1993

Phylogeny Of Lampridiform Fishes

JE Olney
Virginia Institute of Marine Science

GD Johnson
Virginia Institute of Marine Science

CC Baldwin
Virginia Institute of Marine Science

Recommended Citation

Olney, JE; Johnson, GD; and Baldwin, CC, Phylogeny Of Lampridiform Fishes (1993). *Bulletin of Marine Science*, 52(1), 137-169.
https://scholarworks.wm.edu/vimsarticles/1533

BULLETIN OF MARINE SCIENCE, 52(1): 137–169, 1993

PHYLOGENY OF LAMPRIDIFORM FISHES

John E. Olney, G. David Johnson and Carole C. Baldwin

ABSTRACT

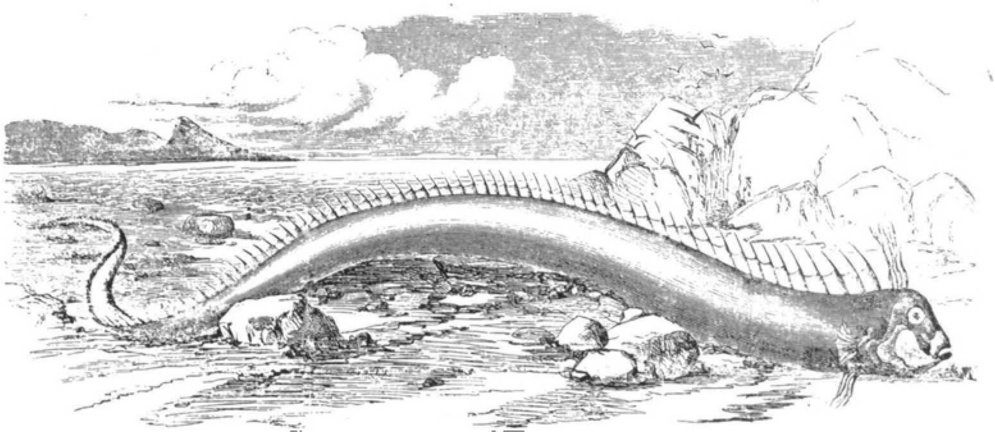
A survey of characters defining the Neoteleostei, Eurypterygii, Ctenosquamata, Acanthomorpha, Paracanthopterygii and Acanthopterygii convincingly places the Lampridiformes within the acanthomorph clade. Lampridiforms are primitive with respect to the Percomorpha but their precise placement among basal acanthomorphs remains unclear. In the absence of a specific sister-group hypothesis, *Polymixia*, percopsiform and beryciform taxa were used as outgroups in a cladistic analysis of the order. Monophyly of Lampridiformes is supported by four apomorphies; three are correlated modifications related to the evolution of a unique feeding mechanism in which the maxilla slides forward with the premaxilla during jaw protrusion. The Veliferidae are the sister group of all other lampridiforms. The deep-bodied (bathysomous) lampridiforms are not monophyletic because *Lampris* is the sister group of the elongate (taeniosomous) families. *Stylephorus* is placed as the sister group of all other taeniosomous families. The Radiicephalidae are hypothesized to be the sister group of the Lophotidae, a clade that forms the sister group of the Regalecidae + Trachipteridae. Ateleopodid, mirapinnid, and eutaeniiophorid fishes are not lampridiforms. †*Bajaichthys* is allied with living lampridiform fishes but †*Pharmacichthys* is not a lampridiform. The affinities of †*Aipichthys* and †*Bathysomous* are unknown.

On January 22nd, 1860, a large, silver fish was observed splashing in shallow water near Hungary Bay, Bermuda. The activity attracted the attention of a member of the Linnean Society of London, Mr. Matthew Jones, who happened to be on the island at the time. Jones believed that the 6 m specimen (an immature male) was an unknown species and his subsequent report of the stranding of this unusual creature appeared in *Harper's Weekly* (Fig. 1) where the sighting was described as the "first appearance of the great sea-serpent on dry land." Almost 50 years later, Charles Tate Regan (1907) provided the first classificatory treatment of the great sea serpent and its relatives. The stranded monster, *Regalecus* Brünnich, was placed along with *Trachipterus* Bloch and Schneider, *Lophotus* Giorna, and a new genus, *Eumecichthys* Regan, within one division, the Taeniosomi, of a new teleostean suborder that Regan named the Allotriognathi from the Greek meaning "strange jaw." Regan (1907) considered the Taeniosomi, along with *Lampris* Retzius and *Velifer* Temminck and Schlegel (placed in the divisions Selenichthyes and Histichthyes, respectively) to form a natural assemblage based on the common possession of several unique characteristics. These included a posteriorly placed mesethmoid and absence of an attachment between the palatines and maxillae, a condition allowing an unusual upper jaw mechanism in which the maxillae are protractile and carry the premaxillae forward in the feeding posture.

Regan's (1907) Allotriognathi (Lampridiformes[1] of Greenwood et al., 1966; =Lampriformes following Steyskal, 1980) comprised four families: Lamprididae, Veliferidae, Lophotidae and Trachipteridae. *Stylephorus* Shaw was later added to the group in the family Stylephoridae (Regan, 1924). Both Starks (1908) and Regan (1924) experienced difficulty in interpreting the highly modified suspensorium of *Stylephorus,* and its position within the Allotriognathi proved prob-

---

[1] Although Steyskal (1980: 171) recommended that the termination of higher taxa based on *Lampris* Retzius should use the stem *lampri-*, we follow C. Patterson (Appendix I) in the use of Lamprididae and Lampridiformes.



THE GREAT SEA-SERPENT, FOUND IN HUNGARY BAY, BERMUDA, ON JANUARY 22, 1860.—From a Sketch by W. D. Munro.—[See preceding Page.]

Figure 1. Reproduction of lithograph published in *Harper's Weekly,* 14 March 1860.

lematic. Regan (1924) considered *Stylephorus* to be intermediate between the Taeniosomi and *Velifer,* and placed it in a separate (although unnamed) suborder, apparently ignoring Starks' (1908) earlier designation of the suborder Atelaxia to accommodate *Stylephorus.* Since Regan's (1907, 1924) classification, several new genera have been accommodated in two lampridiform families: *Zu* Walters and Fitch and *Desmodema* Walters and Fitch (included in the Trachipteridae) and *Metavelifer* Walters (included in the Veliferidae). Furthermore, the Regalecidae was re-erected to accommodate *Regalecus* (originally placed in the Trachipteridae by Regan, 1907) and *Agrostichthys* Phillips (Walters and Fitch, 1960). Thus, in Regan's (1907, 1924) scheme adopted by Greenwood et al. (1966), the Lampridiformes comprised four suborders and six families, a classification soon amended with the addition of the monotypic Radiicephalidae (*Radiicephalus* Osario) by Harrisson and Palmer (1968). As presently understood, these seven families comprise 21 species allocated to 12 genera (Olney, 1984). The families were considered by Oelschläger (1976) to represent two divergent morphological series (Fig. 2): a deep-bodied, generalized Lamprididae and Veliferidae; and the elongate, specialized Lophotidae, Radiicephalidae, Trachipteridae, Regalecidae and Stylephoridae. In a later and more extensive treatment of the functional anatomy and phylogeny of these families, however, Oelschläger (1983) placed lophotids as the sister group to *Lampris,* these taxa together forming the sister group of all other taeniosomes (Fig. 3); thus, he hypothesized that elongate forms may have evolved twice in the lampridiform lineage.

Regan's concept of the Lampridiformes was broadened considerably by Rosen and Patterson (1969) with the provisional addition of ateleopodoid, mirapinnatoid and megalomycteroid fishes. [Oelschläger (1983) did not treat these taxa.] Rosen and Patterson (1969) noted similarities in the upper jaw, cheek musculature, and caudal skeleton among *Ateleopus, Eutaeniophorus,* trachipterids and *Regalecus* (but did not examine specimens of *Mirapinna* or *Megalomycter*). They invoked Regan's (1907) character (absence of a maxillary prong on the palatine) to discount relationship between lampridiforms and the extinct *Asineops* but did not detail the morphology of the suspensorium in *Ateleopus* or *Eutaeniophorus.* One "advanced" character (hypurostegy) was used to unite the Lampridiformes with several extinct taxa (*Palaeocentrotus, Pharmacichthys, Aipichthys* and *Bathysoma*) treated by Patterson (1968). Although not universally recognized by recent workers

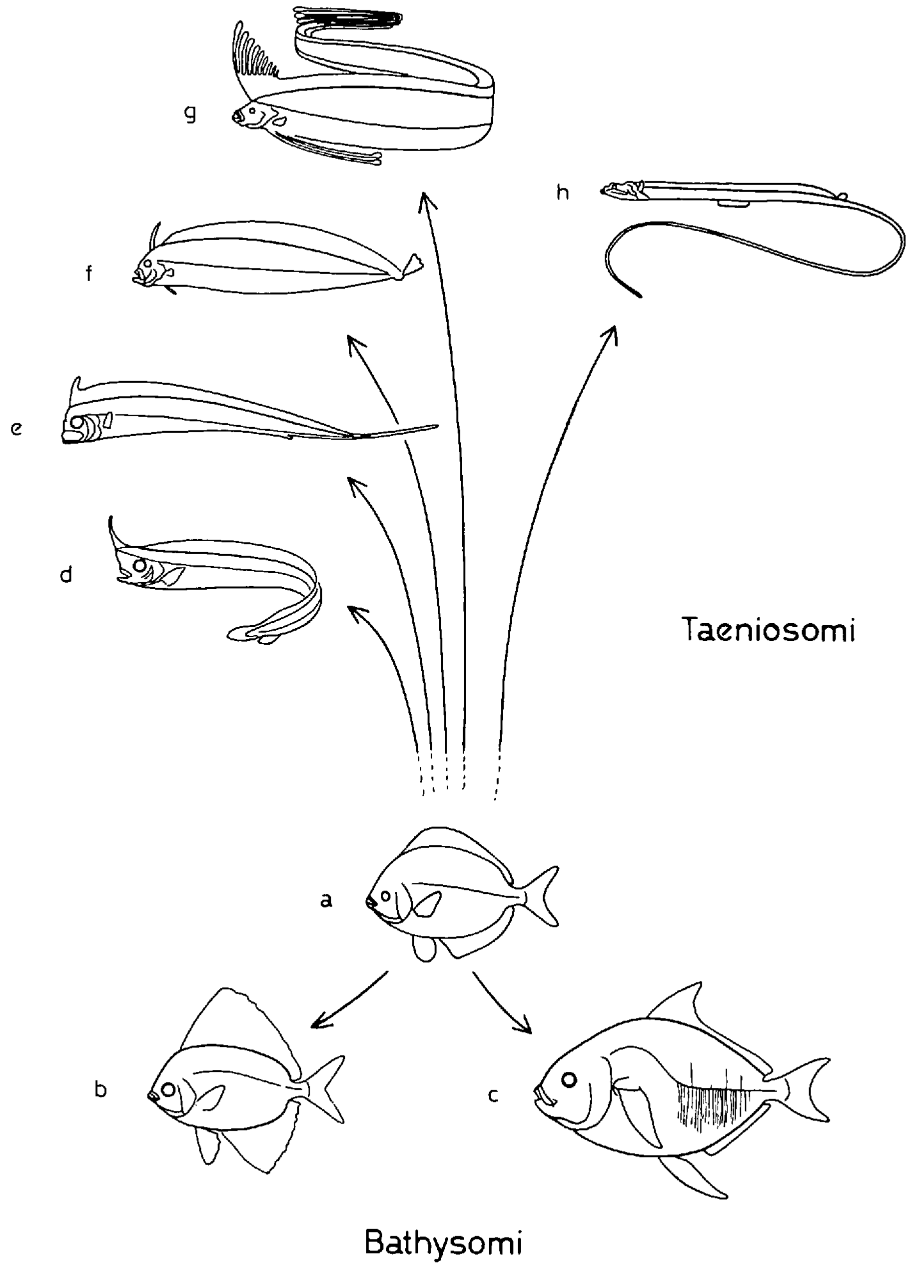


Figure 2. Morphological radiation of Lampridiform (=Allotriognath) families (from Oelschläger, 1976): a) an hypothesized ancestral lampridiform; b) Veliferidae; c) Lamprididae; d) Lophotidae; e) Radiicephalidae; f) Trachipteridae; g) Regalecidae; h) Stylephoridae.

(Oelschläger, 1983; Bertelsen and Marshall, 1984; Olney, 1984) and somewhat altered in subsequent re-examination by Rosen (1973), the expanded Lampridiformes (sensu Rosen and Patterson, 1969) persists in present classifications (Nelson, 1984; Smith and Heemstra, 1986; Eschmeyer, 1990).

Commenting that "... there is no decisive evidence on the nearest relatives of

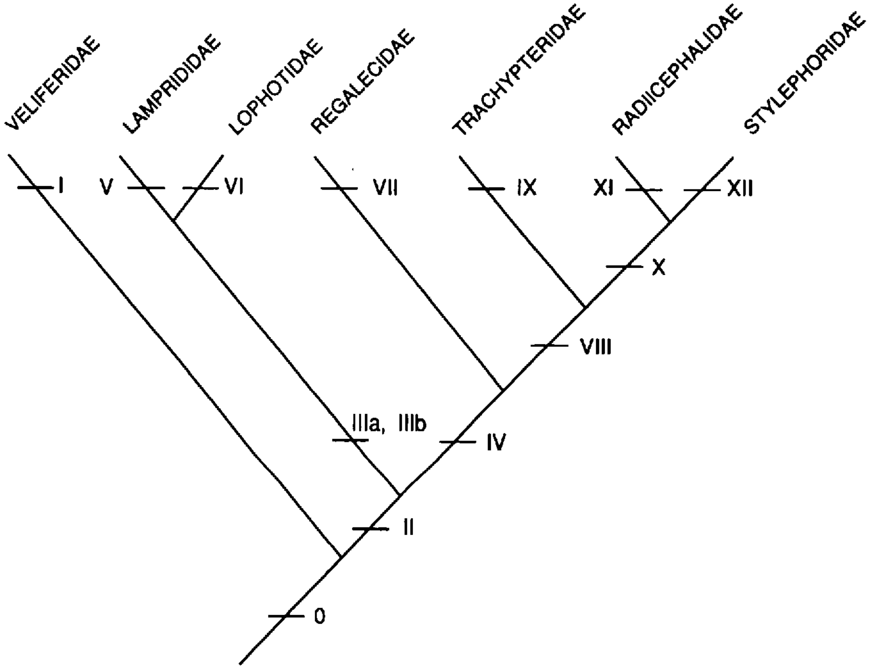


Figure 3. Hypothesis of relationships of lampridiform families proposed by Oelschläger, 1983 and redrawn from his fig. 109. Numbers refer to the following synapomorphies: (0) strongly protractile jaw apparatus for small animal feeding; (I) scaly sheath on dorsal- and anal-fin bases; (II) horizontal pectoral fins; (IIIA) strong separation of coracoid and distal cleithrum; (IIIB) pectoral-fin radials with clearly marked ovoid condyles; (IV) friction reducing skin; (V) shoulder girdle as a secondary swimming apparatus; (VI) frontal-occipital crest with a rostral horn; (VII) pelvic fins with chemical receptive organs; (VIII) symmetric insertion of pectoral erector muscle; (IX) dorsal lobe of caudal fin bears lateral line; (X) ventral lobe of caudal fin bears lateral line; (XI) pelvic fins abdominal; (XII) protractile jaw like a pipette.

the Lampridiformes," Rosen and Patterson (1969: 461) placed lampridiform fishes within the Acanthopterygii ". . . rather than erect yet another higher category. . . ." Few systematists dispute this claim and none has rigorously tested the validity of the classification (Rosen, 1973; Oelschläger, 1983; Lauder and Leim, 1983; Olney, 1984). Four recent studies, however, serve as a starting point for an examination of basal relationships of lampridiform fishes. Johnson (1992) reviewed previous evidence for monophyly of the Neoteleostei, Eurypterygii and Ctenosquamata and provided additional synapomorphies of each clade. Stiassny (1986) identified four derived features supporting the monophyly of the Acanthomorpha (*Polymixia* + Paracanthopterygii + Acanthopterygii) and two that support a sister-group relationship between "acanthopt" and "paracanthopt" fishes. Patterson and Rosen (1989) identified four synapomorphies of the Paracanthopterygii. Finally, in a recent survey of the anatomy of the pelvic-fin girdle among acanthomorph fishes, Stiassny and Moore (1992) identified an additional putative synapomorphy of Acanthomorpha (the ligamentous association of the pelvic girdle with the postcleithrum). Holocentrid fishes were hypothesized to be the sister group of the "higher Percomorpha," a clade consisting of zeiform, scorpaeniform and perciform fishes and united on the basis of a ligamentous association between contralateral pelvic-fin bases. Based solely on pelvic-fin morphology, Stiassny and Moore (1992) considered the position of *Lampris* and its relatives to be the most problematical of all considered acanthomorph lineages. When these hypotheses (Stiassny, 1986; Patterson and Rosen, 1989; Johnson, 1992; Stiassny and Moore, 1992) are considered collectively, however, the position of the Lampridiformes among neoteleostean taxa is less equivocal.

Our first objective is to place "generalized" (and presumably phylogenetically primitive) lampridiform taxa within existing proposals of neoteleostean phylogeny (Stiassny, 1986; Patterson and Rosen, 1989; Johnson, 1992; Stiassny and Moore, 1992). We initially treat the veliferids, *Velifer* and *Metavelifer,* as phylogenetically primitive because they are the most generalized members of the diverse and highly modified lampridiform lineage (Rosen, 1973; Oelschläger, 1983). We will demonstrate the validity of the assumption that veliferids are the sister group of all other lampridiforms in a later section. Lastly, we cladistically test Regan's (1907, 1924) and Oelschläger's (1983) hypotheses of lampridiform monophyly, define the limits of the Lampridiformes and propose a new scheme of intrarelationships.

MATERIALS AND METHODS

Adult lampridiform fishes attain large sizes (Robins et al., 1986; for example, up to 270 kg weight in *Lampris*; up to 17 m total length in *Regalecus*), and are rare in systematic collections. Consequently, all lampridiform specimens that we examined were eggs, larvae or juveniles, and many were damaged by collection and handling. Cleared and stained specimens were dissected, and illustrations were made with the aid of a camera lucida, traced from photographs or prepared with a 35-mm photomicroscope system. In illustrations, cartilage is indicated by larger stippling. Unless otherwise noted, scale bars are 1 mm. In the following, we use standard acronyms for resource collections (Leviton et al., 1985; Leviton and Gibbs, 1988) and list family, genus, species (when determined), museum, catalogue number, and standard length (SL) for material used in this study.

Cleared and Stained.—Polymixiidae: *Polymixia lowei,* VIMS 04421, 68 mm; Aphredoderidae, *Aphredoderus sayanus,* VIMS 21113, 62, 48 mm; Trachichthyidae: *Trachichthys mento,* USNM 269460, 80 mm; *Hoplostethus mediterraneus,* VIMS 4900, 40 mm; Melamphaidae: *Scopelogadus mizolepis,* VIMS 05954, 49 mm; Stephanoberycidae: *Stephanoberyx monae,* USNM 208284, 81 mm; Diretmidae, *Diretmus argenteus,* VIMS uncat., 39 mm SL; *Anoplogaster cornuta,* VIMS unlabelled, 89 mm SL; Ateleopodidae: *Ateleopus japonicus,* AMNH 27680SW, ca. 270 mm (the head of the specimen is separated from the body); Veliferidae: *Metavelifer multiradiatus,* BPBM 23953, 77 mm SL; *Velifer hyselopterus,* RUSI 13821, 138 mm; Lamprididae: *Lampris guttatus,* MCZ 55173, 19.2 mm SL; Stylephoridae: *Stylephorus chordatus,* MCZ 58941, 31 mm SL; Radiicephalidae: *Radiicephalus elongatus,* MCZ 58904, 86 mm SL; Lophotidae: *Lophotus lacepede,* HML uncat., 49 mm SL; *Eumecichthys fiski,* VIMS uncat., 63 mm; Regalecidae: *Agrostichthys parkeri,* ISH 643/71, 300 mm SL; *Regalecus glesne,* HML 6848, 196 mm; Trachiperidae: *Trachipterus* sp., SIO uncat. (rec. 131), 54 mm SL; *Trachipterus* sp., VIMS uncat., 23, 56 mm; *Zu cristatus,* SEFC uncat. (National Marine Fisheries Service, Southeast Fisheries Center, Miami, Florida), 147 mm SL; *Desmodema* sp., MCZ 58907, 41 mm SL.

Whole Specimens.—Veliferidae: *Metavelifer multiradiatus,* BPBM 24712, 72 mm; *Velifer hypselopterus,* MCZ 47010, ca. 230 mm; Lamprididae: *Lampris guttatus,* USNM 271011, 273477, 273479, all skeletons; Stylephoridae: *Stylephorus chordatus,* MCZ 58936, 172 mm SL; Lophotidae: *Eumecichthys fiski,* MCZ 55176, 29 mm; Trachipteridae: unidentified eggs, SWFC uncat. (National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California), Eastropac Station 20.240.

RELATIONSHIPS OF THE VELIFERIDAE

In the following, we briefly survey the distribution of neoteleostean, eurypterygian, ctenosquamate (Johnson, 1992), acanthomorph (Stiassny, 1986), paracanthopterygian (Patterson and Rosen, 1989) and percomorph (Stiassny, 1990) synapomorphies in lampridiforms with special reference to *Metavelifer* and *Velifer.* Characters are labelled with letters to facilitate subsequent discussion.

Neoteleostean Synapomorphies (Johnson, 1992).—A) **Exoccipitals and basioccipital exposed posteriorly and joined in an inverted y-shaped suture**: This condition

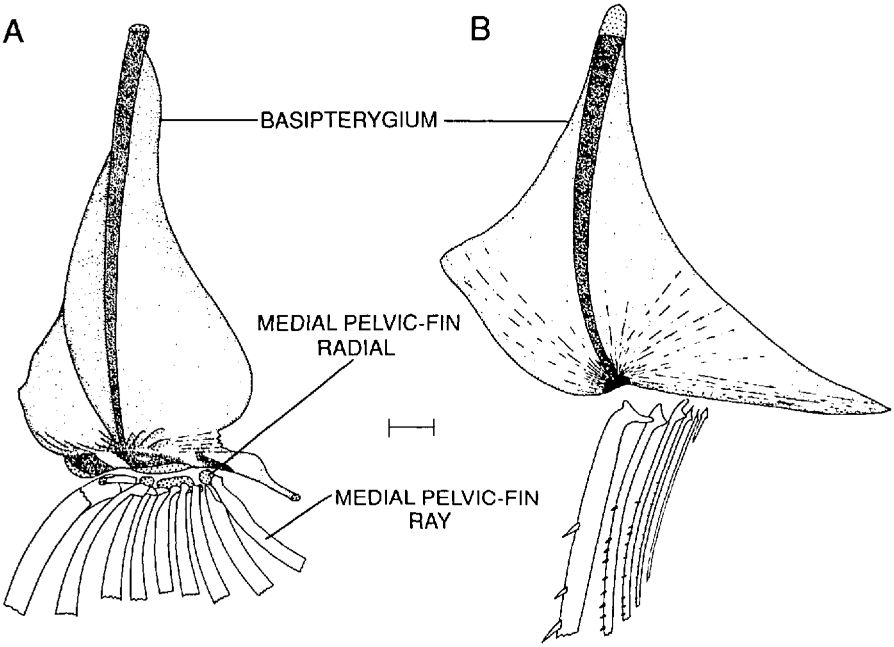


Figure 4. Left lateral view of the pelvic-fin skeleton of (A) *Metavelifer multiradiatus*, BPBM 23953, 77 mm SL; proximal portion of ventral half of most lateral pelvic ray removed; (B) *Zu cristatus*, SEFC uncat., 147 mm SL.

is present in veliferids but modified in *Lampris* (see Lampridiform Monophyly). **B) Type 4 tooth attachment**: Veliferids and *Lampris* lack teeth. The primary jaws and vomer of all other lampridiforms, except our larval specimen of *Desmodema*, bear one to several teeth of mixed types (type 2 teeth in *Zu cristatus* and type 4 teeth in *Radiicephalus elongatus*). **C) Presence of a retractor dorsalis muscle**: The retractor dorsalis is present in all lampridiforms (Rosen, 1973: figs. 104, 105). **D) Insertion of the third internal levator on the fifth upper pharyngeal toothplate**: The fifth upper pharyngeal toothplate is absent in all lampridiforms (see below).

Eurypterygian Synapomorphies (Johnson, 1992).—**E) Toothplate fused to the third epibranchial**: The third epibranchial toothplate is absent in all lampridiforms (Rosen, 1973: figs. 104, 105). **F) Presence of an interoperculohyoid ligament**: This ligament is present in all lampridiforms. **G) Fusion of the ventral half of the medial pelvic ray to the medial pelvic radial**: Both *Velifer* and *Metavelifer* have the ventral half of the medial pelvic ray fused to the medial pelvic radial. In *Velifer* there are two autogenous, ossified lateral radials supporting the remaining pelvic-fin rays. Our juvenile specimen of *Metavelifer* has two large and two smaller autogenous lateral radials; only the lateralmost is partly ossified (Fig. 4A). See "Lampridiform Monophyly" for additional modifications in other lampridiforms.

Ctenosquamate Synapomorphies (Johnson, 1992).—**H) Absence of the fifth upper pharyngeal toothplate and the associated third internal levator muscle**: There is no third internal levator or fifth pharyngeal toothplate in lampridiforms (Rosen, 1973: figs. 104, 105).

Acanthomorph Synapomorphies (Stiassny, 1986).—**I) The maxillo-rostroid ligament originates from the inner face of the maxillary median process just below**

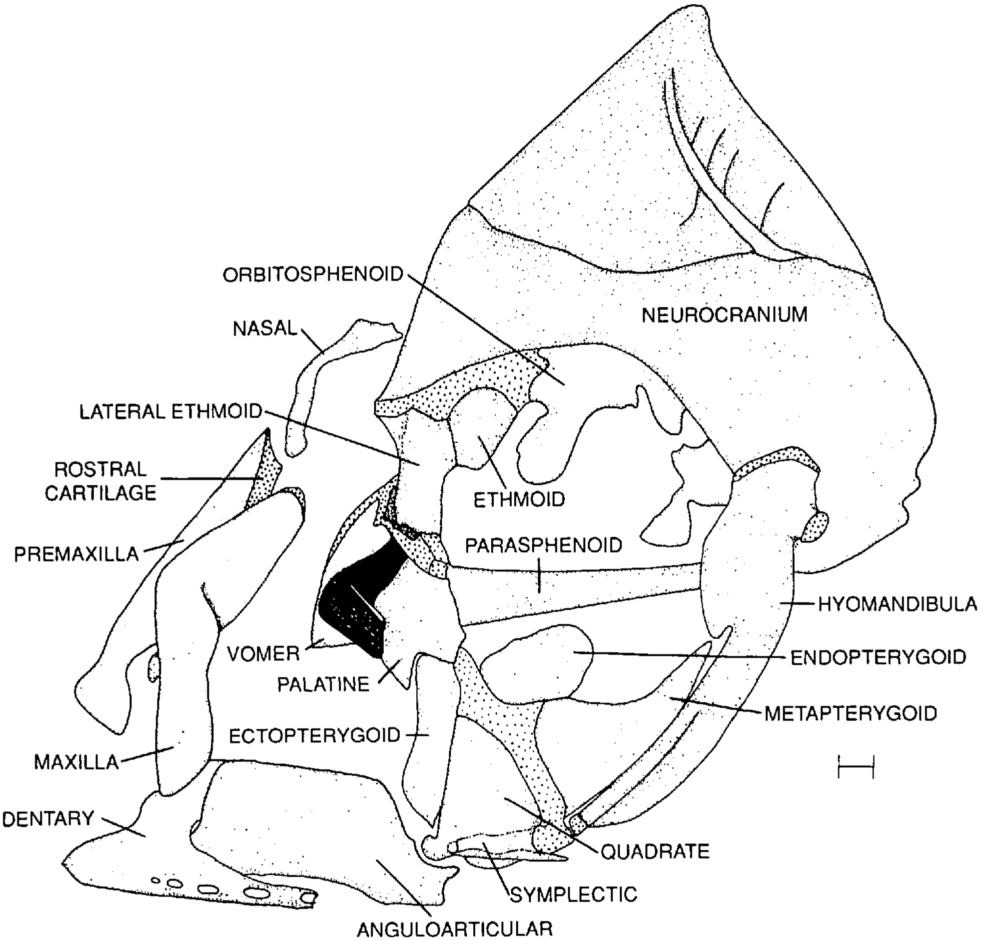


Figure 5. Lateral view of jaws, suspensorium and cranium of *Metavelifer multiradiatus*, BPBM 23953, 77 mm SL. Palato-vomerine ligaments are depicted as dark bands.

the cranial condyle and passes up, out of the folded head, to insert onto the dorsolateral face of the rostral cartilage: The maxillo-rostroid ligament arises from the inner face of the posterior tip of the maxillary ascending process, is closely applied to the rostral cartilage and attaches to the posterior tip of the premaxillary ascending process in all lampridiforms. **J) A spina occipitalis extends ventrally between the epi- and exoccipitals to form the dorsal margin of the foramen magnum**: All lampridiforms lack a spina occipitalis. Although Starks (1908: pl. 2, fig. B) illustrated a spina occipitalis in *Stylephorus*, the condition is not evident in our material. **K) The ethmoid cartilage is reduced and there is a close approximation (often sutural union) of the lateral ethmoids with the vomer**: In veliferids, the ascending processes of the vomer are in close association with (but not sutured to) the lateral ethmoids (Fig. 5). **L) The upper limb of the posttemporal is firmly bound to the epioccipital, and the posttemporal-epioccipital ligament is reduced**: In all lampridiforms, the dorsal limb of the postemporal is firmly bound by ligament to the epioccipital.

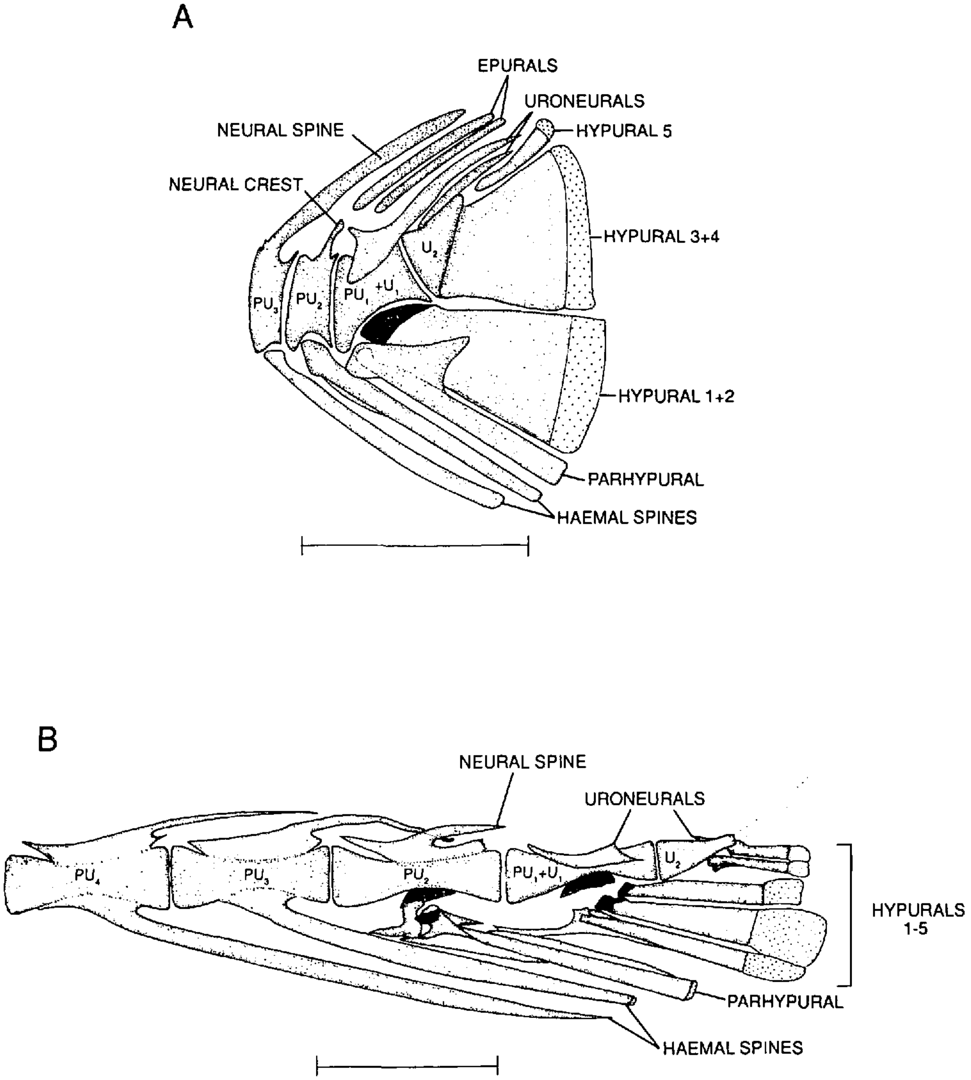


Figure 6. Caudal skeleton of A) *Lampris guttatus*, MCZ 55173, 19.2 mm SL; B) *Radiicephalus elongatus*, MCZ 58904, 86 mm SL. Dark stippling indicates areas of rugosity.

Synapomorphies of Paracanthopterygii + Acanthopterygii (Stiassny, 1986).—**M) The median palato-maxillary ligament is absent, and the body of the palatine is no longer bound to the maxilla**: All lampridiforms possess a highly specialized mechanism of upper jaw protrusion in which the palatine is completely free from the maxilla (see below and Lampridiform Monophyly). Consequently, we consider this character inapplicable to lampridiforms. **N) The palato-vomerine ligament is subdivided into two distinct ligaments, with the anterior subdivision inserting onto the palatine prong**: The palatine is highly modified in lampridiforms, and this character is not applicable for the group. Lampridiforms lack a palatine prong and have an extremely broad palato-vomerine ligament. There is evidence of subdivision of this ligament in some taxa (e.g., *Metavelifer*, Fig. 5) but it is not clear that this condition is homologous with that described by Stiassny (1986).

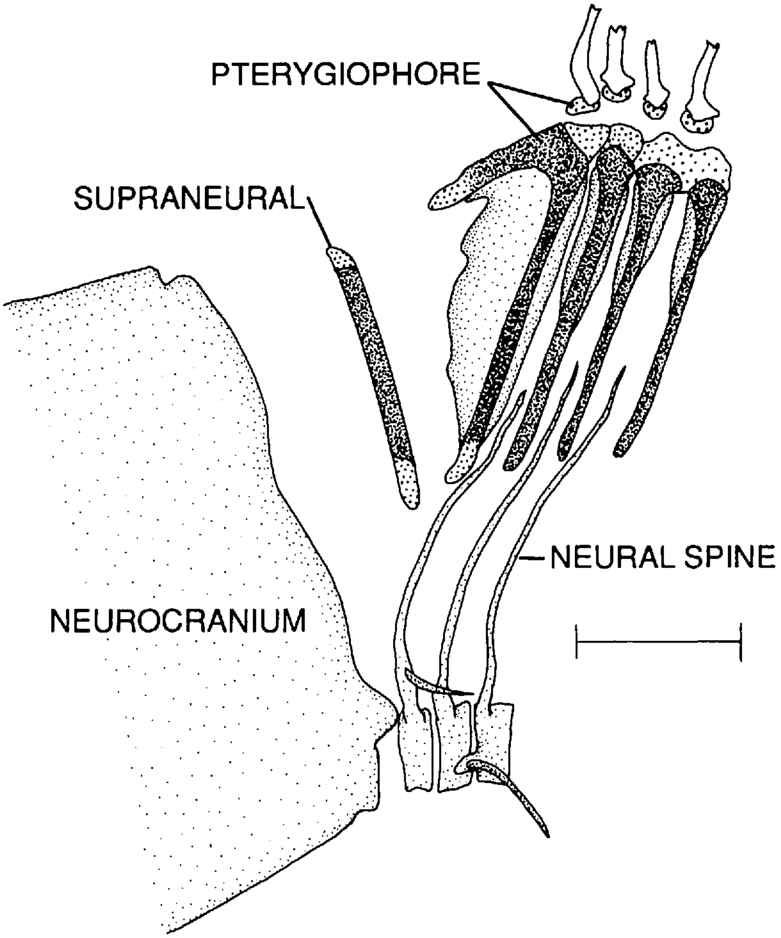


Figure 7. Anterior dorsal fin and vertebrae of *Lampris guttatus*, MCZ 55173, 19.2 mm SL.

Paracanthopterygian Synapomorphies (Patterson and Rosen, 1989).—**O) A full neural spine on PU2**: The neural spine of the second preural centrum is reduced to a low crest in veliferids (Rosen, 1973: fig. 111) and *Lampris* (Fig. 6A). Among other lampridiforms, the condition is variable. Rosen (1973: fig. 112) assessed the full neural spine of *Trachipterus* to be secondarily derived. **P) Two epurals**: Veliferids have three epurals (Rosen, 1973: fig. 111), *Lampris* has two epurals and the remaining lampridiforms have two or fewer (Fig. 6). **Q) A single supraneural behind the first or second neural spine**: *Velifer* has two supraneurals, and the single supraneural of *Metavelifer* and *Lampris* (Fig. 7) is anterior to the first neural spine (see "Lampridiform Monophyly" for modifications in other lampridiforms). **R) The intercalar is enlarged, containing glossopharyngeal foramen, and forming part of cranial wall**: The intercalar in lampridiforms is small and does not contain the glossopharyngeal foramen.

Relationships.—The distribution of characters reviewed above convincingly places lampridiforms within the Acanthomorpha and excludes them from the Paracanthopterygii. Many authors have commented on the absence of spines in the pelvic, dorsal and anal fins of veliferids (Rosen, 1973; Lauder and Liem, 1983).

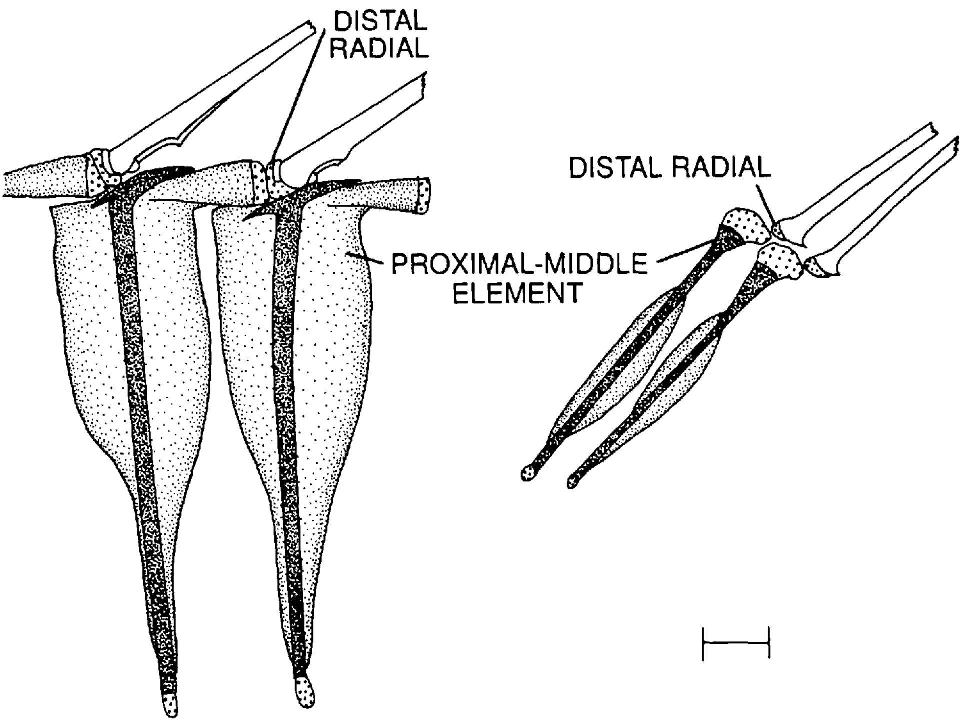


Figure 8. Left lateral view of dorsal-fin pterygiophores of *Metavelifer multiradiatus,* BPBM 23953, 77 mm SL. Left, incipient spine-bearing pterygiophores (12th, 13th); Right, ray-bearing pterygiophores (35th, 36th).

Our relatively small specimens of *Metavelifer* and *Velifer* have one or more anterior rays in the dorsal and anal fins that are bilaterally fused and unsegmented and thus, should be considered true spines. In addition, the majority of elements in each fin are fused bilaterally at their proximal ends, and are bilaterally paired and segmented distally. Bannikov (1990) indicated that these elements become spines ontogenetically in *Metavelifer.* The pterygiophores supporting the incipient spines (Fig. 8A) differ from those that support the posteriormost soft rays (Fig. 8B) in that their distal ends are bent posteriorly, but the transition in form is gradual, i.e., there is no abrupt shift from spine-bearing to ray-bearing pterygiophores. Although true spines are present in veliferids, they differ from those spines of most Percomorpha in that the bases are open and embrace most of the serially corresponding distal radial; they do not exhibit the chain-link support described by Bridge (1896).

Veliferids are also primitive with respect to percomorphs in the following characters: presence of an orbitosphenoid (Fig. 5); absence of an interarcual cartilage (Fig. 9; also Rosen, 1973: fig. 104); 7–14 pelvic-fin rays and no pelvic spine (Fig. 4A; also Olney, 1984); 10 + 9 principal caudal-fin rays (Oelschläger, 1974); and six hypurals (Rosen, 1973: fig. 111).

The percomorph synapomorphy described by Stiassny (1990) and further elaborated by Stiassny and Moore (1992) is equivocal for lampridiforms, though probably lacking. According to those authors, percomorphs have a medially sutured pelvic girdle with ventrally displaced anteromedial processes. In veliferids, each pelvic half is rotated ventromedially. The central axis of the pelvis is directed

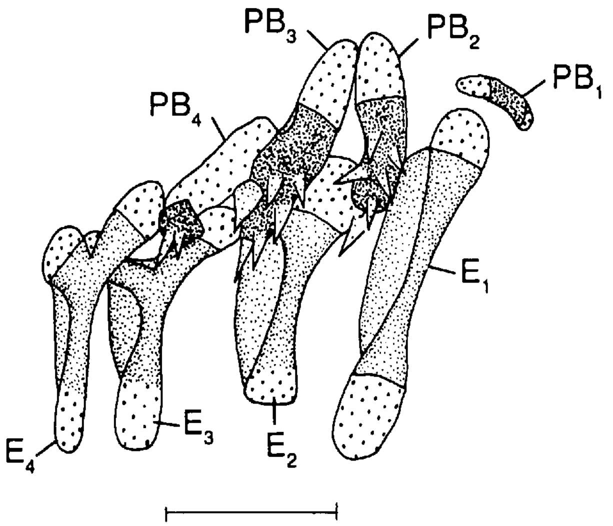


Figure 9. Ventral view of left epibranchials (E_1–E_4) and pharyngobranchials (PB_1–PB_4) of *Lampris guttatus*, MCZ 55173, 19.2 mm SL. Scale bar = 0.5 mm.

dorsally, and the cartilaginous tip of the central process of each girdle half is attached by a strong ligament to the medial face of the cleithrum, a character also considered by Stiassny and Moore (1992) to diagnose percomorphs. The posterior processes are tightly applied along the midline (but there is no suturing), and there are no anteromedial processes.

We conclude here that veliferids and all other lampridiforms are basal acanthomorphs that diverged somewhere below the percomorph clade. Further discussion of the relationships of lampridiforms to basal acanthomorphs is presented by Johnson and Patterson (1993).

MONOPHYLY OF LAMPRIDIFORMES

Below, we review previous evidence of lampridiform monophyly (Regan, 1907, 1924; Oelschläger, 1983) and propose additional synapomorphies based on outgroup comparison with other basal acanthomorphs, including *Polymixia*, percopsiforms, and various beryciforms (see "Materials and Methods"). The discussion of each character is preceded by a brief description of the derived condition.

Character Analysis.—**1) Absence of the anterior palatine process (prong) and the anterior palatomaxillary ligament**: In *Polymixia*, percopsiforms and most beryciforms (as well as most teleosts), the palatine bears a prong that is tipped in cartilage and articulates with the maxilla via the anterior palatomaxillary ligament (Stiassny, 1986). In addition, there is a ligamentous connection between the maxilla and the relatively broad nasal bone. *Anoplogaster* is exceptional in lacking the palatomaxillary ligament and the cartilage-tipped palatine prong, but the maxilla remains tightly bound to the nasal. Furthermore, in all outgroup taxa, the ascending processes of the maxilla and premaxilla are short, and the rostral cartilage is relatively small. Thus, the upper jaws (in particular, the maxilla) of these fishes have limited capability of anterior movement. In all lampridiforms, the anterior palatomaxillary ligament and the palatine prong are absent and the relatively narrow nasals are free from the maxilla (Figs. 5, 10). As a consequence, the maxilla is free to extend, along with the premaxilla, well away from the ethmo-

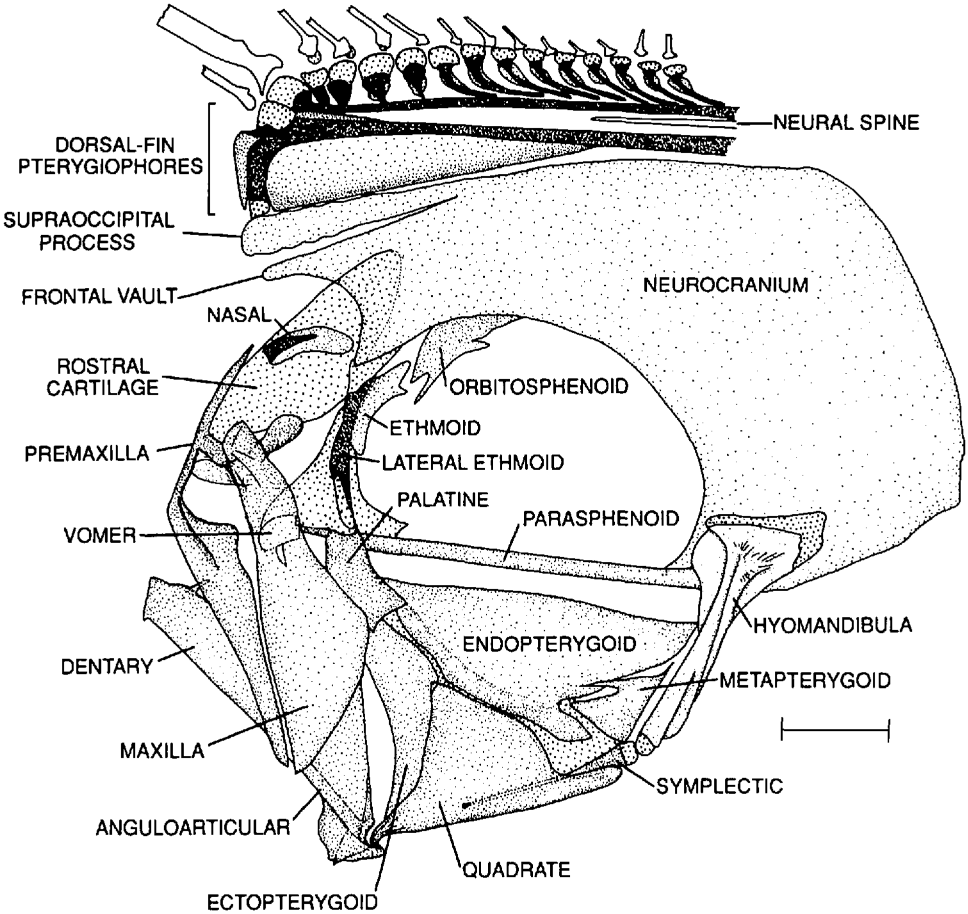


Figure 10. Lateral view of jaws, suspensorium, cranium and anterior pterygiophores of *Lophotus lacepede*, HML uncat., 49 mm SL.

vomerine region during upper jaw protrusion (Plate 1). In veliferids, the palatine bears two cartilaginous heads (Fig. 5), one posteroventrally directed and articulating with the ectopterygoid and the other dorsally directed and associated with the palato-vomerine ligaments. The palatine articulates with a portion of the ethmo-rostroid cartilage that forms the ventral border of the lateral ethmoids. This configuration of articular surfaces and ligaments on the palatine is not considerably altered in other lampridiforms (Figs. 10, 11A) except *Stylephorus* (see "Lampridiform Intrarelationships"). As noted earlier, the absence of a palatomaxillary connection was the primary evidence for Regan's (1907) hypothesis of lampridiform monophyly. **2) Mesethmoid posterior to lateral ethmoids**: In the outgroup taxa, the mesethmoid lies between (in some beryciforms) or is anterior to the lateral ethmoids (Zehren, 1979). In veliferids and all other lampridiforms (Figs. 5, 10, 11A; also Regan, 1907: figs. 166, 167 and Oelschläger, 1983: 14–15, fig. 8), part or all of the mesethmoid is posterior to the lateral ethmoids and is visible through the orbit where it approaches the orbitosphenoid. Oelschläger (1983: 14–15, fig. 8D) did not illustrate a mesethmoid in *Lophotus* but the element is present in our material (Fig. 10). **3) Elongate ascending processes of premaxillae and large rostral cartilage insert into frontal vault or cradle**: In most basal acan-

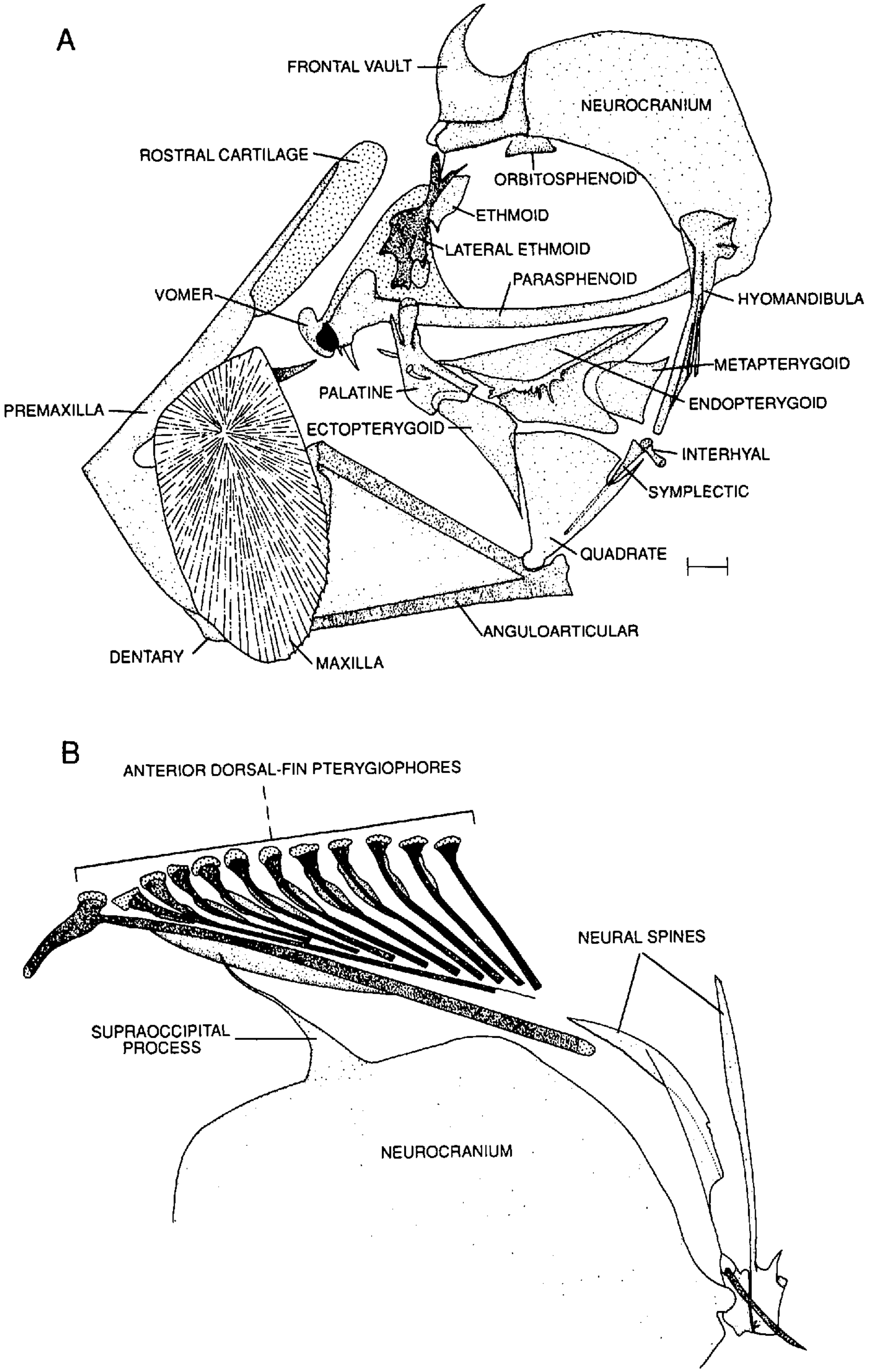


Figure 11. Lateral view of A) jaws, suspensorium, cranium, B) anterior pterygiophores and axial skeleton of *Radiicephalus elongatus*, MCZ 58904, 86 mm SL. The specimen is presently damaged and disarticulated. Illustrations are composites based, in part, on previous photographs of the undamaged specimen. Details, including the supraoccipital spine, of the neurocranium are not shown in view A, and cartilage between suspensorial bones was not stained in the specimen. Darkened area on vomer indicates rugosity.

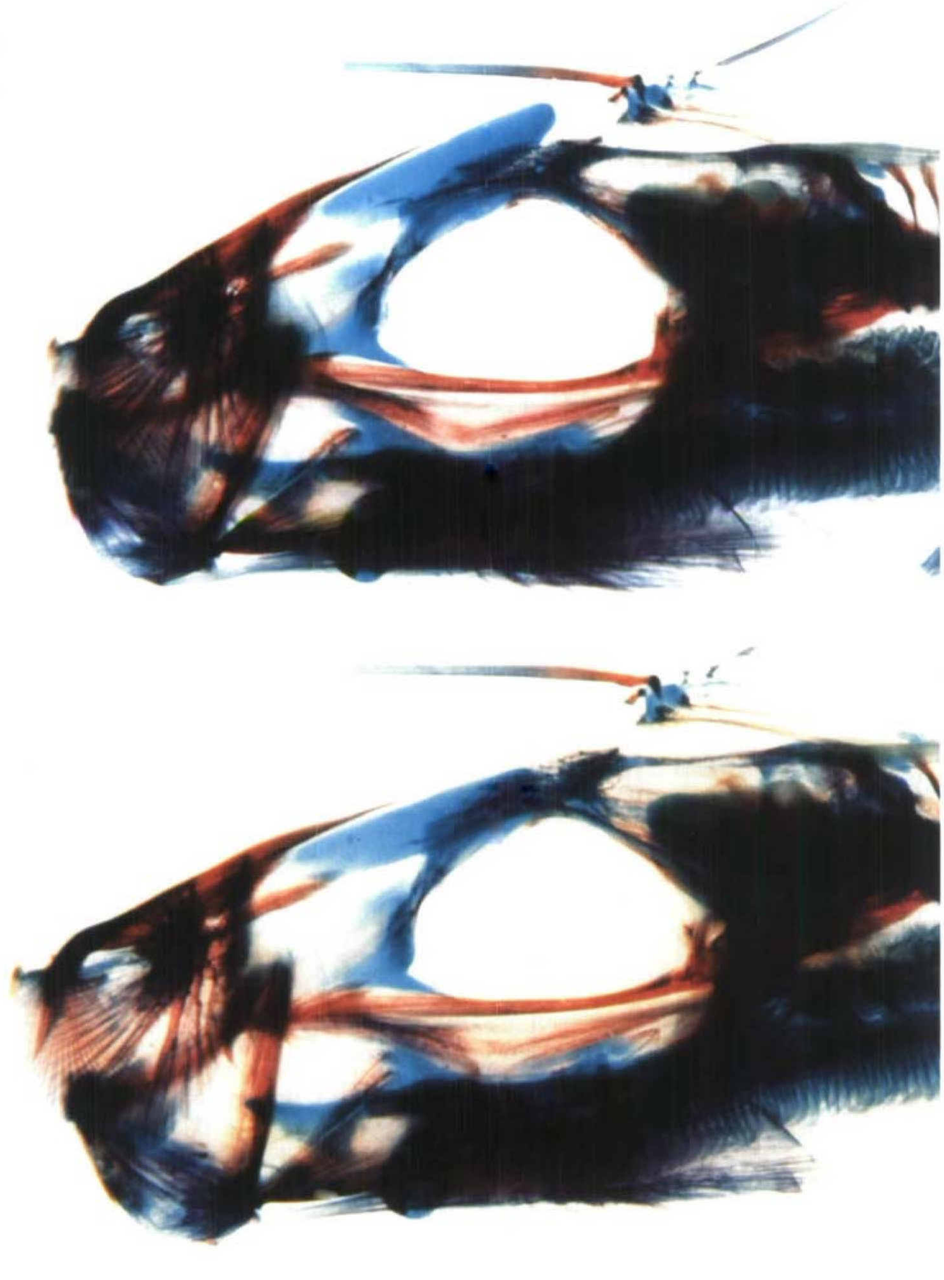


Plate 1. Jaw protrusion in *Agrostichthys parkeri*, ISH 643/71, 300 mm SL. Upper, mouth closed; Lower, jaw partially protruded; Next page, jaw fully protruded.

thomorphs, the ascending processes of the premaxillae are short relative to the alveolar process, and the rostral cartilage rides along the ethmoid cartilage or the mesethmoid (or both), usually abutting the mesethmoid posterodorsally and never extending beyond the anterior margin of the frontals. In many beryciforms, a roof is formed over the rostral cartilage "chamber" by the expanded nasal bones, which

Plate 1. Continued.

Plate 2. Unidentified lampridiform eggs, probably those of *Trachipterus* sp., SWFC uncat. (Eastropac Station 20.240), 1.9 mm chorion diameter.

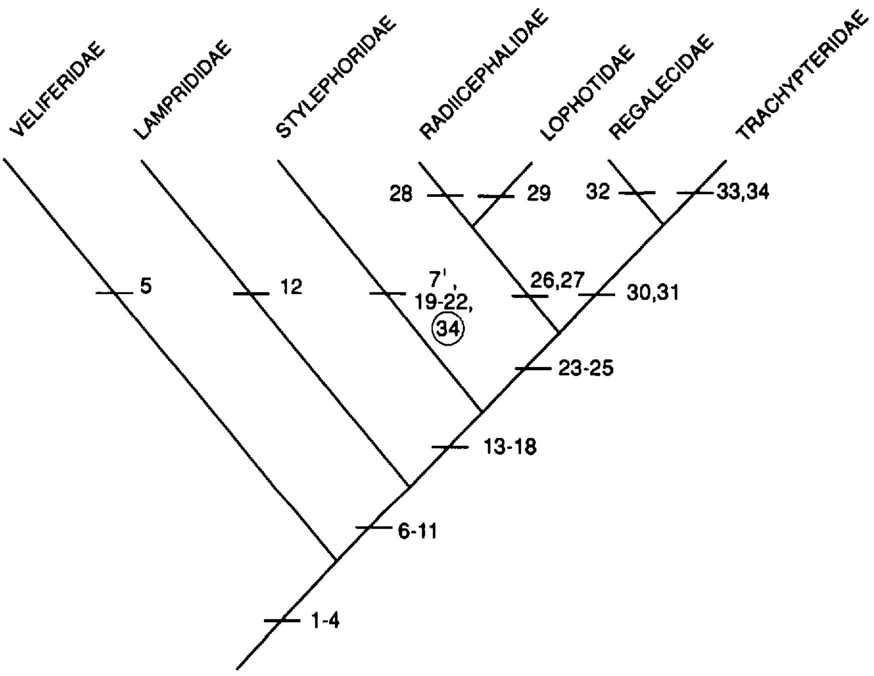


Figure 12. Cladogram depicting hypothesized relationships of lampridiform families. Numbers refer to the following synapomorphies: (1) absence of the anterior palatine process and the anterior palatomaxillary ligament; (2) mesethmoid posterior to lateral ethmoids; (3) elongate ascending processes of premaxillae and large rostral cartilage insert into frontal vault or cradle; (4) first dorsal-fin pterygiophore inserts anterior to first neural spine; (5) dorsal- and anal-fin bases with scaly sheaths; (6) large, pelagic eggs with red-brown chorion; (7) first pectoral-fin radial fused to the scapula, remaining three radials autogenous; (8) absence of uncinate process on first epibranchial; (9) absence of autogenous pelvic-fin radials; (10) more than 40 total vertebrae; (11) second, third and fourth pharyngobranchials columnar, obliquely oriented and with small, posteroventral toothplates; (12) foramen magnum enclosed in cranial condyle; (13) absence of supraneurals; (14) absence of supraoccipital crest; (15) first two dorsal-fin pterygiophores greatly enlarged and inclined sharply forward over the cranium; (16) first neural spine directed anteriorly, usually curving over posterior surface of the cranium; (17) fewer than 20 total caudal-fin rays, some of which are enlarged; (18) first vertebral centrum reduced in length; (19) second neural spine absent, neural arch m-shaped; (20) loss of rostral cartilage; (21) palatine reduced to small, straight rod; (22) posterior shift in first dorsal-fin pterygiophore position; (23) dorsal-fin rays bear lateral spinules; (24) one or two fang-like teeth on the vomer; (25) more than 60 total vertebrae; (26) anteriorly projecting supraoccipital process; (27) ink gland present; (28) elongate haemal spines on PU4–PU6; (29) supraoccipital spine enlarged and supporting first dorsal-fin pterygiophore; (30) absence of anal fin; (31) caudal- and pelvic-fin rays bear lateral spinules; (32) pelvic-fin rays reduced in number to one stout, elongate ray and one small splint-like element; (33) lateral line scales bear spines; (34) absence of pleural ribs. Character 7' is a reversal, and the circled number indicates independent origin.

frequently meet along the midline. In all lampridiforms, the ascending processes of the premaxillae are extremely long (equal to or longer than the alveolar processes) and together with the large rostral cartilage extend much farther posteriorly to insert into a vault or cradle formed by the frontals (Figs. 5, 10, 11A, Plate 1). The rostral cartilage is somewhat trapezoidal (and similar in shape to that of outgroup taxa) in *Metavelifer*; it is semi-elliptical and elongate in *Velifer* and all other lampridiforms (Figs. 10, 11A, Plate 1). In veliferids, lophotids, and radiicephalids (Figs. 5, 10, 11A), the frontals are elevated and arched anteriorly to form the dorsal roof and lateral walls of a chamber (the vault) that accommodates the premaxillae or the rostral cartilage (or both). The floor of the chamber comprises the posterior portion of the ethmoid cartilage and the posteriorly displaced mesethmoid. In regalecids (Plate 1) and trachipterids, the frontals do not meet at the midline anteriorly so the chamber has no roof, only lateral walls, and is thus "cradle-like." The upper jaw apparatus is highly modified in *Stylephorus* which lacks a rostral cartilage and a frontal vault or cradle (see "Lampridiform Intrarelationships"). In most zeoids, for example *Cyttopsis*, the rostral cartilage is large, slides along the anterior edge of a large mesethmoid and inserts just below two supraorbital ridges. The condition superficially resembles that of lampridiforms (Rosen, 1973) but the mesethmoid is anterior to the lateral ethmoids and there is no well-defined frontal chamber. **4) First dorsal-fin pterygiophore inserts anterior to first neural spine**: Insertion of the first dorsal pterygiophore anterior to the first neural spine is unique among basal acanthomorphs to lampridiform fishes (Figs. 7, 10, 11B). The next most anterior placement is found in some holocentrids where the insertion is anterior to the second neural spine. In *Stylephorus* anterior vertebrae are highly modified and the position of the first dorsal pterygiophore is more posterior (it inserts between the third and fourth neural spines, see Intrarelationships section, character 25).

Limits of the Lampridiformes and the Relationships of Ateleopus.—We conclude that monophyly of Lampridiformes is supported by four apomorphies: liberation of the maxilla from the ethmo-vomerine region, posterior displacement of the mesethmoid, insertion of the premaxillae and enlarged rostral cartilage into a frontal cradle or vault and the anterior insertion of the dorsal fin (Fig. 12). [A fifth lampridiform synapomorphy, large pelagic eggs with red-brown chorions (character 6), is putative and discussed in the following section.] Three of these characters are correlated modifications related to the evolution of an unusual feeding mechanism in which the maxilla slides forward with the premaxilla during jaw protrusion (Regan, 1907). Together they represent a functional complex unique to lampridiforms. One of the most unusual features, loss of the palatine prong and palato-maxillary ligament, is also found in the beryciform *Anoplogaster* suggesting a possible sister-group relationship. We reject that hypothesis because considerable evidence supports the affinities of *Anoplogaster* with the Trachichthiiforms (sensu Moore, 1993) or Beryciformes (sensu Johnson and Patterson, 1993), and lampridiforms lack the specializations that diagnose these groups.

Rosen and Patterson (1969) proposed a close relationship between eutaeniiophorids, mirapinnids, ateleopodids and lampridiforms based on perceived similarities in jaw structure and caudal skeleton. Evidence is presented elsewhere in this volume (Moore, 1993) that eutaeniophorids and mirapinnids are related to stephanobercyiforms. Rosen (1973) concluded that the configuration of the dorsal gill-arch elements of ateleopodids is not consistent with a hypothesis of ateleopodid affinities with lampridiforms, but subsequent classifications (Nelson, 1984; Smith and Heemstra, 1986; Eschmeyer, 1990) have continued to follow it. Ateleopodids lack all of the four diagnostic apomorphies of lampridiforms; thus, we agree with Rosen (1973) that there is no close affinity between the two groups. Furthermore, as discussed below, we believe that ateleopodids are not acanthomorphs, and diverged well below the ctenosquamate clade.

Ateleopodids lack all four acanthomorph synapomorphies proposed by Stiassny (1986) and listed above. There is no spina occipitalis, the postemporal is attached

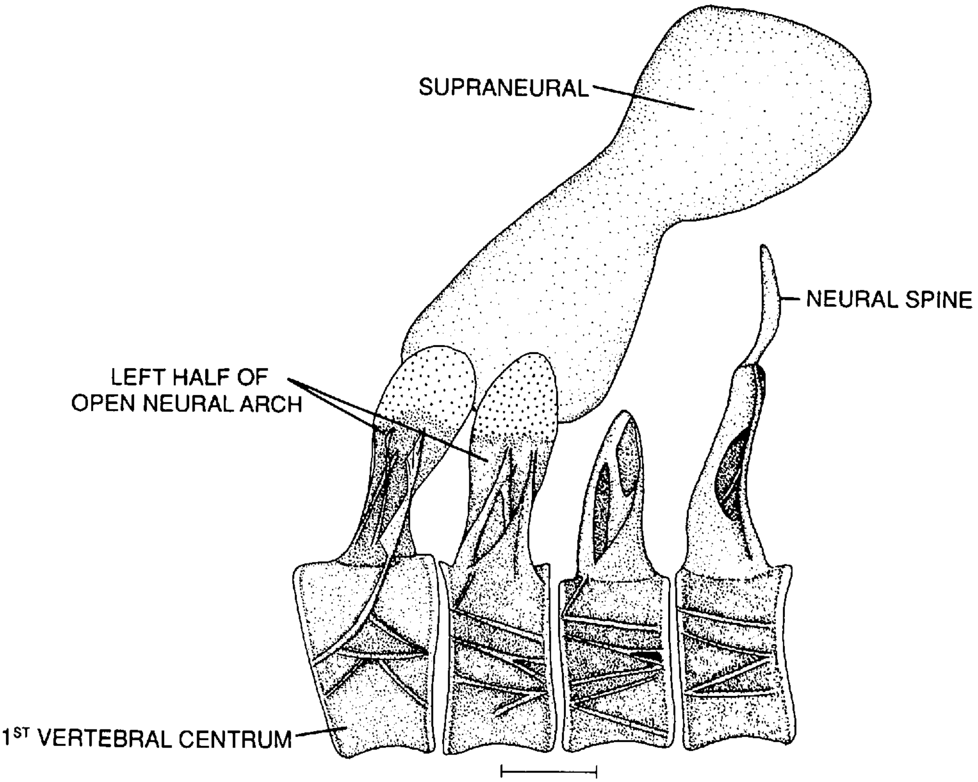


Figure 13. Left lateral view of anterior vertebrae and supraneural of *Ateleopus japonicus*, AMNH 27680SW, ca. 270 mm.

to the cranium by a strap-like postemporal-epioccipital ligament, the lateral ethmoids are widely separated from the vomer, and neither bone bears processes for articulation with the other. Finally, the maxilla does not have a complex folded head, and the maxillo-rostroid ligament arises from the medial face of the maxillary process to insert on the lateral face of the rostral cartilage. Although large and cylindrical, the rostral cartilage of *Ateleopus* is not bound to the premaxillae in the typical acanthomorph fashion, and there are one or two pairs of ancillary cartilages as is frequently the case in non-acanthomorphs. An additional non-acanthomorph feature of ateleopodids is the absence of dorsal- and anal-fin spines.

As Rosen (1973) noted, ateleopodids are unusual in having the upper pharyngeal toothplate fragmented into many small groups of teeth and not fused to their respective pharyngobranchials, which are largely cartilaginous. Although Rosen (1973: 487) stated that pharyngobranchials 2, 3, and 4 are present, his figures 113 and 114 showed correctly that only the second and third are present. We believe that the element labelled UP4 (fourth upper pharyngobranchial toothplate) in those figures is actually UP5. We base this on the observation that the posteriormost internal levator separates distally to form second and third internal levators, the former inserting on the third pharyngobrachial, and the latter on the posteriormost toothplate (Rosen, 1973: fig. 113). Because UP4 never receives insertion of an internal levator, we conclude that the posteriormost upper pharyngeal toothplate of ateleopodids is UP5. Ateleopodids, then, lack the single unequivocal synapomorphy of the Ctenosquamata (see Character H above).

Further corroborating the hypothesis that ateleopodids are not ctenosquamates is the presence of open neural arches on the anterior several vertebrae, with the single, very broad supraneural inserting between those of the first two vertebrae (Fig. 13). The neural arches of at least the first, and usually many succeeding vertebrae remain open in aulopiforms, stomiiforms and most other euteleosts, including ateleopodids. Although not considered as such by Johnson (1992), the presence of a median neural spine on the first vertebra may be synapomorphic for myctophiforms and acanthomorphs.

Ateleopodids are neoteleosts. They possess a retractor dorsalis and have the third internal levator inserting on the fifth upper pharyngobranchial toothplate. They have a tripartite occipital condyle, although the exoccipitals are separated along the midline. They appear to have Type 1 rather than type 4 tooth attachment, but the former is known to be sporadically distributed among neoteleosts (Fink, 1981).

We are confident that ateleopodids are non-ctenosquamate neoteleosts, and find no evidence to support their inclusion within the Euryptergii. They lack the three eurypterygian synapomorphies considered valid by Johnson (1992). The median pelvic ray is not fused with the median pelvic radial, however there are no free pelvic radials and only six pelvic rays. The middle four pelvic rays are extremely reduced and the reduced pelvic girdle is abdominal in position, as it is in most acanthomorphs. Thus, the pelvic girdle and fin are highly modified, and the absence of the medial-ray fusion may be secondary. There is no third epibranchial toothplate (Rosen, 1973: fig. 114), but secondary loss among eurypterygians is not uncommon. There is a well-developed mandibulohyoid ligament and no interoperculohyoid ligament, with no evidence that this condition is secondary. Ateleopodids lack the most convincing synapomorphy of non-ctenosquamate erypterygians (i.e., the Aulopiformes). All aulopiforms share a distinctive configuration of the dorsal gill-arch elements involving lateral displacement of the second pharyngobranchial, concomitant elongation of the uncinate process of the second epibranchial, and absence of a cartilaginous condyle on the third pharyngobranchial for articulation of the second epibranchial (Johnson, 1992). In ateleopodids, the second pharyngobranchial lies directly anterior to the third, and there is no uncinate process on the second epibranchial (compare in Rosen, 1973: figs. 6–16 with 113).

Finally, of the eight stomiiform synapomorphies identified by Fink and Weitzman (1982), ateleopodids lack seven, and we have no information on the eighth (posterior placement of the rete mirabilia). Based on the character information reviewed here, it is most parsimonious to place the ateleopodids in an unresolved trichotomy with stomiiforms and eurypterygians.

INTRARELATIONSHIPS OF LAMPRIDIFORMES

In the following cladistic analysis of lampridiform intrarelationships, characters were polarized by outgroup comparison with other basal acanthomorphs following the methods of Maddison et al. (1984). Once phylogenetically primitive lampridiform taxa are hypothesized, characters within the lineage are polarized on the basis of comparison with those taxa. This phylogeny describes interfamilial relationships. We do not emphasize autapomorphies of terminal taxa, but describe at least one for each family with emphasis on those that are previously unrecognized (for example, see Characters 19–22 below). In doing so, we have not considered a wealth of highly specialized morphological characters, expressed

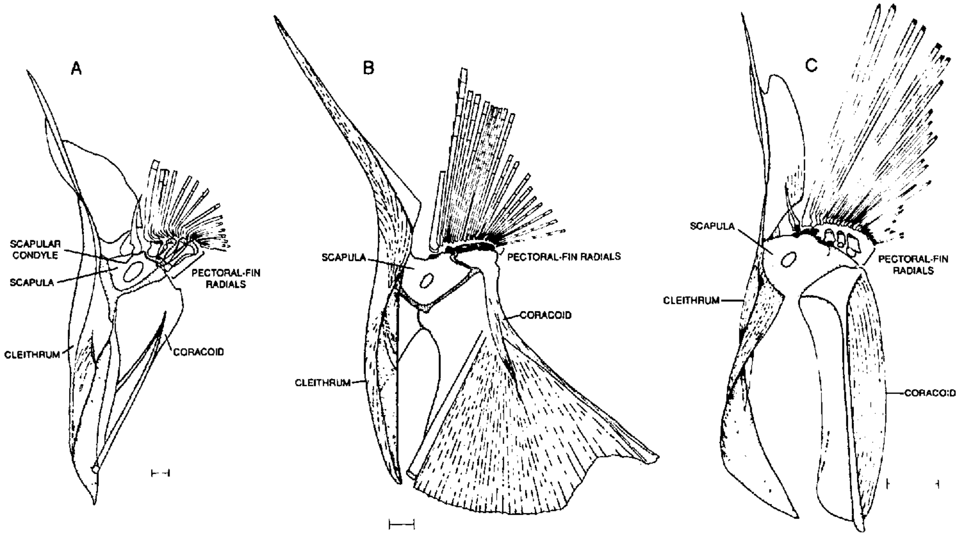


Figure 14. View of left pectoral-fin skeleton of (A) *Metavelifer multiradiatus*, BPBM 23953, 77 mm SL; B) *Diretmus argenteus*, VIMS uncat., 39 mm SL; C) *Lampris guttatus*, MCZ 55173, 19.2 mm SL. Darkened areas indicate rugosity.

uniquely by virtually every lampridiform genus. Numerals designating apomorphies are used in the cladogram (Fig. 12).

VELIFERIDAE. **5) Dorsal- and anal-fin bases with scaly sheaths**: A thick, scaly sheath of skin lies at the base of portions of the dorsal and anal fins in *Velifer* and *Metavelifer* (Oelschläger, 1983; Heemstra, 1986), extending posteriorly along 20–30% of the proximal portion of all but about the last 6 (*Velifer*) to 12 (*Metavelifer*) dorsal- and anal-fin rays. The anterior fin rays can be depressed into this sheath. The sheathed rays are those described as "incipient spines" (see discussion of veliferid relationships above); the true soft rays are unsheathed as reported by Bannikov (1990). This condition is unique among lampridiforms to the Veliferidae and is not present in other basal acanthomorphs.

Lamprididae and above. **6) Large, pelagic eggs with red-brown chorion**: Olney (1984) reviewed available data on lampridiform egg morphology. Eggs of veliferids, radiicephalids and stylephorids are unknown. Eggs of trachipterids (Plate 2), regalecids, lophotids and lamprids are large (1.5–4.1 mm egg diameter), brightly colored (often pink to reddish brown), and possess thick, multi-layered chorions (Olney, 1984: 371, fig. 194). Up to 3 weeks may be required for incubation of lampridiform eggs, and Breder (1962) hypothesized that the distinctive chorions may be a specialization related to intense ultraviolet radiation in the epipelagic environment. Of known euteleostean eggs, only those of exocoetoids are similar, and they clearly have evolved independently (Olney, 1984). Large eggs with colored chorions may characterize all lampridiforms, but in the absence of information on eggs of veliferids, *Stylephorus* and *Radiicephalus*, we tentatively interpret the character as a synapomorphy of *Lampris* and the taeniosomes. **7) First pectoral-fin radial fused to the scapula, remaining three radials autogenous**: In lampridiforms and most teleosts, the base of the medial half of the first pectoral-fin ray is expanded to form an articular surface for the scapular condyle (Fig. 14). In veliferids and all basal acanthomorphs except *Diretmus*, succeeding pectoral-fin rays are supported by four autogenous radials (Fig. 14A). In *Diretmus* (Fig. 14B), none of the four radials is autogenous; the first radial is fused to the scapula and the three posterior radials are fused to one another and together fused to the coracoid. *Lampris* (Fig. 14C) and all other lampridiforms (except *Stylephorus*), share the unique condition of having the first pectoral-fin radial fused to the scapula; the three posterior radials remain autogenous. *Stylephorus* has all four radials autogenous (Regan, 1924: fig. 8), here interpreted as a reversal (character 7′). **8) Absence of uncinate process on first epibranchial**: In veliferids and most basal acanthomorphs, the first epibranchial bears an uncinate process that articulates with the second pharyngobranchial (Rosen, 1973: figs. 88, 104). *Lampris* (Fig. 8) and all other lampridiforms (Rosen, 1973: fig. 106), lack this process. **9) Absence of autogenous pelvic-fin radials**: Primitively in basal acanthomorphs, there are two large autogenous radials associated with each half of the pelvic-fin girdle. They lie lateral to the medial radial which is fused to the ventral half of the medial-most pelvic ray. Autogenous lateral radials are present, although frequently reduced in size, in all beryciforms with the exception of a few stephanoberycoids (Stiassny and Moore, 1992). Among lampridiforms, autogenous lateral radials are present only in veliferids (Fig. 4) where they are large as in *Polymixia* and *Percopsis*. **10) More than 40 total vertebrae**: Veliferids have 33–34, lampridids have 43–46 and all other lampridiform fishes have more than 50 total vertebrae (Olney, 1984). More than 40 total vertebrae are found elsewhere among basal acanthomorphs, only in the highly derived stephanoberycoids, Barbourisiidae, Megalomycteridae and Cetomimidae. **11) Second, third and fourth pharyngobranchials columnar, obliquely oriented and with small, posteroventral toothplates**: In veliferids (Rosen, 1973: 482, fig. 105) and other basal acanthomorphs, the second, third and fourth pharyngobranchials are short, triangular to ovoid with large toothplates bearing relatively small teeth that cover most of the horizontally oriented ventral surface of the element. In other lampridiforms (Fig. 8 and Rosen, 1973: 483, fig. 107), the second, third and fourth pharyngobranchials are elongate, columnar structures with a pronounced oblique orientation and posteroventral tips. The toothplates bear relatively few teeth, most of which are much larger than those of veliferids.

LAMPRIDIDAE. **12) Foramen magnum enclosed in cranial condyle**: In most basal acanthomorphs, the foramen magnum is dorsal to the tripartite condyle formed by the basioccipital and exoccipitals. In *Lampris,* the foramen magnum is bounded laterally by the exoccipital condyles (Oelschläger, 1983: 21, fig. 15).

STYLEPHORIDAE AND ABOVE. **13) Absence of supraneurals**: Supraneurals are present in basal acanthomorphs with the exception of some of the most derived stephanoberycoids. *Velifer* has two supraneurals, *Metavelifer* and *Lampris* have one; all other lampridiforms lack these elements. **14) Absence of supraoccipital crest**: In veliferids and *Lampris,* the supraoccipital bears a large median crest (Fig. 5 and Oelschläger, 1983: 14–15, Fig. 8). All other lampridiforms lack a crest, although some possess supraoccipital processes (see Character 26) that are not structural homologues of the crest in veliferids and lampridids. **15) First two dorsal-fin pterygiophores greatly enlarged and inclined sharply forward over cranium**: In basal acanthomorphs, veliferids and *Lampris,* there is no substantial difference between the first two dorsal-fin pterygiophores and the succeeding ones, although the first is frequently broader than the second. Furthermore, the anteriormost pterygiophores are approximately vertically oriented. In all other lampridiforms, the first two dorsal-fin pterygiophores are greatly enlarged and elongate with respect to succeeding elements (Figs. 10, 11B) and, in all but *Stylephorus,* are inclined sharply forward, so that for much of their length they lie along the medial junction of the frontal bones. These two highly modified pterygiophores support stout, elongate rays in larvae (Olney, 1984). In *Stylephorus*, where the first and second vertebrae are severely reduced (see below), the two enlarged pterygiophores are much shorter than in the other taxa and do not incline forward over the neurocranium. **16) First neural spine inclined anteriorly, usually curving over posterior surface of the cranium**: In veliferids and *Lampris*, the first neural spine is inclined posteriorly (Fig. 7), as in other basal acanthomorphs. In all other lampridiforms, the first neural spine is directed anteriorly and is usually closely associated with the posterodorsal surface of the cranium (Figs. 10, 11B, 15, 16). **17) Fewer than 20 total caudal-fin rays, some of which are enlarged**: Olney (1984) summarized meristic data for lampridiforms based on published accounts. Most basal acanthomorphs have 19 principal caudal-fin rays. Veliferids and *Lampris* have 19 principal and a total of 30–36 caudal-fin rays (Oelschläger, 1974: fig. 1) and the caudal fin is symmetrical, lunate and bears no produced rays (Oelschläger, 1983: 7, figs. 1, 2). All other lampridiforms have 2–17 total caudal-fin rays (data on principal fin-ray formulae are incomplete and difficult to obtain in our fragile and damaged material) and often exhibit bizarre caudal-fin morphology (Oelschläger, 1983: 10–11, figs. 3–7). The lower lobe of the caudal fin of *Stylephorus* bears two stout rays that together form an elongate caudal filament. The caudal fin of regalecids is reduced to 2–3 produced rays, and trachipterids exhibit asymmetry such that the upper lobe comprises elongate and more numerous rays. **18) First vertebral centrum reduced in length**: The first vertebra of veliferids and *Lampris* is approximately as long as the second and both are similar in size or slightly smaller than succeeding centra (Fig. 7, also Oelschläger, 1983: 17, fig. 10). In all other lampridiforms, the first centrum is variously reduced in length but always smaller than the second and succeeding centra (Figs. 11B, 15, 16). Oelschläger (1983) did not figure this condition but we observed it in *Desmodema, Trachipterus*, and *Agrostichhthys*. Oelschläger (1983: 17, fig. 10) mislabelled the first and second vertebral centra in *Stylephorus* (his C1 and C2 are actually the third and fourth vertebral centra); these elements are further modified, as discussed below. Although not present in veliferids and lamprids, a reduced first vertebral centrum appears in some basal acanthomorphs (e.g., *Trachichthys* and *Hoplostethus*). In the absence of a specific outgroup hypothesis, we tentatively consider this character as apomorphic within the order.

STYLEPHORIDAE. **19) Second neural spine absent, neural arch m-shaped**: As noted above, *Stylephorus* shares with all lampridiforms (except veliferids and lamprids) an anteriorly directed first neural spine (Character 16) and a reduction in length of the first vertebral centrum (Character 18). However, in *Stylephorus*, the first and second vertebrae are extremely reduced (Fig. 16A) and appear in ventrolateral aspect (Fig. 16B) as ossified bands that surround a cartilaginous plug and fail to join ventrally. Previous authors (Regan, 1924; Pietsch, 1978; Oelschläger, 1983) failed to recognize these elements as the first and second vertebral centra and have reported 50 total vertebrae. One larval *Stylephorus* (MCZ 58941) that we examined has 53 total vertebrae. The second vertebra (and succeeding thoracic vertebrae) of most lampridiforms bears a full neural spine that tapers distally to a sharp point. In *Stylephorus* (Fig. 16), the second neural spine is absent and the arch is m-shaped and approximately half of the height of the arch of the first vertebra. Furthermore, the arch and spine of the third vertebra in *Stylephorus* (Fig. 16) differs from more posterior vertebrae in lacking a produced anterior prezygapophysis. **20) Loss of rostral cartilage**: Like all basal acanthomorphs, all lampridiforms except *Stylephorus* possess a rostral cartilage (see character 3) tightly bound to the ascending processes of the maxilla and premaxilla by ligaments.

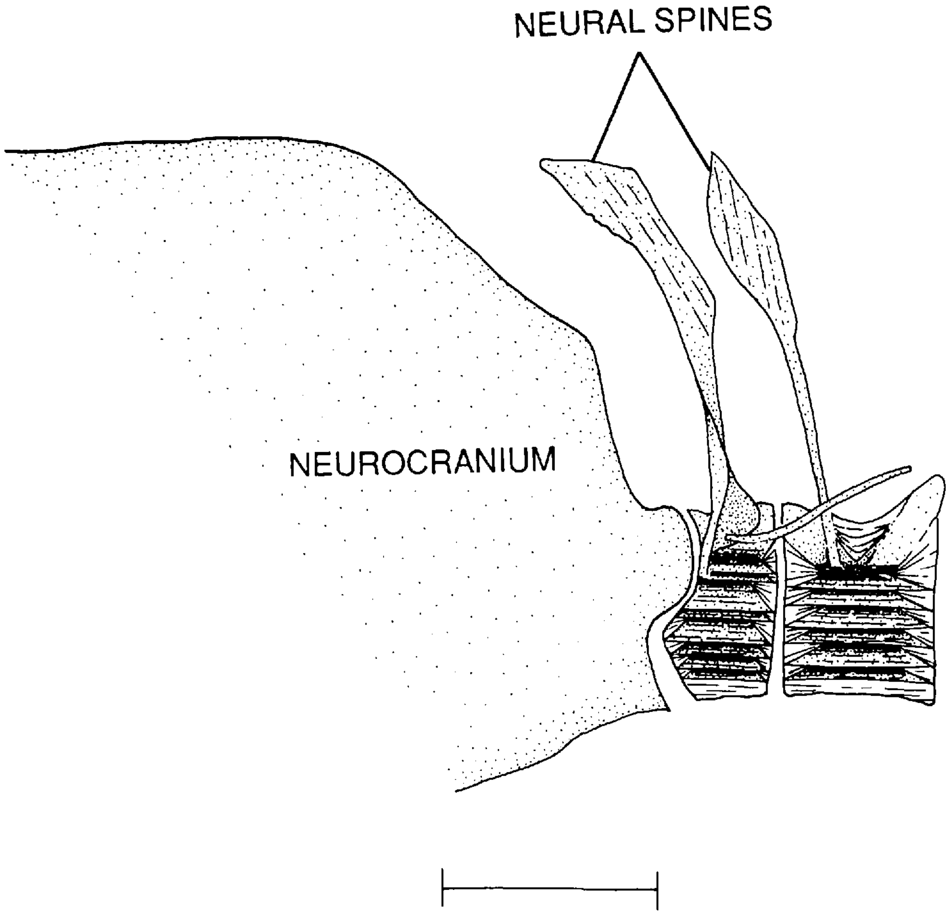


Figure 15. Left lateral view of anterior vertebrae of *Agrostichthys parkeri*, ISH 643/71, 300 mm SL.

The rostral cartilage is absent in *Stylephorus* (Fig. 17). The ascending processes of the maxilla and premaxilla are long as in most lampridiforms but the upper jaws are bound to the dentary to form a tubular mouth (Pietsch, 1978). **21) Palatine reduced to small, straight rod**: In basal acanthomorphs as well as all lampridiforms except *Stylephorus*, the palatine is a broad or slightly narrow element that is bound (by ligaments and/or cartilage) anterodorsally to the lateral ethmoid and vomer and posteroventrally to the pterygoids (Figs. 5, 10, 11A). In *Stylephorus*, the palatine is reduced to a thin, straight rod with cartilaginous tips (Fig. 17) and is not tightly bound to the ethmo-vomerine region. It bears two ligaments posteriorly that attach to a slender, posterior process of the lacrimal (Pietsch, 1978: fig. 7). Pietsch (1978), following Starks (1908) and Regan (1924), incorrectly identified the palatine of *Stylephorus* as an ossified ligament and the lacrimal process as the palatine. Oelschläger (1983: 29, fig. 22) correctly identified the palatine but mislabelled the lacrimal process as the vomer. In *Stylephorus*, the posterior process of the lacrimal rests on a lateral flange of the parasphenoid. Because the palatine of veliferids bears only a single slender ligament that attaches to the lacrimal (but a pair of ligaments that attach to the vomer, see Basal Relationships of the

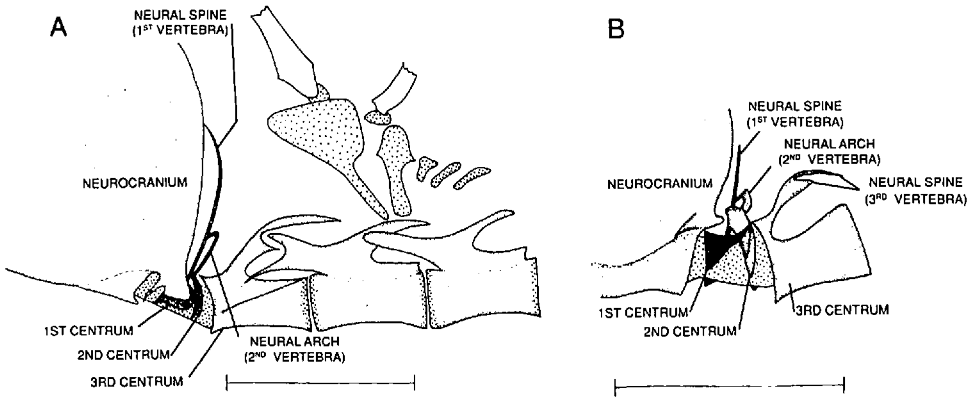


Figure 16. Left lateral view of the anterior vertebrae and dorsal-fin pterygiophores of *Stylephorus chordatus*, MCZ 58941, 31 mm SL; A) first five thoracic vertebrae and anterior dorsal-fin pterygiophores; B) rotated, ventrolateral view of vertebrae 1–3.

Veliferidae, character N), we are not certain that the paired ligaments of *Stylephorus* are the homologues of the palato-vomerine series. **22) Posterior shift in position of first dorsal-fin pterygiophore**: In all lampridiforms except *Stylephorus*, the first dorsal-fin pterygiophore inserts anterior to the first neural spine (see character 4). In *Stylephorus* (Fig. 16A), the first dorsal pterygiophore is more posterior, its proximal tip inserting over the neural arch of the fourth thoracic vertebra between the third and fourth neural spines. The posterior displacement of the dorsal-fin origin in *Stylephorus* is clearly related to the extreme reduction of the anterior two vertebrae and is one of a complex of correlated modifications (characters 19–21) related to the unique feeding mechanism of *Stylephorus* (see Intrarelationships) in which the head is rotated posteriorly in jaw protrusion.

Radiicephalidae, Lophotidae, Regalecidae and Trachipteridae. **23) Dorsal-fin rays bear lateral spinules**: As in most basal acanthomorphs, the dorsal-fin rays of veliferids, lamprids and *Stylephorus* are unornamented. The dorsal-fin rays of all other lampridiforms bear spinules that are sharp and project laterally. The spinules are weakly developed in regalecids and only visible on anterior dorsal-fin rays. In trachipterids, the spinules are stout and conspicuous (Fig. 18). **24) One or two fang-like teeth on the vomer**: Veliferids, *Lampris* and *Stylephorus* lack vomerine teeth (Figs. 5A, 17). Most other lampridiforms have one or two distinctive, fang-like vomerine teeth (Plate 1, Figs. 10, 11A). Similar vomerine teeth do not occur elsewhere among basal acanthomorphs. Our larval specimen (63 mm SL), and a 760-mm specimen of *Eumecichthys fiski* (SIO 75-406, R. Rosenblatt, pers. comm.) lack teeth on the vomer. Although vomerine teeth develop late in some lampridiforms (for example, lacking in a 23-mm specimen of *Trachipterus* but present by 56 mm SL), we consider the condition reversed in *Eumecichthys*. **25) More than 60 total vertebrae**: *Radiicephalus*, lophotids, regalecids and some trachipterids have more than 100 total vertebrae (Olney, 1984). Most trachipterids have 62–96 total vertebrae and the remaining lampridiforms have fewer than 60.

Radiicephalidae and Lophotidae. **26) Anteriorly projecting supraoccipital process**: Like other basal acanthomorphs, veliferids, lampridids, *Stylephorus*, trachipterids and regalecids have no anteriorly projecting supraoccipital processes.

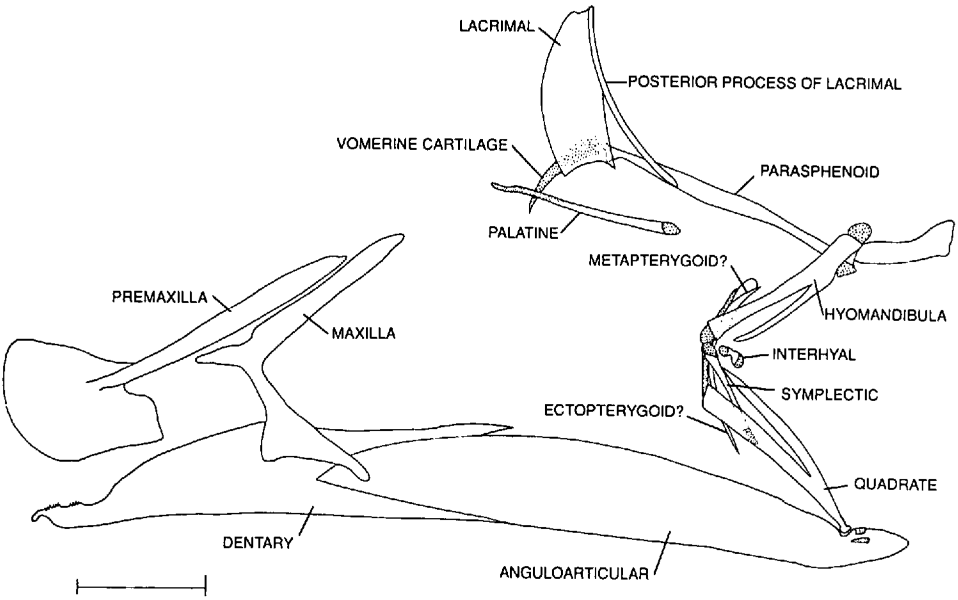


Figure 17. View of jaws and suspensorium of *Stylephorus chordatus*, MCZ 58941, 31 mm SL.

In *Radiicephalus* and lophotids (Figs. 10, 11B), the supraoccipital bears an anteriorly directed process that is variously developed. In *Radiicephalus*, the process arises at the dorsal midline of the cranium and tapers to a thin, wavy distal tip that is closely applied to the first dorsal pterygiophore (Fig. 11B). It is weakly developed, very fragile, spine-like, and probably offers little support to the anterior dorsal-fin rays. In the Lophotidae, the supraoccipital process is well developed (see character 28). **27) Presence of an ink gland**: The ink gland of *Lophotus* (Olney 1984: 379, fig. 201) and *Radiicephalus* is a tubular organ overlying the hindgut and vent. It is filled with a dark, ink-like fluid that is supposedly expelled to confuse predators. Walters and Fitch (1960) reported its presence in *Eumecichthys*, but it is not visible in our two small specimens (MCZ 55176, ca. 35 mm SL; VIMS uncat., ca. 70 mm SL). A comparable structure occurs nowhere else among teleost fishes.

RADIICEPHALIDAE. **28) Elongate haemal spines on PU4-PU6**: In *Radiicephalus*, the haemal spines of the fourth, fifth and sixth preural centra are elongate, exceed the ventral body margin and form the ventral portion of the caudal fin (Fig. 6B). This condition is unique among fishes.

LOPHOTIDAE. **29) Supraoccipital spine enlarged and supporting first dorsal-fin pterygiophore**: As noted above, the supraoccipital of lophotids bears a well developed anterior process (Fig. 10). It is broad, projects anteriorly over the frontal arch, lies directly beneath the first dorsal pterygiophore and supports the large "crest" of *Lophotus* and "horn" of *Eumecichthys* (Robins et al., 1986: pl. 22).

REGALECIDAE AND TRACHIPTERIDAE. **30) Absence of anal fin**: Regalecids and trachipterids are unique among basal acanthomorphs in lacking an anal fin. **31) Caudal- and pelvic-fin rays bear lateral spinules**: The caudal- and pelvic-fin rays of veliferids, lamprids, stylephorids, lophotids and *Radiicephalus* are unornamented. In trachipterids (Figs. 4B, 18; also Rosenblatt and Butler, 1977: 844) and

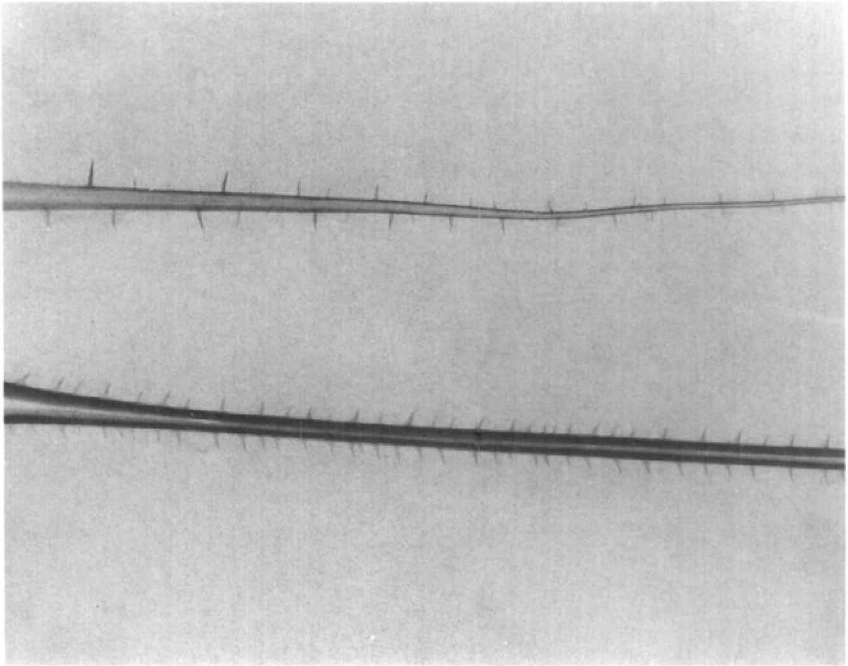


Figure 18. Photomicrograph of 12th dorsal-fin ray (top), and dorsal-most caudal-fin ray (bottom) of *Trachipterus* sp., SIO uncat., 54 mm SL.

regalecids, caudal- and pelvic-fin rays bear spinules that project laterally. In regalecids, the spinules are very weakly developed and reduced to nubbins.

REGALECIDAE. **32) Pelvic-fin rays reduced in number to one stout, elongate ray and one small splint-like element**: Most lampridiforms have three or more pelvic rays. Regalecids have only two; the first is stout, elongate, and articulates in a saddle-like joint with the basipterygium (Oelschläger, 1978: 171, fig. 6); the second is a small, weakly developed splint-like element that is absent on some specimens. Oelschläger (1978) demonstrated that the highly specialized pelvic ray (the oar of "oarfishes") has specialized sensory capability (Fig. 3, character VII).

TRACHIPTERIDAE. **33) Lateral line scales bear spines**: The lateral line scales of all lampridiforms except trachipterids are unornamented. In *Trachipterus, Desmodema* and *Zu* each lateral-line scale bears a median spine that is somewhat curved distally (Fig. 19). The spines are weakly developed in our larval examples of *Desmodema* but stout and conspicuous in other trachipterids. In both *Desmodema* and *Trachipterus,* the spines are uniformly spaced and project laterally. In *Zu,* posterior spines project laterally and ventrally in an alternating pattern. **34) Absence of pleural ribs**: Most lampridiform fishes have pleural ribs. In single specimens of the following taxa, the ribs originate on parapophyses of thoracic vertebra number 3 and total 18 in *Lampris* (3, 18); *Radiicephalus* (5, 34); *Lophotus* (5, 44); *Eumecichthys* (5, 39); *Regalecus* (7, 16); and *Agrostichthys* (3, 27). Pleural ribs are absent in trachipterids and stylephorids. In trachipterids, the parapophyses of each thoracic vertebra are well developed. Parapophyses are absent on anterior vertebrae of our larval examples of *Stylephorus* as well as in adult material (Regan, 1924: fig. 7).

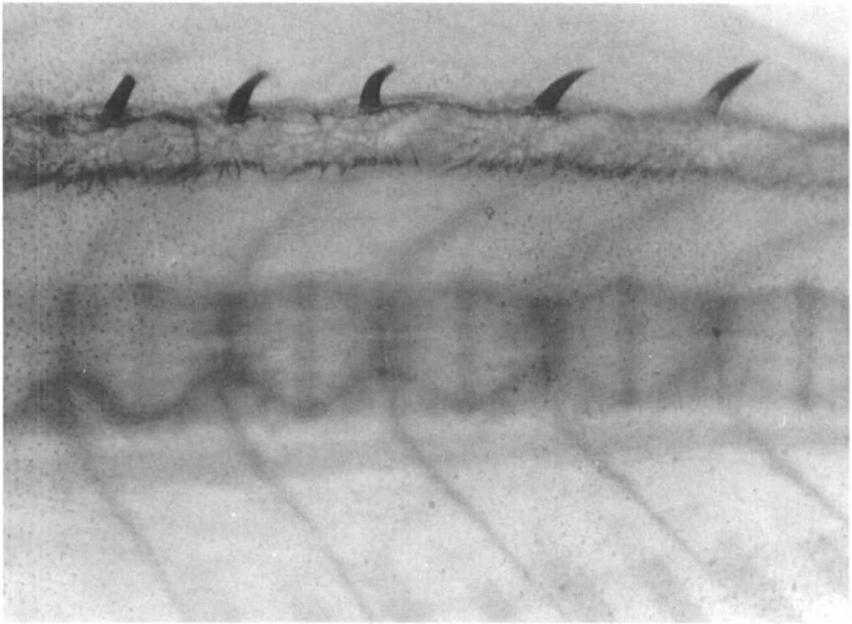


Figure 19. Photomicrograph of the lateral line scales of *Zu cristatus*, VIMS uncat., 78 mm SL.

DISCUSSION

Oelschläger (1983) proposed a familial phylogeny of the Lampridiformes (Fig. 3) based on an eclectic assemblage of 14 morphological and functional traits polarized on the basis of comparison with fossil taxa. Other than the identification of veliferids as the sister group of all other lampridiforms, our hypothesis of intrarelationships (Fig. 12) bears little resemblance to that of Oelschläger (1983). The two most striking disparities in these hypotheses (the presence or absence of sister group relationships between *Lampris* and lophotids and between *Stylephorus* and *Radiicephalus*) can be resolved on the basis of parsimony argumentation. Before summarizing our hypothesis, we comment on several of the characters in Oelschläger's work (including two putative apomorphies of the pectoral-fin skeleton, characters IIIa and IIIb) that we find problematic or could not assess.

Oelschläger (1983) considered a strong separation of the coracoid and cleithrum distally (character IIIa) to be a synapomorphy of *Lampris* and lophotids. There is no obvious resemblance between the coracoid-cleithrum arrangement of *Lampris* and lophotids. We found what might be termed a "strong" separation only in *Lampris* and note that a similar condition occurs in *Diretmus*, and may be associated with extreme body depth. In most basal acanthomorphs, the pectoral-fin base is oriented vertically, and the coracoid extends anteroventrally, terminating at or near the distal portion of the cleithrum. In *Lampris*, the pectoral-fin base is horizontal, and the ventrally-directed coracoid does not closely approach the cleithrum (Fig. 14C), an arrangement possibly derived from a clockwise rotation of a vertical fin base to the horizontal plane. *Diretmus* is similar (Fig. 14B) except that the axis of the coracoid is directed slightly more anteroventrally. In all other lampridiforms, including lophotids, the coracoid curves anteroventrally and ends in close proximity to the cleithrum (Fig. 14A). Oelschläger (1983) also noted that *Lampris* shares with lophotids the presence of ovoid condyles on the pectoral-fin radials (his character IIIb). We were unable to discern substantive differences in the configuration of the pectoral radials of *Lampris,* lophotids and other lampridiforms.

Oelschläger (1983) reported the presence of a specialized integument (his character IV) in all elongate lampridiforms except lophotids. We observed raised tubercles or papillae on the skin of our largest specimens of trachipterids, *Agrostichthys* and *Radiicephalus* but material of comparable size was not available for other taxa. Although unable to fully assess the distribution and homology of this character, we attempt to accommodate the condition in our discussion of intrarelationships below.

The presence of an extension of the lateral line onto the enlarged rays of the lower lobe of the caudal fin (Fig. 3, character X) was believed by Oelschläger (1983) to unite *Stylephorus* and *Radiicephalus.* However, Walters and Fitch (1960) report this condition in some trachipterids. Furthermore, the elongate rays in *Radiicephalus* and *Stylephorus* differ in number and in support: *Radiicephalus* has three rays that are supported by haemal spines of PU2 and PU3; the two rays of *Stylephorus* are supported by the ventral-most hypurals (Pietsch, 1978). Again, we are unable to assess this condition in all lampridiforms but question the homology of the character.

We concur with Oelschläger (1983) that the bathysomous (deep-bodied) lampridiforms are not monophyletic; lampridids are more closely related to the taeniosomous (elongate) lampridiform fishes than to veliferids. Six synapomorphies (6–11) including egg morphology and a number of osteological features (modifications of the vertebrae, pectoral fin, dorsal gill arch elements, and pelvic fin) support this relationship and place veliferids as the sister group of all other lampridiforms.

We do not agree with Oelschläger (1983) that an elongate body form evolved twice within lampridiforms (Fig. 3). Our analysis unequivocally places lophotids within the taeniosomous clade (Fig. 12). If Oelschläger (1983) is correct in his assessment of the homology and distribution of a specialized integument (his character IV, Fig. 3), we must hypothesize its loss in lophotids. Six osteological characters (13–18) defend the monophyly of the clade comprising *Stylephorus* + *Radiicephalus* + Lophotidae + Regalecidae + Trachipteridae. Several of these features are reductive (loss of supraneurals, loss of supraoccipital crest and reduction in size of the first centrum), whereas others are innovative modifications of the vertebral column and anterior dorsal fin. All may be related to the support of elongate dorsal-fin rays in larvae or adults.

Contrary to Oelschläger (1983), who placed *Stylephorus* and *Radiicephalus* as the most derived lampridiform clade, we believe that *Stylephorus* is the sister group of all other elongate lampridiforms. Of 16 synapomorphies (1–4, 6–11, 13–18) that describe basal relationships of lampridiform families, only one (7) is lacking in *Stylephorus. Stylephorus* retains the pleisiomorphic condition of four autogenous pectoral-fin radials, but it is most parsimonious to treat this condition as a reversal (7′, Fig. 12). Three additional character states (absence of the rostral cartilage, a posterior shift in the position of the dorsal fin, and enlarged anterior dorsal-fin pterygiophores that do not arch forward over the neurocranium) are modifications obviously related to the bizarre feeding posture of *Stylephorus.* Expansion of the buccal cavity in most lampridiforms is accomplished when the rostral cartilage slides forward out of a frontal cradle or vault (Pl. 1, character 3), carrying with it the maxilla and premaxilla. In *Stylephorus,* in addition to forward protrusion, the buccal cavity is further expanded by a remarkable posterior rotation of the cranium (Pietsch, 1978). This extreme cranial rotation is undoubtedly facilitated by incompletely ossified anterior vertebrae and the space provided by reductions in neural spines and posteriorly displaced pterygiophores. Thus, in addition to the three conditions described above in *Stylephorus,* there are autapomorphic modifications (apparently associated with feeding) in the anterior vertebrae (first two vertebrae extremely reduced, the second vertebra lacking a neural spine and having an m-shaped neural arch, character 19), the ethmoid region (development of an unusual cartilage anterior to the vomer, Fig. 17), and the suspensorium (change in size and shape of palatine, character 21, Fig. 17). An additional character, absence of pleural ribs (character 34) is shared by stylephorids and trachipterids, but considered to be homoplasous in our hypothesis.

Three characters (lateral spinules on dorsal-fin rays, presence of vomerine teeth, and more than 60 vertebrae) support the monophyly of the remaining taeniosomes, Radiicephalidae + Lophotidae + Regalecidae + Trachipteridae. Absence of vomerine teeth in *Eumecichthys* is interpreted as a reversal.

Historically, the phylogenetic position of *Radiicephalus* has been unclear (Harrisson and Palmer, 1968), and our placement of *Radiicephalus* as the sister group of lophotids is novel. Despite considerable divergence in morphology of the anterior dorsal fin, the families share two specializations, one of which, presence of an ink gland, is unprecedented among teleosts. The second, presence of an anteriorly projecting supraoccipital process, probably has been overlooked because of its small size and fragility in *Radiicephalus.*

Finally, two unique specializations support a sister group relationship between regalecids and trachipterids: absence of an anal fin (character 30) and presence of spinules (character 31) on the caudal- and pelvic-fin rays (vs. only on dorsal rays in other taeniosomous lampridiforms).

A number of fossil taxa have been placed in the Lampridiformes. We have not seen specimens nor extensively reviewed the pertinent literature but discuss below our assessment of some of the taxa based on published description, photographs, and skeletal reconstructions.

Bajaichthys (Sorbini and Bottura, 1988; known from a single juvenile specimen found in Eocene deposits near Verona) possesses a posteriorly placed mesethmoid, lacks a palatine prong and the upper jaws are highly protruded. The nasals are small and the frontals have a curved profile that resembles a crest. The first and second dorsal-fin pterygiophores are inserted anterior to the first neural spine. We concur with the assessment (Sorbini and Bottura, 1988) that *Bajaichthys* is an extinct bathysomous lampridiform that appears to share some derived features (specialized integument, ornamented fin rays) with elongate (taeniosomous) forms.

In the reconstructions of *Aipichthys velifer* (Gayet, 1980), the first dorsal-fin pterygiophore inserts anterior to the first neural spine; the mesethmoid is anterior to the lateral ethmoids; and the palatine is hidden by the lacrimal. However, in another unnamed *Aipichthys* (Gayet, 1980: 48, fig. 29), the palatine bears an anterior process that articulates with the maxilla. Rosen and Patterson (1969) concluded that *Aipichthys* is closely related to the living veliferid fishes, a view not shared by Gayet (1980) who placed the genus within the Paracanthopterygii. More recently, Oelschläger (1983: fig. 108) placed *Aipichthys* and its relatives as the sister group to the Allotriognathi. Although we disagree with Gayet's (1980) conclusion based on the absence of paracanthopterygian synapomorphies enumerated by Patterson and Rosen, 1989, the relationship of *Aipichthys* with veliferids or any other lampridiform is unclear.

Rosen and Patterson (1969) proposed that *Pharmacichthys venenifer* (Patterson, 1964: 399, fig. 85; Gayet, 1980: 30, fig. 14) is a lampridiform closely related to *Aipichthys*. However, the mesethmoid is anterior to the lateral ethmoids, the first pterygiophore of the dorsal fin inserts posterior to the first neural spine and the palatine articulates with the maxilla (Gayet, 1980: 25, fig. 7). The first pterygiophore of the dorsal fin inserts anterior to the first neural spine in *Pharmacichthys numismalis* (Gayet, 1980: 29, fig. 13), but the species otherwise resembles *P. venenifer*. We find little evidence that relates *Pharmacichthys* to the Lampridiformes.

Bathysomus (Patterson, 1964: 423, fig. 90; Oelschläger, 1983: 36, fig. 32) superficially resembles *Lampris* in overall body shape and in the configuration of the pectoral-fin skeleton. The jaws are protractile but the suspensorium, ethmoids and dorsal pterygiophores are apparently lacking in available material. We cannot assess its phylogenetic affinities.

ACKNOWLEDGMENTS

We extend our appreciation to H. Oelschläger for his interest in this study and permission to use or modify some of his original figures. Special thanks to C. Patterson for help with the literature on fossil fishes, for correcting our nomenclature, and for his review of this manuscript. V. Springer provided translations of sections of pertinent papers. R. Rosenblatt read and commented on the manuscript. We thank E. Bertelsen, T. Clark, O. Gon, K. Hartel, G. Moser, D. Markle, J. Randall, and A. Post for generously providing rare material for our extended use. S. Olney, K. Stubblefield, M. Cavalluzzi, and L. Keene offered technical assistance. This is contribution number 1754 of the Virginia Institute of Marine Science, College of William and Mary.

LITERATURE CITED

Bannikov, A. F. 1990. An eocene veliferoid (Teleostei, Lampridiformes) from Bolca. Misc. Paleontologica 6: 161–174.

Bertelsen, E. and N. B. Marshall. 1984. Mirapinnatoidei: development and relationships. Pages 380–383 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds., Ontogeny and systematics of fishes. Amer. Soc. of Ich. and Herp., Spec. Pub. No. 1.

Breder, C. M., Jr. 1962. On the significance of transparency in osteichthid fish eggs and larvae. Copeia 1962: 561–567.

Bridge, T. W. 1896. The mesial fins of ganoids and teleosts. J. Linn. Soc. London, Zool. 25: 530–602.

Eschmeyer, W. N. 1990. Catalogue of the genera of recent fishes. Cal. Acad. Sci., San Francisco, 697 p.

Fink, W. L. 1981. Ontogeny and phylogeny of tooth attachment modes in teleost fishes. J. Morph. 167: 167–184.

——— and S. H. Weitzman. 1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. Bull. Mus. Comp. Zool. Harv. 150: 31–93.

Gayet, M. 1980. Contribution a l'étude anatomic et systématique des poissons cénomamiens du Liban, anciennement placés dans les Acanthoptérygiens. Mem. Mus. Nat. d'Hist. Nat., Ser. C, 44: 1–86.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist. 131: 341–455.

Harrisson, C. M. H. and G. Palmer. 1968. On the neotype of *Radiicephalus elongatus* Osorio with remarks on its biology. Bull. Brit. Mus. Nat. Hist. (Zool.) 16: 187–211.

Heemstra, P. C. 1986. Family No. 118: Veliferidae. Pages 117–118 *in* M. M. Smith and P. C. Heemstra, eds. Smiths sea fishes. Macmillan South Africa, Publishers.

Johnson, G. D. 1992. Monophyly of the euteleostean clades—Neoteleostei, Eurypterygii, and Ctenosquamata. Copeia 1992: 8–25.

——— and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bull. Mar. Sci. 52: 554–625.

Lauder, G. V. and K. F. Liem. 1983. The evolution and interrelationships of the actinopterygian fishes. Bull. Mus. Comp. Zool. 150: 95–197.

Leviton, A. E. and R. H. Gibbs, Jr. 1988. Standards in herpetology and ichthyology: standard symbolic codes for institutional resource collections in herpetology and ichthyology. Supplement No. 1: additions and corrections. Copeia 1988: 280–282.

———, ———, E. Heal and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985: 802–832.

Maddison, W. P., M. J. Donoghue and D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

Moore, J. A. 1993. The phylogeny of the Trachichthiiformes (Teleostei: Percomorpha). Bull. Mar. Sci. 52: 114–136.

Nelson, J. S. 1984. Fishes of the world. John Wiley and Sons, Inc., New York, New York, 2nd Ed. 523 pp.

Oelschläger, H. 1974. Das caudalskelett von *Lampris regius* und seine ableitung von *Velifer hypselopterus* (Teleostei: Allotriognathi). Senckenbergiana Biol. 55: 77–85.

———. 1976. On the evolution and ecological adaptations of the Allotriognathi. Rev. Trav. Inst. Peches Marit. 40: 691–694.

———. 1978. Vergleichend-morphologische und functions-analytische untersuchungen am pelvis der Riemenfische (oar fishes) (Teleostei: Allotriognathi). Zoologische Beiträge 24: 165–192.

———. 1983. Vergleichende und funktionelle anatomie der Allotriognathi (=Lampridiformes), ein beitrag zur evolutionsmorphologie der knochenfische. Abhandlungen der Senckenbergergichen Naturforschenden Gesellschaft 541: 1–127.

Olney, J. E. 1984. Lampridiformes: development and relationships. Pages 368–379 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ich. Herp., Spec. Pub. No. 1.

Patterson, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference those of the English Chalk. Phil. Trans. Roy. Soc. 247: 213–482.

———. 1968. The caudal skeleton in Mesozoic acanthopterygian fishes. Bull. Brit. Mus. (Nat. Hist.), Geol. 17: 47–102.

——— and D. E. Rosen. 1989. The Paracanthoptergii revisited: order and disorder. Pages 5–36 *in* D. M. Cohen, ed. Papers on the systematics of gadiform fishes, Nat. Hist. Mus. Los. Angeles Co. Sci. Ser. 32.

Pietsch, T. W. 1978. The feeding mechanisms of *Stylephorus chordatus* (Teleostei: Lampriformes): functional and ecological implications. Copeia 1978: 255–262.

Regan, T. 1907. On the anatomy, classification and systematic position of the teleostean fishes of the suborder Allotriognathi. Proc. Zool. Soc. London 1907: 634–643.

———. 1924. The morphology of a rare oceanic fish, *Stylephorus chordatus* Shaw; based on specimens collected in the Atlantic by the "Dana" expeditions, 1920–1922. Proc. R. Soc. Lond. 96: 193–207.

Robins, C. R., G. C. Ray, J. Douglas and R. Freund. 1986. The Peterson field guide series, a field guide to Atlantic coast fishes of North America, Houghton Mifflin Comp., Boston. 352 pp.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes. Pages 397–513 *in* Greenwood, P. H., R. S. Miles and C. Patterson, eds. Interrelationships of fishes. J. Linn. Soc. Zool.

——— and C. Patterson. 1969. The structure and relationships of the paracanthopthopterygian fishes. Bull Amer. Mus. Nat. Hist. 141: 357–474, 27 pls.

Rosenblatt, R. H. and J. L. Butler. 1977. The ribbonfish genus *Desmodema*, with a description of a new species (Pisces, Trachipteridae). Fish. Bull. U.S. 75: 843–855.

Smith, M. M. and P. C. Heemstra. 1986. Smith's sea fishes. J.L.B. Smith Inst. Ichthy., Grahamstown. 1047 pp.

Sorbini, L. and C. Bottura. 1988. *Bajaichthys elegans*, an eocene lampridiform from Bolca (Italy). Boll. Mus. civ. St. nat. Verona 14: 369–380.

Starks, E. C. 1908. The characters of Atelaxia, a new suborder of fishes. Bull. Mus. Comp. Anat. 52: 1–22, 5 pls.

Steyskal, G. C. 1980. The grammar of family-group names as exemplified by fishes. Proc. Biol. Soc. Wash. 93(1): 168–177.

Stiassny, M. L. J. 1986. The limits and relationships of the acanthomorph teleosts. J. Zool., Lond. 1(B): 411–460.

———. 1990. Notes on the anatomy and relationships of bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotidae). American Mus. Nov. 2979: 1–33.

——— and J. Moore. 1992. A review of the pelvic girdle of acanthomorph fishes, with a provisional hypothesis of acanthomorph intrarelationships. J. Zool. Lond. 104: 209–242.

Walters, V. and J. E. Fitch. 1960. The families and genera of the Lampridiform (Allotriognath) suborder Trachipteroidei. Calif. Fish Game 46: 441–451.

Zehren, S. J. 1979. The comparative osteology and phylogeny of the Beryciformes (Pisces: Teleostei). Evolutionary Monographs 1. 389 pp.

DATE ACCEPTED: June 10, 1992.

ADDRESSES: *(J.E.O. and C.C.B.) Virginia Institute of Marine Science and School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062;* PRESENT ADDRESS: *(C.C.B. and G.D.J.) Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.*

APPENDIX I

Lampridiformes or lampriform, Lamprididae or Lampridae?

Colin Patterson
British Museum (Natural History), London SW7 5BD

Steyskal (1980) recommended that the termination of higher taxa based on *Lampris* Retzius should use the stem *lampri-*, thus Lampridae, Lampoidei, Lampriformes, rather than the names based on the stem *lamprid-* (e.g., Lamprididae) previously in general use. Steyskal's argument was: "*Lampris* Retzius, 1799 was stated by Agassiz to be based upon the Greek adjective *lampros.* Inasmuch as *lampris* is not attested in Greek lexicons that word can only be considered as having a changed ending (*-os* replaced by Latin or Greek *-is*). The form of the family cited by Nelson, Lampridae, may be considered correct because of lack of evidence that *Lampris* has the stem *lamprid-*. Furthermore . . . Lampridiformes should be Lampriformes, and . . . Lampridoidei should be Lamproidei." The reference to J. L. R. Agassiz is his *Nomenclator Zoologicus* (1842–1847), and the reference to J. S. Nelson is the first edition of *Fishes of the World* (1976).

It is clear from Agassiz's *Nomenclator,* and from his *Index Universalis* (1848), that he had not seen Retzius's original publication (1799), for in contrast to the information accompanying other names in his compilation Agassiz gave neither date nor place of publication for *Lampris,* merely a row of dots in the *Nomenclator* and the date "17.." in the *Index.* Thus Agassiz's statement that the name is based on *lampros* is conjecture, and in fact Retzius gave no indication of etymology. The word *lampris* does not appear in Greek or Latin lexicons, and in such cases Article 29 (b) (ii) of the *Code* (1985 edition) applies: "If a generic name is or ends in a word not Greek or Latin . . . the stem for purposes of the Code is that used by the author who establishes a family-group name based on that generic name." For *Lampris* that author is T. N. Gill, no slouch as a scholar. Gill established the family in 1862, as Lampridoidae, and corrected it to Lamprididae in 1872. He gave no reason for so forming the name in 1903: "The family was originally written *Lamprididae,* and in this form it was adopted by Jordan and Gilbert and by others, but Jordan and Evermann have changed it to *Lampridae.* The reason for the change is not evident and has not been given. It is possible that it may have been from confusion with *lampros* (radiant), but the generic name is not derived directly from the Greek but modified from it, and agrees with such well-known fish names as *Chalcis, Etelis, Julis, Pelamis, Phycis, Smaris, Synagris,* and *Teuthis,* which have -id in the oblique cases (e.g., -idos in the genetive [sic], etc.). The original form of the name is consequently justified by analogy and should be retained." Gill also provided a synonomy of the name Lampridae up to 1903, citing Poey, Jordan and Gilbert, Smitt, Goode and Bean, and Boulenger as using the form Lamprididae, and only Jordan and Evermann using Lampridae. In any case, under Article 29 (b) (ii) of the *Code,* Gill's establishment of the name Lamprididae provides the "evidence that *Lampris* has the stem *lamprid-*" that Steyskal (1980) thought was lacking, and there is no necessity to modify the name of either the family Lamprididae or the order Lampridiformes (established by Goodrich, 1909).

LITERATURE CITED

Agassiz, J. L. R. 1842–1847. Nomenclator zoologicus, 4 vols. Jent and Gassmann, Solothurn. Fishes are fasc. 7–8 (1845) in Vol 1. vi + 69 pp.

———. 1848. Index universalis nomenclatoris zoologicus. Jent and Gassman, Solothurn. X + 1135 pp.

Gill, T. N. 1862. Remarks on the genera and other groups of Cuban fishes. Proc. Acad. Nat. Sci. Philad. 1862: 235–242.

———. 1872. Arrangement of the families of fishes. Smithson. Misc. Colls. 247: i–xlvi, 1–49.

———. 1903. On the relations of the fishes of the family Lamprididae or opahs. Proc. U.S. Nat. Mus. 26: 915–924.

Goodrich, E. S. 1909. Vertebrata Craniata, first fascicle, cyclostomes and fishes. Part 9 *in* E. R. Lankester, ed. A treatise on zoology. A. and C. Black, London. xvii + 518 pp.

Nelson, J. S. 1976. Fishes of the world. John Wiley and Sons, New York. Xiii + 416 pp.

Retzius, A. J. 1799. *Lampris,* en ny Fiskslaegt. K. Svenska VetenskAkad. Handl. 20: 91–100.

Steyskal, G. C. 1980. The grammar of family-group names as exemplified by fishes. Proc. Biol. Soc. Wash. 93: 168–177.