from that of all other osmerids except salangids in two features: it is elongate and unossified except for lateral ethmoids, which appear between about 60 and 100 mm SL, much later than the ethmoid endoskeleton in other osmerids where it is short and always includes at least two perichondral ethmoid bones in addition to the lateral ethmoids. The elongate ethmoid endoskeleton of salangids is unossified.

3. [Begle's 1: Median posterior shaft of vomer present (0) or absent (1). State (1) coded in all Osmeroidei except *Lepidogalaxias*.] Shaft wrongly coded as absent in *Plecoglossus* (Chapman, 1941a; Klyukanov, 1975), galaxiids, and *Lovettia* (McDowall, 1969, 1984). In Begle (1991) the character was different, with (0) for a short shaft and (1) for a long one; coding was wrong in *Lovettia* (1) and *Aplochiton* (0) but correct in galaxiids (0). In *Aplochiton* and salangids the vomer is absent; they represent a third state (2). A vomerine shaft is

present in our *Hypomesus olidus*, and one was illustrated as present in *H. japonicus* and *H. nipponensis* (but absent in *H. olidus*) by Klyukanov (1977, fig. 4).

4. [Begle's 16: Vomerine teeth present (0) or as fangs on head of bone (1) or absent (2). State (1) coded in *Osmerus*, state (2) in galaxiids, *Lovettia, Aplochiton,* salangids, *Alepocephalus,* platytroctids, *Leptoderma, Bathyprion,* and *Bathytroctes.*] Vomerine teeth occur in all platytroctids (Sazonov, 1986; Matsui and Rosenblatt, 1987) but are absent in *Rouleina* (Markle, 1976, 1978). Absence of the vomer in *Aplochiton* and salangids (no. 3) means that they should be coded as (?). In Begle (1991) the character was two-state, presence (0) vs absence (1), with *Spirinchus* wrongly coded (1); inexplicably, *Osmerus* was coded (2) and salangids, *Aplochiton, Lovettia,* and galaxiids were coded (3).

5. [Begle's 103: Vomer ends anteriorly at margin of ethmoid cartilage (0) or extends beyond it (1). State (1) coded in all sampled argentinoids: *Argentina, Bathylagus, Opisthoproctus,* and *Glossanodon.*] *Aplochiton* and salangids, which have no vomer, accordingly coded (0), not (?).

6. [Begle's 58: Orbitosphenoid present (0) or reduced or absent (1). State (1) coded in all osmeroids and in *Alepocephalus, Bathylagus, Opisthoproctus, Bathyprion, Narcetes,* and *Rouleina,* with platytroctids polymorphic.] We commented (Patterson and Johnson, 1995, p. 26). The bone is wrongly coded as present in esocoids and as absent or reduced in *Alepocephalus, Narcetes, Rouleina,* and *Bathylagus* (Chapman, 1943; Kobyliansky, 1986). It is absent in our small *Leptochilichthys.* The orbitosphenoid is present in microstomatids (*Microstoma* and *Nansenia;* Chapman, 1948). In Begle (1991) the character was presence vs absence of the bone.

7. [Begle's 63: Pterosphenoids not reduced, meeting in midline (0) or reduced and widely separated, not meeting in midline (1). State (1) coded in all Osmeroidei and all sampled alepocephaloids.] The character is from Howes and Sanford (1987b, p. 27). We noted (Patterson and Johnson, 1995, p. 27) that the character is ambiguous because widely separated pterosphenoids occur in the most primitive teleosts, such as Jurassic pholidophorids and leptolepids, *Hiodon,* and *Elops* (Howes and Sanford, 1987b, also reported the condition in esocoids, alepocephaloids, and gonorynchiforms). In any case, the pterosphenoids are widely separated in salmonoids, esocoids, *Argentina,* and *Glossanodon,* and in all of these Begle coded them as in contact medially. As presented and coded by Begle, the character is worthless and we discard it.

8. [Begle's 71: Pterosphenoid without (0) or with small ventral flange midway along its length (1). State (1) coded in all Osmeroidei except salangids and *Retropinna.*] The character is not so simple. Among osmerids, *Hypomesus* and *Mallotus* have a ventral flange or process from the anterior part of the pterosphenoid and the pterosphenoid–prootic junction is entirely in cartilage bone. In *Osmerus* there is a process about midway along the bone that is directed posteroventrally, toward a similar anterodorsal process from the prootic. *Spirinchus* resembles *Osmerus,* but the pterosphenoid and prootic processes meet and interdigitate, forming the ventral margin of a foramen between the two bones so that their junction is partly in membrane bone. *Allosmerus* and *Plecoglossus* have both a ventral process from the middle of the bone and a posteroventral process that interdigitates with an anterodorsal process from the prootic, as in *Spirinchus.* In *Thaleichthys* the pterosphenoids are much modified and almost contact the parasphenoid (Klyukanov, 1970), but as in *Allosmerus, Plecoglossus,* and *Spirinchus* a posteroventral process from the pterosphenoid interdigitates with an anterodorsal process from the prootic. Since the process on the anterior part of the pterosphenoid (as in *Hypomesus* or *Mallotus*) and the posteroventral process toward the prootic (as in *Osmerus* or *Spirinchus*) coexist in *Allosmerus* and *Plecoglossus,* the two processes cannot be homologous.

In retropinnids, a broad ventral process (Howes and Sanford, 1987b, fig. 2B) is present in *Prototroctes* and *Stokellia.* In galaxiids the pterosphenoid (like many other structures) is remarkably variable but shares one feature with that of retropinnids and *Aplochiton*: there is a broad and shallow medial arm, ossified perichondrally around the epiphyseal bar and applied to the underside of the frontal. In retropinnids and some galaxiids, the pterosphenoids meet in the midline by means of this epiphyseal arm (cf. preceding character as presented by Begle). Some galaxiids retain a slender anterior, perichondrally and endochondrally ossified arm of the pterosphenoid (e.g., *G. maculatus, G. fontanus, G. zebratus,* and *Neochanna*), but in others and in *Aplochiton* the anterior arm is ossified only in membrane bone, and in others it is missing entirely so that the pterosphenoid is L-shaped in ventral view, with only the posterior and medial (epiphyseal) arms (e.g., *Paragalaxias dissimilis, Galaxias fasciatus,* and *G. platei*). A ventral flange or process (always in membrane bone when present) is variable in galaxiids, even within species and from one side to another in individuals (*G. platei,* dried skeleton); absent in *Paragalaxias dissimilis* and some *Galaxias fasciatus;* and present in *Aplochiton, G. fontanus, G. maculatus, G. brevipinnis,* and some *G. fasciatus.* In *Lepidogalaxias* the pterosphenoid, placed far laterally, lacks the epiphyseal arm (and epiphyseal cartilage), has the anterior part ossified only in membrane bone, and has a minute ventral process from the center of the orbital margin.

Salangids (Roberts, 1984) and *Lovettia* lack a pterosphenoid and so must be coded as (?) for any feature concerning the bone.

Begle's original character 71 should be discarded; it comprises four separate two-state characters: (A) Pterosphenoid present or absent (in salangids and *Lovettia*); (B) pterosphenoid unmodified or with extensive epiphysial arm; (C) pterosphenoid with or without ventral process or flange from anterior half of margin; and (D) pterosphenoid with or without posteroventral process towards prootic. We have not checked all of the non-osmeroids for comparable structures.

9. [Begle's 72: Anterior margin of prootic rounded and smooth (0) or notched, with a small dorsal projection (1). State (1) coded in *Allosmerus* and *Spirinchus*.] We take the dorsal projection to be that which is directed towards or meets a process from the pterosphenoid (no. 8 above). We have also observed this in *Osmerus* (*O. eperlanus* and *O. mordax*), *Thaleichthys* (where the anterior margin of the prootic is almost horizontal, through reduction in the myodome and widening of the otic region), and *Plecoglossus*. See also no. 10, below, in *Allosmerus*, *Plecoglossus*, *Spirinchus*, and *Thaleichthys*.

10. [Begle's 73: Prootic/pterosphenoid contact at dorsal margin of prootic (0) or more medial, by interdigitation of prootic and pterosphenoid (1). State (1) coded in *Osmerus* and *Plecoglossus*.] The medial contact is between the membrane bone processes described in nos. 8 and 9 above. It also occurs in *Allosmerus*, *Spirinchus*, and *Thaleichthys* but is absent in *Osmerus*. The character is best treated as a further state (2) of no. 9.

11. Interorbital septum. In the osmerids *Allosmerus*, *Osmerus*, *Spirinchus*, and *Thaleichthys* there is a cartilaginous interorbital septum in the anterior part of the orbit (Klyukanov, 1970, figs. 1–4; 1975, fig. 8). Klyukanov (1975, p. 13), accepting Weitzman's (1967, p. 533) belief that the orbitosphenoid was primitively absent, regarded the extensive interorbital cartilage in these osmerids (and in some salmonines) as primitive. But presence of the orbitosphenoid is undoubtedly primitive in teleosts (Patterson, 1975, p. 427), and we regard the osmerid cartilage as derived. There is no comparable structure in other osmeroids, or in coregonids, argentinoids, or esocoids. Among alepocephaloids, there is a comparable cartilaginous septum in a few derived forms (e.g., *Rinoctes* and *Photostylus*).

12. [Begle's 57: Basisphenoid present (0) or reduced or absent (1). State (1) coded in all Osmeroidei and all sampled argentinoids and alepocephaloids except *Argentina*, *Talismania*, *Leptoderma*, and *Bathylaco*, with platytroctids polymorphic.] In Begle (1991) the character was presence vs absence of the bone. We commented (Patterson and Johnson, 1995, p. 26) that the basisphenoid is wrongly coded as absent in *Lepidogalaxias*, where the bone is large, and in *Alepocephalus*, *Bathytroctes*, *Narcetes*, *Rouleina*, and *Glossanodon* (Begle's text correctly says that the bone is present in the latter). The basisphenoid is well-developed in some bathylagids (Kobyliansky, 1986), in most platytroctids (Sazonov, 1986), and in the microstomatids *Microstoma* and *Nansenia* (Chapman, 1948). The basisphenoid is present in esocids but absent in umbrids. It is absent in all opisthoproctids.

13. Myodome. The posterior myodome is primitively large in teleosts (Patterson, 1975, p. 543), and an extensive myodome occurs among lower euteleosts in argentinids, alepocephaloids, *Esox*, salmonoids, osmerids, retropinnids, and *Aplochiton*. Among osmeroids the myodome is absent in salangids, *Lepidogalaxias*, *Lovettia*, and some galaxiids. In most of the galaxiids we examined (*Neochanna*, *Nesogalaxias*, *Paragalaxias*, *Galaxias fontanus*, and *G.occidentalis*) there is a myodome with a wide but very shallow orbital opening, whereas in others (*G.zebratus* and *Galaxiella*) it is absent. *Galaxias paucispondylus* shows an intermediate condition, with the prootic bridge developed only at the extreme posterior part of the prootic, so that the myodome is no more than a shallow pit.

14. Buccohypophyseal canal. The buccohypophyseal canal through the parasphenoid is normally closed during ontogeny in teleosts; a patent canal has been recorded only in Mesozoic forms, in *Elops*, *Megalops* (Holstvoogd, 1965), and perhaps in a few clupeomorphs (Patterson, 1975, p. 530). There is an obvious median buccohypophyseal canal through the ossification center of the parasphenoid in *Aplochiton*, *Lovettia*, and in almost all galaxiids (e.g., *G.occidentalis*, *G.zebratus*, *G.paucispondylus*, *Galaxiella*, and *Neochanna*). We have not seen a buccohypophyseal canal elsewhere in osmeroids (it is not there in *Lepidogalaxias*).

15. Basipterygoid process and efferent pseudobranchial artery. Primitively in teleosts, the parasphenoid has a basipterygoid process, penetrated a foramen for the efferent pseudobranchial artery which lies anterior to the internal carotid foramen (Patterson, 1975, pp. 529, 532). In Recent teleosts, a basipterygoid process is recorded only in osteoglossomorphs (osteoglossoids and some mormyroids), except for Gosline's (1969, p. 196) report of "a pair of knob-like projections from the parasphenoid" in the alepocephaloid *Searsia koefoedi*, leading him to

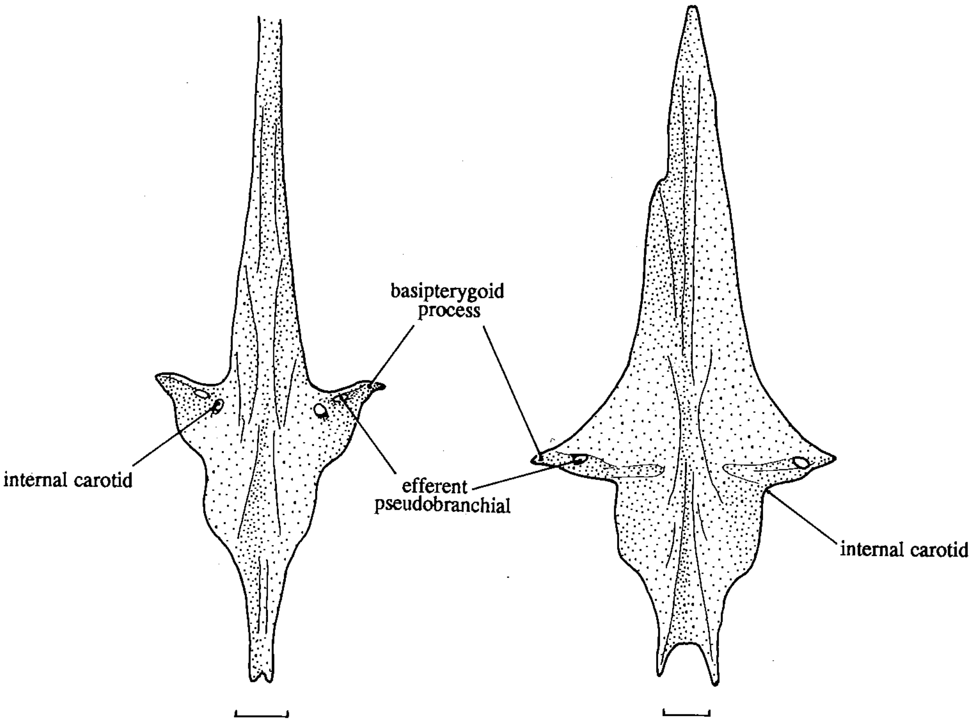

FIGURE 3 Basipterygoid process in alepocephaloids. Parasphenoid, in ventral view, of *Searsioides multispinus* (left, SIO 77-21, 113 mm SL) and *Bathylaco nigricans* (right, SIO 64-15, 86 mm SL). Scale bars: 1 mm. The internal carotid does not pass through the parasphenoid in *Bathylaco* but through the notch indicated.

conclude that it "appears to have a basipterygoid process." Gosline was right: *Searsia* and all other examined platytroctids have a basipterygoid process, penetrated in the usual way by a foramen for the efferent pseudobranchial artery (Fig. 3; also visible in Sazonov, 1986, figs. 10B, 11A). The only other Recent euteleost in which we have found a similar process is *Bathylaco* (Fig. 3). The efferent pseudobranchial foramen persists in various lower euteleosts (e.g, *Argentina*, coregonids, and *Salmo*; Patterson, 1975, p. 532) but is absent in osmerids and retropinnids, where the artery passes lateral to the parasphenoid, as in the majority of teleosts. However, retropinnids show a unique condition: in *Retropinna*, *Prototroctes*, and *Stokellia* there is a conspicuous earlike, paired cartilage projecting lateral to the parasphenoid, just in front of the opening of the myodome, and the cartilage is perforated by a foramen for the efferent pseudobranchial artery. In *Aplochiton* there is no such cartilage, but instead the parasphenoid contains a pair of foramina for the efferent pseudobranchials. There is no efferent pseudobranchial foramen in *Lovettia* or *Lepidogalaxias*, but galaxiids commonly have a foramen (e.g., *G.maculatus* and *G.zebratus*) or notch (e.g., *G.fontanus*, *G.platei*, and *Paragalaxias*) for the artery in the parasphenoid.

16. Otic bulla. In osmerids, there is variation in the form of the otic bulla (lateral wall of the saccular recess). *Thaleichthys* and *Spirinchus* have an inflated otic bulla with a large area of cartilage in its wall (Klyukanov, 1970, figs. 1, 2; 1975, fig. 7). In *Allosmerus*, *Mallotus*, and *Osmerus* the bulla is less inflated and the area of cartilage is smaller (Klyukanov, 1970, figs. 3, 4, 6), whereas in *Hypomesus* and *Plecoglossus* the bulla is uninflated (Klyukanov, 1970, fig. 5; 1975, figs. 5, 7). Klyukanov (1975, p. 13) considered the inflated bulla of *Thaleichthys* and *Spirinchus* to be primitive, but, as he correctly noted, the bulla is not inflated in outgroups, and when an inflated bulla of this type occurs elsewhere in teleosts (e.g., trachichthyid beryciforms) it can be shown to be derived.

17. [Begle's 74: Sphenotic spine blunt (0) or rodlike (1). State (1) coded in galaxiids, *Allosmerus*, *Hypomesus*, *Spirinchus*, and *Mallotus*, with salangids coded as (?) because the sphenotic is not ossified.] Within osmerids, we see no difference between the sphenotic spine (postorbital process) of *Osmerus* and that of *Hypomesus* or *Mallotus*. The spine is sharply pointed in the *Allos-*

merus, Spirinchus, and *Thaleichthys* that we studied. The character was discarded.

18. Lateral extent of frontal. In teleosts the supraorbital sensory canal primitively runs longitudinally approximately along the center of each frontal, and the frontal has a laminar portion, lateral to the sensory canal, that roofs the orbit. In *Lepidogalaxias* and *Lovettia* this lateral laminar portion is absent, and the sensory canal runs along the margin of the bone. Salangids have the frontal so weakly ossified (Roberts, 1984, figs. 3–6) that they cannot be assessed for this feature.

19. Extent of parietals. The parietals in teleosts primitively overlie the supraoccipital medially, meeting in the midline, and are overlapped by the frontals anteriorly so that their exposed surface is relatively small. In osmeroids there are three derived states. First, in all osmerids except *Hypomesus* and *Plecoglossus* the parietals are partially (*Mallotus* and *Osmerus*) or completely (*Allosmerus, Spirinchus,* and *Thaleichthys*) separated by the supraoccipital (they are also partially separated in *Lovettia*). Second, in all southern osmeroids (retropinnids, *Aplochiton, Lovettia, Lepidogalaxias,* and galaxiids) the parietals are not overlapped by the frontals but suture with them and extend forward to or beyond the postorbital process. Third, parietals are absent in salangids (Roberts, 1984).

In other lower euteleosts, the parietals are completely separated by the supraoccipital in all alepocephaloids (Greenwood and Rosen, 1971, p. 33) and esocoids, and in bathylagids and opisthoproctids among argentinoids. Among salmonoids the parietals are partially separated in *Thymallus, Stenodus,* and some *Coregonus* and are completely separated in all salmonines (Sanford, 1987, 1990).

20. Parietals and occipital (supratemporal) commissure. Primitively in teleosts, the parietals do not carry the occipital sensory canal, which lies in the extrascapulars. Among lower euteleosts, the parietal carries the medial part of the occipital commissural sensory canal, presumably through fusion with a medial extrascapular, in all argentinoids except bathylagids, where the commissure is secondarily absent. In argentinids the parietal carries the commissure across its posterior margin, the primitive position, but in microstomatids the lateral extrascapular is a long tube or gutter, directed forward over the autopterotic (the dermopterotic is absent, no. 21 below), and the occipital commissure passes across the anterior margin of the parietal. In opisthoproctids the parietal is rather short rostrocaudally, and the commissure passes across the middle of the bone.

21. Dermopterotic. The dermopterotic is primitively fused to the autopterotic in Recent teleosts. Gosline (1969, p. 197) reported that the dermopterotic is independent in *Alepocephalus rostratus*, and this is true also of our *A.agassizi, A.bairdi,* and *A.tenebrosus*, and of *Leptochilichthys* and *Talismania aphos*. In other alepocephalids we find the dermopterotic and autopterotic fused in *Bajacalifornia, Bathylaco, Bathytroctes, Binghamichthys, Narcetes, Rinoctes, Rouleina,* and *Talismania oregoni* and the dermopterotic absent in *Leptoderma* and *Photostylus*. In platytroctids the same three conditions occur: the dermopterotic and autopterotic are fused in *Paraholtbyrnia*; the dermopterotic is free in *Mentodus, Mirorictus, Pellisolus, Searsia,* and *Searsioides*; and the dermopterotic is absent in *Holtbyrnia, Platytroctes,* and *Sagamichthys*.

The relation between the temporal sensory canal and dermopterotic also varies in alepocephaloids. The primitive pattern, with the canal penetrating the bone from end to end, occurs in some platytroctids (*Paraholtbyrnia*; Sazonov, 1986, fig. 11) and in the alepocephalids *Bathylaco, Narcetes,* and *Talismania*. Derived conditions include a short enclosed canal in the dermopterotic (*Bajacalifornia* and *Binghamichthys*); the canal running superficial to the bone (*Bathytroctes, Rinoctes* and *Rouleina*); the canal running through one or more free ossicles (some platytroctids; e.g., Sazonov, 1986, fig. 10); the canal running superficial to a free bone (some platytroctids, *Alepocephalus,* and *Leptochilichthys*); and no dermopterotic (see above).

Among argentinoids, the dermopterotic is absent in microstomatids, some bathylagids (Kobyliansky, 1986, figs. 2–5), and apparently in all opisthoproctids except *Bathylychnops*.

22. Temporal fontanelles. The osmerids *Spirinchus* and *Thaleichthys* differ from other osmerids by eliminating the temporal fontanelles in the chondrocranial roof during ontogeny (Klyukanov, 1970, fig. 9). Klyukanov (1970) took this condition to be primitive, but comparison with outgroups (e.g., retropinnids and salmonoids) shows that it is derived. Closure of the fontanelles occurs as a derived state in a subgroup of *Oncorhynchus* (Stearley and Smith, 1993, character 1, where *Thaleichthys* is wrongly coded).

23. Posttemporal fossa. Primitively in teleosts the posttemporal fossa is extensive and is roofed by the dermopterotic and parietal. Among lower euteleosts, this primitive type of posttemporal fossa persists only in argentinids and esocids. There is an unroofed posttemporal fossa in other argentinoids (many of which have lost the dermopterotic, no. 21 above) and in salmonoids, osmeroids, and umbrids. Gosline (1969) reported that the alepocephaloids *Alepocephalus, Bathyprion,* and *Xenodermichthys* have no posttemporal fossa but that there is a roofed fossa in *Bathylaco*. We

could find no posttemporal fossa in *Bathylaco* and believe that alepocephaloids are characterized by loss of the fossa. They exhibit two different states. In *Bathylaco, Bathytroctes, Narcetes, Rinoctes,* and *Talismania antillarum,* the posterior margins of the parietal and dermopterotic form a straight transverse line, as in taxa with a roofed posttemporal fossa such as *Elops* and argentinids. In other alepocephaloids the margins of the parietal and dermopterotic, if a contact between them exists, form a "V" open posteriorly, as in taxa with an unroofed posttemporal fossa; we take the second condition to be derived and regard alepocephaloids that lack the dermopterotic (no. 21 above) as a special case of it.

24. [Begle's 25: Basioccipital without (0) or with (1) a caudally projecting peg on either side of the first vertebra, coded as present in galaxiids.] The peg is more restricted; when present, it carries Baudelot's ligament, which is double in some galaxiids, with one originating on the basioccipital and one on V1. In our cleared-and-stained material, pegs are present only in *Galaxias fasciatus* (McDowall, 1969, fig. 2; Begle's source). They are absent in *G. fontanus, G. zebratus, G. maculatus, G. occidentalis, G. paucispondylus, Galaxiella, Neochanna apoda,* and *Paragalaxias dissimilis,* although they may develop in larger individuals of species in which the ligament is double; pegs are absent in dried skeletons of *G. maculatus* and *G. platei* but present in *G. fasciatus.* Variability means that the character must be entered "B" in the matrix (Begle's coding for polymorphic taxa), making it empty if polymorphism for (0) and (1) is treated as (0). Character was discarded.

25. [Begle's 48: Occiput greatly depressed (1) only in salangids.] No comment.

26. [Begle's 55: Occipital condyle formed only by basioccipital (0) or tripartite, with exoccipital condyles (1). State (1) coded in neoteleosts and *Lepidogalaxias,* with salmonoids coded as (?).] Begle's query for salmonoids evidently refers to the primitive state in salmonoids, which might be state (0), as coded in *Coregonus* and *Stenodus* by Stearley and Smith (1993), or state (1), as in salmonines. Stearley and Smith (1993, p. 19) listed the tripartite condyle as a character of Salmonidae (including coregonines) and coded it as present in the coregonine *Prosopium* and in *Thymallus.* In our cleared-and-stained *Prosopium williamsoni* and *Thymallus thymallus* the condyle is not tripartite but is as illustrated by Rosen (1985, fig. 7B). According to Stearley and Smith's (1993) cladogram, the neoteleostean type of condyle (e.g., Rosen, 1985, fig. 3) is therefore synapomorphous for Salmoninae. There is also a tripartite condyle in opisthoproctids (seen in *Opisthoproctus, Bathylychnops, Dolichopteryx, Macropinna,* and *Rhynchohyalus*).

B. Suspensorium

27. [Begle's 35: Palatine without (0) or with (1) distinctive dumbbell shape. State (1) coded in all osmerids, including *Plecoglossus.*] Begle (1991) credited the character to Chapman (1941b) and McAllister (1963), both of whom described the palatine as longer and more slender in *Hypomesus* and (in particular) *Mallotus.* Howes and Sanford (1987a, p. 167) correctly reported the derived state (their "diabolo-shaped") as absent in *Hypomesus* and *Mallotus* but in their second (1987b) paper used it as a character of Osmeridae, secondarily modified in those two genera. In *Hypomesus* the autopalatine is much shorter than in *Mallotus* and (particularly in *H. olidus* and *H. pretiosus*) differs from that of other osmerids in being shallower posteriorly rather than shorter. We find it impossible to discriminate the osmerid dumbbell or diabolo condition from that in, for example, the alepocephaloids *Bathytroctes, Rouleina,* and many platytroctids (Sazonov, 1986, figs. 4, 5).

28. Fusion between autopalatine and dermopalatine. The autopalatine and dermopalatine are separate in retropinnids but fused in *Lepidogalaxias* and all osmerids except *Hypomesus* and *Osmerus.* In *Plecoglossus,* Howes and Sanford (1987a, p. 146) reported fusion late in ontogeny (at ca. 100 mm), but the bones are separate in our specimens of ca. 150 mm. The two bones are separate in *Alepocephalus rostratus* (Gosline, 1969), *A.agassizi,* and *Leptoderma* but fused in our *A.tenebrosus* and in other alepocephalids, platytroctids, argentinoids (Kobyliansky, 1990, fig. 6), salmonoids, and esocoids. The dermopalatine is absent in galaxiids, *Aplochiton,* and *Lovettia* (Figs. 4B–4D), and the autopalatine is absent in salangids.

29. [Begle's 10: Palatine teeth present (0) or absent (1). State (1) coded in salangids, galaxiids, retropinnids, *Aplochiton, Lovettia,* and the alepocephaloids *Leptoderma* and *Rouleina.*] In retropinnids, this character depends on interpreting the single toothed bone that extends from beneath the autopalatine to the quadrate (Fig. 4A). McDowall (1969) and Williams (1987) interpreted the bone as fusion between a toothed palatine and a toothless ectopterygoid, but Begle evidently interpreted it as a toothed ectopterygoid (see no. 32). In one cleared-and-stained *Retropinna* (BMNH 1964.4.30.19) there are two separate bones on the right side, corresponding in position to a long toothed palatine and a short toothless ectopterygoid resembling that bone in *Lovettia* or *Lepidogalaxias* (Figs. 4D and

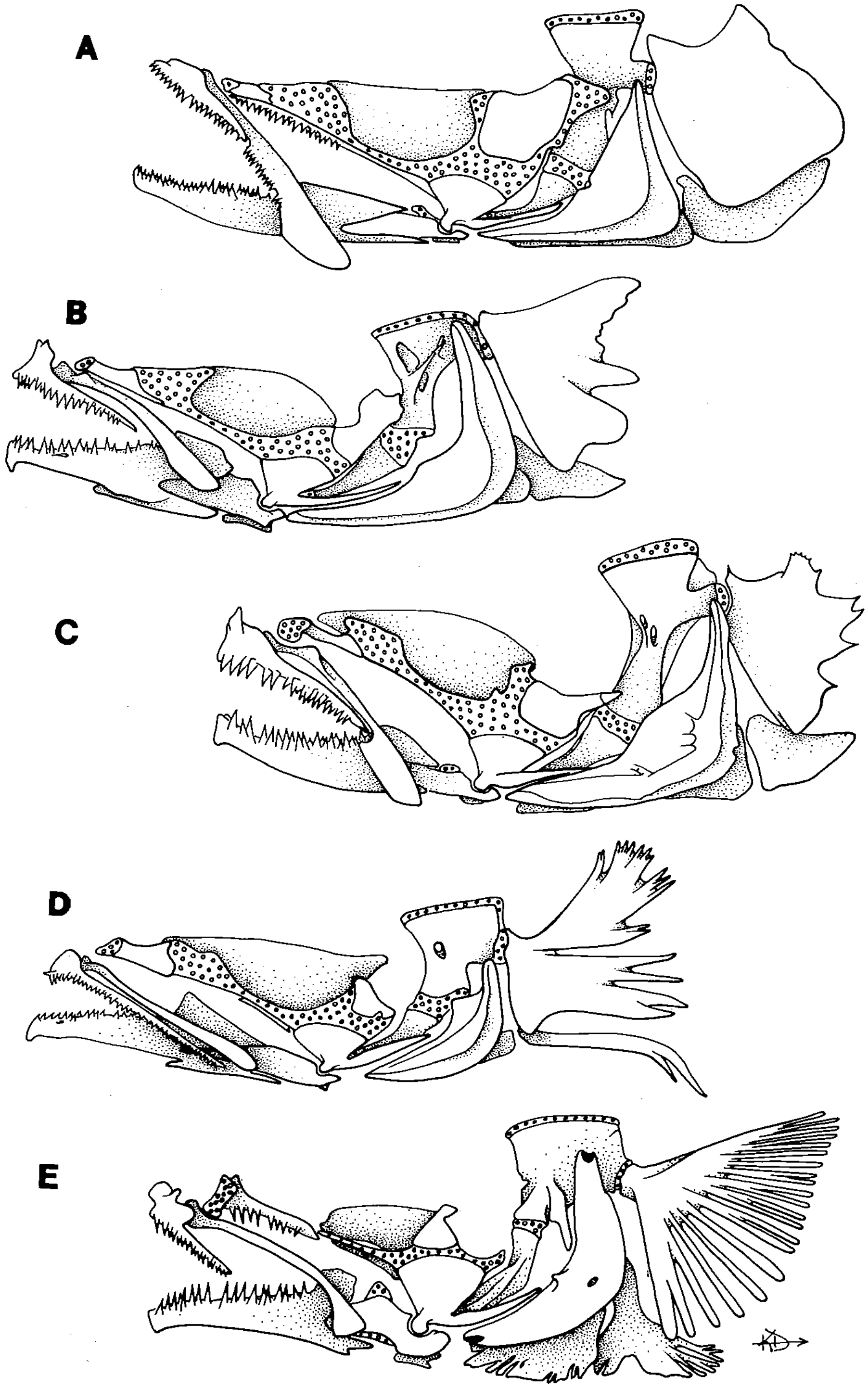

FIGURE 4 Suspensorium in galaxioids. Left jaws, palate, and operculum, in lateral view, of (A) *Retropinna retropinna*, MCZ 58015, 71 mm SL; (B) *Galaxias occidentalis*, AMNH 31478, 46 mm SL; (C) *Aplochiton zebra*, AMNH 31048, 77 mm SL; (D) *Lovettia sealei*, BMNH 1937.8.22.1, 41 mm SL; (E) *Lepidogalaxias salamandroides*, USNM 339265, 44 mm SL.

4E) but with a more extensive contact with the quadrate. On that basis, we agree with McDowall that retropinnids have a toothed palatine, usually fused with a toothless ectopterygoid. There is a similar problem in salangids, where there is a single elongate toothed bone, identified as "= ectopterygoid?" by Roberts (1984). In salangids the bone is well forward on the palatoquadrate and in *Protosalanx* is separated from the quadrate by the endopterygoid; we interpret it as the dermopalatine.

In bathylagids and microstomatids the palatine teeth are in a single row, differing from the patch of teeth that occurs in other argentinoids (argentinids and opisthoproctids; Kobyliansky, 1990, fig. 6).

30. [Begle's 70: Palatine contacting maxilla by a small knob if at all (0) or with lateral knob overlying maxilla (1). State (1) coded in galaxiids, *Lovettia, Aplochiton*, salangids, and *Lepidogalaxias*.] In galaxiids, *Lovettia*, and *Aplochiton* the lateral knob is the anterior end of the palatine cartilage, and the condition is the same as that in retropinnids (Figs. 4A–4D). In *Lepidogalaxias* (Fig. 4E) there is a distinctive cartilaginous lateral process that curves ventrally distally. In salangids the palatine cartilage is unmodified: in *Protosalanx* and *Salangichthys* the dermopalatine extends to the pointed tip of the cartilage, which merely ends in an oblique junction with the ethmoid; in *Neosalanx* the anterior end of the palatine cartilage is widened but does not overlie the maxilla. The derived state is autapomorphous for *Lepidogalaxias*.

31. [Begle's 3: Endopterygoid teeth broadly distributed over oral surface of bone (0) or a narrow band of larger teeth along medial margin (1) or teeth absent (2). State (1) coded in all Osmeroidei except *Lepidogalaxias* and salangids, which have state (2). State (2) also in all sampled argentinoids and alepocephaloids, which were wrongly coded (0) in Begle, 1991.] Esocoids and salmonoids, which lack endopterygoid teeth, are both wrongly coded (0) (Stearley and Smith, 1993, also wrongly code *Novumbra* as having endopterygoid teeth). Endopterygoid teeth, coded by Begle as absent in all Alepocephaloidea, are present in almost all platytroctids (Matsui and Rosenblatt, 1987, table 1), in pattern (1) (Sazonov, 1986, figs. 4 and 5).

Within osmeroids, there is variation in state (1). The endopterygoid teeth are in a single row in *Aplochiton, Lovettia*, galaxiids, and the osmerids *Allosmerus, Mallotus, Osmerus*, and *Thaleichthys;* a single row with 2 or 3 teeth lateral to the posterior end of the row in *Spirinchus;* a single row with 8 to 10 teeth lateral to its posterior end in *Plecoglossus;* and a single row with an extensive patch of teeth scattered lateral to the posterior end of the row in retropinnids and *Hypomesus*.

32. [Begle's 11: Ectopterygoid present (0) or absent (1). State (1) coded in galaxiids, *Aplochiton, Lovettia*, and salangids.] The ectopterygoid is wrongly coded as absent in *Lovettia* (Fig. 4D; McDowall, 1969). In our opinion (no. 29) retropinnids generally lack an independent ectopterygoid but have it fused with the dermopalatine.

33. [Begle's 23: Ectopterygoid posterior to autopalatine (0) or ventral to it (1). State (1) coded in retropinnids, with queries for galaxiids, *Lovettia, Aplochiton*, and salangids.] See no. 29 above; the bone is the dermopalatine and the character is therefore discarded.

34. [Begle's 32: Ectopterygoid with dorsal rim unmodified (0) or with a horizontal flange directed laterally (1). State (1) coded in *Plecoglossus*.] Howes and Sanford (1987a,b) found the derived state in *Hypomesus* and *Osmerus* as well as *Plecoglossus*. We agree with Begle (also Wilson and Williams, 1991, fig. 11) that no obvious flange exists in *Hypomesus* and *Osmerus*.

35. Ectopterygoid teeth. The ectopterygoid is primitively toothed in teleosts, as it is in neoteleosts. In lower euteleosts, the only records of ectopterygoid teeth are in alepocephaloids. In platytroctids, Sazonov (1986) reported ectopterygoid teeth in some individuals of *Sagamichthys* and in the larger species of *Holtbyrnia*, and Matsui and Rosenblatt (1987, p. 131) also found ectopterygoid teeth "variably present in larger individuals" of *Holtbyrnia* and *Sagamichthys* (we have seen such teeth in *H.innesi*). In alepocephalids, Nielsen and Larsen (1968) reported several rows of ectopterygoid teeth in 3 out of 10 specimens of *Bathylaco*, with a few teeth on one side in a 4th specimen, and we observed a single row of teeth (on both ectopterygoids) in a BMNH dried skeleton of *Alepocephalus rostratus*.

36. [Begle's 38: Metapterygoid without lateral shelf (0) or with short lateral shelf (1) or with prominent diagonal shelf (2). State (1) coded in *Mallotus* and *Plecoglossus* (where the shelf is described as horizontal) and state (2) in the other five osmerid genera.] *Mallotus* is wrongly coded, having state (2), so that (1) is autapomorphous for *Plecoglossus*. The shelf is very weak in *Hypomesus pretiosus*. Wilson and Williams (1991) cited "lateral ridge of metapterygoid" as a character of all osmerids.

37. [Begle's 89: Metapterygoid large and broad (0) or reduced and rodlike (1). State (1) coded in *Argentina, Bathylagus, Glossanodon*, and *Opisthoproctus*.] The metapterygoid is absent in *Bathylagus s.s.* and several other bathylagid genera (Kobyliansky, 1986) and is "small and insignificant" in microstomatids (Chapman, 1948, p. 10). In *Leptoderma, Aplochiton, Lovettia, Lepidogalaxias*, and most galaxiids the metapterygoid is also reduced and comparable in size and shape to the symplectic (Figs. 4B–4E). In *Lovettia* and *Lepidogalaxias* it is less than half the size of the symplectic and fails to contact the hyomandibular (Fig. 4; McDowall, 1969, fig. 3D; Roberts, 1984, fig. 22); they are recoded (1).

38. Metapterygoid position. Wilson and Williams (1991, figs. 11 and 12) published a cladistic analysis of osmerids in which *Hypomesus* is the sister of the other six Recent genera and is distinguished from them by one character, position of the metapterygoid: the metapterygoid is posterodorsal to the quadrate in *Hypomesus* but dorsal to it in *Allosmerus, Mallotus, Osmerus, Plecoglossus, Spirinchus,* and *Thaleichthys*. We agree with Wilson and Williams that appropriate outgroups show the same condition as *Hypomesus* [e.g., esocoids; argentinoids; coregonids and *Thymallus,* though not all salmonids (Stearley and Smith, 1993, fig. 7); and retropinnids (Fig. 4)]. In alepocephaloids both conditions occur among platytroctids (Sazonov, 1986, figs. 4 and 5) and among alepocephalids. In salangids the metapterygoid and quadrate are well ossified only in *Protosalanx* (Roberts, 1984, fig. 9), where the condition is as in *Hypomesus* and outgroups.

39. [Begle's 90: Metapterygoid without medial shelf (0) or with shelf at midpoint of bone (1). State (1) coded in all alepocephaloids except *Leptochilichthys, Bathylaco, Narcetes,* and *Rouleina.*] The shelf is the narrow, oblique one shown in most of the platytroctids in Sazonov's illustrations (1986, figs. 4 and 5). It is well-developed in our *Leptochilichthys* and *Rouleina* but absent in *Leptoderma,* where the metapterygoid is reduced with forward displacement of the quadrate (no. 37). Otherwise, we found the structure in our alepocephaloid material to agree with Begle's coding (we were unable to check *Bathyprion*). However, late in our work (July 1995) we saw Williams's (1987) dissertation; he recorded a medial shelf "of some form or another" in all examined alepocephaloids. Williams's sample included all the genera in Begle's except *Leptochilichthys* and *Bathyprion.* On rechecking our material, we found no shelf in *Leptoderma* but a vestige in *Bathylaco* and *Narcetes.* With those problems in interpretation, *Bathylaco* and *Narcetes* would best be coded as (?). Williams (1987) showed that a medial shelf on the metapterygoid like that in alepocephaloids also occurs in all osmerids (including *Plecoglossus*); we confirmed his observations.

40, 41. [Begle's 60, 61: Quadrate (60) and metapterygoid (61) without (0) or with (1) linear ridges, sometimes ramifying. State (1) coded for the quadrate in *Allosmerus, Spirinchus,* and *Thaleichthys* and for the metapterygoid in *Allosmerus* and *Spirinchus.*] The ridges are struts of membrane bone, and are commonly developed elsewhere, for example, on the quadrate in *Bathylagus* and other bathylagids (Kobyliansky, 1986) and on both quadrate and metapterygoid in *Alepocephalus* and platytroctids (Sazonov, 1986), on the quadrate in many salmonoids (e.g., *Oncorhynchus, Salvelinus,* and *Thymallus*), and on the metapterygoid in some of those. In our osmerid material, struts occur on the quadrate in *Allosmerus, Mallotus, Thaleichthys,* and *Spirinchus,* where they are particularly strongly developed, and on the metapterygoid in *Allosmerus, Spirinchus,* and *Thaleichthys.* Polarity is questionable, and the character may be size related.

42. [Begle's 88: Ventral arm of symplectic short, less than half the length of the dorsal arm (0) or longer than the dorsal arm (1). State (1) coded in *Argentina, Glossanodon,* and *Opisthoproctus,* though the text says that it also occurs in *Bathylagus.*] The character expresses the forwardly displaced jaw articulation of argentinoids. The symplectic is primitively a straight bone (e.g., Patterson, 1973, figs. 7, 23, and 26), but in many teleosts it develops a more or less pronounced flexure near its midpoint. In bathylagids (Kobyliansky, 1990, figs. 6–8), *Opisthoproctus* (Trewavas, 1933, fig. 7), and microstomatids (Chapman, 1948, fig. 4) the two arms of the symplectic are about equal in length, as they are in osmerids (Weitzman, 1967, fig. 3), platytroctids (Sazonov, 1986, fig. 5), and umbrids (Wilson and Veilleux, 1982, fig. 7), for example. As presented by Begle, the primitive state is wrongly described, and the derived state occurs only in argentinids.

43. [Begle's 46: Hyomandibula not fused (0) or fused (1) to palatopterygoid. State (1) coded as autapomorphic for salangids.] Roberts (1984), who reported the salangid condition as unique, was unaware that the derived state is also reported in early ontogeny of *Clupea* (Norman, 1926; also *Alosa,* Shardo, 1995), *Sebastes* (Mackintosh, 1923), *Ictalurus* (Kindred, 1919), and *Heterotis* (Daget and d'Aubenton, 1957). Salangids maintain into adulthood a condition that is widespread, though not universal, in teleost embryos.

44. [Begle's 26: Hyomandibular without (0) or with (1) lateral spur at or below the level of the opercular process, projecting caudally to contact the preopercle. State (1) coded in galaxiids, *Aplochiton,* and all osmerid genera except *Thaleichthys.*] In Begle (1991) an undescribed state (2) was entered for the osmerid genera. Fink (1984b) used a lateral hyomandibular spur to characterize galaxiids (excluding aplochitonids), but Begle's wording of this character follows Howes and Sanford (1987b, p. 21). *Lepidogalaxias* (Fig. 4E) and esocoids (Wilson and Veilleux, 1982, fig. 7; Howes and Sanford, 1987b, fig. 5) are wrongly coded as lacking the spur. In osmerids, Wilson and Williams (1991, fig. 11) discriminated a vertical strut (= spur) in outgroups *Hypomesus, Mallotus, Plecoglossus,* and *Thaleichthys* from a lateral strut in *Osmerus, Allosmerus,* and *Spirinchus.*

45. [Begle's 98: Hyomandibular with lateral ridge short, less than half the length of the bone (0) or

longer, sometimes occupying the entire length of the hyomandibular shaft (1), or absent (2). State (1) coded in all osmerids and state (2) in retropinnids.] It is true that retropinnids, like salangids and *Lovettia*, which were both coded (0) by Begle, lack a lateral ridge on the hyomandibular; instead, as in *Aplochiton*, the metapterygoid sends a distinctive cartilaginous process across the hyomandibular towards the preopercle (Fig. 4). But osmerids (coded 1) do not have a long lateral ridge or crest but a short one (no. 44 above), whereas salmonoids, argentinids, alepocephalids (all coded 0), and outgroups such as *Elops* and *Chanos* all have a long one. We are unable to make sense of the character and so we discard it.

46. [Begle's 99: Hyomandibular with lateral ridge contacting (0) or failing to contact preopercle (1). State (1) coded in *Stokellia, Allosmerus, Thaleichthys, Leptoderma, Bathyprion, Bathytroctes, Bathylaco, Narcetes*, and *Rouleina*.] The character repeats no. 44 above and so is redundant in part. The coding is also confused and contradictory, for in the paragraph on the character Begle wrote "ridge contacts the preopercle in *Leptoderma, Bathyprion*, [etc.]," describing state (0), *not* the (1) coded for those genera. In the preceding character (no. 45), he (correctly) coded retropinnids as lacking a lateral ridge on the hyomandibular, but here he coded *Prototroctes* and *Retropinna* as having a ridge that contacts the preopercle. And under character 44 above he coded a "lateral spur . . . projecting caudally to contact the preopercle" as a *derived* feature present in all osmerid genera (including *Allosmerus*, here said to lack the contact) except *Thaleichthys*. With corrected coding the character is redundant except for the potential information on alepocephaloids, which is significant in Begle's cladogram as the only feature distinguishing *Leptochilichthys* (state 0) from the rest of the group (state 1, with reversal to 0 in *Alepocephalus* and platytroctids + *Talismania*). However, the hyomandibular crest unquestionably contacts the preopercle in our *Narcetes* and *Bathytroctes*, and in *Leptoderma* and *Bathylaco* the loss of contact has entirely different causes—forward inclination of the hyomandibular in the short-jawed *Leptoderma* and backward inclination in the long-jawed *Bathylaco*. Character was discarded.

47. [Begle's 100: Hyomandibular with anterior laminar extension (0) or with laminar bone reduced or absent (1). State (1) coded in neoteleosts, all Osmeroidei except *Prototroctes* and *Plecoglossus*, and all argentinoids and alepocephaloids except *Leptochilichthys* and *Narcetes*.] We commented (Patterson and Johnson, 1995, p. 27) at a time when we accepted Begle's accounts of characters and their distribution. We see no difference between the anterior part of the hyomandibular in *Prototroctes* (coded 1) and *Retropinna* (coded 0; Fig. 4A) or between it in *Narcetes* (coded 1) and *Bathytroctes* or *Rouleina* (both coded 0). Laminar bone is certainly not absent on the hyomandibular of neoteleosts (e.g., Johnson *et al.*, 1996, figs. 6, 26–29). Character was discarded.

48. [Begle's 105: Opercular process of hyomandibular dorsally located and straight (0) or curved ventrally (1) or located at or below the midpoint of the bone (2). State (1) coded in platytroctids, *Leptoderma, Leptochilichthys*, and *Bathytroctes*; state (2) said to occur in *Bathyprion*, but it is coded (0).] State (2) occurs in *Bathylaco* (Markle, 1976, fig. 9). Figures 4 and 5 in Sazonov (1986) show the hyomandibular in 10 genera of platytroctids, and both states (0) and (1) occur. The opercular process is identical in our *Bathytroctes* (coded 1) and *Rouleina* (coded 0) and is similar but longer in *Narcetes* (coded 0). Character was discarded.

C. *Jaws*

49. [Begle's 29: Premaxilla with articular process not tightly adhering to maxillary head (0) or syndesmotically attached to it (1). Character from Howes and Sanford (1987a), with state (1) coded only in *Plecoglossus* and *Prototroctes*.] In this and the following two characters, *Opisthoproctus*, which has no premaxilla, is wrongly coded (0) rather than (?) by Begle.

50. [Begle's 66: Ascending process of premaxilla knoblike (0) or sharply triangular (1). State (1) coded in galaxiids and *Aplochiton*.] See no. 49.

51. [Begle's 83: Premaxilla without (0) or with (1) alveolar (postmaxillary) process extending beneath maxilla. State (1) coded in all osmeroids, all argentinoids and alepocephaloids, and neoteleosts, with state (0) in outgroups, salmonoids, and esocoids.] Begle credited the character to Rosen (1985), who regarded the "serial alignment" (p. 37) of the premaxilla and maxilla in salmonids as primitive. We commented (Patterson and Johnson, 1995, p. 27) and regard the character as wrongly coded in outgroups, esocoids, and salmonoids, where it is apomorphic for salmonines (there is an alveolar process in coregonids and *Thymallus*); with corrected coding [state (0) only in some salmonoids] the character is empty and is discarded. In Begle (1991) character 83 was different, referring to a long alveolar process (greater than half the length of the maxilla) coded as autapomorphic for *Stokellia*, but this is also present in *Prototroctes, Aplochiton, Lovettia*, and some galaxiids (Fig. 4; McDowall, 1969, fig. 7).

52. Premaxillary teeth. The premaxilla is primitively toothed. Among lower euteleosts it is toothless only in argentinoids and the alepocephalid *Leptochilichthys*. There is no premaxilla in opisthoproctids.

53. Premaxilla–maxilla contact. Primitively in teleosts the distal end of the alveolar process of the pre-

maxilla is free or attached to the maxilla by loose connective tissue. In bathylagids and microstomatids there is a distinctive articulation between the tip of the premaxilla and a notch or facet on the maxilla (Kobyliansky, 1990, fig. 4; note that there is no premaxilla in opisthoproctids, no. 52 above).

54. [Begle's 30: Maxilla and palatine without (0) or with (1) head-to-head articulation. Character from Howes and Sanford (1987a) with state (1) coded only in *Retropinna* and *Stokellia*.] No comment.

55. [Begle's 67: Maxilla more or less straight (0) or curved dorsally (1) in lateral profile. State (1) coded in galaxiids and *Aplochiton*.] We believe that this character refers to the configurations of retropinnid, aplochitonid, and galaxiid maxillae shown by McDowall (1969, fig. 7) and is based on a misreading of that figure (taking 7H, 7C, and 7F for 7F, 7G and 7H). In fact, the curvature of the maxilla in *Aplochiton* is most closely matched in McDowall's illustration by *Stokellia*. Character was discarded.

56. [Begle's 95: Teeth on maxilla present (0) or absent (1). State (1) coded in argentinoids and in *Alepocephalus*, *Leptoderma*, and *Leptochilichthys*.] The maxilla is also toothless in esocoids, *Prototroctes*, *Stokellia*, *Aplochiton*, *Lovettia*, galaxiids, and *Lepidogalaxias*, all wrongly coded (0).

57. Supramaxillae. Primitively in teleosts there are two supramaxillae. Among lower euteleosts, two supramaxillae occur in platytroctids (Sazonov, 1986, fig. 3) and the alepocephalids *Alepocephalus*, *Bajacalifornia*, *Bathytroctes*, *Binghamichthys*, *Narcetes*, *Rinoctes*, some *Rouleina* (Markle, 1976, p. 27), and *Talismania* among those we examined. There is one supramaxilla in esocoids, salmonoids, osmerids (lost during ontogeny in *Plecoglossus*; Howes and Sanford 1987a), salangids, and the alepocephaloids *Bathylaco*, some *Bathyprion* (Markle, 1976, p. 27), *Leptochilichthys*, *Leptoderma*, *Photostylus*, some *Rouleina*, and *Xenodermichthys* among those we examined. There are no supramaxillae in southern osmeroids (= galaxioids: retropinnids, *Aplochiton*, *Lovettia*, *Lepidogalaxias*, and galaxiids) or in argentinoids.

58. Shape and dentition of dentary. There is significant variation in the dentary dentition in osmerids. In *Hypomesus* (Patterson, 1970, fig. 37; Klyukanov, 1970, fig. 7) teeth are small and confined to the anterior quarter of the jaw, and there is a high coronoid process with a concave anterior margin. In juvenile *Plecoglossus* (Howes and Sanford, 1987a, fig. 4) the coronoid process is similar, and in *Plecoglossus* and *Mallotus* the teeth are also small and are confined to the anterior half of the jaw. In other osmerids (*Allosmerus*, *Osmerus*, *Spirinchus*, and *Thaleichthys*; Klyukanov, 1970, fig. 7; 1975, fig. 9) and in salangids (Roberts, 1984) and southern osmeroids (McDowall, 1969) teeth are larger and occupy more than half the length of the jaw. In outgroups, Stearley and Smith (1993, character 65) assessed the *Hypomesus* pattern, which occurs also in coregonids, as primitive relative to the *Spirinchus* pattern, which occurs also in salmonids.

Among argentinoids, bathylagids and microstomatids share a derived pattern of the dentary, with a long single row of incisorlike teeth (Kobyliansky, 1990, fig. 5).

59. Meckelian fossa. The opening of the Meckelian fossa on the inner face of the dentary in osmerids was discussed by Klyukanov (1975, p. 7) and Howes and Sanford (1987a, p. 157). The opening is very small and placed in the anterior third of the bone in *Hypomesus* (Patterson, 1970, fig. 37) and juvenile *Plecoglossus* (Howes and Sanford, 1987a, fig. 4), similarly placed but slightly larger in *Osmerus* and salangids, larger and beneath the middle of the tooth row in *Mallotus*, and large and beneath the rear of the tooth row in *Allosmerus*, *Spirinchus*, and *Thaleichthys* (Klyukanov, 1975, fig. 9). Howes and Sanford (1987a) noted that the fossa is also small and anteriorly placed in retropinnids and *Aplochiton*. It is similar in coregonids and in *Glossanodon* (Kobyliansky, 1990, fig. 5). Weitzman (1967, p. 529) called the recess "small (or practically nonexistent) and far anterior" in salmonids and esocoids.

60. [Begle's 31: Paired postsymphysial cartilages absent (0) or present (1) at dentary symphysis. Character from Howes and Sanford (1987a), with state (1) coded only in *Osmerus* and *Plecoglossus*.] Howes and Sanford (1987a) found a median postsymphysial bone in one specimen of *O.mordax*; like them, we have seen it only in that specimen and not in other specimens of that species or of *O.eperlanus*. There is no demonstrable shared feature and the character becomes autapomorphous for *Plecoglossus*.

61. [Begle's 37: Dentary without (0) or with (1) medial tusk-like process at symphysis. Character said to be from Howes and Sanford (1987a,b), with state (1) coded in *Osmerus* and *Plecoglossus*.] Howes and Sanford (1987a) did not report a medial tusk-like process in *Osmerus*, and their "symphysial dentary process" (1987b, p. 24) said to be shared by *Osmerus* and *Plecoglossus* probably refers to the "postsymphysial notch" (Howes and Sanford, 1987a, p. 157) present in the margin of the dentary in an *Osmerus mordax* and in *Plecoglossus* of 40 to 60 mm SL. We have found no such notch in other specimens of *O.mordax*, or in *O.eperlanus*, and there is again no demonstrable shared feature so that the character is autapomorphous for *Plecoglossus*.

62. [Begle's 2: Articular fused with angular (0) or absent or greatly reduced, appearing late in ontogeny (1). State (1) coded in all Osmeroidei.] The character is from Fink (1984b), who gave no source or discussion. Howes and Sanford (1987b, p. 26) interpreted it as late ossification of the articular in all osmeroids and reported an osmeroid-like condition in *Argentina sphyraena*. The articular of *Argentina* (Kobyliansky, 1990, fig. 5) does not appear to differ from that of other argentinoids, and we accept the character as true of osmeroids, but it also occurs in esocoids (e.g., Nelson, 1973, fig. 6H and 6K; Jollie, 1975, p. 76).

63. [Begle's 102: Mouth terminal and large (0) or very small (1). State (1) coded in *Argentina*, *Bathylagus*, *Opisthoproctus* and *Glossanodon*.] No comment.

64. Tooth attachment. Fink (1981) identified four modes of tooth attachment in teleosts in a survey of the jaws and pharyngeals of a wide range of species. He distinguished hinged (depressible) teeth as type 4 and found them to be restricted to neoteleosts and the pharyngeals of *Esox*. Our observations on esocoids differ from Fink's (1981) in two ways. First, he assessed only the pharyngeal teeth of *Esox* as type 4, but we find the jaw teeth also to be type 4. Second, among umbrids according to Fink, *Dallia* has type 2 teeth in the jaws and pharyngeals, and *Umbra* has type 1 in both; we found the reverse, type 1 in *Dallia* and type 2 in *Umbra* (also in *Novumbra*). The same patterns as in umbrids are found in some lower neoteleosts (for example, type 1 in *Gonostoma* and type 2 in *Synodus*; Fink, 1981).

D. Circumorbital Bones

65, 66. Antorbital (65) and supraorbital (66). These two bones are primitively both present in teleosts and in lower euteleosts (e.g., platytroctids, argentinids, salmonoids, and osmerids). The antorbital is absent in esocoids, salangids, retropinnids, some galaxiids, and the alepocephalids *Leptoderma* and *Rouleina* (Markle, 1976). From our specimens and the literature, we could not determine whether opisthoproctids have an antorbital or not. The supraorbital is absent in umbrids, opisthoproctids, retropinnids, *Aplochiton*, *Lovettia*, *Lepidogalaxias*, some galaxiids, and the alepocephalids *Alepocephalus*, *Bajacalifornia*, *Bathyprion*, *Leptoderma*, *Narcetes*, *Rouleina*, and *Xenodermichthys* (Markle, 1976).

In bathylagids and microstomatids the supraorbital is long and there is an extensive contact between it and the dermosphenotic above the posterior part of the orbit (Kobyliansky, 1986, fig. 1; 1990, fig. 3).

67. Number of infraorbitals. Primitively in teleosts there are seven canal-bearing infraorbitals, including the antorbital and lachrymal anteriorly and the dermosphenotic posteriorly (Nelson, 1969b). The osmerid *Spirinchus* has an extra infraorbital, with five between the lachrymal and dermosphenotic (Weitzman, 1967). We also found an extra infraorbital on one side of a specimen of *Thaleichthys*. Salangids have one infraorbital (behind the eye) or none (Roberts, 1984). *Aplochiton*, *Lovettia* and galaxiids have two infraorbitals, the lachrymal and the first infraorbital behind it (McDowall, 1969); *Lepidogalaxias* has none.

68. Lachrymal. Primitively, the lachrymal is attached to the lateral ethmoid by loose connective tissue. In *Aplochiton*, *Lovettia*, and galaxiids the lachrymal articulates with the lateral ethmoid by a cartilage-covered condyle. The lachrymal is primitively larger than the succeeding infraorbitals. In bathylagids, microstomatids (Kobyliansky, 1990, fig. 3), and opisthoproctids the first infraorbital is larger than the lachrymal.

E. Ventral Part of Hyoid Arch, Branchiostegals, and Operculum

69. [Begle's 20: Ventral border of ceratohyal straight with branchiostegals along most of its length (0), or deeply concave anteriorly with branchiostegals restricted to area behind the concavity (1), or with rectangular notch (2). State (1) coded in *Prototroctes*, *Retropinna*, and *Stokellia*, and state (2) in *Talismania* and platytroctids.] State (1) also occurs in *Aplochiton* (Chapman, 1944, fig. 5), and in all four genera (*Aplochiton* and retropinnids) cartilage extends along the ventral border of the deep posterior part (fig. 5A). Begle's state (2) refers not to a notch in the ventral border but to an excavation in the *dorsal* border in some alepocephaloids. It is a different character, part of a different transformation series (no. 70 below). In any event, our *Talismania* (*T.antillarum*, *T.aphos*, and *T.oregoni*) all have a rectangular distal ceratohyal with no dorsal notch and no fenestra, making state 2 autapomorphic (and polymorphic, no. 70) in platytroctids in Begle's sample.

70. Dorsal margin of ceratohyal. Begle (1992, character 20) mentioned a notch in the dorsal border of the ceratohyal (no. 69) in platytroctids and the alepocephalid *Talismania* and coded it as a derived feature. Sazonov (1986, figs. 6–8) illustrated the notch in several genera among platytroctids but showed that others have a fenestra in the bone (Fig. 6D), as does the alepocephalid *Rinoctes* (Markle and Merrett, 1980). The notch is clearly homologous with the fenestra (fig. 6). Elsewhere in teleosts, a ceratohyal fenestra ("beryciform foramen" of McAllister, 1968) is a primitive feature (Rosen and Patterson, 1969, p. 408). This

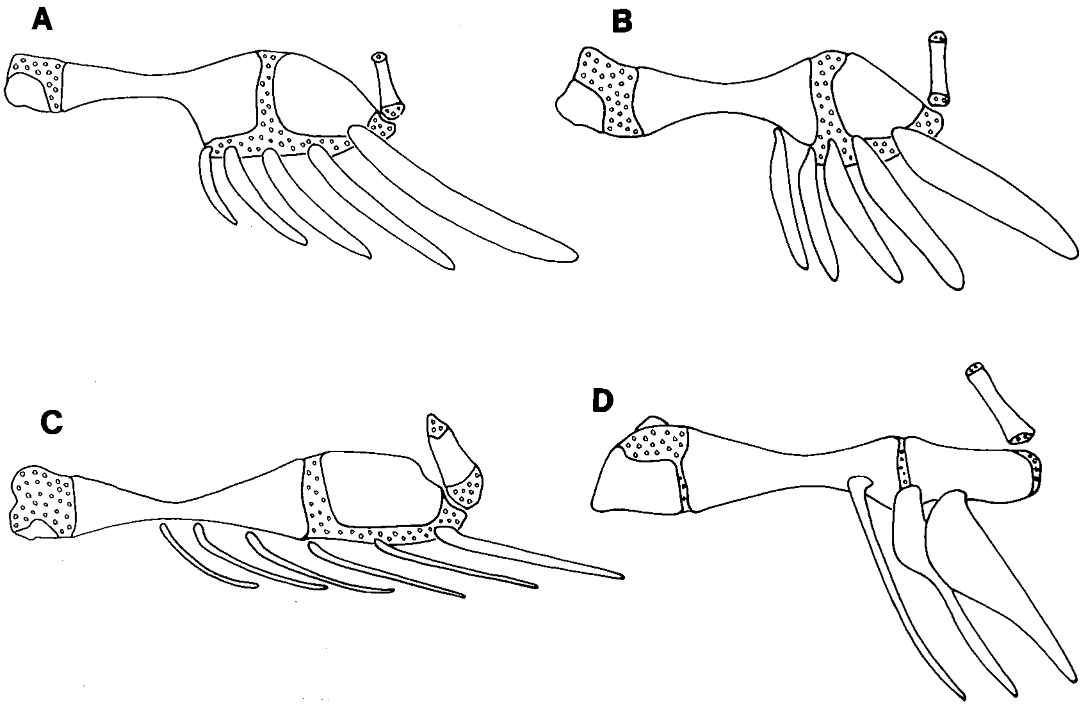

FIGURE 5 Hyoid in galaxioids. Left hyoid bar and branchiostegals, in lateral view, of (A) *Retropinna retropinna;* (B) *Galaxias occidentalis;* (C) *Lovettia sealei;* (D) *Lepidogalaxias salamandroides.* Same specimens as Fig. 3.

primitive, fenestrate type of ceratohyal can be discriminated by the presence of cartilage along the entire dorsal margin, whereas when the fenestra is lost, the dorsal margin is closed by perichondral bone (Fig. 6). The primitive cartilaginous dorsal margin of the ceratohyal is not always associated with an obvious fenestra in the bone, for example, in *Elops, Megalops, Etrumeus,* or *Clupea* (Fig. 6A), and among platytroctids Sazonov (1986, fig. 6) illustrated ceratohyals with a cartilaginous dorsal margin and no fenestra in *Pectinantus* and *Platytroctegen.* Our *Platytroctes* also have a cartilaginous dorsal margin and no fenestra (cf. Sazonov, 1986, fig. 6A). Beyond alepocephaloids, the only other Recent lower euteleosts with a cartilaginous dorsal margin to the ceratohyal are coregonids, where there is also a fenestra (Fig. 6B; Patterson, 1970, fig. 28; Stearley and Smith, 1993, character 90, with the fenestrate condition wrongly coded as derived). The only report of a ceratohyal fenestra in alepocephalids is in *Rinoctes* (Markle and Merrett, 1980; our cleared-and-stained *Rinoctes* lacks the hyoid and gill arches, but an alcohol specimen shows a fenestra). There is a complete cartilage-covered upper margin on the ceratohyal in *Bathylaco, Bathytroctes, Narcetes, Rinoctes, Talismania antillarum* and *T. oregoni,* and *Rouleina attrita* and *R.maderensis,* whereas *R.squamilateratus* and *Bajacalifornia* retain the dorsal notch with cartilage covering the margin of the bone in front of and behind the notch. Other alepocephalids we have seen (including *Talismania aphos;* cf. *T.antillarum* and *T.oregoni* above) have a waisted ceratohyal with the dorsal margin closed by perichondral bone (Fig. 6F). That type of ceratohyal occurs in all esocoids, argentinoids, salmonids (Fig. 6C), and osmeroids. The primitive type of ceratohyal, with a cartilaginous dorsal margin, persists in various neoteleosts (e.g., neoscopelids, many beryciforms, zeiforms, and some percoids).

71. [Begle's 62: Proximal ceratohyal ("epihyal") without (0) or with (1) midlateral foramen. State (1) coded in all osmerids except *Thaleichthys,* although the text implies that the latter should also be coded (1).] The "foramen" is the termination of the groove for the hyoidean artery; it is also present (for example) in *Pantodon, Elops, Megalops, Clupea* (Fig. 6A), and salmonoids (Fig. 6B and 6C) and is primitive for teleosts. We regard state (0) as autapomorphic for *Thaleichthys* (within osmerids) and discard the character.

72. [Begle's 68: Proximal ceratohyal ("epihyal") more than half the length of distal ceratohyal (0) or short, much less than half the length of the distal ceratohyal (1). State (1) coded in galaxiids and *Aplochiton.*] In galaxiids (e.g., Fig. 5B) the proximal ceratohyal is about half the length of the distal, or slightly more. The character is true only of *Aplochiton.*

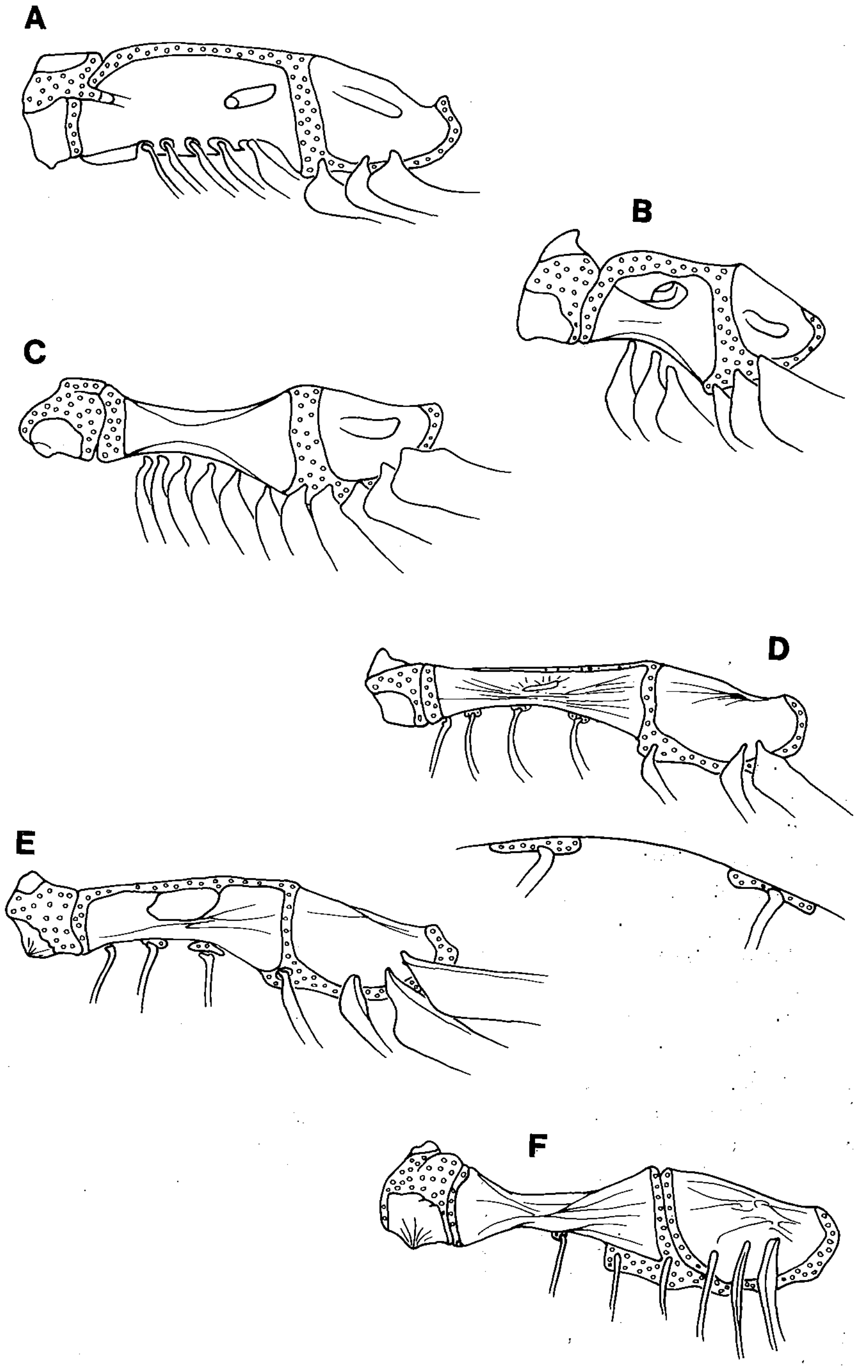

FIGURE 6 Ceratohyals and branchiostegal cartilages. Left hyoid bar, in lateral view, of (A) the clupeid *Clupea harengus*, BMNH 1932.2.15.1, 63 mm SL; (B) the coregonid *Prosopium williamsoni*, BMNH 1892.12.30.340, 81 mm SL; (C) the salmonid *Thymallus thymallus*, BMNH 1970.10.14.3, 70 mm SL; (D) and (E) the platytroctid alepocephaloids (D) *Paraholtbyrnia cyanocephala*, SIO 77-53, 125 mm SL [with (below) a close-up of two branchiostegal cartilages] and (E) *Searsia koefoedi*, SIO 77-38, 115 mm SL; (F) *Alepocephalus tenebrosus*, SIO uncat., 135 mm SL. A, B, and D show the primitive teleostean condition, with the upper border of the distal ceratohyal covered by cartilage and with a foramen (A) or fenestra (B and D) associated with the passage of the hyoidean artery. E shows a more derived condition, in which the fenestra is converted into a notch in the dorsal margin of the bone, though here the notch is still bridged by a strand of cartilage. C and F show the derived condition, typical of most teleosts, in which the distal ceratohyal is a waisted bone with its dorsal margin closed in perichondral bone. Branchiostegal cartilages, found in primitive alepocephaloids, are shown in D–F, with F showing a variant in which the posterior branchiostegal cartilage is continuous with that between the distal and proximal ceratohyals.

73. [Begle's 86: Interhyal elongate and rodlike (0) or short and dumbbell-shaped. State (1) coded in *Argentina, Bathylagus, Opisthoproctus*, and *Glossanodon*.] The character is related to the small mouth and forwardly inclined suspensorium in argentinoids. As described, it is true of argentinids, opisthoproctids, and microstomatids (the last not checked by Begle) but not true of *Bathylagus* (e.g., Kobyliansky, 1986, fig. 10), where the interhyal is as long as the epihyal and no shorter or more waisted than that, for example, of platytroctid alepocephaloids (Sazonov, 1986, fig. 6), *Umbra* (Wilson and Veilleux, 1982, fig. 8) or some galaxioids (Fig. 5). The interhyal is very short, though not always strongly waisted, in primitive salmonoids (e.g., coregonids, *Thymallus*, and *Brachymystax*).

74. [Begle's 87: Small cartilages connecting branchiostegals with hyoid arch absent (0) or present (1). State (1) coded only in *Talismania*.] These cartilages (Fig. 6) are widespread in platytroctids: we have seen them in *Holtbyrnia, Mentodus, Mirorictus, Paraholtbyrnia, Pellisolus, Sagamichthys*, and *Searsia*, but not in *Platytroctes* or *Searsioides*; they are illustrated by Sazonov (1986, figs. 6–8) in all platytroctid genera except *Platytroctes*, including juvenile *Searsioides*. They also occur among alepocephalids in *Bajacalifornia, Bathylaco, Bathytroctes, Leptochilichthys*, and *Rinoctes* and in the osmerids *Mallotus* (on the posterior three of four or five branchiostegals on the distal ceratohyal) and *Hypomesus olidus* (on the second or on the first and second of four branchiostegals on the distal ceratohyal). In *Alepocephalus tenebrosus* (Fig. 6F) a strand of cartilage extends forward along the ventral margin of the ceratohyal as far as the base of the second (of three) branchiostegals on the bone, and there is a separate cartilage at the base of the most anterior branchiostegal. We have not found branchiostegal cartilages in other alepocephaloids we checked (*Leptoderma, Narcetes, Photostylus, Rouleina, Alepocephalus agassizi*, and *Talismania oregoni*).

75. Branchiostegal attachment. In teleosts generally and in lower euteleosts the branchiostegals are normally differentiated into an anterior series inserting on the ventral or internal face of the hyoid bar (ventral or internal branchiostegals of McAllister, 1968) and a posterior series inserting on the external face of the bar (external branchiostegals of McAllister, 1968). These two series are recognizable in all lower euteleosteans except bathylagids and opisthoproctids, where the branchiostegals are all external.

76. [Begle's 82: Opercle extending dorsally above its articulation with the hyomandibular (0) or not (1). State (1) coded in galaxiids, *Lovettia, Aplochiton*, retropinnids, salangids, *Lepidogalaxias*, and all alepocephaloids.] State (1) is not true of *Bathylaco* (Fig. 7J and no. 78 below). The dorsal part of the opercle is also reduced in esocoids (e.g., Wilson, 1984, fig. 9).

77. [Begle's 65: Anterodorsal border of opercle horizontal and without spine (0) or with notch and spine (1) or with deep, narrow notch (2). State (1) coded in *Plecoglossus, Hypomesus, Osmerus*, and *Thaleichthys*; state (2) in *Allosmerus, Mallotus*, and *Spirinchus*.] The anterodorsal border of the opercle is characteristically emarginate in most osmerids (Fig. 7; Klyukanov, 1970, fig. 10; 1975, fig. 10). In our material of the seven genera (Fig. 7) it is unreasonable to regard *Allosmerus, Mallotus*, and *Spirinchus* as having a different condition from the other genera, though if one worked only from Klyukanov's somewhat schematic drawings, that conclusion might be possible. In a blind test where one of us asked the other to sort eight stained opercles, the groups found were *Allosmerus* with *Mallotus*; *Spirinchus* with *Hypomesus pretiosus, Osmerus, Thaleichthys*, and *Plecoglossus*, with the last most divergent; and *H. olidus* (which has an excavation like an inverted keyhole, Fig. 7A) on its own. Other groupings might be detected (Fig. 7), but we see Begle's state (2) only in *Allosmerus* and *Mallotus*. See also no. 78 below.

78. [Begle's 94: Dilatator spine on dorsal margin of opercle absent (0), present (1), or a large spinelike process extending dorsally above opercle (2).] State (1) coded in all alepocephaloids except *Bathylaco*, which has state (2). The character is redundant since it repeats nos. 76 and 77 above (Begle's 65 and 82). When the dorsal part of the opercle is emarginate or reduced the dilatator operculi muscle has to insert somewhere, and there is no difference between the large spine in front of the emargination in osmerids (Fig. 7A–H), *Dolicholagus* (Begle's *Bathylagus*, his 1991, fig. 7) and *Bathylaco* (Fig. 7J), or between the small spine (sometimes merely the dorsal margin of the articular facet, e.g., *Talismania*, Fig. 7K; *Lovettia*, Fig. 4D; *Lepidogalaxias*, Fig. 4E; and *Esox*) in galaxioids, salangids, and other alepocephaloids. If this character were retained, state (2) should be coded in osmerids (duplicating Begle's 65, our 77) and state (1) in galaxioids (duplicating Begle's 82, our 76). We have added *Bathylaco* to character 77 (Begle's 65, state 1) and discarded this character.

79. [Begle's 17: Posterior border of suspensorium rounded/smooth (0) or incised/emarginate (1). State (1) coded in galaxiids, *Aplochiton, Lovettia*, and *Lepidogalaxias*.] The character refers to the serrated or fimbriate margin of the opercle in those fishes, which is particularly deeply incised in *Lovettia* and *Lepidogalaxias* (Fig. 4D and 4E). The margin of the opercle is also

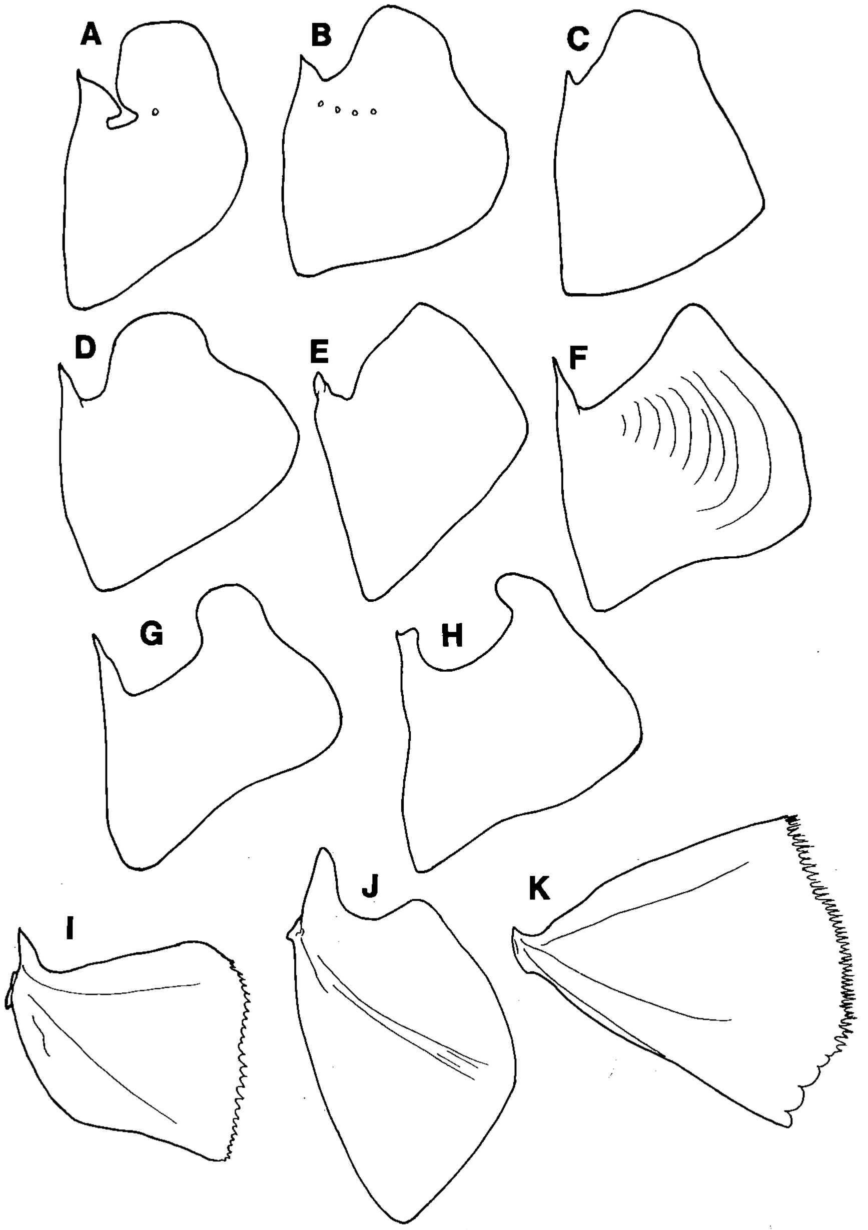

FIGURE 7 Opercles of osmerids and alepocephaloids. Left opercle, in lateral view, of (A) *Hypomesus olidus*, HSU 86-33, 70 mm SL; (B) *H.pretiosus*, HSU 81-87, 55 mm SL; (C) *Plecoglossus altivelis*, BMNH 1984.12.6.16, 63 mm SL; (D) *Osmerus mordax*, HSU 85-46, 75 mm SL; (E) *Spirinchus thaleichthys*, USNM 105639, 110 mm SL; (F) *Thaleichthys pacificus*, USMN 342051, 140 mm SL; (G) *Mallotus villosus*, AMNH 26286, 137 mm SL; (H) *Allosmerus elongatus*, USNM 342050, 90 mm SL; (I) *Pellisolus eubranchus*, SIO 60-287, 95 mm SL; (J) *Bathylaco nigricans*, SIO 64-15, 86 mm SL; (K) *Talismania aphos*, SIO 72-144, 105 mm SL.

fimbriate or incised in most bathylagids (Kobyliansky, 1986, figs. 6–9), and less strongly so in many alepocephaloids, including some platytroctids (Sazonov, 1986, fig. 4), *Alepocephalus*, *Bathytroctes*, *Leptoderma*, *Leptochilichthys*, and *Narcetes* and to some extent *Rouleina* and *Talismania* in Begle's sample. Rather than extend state (1) to all those fishes (in many of which the condition could not reasonably be distinguished from that in *Aplochiton* or some galaxiids), we restrict the derived state to the extremely deep incisions seen in *Lovettia* (Fig. 4D; McDowall, 1969, fig. 3D) and *Lepidogalaxias* (Fig. 4E; Roberts, 1984, fig. 22).

F. Gill Arches

80. [Begle's 106: Basihyal with scattered teeth (0), marginal fangs (1), small teeth on terminus (2), terminal fangs (3), or toothless (4). State (1) coded in salmonoids, galaxiids, *Aplochiton*, *Lovettia*, retropinnids, and all osmerids except *Hypomesus* and *Mallotus*; state (2) in *Glossanodon*; state (3) in *Argentina*; and state (4) in salangids, *Lepidogalaxias*, and all sampled Alepocephaloidea except *Leptochilichthys* (coded ?; the basihyal is absent).] Salangids are wrongly coded since basihyal teeth are present in *Protosalanx* (state 0) and *Salanx reevesi* (a median row) (Nelson, 1970b; Roberts, 1984). Platytroctids are wrongly coded since almost all have basihyal teeth (Matsui and Rosenblatt, 1987, table 1; Begle illustrated them in *Sagamichthys*, 1991, fig. 5), either in a median row or pattern (1). In salmonoids, state (1) is synapomorphous for salmonines (Stearley and Smith, 1993, character 85) since coregonids and *Thymallus* have state (0) (Norden, 1961, pl. 6). *Glossanodon* is polymorphic for states (2) and (4) (Cohen, 1958). Argentinids are the only argentinoids with basihyal teeth (Kobyliansky, 1990, p. 159, fig. 7; Greenwood and Rosen (1971, fig. 19) illustrated a toothed basihyal in the microstomatid *Nansenia* that differs greatly from the toothless bone in our specimens and in Kobyliansky's).

81. Basibranchial dentition. Primitively in teleosts an elongate toothplate covers basibranchials 1–3 (Nelson, 1969a, p. 494; Rosen, 1974, figs. 2–4). Derived states in lower euteleosts are (1) loss of teeth, leaving a toothless dermal bone (Stearley and Smith, 1993, character 89); and (2) loss of both teeth and the dermal bone (Stearley and Smith, 1993, character 88). State (1) occurs in all argentinoids; in all alepocephaloids except platytroctids, where basibranchial teeth are present in most genera (Matsui and Rosenblatt, 1987, table 1), and *Rinoctes* (basibranchial teeth recorded by Markle and Merrett, 1980; confirmed in two USNM specimens); among osmeroids in *Aplochiton*, *Lovettia*, *Lepidogalaxias*, and galaxiids (Rosen, 1974, fig. 5); and among salmonoids in our *Coregonus cylindraceum* (*contra* Stearley and Smith, 1993), *Prosopium*, *Thymallus* (*contra* Stearley and Smith, 1993), and many salmonines. State (2) occurs in salangids (Roberts, 1984). A third derived state is fragmentation ("secondary subdivision," Nelson, 1969a, p. 497) of the basibranchial toothplate, which characterizes esocoids (Rosen, 1974, fig. 1). In salmonids the toothless dermal plate is occasionally divided (*Salvelinus fontinalis* divided in Norden, 1961, pl.6B, but not in Rosen, 1974, fig. 3B and 3C; and *Oncorhynchus keta*, Rosen, 1974, fig. 3E).

82. Toothplate of fourth basibranchial (Bb4). Presence of this toothplate is the single character cited to distinguish esocoids from all other euteleosts (Fink and Weitzman, 1982; Fink, 1984b; Begle, 1992). Patterson and Johnson (1995, p. 25) reviewed the distribution of a Bb4 toothplate in lower teleosts and concluded that the character is questionable; they failed to mention that the toothplate also occurs in percopsiforms (*Amblyopsis*, Rosen, 1962, fig. 13; *Aphredoderus*, Nelson, 1969a, pl. 92, fig. 2; and *Percopsis*, Rosen and Patterson, 1969, pl. 65, fig. 1) and was illustrated by Kobyliansky in the argentinoids *Bathylagichthys* (1986, fig. 11) and *Nansenia* (1990, fig. 8; personal observation), so destroying its validity in distinguishing esocoids.

83. [Begle's 64: First basibranchial unmodified (0) or with ventral cartilaginous vane (1). State (1) coded in retropinnids, osmerids, and all sampled argentinoids and alepocephaloids.] We commented (Patterson and Johnson, 1995, p. 26), noting that Begle's "unmodified" state occurs in argentinids and *Opisthoproctus* (it also occurs in bathylagids). Weitzman's (1974, fig. 75) comparison of the basibranchials in *Spirinchus* and three stomiiforms shows that the latter also have Begle's "derived" state, as do *Elops* (Fig. 8A; Nelson, 1968a, fig. 1) and many clupeoids (e.g., *Chirocentrus*, Fig. 8B; Nelson, 1970a, fig. 5). We see no difference between the configuration in *Argentina* (Fig. 8C) or *Retropinna* (Fig. 8D), both coded (1) by Begle, and in some salmonoids (Figs. 8E–8G), coded (0); *Thymallus* (Fig. 8G) has the "derived" state in much the same form as osmerids (Fig. 8H and 8I) and alepocephaloids (Fig. 8J). If retained, the character would have to be coded (0) in argentinoids and retropinnids but (1) in basal neoteleosts (stomiiforms) and some salmonoids and outgroups. We regard the character as so problematic and subjective that we discard it.

84. [Begle's 97: Basibranchials without (0) or with (1) a narrow median dorsal ridge "separating right and left portions of branchial basket." State (1) coded in all sampled alepocephaloids.] The character originated with Greenwood and Rosen (1971, p. 8) and Rosen (1974, p. 274). Markle (1976, p. 82) wrote, "the sharp medial basibranchial ridge is virtually absent in every alepocephalid [i.e., excluding platytroctids]." *Leptochilichthys* has an extraordinarily deep median keel extending from end to end of the copula and presumably representing a modified toothplate, but we agree with Markle that there is nothing notable in other alepocephalids. In platytroctids, where the basibranchial is normally toothed, the teeth are often arranged longitudinally along a median ridge or crest (Matsui and Rosenblatt, 1987, p. 14). State (1) therefore occurs only in some platytroctids and *Leptochilichthys*.

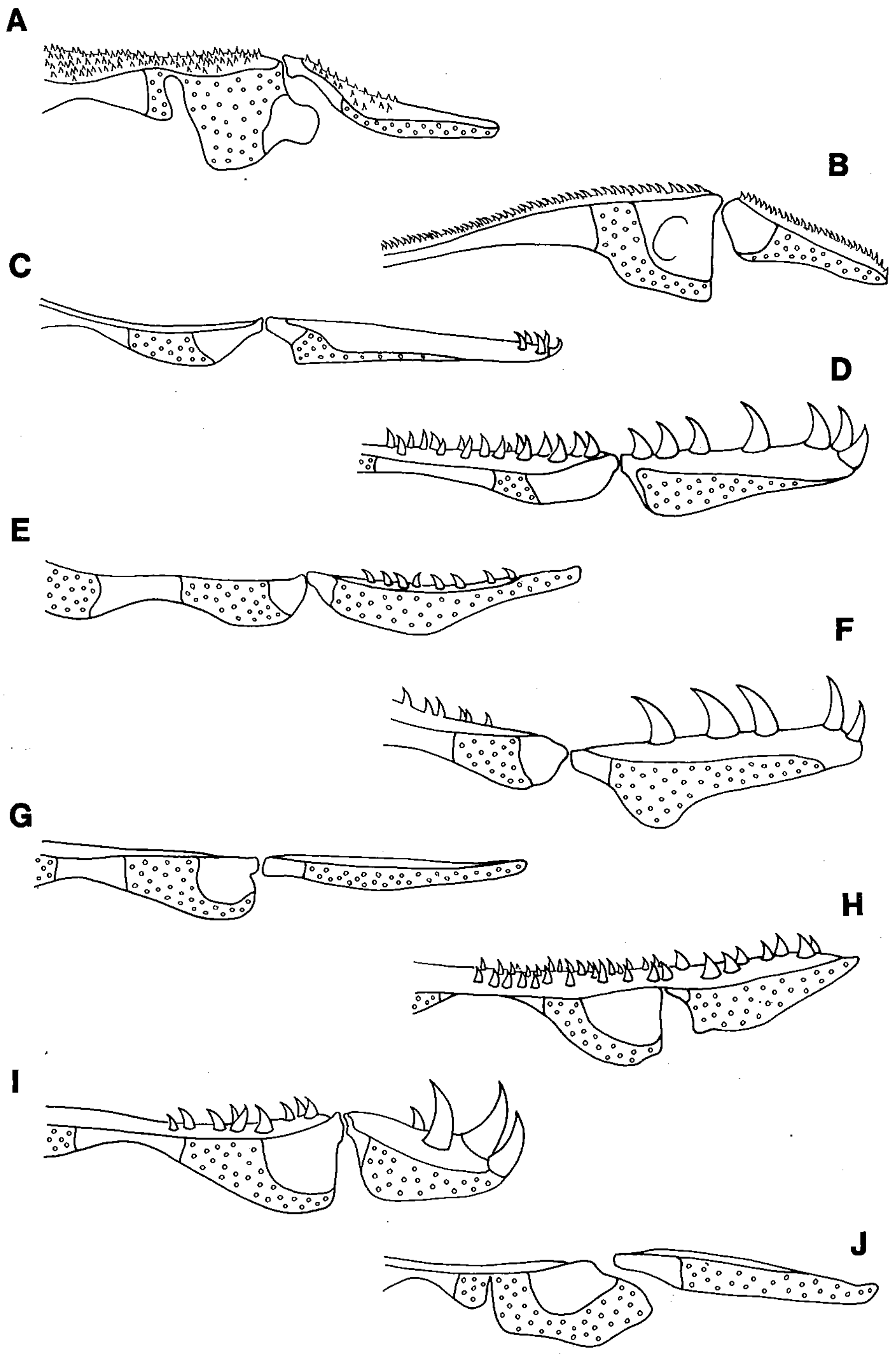

FIGURE 8 Basihyal and first basibranchial, in right lateral view, of (A) *Elops hawaiensis*, BMNH 1962.4.3.1, 69 mm SL; (B) *Chirocentrus dorab*, BMNH 1966.11.16.5, 147 mm SL; (C) *Argentina sphyraena*, USNM 238015, 127 mm SL; (D) *Retropinna retropinna*, BMNH 1964.4.30.19, 83 mm SL; (E) *Stenodus leucichthys*, BMNH 1985.7.16.22, 63 mm SL; (F) *Oncorhynchus clarki*, BMNH 1957.2.20.3, 90 mm SL; (G) *Thymallus thymallus*, BMNH 1970.10.14.3, 71 mm SL; (H) *Hypomesus transpacificus*, BMNH 1984.6.28.11, 65 mm SL; (I) *Osmerus eperlanus*, BMNH 1971.2.16.303, 63 mm SL; (J) *Alepocephalus tenebrosus*, SIO uncat., 135 mm SL.

85. [Begle's 49: Fourth hypobranchial absent (0) or present (1). State (1) coded only in salangids.] The character is from Roberts (1984). Like fusion of the hyomandibula and quadrate (no. 43), this is a larval character persisting into maturity only in salangids. We have observed separate fourth hypobranchials in larval *Coregonus, Salmo, Hypomesus, Osmerus,* and *Galaxias.*

86. [Begle's 79: Fourth ceratobranchial (Cb4) unmodified (0) or much wider in dorsal view than ceratobranchials 1–3, sometimes with distal end expanded (1). State (1) coded in all sampled argentinoids and alepocephaloids.] Begle (1991, fig. 6) illustrated Cb4 broad throughout its length in *Bathylagus* and CB4 expanded distally in the platytroctid *Sagamichthys.* Kobyliansky (1990, fig. 8) illustrated the broad Cb4 in other bathylagids but also showed that it does not occur in argentinids (*Argentina* and *Glossanodon*) or microstomatids. Among alepocephalids, *Alepocephalus, Bathytroctes,* and *Leptoderma* have the platytroctid condition, but other alepocephaloids do not. There appear to be two different states here, recoded (1) for the bathylagid configuration and (2) for the platytroctid.

87. [Begle's 80: Fourth gill arch unmodified (0) or with fleshy membrane along joint of ceratobranchial and epibranchial, partitioning the crumenal organ from the orobranchial chamber (1). State (1) coded in all sampled argentinoids and alepocephaloids.] The membrane is a continuation of esophageal tissue and spans the gap between the fourth arch and the fifth that is created by the accessory cartilage (no. 90, below). No comment.

88. Dentition of fifth ceratobranchial (Cb5). Among lower euteleosts, Cb5 is toothless in bathylagids, microstomatids (Kobyliansky, 1990), opisthoproctids, and in the alepocephalid *Photostylus.* In alepocephaloids other than *Photostylus,* the dentition on Cb5 varies. In *Bajacalifornia* and *Narcetes* there is a longitudinal band of teeth, a pattern that we take to be primitive by comparison with outgroups (e.g., Nelson, 1969a, pl. 85). One derived state is a single longitudinal row of teeth, seen in *Bathylaco.* An alternative derived state is a single marginal row of teeth on a fanlike medial expansion of the bone, seen in platytroctids, *Alepocephalus, Bathytroctes, Leptochilichthys, Leptoderma, Rinoctes, Rouleina,* and *Talismania.*

89. [Begle's 69: Fifth ceratobranchial without (0) or with bony anterior laminar extension, close to medial margin (1). State (1) coded in galaxiids and *Lepidogalaxias.*] In *Lepidogalaxias,* there is a distinctive anteriorly directed process from the anterolateral margin of Cb5, presumably serially homologous with successively larger ventrally directed processes on Cb1–4. In galaxiids, we have seen nothing similar in any of the species examined and the character becomes autapomorphous.

90. [Begle's 78: Accessory cartilage between fifth ceratobranchial and epibranchial absent (0) or present (1). State (1) coded in all sampled argentinoids and alepocephaloids except *Bathyprion* and *Bathylaco.*] The character is from Greenwood and Rosen (1971), and Markle (1976) reported the cartilage absent in *Bathyprion* and *Bathylaco. Opisthoproctus* was wrongly coded (1) (Greenwood and Rosen, 1971, fig. 6), despite comments in Begle's text (1992, p. 356) on alternative evaluations for "absence of an accessory cartilage in opisthoproctids." Like Greenwood and Rosen (1971), we found no accessory cartilage in the opisthoproctids *Opisthoproctus* and *Rhynchohyalus,* or in *Macropinna,* but found it present in *Bathylychnops* and on one side in our *Dolichopteryx.* It is absent in the alepocephalid *Photostylus.*

91. [Begle's 39: Uncinate process on first epibranchial present (0) or absent (1). State (1) coded in galaxiids, *Lovettia,* and *Aplochiton.*] Absent also in *Lepidogalaxias.* In this and the succeeding characters referring to uncinate processes (nos. 92–94, 103–107) salangids should be coded as (?) since there is no ossification and hence no way of recognizing an uncinate process, which can be discriminated from an extension of the cartilaginous head of the structure only once it ossifies.

92. [Begle's 40: Uncinate process on second epibranchial present (0) or absent (1). State (1) coded in galaxiids, *Lovettia,* and *Aplochiton.*] It is absent also in all alepocephaloids except *Bathylaco* and *Bathytroctes* (we could not check *Bathyprion* or *Rinoctes*) and in most bathylagids (Kobyliansky, 1986, fig. 12A; 1990, fig. 9I,K; personal observation), but present in *Melanolagus* (Kobyliansky, 1986, fig. 12C).

93. [Begle's 41: Uncinate process on third epibranchial present (0) or absent (1, only in *Lepidogalaxias*).] No comment.

94. [Begle's 91: Uncinate process on fourth epibranchial (Eb4) present (0) or absent (1). State (1) coded in all sampled argentinoids and alepocephaloids except *Argentina, Glossanodon,* and some platytroctids.] The platytroctid feature may refer to Greenwood and Rosen's (1971) figure of *Searsia koefoedi* or to Sazonov's (1986, p. 70) report of a well-differentiated process in *Barbantus;* we have not been able to study *Barbantus* but have found no process in two cleared-and-stained *S. koefoedi* (probably those used by Matsui and Rosenblatt, 1987, p. 23, who also failed to find it). It might become distinct from the cartilaginous posterodorsal margin in large specimens. Greenwood and Rosen (1971, fig. 4) illustrated an uncinate process

on Eb4 in *Glossanodon pygmaeus*; it is lacking in our *G.polli* and *G.struhsakeri* and in Kobyliansky's (1990, fig. 9) *G.danieli*. The process is absent in *Lepidogalaxias, Hypomesus, Mallotus,* salmonoids, galaxiids, *Aplochiton, Lovettia,* and in our retropinnids (though shown in *Stokellia* by Rosen, 1974, fig. 16E); Begle wrongly coded it as present in all of these. As we argue below, Begle's outgroups and neoteleosts should also be coded for absence.

Rosen (1974, p. 278) gave a careful account of fourth epibranchial configuration in lower teleosts. He noted that the uncinate process is absent in osteoglossomorphs, clupeomorphs, *Chanos,* the ostariophysans he sampled, and *Elops* but is present in other elopomorphs. He inferred that the process might be a derived feature shared by elopomorphs and euteleosts, independently lost in *Elops* and in various euteleostean lineages, but wrote (p. 279) "It would be instructive to attempt a study of this bone in some of the fishes that appear to be primitive sister groups to some or all living forms, for example, in ichthyodectids and in some of the fishes called leptolepids." We checked Eb4 of Jurassic pholidophorids (*Pholidophorus bechei, P.germanicus,* and *P.macrocephalus*) and leptolepids (*Tharsis dubius* and the "Callovian *Leptolepis*" of Patterson, 1975), and it was checked in the Cretaceous ichthyodectiform *Cladocyclus* by Patterson and Rosen (1977, p. 103). In all, there is no uncinate process, as in osteoglossomorphs, *Elops, Chanos,* and clupeomorphs [Begle's outgroups should therefore be coded for absence]. The uncinate process of Eb4 is a derived feature, independently developed in non-elopid elopomorphs and at some level or levels within euteleosts.

Homology of the elopomorph process is established by comparison between *Elops* and *Megalops*. In *Elops,* Nelson (1968b, fig. 6) illustrated an "interarcual cartilage" connecting the tip of the uncinate process of Eb3 with the head of Eb4 (there is no uncinate process); we confirmed his observations and found a corresponding but smaller interarcual cartilage in *Megalops,* where it lies between the articulating tips of the uncinate processes of Eb3 and Eb4. The elopomorph uncinate process therefore develops from the head (anterior end) of Eb4, as one would infer from its shape. Observations of small *Esox* show that the uncinate process develops in the same way, by separation from the head of Eb4. We believe that the uncinate process of Eb4 in osmerids has a different origin; it, and Begle's coding of this character, is discussed with the following character.

95. [Begle's 50: Levator process on fourth epibranchial wide, with width at distal margin up to half the length of the underlying epibranchial (0) or very narrow, narrower than the width of the epibranchial (1). State (1) coded in *Allosmerus, Hypomesus, Spirinchus, Mallotus, Argentina, Bathylagus, Glossanodon,* and *Opisthoproctus* (the latter said to have (0) in Begle's text).] The term levator process applied to the fourth epibranchial (Eb4) seems to originate with Rosen (1974, p. 278), who first differentiated "a distinct process" from the "elevation" found, for example, in *Elops, Hiodon,* and *Thymallus,* where there is continuity between the cartilaginous margin of the elevation and the posterior articular surface of the bone (Nelson, 1967, fig. 1). Later in the same paper, Rosen (1974, p. 279) equated the "reflected dorsal section" or elevation of Eb4 in *Elops* and *Megalops* with the levator process, but this loses a real distinction, and we prefer to restrict the definition to a distinct and separate process on which the fourth external levator muscle inserts. So defined, there is no levator process in osteoglossomorphs, most elopomorphs, and clupeomorphs (Nelson, 1967, figs. 2 and 3), or in salmonoids (Rosen, 1974, fig. 9), alepocephaloids (Greenwood and Rosen, 1971, figs. 1–3), opisthoproctids (Greenwood and Rosen, 1971, fig. 6; Stein and Bond, 1985, fig. 5), retropinnids (Rosen, 1974, fig. 16), galaxiids (Rosen, 1974, fig. 10), or *Lepidogalaxias* (Rosen, 1974, fig. 14). All those fishes also lack an uncinate process on Eb4, except for non-elopid elopomorphs, where the process segments from the anterior tip of Eb4 (no. 94, above).

Among esocoids, esocids have lost the fourth external levator (Holstvoogd, 1965, also personal observation) and there is no levator process or posterior elevation on Eb4, but there is an uncinate process (no. 95, above). In umbrids there is a fourth levator muscle in *Umbra* and *Dallia,* but none in *Novumbra* (personal observation). Rosen (1974, fig. 8) reported a "relic" levator process in one specimen of *Umbra;* in our material, the muscle inserts on the posterior elevation and there is no levator process. Other umbrids (Rosen, 1974, figs. 8 and 15) lack the posterior elevation (in *Dallia* the fourth levator inserts on the broadened posterior part of Eb4) but have an uncinate process, presumably developed from the front end of Eb4, like that of *Esox* (above).

A distinct levator process on Eb4 is present in *Albula* and *Halosaurus* among elopomorphs; in argentinid, microstomatid, and bathylagid argentinoids (Greenwood and Rosen, 1971, figs. 4–6; Kobyliansky, 1986, fig. 12; 1990, fig. 9); in all osmerids (Rosen, 1974, fig. 16), in some clupeomorphs (Nelson, 1967, figs. 2 and 3); in *Chanos* and some ostariophysans (Nelson, 1967, fig. 1; Fink and Fink, 1981, fig. 13); in most lower neoteleosts (consistently in stomiiforms and myctophiforms, variable in aulopiforms); and among examined acanthomorphs in *Polymixia* and percopsiforms (Pat-

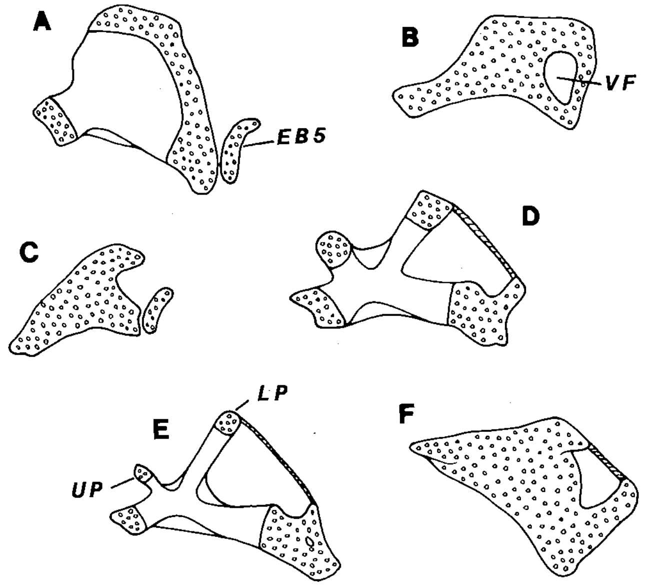

FIGURE 9 Epibranchial configuration in osmeroids. Fourth and fifth epibranchials, medial view of right side, in (A) *Prototroctes maraena,* BMNH 1984.10.3.1, 74 mm SL; (B) *Lovettia sealei,* BMNH 1937.8.22.1, 41 mm SL; (C) *Osmerus* sp., HSU uncat., 29 mm larva; (D) *Osmerus eperlanus,* BMNH 1971.2.16.303, 63 mm SL; (E) *Thaleichthys pacificus,* USNM 342051, 136 mm SL; (F) *Salangichthys microdon,* BMNH 1996.2.6.1, 83 mm SL. Abbreviations: EB5, fifth epibranchial; LP, levator process of fourth epibranchial; UP, uncinate process of fourth epibranchial; VF, vascular foramen for efferent artery, assumed to be enclosed by distal and proximal fusion between fourth and fifth epibranchials.

terson and Rosen, 1989, fig. 13). In all those fishes (except some clupeomorphs), the levator process meets Begle's description—its tip is narrower than the body of Eb4. In Rosen's (1974, fig. 16) illustrations of the process in osmerids, the narrowest is in *Plecoglossus,* coded (0) by Begle. In our material, *Hypomesus olidus* and *H.transpacificus* agree with Rosen's *H.olidus* (1974, fig. 16D), but in *H.pretiosus* the dorsal and ventral tips of the posterior processes are in contact and are fused in one specimen. In *Thaleichthys,* the only osmerid genus not illustrated by Rosen (*Osmerus* is in Greenwood and Rosen, 1971, fig. 7), Fig. 9E shows that Eb4 agrees exactly with that of *Spirinchus* (Rosen, 1974, fig. 16A). Salangids are a special case because Eb4 does not ossify so that (as with uncinate processes, no. 91 above) it is not easy to discriminate a distinct levator process from an extension of the cartilaginous posterior margin of Eb4. Rosen's (1974, fig. 16G) illustration of Eb4 in the salangid *Salangichthys microdon* is very different from our material of that species (Fig. 9F), in which Eb4 resembles Rosen's illustration of *Mallotus* (1974, fig. 16C) except for lack of ossification. In *Protosalanx* Eb4 is like our *Salangichthys* (Fig. 9F), whereas in *Salanx* it is like Rosen's (1974, fig. 16G) "*Salangichthys,*" and in *Neosalanx* it is similar but the upper arm of Eb4 is shorter. Because Eb4 in salangids is so similar in shape to that of osmerids, we regard the levator process as present in salangids. Begle's data are recoded with (1) (presence of levator process) for neoteleosts, osmerids, and salangids, (0) (absence) for *Opisthoproctus;* and (2) for the condition in esocoids.

Among the lower euteleosts with a levator process on Eb4, there is also an uncinate process, articulating with that of Eb3, in *Argentina* and some *Glossanodon* (Greenwood and Rosen, 1971, fig. 4), the bathylagid *Bathylagichthys* (Kobyliansky, 1986, fig. 12), and the osmerids *Osmerus, Plecoglossus, Spirinchus,* and *Thaleichthys* (Fig. 9; Rosen, 1974, fig. 16). In *Allosmerus,* Rosen (1974, fig. 16B) illustrated a specimen in which the cartilaginous head of the levator process is wide and partially separated into what he labelled as uncinate and levator processes; in our *Allosmerus,* three out of six specimens show uncinate and levator processes separated by bone. This, and the configuration in other osmerids, indicates that the osmerid uncinate process of Eb4, wherever it occurs, is segmented from the levator process. It is therefore nonhomologous with the uncinate process in elopomorphs and *Esox,* which is segmented from the anterior tip of Eb4. We lack developmental information on argentinoids but guess from the configuration of Eb4 that the uncinate process, where it occurs, also segments from the anterior tip of Eb4.

The levator process on Eb4 is directed posteriorly and has no articulation or connection with the uncinate process of Eb3. This is so in ostariophysans (e.g., Rosen, 1973, fig. 3; Fink and Fink, 1981, fig. 13), argentinoids (Kobyliansky, 1990, fig. 9), the osmerids *Hypomesus* and *Mallotus* (Rosen, 1974, fig. 16), stomiiforms (Fink and Weitzman, 1982, fig. 11), and various aulopiforms and myctophiforms (Baldwin and Johnson, in this volume; Stiassny, in this volume). In *Aulopus* (Rosen, 1973, fig. 1) and *Parasudis* there is an uncinate process on Eb4 that approaches but does not directly articulate with that of Eb3. In acanthomorphs (e.g., Rosen, 1973, figs. 82–101; Rosen and Patterson, 1990, figs. 30–50) Eb4 has an uncinate process that articulates with and is tightly bound to the uncinate process of Eb3. In *Polymixia* and percopsiforms there is also a levator process on which the fourth levator muscle inserts; in *Aulopus, Parasudis,* and other acanthomorphs the muscle inserts posterior to the uncinate process.

To sum up on the distribution of levator and uncinate processes of Eb4, the levator process is a derived feature developed, presumably independently, within elopomorphs, clupeomorphs, ostariophysans, argentinoids, osmerids, and neoteleosts. Loss of a separate levator process appears to be a synapomorphy of Acanthopterygii, although it may occasionally occur secondarily within percomorphs (e.g., *Pomadasys* and *Lobotes*, Rosen and Patterson, 1990, figs. 7C and 42A). An uncinate process segments off from the levator process in some osmerids. An uncinate process characterizes acanthomorphs. Begle's character 91 (our 94, above), conflated two different kinds of uncinate process: the esocoid or argentinoid type, segmented from the head of Eb4; and the osmerid type, segmented from the levator process. It should be coded with (0) for absence of the uncinate process, (1) for the esocoid/argentinoid type [with (B) for polymorphism in *Glossanodon*], and (2) for the osmerid [with (B) for polymorphism in *Allosmerus*].

96. [Begle's 92: Fifth epibranchial (Eb5) less than half the length of the fourth (0) or almost as long as the fourth (1). State (1) coded in *Bathylagus* and *Opisthoproctus*.] Opisthoproctids (Greenwood and Rosen, 1971, fig. 6; Stein and Bond, 1985, fig. 5) show an elongate Eb5, as does the microstomatid *Nansenia* (Greenwood and Rosen, 1971, fig. 5B; Kobyliansky, 1990, fig. 9; in *Microstoma* the cartilage is partially fused to Eb4). In bathylagids (Greenwood and Rosen, 1971, fig. 6B; Kobyliansky, 1986, fig. 12; 1990, fig. 9) Eb5 varies in length, and in *Bathylagichthys* and *Leuroglossus* it is proportionally no longer than in argentinids. As described the character is autapomorphous for *Opisthoproctus*; if differently phrased it might be a feature of argentinoids but would merely reflect another aspect of the crumenal organ, already coded as two characters (nos. 87 and 90).

97. [Begle's 59: Fifth epibranchial separate (0) or fused to fourth, forming circular foramen for efferent artery (1). State (1) coded in galaxiids, *Lovettia*, *Aplochiton*, and salangids.] There are two different patterns, illustrated in Rosen (1974, figs. 10 and 16), Roberts (1984, figs. 14–17) and Fig. 9. In the galaxiid/aplochitonid pattern, an enclosed vascular foramen, as in *Aplochiton* (Rosen, 1974, fig. 10), *Lovettia* (Fig. 9B), and most galaxiids, is apparently formed by ontogenetic fusion between Eb4 and Eb5, with fusion initiated at the upper ends of the structures (as in Rosen, 1974, fig. 10A, *Galaxias divergens*, and on one side of our *G.fontanus*). In salangids (Fig. 9F), as in adult osmerids (Fig. 9D and E), there is a distinct levator process on Eb4, and a vascular notch is formed by approximation of the levator process and the upper end of Eb5, which fuses ontogenetically to Eb4 at its lower end. These states should be distinguished [(1) for the galaxiid/aplochitonid condition, (2) for the osmerid/salangid condition]. Among osmerids, Eb5 fused to Eb4 at its lower end [state (2)] is shown in *Thaleichthys* and *Osmerus* in Fig. 9 and illustrated by Rosen (1974, fig. 16) in *Allosmerus*, *Hypomesus*, *Mallotus*, and *Spirinchus*. There is a free Eb5 in *Plecoglossus* (Rosen, 1974, fig. 16), but that shown in *Osmerus eperlanus* by Greenwood and Rosen (1971, fig. 7) does not exist in our material except in larvae (Fig. 9C); adult *O.eperlanus* and *O.mordax* both show the condition in Fig. 9D. Among retropinnids, Rosen (1974) illustrated Eb5 fused at its lower end in *Retropinna* and a free Eb5 in *Stokellia*; our material agrees and shows a free Eb5 in *Prototroctes* (Fig. 9A). *Lepidogalaxias* lacks Eb5 and a vascular foramen and so should be coded as (?). In esocoids, there is no Eb5 or vascular foramen in esocids, *Dallia*, and *Novumbra* (Rosen, 1974, fig. 8), but in *Umbra* Rosen illustrated a free Eb5 enclosing a vascular notch, and our specimens confirm the condition. Esocoids should therefore be coded (B), indicating polymorphism, or (?).

98 and 99. Suprapharyngobranchials. Nelson (1968b) reported a suprapharyngobranchial on the first gill arch (Spb1, no. 98) in *Alepocephalus* and wrote that a second suprapharyngobranchial (Spb2, no. 99) occurs among teleosts only in Elopidae. Spb2 is also present in *Megalops*. Markle and Merrett (1980) reported Spb2 in *Rinoctes* (we disregard their third suprapharyngobranchial; it lies in the wrong position, cf. Nelson, 1968b, p. 137). We find Spb1 and Spb2 in several platytroctids (*Holtbyrnia*, *Mirorictus*, *Paraholtbyrnia*, and *Pellisolus*) and in the alepocephalids *Narcetes*, *Rouleina*, and *Talismania*. Spb1 only is present in the platytroctids *Platytroctes*, *Searsia*, and *Searsioides* and in the alepocephalids *Alepocephalus*, *Bajacalifornia*, and *Bathylaco*. *Bathytroctes*, *Leptochilichthys*, *Leptoderma*, and *Photostylus* have no suprapharyngobranchials, as do argentinoids and other lower eutelosts.

100. Pharyngobranchial 1 (Pb1). Pb1 is primitively ossified in teleosts. It is cartilaginous in bathylagids and absent in microstomatids (Kobyliansky, 1990) and *Lepidogalaxias*. In esocoids, Pb1 is conical and its tip is closed in bone, not covered by cartilage, a derived condition that we have found elsewhere only in *Glossanodon*, where the bone is more elongate.

101. Articulation between Pb1 and epibranchials. In osmeroids the pattern varies. We take the primitive condition to be Pb1 articulating with the anterior tip of Eb1, as in *Lepisosteus*, *Amia*, *Hiodon*, *Elops*, argentinids, etc. (Nelson, 1968b). Among osmeroids, this is found in northern taxa—osmerids—and salangids. In southern osmeroids (retropinnids, *Aplochiton*, *Lovettia*, *Lepidogalaxias*, and galaxiids) Pb1 articulates with the lateral surface of Eb1, except in *Lepidogalaxias*, where Pb1 is absent. Among salmonoids, coregonids and *Thymallus* have a broad-based Pb1, articulating

with the tips of both Eb1 and Pb2. In salmonines Pb1 articulates with the lateral surface of Eb1 (Rosen, 1974, fig. 11), as in southern osmeroids. In all examined alepocephaloids except *Leptoderma* and *Photostylus* Pb1 is extremely broad-based and articulates with both Eb1 and Pb2. In *Photostylus* Pb1 is small and articulates only with Eb1; *Leptoderma* lacks Pb1. In esocids Pb1 articulates with both Eb1 and Pb2, whereas in umbrids it usually articulates only with the tip of Pb2; in one *Umbra* its base is broad and also articulates with Eb1.

102. Toothplate of pharyngobranchial 2 (Pb2). Pb2 primitively carries a toothplate in teleosts. Among lower euteleosts the toothplate is absent in esocoids, all argentinoids (Argentinidae, Bathylagidae, Microstomatidae and Opisthoproctidae); the alepocephalids *Alepocephalus, Bajacalifornia, Bathylaco, Bathyprion* (Markle, 1976), *Bathytroctes, Binghamichthys, Leptoderma, Narcetes, Photostylus,* and *Rouleina;* and all salmonoids except *Coregonus* and *Stenodus.*

103. [Begle's 43: Uncinate process on second pharyngobranchial present (0) or absent (1). State (1) coded in galaxiids, *Lepidogalaxias, Aplochiton,* retropinnids, and salangids.] It is also absent in *Lovettia.*

104. [Begle's 45). Uncinate process on second pharyngobranchial directed laterally or caudally (0) or directed anteriorly (1). State (1) coded in all osmerids.] Taxa lacking the process (no. 103 above) are all wrongly coded (0) rather than (?). As with no. 107, below, we found that distinguishing the two states is often subjective. In our judgment, among Begle's sample the process is also anterolaterally directed (as in osmerids) in salmonoids, as it is in *Argentina, Glossanodon,* and *Bathylagus* (e.g., Kobyliansky, 1990, fig. 9). It is anterolaterally directed in *Elops* and microstomatids but laterally directed in *Megalops,* esocoids, and opisthoproctids. In alepocephaloids, the process is directed dorsally rather than laterally; in some alepocephaloids its orientation is anterodorsal and in others dorsolateral. With these problems in evaluating the character, we discard it.

105. Toothplate of pharyngobranchial 3 (Pb3). Pb3 primitively carries a toothplate in teleosts. Among sampled lower euteleosts, the toothplate is absent in all argentinoids (Argentinidae, Bathylagidae, Microstomatidae, and Opisthoproctidae) and in the alepocephalids *Alepocephalus tenebrosus* and *Photostylus.*

106. [Begle's 42: Uncinate process on third pharyngobranchial present (0) or absent (1, only in *Lepidogalaxias*).] It is absent also in our *Retropinna, Lovettia,* and some galaxiids (e.g., *Galaxias maculatus, G. fontanus,* and *G. zebratus*).

107. [Begle's 44: Uncinate process of third pharyngobranchial not extending over second epibranchial (0) or extending well over body of that bone (1). State (1) coded in all osmerids except *Hypomesus.*] As coded by Begle, the derived state distinguishes all osmerids except *Hypomesus* from other osmeroids and outgroups. We could not confirm the implied difference in length or orientation of the uncinate process of PB3 in direct comparisons of three species of *Hypomesus* with other osmerid genera, and although the uncinate process is longer in osmerids than in retropinnids, it is as long and has the same orientation over Eb2 in *Argentina* and various alepocephaloids, for example. Taxa lacking the process (no. 106) were wrongly coded (0) rather than (?) by Begle. Character was discarded.

108. [Begle's 47: Third pharyngobranchial with narrow anterior extension, reaching first pharyngobranchial (0), or without anterior extension (1). State (1) coded in galaxiids, *Lepidogalaxias, Lovettia,* retropinnids, and salangids.] By "reaching" Pb1 we assume that Begle meant Pb3 extends forward almost to the anterior tip of Pb2, as illustrated by Rosen (1974, figs. 11 and 12) in *Salmo* and *Hypomesus.* That condition occurs in all osmerids and in *Aplochiton,* argentinids, and alepocephaloids. Begle's state (1), "without anterior extension," is true, for example, of salangids (Roberts, 1984, figs. 14–16) and *Lepidogalaxias* (Rosen, 1974, fig. 15), though the configuration is very different in the two. It is not true of retropinnids or some galaxiids (e.g., Rosen, 1974, figs. 11C and 12A), where Pb3 has an anterior extension alongside about two-thirds of Pb2. We code the retropinnid state as "intermediate" (1) and recode Begle's state (1) as (2). Some galaxiids (e.g., *Galaxias fasciatus*) have state (0). *Opisthoproctus* has the intermediate state (1), as do other opisthoproctids, microstomatids, and some bathylagids. In esocoids the tip of Pb3 is broad and spatulate (Rosen, 1974, fig. 15); we assess *Esox* as having state (2) and *Umbra* state (0).

109. Upper pharyngeal toothplates (UP4 and UP5). Primitively in teleosts there are two principal upper pharyngeal toothplates (Nelson, 1969a; Johnson, 1992). UP4 is absent and UP5 is minute in bathylagids, microstomatids, and opisthoproctids (UP5 is absent in *Macropinna* and *Opisthoproctus*), and UP4 is absent in the alepocephalid *Photostylus* and in all salmonoids (see below). Identification of the single toothplate in most osmeroids (as either UP4 or UP5) is problematic (see below). In *Lovettia* both UP4 and UP5 are absent, and in *Aplochiton* and galaxiids the toothplate is fragmented, into four small toothplates in *Aplochiton* and into two to four in galaxiids (e.g., Rosen, 1974, figs. 11B and 11C; there is one toothplate in our *G.paucispondylus*).

Esocoids are unique among lower euteleosts in having lost UP5 but retained a large UP4, a condition that

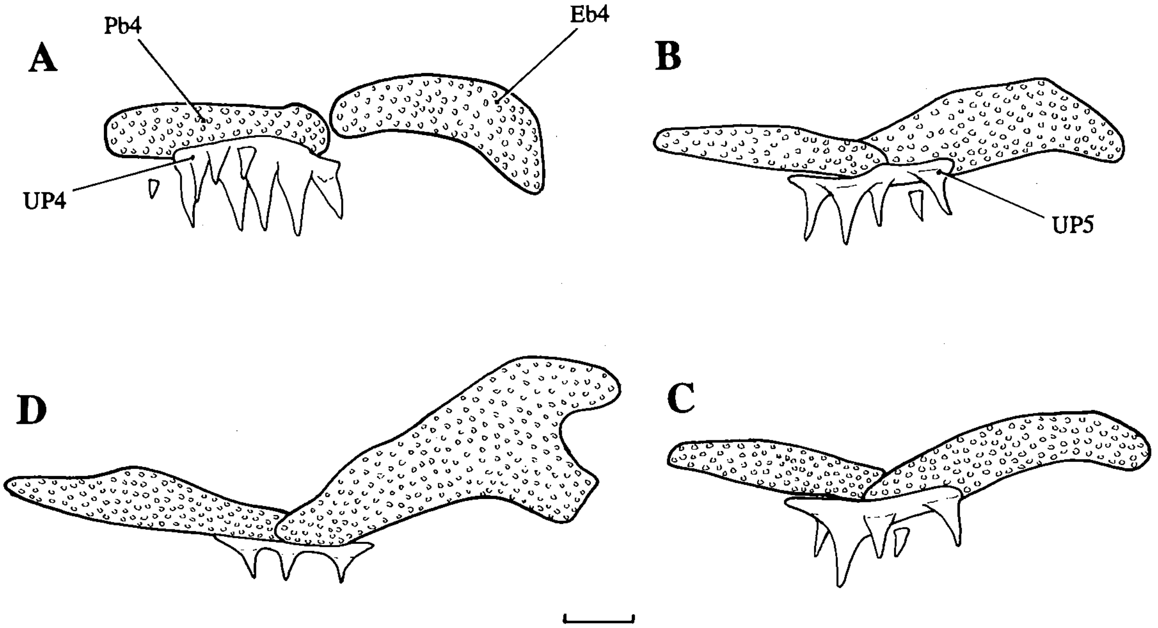

FIGURE 10 Upper pharyngeal toothplate (UP4 or UP5) and fourth pharyngobranchial (Pb4) and epibranchial (Eb4) in larvae. (A) *Esox americanus*, ROM 24422, 15 mm NL, lateral view of left side. (B) *Coregonus clupeaformis*, ROM 68375, 17 mm SL, same view as A. (C) as B, medial view of right side. (D) *Hypomesus* sp., USNM 340198, 33 mm SL, same view as C. Scale bar: 0.1 mm

we previously believed to be unique to ctenosquamates (Johnson, 1992). We base the identification of the toothplate on larval *Esox americanus* (Fig. 10A), where it develops in close association with the ventral surface of Pb4 rather than the tip of Eb4 (cf. Johnson, 1992, fig. 8). In salmonoids, larvae of *Coregonus* (Figs. 10B–10C) indicate by the same criterion that the single toothplate is UP5. In osmeroids the situation is ambiguous. Larval *Hypomesus* (Fig. 10D) suggest that the single toothplate is UP5 because it originates at the tip of Eb4, rather than farther forward, where UP4 originates in *Esox* and in euteleosts with both UP4 and UP5 (Johnson, 1992, fig. 8A). In our larval *Osmerus* there is a single tooth beneath the junction of Pb4 and Eb4, implying UP5, as in *Hypomesus*. In our larval *Mallotus*, there are three separate toothplates, with two beneath Pb4 and one, the smallest, beneath Eb4. In adult *Mallotus* there is usually a single toothplate, but occasionally there are two, one beneath Pb4 and one beneath the junction of Pb4 and Eb4. In our larval galaxiids the single tooth is beneath Pb4, implying UP4, but in adult galaxiids there are two or more toothplates, variable in position. Larval retropinnids might help to resolve the situation, but our assessment is that primitively there is a single toothplate in osmeroids, that it is PB5, and that the ambiguities described above are due to secondary subdivision of the toothplate.

110. [Begle's 54: Retractor dorsalis absent (0) or present (1). State (1) coded in neoteleosts and *Lepidogalaxias*.] Johnson (1992, p. 11) commented further on this.

111. [Begle's 81: Gill rakers on fourth and fifth arches unmodified (0) or expanded/elongate (1). State (1) coded in all sampled argentinoids and alepocephaloids.] We believe that Begle's coding of this character is based on misreading of Greenwood and Rosen (1971) rather than attributes of specimens. In discriminating the crumenal organ of alepocephaloids from that of argentinoids, Greenwood and Rosen (1971, pp. 9, 14) described the gill rakers in the former as broad-based and toothed and in the latter as long, slender, and toothless. However, these are general descriptions of all the gill rakers in alepocephaloids and argentinoids, not just those on the fourth and fifth arches. In argentinids and most alepocephalids, the gill rakers of the fourth and fifth arches are in no way differentiated from those of more anterior arches. In bathylagids, microstomatids, and opisthoproctids the rakers of the fourth and fifth arches are much longer than those on the second and third, and resemble those on the first arch. In some alepocephaloids the rakers on the upper part of the fourth and fifth arches may be slightly larger or more close-packed than those on the lower part of the arches, but there is no general character matching Begle's description.

The derived state, differentiation of the fourth and fifth arch rakers, is restricted to *Bathylagus* and *Opisthoproctus* in Begle's sample.

112. [Begle's 101: Gill rakers toothless (0) or with a series of marginal teeth, sometimes with one or a few fanglike teeth distally (1). State (1) coded in all sampled alepocephaloids.] Polarity is reversed because gill rakers are primitively toothed (they are modified toothplates), as they are in outgroups, esocoids, salmonoids, and primitive neoteleosts. The gill rakers are toothless in *Alepocephalus tenebrosus* and *Photostylus* among the alepocephaloids we have sampled, in argentinoids, and in all osmeroids except *Retropinna* (McDowall, 1969, p. 802). Coding should be (0) for toothed rakers and (1) for toothless.

G. *Axial Skeleton (Including Caudal Skeleton and Fin)*

113. Accessory neural arch. Distribution of the accessory neural arch (ANA) was reviewed by Patterson and Johnson (1995, p. 17). Among lower euteleosts, they recorded ANA in alepocephaloids, salmonoids, northern osmeroids (including salangids), and *Esox*, whereas ANA is absent in argentinoids, southern osmeroids (retropinnids and other galaxioids), and umbrids. With more extensive sampling, we now find that ANA occurs in all osmerid and salangid genera and in *Aplochiton* alone among southern osmeroids; in platytroctid alepocephaloids; and among alepocephalids in *Alepocephalus, Bathylaco, Bathytroctes,* and *Talismania* (where it may carry an epineural); but it is absent in *Bajacalifornia, Leptochilichthys, Leptoderma, Photostylus, Rinoctes,* and *Rouleina*. Among osmerids, *Spirinchus* is notable in having ANA reduced to a minute nubbin, whereas it is large in all others. Previously (Patterson and Johnson, 1995), we were unwilling to decide whether ANA is synapomorphous at some level and has been repeatedly lost or has arisen repeatedly and is nonhomologous from group to group. With more extensive sampling in euteleosts, we are now convinced that ANA was primitively present in that group and has been repeatedly lost.

114. Occipital gap. In osmeroids and outgroups such as salmonoids the articulation between the occipital condyle and V1 is normally close, but in *Lepidogalaxias* and *Lovettia* there is a distinct gap between the two. A gap also occurs in many alepocephaloids.

115. Baudelot's ligament. In teleosts Baudelot's ligament primitively originates on V1 (Patterson and Johnson, 1995, p. 19), as it does in all examined lower euteleosts except southern osmeroids. In retropinnids, *Aplochiton* and *Lovettia* Baudelot's ligament originates on the occiput (the entry of V1 for *Stokellia* in Patterson and Johnson, 1995, table 4, is an error). In *Lepidogalaxias* the ligament originates on V1. In galaxiids it originates only on V1 or has a double origin, on the occiput and V1.

116. Fusion of neural arches to centrum. Teleostean neural arches are primitively autogenous and remain so in most lower euteleosts. Within osmeroids, all neural arches anterior to the dorsal fin are fused to the centra in *Aplochiton, Lovettia, Lepidogalaxias,* and galaxiids. They are also all fused in umbrids (Wilson and Veilleux, 1982).

117. Epineural fusion or autogeny. Epineural bones are primitively fused to neural arches in teleosts (Patterson and Johnson, 1995, p. 11). In lower euteleosts, all but the last two or three epineurals are fused in alepocephaloids (except in *Leptoderma,* where only the first two of about 25 are fused), and more than half of them are fused in argentinids (Patterson and Johnson, 1995, table 4). In salmonoids, the epineural of V1 may be fused (in some coregonid specimens; fused on one side in the *Thymallus* recorded by Patterson and Johnson, 1995, table 4), but the epineurals are generally all autogenous, as they are in all osmeroids. In esocoids the first two to five epineurals are fused in *Esox* (Patterson and Johnson, 1995, fig. 8), and none is fused in umbrids.

118. Epineural origin. Primitively, epineurals originate on the neural arch. In a few lower (nonacanthomorph) teleosts the point of origin of some epineurals descends on to the centrum, as in some osteoglossomorphs, *Esox,* and some aulopiforms (Patterson and Johnson, 1995, p. 12). Extensive sampling of osmerids shows that in all genera (including *Plecoglossus*) except *Hypomesus* epineural origin is displaced onto the anterodorsal part of the centrum from about V10 back to about V30; we also observed this displacement in *Hypomesus olidus* and *H. pretiosus* but not in *H. transpacificus,* where the epineurals remain on the neural arch. In salangids, where the epineural ligaments are unossified, their origin is displaced ventrally in the osmerid pattern in *Neosalanx* and *Protosalanx*; in *Salanx* the cartilage of the neural arches and parapophyses surrounds the centra so that the condition could not occur. In *Salangichthys* we could not clearly see the point of origin of the epineural ligaments. In *Stokellia* the origin of the epineural ligaments (there are no bones) is also displaced on to the centrum from about V8 to V20.

119. Epineural descent. Patterson and Johnson (1995, p. 27) suggested a synapomorphy of Argentinoidei: in the argentinoid and alepocephaloid genera then sampled, the tips of the first three (*Glossanodon, Leptoderma,* and *Searsia*) or four (*Argentina*) epineurals are displaced ventrally relative to their successors, in

the same way as is the distal part of the first epineural in the lampridiform *Velifer* (Johnson and Patterson, 1993, fig. 1). We have now checked other genera and found the first three epineurals descended distally in the alepocephaloids *Bathylaco, Bathytroctes, Mirorictus,* and *Searsioides;* the first four in the argentinoids *Bathylagus* and *Nansenia* and the alepocephaloids *Leptochilichthys* and *Pellisolus;* and among other alepocephaloids about the first 11 epineurals descended in *Rinoctes*, only the first two in *Bajacalifornia, Rouleina, Alepocephalus rostratus,* and *Talismania antillarum*, only the first in *Alepocephalus tenebrosus* and *Talismania aphos*, and none in *Xenodermichthys*. Our specimen of *Platytroctes* is poor, but Matsui and Rosenblatt's drawing (1987, fig. 6) indicates that only the first epineural is descended. The opisthoproctids *Opisthoproctus, Dolichopteryx,* and *Rhynchohyalus* have no epineural on V1 or V2 and none descended thereafter; *Macropinna* has no epineural on V1 and none descended; but *Bathylychnops* has no epineural on V1 and those on V2 and 3 descended. *Microstoma* has extremely long epineurals with none descended, a situation we take to be derived because the microstomatid *Nansenia* has four descended epineurals. There are no ossified epineurals in *Photostylus*, and our specimen of *Narcetes* is too poor to check. Summarizing, descent of the first two to four epineurals seems to stand up as a character of Argentinoidei (argentinoids and alepocephaloids). Genera or species lacking the character (only one descended in *Platytroctes, Talismania aphos,* and *Alepocephalus tenebrosus*, and none in most opisthoproctids, *Microstoma,* and *Xenodermichthys*) are all indicated, by other evidence (see below), as derived members of their subgroups.

120. Epineural ossification. Epineurals are primitively ossified in teleosts. Patterson and Johnson (1995, p. 12) found epineural ligaments but no bones in the retropinnids *Retropinna* and *Stokellia*, the salangid *Salangichthys*, and the umbrids *Dallia* and *Novumbra*, whereas in *Lepidogalaxias* there are no epineural bones or ligaments. We have checked other salangids and galaxioids and found epineural ligaments but no bones in *Prototroctes, Aplochiton,* and *Lovettia* but bones in all galaxiids. In *Novumbra* the epineurals ossify in larger specimens.

121. Cartilaginous and bony epicentrals. The epicentral series of intermusculars is primitively represented by ligaments in teleosts (Patterson and Johnson, 1995, p. 15). Epicentral bones develop in those ligaments in several taxa (e.g., *Megalops*, clupeomorphs, gonorynchiforms, and gymnotoids), and we found cartilages in the distal part of the anterior epicentral ligaments in salmonoids, osmeroids, the stomiiform *Maurolicus*, and the acanthomorph *Polymixia;* epicentral cartilages also occur among aulopiforms in the three genera of Evermannellidae (Baldwin and Johnson, in this volume). Regarding the epicentral cartilages in *Maurolicus* and *Polymixia* as autapomorphous, we (Patterson and Johnson, 1995, p. 26) argued that epicentral cartilages support a grouping of Osmeroidei and Salmonoidei. As with osmerid epipleurals (no. 122, below), our sampling of Argentinoidei was deficient, as was the quality of our material. We have now found cartilage rods in the epicentrals of all argentinid, bathylagid, and opisthoproctid genera in which our material is sufficiently well prepared to show them (*Argentina*, the bathylagids *Bathylagus* and *Leuroglossus*, the microstomatid *Nansenia*, and the opisthoproctids *Bathylychnops, Dolichopteryx,* and *Macropinna*). Among alepocephaloids, cartilaginous epicentrals are absent in all examined platytroctids (we have good material of seven genera) and absent in *Alepocephalus, Leptoderma, Photostylus,* and *Talismania* but present in *Bathylaco* (in the epicentrals of V1–3 only) and *Rinoctes* (in an occipital epicentral and those of V1–5). We do not yet have good enough material to check for them in other alepocephaloid genera.

Among Osmeroidei, in addition to the records in Patterson and Johnson (1995), we have now seen cartilaginous epicentrals in all osmerid genera and in *Aplochiton* and have confirmed that the epicentral cartilages ossify in *Lepidogalaxias* by study of a size range of double-stained specimens. There are no cartilaginous epicentrals in *Lovettia* or in our material of the four genera of salangids; in all those fishes, and in *Aplochiton*, there are no ossified intermusculars. Cartilage rods in the epicentrals therefore characterize osmeroids (all osmerids and retropinnids, *Aplochiton, Lepidogalaxias,* and many galaxiids), salmonoids (Patterson and Johnson, 1995, p. 14), argentinoids, and a minority of sampled alepocephaloids. Given that argentinoids and alepocephaloids are sister-groups (Argentinoidei of Greenwood and Rosen, 1971), the most economical interpretation is that cartilaginous epicentrals characterize a group comprising Argentinoidei, Osmeroidei, and Salmonoidei and are secondarily absent in most alepocephaloids (as they are in salangids, *Lovettia,* and some diminutive galaxiids among osmeroids).

122. Epipleural bones. Ossified epipleurals are primitively present in elopocephalans (Patterson and Johnson, 1995, p. 13). We argued (Patterson and Johnson, 1995, p. 26) that the absence of epipleural bones in salmonoids and osmeroids is a derived feature indicating that they are sister-groups. Our interpretation of osmerids was deficient both in sampling and in literature search.

We recorded the intermusculars of three osmerids, *Hypomesus transpacificus*, *Osmerus mordax*, and *Plecoglossus* (Patterson and Johnson, 1995, table 3), and found no epipleural bones in them. We did see epipleural bones in *Spirinchus* (Patterson and Johnson, 1995, p. 26), but because that genus occupies a derived position in Begle's (1991) cladogram of osmerids, we regarded its epipleurals as secondary (reversal) and argued that osmerids primitively lack epipleural bones. But Klyukanov (1975) described epipleurals in *Thaleichthys* (from ca. V20 back into the caudal region), *Spirinchus* (on 7–13 abdominal vertebrae and "possibly" 1–2 caudal vertebrae), *Allosmerus* (on 7–9 abdominal vertebrae) and *Mallotus* (on 25–27 abdominal and 7–10 caudal vertebrae). Wilson and Williams (1991, fig. 11) recorded epipleural bones in all osmerid genera except *Plecoglossus*. We have now examined all osmerid genera and agree with Klyukanov that epipleural bones occur in *Thaleichthys* (on about the last 20 abdominal but not on the first caudal vertebra in fishes ca. 60–150 mm SL), *Spirinchus* (absent, or ossified only on 2 or 3 posterior abdominal vertebrae in fishes ca. 45 mm SL; present on the last 7–12 abdominal vertebrae in fishes ca. 100 mm SL), *Allosmerus* (on 5–12 posterior abdominal vertebrae and sometimes on the first 1 or 2 caudals in fishes ca. 80–100 mm SL) and *Mallotus* (absent in a 55 mm specimen, ossified on ca. 20 posterior abdominal vertebrae and 2 caudal vertebrae in a 60 mm specimen, present on ca. 25 abdominal and 5 caudal vertebrae in fishes ca. 140 mm SL). In agreement with Klyukanov (1975), and in contrast to Wilson and Williams (1991), we have found no epipleurals in *Osmerus* (*O.mordax* and *O.eperlanus*) or *Hypomesus* (*H.olidus*, *H.pretiosus*, and *H.transpacificus*). A decision on whether epipleural bones are primitive or derived for osmerids depends on relationships within the group (Section IVB below), but the pattern of epipleurals in osmerids is distinctive. Primitively in elopocephalans the epipleural bones occur on roughly equal numbers of abdominal and caudal vertebrae (Patterson and Johnson, 1995, tables 3 and 4), ossifying rostrally and caudally from a focus around the first caudal vertebra. When epipleural bones are present in osmerids, they are generally confined to the posterior abdominal vertebrae (see above).

In galaxiids, we (Patterson and Johnson, 1995, p. 26, table 4) recorded epipleural bones in *Galaxias zebratus* and noted McDowall's (1969, 1978) records of them in *Galaxias* and *Paragalaxias*. We have now seen a larger sample of galaxiids. Epipleurals are present in all our cleared-and-stained *Galaxias* species and also in our *Galaxiella*, *Nesogalaxias*, *Paragalaxias*, and in rudimentary form (small nubbins) in some *Neochanna* but not in others.

123. Epipleural extent. Primitively, epipleural bones are absent on the anterior vertebrae in teleosts, but they extend unusually far forward in two groups, aulopiforms and alepocephaloids (Patterson and Johnson, 1995, p. 14). We (Patterson and Johnson, 1995, p. 27) proposed that monophyly of alepocephaloids is corroborated by the fact that the ossified epipleural series extends forward to V3 in *Bathytroctes*, *Leptochilichthys*, *Rinoctes*, *Searsia*, and *Talismania*. Matsui and Rosenblatt (1987, fig. 6) illustrated that condition in *Mirorictus*, and we have now also observed it in *Alepocephalus tenebrosus*, *Bathylaco*, *Narcetes*, *Rouleina*, and the platytroctids *Paraholtbyrnia*, *Pellisolus*, and *Searsioides*. The epipleurals extend to V2 in our *Bajacalifornia* (in which the first rib is on V1) and *Alepocephalus agassizi* (first rib on V2), to V4 in *Bathyprion* (Markle, 1976) and *Alepocephalus agassizi*, to V6 in *Holtbyrnia* and *Sagamichthys*, to V7 in *Platytroctes*, to V9 in *Leptoderma* and *Rinoctes* [in contrast to the report of V3 in *Rinoctes* by Patterson and Johnson (1995); Markle and Merrett (1980), reported epipleurals to V7], and to V11 in *Xenodermichthys*; in *Photostylus* there are no ossified epipleurals. Gosline (1969, fig. 11) illustrated an epipleural on V2 in *Alepocephalus rostratus*, and Markle (1976) reported epipleurals to V2 in *Bathylaco*, *Asquamiceps*, and *Talismania oregoni*, V4 in *Bathytroctes*; V6 in *Alepocephalus bicolor*; V8 in *Ericara*; V11 in *Leptoderma*; and V12 in *Conocara* and *Xenodermichthys*. We take conditions in *Rinoctes* (V7–9), *Leptoderma* (V9–11), *Ericara* (V8), *Conocara* and *Xenodermichthys* (V12), and *Photostylus* (none) to be derived since in our view (Section VIII) all that we have examined are derived alepocephaloids.

124. Proximal forking of epineurals and epipleurals. Patterson and Johnson (1995, p. 28) proposed that monophyly of salmoniforms (argentinoids, alepocephaloids, salmonoids, and osmeroids) might be corroborated by absence of proximal forking of the epineural and epipleural bones. Proximal forking of the epineurals and epipleurals is general in elopomorphs, clupeomorphs, ostariophysans, and myctophiforms. It does not occur in stomiiforms; in esocoids proximal forking occurs only in the epineurals (esocids) or in no more than three or four bones in each series (*Umbra*); and in aulopiforms the bones are forked only in chlorophthalmids and some paralepids (Baldwin and Johnson, in this volume). The lack of proximal forking of intermusculars in stomiiforms, the basal neoteleostean group, weakens it as a salmoniform character, unless (as proposed in Section X) esocoids belong between salmoniforms and neoteleosts.

125. Supraneural pattern. There are two basic patterns of supraneural development in teleosts. In the first, exemplified in Fig. 11A by larval *Clupea*, the

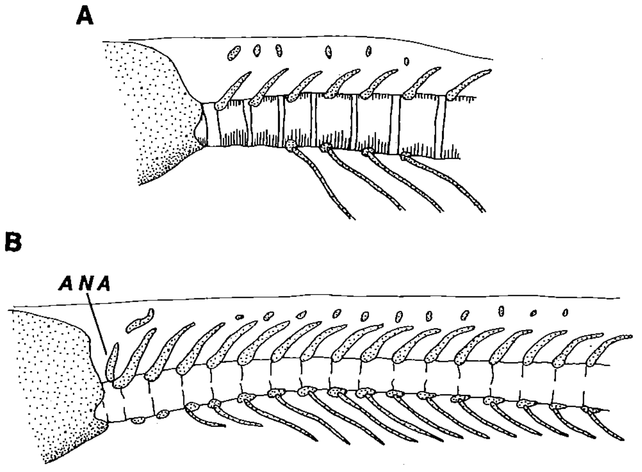

FIGURE 11 Patterns of supraneural development in larvae. Anterior vertebrae and supraneurals in (A) larval *Clupea harengus*, BMNH 1996.2.6.4, 20 mm SL; (B) larval *Salmo salar*, BMNH 1932.11.13.3, 19 mm SL. Cartilage stippled; chordacentra in A hatched. A shows the primitive pattern 1; B shows the euteleostean pattern 2. The accessory neural arch (ANA) is present in both *Clupea* and *Salmo*, but in *Clupea* (or in this lot of cleared-and-stained larvae) it develops late; it is present and already ossifed only in the largest specimen in the lot, 35 mm SL.

supraneurals develop caudally in series from the first, which lies anterior to the neural spine of V1. In adults resulting from this mode of development (Figs. 12A and 12B) there is normally no differentiation between the first and second supraneurals, and they are separated by the neural spine of V1. We will call this pattern 1. In the second (pattern 2), exemplified in Fig. 11B by larval *Salmo*, the first supraneural (anterior to the neural spine of V1) develops independently, and the remainder differentiate in rostral and caudal gradients from a focus roughly midway between the occiput and dorsal fin origin. In adults resulting from this mode of development (Figs. 12C, 12D, and 12H) the first supraneural is usually differentiated from the second (the first is substantially larger or thicker), and the two are separated by two (or more) neural spines. We have observed or inferred pattern 1, development in rostrocaudal series, in *Amia, Hiodon, Elops* (Fig. 12A), *Megalops, Albula, Denticeps*, several clupeoids (Fig. 11A), *Umbra* (Wilson and Veilleux, 1982, fig. 12E), microstomatids, bathylagids (Fig. 12B), and the alepocephalids *Bajacalifornia, Bathytroctes, Binghamichthys, Narcetes, Rinoctes*, and *Talismania antillarum*. We have observed or inferred pattern 2, differentiation of the first supraneural and a gap between it and the second, in *Esox*, salmonoids (Figs. 11B and 12D), osmeroids, argentinids (Fig. 12C), opisthoproctids, the stomiiforms *Diplophos* (Fink and Weitzman, 1982, fig. 5) and *Pollichthys, Aulopus*, the neoscopelid *Scopelengys*, and the alepocephalids *Alepocephalus agassizi, Bathylaco, Talismania oregoni*, and *T.aphos*. Taxa with only one supraneural (over V1), such as *Chirocentrus* and the alepocephalids *Alepocephalus tenebrosus* and *Leptochilichthys*, cannot be assigned to pattern 1 or 2.

Two variants of pattern 2 occur in osmeroids: the first (pattern 2A) in osmerids and salangids and the second (pattern 2B) in galaxioids (retropinnids, *Aplochiton, Lovettia, Lepidogalaxias*, and galaxiids). In pattern 2A (Figs. 12E and 12F), the first supraneural is associated with the first two neural arches; this pattern also occurs in argentinids (*Argentina* and *Glossanodon*, Fig. 12C). In the galaxioid pattern, 2B, the first supraneural develops in continuity with the neural arch (Fig. 12I), and in the adult (Figs. 12G and 12H) V1 has no neural spine, and the supraneural is closely articulated or continuous by cartilage with the neural arch.

A different variant of pattern 2 occurs among esocoids in *Dallia, Novumbra*, and the Paleocene *Esox tiemani* (Wilson and Veilleux, 1982; Wilson, 1984): the supraneurals develop rostrally and caudally from a focus midway between the occiput and dorsal fin, as usual, but there is no anterior supraneural.

Ostariophysans show a third pattern (pattern 3) of supraneural development. Fink and Fink (1981, p. 324) identified absence of the supraneural anterior to the neural arch of V1 as an ostariophysan synapomorphy. *Chanos* (Rosen and Greenwood, 1970, fig. 3; Fink and Fink, 1981, fig. 6) and the early Cretaceous *Tharrhias* (Patterson, 1984b, fig. 3) lack that first supraneural but otherwise show a caudal gradient of supraneurals from above V2. In gonorynchid (Patterson and Johnson, 1995, fig. 5; Gayet, 1993, figs. 8 and 9) and kneriid (Lenglet, 1974, fig. 17; Grande, 1994, fig. 9) gonorynchiforms, the supraneural anterior to the neural spine of V2 is either absent or is smaller than its successors, and the supraneurals evidently develop rostrally and caudally from over V3. Otophysans (e.g., Fink and Fink, 1981, figs. 14–18; Patterson, 1984a, figs. 14 and 16) show the same pattern, with the supraneural over V2 either absent (characiphysans) or smaller than its successor (cypriniforms and the Eocene *Chanoides*; Patterson, 1984a, p. 445).

A fourth pattern of supraneural development (pattern 4) occurs in platytroctid alepocephaloids and in *Rouleina* and *Xenodermichthys*—the supraneurals are evenly spaced, with one every two or three vertebrae (Matsui and Rosenblatt, 1987, fig. 6).

A synapomorphy of eurypterygians (aulopiforms, myctophiforms and acanthomorphs), additional to the three listed by Johnson (1992), is that they have no more than three supraneurals. Exceptions to that statement, such as four supraneurals in the neoscope-

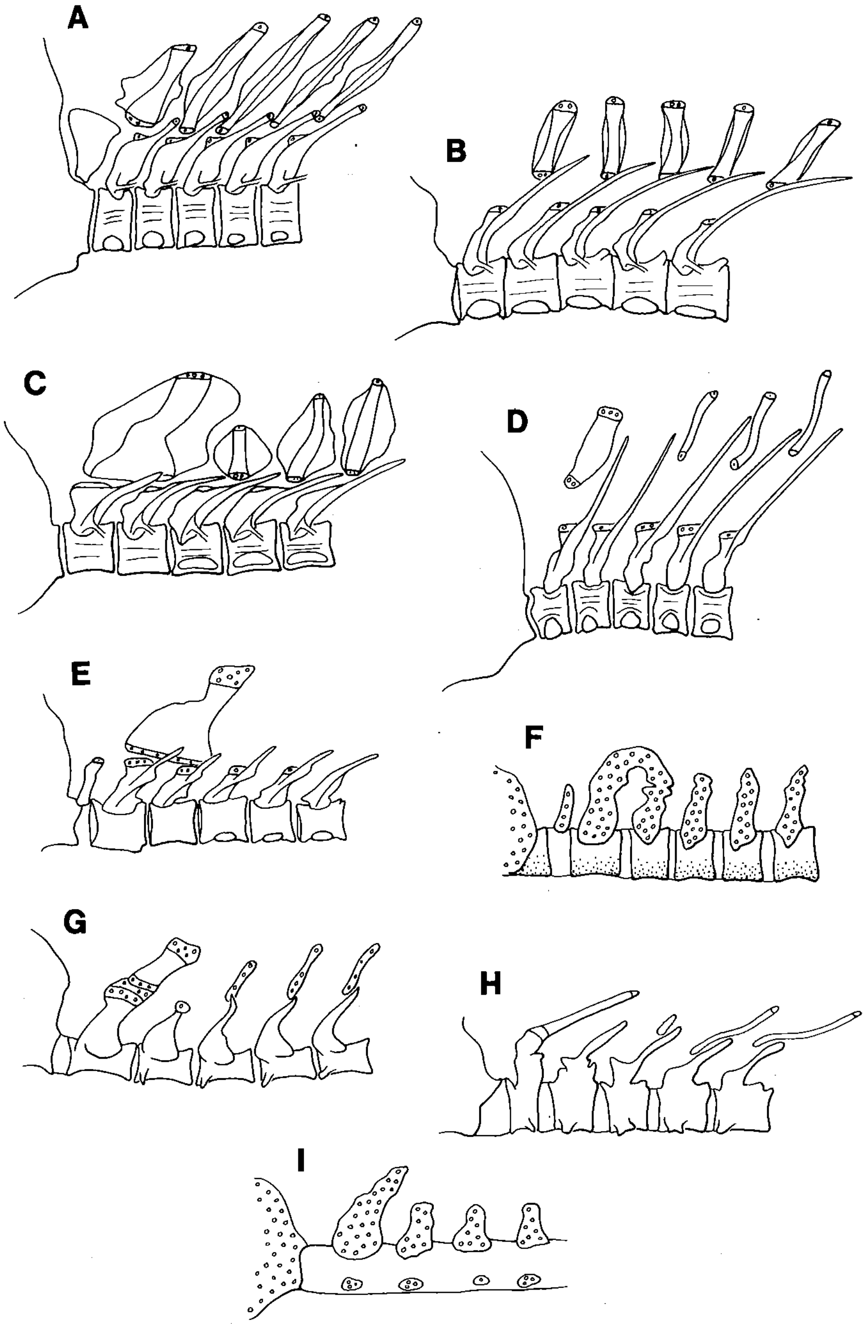

FIGURE 12 Anterior vertebrae and supraneurals in (A) *Elops hawaiensis*, BMNH 1962.4.3.1, 69 mm SL; (B) *Bathylagoides* sp., USNM 234768, 43 mm SL; (C) *Glossanodon polli*, USNM 203236, 101 mm SL; (D) *Oncorhynchus clarki*, BMNH 1957.2.20.3, 90 mm SL; (E) *Mallotus villosus*, AMNH 26286, 137 mm SL; (F) *Protosalanx chinensis*, HSU 85-38, 65 mm SL; (G) *Lovettia sealei*, BMNH 1937.8.22.1, 41 mm SL; (H) *Lepidogalaxias salamandroides*, USNM 339265, 44 mm SL; (I) Galaxiidae indet. larva, USNM 340197, 25 mm SL.

lids *Neoscopelus* and *Solivomer*, five in the stephanoberyciforms *Rondeletia* (Moore, 1993) and *Hispidoberyx*, eight in *Barbourisia* (Moore, 1993), and four or more in a few percomorphs (Johnson, 1984; Smith-Vaniz, 1984; Mabee, 1988), are all most economically explained by secondary increase, as demonstrated in centrarchids by Mabee (1988). We interpret supraneural development in lower eurypterygians (aulopiforms and myctophiforms) as pattern 2 and in acanthomorphs (Mabee, 1988) as a modified pattern 1.

Summarizing, pattern 1 supraneurals occur in osteoglossomorphs, elopomorphs, and clupeomorphs, and pattern 2 occurs in basal euteleosts (argentinids, some alepocephalids, salmonoids, osmeroids and stomiiforms) and lower neoteleosts, with the majority of that group (acanthomorphs) having a modifed pattern 1. Esocoids exhibit both pattern 1 (*Umbra*) and 2 (*Esox*).

126. Number of supraneurals. Primitively in teleosts the supraneurals are numerous, with one above each vertebra from the occiput back to the dorsal fin origin. That pattern persists in most lower euteleosts (argentinids, bathylagids, microstomatids, opisthoproctids, salmonoids, umbrids, and in the Paleocene *Esox tiemani* among esocids; Patterson and Johnson, 1995, p. 24). Among osmeroids, the primitive pattern occurs in most osmerids (see below) and in *Aplochiton, Lovettia, Lepidogalaxias,* and galaxiids. Retropinnids have a reduced number of supraneurals, covering half or fewer of the vertebrae between the occiput and dorsal origin. Salangids have a single supraneural, over V1 and V2 (Fig. 12F). Among osmerids, *Hypomesus, Osmerus, Plecoglossus, Spirinchus,* and *Thaleichthys* show the primitive pattern, with supraneurals extending almost to the dorsal origin (D). *Allosmerus* has about 16 supraneurals, with D at about V28, and *Mallotus* (Fig. 12E) has 1–8 supraneurals, with the same dorsal origin. Among alepocephaloids, the number of supraneurals is reduced in platytroctids, *Rouleina*, and *Xenodermichthys*, which have one supraneural to every two or three vertebrae (no. 125 above) and a total of about 5 supraneurals. In other sampled alepocephalids the most complete series of supraneurals is in *Bathylaco*, with 13 supraneurals and D at V19. *Bajacalifornia* also has 13 supraneurals with D at V21, *Bathytroctes* has 11 with D at V18, and *Talismania antillarum* has 11 with D at V19. Other alepocephalids have fewer than 10 supraneurals: *Talismania aphos* 9, D at V20; *Rinoctes*, 8, D at V20; *Narcetes*, 7, D at V23; *Alepocephalus agassizi*, 2; *A.tenebrosus* and *Leptochilichthys*, 1; and *A.bairdii, Leptoderma,* and *Photostylus*, none.

127. Laminar supraneurals. Supraneurals are primitively rodlike cartilages sheathed by a tube of perichondral bone. In *Argentina* and *Glossanodon* the anterior supraneurals are expanded rostrocaudally by sheets of membrane bone (Fig. 12C). The character is trivial but is one of the few indicators of argentinid monophyly.

128. Condition of last few neural and haemal spines. Gosline (1960, p. 332), in grouping salmonoids, osmeroids, and argentinoids (his Salmonoidei, which did not include alepocephaloids), wrote

> the caudal skeletons of adult members ... are, with the exception of those of the Salangidae and of the neotenic aplochitonid *Lovettia*, the most easily recognizable.... the last few preterminal vertebrae have neural and haemal spines with flattened, anteroposteriorly oriented blades. These together make up a flange or keel running above and below the posteriormost portion of the vertebral column.

Greenwood and Rosen (1971) illustrated these blades (their "preural flanges") in several argentinoids and in the alepocephaloid *Searsia*, and Markle (1976), Kobyliansky (1986, 1990), Sazonov (1986), and Fujita (1990) illustrated them in several other alepocephaloids and in argentinoids. In all these alepocephaloids and argentinoids, the preural flanges, when present, are confined to the proximal part of the anterior margin of the neural and haemal spine in a configuration that seems no different from that in (for example) *Chanos*, cyprinids, and chlorophthalmids (Fig. 13A; Fujita, 1990, figs. 30, 36, 41, and 98–100). But in salmonoids and osmeroids the last few neural and haemal arches generally have the structure described by Gosline (1960): they have laminar bone on both the anterior and posterior margins and tend to contact their neighbors in the midline, forming the "keel" above and below the column that Gosline described (Figs. 13C, 13E and 13F). This condition is illustrated by Rosen (1974, figs. 18 and 25–27) in several galaxiids, *Plecoglossus, Retropinna, Stokellia, Aplochiton, Lovettia* and several salmonoids, and by Fujita (1990, figs. 61–63 and 66–71) in *Hypomesus, Plecoglossus,* and several salmonoids. Other salmonoids showing the condition are illustrated in Shaposhnikova (1968a,b), Nybelin (1971, pl. 6) and Arratia and Schultze (1992). Among osmeroids, the condition does not occur (the neural and haemal spines are slender distally) in *Allosmerus, Osmerus* (Fujita, 1990, fig. 60), *Spirinchus* (Weitzman, 1967, fig. 4), *Thaleichthys* (Chapman, 1941b, fig. 15), salangids (Roberts, 1984, fig. 21; Fujita, 1990, fig. 64), *Lepidogalaxias* (Rosen, 1974, fig. 24) and some galaxiids (e.g., *Galaxias maculatus*, Fujita, 1990, fig. 65). In *Mallotus* the neural and haemal spines are normally slender distally, but they become laminar in large specimens.

129. Condition of NPU2. The condition of the neural spine of PU2 (NPU2) in lower eutelosts has been debated, particularly by Rosen (1973, pp. 422–432), who took the "broad half-spine" found in *Elops, Pterothrissus,* osmerids, and *Aulopus*, for example, to be derived and to characterize Eurypterygii or (Rosen, 1985, p. 52) eurypterygians plus osmeroids. Johnson (1992, p. 12) reviewed subsequent evaluations.

Fujita (1990, table 2) recorded a short NPU2 in *Elops, Pterothrissus, Hypomesus, Plecoglossus, Coregonus, Thymallus,* and *Diplophos* among the pre-eurypterygian teleosts he sampled. It also occurs in all other osmer-

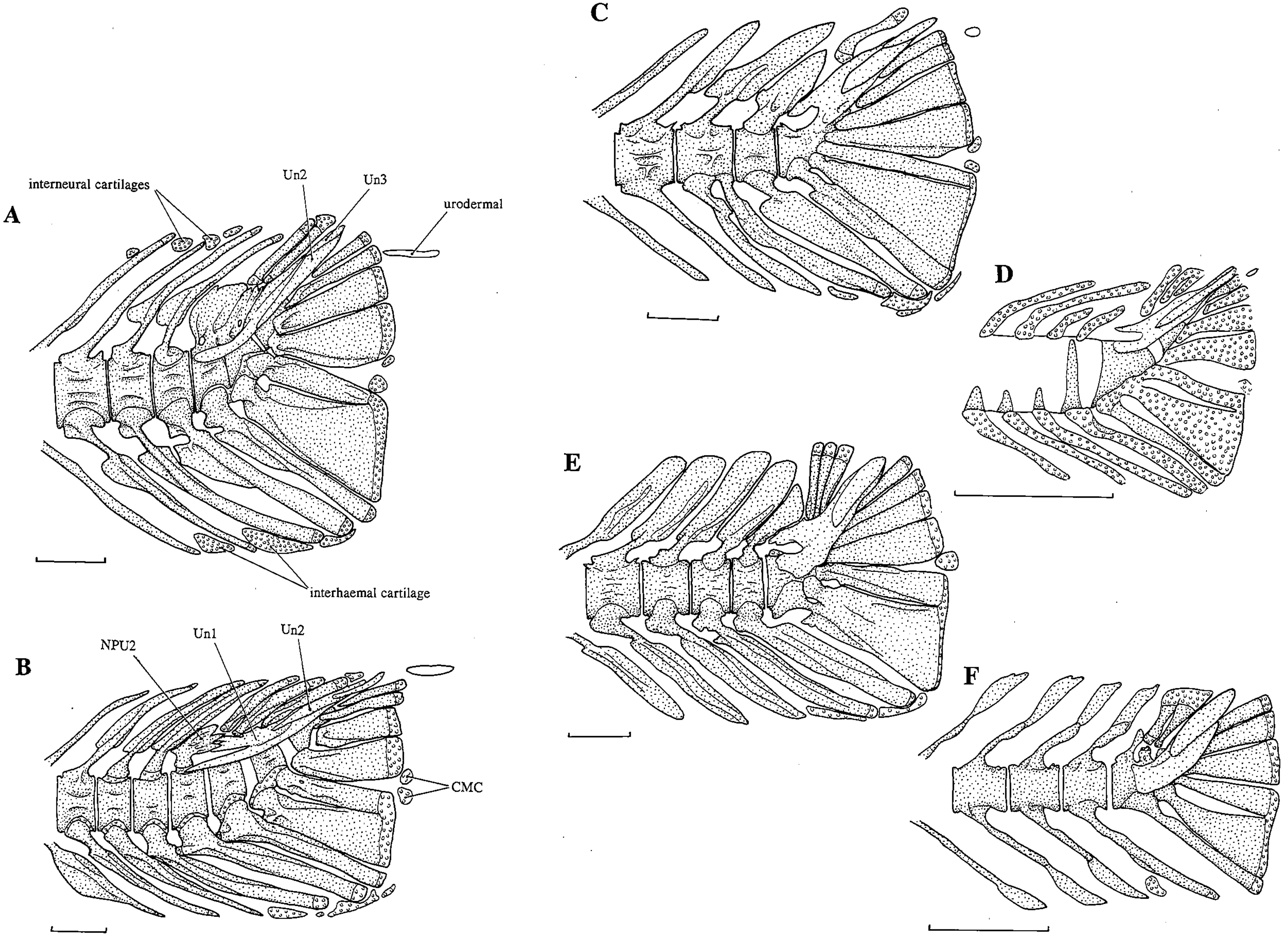

FIGURE 13 Caudal skeleton in (A) *Argentina silus*, BMNH 1967.3.5.2, 78 mm SL; (B) *Coregonus lavaretus*, BMNH 1996.2.6.20, 73 mm SL; (C) *Hypomesus transpacificus*, BMNH 1984.6.28.11, 65 mm SL; (D) *Hypomesus* sp., larva, USNM 340198, 33 mm SL; (E) *Retropinna retropinna*, BMNH 1964.4.30.19, 83 mm SL; *(F) Lovettia sealii*, BMNH 1937.8.22.1, 41 mm SL. Abbreviations as in text; scale bars = 1 mm. A shows the normal position of Un2 in teleosts, posteroventral to Unl, whereas B–F show the derived condition characteristic of salmonoids and osmeroids, where Un2 is anterodorsal to Unl. A shows the derived, long NPU2 characteristic of argentinoids (and many other groups) whereas B–E show the primitive, short NPU2. C and E–F show the laminar distal parts of the last few neural and haemal spines characteristic of salmonoids and osmeroids; these do not develop in *Coregonus lavaretus* but are conspicuous in other species (e.g., Nybelin, 1971, pl. 6; *C. nasus* and *C. albula*) and in *Prosopium*.

ids, all retropinnids, and commonly in alepocephaloids (Fig. 13; Greenwood and Rosen, 1971, fig. 11, *Searsia*; Markle, 1976, fig. 13A, *Bathylaco*; Sazonov, 1986, figs. 17–19, *Platytroctes*, *Barbantus*, *Mirorictus*, *Persparsia*, *Holtbyrnia*, and *Sagamichthys*; Matsui and Rosenblatt, 1987, fig. 7, *Paraholtbyrnia*; and in our *Pellisolus* as well as several of the mentioned genera).

Among the Jurassic teleosts studied by Arratia (1991, character 19), NPU2 is coded as equal in length to NPU3 only in the ichthyodectiform *Allothrissops* and in the *incertae sedis* taxa *Daitingichthys*, *Orthogonicleithrus*, *Pachythrissops*, and *Leptolepis talbragarensis* (it is variable in the last and in ichthyodectiforms; Patterson and Rosen, 1977, p. 110, fig. 46). Among generalized elopomorphs, NPU2 is long in *Megalops* and *Albula* but short in the Jurassic *Anaethalion* and the Cretaceous megalopid *Sedenhorstia* (Goody, 1969).

In salmonoids, Stearley and Smith (1993, character 97), in agreement with Arratia and Schultze (1992), referred to the short neural spine in coregonids and *Thymallus* as a neural arch with a detached neural spine. *Thymallus* and coregonids may give that impression, because in some specimens NPU2 is tipped with cartilage (Arratia and Schultze, 1992, figs. 21 and 22) and appears to be associated with the tip of the first epural. Occasional specimens have two neural arches on PU2, apparently associated distally with tips of the first and second epurals, whereas in other coregonids the tip of NPU2 is without cartilage and lies in front of the tip of the epural (Fig. 13B; Nybelin, 1971, pl. 6).

In the most primitive teleosts, such as the early Jurassic pholidophorids and *Pholidolepis* (Patterson, 1968), NPU2 is shorter than NPU3 but like NPU3 was ossified in cartilage and tipped with cartilage in life. The same is true of Jurassic "leptolepids" such as *Leptolepis coryphaenoides*, *Todiltia*, *Ascalabos*, and *Tharsis*, and of the Jurassic ichthyodectiforms *Allothrissops* and *Thrissops* (Patterson, 1968; Patterson and Rosen, 1977; Arratia, 1991). A bladelike or leaflike NPU2 tipped with membrane bone, like that of *Elops*, first appears in late Jurassic teleosts such as *Anaethalion* and *Luisichthys* (Patterson and Rosen, 1977; Arratia, 1991). It occurs commonly in Lower Cretaceous teleosts, for example in *Crossognathus* and pachyrhizodontids (Forey, 1977; Taverne, 1989), *Scombroclupeoides* (Patterson and Rosen, 1977, fig. 47) and "*Leptolepis*" *neocomiensis* (Patterson, 1970, fig. 48). This leaflike NPU2 is derived relative to the cartilage-tipped NPU2 of pholidophorids and true leptolepids, but in our view its distribution clearly indicates that it is primitive relative to a long NPU2.

130. [Begle's 5: Rudimentary neural arches in caudal skeleton independent (0) or fused to centrum followed in some cases by fusion to first uroneural (1) or fused to first uroneural followed in some cases by fusion to centrum (2). State (0) coded in outgroups, salmonoids, neoteleosts, *Lepidogalaxias*, and esocoids; state (1) in all argentinoids, all alepocephaloids except platytroctids, *Talismania*, *Bathylaco*, and *Leptoderma*, all southern osmeroids and *Thaleichthys*; state (2) in Osmeridae (minus *Thaleichthys*) and salangids. Platytroctids and *Talismania* are coded as polymorphic for (0) and (1); *Bathylaco* and *Leptoderma* are coded (?).] Begle's text implies that the (1) entered for *Thaleichthys* is an error. We commented on this character (Patterson and Johnson, 1995, p. 27). It is taken from Fink (1984b), and the "followed in some cases" in the description of states (1) and (2) refers to ontogenetic information on neural arches over PU1 in *Osmerus* and galaxiids presented by Fink and Weitzman (1982, p. 83). In Begle (1991) the character was two-state and referred to the first uroneural (Un1) as well as caudal neural arches; the derived state was coded only in osmerids and salangids, as in Fink (1984b). It is easy enough to determine whether Un1 is free or fused to a centrum, but determining the ontogenetic history of rudimentary neural arches from adult specimens is problematic. The effect of Begle's (1991) coding was to distinguish osmerids plus salangids from the remaining taxa in his sample, whereas the effect of his 1992 coding was also to distinguish all argentinoids and osmeroids (except *Lepidogalaxias*) from outgroups.

This part of the caudal skeleton of argentinoids and osmeroids has been discussed often and at length over the past quarter-century (Patterson, 1970; Greenwood and Rosen, 1971; Rosen, 1974; Markle, 1976; Fink and Weitzman, 1982) without any real agreement on its significance. Begle's (1992) coding of (1) for most alepocephaloids is not supported by the descriptions and illustrations in Greenwood and Rosen (1971), Markle (1976) and Sazonov (1986). In alepocephaloids, the neural arches of PU1 and U1, when present, usually remain autogenous, in state (0). In argentinoids (Fig. 13A; Patterson, 1970; Greenwood and Rosen, 1971; Kobyliansky, 1986, 1990; Fujita, 1990) the first uroneural is free (*Argentina* and opisthoproctids) or fused to PU1, and the caudal neural arches are generally well-developed and fused to the centra (except in opisthoproctids), justifying Begle's (1) in all except opisthoproctids. In retropinnids (Fig. 13E; McDowall, 1969; Rosen, 1974) the first uroneural is free, and there are no caudal neural arches; they should be coded (0).

131. [Begle's 77: PU1 bearing one (1) or more (0) rudimentary neural arches. State (1) coded in esocoids and *Lepidogalaxias*.] Begle (1991) referred this character to Rosen (1974) and Fink and Weitzman (1982); we cannot understand it. The primitive condition in tele-

osts is to have one arch per centrum, and to have one arch, rudimentary or not, over PU1 can only be primitive. Working through Fujita's (1990) figures, which are arranged systematically, the first fish one encounters with *no* (rather than one) neural arch over PU1 is *Esox* (Fujita, 1990, fig. 54), and the first fish in which the configuration might imply more than one arch is *Argentina*. Rosen's (1974) extensive sample of variant caudal skeletons in lower euteleosts shows more than one arch [Begle's (1)] in some galaxiids and in *Aplochiton* and an arch that bifurcates distally in some *Dallia*. Our *Lepidogalaxias*, like Rosen's (1974, fig. 24), all have a single arch with a complete neural spine on PU1. Character was discarded.

132. [Begle's 108: U1 free (0) or fused to PU1 (1). State (1) coded in *Bathylagus* and *Opisthoproctus*.] State (1) does not occur in *Opisthoproctus* (Greenwood and Rosen, 1971, fig. 15; checked in two further specimens, including that used by Begle). Begle's text assigns the fusion to argentinids, though it is not coded in them. Argentinids are variable, with fusion in most species (or individuals) of *Argentina* (fused in Gosline, 1960, fig. 10; Rosen and Patterson, 1969, fig. 71; Patterson, 1970, fig. 38; Greenwood and Rosen, 1971, fig. 12; unfused in Fig. 13A and Fujita, 1990, fig. 56) and *Glossanodon* (fused in Greenwood and Rosen, 1971, fig. 12; Fujita, 1990, fig. 57; unfused in Kobyliansky, 1990, fig. 14). State (1) occurs in microstomatids (Kobyliansky, 1990, fig. 14) and among Begle's sample in all neoteleosts, all Osmeroidei except *Lepidogalaxias*, several platytroctids (Sazonov, 1986, figs. 17–19), and *Leptoderma* (Greenwood and Rosen, 1971, fig. 9; personal observation). They are wrongly coded.

133. [Begle's 18: Number of hypurals six (0) or five (1). State (1) coded in galaxiids, *Aplochiton*, *Lovettia*, and *Lepidogalaxias*.] *Leptoderma* also has five (or fewer) hypurals (Greenwood and Rosen, 1971; Markle, 1976; personal observation) and is miscoded. There are no more than five hypurals in the umbrids *Dallia* and *Umbra* (Rosen, 1974; Wilson and Veilleux, 1982). Fusion between hypurals occurs in some galaxiids (Rosen, 1974, fig. 18) and salangids (Roberts, 1984, p. 201). In retropinnids (*Prototroctes*, *Retropinna*, *Stokellia*) hypural 1 is fused to the parhypural (Fig. 13E; McDowall, 1969, fig. 4; Rosen, 1974, fig. 27), an unusual condition that we have not observed elsewhere in lower euteleosts (cf. Fujita, 1990, table 2.1).

134. Number of epurals. Three epurals, primitive for Recent teleosts, occur in most lower euteleosts. There are no more than two epurals in argentinids; platytroctids and all alepocephalids except *Bathylaco* and *Narcetes* (Markle, 1976; Sazonov, 1986); a derived subgroup of salmonids (Stearley and Smith, 1993, character 98; reversal to three inferred in *Oncorhynchus*); *Hypomesus*, *Mallotus*, and *Plecoglossus* among osmerids; *Aplochiton* and *Lovettia* among galaxioids; and umbrids among esocoids.

There is one epural in the alepocephalid *Leptochilichthys*, opisthoproctids, and galaxiids, and none in the alepocephalid *Leptoderma* or in *Lepidogalaxias*.

135. [Begle's 76: Uroneurals more than one (0) or one (1). State (1) coded in esocoids and *Lepidogalaxias*.] There is one uroneural in *Leptoderma* (Markle, 1976; personal observation), whereas our *Lepidogalaxias* consistently have two uroneurals.

136. Uroneural 1 (Un1) autogenous or fused. Begle (1991, character 5) correctly coded the fusion of Un1 with the compound centrum in all osmerids and salangids. Begle (1992) altered the character to a description of ontogenetic fusions between ural neural arches and other structures (no. 130, above). Fusion of Un1 also occurs in *Glossanodon*, bathylagids, and microstomatids (though it is drawn as if separate in *Microstoma* and *Nansenia* by Greenwood and Rosen, 1971, fig. 13; cf. Kobyliansky, 1990, fig. 14).

137. Membranous outgrowth of Un1. Begle (1992, fig. 9) cited a "membranous outgrowth of first uroneural" as a synapomorphy uniting all euteleosts (esocoids, ostariophysans, salmonoids, his Osmerae, and neoteleosts). The character is problematic and has involved unsubstantiated speculation on ontogenetic processes (e.g., Greenwood and Rosen, 1971; Rosen, 1974). The structure in question is the "stegural" of Monod (1968, pp. 62, 594), for which the type locality is *Salmo* and other salmonids. Ontogeny is now well known in salmonoids (Arratia and Schultze, 1992), and contrary to earlier suggestions there is no indication that the structure is compound in origin. Stearley and Smith (1993, character 96) considered the large, fan-shaped membranous outgrowth in salmonines to be derived relative to the smaller outgrowth in *Thymallus* and coregonids (Fig. 13B; Norden, 1961, pls. 14 and 15; Arratia and Schultze, 1992, figs. 21 and 25). The form of the membranous outgrowth, if present, can be assessed accurately only when Un1 is autogenous. In alepocephaloids, where Un1 is always free, it has a substantial anterodorsal outgrowth in platytroctids (Sazonov, 1986, figs. 17–19) and in most alepocephalids (Markle, 1976; outgrowth absent in *Alepocephalus*, *Asquamiceps*, *Bathytroctes*, *Conocara*, *Ericara*, *Leptoderma*, and *Talismania*). In argentinoids, Un1 is usually fused to the underlying compound centrum, but when it is free (*Argentina*, Fig. 13A; Patterson, 1970, fig. 38; Fujita, 1990, fig. 57; opisthoproctids; a 22 mm bathylagid larva) there is no conspicuous membranous outgrowth. In osmeroids, Un1 is fused to the compound centrum in osmerids and salangids, but

the configuration is very like that in retropinnids (Figs. 13C and 13E; Rosen, 1974, figs. 26 and 27), where Un1 is free and has a membranous outgrowth like that in salmonoids, and larval osmerids (Fig. 13D) confirm the condition. In other southern osmeroids (*Aplochiton, Lovettia, Lepidogalaxias*, and galaxiids) the membranous outgrowth is small or absent (Fig. 13F; Rosen, 1974, figs. 18, 19, and 24; in our larval galaxiids, ca. 25 mm SL, there is no conspicuous outgrowth). In esocoids (Rosen, 1974, figs. 20–23; Wilson and Veilleux, 1982, figs. 13 and 14; Fujita, 1990, figs. 54 and 55) the membranous outgrowth of Un1 is small but distinct, except in *Umbra krameri* and some *Dallia*, where it is absent. The membranous outgrowth on Un1 is generally well developed in neoteleosts (e.g., Fujita, 1990, figs. 72, 84, 96–102, 115–117, 175–178). In ostariophysans Un1 is free only in early Cretaceous stem gonorynchiforms such as *Dastilbe* (Blum, 1991, p. 279), *Tharrhias* (Patterson, 1984b, fig. 2), *Gordichthys*, and *Rubiesichthys* (Poyato-Ariza, 1994, figs. 16, 17). Although some specimens of *Gordichthys* have been interpreted as showing a membranous outgrowth (Poyato-Ariza, 1994, p. 28), the structure in question is no more distinctive than the low ridge developed in several Jurassic "leptolepids' (Arratia, 1991, p. 297) or in large *Elops* (Schultze and Arratia, 1988, p. 289). In clupeomorphs Un1 is free only in *Denticeps* (Greenwood, 1968, fig. 29; Monod, 1968, fig. 263; Grande, 1985, fig. 7) and in Cretaceous stem clupeomorphs (Grande, 1982, 1985). As in stem gonorynchiforms (above) there may be a low ridge on the anterodorsal surface of Un1, but there is no distinctive membranous outgrowth.

Summing up, an anterodorsal membranous outgrowth on Un1 characterizes euteleosts if ostariophysans are excluded and if absence of the outgrowth in argentinoids is considered secondary.

138. Extent of Un1. Primitively in Recent teleosts Un1 extends forward to PU2 [e.g., *Hiodon, Elops, Megalops*, many alepocephaloids (Markle, 1976; Sazonov, 1986), and salmonoids (Fig. 13B; Fujita, 1990)]. When Un1 is fused to the the compound centrum (no. 136 above), it never extends beyond PU1. It also never extends beyond PU1 in esocoids or in neoteleosts (Fujita, 1990).

139. Position of Un2. Greenwood and Rosen (1971, p. 25, fig. 16) mentioned one feature that they took to be evidence of relationship between osmeroids and salmonoids, the position of the second uroneural (Un2), as first described in salmonoids by Cavender (1970). Primitively, Un2 in teleosts is elongate, with a slender, tapering anterior portion that lies posteroventral to Un1 (e.g., Fig. 13A and Fujita, 1990, figs. 6–8, 15–30, 47–48, and 56–58, of elopomorphs, clupeomorphs, *Chanos*, characins, and argentinoids). In all salmonoids and osmeroids Un2 is rather broad and lies anterodorsal to Un1 (e.g., Figs. 13B–13F; Rosen, 1974, figs. 18, 19, and 25–27; Fujita, 1990, figs. 60–71; Arratia and Schultze, 1992). The character is not perfectly clean, since Fujita's illustrations of cyprinoids (1990, figs. 35–45) and of most aulopiforms (1990, figs. 100 and 103–114) show a configuration like that in osmeroids and salmonoids.

140. Third uroneural (Un3). Un3 is primitively present in lower euteleosts, as it is in salmonoids and osmerids. Un3 is absent in our salangid material (illustrated in *Salangichthys ishikawae* by Fujita, 1990, fig. 64, but unusual in form) and in southern osmeroids (retropinnids, *Aplochiton, Lovettia, Lepidogalaxias*, and galaxiids). Among argentinoids Un3 is present in argentinids, microstomatids, and opisthoproctids, and in *Bathylagichthys* and *Lipolagus* among bathylagids (Greenwood and Rosen, 1971; Kobyliansky, 1986, 1990). Among alepocephaloids, Un3 is present in most platytroctids (Sazonov, 1986) and most alepocephalids (Markle, 1976). It is absent in the alepocephalids *Leptoderma, Photostylus*, and *Rouleina* (Greenwood and Rosen, 1971; Markle, 1976). Esocoids lack Un3, as do all neoteleosts.

141. Interneural and interhaemal cartilages. Kobyliansky (1986, fig. 19) and Fujita (1990, figs. 58 and 59) illustrated the extensive series of large interneural and interhaemal cartilages in bathylagids: they may extend forward to about PU12, and always extend at least to PU5. The microstomatid *Nansenia* also has conspicuous interneural and interhaemal cartilages (Kobyliansky, 1990, fig. 14), extending forward to about PU7; there are fewer in *Microstoma*. The only other teleosts with comparable development of the interneural and interhaemal cartilages are myctophids and some stomiiforms (Fujita, 1990, table 3). In argentinids the interneural cartilage series sometimes extends to PU5 (Fig. 13A); in opisthoproctids interneural and interhaemal cartilages do not extend forward beyond PU4.

142. Caudal median cartilages (CMCs, Fujita, 1990). CMCs (Figs. 13 and 14) are two cartilages lying in the gap between the distal parts of hypurals 2 and 3, one at the posteroventral corner of H3 and one at the posterodorsal corner of H2. They occur only in euteleosts (Fujita, 1990, table 3), where their presence is unambiguously primitive for argentinoids, osmeroids, salmonoids and neoteleosts. There is a single CMC, rather than two, in *Mallotus*, retropinnids (*Prototroctes, Retropinna*, and *Stokellia*), some salmonids (Fujita, 1990, figs. 67–69), some *Salangichthys* (Fujita, 1990, fig. 64, *S.ishikawae*; there are two in our *S.microdon*), and some *Salanx* (our *S.prognathus*; there are two

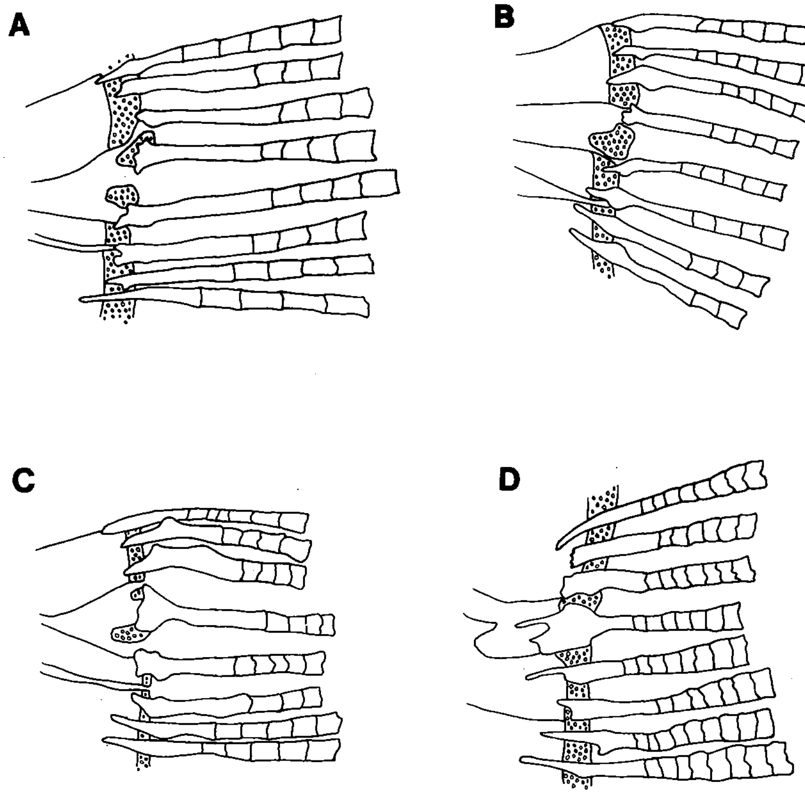

FIGURE 14 Caudal median cartilages (CMCs) in argentinoids. The figures show the distal parts of hypurals 1–3, the CMCs, and the bases of the central caudal fin rays. (A) *Osmerus mordax*, BMNH 1984.11.29.11, 85 mm SL, showing the configuration normal in lower euteleosts, with the CMCs each carrying the innermost ray of the upper and lower caudal lobes. (B) *Pseudobathylagus milleri*, SIO 80-258, 155 mm SL, with a single CMC lying between the innermost caudal rays. (C) *Argentina sphyraena*, USNM 238015, 127 mm SL, and (D) *Bathylaco nigricans*, USNM 206693, 285 mm SL, show the condition characteristic of primitive argentinoids and alepocephaloids, with the CMCs carrying only the lowermost ray of the upper caudal lobe. We interpret the bathylagid condition (B) as derived relative to the condition in C and D.

in our *S.ariakensis* and in Roberts's *S.cuvieri*, 1984, fig. 21). CMCs are secondarily absent in acanthomorphs, and primarily absent in osteoglossomorphs, elopomorphs, clupeomorphs, and ostariophysans. Among lower euteleosts, they are absent in *Aplochiton*, *Lovettia*, *Lepidogalaxias*, galaxiids, the alepocephalids *Leptoderma* and *Photostylus*, and in esocoids. Their absence in esocoids is problematic. Patterson and Johnson (1995, p. 25) used CMCs as a character to distinguish esocoids from other euteleosts (excluding ostariophysans). However, we now infer that CMCs have been lost in at least six euteleostean lineages: southern osmeroids (except retropinnids); some alepocephalids; stomiid stomiiforms (Fujita, 1990, figs. 84 and 85); synodontoids and a subgroup of ipnopids among aulopiforms (Baldwin and Johnson, this volume); and acanthomorphs (Johnson and Patterson, 1993). Whether the absence of CMCs in esocoids is primary or secondary must be resolved by congruence with other characters.

143. CMCs and caudal finrays. Primitively, the upper CMC supports the lowermost ray of the upper caudal lobe, and the lower CMC supports the uppermost ray of the lower lobe (Fig. 14A; Fujita, 1990, figs. 60–63 and 73–78). In argentinids (*Argentina* and *Glossanodon*), microstomatids (*Microstoma* and *Nansenia*), the opisthoproctid *Bathylychnops*, platytroctid alepocephaloids (10 genera examined), and the alepocephalids *Bathylaco* and *Narcetes*, the CMCs together support the lowermost ray of the upper caudal lobe (Figs. 14C and 14D). This condition was illustrated in argentinids by Fujita (1990, figs. 56 and 57) and was reported in *Bathylaco*, *Narcetes*, and the platytroctid *Mentodus* by Markle (1976). Its distribution implies that the derived condition, with one finray on both CMCs, is synapomorphous for Argentinoidei (argen-

tinoids + alepocephaloids). If so, three reversals to the primitive pattern must be accepted: in bathylagids (Fig. 14B), opisthoproctids (except *Bathylychnops*), and alepocephalids (all except *Bathylaco* and *Narcetes*).

144. Caudal scutes. Fujita (1990, table 2) recorded upper and lower caudal scutes in *Elops*, a few clupeids, *Chanos, Alestes, Argentina, Glossanodon, Osmerus, Hypomesus,* and various aulopiforms. Their distribution correlates well with that of the urodermal (no. 146, below); the only substantial differences are that scutes occur in a few clupeomorphs and ostariophysans, where no urodermal is recorded, and scutes are not recorded in coregonids or myctophiforms, where there is a urodermal. It can be difficult to discriminate a small caudal scute (unpaired) from a procurrent ray (paired) [for example, we believe that *Plecoglossus* has caudal scutes, whereas Fujita (1990, fig. 63) took the structures to be procurrent rays].

145. [Begle's 9: Principal caudal rays 10/9 (0), 9/9 (1), or 8/8 (2). State (1) coded in retropinnids, state (2) in galaxiids, *Lovettia, Aplochiton,* and *Lepidogalaxias.*] In Begle (1991) the character was two-state, with (1) for 9/9 or less, and an undescribed state (2) was coded for galaxiids, *Lovettia, Aplochiton,* and *Lepidogalaxias.* Also (Begle, 1991, p. 53) retropinnids were wrongly diagnosed by "Principal caudal rays 8/8" rather than 9/9.

146. Urodermal. Fujita (1990, table 2) recorded a urodermal in *Elops, Argentina* (Fig. 13A), *Glossanodon, Osmerus, Hypomesus* (Fig. 13C), *Plecoglossus, Coregonus* (Fig. 13B), a few aulopiforms, and several myctophiforms. There is also a urodermal in microstomatids and opisthoproctids (Greenwood and Rosen, 1971, figs. 13 and 15; Kobyliansky, 1990, fig. 14), in the bathylagid *Bathylagichthys* (Kobyliansky, 1986, fig. 19), in the coregonids *Prosopium* (Arratia and Schultze, 1992) and *Stenodus,* and in all other osmerids (*Allosmerus, Mallotus, Spirinchus,* and *Thaleichthys*). No urodermal is recorded in Recent osteoglossomorphs, non-elopid elopomorphs, clupeomorphs, ostariophysans, alepocephaloids, salmonids, galaxioids, salangids, esocoids, stomiiforms, or acanthomorphs. In some Jurassic teleosts there are two urodermals (e.g., *Allothrissops, Ascalabos, Tharsis,* and various "*Leptolepis*" spp.; Patterson and Rosen, 1977; Arratia, 1991), whereas others have one (e.g., *Anaethalion* and *Leptolepides*). Arratia and Schultze (1992, p. 247) proposed that the urodermal is "independently acquired" in coregonids, osmerids and/or argentinids, and myctophiforms, but to us its distribution indicates that it is homologous throughout Recent teleosts and has been lost repeatedly.

147. [Begle's 27: Caudal fin margin incised/deeply forked (0) or rounded/emarginate (1). State (1) coded in *Lepidogalaxias* and reported in some galaxiids.] State (1) also occurs in umbrids.

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148. [Begle's 12: Extrascapular present (0), attached to pterotic (1), or absent (2). State (1) coded in *Argentina* and *Glossanodon*, and state (2) in galaxiids, *Aplochiton, Lovettia, Lepidogalaxias,* and salangids. In Begle (1991) the character was two-state, with (1) for absence.] State (1), "extrascapular is attached to the pterotic in the Argentinidae (Chapman, 1942a)" (Begle, 1992, p. 361), is evidently taken from Ahlstrom *et al.* (1984, tables 42 and 43), who characterized argentinids in that way, probably based on Cohen (1958, p. 101; 1964, p. 3). The character is nonexistent and comes from a misunderstanding of Chapman (1942a), who described the dermal portion of the pterotic in *Argentina* as the "supratemporal." McDowall (1969, p. 819) incorrectly reported that extrascapulars are absent in *Plecoglossus, Spirinchus,* and *Mallotus;* in all there are several ossicles, as in other osmerids (no. 179, below). Among alepocephaloids, extrascapulars are absent in *Leptoderma,* wrongly coded by Begle, and in *Photostylus, Rinoctes, Rouleina squamilaterata,* and *Platytroctes* in our sample. Among esocoids there is an extrascapular in *Esox* and *Novumbra* but none in *Kenoza, Dallia,* or *Umbra.* Begle's state (1) should be deleted and his (2) changed to (1).

149. Internal limb of posttemporal. The internal limb of the posttemporal is primitively ossified in teleosts and attaches to the intercalar. The internal limb is unossified in all southern osmeroids (retropinnids, *Aplochiton, Lovettia, Lepidogalaxias,* and galaxiids). The internal limb is typically ossified in esocoids, salmonoids, alepocephaloids, and argentinoids except opisthoproctids.

150. [Begle's 13: Cleithrum with ventral process descending to meet coracoid just in front of its articulation with scapula (0) or without such a process (1). State (1) coded in galaxiids, *Aplochiton, Lovettia, Lepidogalaxias,* and salangids.] The character is from McDowall (1969). The ventral process is also absent in *Stokellia,* esocoids, *Bathylagus, Opisthoproctus,* and all examined alepocephaloids except *Bathylaco* and some platytroctids; these are all wrongly coded (0). In argentinids, *Bathylaco,* platytroctids, salmonoids, and outgroups such as elopiforms, *Clupea, Chanos, Triplophos,* and *Aulopus* the process is present but different in form from that in osmerids and *Retropinna.* In the latter, the process is narrow-based and straight-sided, extending down to interdigitate with the margin of the coracoid (in *Prototroctes* the process is very small but does interdigitate with the coracoid). In ar-

gentinids, *Bathylaco*, platytroctids, salmonoids, and outgroups the process is long-based and triangular, and the coracoid lies against it. We therefore believe that there are three states of the character: a long-based triangular process (0), a narrow, columnar process (1), and absence (2).

151. Postcleithra. Primitively in teleosts there are three principal postcleithra (Pcl 1–3 of Gottfried, 1989). One or more extra bones, lateral to Pcl 2 and 3, have been reported in *Elops* and most salmonoids [Arratia and Schultze (1987) illustrated two in *Oncorhynchus gairdneri*, and Sanford (1987) recorded one as present in all salmonoids except *Prosopium* and *Thymallus*, with four on one side in an *O.gorbuscha*]; these extra bones are neglected here. Osteoglossomorphs have only one (or no) postcleithrum, positionally homologous with Pcl 1. Generalized clupeomorphs and characiform ostariophysans have three, as do many aulopiforms (Baldwin and Johnson, in this volume). Ctenosquamates have only two, positionally homologous with Pcl 2 and 3 (Gottfried, 1989). Postcleithra are apparently absent in stomiiforms. In lower euteleosts, Pcl 1–3 are present in salmonoids, argentinids, microstomatids (Kobyliansky, 1990, figs. 11 and 12), and the bathylagid *Bathylagichthys* (Kobyliansky, 1986, fig. 18). Other bathylagids have Pcl 2 and 3, Pcl 2 only, or none (Kobyliansky, 1986). Opisthoproctids lack postcleithra. Among alepocephaloids there is a single postcleithrum, positionally homologous with Pcl 1, in most platytroctids (Sazonov, 1986, figs. 12–15). In the alepocephalids *Bathylaco*, *Bathytroctes*, and *Narcetes* there is a single postcleithrum (Markle, 1976), placed lower than that in platytroctids and which might therefore be Pcl 2. Other alepocephalids lack postcleithra. Osmerids, salangids, retropinnids, *Aplochiton*, and *Lepidogalaxias* lack postcleithra [the "postcleithrum" illustrated in *Salanx* by Roberts (1984, fig. 18) is a cartilage]. In galaxiids, McDowall (1969) illustrated one rodlike postcleithrum (corresponding to Pcl 3) in *Galaxias fasciatus* and reported no postcleithra in several other species. We find a rodlike Pcl 3, sometimes merely a sliver of bone dissociated from the cleithrum, in *Galaxias fasciatus*, *G.maculatus*, *G.occidentalis*, *G.platei*, *G.zebratus*, *Galaxiella*, and *Paragalaxias* and nothing in *Galaxias fontanus*, *G.paucispondylus*, *Neochanna* and *Nesogalaxias*. There is a rodlike postcleithrum, dissociated from the cleithrum, in *Lovettia*. Esocoids have one postcleithrum, positionally homologous with Pcl 3.

In summary, among noneurypterygian euteleosts, absence of postcleithra characterizes stomiiforms, opisthoproctids, and osmeroids, with Pcl 3 reacquired in *Lovettia* and some galaxiids; absence of Pcl 3 characterizes alepocephaloids; and absence of Pcl 1 and 2 characterizes esocoids.

152. [Begle's 7: Mesocoracoid present (0) or absent (1). State (1) coded in galaxiids, *Aplochiton*, *Lovettia*, retropinnids, *Lepidogalaxias*, salangids, esocoids, *Bathylagus*, *Leptoderma*, *Opisthoproctus*, and *Bathyprion*.] The bathylagids sampled by Begle (his "*Bathylagus*") were *Bathylagoides wesethi* and *Dolicholagus longirostris*, both of which lack the mesocoracoid; it is present in *Bathylagichthys* and *Melanolagus* (Kobyliansky, 1986).

153. [Begle's 93: Coracoid with ventral process short, not extending below ventral margin of pectoral girdle (0), or narrowly elongate, extending below pectoral girdle (1). State (1) coded in *Alepocephalus*, *Talismania*, platytroctids, *Leptoderma*, *Bathyprion*, and *Rouleina*.] The "ventral process" (e.g., Markle and Merrett, 1980, fig. 5; Markle and Krefft, 1985, fig. 3) is the postcoracoid process, which is long in all larval teleosts; retention of the process, as in many alepocephaloids and in salangids (Fig. 15F; Roberts, 1984, fig. 18) and *Lovettia* (Fig. 15I), is a paedomorphic feature. Platytroctids (Sazonov, 1986, figs. 12–15) have a short postcoracoid process, comparable to that illustrated by Markle (1976, figs. 22 and 23) in *Narcetes* or *Bathylaco*, both coded (0) by Begle.

154. Number of pectoral radials. Primitively there are four pectoral radials in teleosts, and this number is remarkably constant. In alepocephalids, there are two radials in *Bathylaco*, two in *Bathyprion*, three or four in *Leptoderma*, three in *Photostylus*, three or four in *Rinoctes*, two or three in *Rouleina*, and three in *Xenodermichthys* (Markle, 1976; Markle and Merrett, 1980; personal observation). Among bathylagids, there are three radials in *Dolicholagus* and *Lipolagus* (Kobyliansky, 1986, figs. 14 and 15).

155. Form of first pectoral radial. In most osmerids and in retropinnids the first pectoral radial is modified in comparison with outgroups (Figs. 15A and 15B): it is enlarged, thickened, and embraces the scapula proximally (Figs. 15C and 15D). The first pectoral radial is unmodified in *Mallotus*, salangids, *Aplochiton*, *Lovettia*, *Lepidogalaxias*, and galaxiids (Fig. 15).

156. Proximal articulation of third pectoral radial. In salangids, *Lovettia*, and *Lepidogalaxias* the third pectoral radial tapers proximally and fails to reach the scapulocoracoid (Figs. 15I and 15J).

157. Proximal articulation of fourth pectoral radial. In the osmerids *Allosmerus*, *Osmerus*, *Plecoglossus*, *Thaleichthys*, and in large *Mallotus* (Fig. 15G), the fourth pectoral radial tapers proximally and fails to articulate with the scapulocoracoid. In *Hypomesus* and *Spirinchus* (Fig. 15C), as in outgroups (Figs. 15A, 15B,

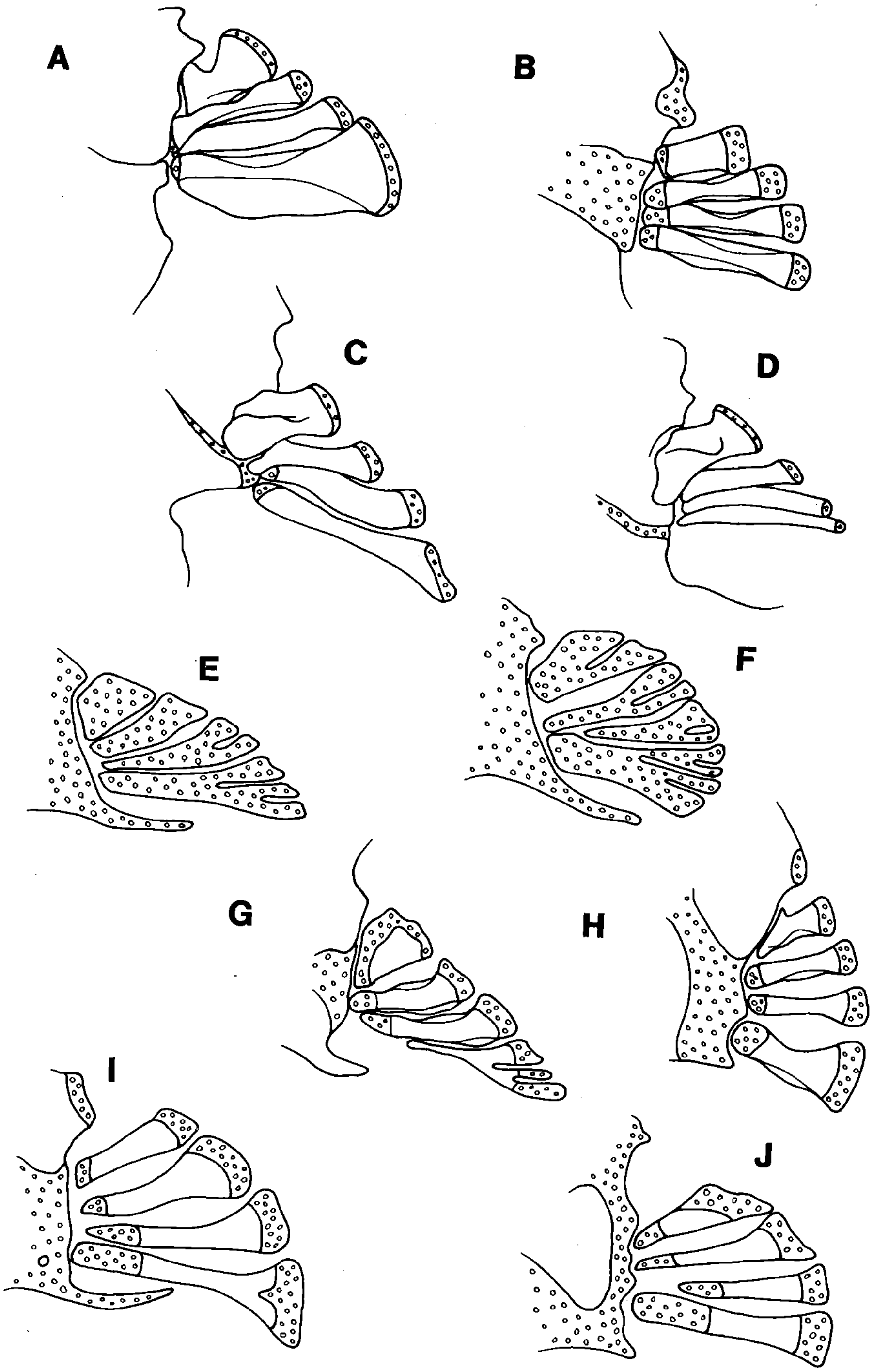


FIGURE 15 Pectoral radials of left side, lateral view, in (A) *Argentina sphyraena,* USNM 238015, 127 mm SL; (B) *Salmo trutta,* BMNH 1983.10.17.5, 74 mm SL; (C) *Spirinchus starksi,* USNM 342052, 95 mm SL; (D) *Retropinna retropinna,* BMNH 1964.4.30.19, 83 mm SL; (E) *Mallotus villosus,* HSU 89-282, 61 mm SL; (F) *Salangichthys microdon,* BMNH 1996.2.6.1, 81 mm SL; (G) *Mallotus villosus,* AMNH 26286, 137 mm SL; (H) *Galaxias occidentalis,* AMNH 31478, 79 mm SL; (I) *Lovettia sealei,* BMNH 1937.8.22.1, 41 mm SL; (J) *Lepidogalaxias salamandroides,* USNM 339265, 44 mm SL.

and 15D), the radial articulates with the scapulocoracoid.

158. Form of fourth pectoral radial. In *Mallotus* and salangids the fourth pectoral radial is multifid distally (Figs. 15E–15G), with at least three branches in *Mallotus* and often more in salangids. Sazonov (1986, fig. 12) illustrated a similar modification in the alepocephaloid *Platytroctes*. In salangids the distal parts of all the pectoral radials are subdivided (Fig. 15F; Roberts, 1984, fig. 18). In adult *Mallotus* the lowermost radial is trifid or quadrifid in all our specimens, and in small fishes the third radial is also bifid (Figs. 15E and 15G).

159. [Begle's 107: Pectoral fin small, develops late in ontogeny (0) or large and develops early in ontogeny (1). State (1) coded in *Argentina, Bathylagus,* and *Glossanodon*.] The character is taken from Ahlstrom *et al.* (1984). Begle's text allocates the derived state to all argentinoids (i.e., including *Opisthoproctus*). In either case Begle's coding appears to be based on misreading of Ahlstrom *et al.* (1984, p. 161, tables 42 and 43), who credited the derived state to Microstomatidae and Opisthoproctidae. So coded, the character becomes autapomorphous for *Opisthoproctus* in Begle's sample.

I. *Pelvic Girdle and Fin*

160. [Begle's 14: Posterior pubic symphysis present (0) or absent (1). State (1) coded in galaxiids, *Aplochiton, Lovettia, Lepidogalaxias,* and salangids.] The character is from Fink (1984b). The symphysis is also absent in esocoids (Wilson and Veilleux, 1982, fig. 11), *Opisthoproctus* (and other opisthoproctids), and in Begle's sample of bathylagids (though not in *Bathylagichthys*, Kobyliansky, 1986, fig. 13). In all osmerids except *Hypomesus, Osmerus,* and *Plecoglossus*, the symphysis is narrow, ligamentous, and very weak (Fig. 16D).

161. [Begle's 34: Pelvic bone without (0) or with (1) ventral condyle articulating with the first three or four hemitrichia. State (1) coded in all Osmeroidei except *Lepidogalaxias*.] The character originated with McDowall (1969, table 2) and was discussed by Howes and Sanford (1987b, p. 27). The osmerid condition is shown in Figs. 16C and 16D. There is no trace of this condyle in galaxiids, *Aplochiton,* or *Lovettia,* as Figs. 16F and 16G and McDowall's illustration (1969, fig. 6) show. We agree with Fink's (1984b, fig. 107) assessment that the condyle occurs only in osmerids, some salangids, and retropinnids.

162. Form of pelvic articular surface. In the osmerids *Hypomesus, Osmerus* and *Plecoglossus* the articular surface of the pelvic girdle is short and almost transverse, as in retropinnids and salmonoids (Fig. 16; Klyukanov, 1975, fig. 12). In other osmerid genera and in salangids (Figs. 16D and 16E) the girdle has a long cartilaginous medial border that does not project medially beyond the level of the ossified margin in front of it, and the articular surface of the girdle is elongate and oblique, lying at about 45^0 to the long axis of the fish [Weitzman (1967, fig. 5) and Klyukanov (1975, fig. 12) show the oblique articular surface in *Spirinchus* and *Thaleichthys* but do not indicate the extent of the cartilaginous symphyseal area].

163. Medial membrane bone extension of pelvic girdle. In *Lovettia* and *Lepidogalaxias* (Figs. 16G and 16H) the pelvic bone has a medial membrane bone lamina with a fimbriate margin. Though trivial, we have not observed this configuration elsewhere in osmeroids.

164. Pelvic radials. Primitively in teleosts there are three pelvic radials (Johnson, 1992), as in alepocephaloids (Sazonov, 1986, fig. 16), argentinids, salmonoids and osmeroids (Fig. 16). Esocoids are unique among lower euteleosts in having no pelvic radials (Johnson, 1992). The number of pelvic radials varies within alepocephalids. Most have three, but *Leptochilichthys* and *Photostylus* have two, and *Leptoderma* has one.

165. [Begle's 85: Pelvic splint present (0) or absent (1). State (1) coded in *Lovettia*, salangids, *Bathylagus, Talismania,* platytroctids, *Leptoderma, Opisthoproctus,* and *Rouleina,* with *Glossanodon* polymorphic.] *Lepidogalaxias* is wrongly coded (0), whereas *Lovettia* and *Bathylagus* (Kobyliansky, 1986, fig. 13) are wrongly coded (1). Platytroctids are polymorphic; there is a splint in *Matsuichthys* (Sazonov, 1992, p. 28), and we have observed one in *Pellisolus,* though not in several other platytroctid genera.

J. *Median Fins*

166. [Begle's 8: Dorsal fin anterior (0) or posterior (1). State (1) coded in all galaxioids, salangids, *Alepocephalus, Talismania* and *Leptoderma*.] However the character is defined, esocoids are mistakenly coded (0) [coded (1) in Begle (1991)]. We have assumed that "posterior" means originating behind the pelvics since that is the only definition that would differentiate *Aplochiton* or *Prototroctes* from *Mallotus* or *Allosmerus*. By that definition, all alepocephaloids have state (1).

167. Middle radials in dorsal and anal fin. Esocoids (esocids and umbrids) share a derived condition: in the dorsal and anal fins of *Esox* (Bridge, 1896) and *Umbra* (Wilson and Veilleux, 1982) ossified middle radials develop only on the central pterygiophores (none ossify in *Dallia* or *Novumbra*), not through to

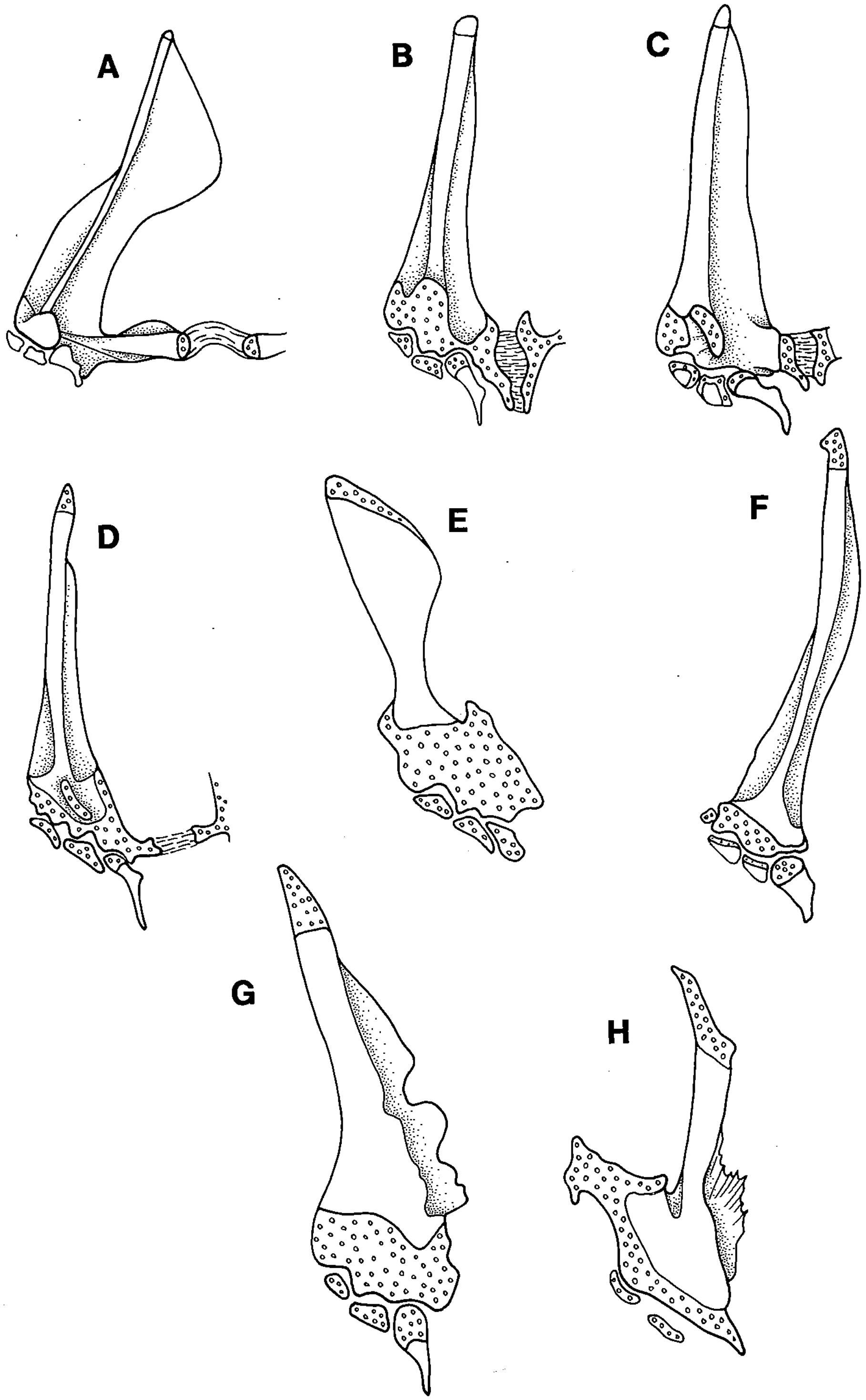


FIGURE 16 Right pelvic girdle, in ventral view, in an argentinid (A), a coregonid (B) and osmeroids (C–H). (A) *Argentina georgei*, USNM 187834, 125 mm SL; (B) *Coregonus lavaretus*, BMNH 1996.2.6.20, 73 mm SL; (C) *Hypomesus transpacificus*, BMNH 1984.6.28.11, 65 mm SL; (D) *Mallotus villosus*, AMNH 26286, 137 mm SL; (E) *Salangichthys microdon*, BMNH 1996.2.6.1, 83 mm SL; (F) *Galaxias fontanus*, BMNH 1983.6.21.1, 72 mm SL; (G) *Lovettia sealei*, BMNH 1937.8.22.1, 41 mm SL; (H) *Lepidogalaxias salamandroides*, USNM 339265, 44 mm SL.

the terminal pterygiophores as they do in other lower euteleosts. Thus esocoids maintain into maturity a state that is transient in the ontogeny of outgroups.

168. Fusion between posterior dorsal pterygiophores. All osmerids (including *Plecoglossus*) and salangids share a derived fusion between the distal parts of the posterior dorsal fin pterygiophores (Fig. 17). This also occurs in some specimens of *Lovettia* (three of four cleared-and-stained). Fusion between dorsal pterygiophores is reported elsewhere only in the aulopiform *Uncisudis* and in veliferid acanthomorphs (Baldwin and Johnson, this volume).

169. [Begle's 28: Adipose fin present (0) or absent (1). State (1) coded in galaxiids and *Lepidogalaxias.*] Although Begle's text (correctly) reports absence in esocoids and all alepocephaloids, presence of the adipose fin is shown as one of three characters uniting esocoids with other euteleosts (Begle, 1992, fig. 9).

170. [Begle's 36: Adipose cartilage absent (0), present (1), or present and pear-shaped (2). State (1) coded in salangids, *Allosmerus, Mallotus,* and *Spirinchus,* state (2) in *Hypomesus, Osmerus, Plecoglossus,* and *Thaleichthys.*] The character originated with Matsuoka and Iwai (1983) and was discussed by Howes and Sanford (1987b). Matsuoka and Iwai described state (2) in *Hypomesus, Osmerus, Plecoglossus,* and *Thaleichthys* and state (1) (a horizontal, fenestrated plate, arched dorsally in transverse section) in the salangid *Salangichthys* and the osmerid *Spirinchus.* According to our observations, Begle wrongly coded *Allosmerus,* which has state (2), and salangids, which exhibit both state (1) (*Salanx* and *Salangichthys*) and state (2) (*Protosalanx* and *Neosalanx*); and *Spirinchus* was miscoded by Begle and misidentified by Matsuoka and Iwai since our material of *S.starksi, S.dilatus,* and *S.lanceolatus* (the species named by Matsuoka and Iwai) shows state (2), and the specimen illustrated by Matsuoka and Iwai (1983, fig. 2b) is clearly *Mallotus.* Begle's state (2) therefore occurs in all osmerids except *Mallotus* and all salangids except *Salanx* and *Salangichthys.*

K. Squamation

171. [Begle's 15: Scales present (0) or absent (1). State (1) coded in galaxiids, *Aplochiton, Lovettia,* salangids, and *Leptoderma.*] Scales are present in mature male salangids, in a row above the anal fin (Roberts, 1984, p. 182), so they either represent a third state (2) or should be coded (0). Among alepocephalids, scales are also absent in *Mirognathus, Photostylus, Rinoctes,* and *Xenodermichthys* and are confined to lateral line ossicles in *Rouleina* (Markle and Merrett, 1980).

172. Radii on scales. Sanford (1987, 1990; fig. 1D) proposed absence of radii on the scales as a character relating salmonoids to osmeroids and argentinoids in the taxon Salmonae. While radii are apparently absent on the scales of all salmonoids and osmeroids (Kobayasi, 1955; personal observation), we have observed well-developed radii on scales of the alepocephaloids *Bajacalifornia, Bathytroctes, Narcetes,* and *Talismania,* and they are illustrated in *Bathylaco* by Nielsen and Larsen (1970, fig. 3) (alepocephaloids usually lose all or most of their scales during capture). In argentinoids, radii are absent in *Argentina* (Cohen, 1964, fig. 4; Roberts, 1993, fig. 8; personal observation on *A.silus* and *A.sialis*), but we have observed them in the microstomatid *Microstoma,* and they occur in *Pseudobathylagus* (*P.milleri;* R. H. Rosenblatt, personal communication). We could find no scales in available specimens of *Glossanodon* or in other bathylagids and opisthoproctids. The presence of radii in alepocephaloids, bathylagids, and microstomatids (as in generalized elopomorphs and in clupeomorphs, ostariophysans, esocoids, and neoteleosts) indicates that absence of radii characterizes salmonoids and osmeroids.

173. Scaling of cheek and operculum. A synapomorphy of esocoids (esocids and umbrids) is that the cheek and operculum are scaled. This derived condition is otherwise found only in eurypterygians (aulopiforms and ctenosquamates), derived elopomorphs (halosaurs, notacanths, and scaled eels), and apparently in one alepocephalid, *Bathytroctes squamosus* Alcock (type-species of *Lepogenys* Parr, 1951).

L. Sensory Canals and Associated Bones

174. Postorbital contact between supraorbital and infraorbital canals. Primitively in teleosts, the supraorbital and infraorbital sensory canals are independent: the supraorbital canal runs straight back through the frontal to the parietal, and the infraorbital canal turns laterally from the dermopterotic into the dermosphenotic (e.g., Patterson, 1975, figs. 145 and 147). This pattern occurs sporadically in Recent lower teleosts (e.g., *Hiodon, Chanos,* many cypriniforms, and some characiforms; Gosline, 1965; Nelson, 1972), and in all alepocephaloids according to Gosline (1969, p. 191; also Matsui and Rosenblatt, 1987, p. 18, on platytroctids; but see *Leptoderma,* Greenwood and Rosen, 1971, fig. 23). Two derived states may be recognized. In the first, there is a postorbital junction between the supraorbital and infraorbital canals, but the primitive posterior (parietal) branch of the supraorbital canal is retained, as in *Elops, Megalops, Argentina, Glossanodon, Hypomesus,* and *Osmerus* (Nelson, 1972, figs. 13, 14, and 16; Patterson, 1970, fig. 29; Greenwood and Rosen, 1971, fig. 21). In the second, there is a postorbital junction between the canals, and the parietal branch

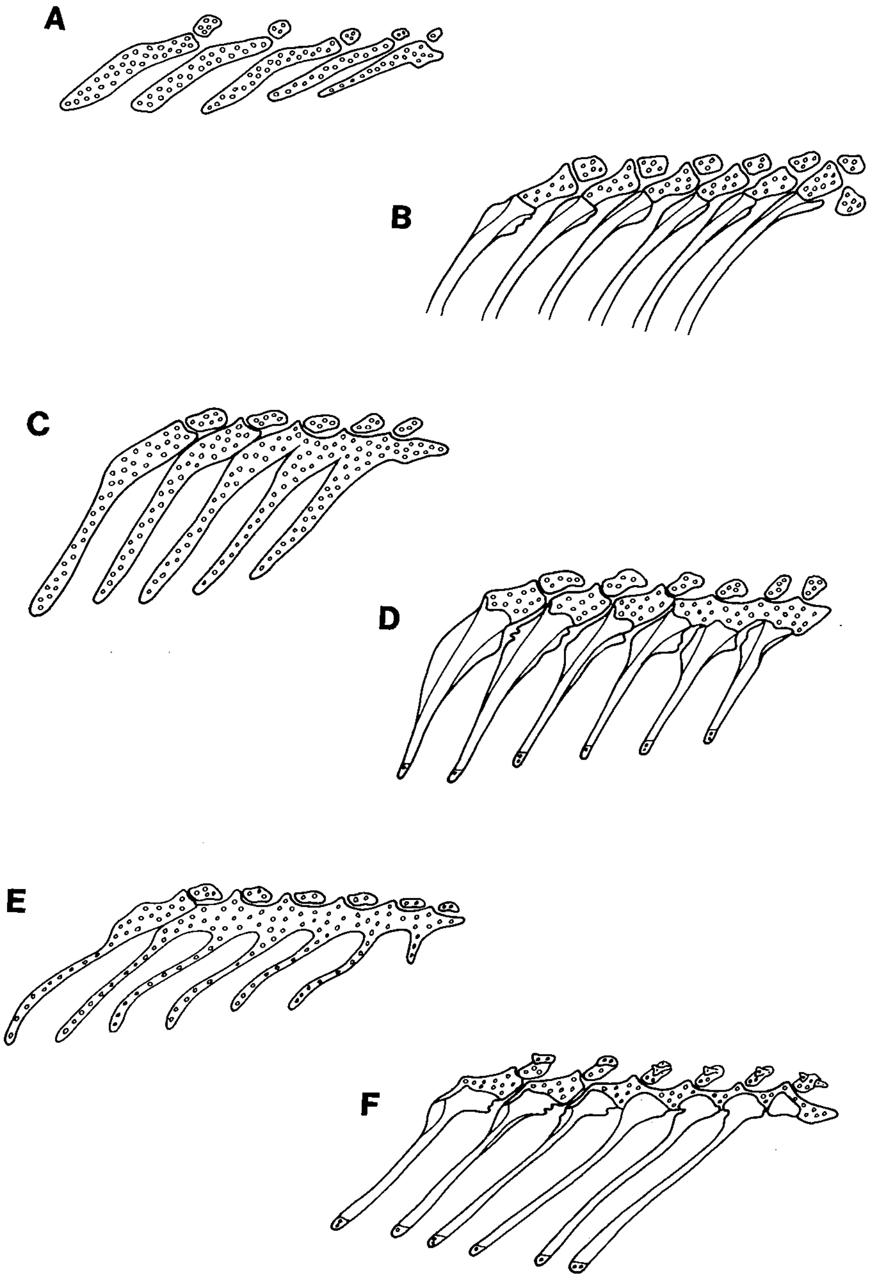


FIGURE 17 Posterior pterygiophores of dorsal fin in (A) Galaxiidae indet. larva, USNM 340197, 26 mm SL; (B) *Coregonus cylindraceus*, BMNH 1963.1.7.10, 49 mm SL; (C) *Osmerus* sp. larva, HSU uncat., 34 mm SL; (D) *Hypomesus olidus*, HSU 86-33, 46 mm SL; (E) *Salangichthys microdon*, BMNH 1996.2.6.1, 83 mm SL; (F) *Mallotus villosus*, AMNH 26286, 137 mm SL. A and B show the primitive teleostean condition, with separate posterior pterygiophores, both in larvae and adults. C–E show the derived osmerid condition, with fusion between the distal parts of the posterior pterygiophores, both in larvae and adults.

is absent, as in esocoids, *Thymallus*, and *Synodus* (Nelson, 1972, figs. 1–4, 7, 8, 14, and 16). In salmonoids, whereas *Salmo*, *Oncorhynchus*, and *Parahucho* have the same derived condition as *Thymallus* (Cavender, 1970, figs. 3 and 4), coregonids and primitive salmonines such as *Brachymystax* and *Hucho* seem to retain the parietal branch but have it displaced laterally in the frontal so that it is directed towards the lateral margin of the parietal (e.g., Berg, 1940, figs. 120 and 122; Shaposhnikova, 1968a, figs. 11–26; Cavender, 1970, fig. 2). In neoteleosts the postorbital junction between the supraorbital and infraorbital canals seems always to occur; the parietal branch persists, for example, in myctophids, *Polymixia*, and many beryciforms.

175. [Begle's 6: Infraorbital sensory canal turning upward behind the eye (0) or deflected posteroventrally (1). State (1) coded in galaxiids, *Aplochiton, Lovettia*, retropinnids, salangids, and *Lepidogalaxias*.] Salangids have state (0) and are wrongly coded (Nelson, 1972, fig. 15B). *Lepidogalaxias* is also wrongly coded since it lacks the infraorbital canal (Nelson, 1972, p. 35). Following Nelson's (1972) and Rosen's (1974, p. 272) comments, we recognize four states: infraorbital canal uninterrupted and unmodified (0); infraorbital canal interrupted, with the anterior portion running posteroventrally to cross the preopercular canal (1), in retropinnids; postorbital infraorbital bones and sensory canal absent (2), in galaxiids, *Aplochiton*, and *Lovettia*; and infraorbital bones and canal absent (3), in *Lepidogalaxias*.

176. [Begle's 19: Infraorbital canal extending to preopercle (1) or not (0). State (1) coded in retropinnids.] If character 94 is coded as suggested above, this character is redundant.

177. [Begle's 52: Supraorbital and preopercular canals each with five or more pores (0) or with three (1). State (1) coded in retropinnids.] The character is from Nelson (1972, p. 38). *Lepidogalaxias* also has three preopercular pores and lacks the supraorbital canal (Nelson, 1972, p. 35).

178. [Begle's 56: Temporal sensory canal present (0) or absent (1). State (1) coded in galaxiids, *Aplochiton, Lovettia*, salangids, and *Lepidogalaxias*.] The character is from Nelson (1972). Salangids have state (0) (Nelson, 1972, fig. 15B) and are wrongly coded.

179. Condition of extrascapular. The teleostean extrascapular is primitively a triangular bone (often with a posterior notch or some other indication of development from two primordia; Ridewood, 1904), carrying a triradiate sensory canal which is received from the posttemporal posteriorly, passes to the pterotic anteriorly, and communicates with its fellow in the midline in the occipital or supratemporal commissure (e.g., *Hiodon, Elops*, and *Megalops*). In several teleostean groups the medial portion of the occipital commissure is carried by the parietal, presumably by fusion of a medial extrascapular, as in argentinoids (no. 20, above), where only the lateral extrascapular occurs. Extrascapulars are absent in several alepocephaloids, osmeroids, and esocoids (no. 145, above). In other lower euteleosts the extrascapular is commonly fragmented into two or more ossicles, often no more than bony tubes surrounding parts of the sensory canal. In coregonids and *Thymallus* there is a tabular (Stearley and Smith, 1993, character 84), triradiate lateral extrascapular, as in argentinids, *Bathylaco*, and some platytroctids (e.g., *Paraholtbyrnia*). In retropinnids there is a tubular, triradiate lateral extrascapular, as in salmonines, some platytroctids (e.g., *Searsia*), and some alepocephalids (e.g., *Alepocephalus bairdii, Binghamichthys*). In all osmerids the lateral extrascapular is fragmented into three (or more) separate ossicles, as it is in several platytroctids (Sazonov, 1986, fig. 3) and alepocephalids (e.g., *Alepocephalus agassizi, Narcetes, Rouleina maderensis*, and *Talismania*). In bathylagids (Kobyliansky, 1986, fig. 1), microstomatids (Kobyliansky, 1990, fig. 3), and most opisthoproctids (Chapman, 1942b, fig. 2, "ST"; Trewavas, 1933, fig. 5, "doc") there are one or more elongate, tubular ossicles extending anterodorsally above the pterotic, towards the rear end of the frontal. To determine whether these bones are extrascapulars [Kobyliansky's (1986, 1990) interpretation] or detached parts of the pterotic requires study of innervation. The opisthoproctid *Bathylychnops* has extremely wide or inflated sensory canals; the extrascapular comprises two cavernous ossicles, one gutterlike and one basically triradiate, from which the temporal canal passes forward to the dermopterotic and the occipital commissure passes medially to the parietal.

180. Sensory canal in posttemporal. Primitively in teleosts, the lateral part of the posttemporal is penetrated by the lateral line, passing forward from the supracleithrum to the extrascapular. This pattern persists in many generalized lower euteleosts: in salmonoids; *Allosmerus, Hypomesus, Osmerus*, and *Plecoglossus* among osmerids; *Holtbyrnia* (Sazonov, 1986, fig. 3), *Paraholtbyrnia, Pellisolus*, and *Searsia* among platytroctids; *Bathylaco* among alepocephalids; and *Argentina, Glossanodon, Bathylagichthys* (Kobyliansky, 1986, fig. 18), *Microstoma, Nansenia*, and the opisthoproctid *Bathylychnops* among argentinoids. Two derived states are recognizable. In the first, there is a separate sensory canal ossicle superficial to the posttemporal, as in *Mallotus, Spirinchus*, and *Thaleichthys* among osmerids; several platytroctids (e.g., *Mentodus, Mirorictus*, and *Searsioides*) and alepocephalids (e.g., *Talismania oregoni, Bathytroctes*, and *Narcetes*); all bathylagids except *Bathylagichthys* (Kobyliansky, 1986, figs. 14–17); and the opisthoproctids *Opisthoproctus* and *Rhynchohyalus*. In the second pattern, there is no canal in the posttemporal and no superficial ossicle, as in esocoids (Jollie, 1975); salangids, retropinnids, *Aplochiton, Lovettia, Lepidogalaxias*, and galaxiids among osmeroids; and *Leptoderma, Platytroctes, Photostylus*, and *Rouleina* among alepocephaloids.

181. Sensory canal in supracleithrum. As with the posttemporal (no. 180), the supracleithrum of teleosts

is primitively penetrated by the lateral line, and there are two derived states, a separate sensory canal ossicle superficial to the bone and no superficial ossicle or canal in the bone. There is general correlation between the condition of the supracleithrum and posttemporal, but some taxa retain the canal through the supracleithrum while having a separate ossicle or nothing over the posttemporal [*Esox*, the osmerids *Mallotus* and *Spirinchus*, the alepocephalids *Bathytroctes*, *Narcetes*, and *Talismania*, the bathylagids *Bathylagus*, *Leuroglossus*, and *Pseudobathylagus* (Kobyliansky, 1986, figs. 15 and 16), and *Opisthoproctus*]. There is an ossicle over the supracleithrum in the osmerid *Thaleichthys*.

M. Reproductive Structures

182. [Begle's 4: Egg not adhesive (0) or surrounded by adhesive "anchor membrane" (1). State (1) coded in all osmerids.] Salangid eggs have "instead of an anchor membrane, an anchoring structure that is composed of various types of filaments that turn out and onto the substrate (Wakiya and Takahashi, 1913 [1937 intended])" (Hearne, 1984, p. 155). According to Begle's (1992) description ("rupturing of an outer 'chorion' . . . producing a structure which adheres to the underlying substrate") the salangid structure qualifies as state (1), and the illustrations of osmerid and salangid eggs in Wakiya and Takahashi (1937, pl. 21), Korovina (1977), and especially Chyung (1961, pl. 51, figs. 242 and 243), indicate that the comparison is sensible.

183. [Begle's 22: Left and right ovaries present (0) or right ovary only (1). State (1) coded in retropinnids.] The character was credited by Begle (1991) to McDowall (1969), who wrote that *Retropinna* and *Stokellia* have only the *left* ovary and that *Prototroctes* has both. The derived state (left ovary only) was later reported in *Prototroctes* (McDowall, 1976, 1984); it also occurs in *Plecoglossus* (Chapman, 1941a).

184. [Begle's 104: Membranous ovarian tunic absent (0) or present (1). State (1) coded in *Talismania*, *Bathyprion*, and *Bathylaco*.] The character is from Markle (1976). According to Markle and Merrett (1980, p. 228), *Bathylaco* has the exposed type of ovary that they consider primitive, whereas *Leptoderma* has the enclosed type. Begle's coding is reversed for those two genera. *Bathyprion* has a type of enclosed ovary different from that in *Leptoderma*, *Rinoctes*, *Talismania*, etc.: it hangs free in the coelom rather than being enclosed by fusion between the ovarian tunic and peritoneum (Markle and Merrett, 1980, fig. 1).

185. Sperm structure. Patterson and Johnson (1995) noted a possible salmoniform character in Jamieson's (1991) records of a single annular mitochondrion in the sperm of alepocephaloids, salmonids, and *Galaxias*. Mattei (1991) also commented on sperm ultrastructure in alepocephaloids and salmonids, citing three characters that seem to relate the two groups, though an annular mitochondrion does not occur in all sampled alepocephaloids or salmonids.

186. [Begle's 33: Nuptial tubercles present (0) or absent (1). State (1) coded in galaxiids, *Aplochiton*, salangids, *Prototroctes*, *Lepidogalaxias*, and all argentinoids and alepocephaloids.] The character is from Wiley and Collette (1970; also Collette, 1977). Presence of nuptial tubercles is one of three characters used by Begle (1992, fig. 9) to unite esocoids with other euteleosts; esocoids lack nuptial tubercles and are wrongly coded (0). Salangids are wrongly coded (1) (Roberts, 1984, p. 183). Among Neoteleostei, tubercles are recorded only in Percidae and *Gadus* (Vladykov *et al.*, 1985), so the group should be coded (1). In salmonoids, tubercles occur only in the three coregonine genera and in *Salvelinus namaycush* (Stearley and Smith, 1993), so that the primitive state for the group is ambiguous. Polarity of the character is also questionable; Begle entered (0) for outgroups, but the only outgroup taxa with tubercles are ostariophysans. *Lovettia* was coded as lacking tubercles in Begle (1991) and as having them in Begle (1992); the latter seems correct (McDowall, 1971).

187. [Begle's 53: Anal fin rays and scales unmodified in males (0), scales anterior to anal fin greatly enlarged and anal fin skeleton modified in males (1), or both preanal scales and anal fin skeleton greatly modified (2). State (1) coded in *Mallotus* and salangids; state (2) in *Lepidogalaxias*.] In Begle (1991) the character was two-state, with an undescribed state (2) entered for *Lepidogalaxias*. No comment.

N. Other Soft Anatomical Features

188. [Begle's 51: Nasal lamellae arranged in a rosette (0) or parallel and longitudinal (1). State (1) coded in galaxiids, *Aplochiton*, *Lovettia*, retropinnids, and *Lepidogalaxias*.] The character is from Howes and Sanford (1987b). No comment.

189. Iris. In *Argentina* and *Glossanodon* there is a crescent of white tissue above the iris (Cohen, 1964). The character is trivial but like no. 127 is one of the few indicators of argentinid monophyly.

190. Swimbladder. Ahlstrom *et al.* (1984) cited a unique synapomorphy of Argentinoidea: the swimbladder (when present; it is absent in bathylagids and some opisthoproctids) is served by microrete mirabilia. All Alepocephaloidea are characterized by ab-

sence of the swimbladder (Greenwood and Rosen, 1971; Markle, 1976).

191. [Begle's 75: Pyloric caeca present (0) or absent (1). State (1) coded in *Lepidogalaxias* and esocoids.] Caeca are also absent in salangids (Roberts, 1984), *Allosmerus* (McAllister, 1963), *Lovettia* (McDowall, 1971), retropinnids (McDowall, 1976, 1979), and among galaxiids in many species of *Galaxias* and in *Galaxiella* and *Paragalaxias* (McDowall and Frankenberg, 1981, figs. 45 and 46).

192. Bone cells. The bones of teleosts are primitively cellular. In lower euteleosts, acellular bone is recorded in two groups, osmeroids and esocoids. In osmeroids acellular bone is reported in *Hypomesus*, *Osmerus*, *Thaleichthys*, and *Galaxias* (Kölliker, 1859; Moss, 1961, 1965). In esocoids it is reported in *Esox*, *Umbra*, and *Dallia* (Kölliker, 1859; Moss, 1961, 1965). Acellular bone has also been recorded in other lower teleosts by Moss (1961, 1965): in both species of *Hiodon* (Kölliker, 1859, found cellular bone, if his "*Hyodon claudulus*" is the same as *Hiodon clodalus* Lesueur, = *H.tergisus*); in the siluroid *Ictalurus* (Kölliker, 1859, also found acellular bone in *Trichomycterus*); and in the eel *Gymnothorax* (Kölliker, 1859, also found acellular bone in *Conger*, *Ophisurus* and *Nettastoma*). Thus bone cells have certainly been lost more than once in teleostean history.

193. [Begle's 96: Saclike shoulder organ absent (0) or present (1, platytroctids only).] No comment.

194. [Begle's 21: Horny midventral abdominal keel absent (0) or present (1). State (1) coded in retropinnids.] The character is from McDowall (1969). There is also a "ventral abdominal keel" (McDowall, 1978, p. 118) in various galaxiids, sometimes in males only. McDowall (1969, p. 810) wrote that this is "not comparable with the keel of retropinnids" but did not say why it is not homologous.

195. Peduncular flanges. In many galaxiids there are prominent fleshy or adipose "caudal peduncle flanges" (McDowall, 1970, p. 354; 1971, p. 39, etc.) extending forward from the caudal fin along the dorsal and ventral margins of the caudal peduncle. These structures are also present in *Lepidogalaxias*.

196. Photophores. In lower euteleosts, photophores occur in most platytroctids (Matsui and Rosenblatt, 1987, table 2; absent in *Barbantus*, *Mirorictus*, *Pellisolus*, *Platytroctegen*, *Tragularius*, and some *Holtbyrnia*), a few alepocephalids (*Anomalopterichthys*, *Rouleina*, *Xenodermichthys*, and *Photostylus*; Markle, 1976), and some opisthoproctids (Cohen, 1964).

197. [Begle's 24: Distinctive cucumber odor of fresh specimens absent (0) or present (1). State (1) coded in retropinnids, *Osmerus* and *Thaleichthys*.] Occurs also in *Argentina* (e.g., Yarrell, 1838; Smitt, 1895, p. 919) and *Mallotus* (Smitt, 1895, p. 879, "stale cucumbers"), and the responsible substance has been isolated in *Hypomesus* (McDowall *et al.*, 1993). The odor also characterizes an Australasian chlorophthalmid, *Chlorophthalmus nigripinnis*, the "Cucumber fish" (Gomon et al., 1994, p. 268). Berra *et al.* (1982), noting that H. B. Bigelow and W. C. Schroeder were unable to detect the odor in *Osmerus*, tested six people with a *Prototroctes* and found that only three could detect the cucumber. One wonders how many qualified sniffers have put fresh *Glossanodon*, opisthoproctids, and alepocephaloids to the test, and what weight to attach to the lack of positive reports in other osmerids and in salangids.

198. [Begle's 84: Midlateral band of silver pigment absent (0) or present (1, *Allosmerus* only).] No comment.

O. Life Cycle

199. Anadromy and diadromy. Anadromy is a life history including a spawning migration from the sea into rivers; diadromy is a more general term, including anadromy, catadromy (spawning migration from rivers to the sea), and amphidromy (migration from sea to freshwater or vice versa, with no relation to reproduction). McDowall (1988, 1993) reviewed the distribution of the two life history patterns in actinopterygians. Among actinopterygians, anadromy occurs in some sturgeons, some alosine clupeids, some percoids, etc. (review in McDowall, 1988), but only in osmeroids and salmonoids can it be considered primitive for suprafamilial taxa. McDowall's (1993) survey of diadromy, the more general phenomenon, shows that osmeroids, salmonoids, and gobioids are the only actinopterygian higher taxa in which diadromy can be considered primitive. Among osmeroids, anadromy occurs in all osmerids except *Allosmerus*, *Hypomesus pretiosus*, *Mallotus*, and *Spirinchus starksi* (all marine), and *Plecoglossus* (amphidromous, larvae move into the sea and over winter before a return migration); in salangids (perhaps not in all; McAllister, 1988, p. 57); in retropinnids except *Prototroctes* (amphidromous, as *Plecoglossus*); and in *Lovettia*. *Aplochiton* is poorly known and may be anadromous or amphidromous. Among salmonoids anadromy occurs in coregonids (*Coregonus* and *Stenodus*) and in many salmonines and is therefore assessed as primitive for the group. *Galaxias* includes one catadromous species (*Galaxias maculatus*) and several amphidromous species; other galaxiids are freshwater, as is *Lepidogalaxias*. Anadromy and diadromy do not occur elsewhere in lower euteleosts.

200. Heterochrony. Paedomorphosis or neoteny is evident in salangids and to some extent in *Mallotus*

and *Lovettia* among osmeroids. The opposite phenomenon, peramorphosis or acceleration, is evident in *Lepidogalaxias*. Gosline (1960, pp. 345, 351) referred to *Lovettia* as "neotenic," citing its "definitely larval appearance," "membranous" median area of the skull roof, and absence of flanges or lamellae on the distal parts of the last few neural and haemal spines (in fact, those flanges are present, Fig. 13F). In the *Lovettia* we studied [40–45 mm SL, average adult size (Blackburn, 1950)] the braincase is largely cartilaginous, the pectoral endoskeleton is unossified in some specimens, there is a long postpectoral process (Fig. 15I), and the supraneurals are unossified. We agree with Gosline's assessment. In salangids, neoteny is documented by Roberts (1984). Early life-history stages of *Mallotus*, *Hypomesus*, *Osmerus*, *Plecoglossus*, and salangids are shown in Okiyama (1988, pp. 66–73). By about 30 mm SL, *Hypomesus*, *Osmerus*, and *Plecoglossus* look much like adults, whereas at 40 mm SL *Mallotus* still looks like a larva, and resembles salangids much more than it resembles osmerids of comparable size. Many details of skeletal development in *Mallotus* could be cited to back up the claim of neoteny; the resemblance in the pectoral endoskeleton between a 60 mm *Mallotus* and a salangid (Figs. 15G and 15H) will serve as an example. *Lepidogalaxias* exhibits peramorphosis, a unique acceleration of skeletal development, so that at an adult size of less than 60 mm SL it ossifies structures that remain cartilaginous or fail to develop in any of its much larger relatives. Examples of those structures include a septal bone and basisphenoid, ossified in the cartilage flooring the orbit and both otherwise absent in all osmeroids; the ossified epicentral cartilages, unknown elsewhere in teleosts; and the scales, absent in all galaxiids and in *Aplochiton* and *Lovettia*. Comparison between preflexion larvae of *Lepidogalaxias* (7 mm NL) and *Galaxiella* (8 mm NL) shows, for example, that in *Lepidogalaxias* all the gill arch elements are ossified, with well-developed teeth on CB5 and UP5, whereas in *Galaxiella* no gill arch elements are ossified and there are no pharyngeal teeth. In the vertebral column, however, *Lepidogalaxias* lags behind *Galaxiella*. By 13.5 mm SL, *Lepidogalaxias* has the head skeleton ossified essentially as in the adult, but centra are still undifferentiated; *Galaxiella* already has the anterior centra differentiated at 8 mm NL. This may explain the separation of PU1 and U1 in *Lepidogalaxias*, whereas the two are fused in all other osmeroids.

P. Molecular Sequence Data

Lower euteleosts are still very poorly sampled for molecular sequences. There are, so far as we know, no sequence data from any alepocephaloid, argentinoid or osmeroid, and the only comparative data are for a few homologous sequences from salmonoids and *Esox*.

Lê *et al.* (1989) presented a partial sequence (ca. 300 nucleotides) of large subunit ribosomal RNA (rRNA) in *Esox*, six other teleosts, and a range of outgroup taxa, but since their teleost sample included only *Clupea* and five acanthomorphs in addition to *Esox*, the results are not helpful (*Esox* as sister-group of acanthomorphs). In subsequent work by Lê (1991; Lê *et al.*, 1993) with a more extensive sample of teleosts, including *Salmo*, and longer 28S rRNA sequences, *Esox* was omitted. Müller-Schmidt *et al.* (1993) analyzed the amino-acid sequence of ependymins of *Esox*, *Oncorhynchus* (two paralogous sequences), *Clupea*, and the cyprinids *Carassius* (two paralogous sequences), and *Brachydanio*. Their work, particularly their evidence for a clupeomorph/ostariophysan clade, is discussed by Lecointre and Nelson (this volume). With no outgroup, they were restricted to phenetic methods. Nevertheless, because their alignment includes two paralogous pairs of sequences (*Oncorhynchus* and *Carassius*) and one from *Salmo salar* (not included in their analysis), it is possible to draw some inferences. If one assumes that divergence between the paralogous *Oncorhynchus* sequences dates from the tetraploidization of the salmonoid genome, the mid-Eocene salmonine *Eosalmo* places that event at least 60 MYA. The *Salmo* sequence differs from its orthologue in *Oncorhynchus* by only three residues (compared with 21 differences between the *Oncorhynchus* paralogues); *Oncorhynchus* and *Salmo* have been distinct for at least 6 MY (Stearley and Smith, 1993). The corrected DNA divergence between *Esox* and the *Oncorhynchus* paralogues (ca. 15.5%) is about 1.6 times as great as that between the *Oncorhynchus* paralogues (9.5%), placing the esocoid/salmonoid divergence at or before roughly 1.6 × 60 or 95 MYA, in the Cenomanian or earlier.

Bernardi *et al.* (1993) analysed the amino-acid sequence of growth hormone (ca. 180 residues) in 25 species of teleosts including four salmonines and *Esox*, with a shark and a sturgeon as outgroups. In their parsimony trees, *Esox* is twinned with the four salmonines in the sister clade to Percomorpha (13 perciforms and a pleuronectiform), with bootstrap support of 69% for the *Esox*/salmonine clade, as against 62% for salmonines. Scanning the alignment, the support for an *Esox*/salmonine clade looks remarkably strong (including several shared residues omitted in the phylogenetic analysis of Bernardi *et al.*), and there is no indication that *Esox* belongs either below salmonines (as in Figs. 1C, 1D, 1F, and 1G) or above them (as the sister of percomorphs in the sample of Bernardi *et al.*).

Complete small subunit rRNA sequences are now available from a range of teleosts, including *Salmo* and *Esox* (Littlewood *et al.*, 1996). The position of *Esox* is labile in parsimony trees generated from those data: it may appear as the sister of (i) *Chanos* + *Clupea* (the only ostariophysan and clupeomorph in the sample); (ii) as the sister of *Salmo* + Acanthomorpha (the only other euteleosts in the sample; nine acanthomorphs sequenced); or (iii) as the sister of *Salmo*. Position (i) is favored by the most conservative alignment, omitting portions where there is any doubt, and may be an effect of "long-branch attraction," since *Esox* is a comparatively long branch terminal, and the *Chanos* + *Clupea* branch is very long. Position (ii) is favored by a less restrictive alignment with all sites equally weighted, and position (iii) by the same alignment with transversions weighted twice as heavily as transitions, which is normally a sound strategy. None of the three solutions has significant bootstrap support.

Phillips *et al.* (1995) reported data from restriction maps (not sequences) of nuclear ribosomal DNA in *Osmerus* and a range of salmonoids. Their data indicate that *Hucho* is paraphyletic, with *H.hucho* closely related to *Brachymystax* and *H.perryi* (genus *Parahucho*) related to other salmonines. Their matrix of percent sequence divergence is interesting in showing the same distance (1.97%) between *Osmerus* and *Coregonus* as between *Coregonus* and *Thymallus* or *Brachymystax* and *H.hucho*, implying close relationship between osmerids and salmonoids.

To sum up, the molecular evidence concerns only salmonoids and esocoids. Growth hormone (rather strongly) and small subunit rRNA (very weakly) support salmonoid/esocoid relationship, for which there is, to our knowledge, no morphological support whatever. Restriction maps of rDNA suggest osmeroid/salmonoid relationship.

III. Discussion of Begle's (1991, 1992) Analyses

Begle's (1992) data matrix contained 108 characters, coded in 33 taxa, of which 26 are genera and 7 are collective at higher levels: outgroups (a hypothetical ancestor comprising a row of zeros), salmonoids, esocoids, neoteleosts, Platytroctidae, Salangidae, and Galaxiidae.

Eleven characters (his nos. 25, 27, 32, 41, 42, 46, 48, 49, 84, 87, and 96) are autapomorphic in Begle's matrix, but after checking and recoding, 4 of those (his nos. 27, 42, 46, and 87) turn out not to be so, whereas a further 7 characters are autapomorphic (his nos. 31, 37, 68, 69, 70, 92, and 107).

As shown in Section II, according to our reading of specimens and the literature, Begle's (1992) matrix contains errors of fact (not interpretation), ranging from minor to gross, in 89 (82%) of his 108 characters. In addition, in our opinion there are errors of interpretation in a further 3 characters (Begle's 10, 23, and 74), leaving 16 characters or 15% that we accept as coded in Begle's publications. Of those 16 characters, 6 (Begle's nos. 32, 46, 48, 49, 84, and 96) are autapomorphic, leaving only 10 that can be used to group taxa. And those 10 are all lifted intact from previous cladistic analyses (Begle's nos. 7, 9, 19, 21, and 54 from Fink, 1984b; nos. 30 and 51 from Howes and Sanford, 1987a,b; no. 53 from Rosen, 1974; and nos. 80 and 102 from Greenwood and Rosen, 1971).

Begle wrote (1991, p. 36; 1992, p. 351) "Every specimen was examined for every character, to check the observed variation against that described in the literature." Apart from the question of claiming to check cucumber odor, ovarian membranes, pyloric caeca, egg structure, etc. in cleared-and-stained specimens, the claim is demonstrably untrue since in a few genera we studied the same specimens (e.g., *Bathylaco*, USNM 206693; *Bathytroctes*, USNM 215493; *Lepto-*

TABLE 1 **Key Relating the Character Numbers in This Paper to Those in Begle (1992)**

1	3
2	62
3	31
4	182
5	130
6	175
7	152
8	166
9	145
10	29
11	32
12	148
13	150
14	160
15	171
16	4
17	79
18	133
19	176
20	69
21	194
22	183
23	33
24	197
25	24
26	44
27	147
28	169
29	49
30	54
31	60
32	34
33	186
34	161
35	27
36	170
37	61
38	36
39	91
40	92
41	93
42	106
43	103
44	107
45	104
46	43
47	108
48	25
49	85
50	95
51	188
52	177
53	187
54	110
55	26
56	178
57	12
58	6
59	97
60	40
61	41
62	71
63	7
64	83
65	77
66	50
67	55
68	72
69	89
70	30
71	8
72	9
73	10
74	17
75	191
76	135
77	131
78	90
79	86
80	87
81	111
82	76
83	51
84	198
85	165
86	73
87	74
88	42
89	37
90	39
91	94
92	96
93	153
94	78
95	56
96	193
97	84
98	45
99	46
100	47
101	112
102	63
103	5
104	184
105	48
106	80
107	159
108	132

Note. The upper numbers (1–108, in numerical order) are Begle's, and the lower numbers (in random order) show where those 108 are covered in our survey of 200 characters.

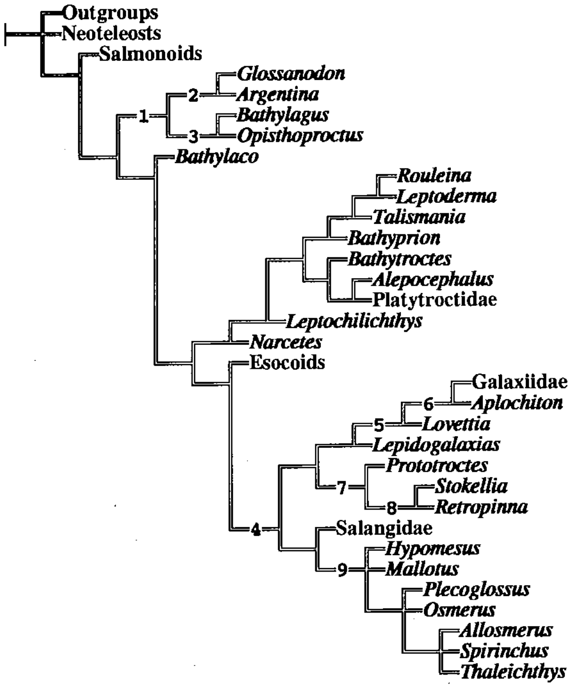


FIGURE 18 Result of parsimony analysis of Begle's (1992) data after correction and recoding. Strict consensus of three equally parsimonious trees, length 231 steps, C.I. 0.42, R.I. 0.73, found by Hennig86 (Farris, 1988). Numbers on branches indicate clades common to this tree and Begle's (Fig. 2).

derma, USNM 215604; *Narcetes*, VIMS 2120; and *Opisthoproctus*, MCZ 61958) and found them insufficiently dissected or incapable of yielding information supposedly checked in them.

Following the general acceptance of cladistic method, it is now fashionable in systematic ichthyology to present only brief descriptions of structure and to concentrate on lists of characters, a matrix, and the results from parsimony analyses. We believe that this fashion merely replaces one black box (evolutionary systematics) by another (the matrix). It is unproductive to divert the systematist's effort from what is primary—studying the fishes with as much care as possible—to what is secondary (and futile if the primary work is not done properly)—manipulating the matrix.

When we ran Begle's (1992) matrix, as published, on Hennig86 (Farris, 1988) we obtained the same result as Begle (Fig. 2).

When we ran the corrected matrix (to be published elsewhere) on Hennig86, not surprisingly, we found a very different result. There are three equally parsimonious trees with the strict consensus shown in Fig. 18. Comparison of Figs. 2 and 18 shows that of the 28 nodes in Fig. 2, only nine (less than one-third) are reproduced in Fig. 18 (numbered 1–9): those linking the four argentinoids, *Argentina* with *Glossanodon*, and *Bathylagus* with *Opisthoproctus*; that linking all osmeroids; that linking the seven osmerid genera; those linking the three retropinnids and *Retropinna* with *Stokellia*; and those linking *Aplochiton* with galaxiids and *Lovettia* with those two.

The most striking difference between Figs. 2 and 18 is in the position of esocoids, which are in the basal polychotomy in Fig. 2 and are the sister group of osmeroids in Fig. 18. Unfortunately, this does not help to resolve the true position of esocoids but is more a reflection of the miscoding of esocoids in Begle's matrix (incorrect in 18 characters, fewer than in several other taxa, but effective because the number of non-zero entries increases from 4 to 17) and of the quality of Begle's data. The characters that place esocoids with osmeroids in Fig. 18 are absence of the orbitosphenoid, mesocoracoid and pubic symphysis, and reduction of the articular and the dorsal portion of the opercle; they are not convincing evidence that the two groups are immediately related.

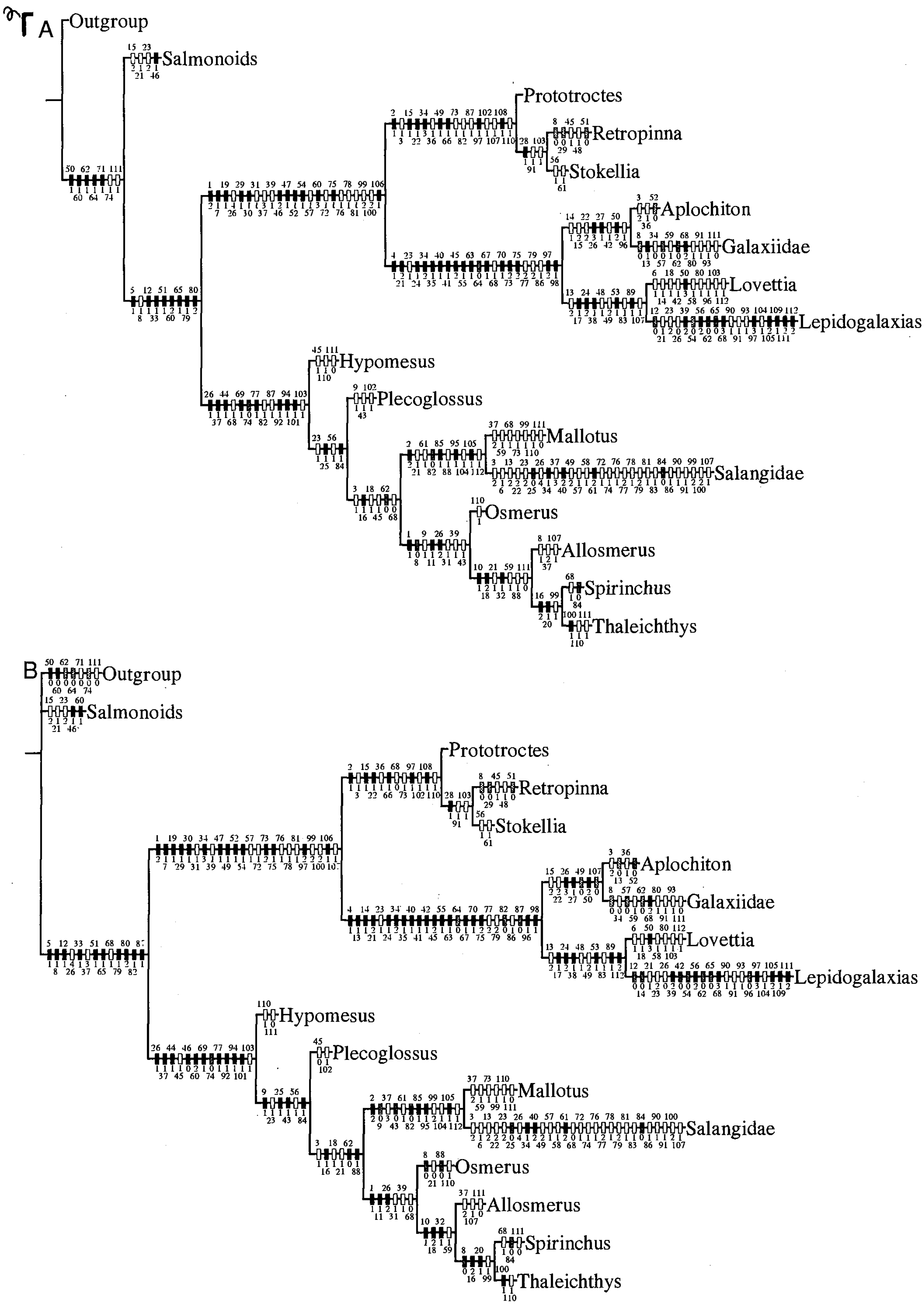
Another major difference between Figs. 2 and 18 is in the position of salangids, which move from within galaxioids to the osmerids. This is a reflection of gross miscoding of salangids by Begle (incorrect in 27 characters, more than any other taxon) and approximates what we believe to be the true position of salangids (below).

IV. Monophyly and Interrelationships of Osmeridae

Osmerids are included with other osmeroids in Appendix 1, a matrix of 112 characters compiled from the survey in Section II by abstracting characters with potential to group two or more osmeroids (i.e., excluding autapomorphies of terminals). Analyzed by Hennig86 and Clados, Appendix 1 generates the trees in Fig. 19. Rather than work through every character at each node in Fig. 19, in this section we evaluate previous work on osmerid interrelationships and comment on the characters that justify our main conclusions. Unless there is an explicit reference to Section II, character numbers in this section are those in Fig. 19 and Appendix 1, where each is tied to the main survey in Section II.

A. Relationships of Salangidae

Salangids have generally been associated with Osmeridae (review in Roberts, 1984) but have not previously been included within that group. The result of our analysis (Fig. 19) is that salangids are nested well within osmerids, as the sister group of *Mallotus*.


A
Outgroup
Salmonoids
Prototroctes
Retropinna
Stokellia
Aplochiton
Galaxiidae
Lovettia
Lepidogalaxias
Hypomesus
Plecoglossus
Mallotus
Salangidae
Osmerus
Allosmerus
Spirinchus
Thaleichthys
B
Outgroup
Salmonoids
Prototroctes
Retropinna
Stokellia
Aplochiton
Galaxiidae
Lovettia
Lepidogalaxias
Hypomesus
Plecoglossus
Mallotus
Salangidae
Osmerus
Allosmerus
Spirinchus
Thaleichthys

Unambiguous synapomorphies supporting that relationship are those at the *Mallotus*–salangid node under the alternative optimizations of the two trees in Fig. 19: the elongate, unossified ethmoid (2); fourth pectoral radial branched distally (85, Fig. 15; in young *Mallotus*, Fig. 15E, the third radial is also branched distally, as in salangids); adipose cartilage a fenestrate plate (95, only in *Salangichthys* and *Salanx* among salangids); and modification of the anal fin skeleton in males (105). In addition, *Mallotus* and salangids share reduction in the number of supraneurals (61, 1–8 in *Mallotus*, one in salangids; homoplasy with *Stokellia*, where the condition is clearly nonhomologous); reversal to the unmodified condition of the first pectoral radial (82, homoplasy with non-retropinnid southern osmeroids); modified scales on the anal fin in males (104, homoplasy with *Lepidogalaxias*); and retardation of skeletal ontogeny (112, homoplasy with *Lovettia*). Further, the adipose fin of *Mallotus* differs from that of all other osmerids in being long-based (McAllister, 1963; Matsuoka and Iwai, 1983, fig. 1, where "*Spirinchus*" = *Mallotus*; see character 170, section II) and resembles the adipose in salangids; and *Mallotus* has 17–22 pectoral fin rays, more than any other osmerid but comparable with the counts in primitive salangids (22–27 in *Protosalanx* and 17–28 in *Salangichthys*).

B. Relationships within Osmeridae

Seven published osmerid phylogenies are summarized in Fig. 20. In our experience, osmerids are unique in the disparity of opinion on their interrelationships. Components common to more than one phylogeny (numbered in Fig. 20) comprise a *Hypomesus* + *Mallotus* clade in Figs. 20A–20D, an *Allosmerus* + *Osmerus* clade in Figs. 20A and 20D, an *Osmerus* + *Allosmerus* + *Spirinchus* clade in Figs. 20C and 20D, an *Osmerus* + *Plecoglossus* clade in Figs. 20E and 20G, and a clade of five genera (excluding *Thaleichthys*) in Figs. 20A, 20C, and 20D. No other groups are shared by any two of the seven interpretations in Fig. 20. There is also notable disagreement on which osmerid genus is the most basal, though four of the seven schemes place *Thaleichthys* at the base of the tree.

Osmerid interrelationships are clearly a difficult problem. Although we do not regard our result (Fig. 19) as the final solution, we are confident about two aspects of it: that *Thaleichthys* and *Spirinchus* are derived osmerids, not basal as Weitzman (1967) and others (Fig. 20) have argued; and that *Hypomesus* is the basal genus (cf. Fig. 20F).

Primitive characters distinguishing *Hypomesus* from all other osmerids (Fig. 19) include the following: endopterygoid teeth in a patch posteriorly, rather than a single row (23); position of metapterygoid (25); all epineurals originating on the neural arch (56, *H. transpacificus* only); and unmodified fourth pectoral radial (84). Primitive characters distinguishing *Hypomesus* and *Plecoglossus* from all other osmerids include the following: presence of vomerine shaft (3, absent in some *Hypomesus*); uninflated otic bulla (16); parietals fully in contact (18); and distal keels on last few neural and haemal arches (62). Primitive characters distinguishing *Hypomesus*, *Plecoglossus*, and *Mallotus* plus salangids from other osmerids include the following: unpaired dermethmoid (1); absence of cartilaginous interorbital septum (11); hyomandibular crest not a triangular spur (26); and form of the lower jaw (31) and basihyal dentition (39).

If *Thaleichthys* and/or *Spirinchus* were basal osmerids (Figs. 20A, 20C, 20D, and 20G; Weitzman, 1967), all the characters cited in the previous paragraph must be wrong or misinterpreted. In Fig. 19, *Spirinchus* and *Thaleichthys* are paired as the most derived osmerids by three characters: globose otic bulla (16), closure of fontanelles in braincase roof (20), and separate sensory canal ossicle over posttemporal (99, also in *Mallotus*). *Allosmerus* is grouped with *Spirinchus* and *Thaleichthys* by a futher four characters: contact in membrane bone between pterosphenoid and prootic (10), complete separation of parietals (18), large Meckelian fossa (32), and presence of epipleural bones (59, also in *Mallotus*).

Thaleichthys has the posterior myodome reduced and the orbitotemporal and otic regions of the braincase wider and shallower than other osmerids, with the pterosphenoids displaced ventrally so that they almost contact the parasphenoid anteriorly (Klyukanov, 1975, fig. 8A). The deep myodome of other osmerids is shared with outgroup taxa such as retropinnids, salmonoids, and argentinids. In *Thaleichthys* there is a separate canal-bearing ossicle over the su-

FIGURE 19 Cladograms of osmeroids based on the data in Appendix 1 analyzed by Hennig86 (Farris, 1988); trees produced with Clados (Nixon, 1992). The single shortest tree is 259 steps long, C.I. 0.59, R.I. 0.77. The two trees show alternative optimizations of characters for which there are equally parsimonious solutions, with A favoring reversals and B favoring forward changes. Character numbers are printed alternately above and below hashmarks, with character states immediately below hashmarks. Black hashmarks indicate uncontradicted synapomorphies, white hashmarks indicate homoplastic forward changes, and grey hashmarks indicate homoplastic reversals. Placing *Osmerus* as the sister of *Mallotus* + salangids and the three terminal osmerid genera increases tree length by three steps, or 1.2%.

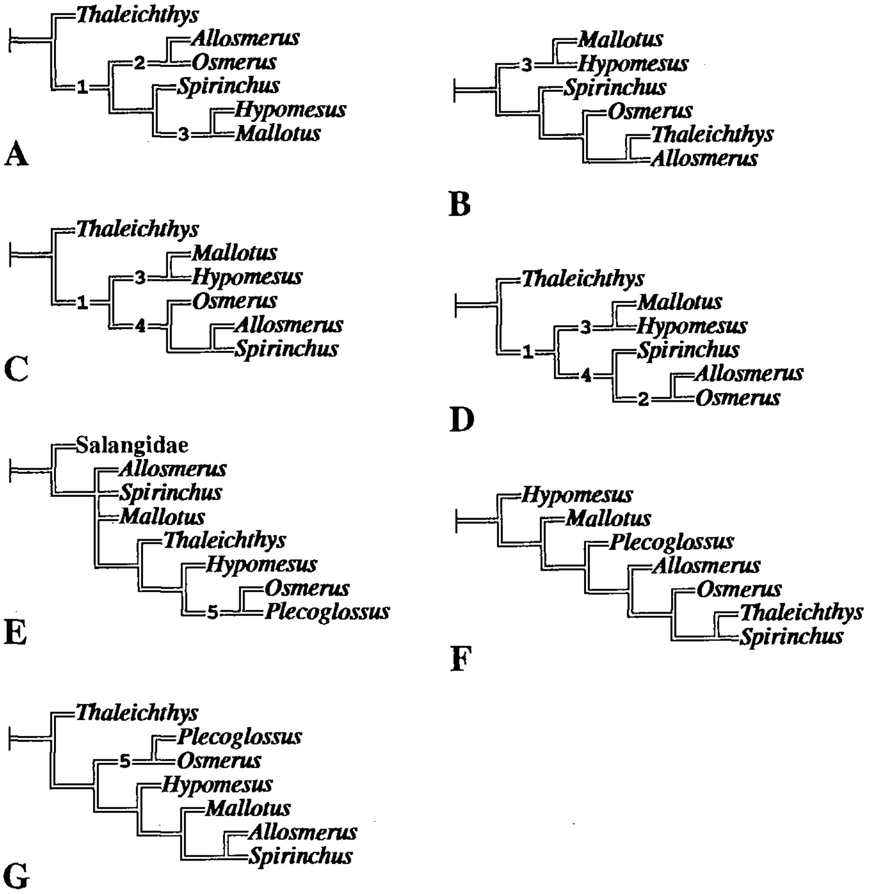


FIGURE 20 Alternative patterns of osmerid relationships. (A) Chapman (1941b). (B) McAllister (1963). (C) McAllister (1966). (D) Klyukanov (1977). (E) Howes and Sanford (1987b). (F) Wilson and Williams (1991). (G) Begle (1991). Numbers on branches denote components common to more than one tree.

pracleithrum, whereas in other osmerids the lateral line penetrates the bone (except in salangids, where the canal is superficial).

Spirinchus has the intercalar small, failing to extend forward toward the prootic as it does in other osmerids; the accessory neural arch (ANA) reduced to a tiny nubbin, whereas it is large in all other osmerids; and seven infraorbitals, whereas other osmerids and outgroups have six (we also observed seven infraorbitals on one side of a specimen of *Thaleichthys*).

While we have confidence in the distal (*Allosmerus*, *Spirinchus*, and *Thaleichthys*) and proximal (*Hypomesus* and *Plecoglossus*) parts of the osmerid tree in Fig. 19, we believe that the central part (*Osmerus* and *Mallotus* + salangids) is less secure. As noted in the legend to Fig. 19, exchanging the positions of *Osmerus* and *Mallotus* plus salangids increases tree length by only three steps, or 1.2%.

Hypomesus, the basal osmerid genus, contains four species. Our examination of three of them (we lacked *H.nipponensis*) yielded suggestions that the genus may be paraphyletic because a primitive state occurs only in one or two of the three species. The characters concerned are vomerine shaft present only in *H.olidus*; palatine most slender in *H.olidus* and *H.pretiosus*; basihyal toothplate least modified in *H.pretiosus*; and all epineurals on the neural arch in *H.transpacificus*. One character that might be derived and is shared by the three species that we studied is the form of the fourth epibranchial (Rosen, 1974, fig. 16). Two epurals also occur in all *Hypomesus*, but the same is true of *Plecoglossus* and *Mallotus*, and in Fig. 19 reversal to three epurals characterizes a derived group of osmerids (character 68).

C. Monophyly of Osmeridae

With the data in Appendix 1, unequivocal synapomorphies of Osmeridae are those that appear at the osmerid node in Fig. 19 under both optimizations: a short hyomandibular crest (26); opercle with a dorsal notch (37); levator process on Eb4 (44); fusion between Un1 and PU1 (69); fragmentation of extrascapular into several ossicles (77, extrascapular absent in salangids); confluence of posterior dorsal pterygiophores (92); adipose cartilage (94); and adhesive membrane of egg (101). Pattern 2A supraneurals (60, state 2) characterize osmerids but appear at the osmerid node only in Fig. 19B. In Fig. 19A the character is at the osmeroid node, with pattern 2B (60, state 3) correctly characterizing galaxioids, whereas in Fig. 19B pattern 2B appears nowhere on the tree. We cannot explain this foible of the Clados program.

Begle (1991, p. 51) listed nine characters of Osmeridae in his sense (including *Plecoglossus* but excluding Salangidae). Three of them (nos. 69, 94, and 101) also occur in salangids and so characterize Osmeridae as we interpret the group. Two of the characters occur in all osmerids (sensu Begle) but not in salangids: metapterygoid shelf (no. 36 in section II; the metapterygoid is unossified in salangids except in *Protosalanx* and some *Salangichthys*) and notch in dorsal margin of opercle (37; salangids have the dorsal part of the opercle reduced). The remaining four characters comprise one that also occurs in salangids but is primitive at this level (103, nuptial tubercles), two that do not exist (orientation of uncinate processes on Pb2 and Pb3, nos. 104 and 107 in section II), and one that is questionable (dumbbell-shaped autopalatine, no. 27 in section II).

V. Monophyly and Interrelationships of Osmeroidei

Appendix 1 is a matrix of 112 characters in osmeroids that generates the trees in Fig. 19. As in the previous section, rather than work through every character at each node in Fig. 19, we here evaluate previous work on osmeroid interrelationships and describe the characters that justify our main conclusions. Unless there is an explicit reference to Section II, character numbers in this section are those in Fig. 19 and Appendix 1, where each is tied to the main survey in section II.

A. Relationships of *Lepidogalaxias*

The phylogenetic position of *Lepidogalaxias* has long been a problem. Begle (1991) reviewed that problem and placed *Lepidogalaxias* as the sister-group of salangids, *Aplochiton*, *Lovettia*, and galaxiids (Fig. 2). That conclusion was facilitated by gross miscoding of salangids (incorrect in 27 characters). In our view, the key to understanding *Lepidogalaxias* is its unique acceleration of skeletal development, detailed under no. 200 in Section II. Searching for the sister group of *Lepidogalaxias*, we tried hard to place it within Galaxiidae, for example, as related to the diminutive *Galaxiella* (McDowall, 1978; McDowall and Frankenberg, 1981), particularly to *G.munda* or *G.nigrostriata*, with which it is sympatric. *Galaxiella* shares with *Lepidogalaxias* extremely well-developed caudal peduncle flanges, a rounded caudal fin, sexual dimorphism, and aestivation (McDowall and Pusey, 1983), but we were unable to find any skeletal features that support such a relationship. Instead, our analysis (Fig. 19) places *Lepidogalaxias* as sister to the Tasmanian *Lovettia*, a fish comparable in size to *Lepidogalaxias* (up to 70 mm SL). Although the two look very different (*Lovettia* looks like a smelt; *Lepidogalaxias* looks like a galaxiid), they share several features: absence of myodome (13, homoplasy with salangids); frontals lacking the posterolateral laminar portion that roofs the orbit (17) so that the pterosphenoid of *Lepidogalaxias* (a bone lacking in *Lovettia*) appears almost as a roofing bone; metapterygoid greatly reduced and removed from hyomandibular (24, state 2); opercle with deeply incised margin (38, Fig. 4; the subopercle is also deeply incised in *Lepidogalaxias*, whereas it is rodlike in *Lovettia*, with a single distal incision in some specimens); uncinate process of Pb3 absent (48, homoplasy with some galaxiids and *Retropinna*); Pb3 without anterior extension (49, state 2, homoplasy with salangids); gap between occiput and V1 (53); pectoral radials (Fig. 15I and 15J) with an identical configuration, the third tapering proximally and failing to contact the girdle (83, homoplasy with salangids); and a medial, membrane bone lamina on the pelvic girdle (89, Figs. 16G and 16H). *Lepidogalaxias* and *Lovettia* are also the only galaxioids to retain a separate ectopterygoid and agree in the shape of the hyoid bar (Fig. 5), which is shallow, without the abrupt deepening of the proximal ceratohyal seen in other galaxioids. Of course there are many differences between *Lepidogalaxias* and *Lovettia*, most of them due to autapomorphies of *Lepidogalaxias* such as the basisphenoid, vomerine and palatine teeth, epicentral bones, separate PU1 and U1, and scales; *Lovettia* agrees with *Aplochiton* and galaxiids in lacking these features.

B. Relationships of *Aplochiton*

If *Lepidogalaxias* and *Lovettia* are sister-groups, *Aplochiton* is the sister of Galaxiidae (Fig. 19), in agreement with Begle (1991). Begle cited four characters supporting this relationship; we accept two of them, the spurlike posterodorsal crest on the hyomandibular (26, state 3; crest very small in *Aplochiton*) and the form of the premaxillary ascending process (27). The only additional features we have noted that support immediate relationship between *Aplochiton* and galaxiids are passage of the efferent pseudobranchial artery through a notch or foramen in the parasphenoid (15, state 2), absence of the ectopterygoid (22, state 2, homoplasy with salangids), and fragmentation of the upper pharyngeal toothplate (50, state 2).

C. *Relationships within Galaxioidea*

Within Galaxioidea, Retropinnidae (*Retropinna, Prototroctes,* and *Stokellia*) are shown to be monophyletic by the unossified ethmoid (2); earlike sphenoid cartilage (15, state 1); fusion of ectopterygoid and dermopalatine (22); absence of both supraorbital and antorbital (34, state 3); fusion between first hypural and parhypural (66); single CMC (73, homoplasy with *Mallotus*); infraorbital canal extending to preopercle (97, state 1); right ovary absent (102, homoplasy with *Plecoglossus*); and horny abdominal keel (108). Begle (1991, p. 53) listed the last three of these, together with three pores in the supraorbital and preopercular sensory canals (177, section II), and three other characters that we reject.

Within retropinnids, our data, like Begle's (1991), indicate pairing of *Retropinna* and *Stokellia*. The three characters favoring that group are maxillo–palatine articulation (28), dorsal fin position (91), and absence of nuptial tubercles (103). However, this pattern of relationships requires independent loss of maxillary and gill-raker dentition in *Prototroctes* and *Stokellia* (or reacquisition of both in *Retropinna*).

Retropinnidae are the sister-group of Galaxiidae s.l. (*Aplochiton, Lovettia, Lepidogalaxias,* and galaxiids), a remarkably well characterized group (Fig. 19) shown to be monophyletic by: toothless vomer (4); buccohypophysial canal in parasphenoid (14, closed in *Lepidogalaxias*); absence of dermopalatine (21, state 2, reversed in *Lepidogalaxias*); reduced metapterygoid (24); lachrymal with cartilage-covered condyle meeting lateral ethmoid (35, no lachrymal in *Lepidogalaxias*); absence of basibranchial teeth (40) and of uncinate process on Eb1 (41) and Eb2 (42, reversed in *Lepidogalaxias*); Eb5 fused to Eb4 to form an enclosed vascular foramen (45, state 2, absent in *Lepidogalaxias*); all anterior neural arches fused to centrum (55); full-length NPU2 (63); well-developed NPU1 (64); five hypurals (67); loss of membranous outgrowth of Un1 (70) and CMCs (73); 16 principal caudal rays or fewer (75, state 2); and absence of extrascapular (77, state 2, homoplasy with salangids), ventral process of cleithrum (79, state 2, homoplasy with salangids), pubic symphysis (86, homoplasy with salangids), ventral pelvic condyle (87), scales (96, reversed in *Lepidogalaxias*), and posterior part of infraorbital (97, state 2) and temporal (98) sensory canals.

Retropinnidae and Galaxiidae s.l. together make up the Galaxioidea. Begle's (1991) Galaxioidea differed from ours in including Salangidae. He listed nine galaxioid characters, of which we accept four: absence of uncinate process on Pb2 (47), 18 or fewer principal caudal fin rays (75, state 1), absence of mesocoracoid (81, homoplasy with salangids), and nasal lamellae parallel (106). Other galaxioid characters include dermethmoid absent (1); pterosphenoid with extensive medial epiphysial arm (7); parietals extending forward to postorbital process (19); no supramaxilla (30); Pb1 articulating with lateral surface of Eb2 (46, state 2); Baudelot's ligament on occiput (54, reversed in *Lepidogalaxias;* double ligament in some galaxiids); no ossified epineurals (57, reversed in galaxiids and homoplastic with salangids); pattern 2B supraneurals (60, state 3); and absence of third uroneural (72, homoplasy with salangids), caudal scutes (74, homoplasy with salangids and salmonoids), urodermal (76, homoplasy with salangids), internal limb of posttemporal (78, homoplasy with salangids), and sensory canal in posttemporal and supracleithrum (99, 100, further homoplasies with salangids). Parsimony also resolves absence of maxillary teeth and ANA as galaxioid characters, with reversal of the first in *Retropinna* (Fig. 19, no. 29) and of the second in *Aplochiton* (Fig. 19, no. 52), but we know of no other well-attested instance of reacquisition of maxillary teeth or ANA.

D. *Monophyly of Osmeroidei*

Within Osmeroidei, Osmeridae (including Plecoglossidae and Salangidae; = Osmeroidea) are the sister-group of Galaxioidea. Begle (1992, p. 353) proposed eight osmeroid characters: vomer with a short shaft (no. 3 in Appendix 1 and Fig. 19; character coded by Begle as shaft absent), loss of orbitosphenoid (5), ventral process on pterosphenoid (8 and 9), reduced articular (33), ventral condyle on the pelvic girdle (87), reduced pterosphenoid (no. 7 in Section II), modified endopterygoid dentition (23), and marginal basihyal teeth (39). The last three were listed by Begle as "additional characters" whose occurrence at the osmeroid node varies with optimization. Absence of the orbitosphenoid, reduced articular, and ventral pelvic condyle withstand criticism, except that the first two characters also occur in esocoids, and the third appears at the osmeroid node only under one optimization (Fig. 19B). The vomerine shaft and basihyal dentition are ambiguous because of variation within osmerids and galaxioids. The pterosphenoid process and reduced pterosphenoid are wrongly interpreted, and the endopterygoid dentition fails because the osmeroid pattern also occurs in platytroctid alepocephaloids. Absence of the basisphenoid (12), a columnar coracoid process of the cleithrum (79), and fusion of PU1 and U1 (65) are additional osmeroid characters, the first miscoded by Begle and so placed as a character of osmeroids + argentinoids, the second miscoded as primitive, and the third miscoded and placed as a character only of a subgroup of Argentinoidea. The coracoid process is lost in Galaxiidae s.l., and the other two characters are reversed in *Lepidogalaxias*.

Further osmeroid characters include enlarged and modified first pectoral radial (82; reversed in *Mallotus*, salangids, and Galaxiidae s.l.), and postcleithra absent (80, state 2; Pcl 3 reappears in *Lovettia* and some galaxiids). Parsimony also resolves toothless gill rakers (51) as an osmeroid character, with reversal in *Retropinna*. We know of no other well-attested instance of reaquisition of gill-raker dentition.

The cucumber odor in osmeroids remains problematic. Under both optimizations in Fig. 19 the character (110) is resolved as independently acquired in retropinnids, *Hypomesus*, *Mallotus*, and *Spirinchus*. It occurs also in *Argentina* and a chlorophthalmid (no. 197, Section II); further sampling is needed, preferably using the methods of Berra *et al.* (1982) and McDowall *et al.* (1993).

Comparison of Fig. 19 with Begle's cladogram of osmeroids (Fig. 2) shows only three internal nodes (out of 13) in common, the pairing of *Aplochiton* and galaxiids, the three retropinnids, and the pairing of *Retropinna* and *Stokellia*.

E. Classification

The relationships indicated in Fig. 19 can be expressed in the following sequenced classification:

- Suborder Osmeroidei
  - Superfamily Osmeroidea
    - Family Osmeridae
      - Subfamily Hypomesinae
        - *Hypomesus*
      - Subfamily Plecoglossinae
        - *Plecoglossus*
      - Subfamily Osmerinae
        - Tribe Salangini
          - *Mallotus*
          - *Protosalanx*
          - *Salangichthys*
          - *Salanx*
          - *Neosalanx*
        - Tribe Osmerini
          - *Osmerus*
          - *Allosmerus*
          - *Spirinchus*
          - *Thaleichthys*
  - Superfamily Galaxioidea
    - Family Retropinnidae
      - *Prototroctes*
      - *Retropinna*
      - *Stokellia*
    - Family Galaxiidae
      - Subfamily Lepidogalaxiinae
        - *Lovettia*
        - *Lepidogalaxias*
      - Subfamily Galaxiinae
        - Tribe Aplochitonini
          - *Aplochiton*
        - Tribe Galaxiini
          - *Brachygalaxias*
          - *Galaxias*
          - *Galaxiella*
          - *Neochanna*
          - *Nesogalaxias*
          - *Paragalaxias*

VI. Monophyly of Argentinoidei (sensu Rosen and Greenwood, 1971; Argentinoidea + Alepocephaloidea)

Begle (1992, p. 355), like Greenwood and Rosen (1971), found that the only unambiguous characters of Argentinoidei are those drawn from the crumenal organ. Begle offered five additional characters whose occurrence at the argentinoid node varied with optimization: reduction in endopterygoid teeth and loss of nuptial tubercles, uncinate process on Eb4, maxillary teeth, and basihyal teeth. Those characters are discussed above (nos. 31, 56, 80, 94, and 186 in Section II), and none can be used to characterize Argentinoidei. The survey in Section II yields two further argentinoid synapomorphies. The first is ventral displacement or descent of the distal parts of the first two to four epineurals (no. 119 in Section II). As concluded in our discussion of the character, argentinoid genera or species in which it is lacking (only one descended in *Platytroctes*, *Talismania aphos*, and *Alepocephalus tenebrosus* and none in most opisthoproctids, *Microstoma*, and *Xenodermichthys*; no ossified epineurals in *Photostylus*) are all indicated, by other evidence (see below), as derived members of their subgroups. The second new argentinoid synapomorphy is no. 143 in Section II, support of the lowermost fin ray of the upper caudal lobe by both caudal median cartilages (CMCs, Figs. 14C and 14D). This occurs in argentinids (*Argentina* and *Glossanodon*), microstomatids (*Microstoma* and *Nansenia*), the opisthoproctid *Bathy-*

lychnops, platytroctids (10 genera examined) and the alepocephalids *Bathylaco* and *Narcetes*. It has not been reported elsewhere. In argentinoids, three reversals to the primitive pattern must be accepted: in bathylagids (Fig. 14B), opisthoproctids (except *Bathylychnops*), and alepocephalids.

In summary, Argentinoidei are characterized by three features: crumenal organ, descent of the first two to four epineurals, and CMCs together supporting the lowermost ray of the upper caudal lobe.

VII. Monophyly and Interrelationships of Argentinoidea

Begle (1992, p. 353) proposed six unambiguous characters of Argentinoidea: narrow levator process on Eb4; short, dumbbell-shaped interhyal; reduced metapterygoid; small, terminal mouth; anterior expansion of vomer; and fusion between PU1 and U1 (he omitted the elongate symplectic, his character 88, which he also found only in Argentinoidea). The characters are evaluated above (nos. 5, 37, 63, 73, 95, and 132 in Section II). Those that withstand criticism (nos. 5, 37, and 63) are related to the small mouth and forwardly displaced jaw articulation. Begle also discussed other characters proposed for Argentinoidea by Greenwood and Rosen (1971) and Ahlstrom *et al.* (1984). He accepted two of Greenwood and Rosen's characters, premaxilla freed from its ethmoid articulation and large supraneural laminae over PU1 and U1; and three characters of Ahlstrom *et al.*, development of dorsal and anal fins within the larval finfold, pustules on the chorion, and micro-rete mirabilia in the swimbladder.

Within Argentinoidea, Begle (1992) summarized divergent recent opinions on relationships, reanalyzed data of Ahlstrom *et al.* (1984), and settled on the pattern [Argentinidae [Microstomatidae [Bathylagidae, Opisthoproctidae]]]. However, Kobyliansky (1990) argued in detail that Microstomatidae and Bathylagidae should be combined as subfamilies of Microstomatidae (the older name); Kobyliansky did not discuss opisthoproctids, but his opinion that bathylagids and microstomatids are sister-groups coincides with Greenwood and Rosen (1971) and differs from Begle (1992).

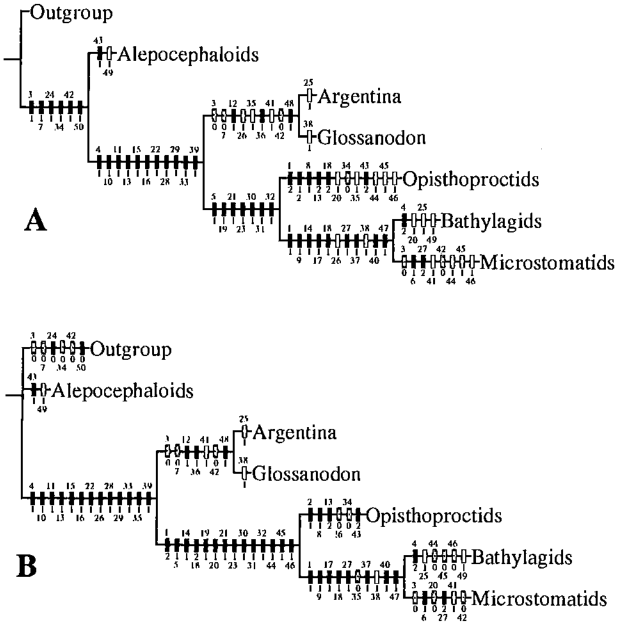


FIGURE 21 Cladograms of Argentinoidea based on the data in Appendix 2 analyzed by Hennig86 (Farris, 1988); trees produced with Clados (Nixon, 1992). Conventions as in Fig. 19. The single shortest tree is 74 steps long, C.I. 0.75, R.I. 0.70. The two trees show alternative optimizations, with A favoring reversals and B favoring forward changes.

Kobyliansky (1986, 1990) showed that *Bathylagichthys* is more primitive than the other seven bathylagid genera that he recognized in retaining a sensory canal ossicle fused to the posttemporal, an opercle without marginal serrations, a toothplate on Bb4, an uncinate process on Eb4, three postcleithra (vs two or fewer), and a urodermal. In microstomatids, we agree with Kobyliansky (1990, p. 174) that *Nansenia* is more primitive than the other two genera (*Microstoma* and *Xenophthalmichthys*, distinguished by "little but the tubular eyes" in the latter; Cohen, 1964, p. 23). *Nansenia* differs from *Microstoma*, and resembles primitive bathylagids, in having a toothplate on Bb4, a free Eb5, descended anterior epineurals, an adipose fin, and numerous interneural and interhaemal cartilages. We studied five of the six genera of opisthoproctids (*Bathylychnops, Dolichopteryx, Macropinna, Opisthoproctus*, and *Rhynchohyalus*). Among those five, *Bathylychnops* differs from the other four and resembles other primitive argentinoids in having a dermopterotic, a sensory canal in the posttemporal, an accessory cartilage between Cb5 and Eb5 (present also on one side in our *Dolichopteryx*), anterior epineurals descended distally, and CMCs together supporting a single finray.

Appendix 2 is a matrix of 50 characters in argentinoid subgroups, alepocephaloids, and an outgroup. Analyzed with Hennig86 (Farris, 1988) and Clados (Nixon, 1992) that matrix gives the trees in Fig. 21. The pattern resolved, [Argentinidae [Opisthoproctidae [Bathylagidae, Microstomatidae]]], is congruent with the conclusions of Greenwood and Rosen (1971) and Kobyliansky (1990), and it contradicts those of Ahlstrom *et al.* (1984) and Begle (1992). A sequenced classification of the group might be (genera in alphabetical order within family-group taxa):

- Superfamily Argentinoidea
  - Family Argentinidae
    - *Argentina*
    - *Glossanodon*
  - Family Opisthoproctidae
    - *Bathylychnops*
    - *Dolichopteryx*
    - *Macropinna*
    - *Opisthoproctus*
    - *Rhynchohyalus*
    - *Winteria*
  - Family Microstomatidae
    - Subfamily Bathylaginae
      - Tribe Bathylagichthyini
        - *Bathylagichthys*
      - Tribe Bathylagini
        - *Lipolagus*
        - *Melanolagus*
        - *Dolicholagus*
        - *Leuroglossus*
        - *Bathylagoides*
        - *Pseudobathylagus*
        - *Bathylagus*
    - Subfamily Microstomatinae
      - Tribe Nanseniini
        - *Nansenia*
      - Tribe Microstomatini
        - *Microstoma*
        - *Xenophthalmichthys*

Characters of the nonterminal groups (based on interpretation of Fig. 21; character numbers from Appendix 2 in brackets) are as follows. Argentinoidea: Parietals carrying medial part of occipital commissural sensory canal (4), endopterygoid teeth absent (10), metapterygoid reduced (11), premaxilla and maxilla toothless (13 and 15), no supramaxillae (16), basibranchials 1–3 toothless (22), Pb2 and Pb3 toothless (28 and 29), ANA absent (33), and Un1 without membranous anterodorsal outgrowth (39). Argentinidae: Ventral arm of symplectic shorter than dorsal arm (12), anterior supraneurals expanded rostrocaudally (36) and white crescent above iris (48). Opisthoproctidae + Microstomatidae: occipital commissure anteriorly placed on parietal (5), lachrymal smaller than succeeding infraorbitals (19), basihyal and Cb5 toothless (21 and 23), UP4 absent (30), UP5 minute (31), and gill rakers of arches four and five differentiated from those of arches two and three (32). Microstomatidae: Mesethmoid with separate laminar dorsal and ventral ethmoids (1), palatine teeth in a single row (9), premaxilla articulating with maxilla posteriorly (14), bladelike dentary teeth (17), supraorbital and dermosphenotic in contact above orbit (18), Pb1 unossified or absent (27), pattern 1 supraneurals (35), PU1 and U1 fused (37), numerous caudal interneural and interhaemal cartilages (40), and extrascapular ossicles present above pterotic (47) (see also Kobyliansky, 1990, table 1).

VIII. Monophyly and Interrelationships of Alepocephaloidea

Begle (1992) proposed four alepocephaloid synapomorphies and two additional characters that might diagnose the group: dorsally reduced opercle, dilatator spine on opercle, middorsal ridge on basibranchials, and toothed gill rakers, with reduced pterosphenoid and toothless maxilla as additional characters. These are discussed above (Section II, our nos. 7, 56, 76, 78, 84, and 112). The dorsally reduced opercle remains uncontradicted (except perhaps in *Bathylaco*, Fig. 7J) but also occurs in all galaxioids and in salangids and esocoids; the dilatator spine is merely another way of describing it. The middorsal ridge on the basibranchials exists only in some platytroctids (toothed) and *Leptochilichthys* (very high and toothless); toothed gill rakers are primitive; and reduced pterosphenoids and a toothless maxilla occur only in a few derived alepocephaloids. The configuration of the opercle is the only character to withstand criticism, a conclusion also reached by Matsui and Rosenblatt (1987, p. 23). Thus alepocephaloid monophyly is unsupported by Begle's data, as is evident from Fig. 18.

Greenwood and Rosen (1971) suggested a few more alepocephaloid characters: separation of parietals, and absence of adipose fin, swimbladder, and urodermal. Patterson and Johnson (1995, p. 27) proposed that monophyly of alepocephaloids is corroborated by the fact that the ossified epipleural series extends unusually far forward, to about V3. More extensive sampling (detailed under no. 123 in Section II) confirms the character, with partial reversal in a few derived genera (epipleurals to V9 in *Rinoctes*, V9–11 in *Leptoderma*, V8 in *Ericara*, V12 in *Conocara* and *Xenodermichthys*, and no epipleurals in *Photostylus*). Reviewing Begle's (1992) data has produced one further plausible alepocephaloid character, branchiostegal cartilages connecting the branchiostegals with the ceratohyal (Section II, no. 74). Elsewhere, we found these only in two osmerids, *Mallotus* and *Hypomesus olidus*, whereas they are widespread in alepocephaloids.

Appendix 3 is a matrix of 59 characters of platytroctids and selected alepocephalid genera (principally those sampled by Begle, 1992), together with argentinids and a hypothetical outgroup to root the tree. Analyzed by Hennig86, that matrix generates 14 shortest trees (length 170 steps, C.I. 0.51, R.I. 0.55) with a strict consensus giving no resolution beyond a monophyletic Alepocephaloidea; platytroctids or *Bathylaco* as the sister of the remaining alepocephaloids; and the terminal grouping [*Rouleina* [*Leptoderma, Photostylus*]]. The 14 trees fall into two sets: 12 in which *Bathylaco* is the basal alepocephaloid taxon and two in which platytroctids are basal. We reject the first set because they imply reacquisition of teeth on the endopterygoid, basihyal, basibranchial, and Pb2 in platytroctids (or independent loss of all in *Bathylaco*); the pattern is favored by parsimony only because the immediate outgroup, argentinids, also lacks teeth on the endopterygoid, basibranchial, and Pb2. In the second set of trees (platytroctids basal) the remaining alepocephaloids are grouped by loss of basihyal teeth (no. 21 in Appendix 3, redeveloped or retained in one lot of *Bajacalifornia*). Beyond platytroctids and *Bathylaco*, the 14 trees place the genera *Alepocephalus, Bajacalifornia, Bathyprion, Bathytroctes, Leptochilichthys, Narcetes*, and *Rinoctes* in a variety of patterns in relation to each other and to the terminal [*Rouleina* [*Leptoderma, Photostylus*]] group.

In order to eliminate the set of trees in which *Bathylaco* is the basal alepocephaloid, we weighted character 21 (basihyal teeth) at 2. With that weighting, the data in Appendix 3 give two trees. One is shown in Fig. 22; the second tree differs from it in pairing *Bajacalifornia* and *Narcetes* as the sister-group of the eight genera beyond them in Fig. 22 and placing those genera in the pattern [*Talismania* [*Rinoctes* [*Leptochilichthys* [*Bathyprion* [*Alepocephalus* [*Rouleina* [*Leptoderma, Photostylus*]]]]]]].

Based on Appendix 3 and Fig. 22, characters of Alepocephaloidea are parietals separated by supraoccipital (no. 5), posttemporal fossa absent (8), branchiostegal cartilages present (18), dorsal part of opercle reduced (19), epipleural bones extending forward to about V3 (32), urodermal absent (43), no more than one postcleithrum (45), and absence of adipose fin (52) and swimbladder (58).

Platytroctids are the sister-group of other alepocephaloids, as indicated by their possession of teeth on the endopterygoid (11), basihyal (21), and basibranchial (22). Platytroctids were originally held to be monophyletic because of one derived character, the shoulder organ (Parr, 1951; Markle, 1976). Matsui and Rosenblatt (1987, p. 23) proposed two further characters: the subcutaneous canal system [which we have not tried to evaluate, but Sazonov (1986, 1992) found it to be restricted to his subfamily Searsiinae] and supraneurals spaced over every second or third vertebra (pattern 4, no. 125, Section II); the same pattern occurs in *Rouleina* and *Xenodermichthys*, where we infer that it is independently derived (33, state 2, Fig. 22). Matsui and Rosenblatt suggested three other platytroctid characters in the caudal skeleton: PU1–3 only half the length of more anterior centra (e.g., PU5); U2 overlapped laterally by the extended bases of hypurals 3 and 4; and first epural much longer than the second. We found that none of these characterizes platytroctids. The length of PU1–3 fails among platytroctids in *Mirorictus, Mentodus, Sagamichthys*, and some *Searsia koefoedi* in our material, and in *Pectinantus* and *Persparsia* as illustrated by Sazonov (1986, figs. 16 and 18), whereas among our alepocephalid material, *Bathylaco* has the "platytroctid" condition. U2 is fully embraced by the bases of hypurals 3 and 4 in several of our platytroctids, but in others (e.g., *Holtbyrnia* and *Pellisolus*) the hypural bases cover less than half the centrum. In alepocephalids, *Bathylaco* has U2 fully embraced by the hypural bases, and in *Talismania aphos* they cover more than half of U2. The ratio between the lengths of the second and first epurals (E2/E1) seems variable within species. In our platytroctids the ratio is >3/4 in *Pellisolus*, and in Sazonov's (1986) illustrations it is >3/4 in *Pellisolus, Holtbyrnia, Maulisia, Persparsia*, and *Platytroctegen*. In alepocephalids the ratio is <3/4 in *Bajacalifornia* and *Rouleina*.

Beyond platytroctids, *Bathylaco* is the sister-group of other alepocephalids, which are united by loss of the basipterygoid process (4), fewer supraneurals (34), a long NPU2 (37), cleithrum without a ventral process (44), reduced extrascapular (54), and absence of sensory canal in posttemporal (55). In Fig. 22, and in the alternative tree, *Bathytroctes* is placed as the sister of the remaining alepocephalids. The characters of *Bathytroctes* tending to favor this are presence of the supraorbital (16), uncinate process on Eb2 (25, otherwise present only in *Bathylaco*), ANA (29), numerous supraneurals (34), and postcleithrum (54). In some other respects, *Bathytroctes* is derived (e.g., characters 7, 18, 26, 27, and 35), and we think it possible that *Narcetes* (for which information is lacking in several characters) is the sister of the remaining alepocephalids, as suggested by its three epurals (38), argentinoid–platytroctid pattern of CMCs and fin rays (42), and other characters in which it seems more primitive than *Bathytroctes*.

We have little confidence in the characters in Appendix 3, too many of which are merely loss of primitive characters, and as the low C.I. and R.I. indicate, they are riddled with homoplasy. There is also much missing data in Appendix 3. Hence we have no confidence in the tree in Fig. 22 as an estimate of

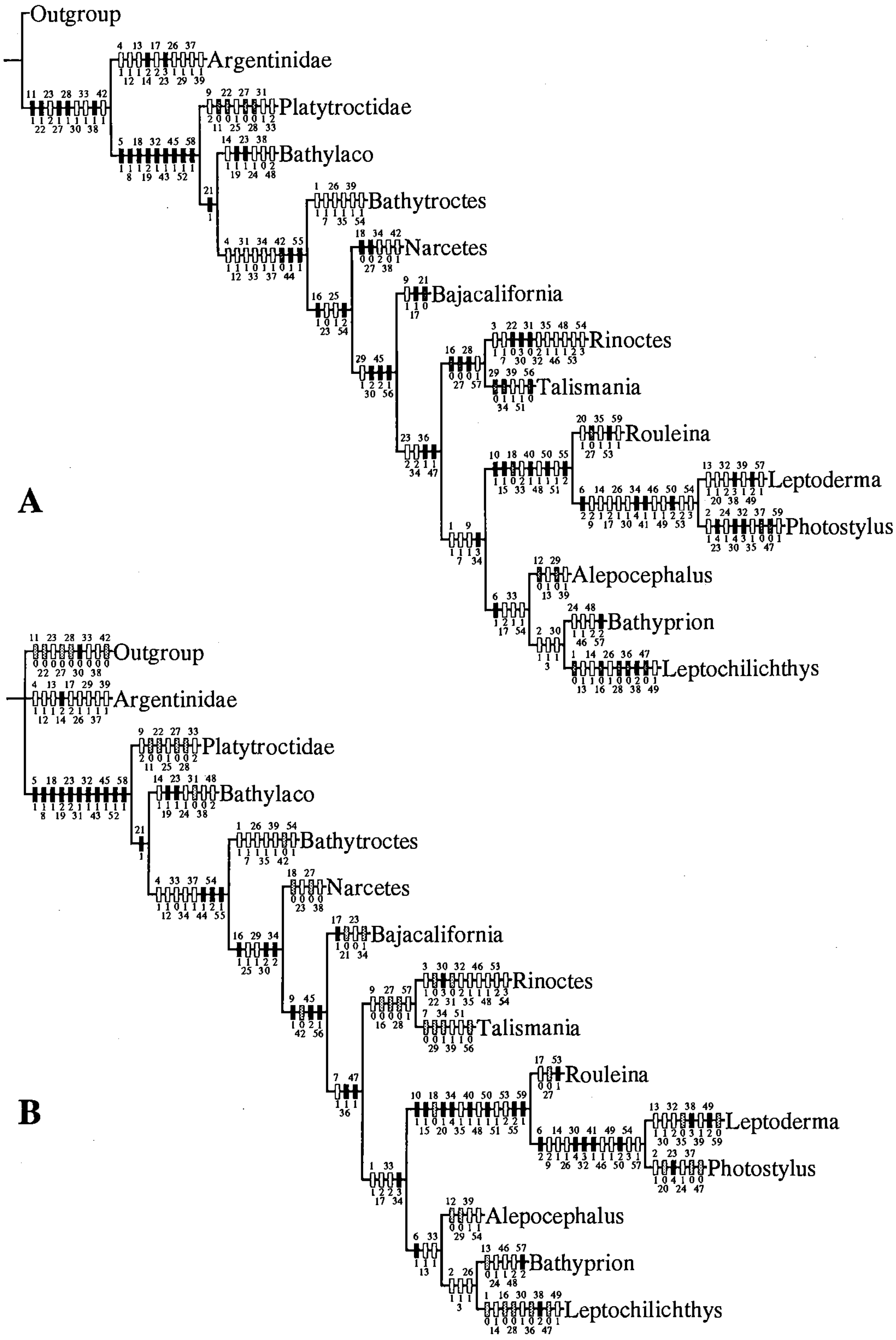


FIGURE 22 Cladograms of Alepocephaloidea based on the data in Appendix 3 analyzed with Hennig86 (Farris, 1988); trees produced with Clados (Nixon, 1992). Conventions as in Fig. 19; weighting as described in text. The two trees show alternative optimizations, with A favoring reversal and B favoring forward changes.

alepocephaloid interrelationships and will not detail characters at the nodes beyond *Bathytroctes*. Alepocephaloids are badly in need of study with better and more comprehensive material than we were able to assemble. Even with our limited material, it seems clear that some genera (*Alepocephalus* and *Talismania*) are nonmonophyletic (e.g., comments in Section II under characters 21, 23, 70, 74, 112, 119, 123, 125, and 179).

In Begle's (1992) cladogram of alepocephaloids (Fig. 2), the only other cladistic analysis of the group, *Leptochilichthys* is at the base, and in the terminal dichotomy platytroctids are twinned with *Talismania*. Platytroctids were misplaced by a combination of miscoding (incorrect in 18 characters) and misinterpreting primitive characters as derived (e.g., the two characters twinning platytroctids and *Talismania* are the condition of the dorsal border of the ceratohyal, and contact between the lateral crest of the hyomandibular and the preopercle). Other nodes in Begle's cladogram involve similar miscoding and/or misinterpretation (e.g., reacquisition of orbitosphenoid and basisphenoid).

On the basis of Fig. 22, a sequenced classification of alepocephaloids might be as follows:

Superfamily Alepocephaloidea
  Family Platytroctidae, ca. 14 genera
  Family Bathylaconidae, *Bathylaco, Herwigia*
  Family Alepocephalidae, ca. 23 genera

IX. Monophyly and Relationships of Salmonoidei

The interrelationships of salmonoids seem now firmly established (Sanford, 1987, 1990; Stearley and Smith, 1993): Coregonidae (*Coregonus, Prosopium*, and *Stenodus*) are the sister-group of Salmonidae, which comprise Thymallinae (*Thymallus*) and Salmoninae (eight Recent genera in Stearley and Smith's scheme; Phillips *et al.*, 1995, add *Parahucho*). Our character survey (Section II) provides a few characters, additional to those listed by Sanford (1990) and/or Stearley and Smith (1993), which reinforce or clarify the monophyly of Salmonidae and Salmoninae. Additional salmonid characters are a distal ceratohyal with no fenestra and closed dorsally by perichondral bone (no. 70, Section II), toothless Pb2 (no. 102), and no urodermal (no. 146). Additional salmonine characters are a tripartite occipital condyle (no. 26; in agreement with Sanford, 1990) and a long NPU2 (no. 129; in agreement with Stearley and Smith, 1993, but reversing their polarity).

Salmonoid monophyly is not in question, although among the salmonoid characters listed by Sanford (1990) and Stearley and Smith (1993), the most striking is still the tetraploid karyotype. The outgroup relationships of salmonoids are unsettled (Fig. 1). The sister-group relationship proposed between salmonoids and galaxiids (Rosen, 1974; Fig. 1B) and between salmonoids and neoteleosts (Fink, 1984b; Fig. 1C) can be dismissed as without support from plausible shared derived characters. Williams (1987; also Nelson, 1994, p. 175; Fig. 1E) proposed a sister-group relationship between salmonoids and esocoids on the basis of two characters of the suspensorium and jaw musculature. The first is an anteroventral wing of the hyomandibular that overlaps the medial face of the metapterygoid. Williams recorded this structure in all esocoids and coregonids but found it to be absent in most salmonids. Sanford (1987, 1990) found the anteroventral process only in *Coregonus* and *Prosopium* and used it as a synapomorphy of those genera. Williams's second character is an adductor mandibulae that inserts directly on the lower jaw and has no ligamentous connection with the maxilla. He recorded that condition in all esocoids, all salmonids, and *Coregonus*, but because *Prosopium* and *Stenodus* have the condition he took to be primitive, he regarded the character as questionable. Our survey has not yielded any characters indicative of immediate relationship between esocoids and salmonoids (Section II and Appendix 4). Relationships between salmonoids and all (Fig. 1F) or some (Figs. 1A, 1D, and 1G) argentinoids + osmeroids (= Osmerae of Begle) remain to be evaluated.

Sanford (1987, 1990; Fig. 1D) proposed two characters relating salmonoids to osmeroids and argentinoids: absence of radii on the scales and well-developed teeth on the margin of the basihyal, a character first proposed and discussed by Nelson (1970b; Fig. 1A). The two characters are discussed above (Section II, nos. 80 and 172). Radii are apparently absent on the scales of all salmonoids and osmeroids but occur in alepocephaloids (e.g., *Bajacalifornia, Bathylaco, Bathytroctes, Narcetes*, and *Talismania*) and argentinoids (e.g., *Microstoma* and *Pseudobathylagus*). Marginal basihyal teeth, Sanford's (1987, 1990) second character, do not occur in Argentinoidea, where the teeth are terminal in *Argentina* and some *Glossanodon*, but are otherwise absent. In alepocephaloids, marginal basihyal teeth occur in the platytroctids *Barbantus, Platytroctes, Sagamichthys, Searsia*, and *Searsioides* (Matsui and Rosenblatt, 1987, table 1), but others have a median row of teeth. Among osmeroids, primitive osmerids (*Hypomesus* and *Plecoglossus*) and *Prototroctes* have the marginal basihyal teeth no better developed than in umbrids (Rosen, 1974; figs. 1, 2, and 4), and the same is true of primitive salmonoids (coregonids and *Thymallus*).

Begle (1991, 1992; Fig. 2) placed argentinoids + osmeroids (his Osmerae) as the sister-group of Neoteleostei, with salmonoids more remote. He offered two characters relating Osmerae and neoteleosts (1992, p. 354): extended alveolar process of premaxilla and reduction of laminar bone on anterior margin of hyomandibular. Both characters (discussed above, Section II, nos. 47 and 51) are wrongly interpreted. Begle (1992, p. 354) offered seven characters supporting monophyly of his Osmerae: reduction or loss of basisphenoid (no. 12 in Section II); ventral vane on Bb1 (no. 83); fusion of rudimentary neural arches to centra in caudal skeleton (no. 130); reduction of pterosphenoid (no. 7); loss of endopterygoid teeth (no. 31); form of basihyal teeth (no. 80); and loss of nuptial tubercles (no. 186) (Begle cited the last four as "additional characters" whose occurrence at the osmeriform node varied with optimization). The seven characters are discussed in Section II. All are shown to involve errors of coding and/or interpretation.

Patterson and Johnson (1995) described two characters relating salmonoids to osmeroids: presence of cartilaginous epicentrals (Section II, no. 121), and absence of epipleural bones (no. 122). They suggested one character relating Argentinoidei to osmeroids + salmonoids as Salmoniformes, lack of proximal forking of intermuscular bones (no. 124), and noted a further possible salmoniform character in Jamieson's (1991) records of a single annular mitochondrion in the sperm of alepocephaloids, salmonids, and *Galaxias* (no. 185). Cartilaginous epicentrals are now found also to occur widely in Argentinoidea and in a few alepocephaloids. The group they characterize, then, is not osmeroids + salmonoids but those plus argentinoids and alepocephaloids. Epipleural bones occur in most osmerid and galaxiid genera, but their pattern in osmerids and their distribution in osmerids and galaxioids imply that they are secondarily derived within each group (character 59, Fig. 19) so that absence of the bones as a salmonoid + osmeroid character is not contradicted. Proximal forking of the epineurals and epipleurals is general in elopomorphs, clupeomorphs, ostariophysans, and myctophiforms. In stomiiforms it does not occur; in esocoids proximal forking occurs only in the epineurals (esocids) or in no more than three or four bones in each series (*Umbra*); and in aulopiforms the bones are forked only in chlorophthalmids and some paralepids (Baldwin and Johnson, in this volume). The lack of proximal forking of intermusculars in stomiiforms, the basal neoteleostean group, weakens it as a salmoniform character, unless (as suggested below) esocoids belong between salmoniforms and neoteleosts.

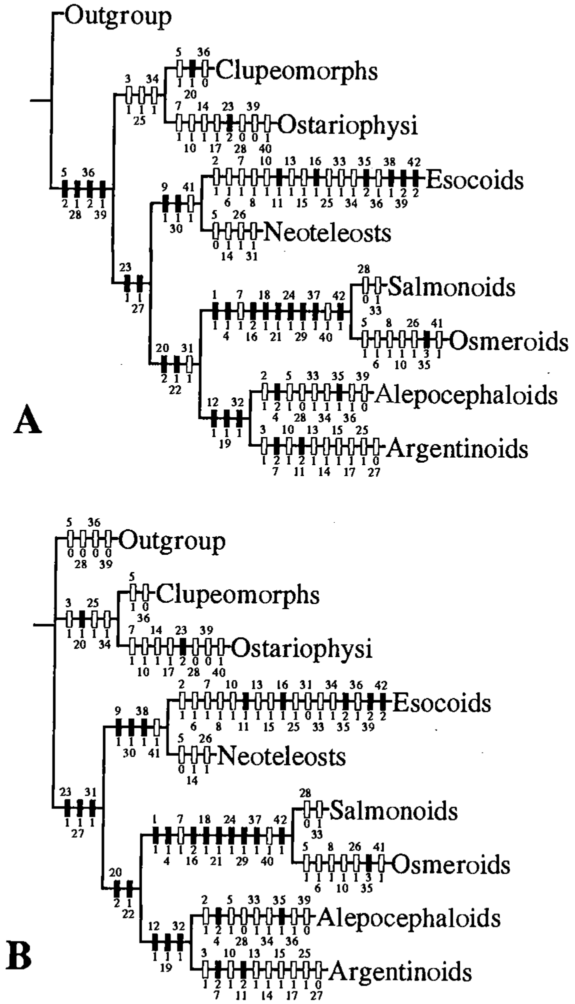


FIGURE 23 Cladograms of the major groups of Clupeocephala based on the data in Appendix 4 analyzed with Hennig86 (Farris, 1988); trees produced with Clados (Nixon, 1992). Conventions as in Fig. 19. The single shortest tree is 89 steps long, C.I. 0.60, R.I. 0.46. The two trees show alternative optimizations, with A favoring reversal and B favoring forward changes.

Appendix 4 is a matrix of 42 characters, abstracted from Section II, in salmonoids, the other major euteleostean groups, clupeomorphs, ostariophysans, and a hypothetical outgroup to root the tree. Analysed by Hennig86, that matrix produces one shortest tree, shown in Fig. 23. Salmonoids fall out as the sister group of osmeroids. Characters of that grouping are separate dermethmoid and supraethmoid (no. 1 in Appendix 4 and Fig. 23); open posttemporal fossa (no. 4); a single supramaxilla (7, homoplasy in ostariophysans and esocoids); UP4 absent (16, state 2); epineurals fused to neural arches on no more than V1 (18); no epipleural bones (21); last few neural and haemal spines keellike distally (24); Un2 anterodorsal to Un1 (29); scales without radii (37); nuptial tubercles (40, homoplasy with ostariophysans); and diadromy (42). With these 11 characters, the grouping of salmonoids and osmeroids has stronger support than any other in Fig. 23. It is perhaps surprising that the group has not been recognized before (Fig. 1).

In Fig. 23, salmonoids + osmeroids are grouped with alepocephaloids + argentinoids by two characters: cartilaginous epicentrals (no. 20) and absence of forking in epineurals and epipleurals (22, entered in Appendix 4 as a query for neoteleosts but resolved by parsimony as general there). Those two characters may seem far from convincing, but we know of no valid characters to support any other pattern of relationships for these groups.

X. Monophyly and Relationships of Esociformes

Esociforms or esocoids comprise only Esocidae (*Esox*, five Recent species) and Umbridae (*Dallia*, *Novumbra*, *Umbra*, and five Recent species). Monophyly of the group was first proposed in a cladistic framework by Nelson (1972) on the basis of modifications of the cephalic sensory-canal system. Among the esocoid characters given by Rosen (1974), the only striking ones are the paired, elongate proethmoids and modification of Eb4 by loss of the levator process or elevation (questionable in *Umbra* and also absent in *Lepidogalaxias*). Our character survey (Section II) yields six further characters supporting esocoid monophyly. First, the basibranchial toothplate is fragmented into two (no. 81, Section II). Second, Pb1 is conical and its tip is closed in bone (no. 100, Section II). Third, the single upper pharyngeal toothplate is UP4, not UP5 (no. 109, Section II). Fourth, there is only a single postcleithrum, homologous with postcleithrum 3 of other teleosts (no. 151, Section II). To our knowledge, the only other teleosts with postcleithrum 3 alone are some galaxioids, the aulopiform *Bathypterois*, and some derived acanthomorphs. Fifth, in the dorsal and anal fins of *Esox* and *Umbra* ossified middle radials develop only on the central pterygiophores (or on none of them in *Dallia* and *Novumbra*) (no. 167, Section II). And sixth, the cheek and operculum are scaled (no. 173, Section II), a derived feature otherwise found only in eurypterygians (aulopiforms and ctenosquamates), derived elopomorphs, and in one alepocephalid.

Within esociforms, monophyly of esocids and umbrids was justified by Nelson (1972). Relationships within umbrids were discussed in detail by Wilson and Veilleux (1982), who agreed with Nelson (1972) that *Novumbra* is the sister of *Dallia* and *Umbra*. Reist (1987) conducted a phenetic analysis of morphometric characters in umbrids, criticized some of the characters used by Wilson and Veilleux, and concluded that *Novumbra* and *Umbra* are more closely related to each other than to *Dallia*. His argument is not convincing, and we accept Nelson's and Wilson and Veilleux's evidence that *Dallia* and *Umbra* are sisters. If so, one equivocal character of esocoids can be resolved. Supraneural pattern (no. 125 in Section II) in esocoids is equivocal because Recent esocids have pattern 2, *Umbra* has pattern 1, and *Dallia*, *Novumbra*, and the Paleocene *Esox tiemani* have a variant of pattern 2 in which the first supraneural is absent. Parsimony resolves pattern 2 or a modification of it as primitive for the group.

Esociform relationships are problematic. Patterson and Johnson (1995, p. 25) reviewed the recent consensus that esocoids are the sister-group of all other euteleosts, including ostariophysans. Begle (1992, fig. 9) summarized that hypothesis with a cladogram in which esocoids are linked with other euteleosts by three characters and are distinguished from them by one. Only one of the three euteleostean characters occurs in esocoids. The three are the adipose fin (absent in all esocoids), nuptial tubercles (absent in all esocoids), and membranous outgrowth of first uroneural. The single character cited to distinguish all other euteleosts from esocoids is the toothplate of Bb4 (no. 82, Section II), present also in some characiforms, bathylagids, microstomatids, and percopsiforms.

Johnson and Patterson (1993, p. 600) distinguished esocoids from other euteleosts (excluding ostariophysans) by the absence in esocoids of median caudal cartilages (CMC of Fujita, 1990). However, as discussed under no. 142 in Section II, we now infer that CMCs have been lost in at least six euteleostean lineages so that whether the absence of CMCs in esocoids is primary or secondary must be resolved by congruence with other characters.

Esocoids are included with clupeomorphs, ostariophysans, and the other major euteleostean groups in the matrix of 42 characters in Appendix 4 and in the trees generated from that matrix in Fig. 23. Esocoids are resolved as the sister group of neoteleosts. The unambiguous characters supporting that relationship are type 4 tooth attachment (no. 9 in Appendix 4) and acellular skeleton (no. 41, homoplasy with osmeroids). Parenti (1986) first used those characters to propose relationship between esocoids and neoteleosts. Less trustworthy characters (to us) are absence of Un3 (no. 30, homoplasy with derived members of several other groups, e.g., galaxioids and salangids) and scaling of cheek and operculum (no. 38), which may be interpreted equally parsimoniously as a character of esocoids and neoteleosts which is lost in stomiiforms, or as homoplastic in esocoids and neoteleosts. Presence of UP4 only (no. 16) is shared by esocoids and ctenosquamates.

Although the evidence relating esocoids to neoteleosts may seem anything but compelling, the alternative solutions have even less in their favor. The current consensus, that esocoids are the sister of all other euteleosts, with (Figs. 1C, 1D, and 1G) or without (Figs. 1F and 1H) ostariophysans, boils down to alternative evaluations of the adipose fin and CMCs. With the data in Appendix 4, the tree in Fig. 1F is 102 steps long, much less parsimonious than the shortest tree (length increased by 13 steps or 15%), whereas the tree in Fig. 1H is 93 steps long, an increase of four steps or 4.5%. We have found no new characters discriminating esocoids from all other euteleosts. The second suggestion (Williams, 1987; Fig. 1E) is that esocoids are the sister of salmonoids. With the data in Appendix 4, the tree in Fig. 1E is 103 steps long, 14 steps or 16% longer than the shortest. We have found no new characters indicating that esocoids are related to salmonoids.

If the pattern shown in Fig. 23 is correct, with esocoids the sister of neoteleosts, parsimony resolves one more of the problematic characters in esocoids. Absence of the adipose fin (no. 36 in Fig. 23) is secondary.

As for the molecular evidence on esocoids (Section IIP), sampling is grossly deficient in all four molecules so far sequenced in *Esox*, but growth hormone (rather strongly) and small subunit rRNA (weakly) both support a salmonoid–esocoid relationship for which there is, to our knowledge, no morphological support.

XI. Monophyly and Relationships of Euteleostei

The euteleost problem is discussed by Lecointre and Nelson (in this volume), who point out difficulties with each of the "characters" previously invoked to define Euteleostei: adipose fin (absent in esocoids and alepocephaloids); nuptial tubercles (absent in esocoids, argentinoids, alepocephaloids, and most neoteleosts); and stegural (questionable in argentinoids and, in their view, esocoids). We accept the molecular evidence (discussed by Lecointre and Nelson) that Clupeomorpha and Ostariophysi are sister-groups. This simplifies the euteleost problem by eliminating ostariophysans, but contributes to the question of how Euteleostei (minus Ostariophysi) might be defined only in a negative way, by indicating that there are teleostean higher taxa (e.g., Clupeomorpha + Ostariophysi) without demonstrable morphological characters.

Appendix 4 and Fig. 23 suggest three characters that distinguish Euteleostei (minus Ostariophysi). The first is pattern 2 supraneurals (no. 23 in Appendix 4). Pattern 2 does not occur in osteoglossomorphs, elopomorphs, clupeomorphs, or ostariophysans; the first three have pattern 1, and the last has a pattern of its own which we call pattern 3. Pattern 2 occurs in all salmonoids and osmeroids, and in basal argentinoids and neoteleosts. Among alepocephaloids it occurs only in the primitive *Bathylaco* and the derived *Alepocephalus*, with platytroctids having the autapomorphous pattern 4. Parsimony resolves pattern 2 as primitive for salmoniforms, but the alepocephaloids are problematic.

The second euteleostean character is the stegural, Un1 with a membranous anterodorsal outgrowth (no. 27 in Appendix 4). This occurs in all euteleostean groups except argentinoids, where parsimony resolves absence as secondary. The third euteleostean character is caudal median cartilages (CMCs, no. 31 in Appendix 4). Their absence in esocoids is problematic, and, as Fig. 23 shows, it is equally parsimonious to treat them as a euteleostean character lost in esocoids or as independently acquired in salmoniforms and neoteleosts.

As for molecular evidence, the ostariophysan plus clupeomorph grouping has very strong support in trees based on partial sequences of large subunit ribosomal RNA (rRNA; Lê *et al.*, 1993) and complete sequences of small subunit rRNA (T. Littlewood, C. Patterson, and A. B. Smith, 1996). In those molecular trees Euteleostei (minus Ostariophysi) are only weakly distinct (bootstrap <50% for both large and small subunit samples), but in the small subunit alignment and on the present (admittedly rudimentary) sample euteleosts are clearly distinguished by the molecular synapomorphy shown in Fig. 24.

Our current estimate of higher level euteleostean relationships (Fig. 23) is summarized in the following classification, which introduces some new rankings and one new name and adapts two old names to new uses.

Clupeocephala
  Otocephala (new)
    Clupeomorpha
    Ostariophysi
  Euteleostei
    Protacanthopterygii
      Order Argentiniformes (new)

Branchiostoma	GUUUUC****G***GAAC
Lampetra	GUUUUC****G***GAAC
Squalus	GUUUUC****G***GAAC
Raja	GUUUUC****G***GAAC
Latimeria	GUUUUC****G***GAAC
Homo	GUUUUC****G***GAAC
Polyodon	GUUUCC****U***GAAC
Lepisosteus	GUUUCC****G***GAAC
Amia	GUUUCC****U***GAAC
Hiodon	GUUUCC****C***GAAC
Elops	GUUUCC****C***GAAC
Megalops	GUUUCC****G***GAAC
Albula	GUUUCC****U***GAAC
Ophichthus	GUUUCC****C***GAAC
Clupea	GUUUUC****G***GAAC
Chanos	GUUUCC****G***GAAC
Esox	GUUUUC***CCC**GAAC
Salmo	GUUUUU**CUUCU*GAAC
Lampris	GUUUUC*UUCUCU*GAAC
Polymixia	GUUUUC*UUCUCU*GAAC
Holocentrus	GUUUUC**UCUCU*GAAC
Lophius	GUUUUCUCUUCUCUGAAC
Fundulus	GUUUUU**CUCCU*GAAC
Sebastolobus	GUUUUC**UUUCU*GAAC
Solea	GUUUUC*UCUCUCUGAAC
Mola	GUUUUC*UUCUCU*GAAC

FIGURE 24 A molecular synapomorphy of Euteleostei (minus Ostariophysi). Positions 924–942 in an alignment of small subunit ribosomal RNA from a sample of craniates. However the nucleotides in bold type are aligned, insertions are synapomorphous for euteleosts.

    Suborder Argentinoidei
    Suborder Alepocephaloidei
  Order Salmoniformes
    Suborder Salmonoidei
    Suborder Osmeroidei
Neognathi
  Order Esociformes
  Neoteleostei

In the first *Interrelationships* the Protacanthopterygii of Greenwood *et al.* (1966) were omitted, as we noted in the first sentence of this paper. We find it necessary to revive Protacanthopterygii, in something close to its original meaning, because of problems in ranking within "salmoniforms." To express the relationships in Fig. 23, either the current Osmeroidei and Salmonoidei must be downgraded, or the current Alepocephaloidea and Argentinoidea must be upgraded. We chose the latter because lowering the rank of Osmeroidei would raise problems in expressing well-resolved relationships within that group using conventional ranks, whereas raising the rank of Alepocephaloidea leaves room to express relationships within a diverse group when they are resolved. The name Neognathi was introduced by Rosen (1973) in the first *Interrelationships* for Euteleostei minus Ostariophysi. That group is now equivalent to Euteleostei. Previously (Patterson and Johnson, 1995, fig. 9) we proposed using Neognathi for Euteleostei minus Esociformes, a group that no longer exists. We now adapt Neognathi for esocoids and neoteleosts, where it is appropriate for fishes characterized by the derived type 4 tooth attachment.

XII. Conclusions

We began this paper with an agenda provided by Fink (1984a). We repeat his seven questions here, with an answer to each. (1) What are the relationships of the Esocoidei? This is still the hardest question to answer, but the solution now current, that esocoids are the sister group of all other euteleosts, has no support, and we propose, like Parenti (1986), that esocoids are the sister-group of neoteleosts. The two groups share type 4 tooth attachment and an acellular skeleton. (2) What are the relationships of the Ostariophysi? Do these fishes lie above or below the Esocoidei? Ostariophysans are the sister-group of clupeomorphs (Lecointre and Nelson, this volume) and esocoids belong above them. (3) What is the pattern of relationships among the traditional 'salmoniform' taxa, exclusive of the Esocoidei and Ostariophysi? See Figs. 19, 21, 22, and 23. (4) What are the relationships of and within the Argentinoidei (sensu Greenwood and Rosen, 1971, i.e., argentinoids plus alepocephaloids)? Argentinoidei, which we rank as Argentiniformes, are the sister-group of Salmoniformes, Salmonoidei + Osmeroidei. See Fig. 21 for relationships within argentinoids. Figure 22 shows our attempt at analyzing relationships within alepocephaloids, but we lacked material and opportunity for a proper study of the group. (5) What are the relationships of and within the Osmeroidei? Osmeroids are the sister-group of Salmonoidei. See Fig. 19 for relationships within osmeroids. (6) What are the relationships of and within the Salmonidae? See (5), Sanford (1990), Stearley and Smith (1993) and Section IX above. (7) Where does *Lepidogalaxias* belong? It is a galaxioid, the sister of *Lovettia*.

Much of this paper, and much of our effort in working towards it, have been effectively wasted in criticizing Begle's (1991, 1992) work. The criticism was necessary only because the work is published, in respected journals and so will be regarded by other biologists as reliable. As we have shown, it is not. In the present context—a volume on the state of the art in fish systematics—we cannot leave the matter without a final comment. The disregard for truth we found in Begle's two papers is ultimately the responsibility of the author, but also indicates in this instance a failure of the system of checks and balances that maintains standards in our science. Surely, at some stage between Begle's writing his papers and their publication, some ichthyologist might have cast an eye over the work and noticed absurdities like crediting *Esox* with an adipose fin, an anteriorly placed dorsal fin, nuptial tubercles, an orbitosphenoid, and endopterygoid and maxillary teeth. To discover that *Esox* lacks some of these features would not need Edward Phelps Allis; a few words with an angler or someone who had glanced at a print of pike in a pub should be enough.

XIII. Summary

Review and reanalysis of published data, together with new characters, suggest the following pattern of relationships among lower euteleosts: [[[[Platytroctidae, Alepocephalidae] [Argentinidae [Opisthoproctidae [Microstomatinae, Bathylaginae]]]] [[Coregonidae [Thymallinae, Salmoninae]] [Osmeridae (including Salangidae, Plecoglossidae) [Retropinnidae [[*Lovettia, Lepidogalaxias*] [*Aplochiton*, Galaxiidae]]]]]] [Esociformes, Neoteleostei]]. That is, salmonoids and osmeroids are sister-groups; together they are the sister-group of alepocephaloids plus argentinoids; and esocoids are the sister-group of neoteleosts. We group salmonoids and osmeroids as Salmoniformes; alepocephaloids and argentinoids as Argentiniformes; Argentiniformes plus Salmoniformes as Protacanthopterygii; Esociformes plus Neoteleostei as Neognathi; and Protacanthopterygii plus Neognathi as Euteleostei. Within Alepocephaloidei, we lacked material for a proper study of the group. However, platytroctids are not a derived subgroup within Alepocephalidae but are the sister-group of all other alepocephaloids, and bathylaconids are the sister of alepocephalids. Monophyly of Alepocephaloidei is supported by branchiostegal cartilages and epipleural bones that extend unusually far forward. Within Argentinoidei, bathylagids (including microstomatids) are the sister of opisthoproctids, and argentinids are the sister of those two combined. Monophyly of Argentinoidei is supported by about a dozen characters, mostly related to the small mouth and reduced dentition. Monophyly of Argentiniformes is supported by the crumenal organ, ventral displacement of the first three or four epineural bones, and support of a single caudal fin ray by the caudal median cartilages. Salangids are osmerids, not galaxioids. Within Osmeridae, *Hypomesus* is the basal genus, *Spirinchus* and *Thaleichthys* are derived, not primitive, and salangids are the sister group of *Mallotus*. Within Galaxioidei, *Lepidogalaxias* is the sister of the Tasmanian *Lovettia*, and *Aplochiton* is the sister of galaxiids. The grouping of salmonoids and osmeroids (Salmoniformes), although not previously proposed, is among the most strongly supported in lower euteleosts, with 11 characters, including separate dermethmoid and supraethmoid, absence of epipleural bones, features of the caudal skeleton, scales without radii, nuptial tubercles, and anadromy. Monophyly of Protacanthopterygii is supported by epicentral cartilages and lack of proximal forking in the intermuscular bones. We find no morphological evidence to support the current view that Esociformes (Esocidae and Umbridae) are the most primitive euteleosts; a sister-group relationship between esociforms and Neoteleostei is supported by type 4 tooth attachment and an acellular skeleton. Monophyly of Euteleostei is supported by pattern of supraneural development and presence of a stegural and caudal median cartilages in the caudal skeleton.

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I (GDJ) began collaborating with Colin Patterson in 1991, and since that time I have spent hundreds of hours working next to him at the microscope, usually surrounded by precariously stacked boxes of glycerin. Many of those hours produced exciting discoveries; even more were spent painfully struggling to find characters, confronting our previous errors, or wallowing in what seemed like hopeless homoplasy. We have smiled and often laughed through most of those hours and they remain memorable among all those I have spent looking at fishes over the past 25 years. Working with Colin, there is obviously much to admire and benefit from—his deep knowledge of the fishes and the literature, his facility with words on the page, the intellect, focus and seemingly boundless energy he brings to the work and, of course, an unwavering determination to get everything right.

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Material Examined

List of specimens examined, in systematic sequence. Institutional abbreviations follow Leviton *et al.* (1985). All specimens are cleared and stained except those with the suffix (d), = dried skeleton; or (f), = fossil; or (s), = spirit specimen.

Outgroups

Amia calva L., BMNH 1996.2.6.14-15
Pholidophorus bechei Agassiz, BMNH P.64021 (f)
P. germanicus Quenstedt, BMNH P.3704 (f)
P. macrocephalus Agassiz, BMNH P.52518 (f)
Tharsis dubius (Blainville), BMNH P.12070 (stomach contents of *Pholidophorus macrocephalus*) (f)
"Callovian *Leptolepis*" of Patterson (1975), BMNH P.64022 (f)
Hiodon alosoides (Rafinesque), AMNH 23754SW (2), BMNH 1980.7.7.6
H. tergisus Lesueur, USNM 167970 (2)
Pantodon buchholzi Peters, USNM 336676
Elops hawaiensis Regan, BMNH 1962.4.3.1

E. machnata Forsskål, BMNH 1962.8.28.1
E. saurus L., USNM 272928
Megalops atlanticus Cuvier and Valenciennes, USNM 132933
M. cyprinoides (Broussonet), BMNH 1855.9.19.832
Albula vulpes (L.), USNM 128509, USNM 128391 (4), USNM 128393 (3)
Halosaurus guentheri Goode and Bean, USNM 319535
Denticeps clupeoides Clausen, BMNH 1969.4.28.1
Chirocentrus dorab (Forsskål), BMNH 1966.11.16.5–6
Clupea harengus L., BMNH 1932.2.15.1, BMNH 1970.2.17.22 (2)
larval *Clupea harengus*, BMNH 1996.2.6.4.4-12
Etrumeus teres (De Kay), USNM 188950
Pellona flavipinnis (Valenciennes), USNM 229344
Chanos chanos (Forsskål), BMNH 1996.2.6.16-19

Salmonoids

Coregonidae

Coregonus cylindraceus (Pallas), BMNH 1963.1.7.10 (3)
C. lavaretus (L.), BMNH 1996.2.6.20-21
larval *C. clupeaformis* (Mitchill), ROM 68375 (10)
Stenodus leucichthys (Güldenstadt), BMNH 1985.7.16.22 (5)
Prosopium williamsoni (Girard), BMNH 1892.12.30.340

Salmonidae

Thymallus thymallus (L.), BMNH 1970.10.14.3, BMNH 1986.5.20.259 (4)
Brachymystax lenok (Pallas), BMNH 1974.8.6.1
Hucho hucho (L.), BMNH 1985.1.25.1 (2)
Oncorhynchus clarki (Richardson), BMNH 1957.2.20.3
O. kisutch (Walbaum), BMNH 1979.7.18.1
Salmo gairdneri Richardson, BMNH 1985.12.20.1
S. salar L., BMNH 1996.2.6.22-24
larval *S. salar*, BMNH 1932.11.13.3 (16)
S. trutta L., BMNH 1981.9.22.81, BMNH 1983.10.17.5 (3), BMNH 1996.2.6.25-26
Salvelinus alpinus (L.), BMNH 1957.9.20.1-3
S. fontinalis (Mitchill), USNM 272669

Osmeroids

Osmeridae

Allosmerus elongatus (Ayres), USNM 342050 (4), UMMZ 93883 (2)
Hypomesus olidus (Pallas), HSU 86-33 (3)
H. pretiosus (Girard), HSU 81-187 (3)
H. transpacificus McAllister, BMNH 1984.6.28.11 (2)
larval *Hypomesus* sp., USNM 340198 (2)
Mallotus villosus (Müller), AMNH 26286 (2), HSU 89-282 (2), BMNH 1970.11.17.27 (2), BMNH 1970.11.17.18, BMNH 1970.11.17.55-56, USNM 306413 (3), USNM 130301 (3)
Neosalanx brevirostris (Pellegrin), HSU 85-38 (3), UMMZ 180147
Osmerus sp., larvae, HSU uncat.
O. eperlanus (L.), BMNH 1971.2.16.303
O. mordax (Mitchill), HSU 85-46, BMNH 1984.11.29.11, BMNH 1984.11.2.5
Plecoglossus altivelis Temminck & Schlegel, BMNH 1984.12.6.12-16, HSU 93-059 (2)
Protosalanx chinensis (Basilewsky), HSU 85-38 (3)
Salangichthys microdon Bleeker, BMNH 1996.2.6.1-3
Salanx (Salanx) ariakensis (Kishinouye), UMMZ 180137
S. (Hemisalanx) prognathus (Regan), UMMZ 180152 (2)
Spirinchus lanceolatus (Hikita), USNM 085563 (s)
S. starksi (Fisk), USNM 342052 (4)
S. thaleichthys (Ayres), USNM 104689 (2), USNM 104690 (6), USNM 105639
Thaleichthys pacificus (Richardson), USNM 342051 (2), UMMZ 129011, USNM 188123

Retropinnidae

Retropinna retropinna (Richardson), MCZ 58015, BMNH 1964.4.30.19, BMNH uncat. (d)
Prototroctes maraena Günther, BMNH 1984.10.3.1, UMMZ 212764 (2)
Prototroctes oxyrhynchus Günther, BMNH 1873.12.13.69 (d)
Stokellia anisodon (Stokell), BMNH 1984.64.30.11 (2)

Galaxiidae

Aplochiton taeniatus Jenyns, HSU 81-192 (10)
Aplochiton zebra Jenyns, AMNH 31048, HSU 81-192 (2), MCZ 46272 (2), BMNH 1868.6.22.9 (d)
Lovettia sealii (Johnston), BMNH 1937.8.22.1 (4)
Lepidogalaxias salamandroides Mees, USNM 339265 (3), larvae, USNM 342027 (3), BMNH uncat. (4)
Galaxiidae indet. larvae, USNM 340197 (12)
Galaxias brevipinnis Günther, BMNH uncat. (d)
G. fasciatus Gray, BMNH 1965.12.16.1 (2), BMNH 1853.2.14.8 (d), BMNH 1843.3.7.4 (d)
G. fontanus Fulton, BMNH 1983.6.21.1 (2)
G. maculatus (Jenyns), BMNH 1971.11.15.35, BMNH 1894.4.13.60 (d), BMNH 1896.6.17.79 (d)
G. occidentalis Ogilby, AMNH 31478 (3)
G. paucispondylus Stokell, AMNH 30889SW (2)
G. platei Steindachner, BMNH 1894.4.13.50 (d)
G. vulgaris Stokell, USNM 203883 (10)
G. zebratus (Castelnau), BMNH 1975.12.29.544 (2)
Galaxiella munda McDowall, AMNH 48833

G. nigrostriata (Shipway), larvae, USNM 342026 (4)
Nesogalaxias neocaledonicus Weber & de Beaufort, AMNH 31036SW, USNM 203885
Paragalaxias dissimilis (Regan), BMNH 1976.8.13.1
Neochanna apoda Günther, AMNH 30135, BMNH 1872.1.23.5 (d)

Argentinoids

Argentinidae

Argentina georgei Cohen and Atsaides, USNM 187834
A. silus (Ascanius), BMNH 1967.3.5.2 (2)
A. sphyraena L., USNM 238015, BMNH 1970.2.17.87 (2)
A. striata Goode and Bean, USNM 272945 (2)
Glossanodon polli Cohen, USNM 203236 (3)
G. struhsakeri Cohen, USNM 36618

Opisthoproctidae

Bathylychnops exilis Cohen, OS 012209
Dolichopteryx longipes (Vaillant), SIO 51-85
Macropinna microstoma Chapman, USNM 220876
Opisthoproctus soleatus Vaillant, AMNH 29688SW, BMNH 1933.5.23.1, MCZ 61958, SIO uncat.
Rhynchohyalus natalensis (Gilchrist and von Bonde), AMNH 29689SW

Bathylagidae

Bathylagoides sp., USNM 234768 (2)
B. wesethi (Bolin), USNM 339262 (3)
Bathylagus bericoides (Borodin), USNM 199825 (2)
indet. bathylagid larva, USNM 332419
Leuroglossus stilbius Gilbert, USNM 327747 (10)
Pseudobathylagus milleri (Jordan and Gilbert), SIO 80-258
Microstoma microstoma (Risso), AMNH 291684SW, BMNH 1888.11.29.67 (d)
Nansenia oblita (Facciola), AMNH 29685SW
Nansenia sp., USNM 203439

Alepocephaloids

Platytroctidae

Holtbyrnia latifrons Sazonov, SIO 71-112
H. innesi (Fowler), USNM 326306 (s)
Mirorictus taningi Parr, SIO 82-85, SIO 66-20
Mentodus rostratus (Günther), USNM 215612
Paraholtbyrnia cyanocephala Krefft, SIO 77-53
Pellisolus eubranchus Matsui and Rosenblatt, SIO 60-287
Platytroctes apus Günther, USNM 201650
Sagamichthys abei Parr, SIO 66-488
Searsia koefoedi Parr, SIO 77-38, SIO 77-53
Searsioides multispinus Sazonov, SIO 77-21

Alepocephalidae

Alepocephalus agassizi Goode and Bean, USNM 215572
A. bairdii Goode and Bean, BMNH 1996.2.6.27
A. rostratus Risso, BMNH 1886.8.4.7 (d), BMNH uncat. (d)
A. tenebrosus Gilbert, SIO uncat.
Bajacalifornia burragei Townsend and Nichols, LACM 9714-19, SIO 69-489
Bathylaco nigricans Goode and Bean, SIO 91-19, SIO 64-15, USNM 206693
Bathytroctes (*Grimatroctes*) sp., USNM 339266
B. microlepis Günther, USNM 215493
Binghamichthys sp., USNM 339263
Leptochilichthys agassizi Garman, USNM 200518
Leptoderma macrops Vaillant, USNM 215604, USNM 215605 (2)
Narcetes stomias (Gilbert), VIMS 2120
Photostylus pycnopterus Beebe, USNM 215656
Rinoctes nasutus (Koefoed), USNM 268400, USNM 189010 (s), USNM 215517 (s)
Rouleina attrita (Vaillant), USNM 215480
R. maderensis Maul, USNM 215473
R. squamilaterata (Alcock), USNM 137752, USNM 307293
Talismania antillarum (Goode and Bean), USNM 215556
T. aphos (Bussing), SIO 72-144
T. oregoni Parr, USNM 304453
Xenodermichthys copei (Gill), USNM 215524

Esociformes

Esocidae

Esox lucius L., ROM 598CS (2)
E. americanus Gmelin, BMNH 1982.11.10.16 (3)
larval *E. americanus*, ROM 24422 (9)

Umbridae

Dallia pectoralis Bean, AMNH 38034SW, BMNH 1984.6.26.2
Novumbra hubbsi Schultz, AMNH 45019 (2), AMNH 30883SW (4)
Umbra krameri Walbaum, BMNH 1979.7.23.1 (2), USNM 205523
U. limi (Kirtland), USNM 179712 (15)
U. pygmaea (DeKay), BMNH 1966.10.14.5, BMNH 1996.2.6.28, AMNH 33406 (3)

Neoteleosts

Stomiiformes

Diplophos taenia Günther, USNM 206614
Triplophos hemingi (McArdle), USNM 199832
Pollichthys mauli (Poll), BMNH 1984.1.1.13

Aulopiformes

Aulopus filamentosus Cloquet, USNM 292105
A. japonicus Günther, AMNH 28635SW

Myctophiformes

Neoscopelus macrolepidotus Johnson, USNM 188056 (2), USNM 317160
Notoscopelus resplendens (Richardson), AMNH 25928
Scopelengys tristis Alcock, AMNH 97466
Solivomer arenidens Miller, USNM 29507

Acanthomorpha

Polymixia lowei Günther, USNM 308378

Appendix 1

Matrix of 112 Morphological and Other Characters of Osmeroids, with Salmonoids and a Hypothetical Outgroup

	Character
	1111111111111
	1111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990000000000111
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012
Outgroup	00000000000000000000000000000000000000000000?000000000000000000000000000000000000000000000000?0000000000000000
Salmonoids	000000000000000200000102000000000000000000000010001000000000101010000000100100000000000000000000?0000000B000000010
Hypomesus	00B010010001000000000000001000000010001000000011000011000000B000201011001101000000101201000010000101000000010100000001B0
Plecoglossus	000010011001000000000000101100000001000100000011000001100001000201011001101000000101201010010000101000000011100000000010
Mallotus	021010010001000101001010110000000100020000000110000110000100121001100110101000101200011011000101100010101110000101
Salangidae	022?11????01200????0?220040000B011003002???110??2110000111022001100010110101212210101111011101100022101110100011
Allosmerus	101010011111000102001010120000111000201000B11000011000010012000110001010000010120101001100010100000010100010000
Osmerus	1010100010110001010000101200001010001010001110000110000100020001100010100000101201010010000101000000101000000110
Spirinchus	10101000111100020201101012000011100010100011100001100001001200011001101000001012010000110001010000101010B00000B0
Thaleichthys	1010100011110002020110101200001110001010001110000110000100120001100010100000101201010011000101000011101000000110
Retropinna	2110101000010010001001000401011013013010000012111101010010030101110000111111011211000010001000?01022011001110110
Prototroctes	2110101100010010001001000400111013013010000002101111010010030101110000111111011211000010000000?01022010001110110
Stokellia	2110101100010010001001000401111013013010000002101111010110031101110000111111011211000010001000?01022011001110110
Aplochiton	202?101100010120001022110310111012113011110022100210011010030110101101112121212210000100000000?12122000001000010
Lovettia	200111????012100111020120400111012103111110022112311111011030110101101112121212110100100100B00?12122001001100011
Lepidogalaxias	2001101100002000101010220000111012?031211000??112111101210030010001301112121212210100100111010?03122000121101022
Galaxiidae	2001101B000111200010221103101110101030111100221BB211011000130B101012B1112121212110000100001010?12122000001B0B0B0

Note. "B" Indicates Polymorphism for States (0) and (1)

Characters

In the following list, an asterisk after a number indicates a multistate character treated as unordered in the parsimony analysis. Numbers in square brackets after character numbers refer to the numbered sequence in Section II.

1* [1]. Dermethmoid median (0), paired (1) or absent (2).

2* [2]. Ethmoid endoskeleton short with one or more perichondral ossifications anterior to the lateral ethmoids (0), short and unossified (1), or long and unossified (2).

3* [3]. Vomer with (0) or without (1) shaft, or vomer absent (2).

4 [4]. Vomer toothed (0) or toothless (1) [vomer absent = (?)].

5 [6]. Orbitosphenoid present (0) or absent (1).

6 [8]. Pterosphenoid present (0) or absent (1).

7 [8]. Pterosphenoid unmodified (0) or with extensive medial epiphysial arm (1).

8 [8]. Pterosphenoid with (1) or without (0) ventral process or flange from anterior half of ventral margin.

9 [8]. Pterosphenoid with (1) or without (0) posteroventral membrane–bone process towards anterodorsal process from prootic.

10 [9]. Contact (1) or lack of it (0) between anterodorsal process of prootic and pterosphenoid.

11 [11]. Cartilaginous interorbital septum present in anterior part of orbit (1) or absent (0).

12 [12]. Basisphenoid present (0) or absent (1).

13 [13]. Posterior myodome deep and extending into basioccipital (0), small and shallow (1), or absent (2).

14 [14]. Buccohypophysial canal in parasphenoid absent (0) or present (1).

15* [15]. Efferent pseudobranchial artery passing lateral to parasphenoid and sphenoid endoskeleton (0), through an earlike cartilage projecting beyond the parasphenoid (1), or though a notch or canal in the parasphenoid (2).

16 [16]. Otic bulla not inflated and with little or no cartilage in its wall (0), somewhat inflated (1), or globose (2).

17 [18]. Frontals with (0) or without (1) laminar lateral part roofing orbit.

18 [19]. Parietals in contact medially (0), or partially (1) or completely (2) separated by supraoccipital. [There is no supraoccipital in salangids, coded (?); *Lovettia* has parietals separate, but supraoccipital does not extend between them].

19 [19]. Parietals overlapped anteriorly by frontals, so that their exposed area is relatively small (0), or sutured with frontals and extending forwards to or beyond the postorbital process (1).

20 [22]. Fontanelles in cartilaginous roof of otic region remaining open (0) or closed during ontogeny (1).

21* [28]. Dermopalatine and autopalatines separate (0) or fused (1), or dermopalatine absent (2) [unossified autopalatine coded ?; *Plecoglossus* coded (0) despite Howes and Sanford's (1987a) report of fusion].

22* [29, 32]. Ectopterygoid present (0), fused with palatine (1), or absent (2).

23* [31]. Endopterygoid teeth concentrated along dorsal margin of bone, with a patch of teeth posteriorly (0), or in a single row (1) or absent (2).

24 [37]. Metapterygoid large (0), comparable in size to symplectic (1), or reduced, less than half as large as symplectic and not contacting hyomandibular or symplectic (2).

25 [38]. Anterior margin of metapterygoid above (0) or anterior (1) to quadrate.

26* [44, 45]. Hyomandibular with a vertically elongate lateral crest (0), a short vertical crest fitting against the propercular (1), a triangular spur (2), an obliquely orientated spurlike crest (3), or no preopercular crest (4).

27 [50]. Ascending process of premaxilla knoblike (0) or sharply triangular (1).

28 [54]. Maxilla and palatine with (1) or without (0) head-to-head articulation.

29 [56]. Maxilla toothed (0) or toothless (1).

30 [57]. Supramaxilla present (0) or absent (1).

31 [58]. Dentary with toothed margin occupying less than half of length of lower jaw (0) or more than half (1) [*Plecoglossus* scored as juvenile (Howes and Sanford, 1987a, fig. 4)].

32 [59]. Meckelian fossa small and anteriorly placed (0) or large and opening beneath the hind end of the dentary tooth row (1).

33 [62]. Anguloarticular with substantial endoskeletal (articular) component (0) or with articular component small (1).

34* [65, 66]. Supraorbital and antorbital present (0), supraorbital only (1), antorbital only (2), or neither (3). Galaxiids exhibit all four conditions and are coded (0).

35 [68]. Lachrymal with (1) or without (0) cartilage-covered condyle at its articulation with lateral ethmoid [lachrymal absent in *Lepidogalaxias*; coded (?)].

36 [69]. Branchiostegals extend forward to ossified ventral border of distal ceratohyal (0) or are restricted to cartilage-covered margin of the deep posterior part of the hyoid bar (1) (Fig. 4).

37* [76, 77]. Dorsal margin of opercular entire and unmodified (0), with an anterodorsal notch (1), with notch and a tongue-like process behind it (2), or not extending above articulation with hyomandibular (3).

38 [79]. Posterior margin of opercular and subopercular deeply incised (1) or not (0).

39* [80]. Basihyal with scattered teeth (0), marginal fangs (1), or toothless (2).

40 [81]. Basibranchial teeth present (0), toothless dermal plate (1), or dermal plate absent (2).

41 [91]. Uncinate process on first epibranchial present (0) or absent (1).

42 [92]. Uncinate process on second epibranchial present (0) or absent (1).

43 [94]. Uncinate process on fourth epibranchial absent (0) or present (1).

44 [95]. Distinct levator process on fourth epibranchial absent (0) or present (1).

45* [97]. Epibranchial 5 free (0) or fused to Eb4 at its lower end (1) or at both ends (2) [Eb5 absent in *Lepidogalaxias*; coded (?)].

46* [101]. Base of first pharyngobranchial articulating with anterior tip of Eb1 (0), with both Eb1 and Eb2 (1), or with lateral surface of Eb1 (2) [Pb1 absent in *Lepidogalaxias*; coded (?)].

47 [103]. Uncinate process on second pharyngobranchial present (0) or absent (1).

48 [106]. Uncinate process on third pharyngobranchial present (0) or absent (1).

49 [108]. Third pharyngobranchial with narrow anterior extension reaching Pb1 or tip of Pb2 (0), without anterior extension (2), or intermediate (1).

50* [109]. Fourth and fifth upper pharyngeal toothplates (UP4, UP5) distinct and separate (0), a single toothplate (1), two to four separate toothplates (bearing no relation to the original two) (2), or toothless (3).

51 [112]. Gill rakers toothed (0) or toothless (1).

52 [113]. Accessory neural arch (ANA) present (0) or absent (1).

53 [114]. Unossified gap between occipital condyle and first centrum absent (0) or present (1).

54 [115]. Baudelot's ligament originating on first vertebra (0) or on occiput (1) [in galaxiids the ligament may show state (1) or may originate on both structures; they are coded (1)].

55 [116]. Neural arches of some vertebrae anterior to dorsal fin autogenous (0) or all fused to centrum (1).

56* [118]. Epineural bones and/or ligaments originate on neural arch (0), on centrum on several anterior vertebrae (1), or absent (2).

57 [120]. Epineural bones present (0) or absent (1).

58 [121]. Cartilage rods in epicentral ligaments present (0) or absent (1).

59 [122]. Epipleural bones absent (0) or present (1).

60* [125]. Supraneurals develop in pattern 1 (0), pattern 2 (1), pattern 2A (2), or pattern 2B (3).

61 [126]. Supraneurals numerous, ca. 15 or more (0), fewer than ten (1), or one (2).

62 [128]. Median keels of laminar bone absent (0) or present (1) on distal parts of last few neural and haemal spines.

63 [129]. NPU2 leaflike and about half the length of NPU3 (0) or similar in form to NPU3 (1).

64 [130]. NPU1 leaflike (0) or rudimentary or absent (1).

65 [132]. U1 free (0) or fused to PU1 (1).

66 [133]. Parhypural and hypural 1 separate (0) or fused (1).

67 [133]. Hypurals six (0) or five (1).

68* [134]. Epurals three (0), two (1), one (2) or none (3) [polymorphisms coded as greatest number observed].

69 [136]. First uroneural free (0) or fused to PU1 (1).

70 [137]. Membranous outgrowth of Un1 present (0) or absent (1).

71 [139]. Second uroneural slender and posteroventral to first (0) or broad and lateral or dorsolateral to first (1).

72. [140]. Number of uroneurals three (0) or two (1).

73* [142]. Upper and lower caudal median cartilages (CMCs) present (0), a single cartilage (1), or absent (2).

74 [144]. Upper and lower caudal scutes present (0) or absent (1).

75 [145]. Principal caudal rays 10/9 (0), 9/9 (1), or 8/8 (2).

76 [146]. Urodermal present (0) or absent (1).

77* [148, 179]. Extrascapular single or double (0), several canal-bearing ossicles (1), or absent (2).

78 [149]. Posttemporal with lower (intercalar) limb ossified (0) or not (1).

79* [150]. Cleithrum with long-based triangular ventral process towards coracoid (0), with narrow columnar process (1), or with no process (2).

80* [151]. Number of postcleithra three (0), one (1), or zero (2).

81 [152]. Mesocoracoid present (0) or absent (1).

82 [155]. First pectoral radial unmodified (0), or enlarged and embracing scapula (1) (Fig. 12C, D).

83 [156]. Third pectoral radial unmodified (0) or tapering proximally and failing to reach scapulocoracoid (1).

84 [157]. Fourth pectoral radial articulating with glenoid (0) or tapering proximally and failing to articulate with glenoid (1).

85 [158]. Fourth pectoral radial single (0) or multifid distally (1).

86 [160]. Posterior pubic symphysis present (0) or absent (1).

87 [161]. Pelvic girdle with (1) or without (0) ventral condyle.

88 [162]. Articular surface for pelvic fin short and transverse (0) or elongate and oblique (1).

89 [163]. Shaft of pelvic girdle with (1) or without (0) laminar medial membrane–bone expansion.

90 [165]. Pelvic splint present (0) or absent (1).

91 [166]. Dorsal fin placed above or close behind pelvics (0), or above or close to anal (1).

92 [168]. Posterior dorsal pterygiophores confluent (1) or nor (0).

93 [169]. Adipose fin present (0) or absent (1).

94 [170]. Adipose cartilage present (1) or absent (0).

95 [170]. Adipose cartilage beanlike (0) or a transversely arched, fenestrate plate (1) [taxa lacking the cartilage coded (?)].

96 [171]. Scales present (0) or absent (1).

97* [175, 176]. Infraorbital sensory canal uninterrupted and unmodified (0), interrupted, with the anterior portion running posteroventrally to cross the preopercular canal (1), postorbital infraorbital bones and sensory canal absent (2), or all infraorbital bones and canal absent (3).

98 [178]. Temporal sensory canal present (0) or absent (1).

99* [180]. Posttemporal penetrated by lateral line (0), with a separate canal-bearing ossicle (1), or with no relation to sensory canal (2).

100* [181]. Supracleithrum penetrated by lateral line (0), with a separate canal-bearing ossicle (1), or with no relation to sensory canal (2).

101 [182]. Egg with (1) or without (0) adhesive membrane or filaments.

102 [183]. Both ovaries present in females (0) or left only (1).

103 [186]. Nuptial tubercles absent (0) or present (1).

104 [187]. Scales on anal fin base of mature males unmodified (0) or enlarged (1).

105* [187]. Anal fin skeleton unmodified in mature males (0), anterior anal endoskeleton and central finrays modified (1), or entire anal fin skeleton greatly modified (2).

106 [188]. Nasal lamellae in a rosette (0) or parallel and longitudinal (1).

107 [191]. Pyloric caeca present (0) or absent (1).

108 [194]. Horny midventral abdominal keel absent (0) or present (1).

109 [195]. Prominent adipose "caudal peduncle flanges" absent (0) or present (1).

110 [197]. Cucumber odor absent (0) or present (1).

111* [199]. Life cycle entirely marine (0), diadromous (anadromous or amphidromous) (1), or entirely freshwater (2).

112* [200]. Skeletal ontogeny unmodified (0), retarded relative to sexual maturity (1), or accelerated (2).

Appendix 2

Matrix of 50 Morphological Characters in Subgroups of Argentinoids, Alepocephaloids, and an Outgroup.

	Character
	11111111112222222222333333333344444444445 12345678901234567890123456789012345678901234567890
Outgroup	00000000000000000000000000000000000000000000000000
Alepocephaloids	00100010000000000000000010000B000001B00000B11000001?
Argentina	000100000111101100000101110110001111B0101000000101
Glossanodon	000100000111101100000101B10110001111B1101000000101
Bathylagids	1012?01011101111111111111111111111001111010000101?
Microstomatids	10011110111011111110111101211111110011111001111001
Opisthoproctids	2111101101102?1102111111000111111010001001211100B1

Note. "B" Indicates Polymorphism for States (0) and (1).

Characters

In the following list, an asterisk after a number indicates a multistate character treated as unordered in the parsimony analysis. Numbers in square brackets after character numbers refer to the numbered sequence in Section II. Bathylagids are coded from *Bathylagichthys* where information is available (Kobyliansky, 1986, 1990), microstomatids are coded from *Nansenia*, and opisthoproctids from *Bathylychnops*.

1* [2]. Mesethmoid fully ossified (0), with separate laminar dorsal and ventral ethmoids (Kobyliansky, 1990, fig. 10) (1), or unossified (2).

2 [6]. Orbitosphenoid present (0) or absent (1).

3 [19]. Parietals in contact medially (0) or separated by supraoccipital (1).

4* [20]. Parietal with no direct relation to occipital commissural sensory canal (0), or carrying canal (presumably through fusion with a medial extrascapular) (1), or occipital commissure absent (2).

5 [20]. Occipital commissural canal crosses posterior margin of parietal (0) or lies anteriorly on the bone (1).

6 [21]. Dermopterotic present (0) or absent (1).

7 [23]. Posttemporal fossa roofed (0) or open (1).

8 [26]. Occipital condyle formed only by basioccipital (0) or tripartite, with exoccipital condyles (1).

9 [29]. Palatine teeth in a patch (0) or a single row (1).

10 [31]. Endopterygoid teeth present (0) or absent (1).

11 [37]. Metapterygoid large (0) or reduced (1).

12 [42]. Ventral arm of symplectic equal in length to dorsal arm (0) or shorter (1).

13* [52]. Premaxilla toothed (0), toothless (1), or absent (2).

14 [53]. Premaxilla articulating with maxilla posteriorly (1) or not (0).

15 [56]. Maxilla toothed (0) or toothless (1).

16 [57]. Two supramaxillae (0) or none (1).

17 [58]. Dentary with scattered small teeth (0) or with a long, single row of bladelike teeth (1).

18* [66]. Supraorbital and dermosphenotic in contact (1) above orbit or not (0), or supraorbital absent (2).

19 [68]. Lachrymal (foremost infraorbital) larger (0) or smaller (1) than succeeding infraorbital.

20 [75]. Anterior branchiostegals carried on medial or ventral margin of ceratohyal (0) or all branchiostegals on external face of ceratohyal (1).

21 [80]. Basihyal teeth present (0) or absent (1).

22 [81]. Basibranchials 1–3 with (0) or without (1) teeth.

23 [88]. Cb5 toothed (0) or toothless (1).

24 [90]. Accessory cartilage at tip of Cb5 absent (0) or present (1).

25 [94]. Uncinate process on Eb4 absent (0) or present (1).

26 [95]. Eb4 with (1) or without (0) distinct levator process.

27 [100]. Pb1 ossified (0), cartilaginous (1), or absent (2).

28 [102]. Pb2 toothed (0) or toothless (1).

29 [105]. Pb3 toothed (0) or toothless (1).

30 [109]. UP4 present (0) or absent (1).

31 [109]. UP5 normal (0) or minute (1).

32 [111]. Gill rakers on fourth and fifth arches similar to those on third (0) or much longer (1).

33 [113]. ANA present (0) or absent (1).

34 [119]. First two to four epineurals unmodified (0) or descended distally (1).

35 [125]. Supraneurals develop in pattern 1 (0) or pattern 2 (1).

36 [127]. Anterior supraneurals rodlike (0) or rostrocaudally expanded (1).

37 [132]. PU1 and U1 separate (0) or fused (1).

38 [136]. Un1 fused to PU1 (1) or free (0).

39 [137]. Membranous outgrowth of Un1 present (0) or absent (1).

40 [141]. Caudal interneural and interhaemal cartilages three or fewer (0) or four or more (1).

41 [143]. CMCs each support a fin ray (0), or together support lowermost ray of upper caudal lobe (1).

42 [144]. Caudal scutes present (0) or absent (1).

43 [151]. Postcleithra three (0), one (1) or none (2).

44 [152]. Mesocoracoid present (0) or absent (1).

45 [159]. Pectoral fin develops small and late (0) or early and large (1).

46 [165]. Pelvic splint present (0) or absent (1).

47 [179]. Lateral extrascapular single, triradiate and lying behind pterotic (0) or represented by one or more tubular ossicles extending forward above pterotic (1).

48 [189]. Eye with (1) or without (0) a crescent of white tissue above the iris.

49 [190]. Swimbladder present (0) or absent (1) (absent in *Bathylychnops*; present in *Opisthoproctus*).

50 [190]. Swimbladder with (1) or without (1) microrete mirabilia [swimbladder absent coded (?)].

Appendix 3

Matrix of 59 Morphological Characters in Subgroups of Alepocephaloidea, Argentinidae, and a Hypothetical Outgroup

	Character
	11111111112222222222333333333344444444445555555555 12345678901234567890123456789012345678901234567890123456789
Outgroup	00000000000000000000000000000000000000000000000000000000000
Argentinidae	00010000001112002000013001111100100011100100000000000000000
Platytroctidae	00001BB1200B00000120002010B001112?00B100011B100000B10BBB01B
Alepocephalus	10011111101B100121201120101102111301111000112010000101111010
Bajacalifornia	00011001101100011120B100101112?1010011000011200000010211010
Bathylaco	00001001001B0100011011110011010110000000011010020001000000010
Bathyprion	11111??1?0110B01??2011?1???1???1??011100001?211200010???210
Bathytroctes	10011011001100000120112001110 1?101101110001110000001011 0010
Leptochilichthys	01111111?01111002120112011101 1?1?300120000112000100 10?11010
Leptoderma	100112112111111120211120111111 2?4011311 1?112111221123 21110
Narcetes	00011001001100010020110010 01???10200100001111000000102 10010
Photostylus	110112112111011120201141111114 13?41101011?11210112112321?11
Rinoctes	001110110011000001201020?00013020211110000112111000123 11110
Rouleina	1001101111110B11B02111201001 12?12?11110100112011011112221011
Talismania	00011B01B0110000012011201000 0211B1011110001120100011021 0110

Note. "B" Indicates polymorphism for States (0) and (1).

Characters

In the following list, an asterisk after a number indicates a multistate character treated as unordered in the parsimony analysis. Numbers in square brackets after character numbers refer to the numbered sequence in Section II.

1 [4]. Vomerine teeth present (0) or absent (1).

2 [6]. Orbitosphenoid present (0) or absent (1).

3 [12]. Basisphenoid present (0) or absent (1).

4 [15]. Basipterygoid process present (0) or absent (1).

5 [19]. Parietals in contact (0) or separated by supraoccipital (1).

6* [21] Dermopterotic and autopterotic fused (0), separate (1), or dermal component absent (2).

7 [21]. Temporal sensory canal enclosed in pterotic (0) or not (1).

8 [23]. Posttemporal fossa extensive and roofed (0) or absent (1).

9* [23]. Posterior margins of parietal and dermopterotic continuous and transverse (0), forming a "V" open posteriorly (1), or no contact between the bones (2, including dermopterotic absent).

10 [29]. Palatine teeth present (0) or absent (1).

11 [31]. Endopterygoid teeth present (0) or absent (1).

12 [35]. Ectopterygoid teeth present (0) or absent (1).

13 [56]. Maxillary teeth present (0) or absent (1).

14* [57]. Supramaxillae two (0), one (1) or none (2).

15 [65]. Antorbital present (0) or absent (1) (information from Markle, 1976).

16 [66]. Supraorbital present (0) or absent (1) (information from Markle, 1976).

17* [70]. Ceratohyal with dorsal margin covered by cartilage (0), with cartilage cover interrupted by a notch (1), or covered by perichondral bone (2) (Fig. 16).

18 [74]. Branchiostegal cartilages absent (0) or present (1).

19* [76, 78]. Dorsal part of opercular normal (unreduced) (0), with large dilatator spine (1), or with small spine (2).

20. Subopercular normal (0) or dagger-like (1) (information from Markle, 1976).

21 [80]. Basihyal teeth present (0) or absent (1).

22 [81]. Basibranchial teeth present (0) or absent (1).

23* [88]. CB5 dentition a longitudinal band of teeth (0), a longitudinal single row (1), a single marginal row on a fanlike medial expansion (2), a cluster at the anterior end of the bone (3), or absent (4).

24 [90]. Accessory cartilage above Cb5 present (0) or absent (1).

25 [92]. Uncinate process on Eb2 present (0) or absent (1).

26 [98]. Suprapharyngobranchial 1 present (0) or absent (1).

27 [99]. Suprapharyngobranchial 2 present (0) or absent (1).

28 [102]. Pb2 toothed (0) or toothless (1).

29 [113]. ANA present (0) or absent (1).

30* [119]. Distal parts of epineurals displaced ventrally on no vertebrae (0), on first three or four (1), on first one or two (2), or on more than four (3), or epineurals absent (4).

31 [121]. Epicentral cartilages present (0) or absent (1).

32* [123]. Epipleural bones not extending forward beyond about V20 (0), extending forward to V2–4 (1), to about V9 (V6–11) (2), or absent (3).

33* [125]. Supraneurals develop in pattern 1 (0), pattern 2 (1) or pattern 4 (2) [taxa with one supraneural or none coded (?)].

34 [126]. Number of supraneurals more than 70% of number of predorsal vertebrae (0), 50–70% (1), 30–50% (2), or only one or two supraneurals (3), or none (4) [taxa with pattern 4 supraneurals coded (?)].

35. Number of abdominal vertebrae greater than number of caudal vertebrae by six or more (0), or approximately equal (± 5) (1) (Markle, 1976).

36. Laminar bone developed on last few neural and haemal arches (0) or not (1) [information from Markle and Merrett, 1980].

37 [129]. NPU2 about half as long as NPU3 (0) or as long as NPU3 (1).

38* [134]. Number of epurals three (0), two (1), one (2), or zero (3).

39 [137]. Membranous anterodorsal outgrowth on Un1 present (0) or absent (1).

40 [140]. Un3 present (0) or absent (1).

41 [142]. CMCs present (0) or absent (1).

42 [143]. Each CMC supports a fin ray (0) or both support lowermost ray of upper lobe (1) (Fig. 14) [CMCs absent coded (?)].

43 [146]. Urodermal present (0) or absent (1).

44 [150]. Cleithrum with (0) or without (1) ventromedial process meeting coracoid.

45 [151]. Postcleithra three (0), one (1), or none (2).

46 [152]. Mesocoracoid present (0) or absent (1).

47 [153]. Postcoracoid process short (0) or long (1).

48* [154]. Pectoral radials four (0), three (1), or two (2).

49 [164]. Pelvic radials three (0), two (1), or one (2).

50. Pelvic rays 8 or 9 (0), 7 (1), or 6 or fewer (2).

51 [165]. Pelvic splint present (0) or absent (1).

52 [169]. Adipose fin present (0) or absent (1).

53* [171]. Scales present (0), restricted to lateral line (1), or absent (2).

54* [179]. Extrascapular a substantial triradiate bone (0), a triradiate tubular ossicle (1), two or more tubular ossicles (2), or absent (3).

55* [180]. Posttemporal containing sensory canal (0), canal passes through separate ossicle or ossicles (1), or no ossicle (2).

56 [181]. Supracleithrum containing sensory canal (0) or not (1).

57* [184]. Ovary exposed to coelom laterally (0), ovary enclosed by fusion of ovarian tunic with peritoneum (1), or ovary enclosed by tunic but hanging free in coelom (2).

58 [190]. Swimbladder present (0) or absent (1).

59 [196]. Photophores absent (0) or present (1).

Appendix 4

Matrix of 42 Characters in Clupeomorphs, the Major Groups of Euteleosts, and a Hypothetical Outgroup

	Characters
	111111111122222222223333333333444
	123456789012345678901234567890123456789012
Outgroup	000000000000000000000000000000000000000000
Clupeomorphs	001010000000000000010000100100000100001000
Ostariophysi	0010201001000100100?0020100000000102000100
Esocoids	0100211111101011000000101011?1001121012012
Alepocephaloids	0102100000001000001201?0001000111111000000
Argentinoids	001020200121111010120110100100110002001000
Salmonoids	100120100000000201021111001010101002101101
Osmeroids	1001111101000?0201021111011110100032101111
Neoteleosts	000000001000010000000?100111011000020?1010

Note. The characters are abstracted from the survey in Section II. Polymorphism within terminals is not coded. Instead, the primitive condition is entered if it occurs in basal members of a group. Queries are entered where the condition in basal members is questionable, as specified in the character descriptions, or where the character is inapplicable.

Characters

In the following list, an asterisk after a number indicates a multistate character treated as unordered in the parsimony analysis. Numbers in square brackets after character numbers refer to the numbered sequence in Section II.

1 [2]. Dermethmoid and supraethmoid fused (0) or separate (1).

2 [19]. Parietals in contact in midline (0) or separated by supraoccipital (1).

3 [20]. Parietals carrying the occipital commissural sensory canal (1) or not (0).

4* [23]. Posttemporal fossa roofed (0), open (1), or absent (2). [Clupeomorphs coded from Cretaceous ellimmichthyids.]

5* [31]. Endopterygoid teeth cover medial surface of bone (0), are restricted to a row along the medial margin (1), or absent (2). [Clupeomorphs coded from Cretaceous ellimmichthyids.]

6 [45]. Lateral crest of hyomandibular long (0) or short (1).

7* [57]. Two supramaxillae (0), one (1), or none (2).

8 [62]. Articular well-developed (0) or reduced (1).

9 [64]. Tooth attachment type 1–3 (0) or type 4 (1).

10 [70]. Dorsal margin of distal ceratohyal cartilaginous (0) or closed in perichondral bone (1).

11* [81]. Basibranchial toothplate covers basibranchials 1–3 (0), fragmented into two (1), or toothless (2).

12 [90]. Accessory cartilage between Cb5 and Eb5 absent (0) or present (1).

13 [94]. Uncinate process on Eb4 absent (0) or present (1). [Neoteleosts coded (?) because process is absent in stomiiforms].

14 [95]. Levator process on Eb4 absent (0) or present (1). [Osmeroids coded (?) because primitive condiion might be (0), as in galaxioids, or (1) as in osmerids.]

15 [102]. Toothplate of Pb2 present (0) or absent (1).

16* [109]. UP4 and UP5 present (0), UP4 only (1), or UP5 only (2).

17 [113]. ANA present (0) or absent (1).

18 [117]. Epineural bones fused to neural arches on several (five or more) anterior neural arches (0) or fused on no more than one (1). [Ostariophysans coded from the Eocene *Chanoides*.]

19 [119]. Distal parts of first two to four epineurals in series with their successors (0) or descended (1).

20* [121]. Epicentrals ligamentous (0), ossified (1), or with cartilage rods distally (2). [Ostariophysans coded (?) because epicentral bones are present in gonorynchiforms, absent in otophysans.]

21 [122]. Epipleurals ossified (0) or ligamentous (1).

22 [124]. Epineurals and epipleurals (when present) forked proximally (0) or not (1). [Neoteleosts coded (?) because primitive state is questionable.]

23* [125]. Supraneurals develop in pattern 1 (0), pattern 2 (1), or pattern 3 (2). [Alepocephaloids exhibit patterns 1, 2, and 4 and are coded (?).]

24 [128]. Last few neural and haemal spines slender distally (0) or expanded rostrocaudally, forming a keel above and below the vertebrae (1).

25 [129]. NPU2 leaflike, about half as long as NPU3 (0), or as long as NPU3 (1).

26 [132]. PU1 and U1 separate (0) or fused (1). [Ostariophysans coded from Cretaceous gonorynchiforms.]

27 [137]. Membranous anterodorsal outgrowth of Un1 absent (0) or present (1).

28 [138]. Un1 extends forwards to PU2 (0) or only to PU1 (1). [Ostariophysans coded from Cretaceous gonorynchiforms.]

29 [139]. Un2 slender and posteroventral to Un1 (0) or broad and anterodorsal to Un1 (1). [Inapplicable in esocoids; coded (?).]

30 [140]. Un3 present (0) or absent (1).

31 [142]. CMCs absent (0) or present (1).

32 [143]. CMCs each support a finray (0) or together support the lowermost ray of the upper caudal lobe (1) [absence of CMCs coded (0)].

33 [144]. Caudal scutes present (0) or absent (1).

34 [146]. Urodermal present (0) or absent (1).

35* [151]. Postcleithra 1–3 present (0), only Pcl 1 (1), only Pcl 3 (2), or none (3).

36* [166, 169]. Adipose fin absent, dorsal fin over pelvics (0); adipose fin absent, dorsal fin posterior (1); or adipose fin present (2).

37 [172]. Scales with (0) or without (1) radii.

38 [173]. Cheek and operculum naked (0) or scaled (1). [Neoteleosts coded (?) because state (1) occurs in eurypterygians but not in stomiiforms.]

39* [74]. Supraorbital sensory canal without postorbital junction with infraorbital canal and with parietal branch (0), with both postorbital junction and parietal branch (1), or with postorbital junction and no parietal branch (2).

40 [186]. Nuptial tubercles absent (0) or present (1).

41 [192]. Skeleton cellular (0) or acellular (1).

42* [199]. Marine (0), diadromous (1), or freshwater (2). [Ostariophysans coded from primitive gonorynchiforms and the Eocene *Chanoides*.]