

ROBERT H. GIBBS, JR. AWARD CONTRIBUTION

Phylogenetic Relationships of Deep-sea Anglerfishes of the Suborder Ceratioidei (Teleostei: Lophiiformes) Based on Morphology

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Phylogenetic relationships of the 11 families and 35 genera of deep-sea anglerfishes of the lophiiform suborder Ceratioidei, characterized most strikingly by an extreme sexual dimorphism that extends to all taxa, were analyzed on the basis of 71 morphological characters applicable to metamorphosed females. All characters were treated as unordered and unweighted, and were polarized by outgroup comparison with taxa of the lophiiform suborders Lophioidei, Antennarioidei, Chaunacoidei, and Ogcocephaloidei. The analysis produced five equally parsimonious trees, with a total length of 153, a consistency index of 0.5560, and a retention index of 0.7952. Lack of resolution was totally attributed to a single family, the relatively poorly understood Oneirodidae, containing 16 genera and 65 species, nearly 40% of all recognized ceratioids. Monophyly for the Ceratioidei was confirmed and all ceratioid genera were placed in currently recognized monophyletic families. Sister families Centrophrynidae and Ceratiidae were found to be basal in position relative to all other ceratioids. The Himantolophidae, Diceratiidae, and Melanocetidae diverge next in sequential step-wise fashion, the latter family forming the sister group of all remaining ceratioids. The integrity of the Thaumatchthyidae to include both *Lasiognathus* and *Thaumatchthys* was maintained, this family forming the sister group of the Oneirodidae. Contrary to its basal position in most all previously proposed hypotheses, the Caulophrynidae was found to be deeply embedded within the suborder, forming the sister group of a monophyletic assemblage containing the Gigantactinidae, Neoceratiidae, and Linophrynidae. Sister families Gigantactinidae and Neoceratiidae were found to form the sister group of the Linophrynidae. A second analysis, with characters of metamorphosed males and larvae added to the matrix, resulted in a collapse of several of the deeper nodes of the tree (because of incomplete sampling; males are unknown for eight of the 30 ceratioid genera available for analysis, and larvae are unknown for nine), producing 352 equally parsimonious trees with a total length of 202. Mapping modes of reproduction on the resulting trees reaffirmed the hypothesis that sexual parasitism has evolved independently more than once within the suborder and perhaps as many as seven times. Whether facultative parasitism and temporary attachment of males to females are precursors to obligate parasitism, or the former are more derived states of the latter, remains unknown.

We may assume an ogcocephalid or chaunacid-like ancestral ceratioid which, from the benthic or littoral environment of its ancestors, has invaded the bathypelagic zone of the ocean. Probably this evolution passed through forms in which the adults were benthic, while the juveniles after metamorphosis continued the pelagic life of the larvae during adolescence as, for instance, found in the family Chaunacidae and as retained or reestablished in the [benthic] ceratioid genus Thaumatchthys. This move to a new adaptive zone has led to a dimorphism which separates the tasks of the two sexes, the females attaining adaptations to the bathypelagic conditions of the lophiiform feeding strategy by passive lurking, the males being adapted solely to actively search for a sexual partner.

—E. Bertelsen, 1984:330

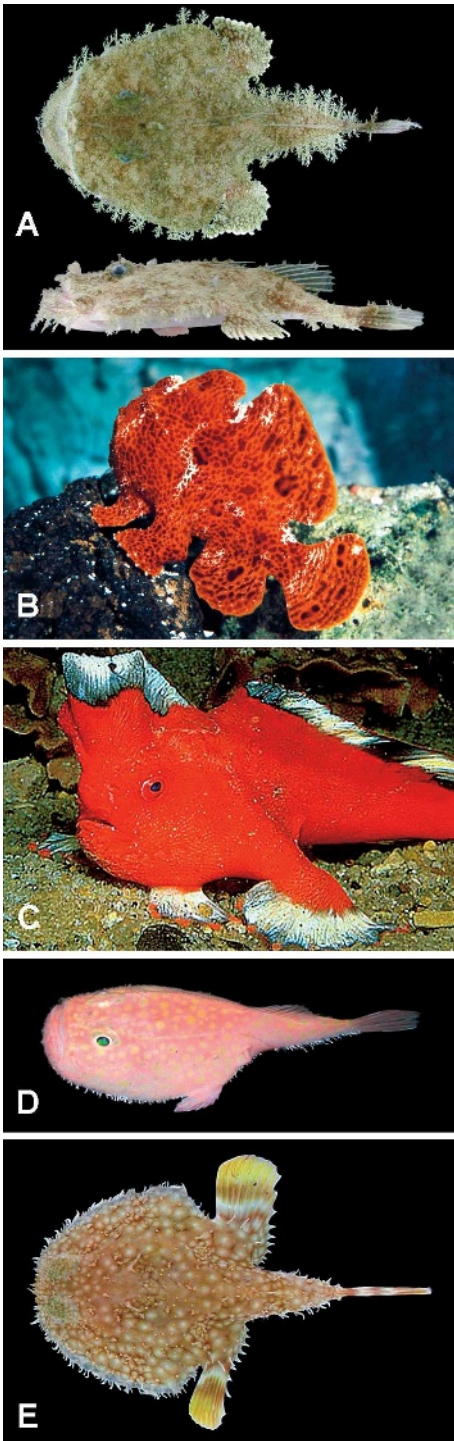


Fig. 1. Representatives of lophiiform taxa used for outgroup comparison with ceratioids: (A) *Lophiodes reticulatus*, 157 mm SL, UF 158902, dorsal and lateral views (photo by J. H. Caruso); (B) *Antennarius commerson*, 111 mm SL, UW 20983 (photo by D. B. Grobecker); (C) *Brachionichthys*

LOPHIIFORM fishes constitute a morphologically diverse assemblage of taxa, most of which share a peculiar and unique mode of feeding characterized most strikingly by the structure of the first dorsal-fin spine, placed out on the tip of the snout and modified to serve as a luring apparatus (illicium). The 18 families, 66 genera, and approximately 321 living species are distributed among five suborders (Pietsch and Grobecker, 1987): the Lophioidei, containing a single family, four genera, and 25 species of shallow to deep-water, nearly all dorsoventrally flattened forms (Caruso, 1985; Fig. 1A); the Antennarioidei, four families, 15 genera, and about 52 species of laterally compressed, shallow to moderately deep-water, benthic forms (Pietsch, 1981; Pietsch and Grobecker, 1987; Fig. 1B, C); the Chaunacoidei, two genera and at least 14 species of globose, deep-water benthic forms (Caruso, 1989a, 1989b; Fig. 1D); the Ogocephaloidei, a single family of ten genera and about 68 species of dorsoventrally flattened, shallow to deep-water benthic forms (Bradbury, 1967, 1980, 1988, 1999; Endo and Shinohara, 1999; Fig. 1E); and the Ceratioidei, containing 11 families, 35 genera, and 162 currently recognized species of globose to elongate, mesopelagic, bathypelagic, and abyssal-benthic forms (Bertelsen, 1951; Figs. 2–6).

The most phylogenetically derived of these suborders is the deep-sea Ceratioidei (Bertelsen, 1984; Pietsch, 1984; Pietsch and Grobecker, 1987), distributed throughout the world's oceans below a depth of 300 m. With 162 currently recognized species, it constitutes by far the most species-rich vertebrate taxon within the bathypelagic zone, containing more than twice as many families and genera, and more than three times the number of species, as the Cetomimoidei, the next most species-rich, bathypelagic, vertebrate taxon (Paxton, 1998; Herring, 2002). At the same time, new species are being added to the suborder at a steady if not increasing rate. Members of the group differ remarkably from their shallow-water relatives by having an extreme sexual dimorphism (shared by all contained taxa) and a unique mode of reproduction in which the males are dwarfed—those of some linophrynids, adults at 6–10 mm standard length (SL), competing for the title of world's smallest

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politus, specimen not retained (photo by R. Kuitert); (D) *Chaunax suttkusi*, 107 mm SL, TU 198058 (photo by J. H. Caruso); (E) *Halieutichthys aculeatus*, 80 mm SL, specimen not retained, dorsal view (photo by J. H. Caruso).

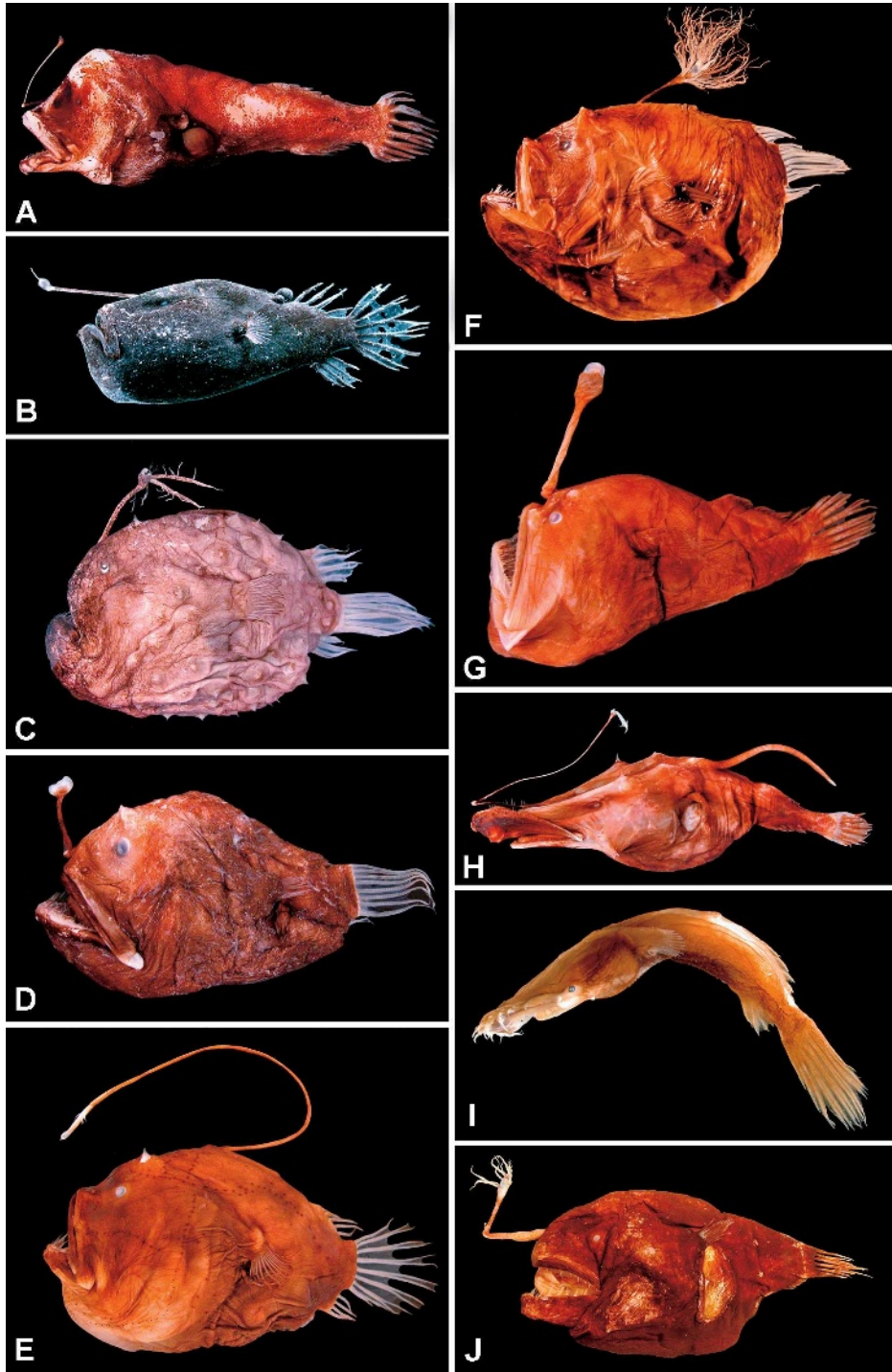


Fig. 2. Females of ceratioid taxa used in the present study: (A) *Centrophryne spinulosa*, 136 mm SL, LACM 30379-1; (B) *Cryptopsaras couesii*, 34.5 mm SL, BMNH 2006.10.19.1 (photo by E. A. Widder); (C) *Himantolophus appeli*, 124 mm SL, CSIRO H.5652-01; (D) *Diceratias trilobus*, 86 mm SL, AMS I.31144-004; (E) *Bufoceratias wedli*, 96 mm SL, CSIRO H.2285-02; (F) *Bufoceratias shaoi*, 101 mm SL, ASIZP 61796 (photo by H.-c. Ho); (G) *Melanocetus eustales*, 93 mm SL, SIO 55-229; (H) *Lasiognathus amphirhamphus*, 157 mm SL, BMNH 2003.11.16.12; (I) *Thaumatchthys binghami*, 83 mm SL, UW 47537 (photo by C. Kenaley); (J) *Chaenophryne*, new species, 157 mm SL, SIO 72-180.

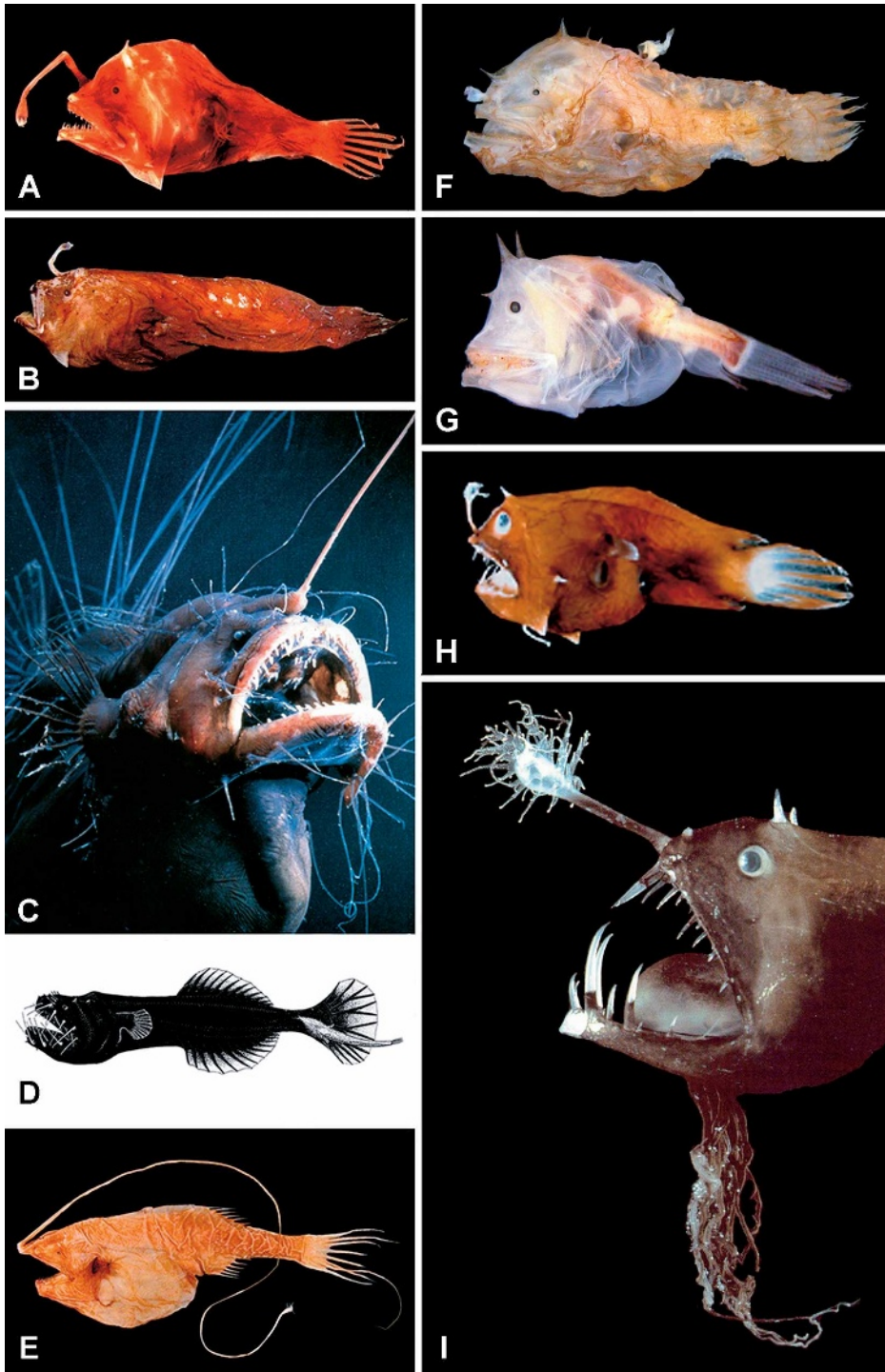


Fig. 3. Females of ceratioid taxa used in the present study: (A) *Oneirodes* sp., 31 mm SL, MCZ 57783 (photo by C. P. Kenaley); (B) *Spiniphryne duhameli*, 117 mm SL, SIO 60-239; (C) *Caulophryne pelagica*, 183 mm SL, BMNH 2000.1.14.106 (photo by D. Shale); (D) *Neoceratias spinifer*, 52 mm SL, with 15.5-mm SL parasitic male, ZMUC P921726 (after Bertelsen, 1951); (E) *Gigantactis gargantua*, 166 mm SL, LACM 9748-028; (F) *Photocorynus spiniceps*, 46 mm SL, with 6.2-mm SL parasitic male, SIO 70-326; (G) *Haplophryne mollis*, 36 mm SL, MNHN 2004-0811; (H) *Linophryne macrodon*, 28 mm SL, UW 47538 (photo by C. P. Kenaley); (I) *Linophryne polyogon*, 33 mm SL, BMNH 2004.9.12.167 (photo by P. David).

vertebrate (Watson and Walker, 2004; Pietsch, 2005; Kottelat et al., 2006)—and attach themselves (either temporarily or permanently) to the bodies of relatively gigantic females (Fig. 4). In *Ceratias holboelli*, where the most extreme examples are found, females may be more than 60 times the length and about a half a million times as heavy as the males (Bertelsen, 1951; Pietsch, 1976, 2005). The males lack a luring apparatus and those of most species are equipped with large, well-developed eyes (Munk, 1964, 1966) and relatively huge nostrils (Marshall, 1967a), the latter used apparently for homing in on a female-emitted, species-specific pheromone (Bertelsen, 1951; Pietsch, 1976, 2005; Munk, 1992). In some taxa, attachment is followed by fusion of epidermal and dermal tissues and, eventually, by connection of the circulatory systems so that the male becomes permanently dependent on the female for blood-transported nutrients, while the host female becomes a kind of self-fertilizing hermaphrodite (Regan, 1925a; Bertelsen, 1951; Munk, 2000).

Ceratioid anglerfishes differ further from their shallow-water relatives in having a bacterial bioluminescent bait or lure (esca)—exceptions among members of the suborder include the monotypic family Neoceratiidae (Bertelsen, 1951), the three species of the gigantactinid genus *Rhynchactis* (Bertelsen et al., 1981; Bertelsen and Pietsch, 1998), and the five species of the Caulophrynidae (Pietsch, 1979). Parr (1927) was the first to recognize the diagnostic value of the external morphology of escae in ceratioids, pointing out the need for a closer examination of individual variation in the structure of this organ. Since that time, differences in the number, shape, and size of escal appendages and filaments, as well as variation in external escal pigment patterns, have been, for the most part, the sole basis on which new species have been described (Pietsch, 1974; Bertelsen, 1982; Bertelsen and Krefft, 1988).

The internal structure of ceratioid escae is infinitely more complex, involving a confusing array of bacteria-filled vesicles, light-absorbing pigment layers, reflecting tissues, tubular light-guiding structures, nerves, blood vessels, and smooth muscle fibers (Munk and Bertelsen, 1980; Munk et al., 1998; Munk, 1999). There is some evidence also that ceratioid escae contain pheromone-producing secretory glands that function to attract a conspecific male (Munk, 1992), but the true nature and adaptive significance of these structures and most of the other internal parts of escae are unknown.

In addition to the esca, all 21 currently recognized species of the ceratioid genus *Lino-*

phryne (family Linophrynidae) bear an elaborate bioluminescent hyoid barbel, the light of which does not originate from symbiotic luminescent bacteria, but rather from a complex array of intrinsic, intracellular, paracrystalline photogenic granules; the bacteria-filled esca is ectodermal in origin, whereas the barbel light organ appears to be derived from the mesoderm (Hansen and Herring, 1977). This remarkable dual system, involving two entirely separate mechanisms of light production, is unique among animals.

In summary, ceratioid anglerfishes are among the most intriguing of all animals, possessing a host of spectacular morphological, behavioral, and physiological innovations found nowhere else. The suborder is taxonomically diverse: with 162 currently recognized species, it makes a major contribution to the biodiversity of the deep-sea. It is exceedingly widespread geographically, occurring in deep waters of all major oceans and seas of the world, from high Arctic latitudes to the Southern Ocean; while some species appear to be almost cosmopolitan in distribution, many others have surprisingly small, restricted, vertical and horizontal ranges. Their relative abundance, high species diversity, and trophic position as the top primary carnivores in meso- and bathypelagic communities make them important ecologically. Their unique mode of reproduction has significant biomedical implications to the fields of endocrinology and immunology. Yet, despite these many aspects of biological interest and importance, as well as a large amount of revisionary work published in the 1970s and early 1980s, no satisfactory hypothesis of relationships exists for the suborder.

Historical perspective.—A monophyletic origin of the Lophiiformes seems certain based on six morphologically complex synapomorphic features (Pietsch, 1981, 1984; Pietsch and Grobecker, 1987). The group has been traditionally allied with the order Batrachoidiformes. Regan (1912:277) initially believed these two groups to be so closely related that he included them as suborders of an order he called the “Pediculati.” Later, however, in his review of “The Pediculate Fishes of the Suborder Ceratioidei,” Regan (1926:3) separated the Lophiiformes from the Batrachoidiformes, but kept them side-by-side (therefore implying a sister-group relationship), stating that “although the resemblances in the pectoral arch may be due to relationship, the differences in other characters are sufficient to keep them apart.” Since that time, Regan’s revised opinion has been almost universally accepted (Berg, 1940; Monod, 1960; Rosen and Patterson, 1969; for a return to Regan’s, 1912, original proposal, see Gosline, 1971), and the

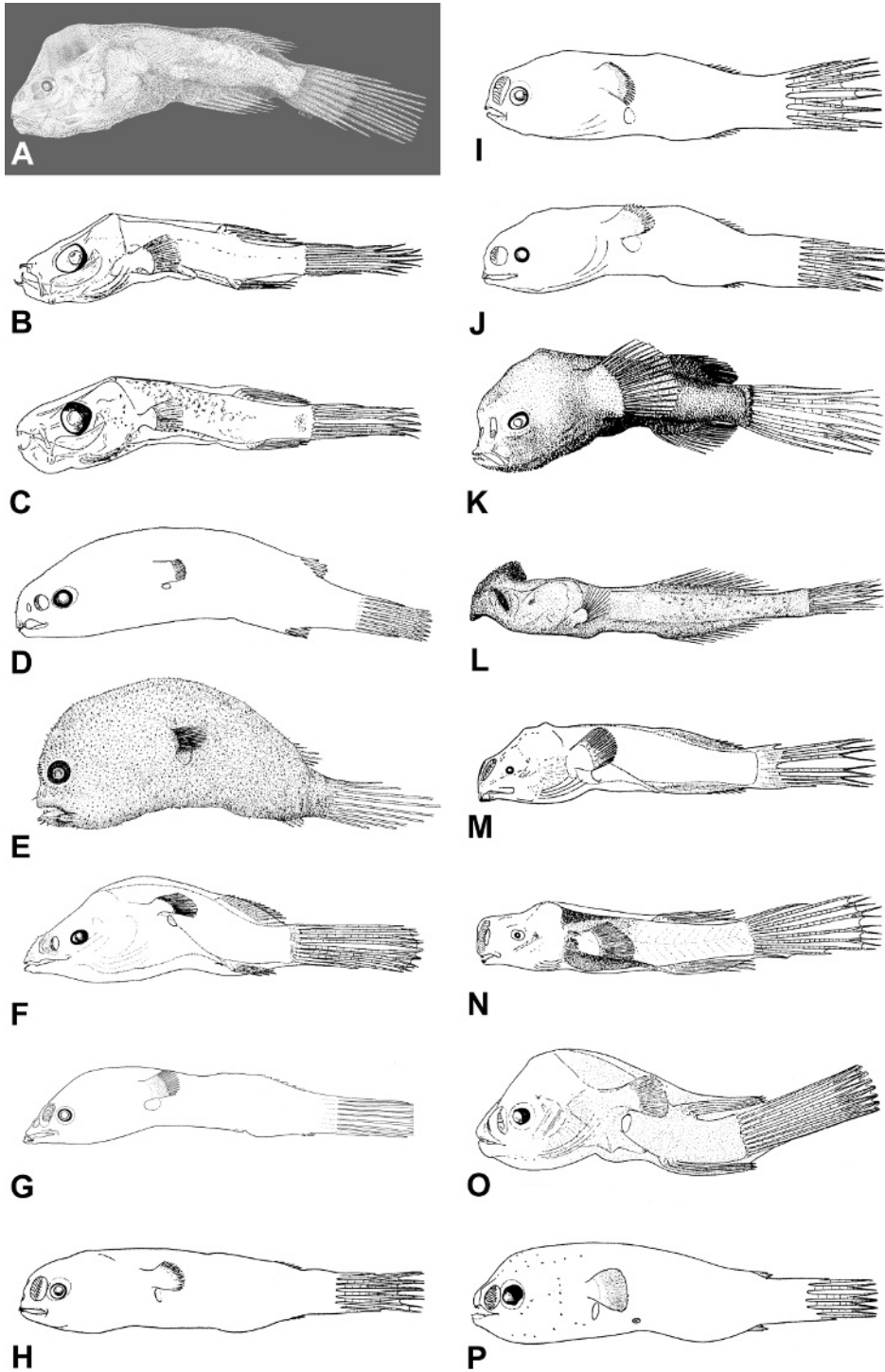


Fig. 4. Free-living metamorphosed males of ceratioid taxa used in the present study: (A) *Centrophryne spilulosa*, 12.8 mm SL, SIO 70-347; (B) *Ceratias* sp., 10.8 mm SL, specimen sacrificed for histology (Munk, 1964); (C) *Cryptopsaras couesii*, 10.2 mm SL, specimen sacrificed for histology (Munk, 1964); (D) *Himantolophus* sp., 34.5 mm SL, ZMUC P92675; (E) *Diceratias* sp., 14 mm SL, LACM 36091-4; (F) *Melanocetus* sp., 20 mm SL, ZMUC P92458; (G) *Thaumatchichthys* sp., 31 mm SL, ZMUC P921946; (H) *Chaenophryne draco*-group, 14 mm SL, ZMUC P92686; (I) *Dolopichthys* sp., 12.5 mm SL, ZMUC P92799; (J)

hypothesis has been strengthened more recently by Patterson and Rosen (1989). The only exceptions to this notion are the recent molecular findings of Miya et al. (2003, 2005), Holcroft (2004, 2005), and Simmons and Miya (2004), which indicate that lophiiforms are deeply nested within the Perciformes (i.e., with a close alignment to tetraodontiforms, and caproids and siganids; see below).

Phylogenetic relationships of the five currently recognized lophiiform suborders are relatively well understood. Based primarily on comparative osteological studies, Pietsch (1984) and Pietsch and Grobecker (1987) concluded that the Lophioidei is the sister group of all other lophiiforms; the Antennarioidei is the sister group of the Chaunacoidei, Ogocephaloidei, and Ceratioidei; and the Chaunacoidei is the sister group of the Ogocephaloidei and Ceratioidei. In addition to the extreme sexual dimorphism—including the presence of denticular bones in the males, used to grasp and hold fast to a prospective mate, as well as numerous associated features that allow for a unique mode of reproduction—monophyly for the Ceratioidei is supported by loss of palatine teeth, the basihyal, and pelvic fins; a loss of the benthic ambulatory function and a consequent repositioning of the pectoral fins; and a general trend toward a reduction in body density by a loss of bony parts, an overall decrease in ossification and the extent of muscle development, and the infusion of lipids throughout.

The taxonomy and present classification of the Ceratioidei is based primarily on studies of metamorphosed females (only 22 of the 35 recognized ceratioid genera are represented by males). Except for larval stages (Figs. 5–6) and the few basic meristic and osteological characters shared by both sexes, synonymies, diagnoses, and descriptions require separate treatment of females and males. The families of the suborder form well-defined, highly distinct taxa, separated primarily by osteological characters, which are more often than not autapomorphic for each; the females of each family possess strikingly unique features that separate them from those of all other families (Bertelsen, 1984).

Likewise, the separation and definition of genera are based primarily on characters present

only in females. However, some of the distinguishing meristic and osteological characters are shared with the males, such as fin-ray counts, which in some families show distinct intergeneric differences. Structures unique to the males, such as denticular teeth and nostril morphology, show distinct intergeneric differences, in full agreement with separations based on characters of the females. In most cases, however, it has not been possible to separate free-living males into taxa below the generic level, and studies of males attached to females have not revealed characters that will allow specific identification (Bertelsen, 1984).

Based on the limited amount of material available at the time, Regan and Trewavas (1932:26) thought it “probable that the families in which the males are parasitic form a natural group, but apart from this, the evidence from the skeleton would point to the Melanocetidae, Diceratiidae, and Himantolophidae as closely related families to be placed first, and the Photocorynidae and Linophryniidae [the former since placed in the synonymy of the latter] as forming a pair to be placed at the end of the series. The Oneirodidae are perhaps not very remote from the Diceratiidae, but the remaining families appear to be rather isolated.” While agreeing with almost everything else, Bertelsen (1951:28) argued against the notion that families that exhibit sexual parasitism form a natural assemblage. Because the Caulophryniidae, the males of which become sexually parasitic on females, displays a number of primitive characters (caulophrynid larvae apparently lack sexual dimorphism in the luring apparatus; adult females lack the bulbous bacteria-filled esca; and caulophrynid larvae retain pelvic fins, which are absent in larvae and adults of all other ceratioids), Bertelsen (1951:28) placed this family “first in the suborder.” At the same time, he argued that linophryniids, which also have parasitic males, show “such a highly specialized condition that they must be placed last.” For unstated reasons, Greenwood et al. (1966:397) implied a much closer relationship between the Caulophryniidae and Linophryniidae. Likewise, Pietsch (unpubl. data) reported (at the 1975 Annual Meeting of the American Society of Ichthyologists and Herpetologists at Williams-

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Oneirodes sp., 12.5 mm SL, ZMUC P921016; (K) *Caulophryne* sp., 11 mm SL, MCZ 69324; (L) *Neoceratias spinifer*, 15.5-mm SL parasitic male (free-living males unknown), ZMUC P921726; (M) *Gigantactis* male group II, 14.5 mm SL, ZMUC P921533; (N) *Rhynchactis* sp., 18.5 mm SL, ZMUC P921732; (O) *Borophryne apogon*, 15 mm SL, ZMUC P921771; (P) *Linophryne* sp., 17 mm SL, ZMUC P921799. After Bertelsen (1951, 1983) and Bertelsen and Struhsaker (1977).

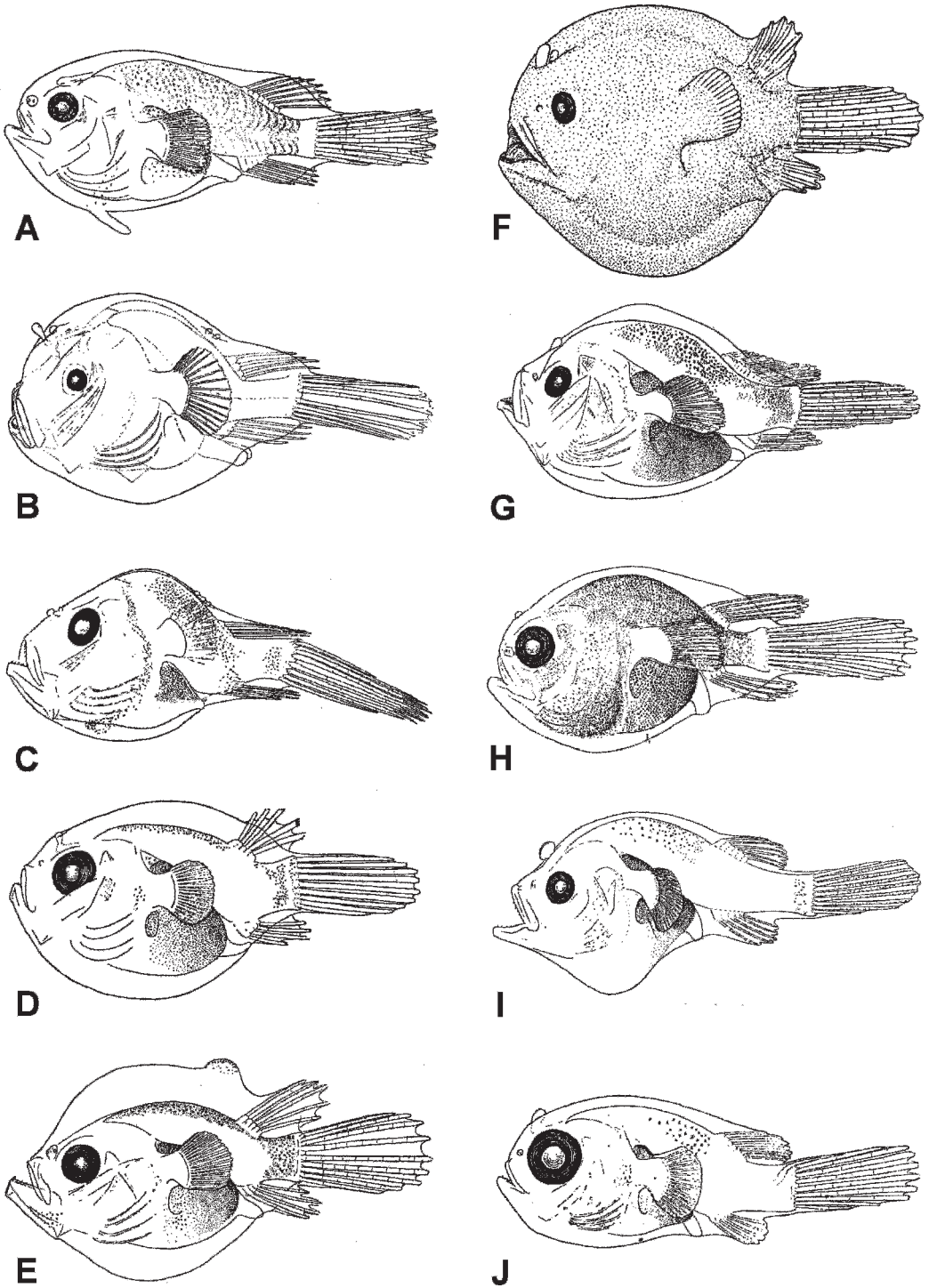


Fig. 5. Larvae of ceratioid taxa used in the present study: (A) *Centrophryne spinulosa*, male, 7.2 mm SL, ZMUC P92153; (B) *Ceratias* sp., female, 7.6 mm SL, ZMUC P921133; (C) *Cryptopsaras couesii*, female, 5.0 mm SL, ZMUC P921423; (D) *Himantolophus groenlandicus*-group, female, 6.0 mm SL, ZMUC P92668; (E) *Himantolophus albinarex*-group, male, 7.1 mm SL, ZMUC P92583; (F) Diceratiidae sp., female, 10.5 mm SL, ZMUC P92676; (G) *Melanocetus* sp., female, 12.0 mm SL, ZMUC P92207; (H) *Thaumatischthys* sp., female, 6.4 mm SL, ZMUC P921956; (I) *Pentherichthys* sp., female, 10.6 mm SL, ZMUC P921119; (J) *Chaenophryne draco*-group, 4.0 mm SL, ZMUC P92735. All after Bertelsen (1951).

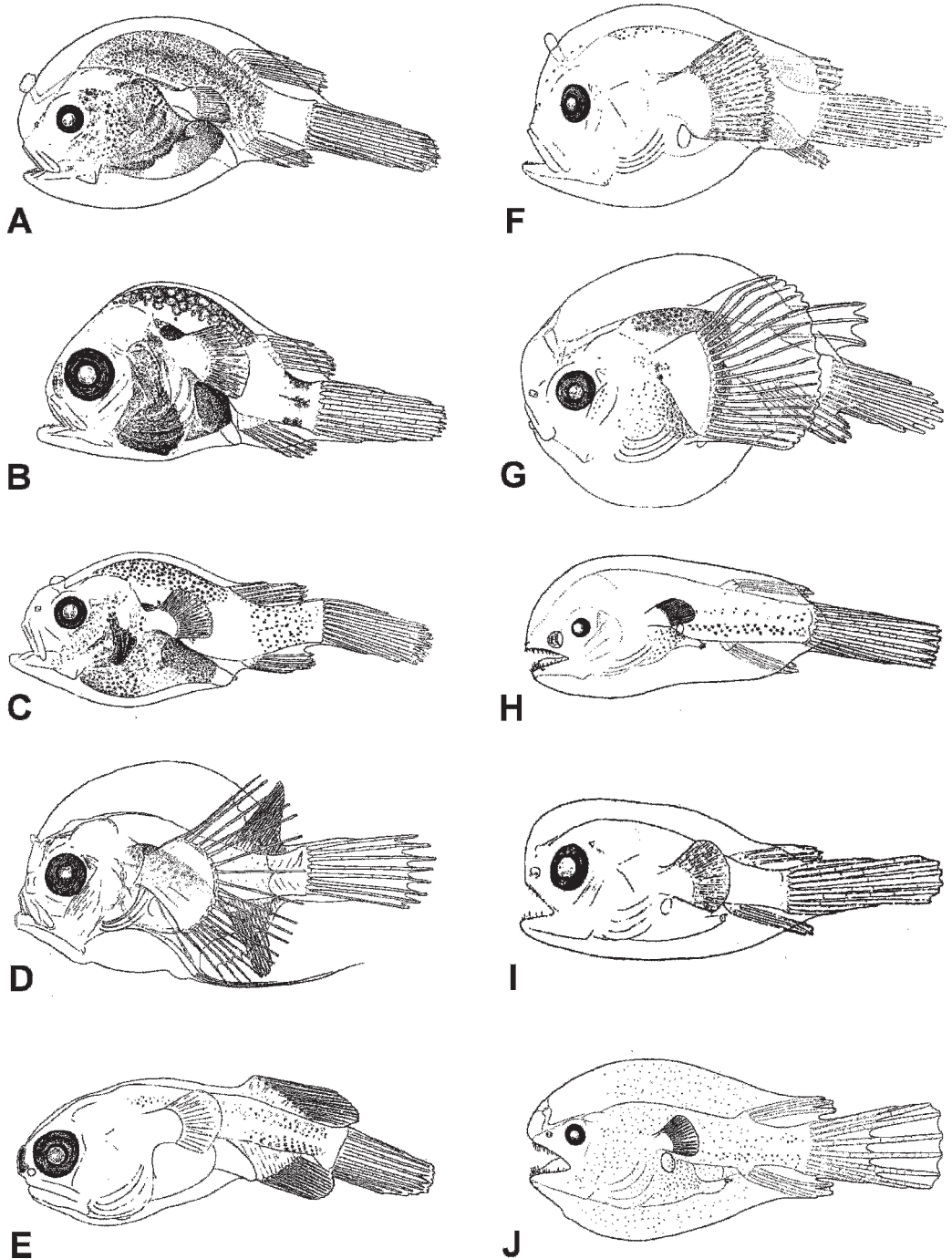


Fig. 6. Larvae of ceratioid taxa used in the present study: (A) *Oneirodes* sp., female, 8.0 mm SL, ZMUC P921073; (B) *Dolopichthys* sp., male, 5.4 mm SL, ZMUC P92818; (C) *Microlophichthys* sp., female, 9.0 mm SL, ZMUC P92976; (D) *Caulophryne* sp., sex unknown, 6.6 mm SL, ZMUC P92192, showing presence of pelvic fins; (E) *Neoceratias spinifer*, sex unknown, 6.3 mm SL, ZMUC P921725; (F) *Gigantactis* sp., female, 8.5 mm SL, ZMUC P921682; (G) *Rhynchactis* sp., female, 7.2 mm SL, ZMUC P921753; (H) *Haplophryne mollis*, male, 13.2 mm SL, ZMUC P921901; (I) *Borophryne apogon*, male, 4.3 mm SL, ZMUC P921759; (J) *Linophryne* subgenus *Rhizophryne* sp., female, 17.5 mm SL, ZMUC P921812. All after Bertelsen (1951).

burg, Virginia) numerous, apparently derived character states shared by these two families as well as with the Gigantactinidae and Neoceratiidae. He presented a phylogeny that argued for a monophyletic origin of sexual parasitism within a lineage derived from some oneirodid-like ancestor (Pietsch, 1976; see also Pietsch, 1979).

In the most recent attempt to determine the phylogenetic relationships of ceratioid taxa, Bertelsen (1984:331) expressed frustration that "most of the derived osteological characters shared by two or more families are reduction states or loss of parts . . . and similarities among such characters may in many cases represent convergent developments. At the same time, most of the diagnostic family characters which represent new structures or specialization of organs are autapomorphic." Nevertheless, he was able to shed new light on the subject, analyzing a list of 30 characters, including ten shared by both sexes, another ten confined to metamorphosed females, six that describe only metamorphosed males, and another four restricted to larvae. Following a discussion of character-state evolution for each of the 30 characters, Bertelsen (1984:333, fig. 171) presented a tree that by his own admission "should be regarded only as a very schematic compilation of expressed views." He (1984:334) concluded by saying that "ceratioids are still very incompletely known and future studies on additional characters and as yet unknown forms may bring answers to at least some of the many questions about their phylogenetic relationships."

Thus, despite numerous efforts, the several hypotheses of phylogenetic relationship that have been proposed for the Ceratioidei are unsatisfactory, mostly contradicting one another and containing one or more unresolved polytomies. It should be emphasized, however, that a rigorous and complete cladistic analysis has never been made. Taxa have been grouped by inspection only; no computer-generated trees have ever been constructed. Here, with the advantage of more than 20 years of additional accumulated data since Bertelsen's (1984) attempt, coupled with a reexamination of all previously identified characters—combined with the results of analyses of new characters and the incorporation of morphological variation taken from newly discovered taxa—we present the first computer-assisted cladistic analysis of relationships of ceratioid families and genera.

MATERIALS AND METHODS

The present analysis was based on an examination of all 66 known lophiiform genera, including

cleared-and-stained material of all except a few unavailable ogcocephaloid genera and five extremely rare ceratioid genera (*Dermatias*, *Tyrannophryne*, *Ctenochirichthys*, *Robia*, and *Acentrophryne*) known only from type specimens (for lists of material examined, see the various papers of Bertelsen and Pietsch cited herein, especially Bertelsen, 1951; and Pietsch, 1972, 1974, 1981). A data matrix of 34 taxa (four outgroups and 30 ingroups, the five unavailable ceratioid genera excluded) and 71 characters applicable to metamorphosed females, plus another 17 characters applicable only to metamorphosed males and larvae (for a total of 88), was constructed (but note that ceratioid males and larvae are rare in collections and generally poorly described anatomically, the males unknown for 13 of the 35 ceratioid genera, and larvae unknown for 11 of the 35 ceratioid genera; Pietsch, 1984; Bertelsen, 1984). Two separate analyses were conducted: one with only those characters applicable to metamorphosed females, and a second with all 88 characters, including those applicable to metamorphosed males and larvae. All characters were treated as unordered and unweighted and were polarized using the lophiiform suborders Lophioidei, Antennarioidei, Chaunacoidei, and Ogcocephaloidei as outgroups (Fig. 1). Characters for outgroup taxa were coded as a single state when all members of the suborder shared the same character state; when the state differed among subtaxa, the state was coded as polymorphic. All except 17 characters were binary. Character states that do not extend to or are unknown for a particular taxon are indicated in the data matrix by a question mark. Character states were coded 0–3 and indicated within parentheses after each respective character-state description. A matrix of character states for all taxa is given in Appendix 1. The matrix was analyzed with PAUP (v. 4.0b10, D. L. Swofford, PAUP*: Phylogenetic Analysis Using Parsimony and Other Methods, Sinauer Associates, Sunderland, MA, 2002), using the branch and bound algorithm, with accelerated transformation (ACCTRAN) to optimize characters. To evaluate branch support, a heuristic bootstrap analysis of 100 replicates was conducted, with random addition sequence and TBR (tree bisection-reconnection) branch swapping options. Bremer decay values (Bremer, 1988) were calculated using TREEROT (v.2, M. D. Sorenson, TREEROT.v2, Boston University, Boston, MA, 1999). When referring to a figure reproduced herein, "Fig." is capitalized but presented in lower case when referring to figures found in the literature cited. Symbolic codes for institutions are those provided by Leviton et al. (1985).

RESULTS

The following characters are divided into three categories: those that describe metamorphosed females (1–71), those restricted to metamorphosed males (72–81), and those that extend only to larvae (82–88). Within each category, characters are arranged by anatomical complex: cranium (1–14), suspensorium (15–18), opercular apparatus (19–24), jaws (25–35), hyoid and gill arches (36–47), axial skeleton and caudal fin (48–53), dorsal and anal fins (54–62), pectoral and pelvic fins (63–67), skin spines (68), additional soft structures unique to lophiiforms (69–71); sexual dimorphism (72), eyes (73–74), olfactory organs (75–76), jaws, teeth, and denticular bones (77–81); size and shape of head and body (82–84), body inflation (85), illicial apparatus (86), and pectoral and pelvic fins (87–88). For the tree derived from characters applicable to metamorphosed females, consistency and retention indices (CI and RI) were produced as a whole and for each character individually. The indices listed for characters of metamorphosed males and larvae were taken from the tree derived from all 88 characters combined. Both CI and RI are presented below in bold font after each character description.

Characters of metamorphosed females.—1. The supraethmoid is usually well developed in lophiiforms (0), but very much reduced or absent in the Thaumatchthyidae (Bertelsen and Struhsaker, 1977:9, figs. 1, 2), and absent in lophioids and the Gigantactinidae (a tiny rudiment observed in a single specimen of *Gigantactis*; Bertelsen et al., 1981:10, fig. 12) (1) (CI 0.33, RI 0.50).

2. An ossified vomer is present in nearly all lophiiforms (0), but absent in juvenile and adult females of both genera of the Gigantactinidae (1) (1.00).

3. Vomerine teeth are well developed in nearly all lophiiforms (0); lost with growth in the oneirodid genera *Dolopichthys* and *Bertella*, and in some species of *Ceratiias* (Pietsch, 1986:481, table 1) (1); and absent in some ogcocephaloids and all members of the Himantolophidae, Thaumatchthyidae, the oneirodid genera *Lophodolos* and *Pentherichthys*, and the linophrynid genera *Photocorynus* and *Haplophryne* (2) (0.33, 0.43).

4. The dorsal margin of the frontal bone is smooth in nearly all lophiiforms or interrupted in some lophioids by a series of short conical knobs or spines ("rugose ridge" of Caruso, 1985:873, fig. 3) (0); a conspicuous, rounded, laterally compressed frontal protuberance is present in the linophrynid genera *Borophryne*

and *Linophryne* (Regan and Trewavas, 1932:46, figs. 65, 66) (1); the frontal protuberance forms a sharp spine in the linophrynid genera *Photocorynus* and *Haplophryne* (Regan and Trewavas, 1932:44, figs. 59, 62) (2) (0.67, 0.50).

5. The frontals of all the outgroups, as well as those of the Centrophrynidae, Ceratiidae, Caulophrynidae, Neoceratiidae, and the linophrynid genus *Photocorynus*, meet posteriorly on the midline (or are narrowly separated by cartilage) in front of the supraoccipital (0); those of all remaining lophiiform taxa are widely separated along their dorsal margins (1) (0.25, 0.67).

6. The anterior end of the frontals of most lophiiforms are simple, more or less tapering, truncate, or slightly concave (Pietsch, 1981:397, figs. 4, 6, 15–19) (0); but strongly bifurcate in the Ceratiidae, the thaumatchthyid genus *Lasiognathus*, the Oneirodidae, and Linophrynidae (Regan and Trewavas, 1932:40, 44, figs. 52, 61, 62, 65; Pietsch, 1974:6, 18, figs. 1, 2, 4, 19–38; Bertelsen and Struhsaker, 1977:32, fig. 18) (1) (0.25, 0.77).

7. In most lophiiforms, the anterior extension of the frontal bone overlaps a small distal portion of the lateral ethmoid (Pietsch, 1981:397, figs. 4, 6, 15–19) (0); in the thaumatchthyid genus *Lasiognathus*, the Oneirodidae, and Linophrynidae the frontal overlaps the full length of the lateral ethmoid (Regan and Trewavas, 1932:44, figs. 61, 62, 65; Pietsch, 1974:6, 18, figs. 1, 2, 4, 19–38; Bertelsen and Struhsaker, 1977:32, fig. 18) (1) (0.33, 0.87).

8. The frontals of most lophiiforms, including all outgroup taxa, are relatively simple elongate bones, without ventromedial extensions (0); those of the Himantolophidae, Diceratiidae, and Melanocetidae bear prominent ventromedial extensions that approach one another on the midline and are narrowly separated by cartilage from the supraethmoid anteriorly and the supraoccipital posteriorly, but make no contact with the parasphenoid (Pietsch and Van Duzer, 1980:62, figs. 1–4; Fig. 7A) (1); the ventromedial extension of each frontal is bifurcated in the thaumatchthyid genus *Lasiognathus* and all oneirodid genera (except *Lophodolos*), the anterior branch making contact with the supraethmoid, the posterior branch closely approaching or making contact with the supraoccipital as well as the parasphenoid (Pietsch, 1974:6, figs. 1, 2, 30; Fig. 7B) (2) (0.50, 0.87).

9. The parietals are present in nearly all lophiiforms (0), but absent in the Himantolophidae and the gigantactinid genus *Rhynchactis* (1); they are very much enlarged in the Centrophrynidae and Ceratiidae (Bertelsen, 1951:128, fig. 88B, C; Pietsch, 1972:28, figs. 7, 8) (2) (0.67, 0.67).

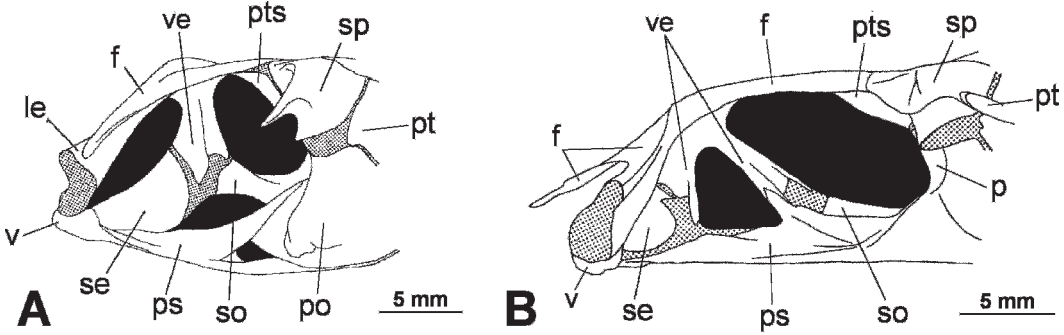


Fig. 7. Left lateral views of anterior portion of cranium of ceratioids: (A) *Melanocetus johnsonii*, 75 mm SL, LACM 32786-1, showing simple ventromedial extension of frontal bone (ve), far removed from parasphenoid (ps); (B) *Chaenophryne draco*, 88 mm SL, LACM 30427-17, showing bifurcated ventromedial extension of frontal bone (ve), posterior branch making direct contact with parasphenoid (ps). Vomerine teeth not shown. Cartilage stippled, open space rendered in solid black. f = frontal; le = lateral ethmoid; po = prootic; pt = pterotic; pts = pterosphenoid; se = supraethmoid; so = supraoccipital; sp = sphenotic; v = vomer.

10. Pterosphenoids are nearly always present (0), but reduced in the Diceratiidae (Uwate, 1979:130, figs. 2, 3) (1) and absent in the Ceratiidae, the oneirodid genus *Lophodolos*, the Caulophrynidae, Gigantactinidae, and Linophrynidae (Pietsch, 1974:19, fig. 33) (2) (0.40, 0.70).

11. The parasphenoid is simple in nearly all lophiiforms (0); in all oneirodid genera (except *Lophodolos*) this bone bears a pair of anterodorsal extensions each overlapping or approaching the distal end of the respective posterior, ventromedial extension of the frontal (Pietsch, 1974:6, 18, figs. 1, 2, 30; Fig. 7B) (1) (1.00).

12. Sphenotic spines are absent in most of the outgroups (0), but present in lophioids and in the Himantolophidae, Diceratiidae, the thaumatichthyid genus *Lasiognathus*, all oneirodid genera except *Chaenophryne*, the Caulophrynidae, and Linophrynidae (Pietsch, 1974:19, fig. 37; 1975:79, fig. 1; Fig. 8) (1) (0.17, 0.55).

13. In nearly all lophiiforms the pterotic makes contact with, but bears no discrete process that overlaps, the respective sphenotic (0); in the Oneirodidae a narrow, elongate, distally rounded, anterodorsally directed process overlaps the posterolateral surface of the sphenotic (Pietsch, 1974:19, figs. 2, 28–37; Fig. 7B) (1); in the Linophrynidae, the pterotic bears a similar, but tapering and distally pointed process (2) (1.00).

14. In nearly all lophiiforms, the supraoccipital is situated posterior relative to other elements of the cranium (0); the supraoccipital is displaced anteriorly in metamorphosed females of the Gigantactinidae, most of its dorsal surface lying in the vertical plane, providing an abutment for the pterygiophore of the illicium (Bertelsen et al., 1981:10, fig. 11) (1); it is displaced anteriorly and narrowly separated by cartilage from the

distal ends of the posterior ventromedial extensions of the frontals in the Himantolophidae, Diceratiidae, Melanocetidae, and all oneirodid genera except *Lophodolos* (Pietsch, 1974:4, 15, figs. 1–4; Pietsch and Van Duzer, 1980:63, figs. 1–7; Bertelsen and Krefft, 1988:16, fig. 3; Fig. 7) (2) (0.50, 0.88).

15. The dorsal end of the hyomandibular bone is distinctly bifurcated, forming two heads in nearly all lophiiform taxa (0); the hyomandibula bears only a single expanded dorsal head in the oneirodid genus *Bertella* and in the Neoceratiidae, Gigantactinidae, and Linophrynidae (Pietsch, 1973:199, fig. 1) (1) (0.50, 0.86).

16. Endopterygoids (mesopterygoids of Bertelsen and Pietsch) are usually present (0), but absent in the antennarioid families Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae (Pietsch, 1981:393, 400, figs. 9, 22, 23), and in the ceratioid families Neoceratiidae, Gigantactinidae, and Linophrynidae (1) (1.00).

17. The palatines are well-developed toothed elements in all the outgroups, except for the Tetrabrachiidae and Brachionichthyidae (Pietsch, 1981:393, 400, figs. 9, 23), and some genera of the Ogocephaloidei (Endo and Shinohara, 1999) (0); they are reduced and toothless in all ceratioids (1) (1.00).

18. The quadrate of most lophiiforms usually bears no more than a small projection at its articulation with lower jaw (0), but this projection forms a highly conspicuous, laterally directed spine in the thaumatichthyid genus *Lasiognathus* and most oneirodid genera (excluding *Pentherichthys*, *Chaenophryne*, *Spiniphryne*, and *Ctenochirichthys*) (Pietsch, 1974:10, figs. 6, 40–47; Bertelsen and Struhsaker, 1977:32, fig. 18; Fig. 8) (1) (0.33, 0.80).

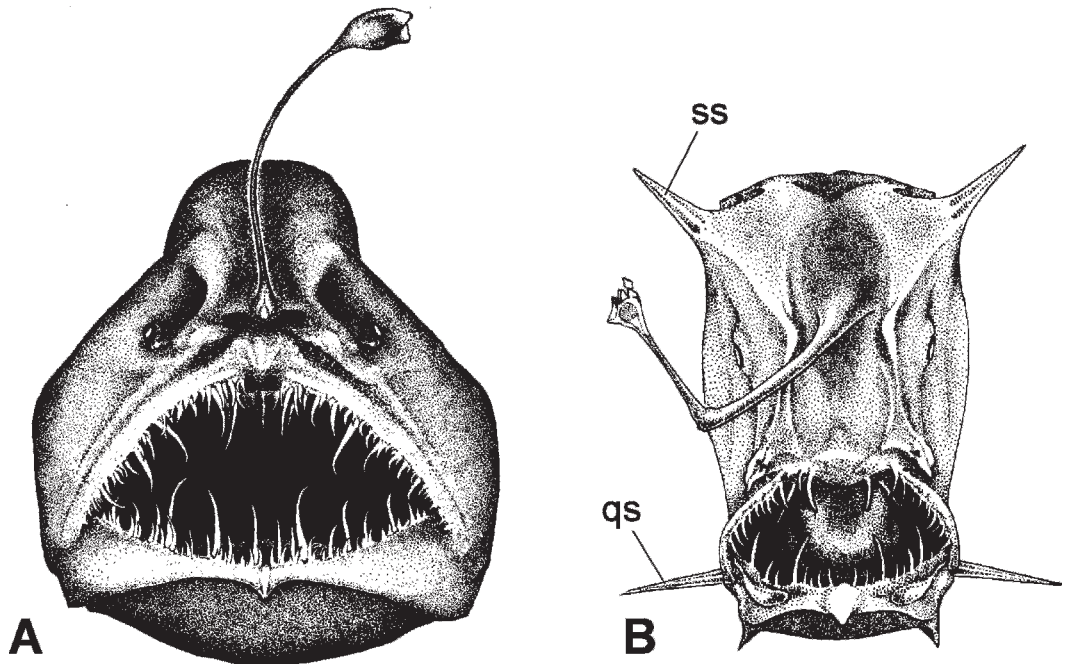


Fig. 8. Anterior views of ceratioids contrasting smooth contour of a melanocetid, with spiny head characteristic of most oneirodids: (A) *Melanocetus johnsonii*, 85 mm SL, LACM 31484-1 (drawn by E. A. Hoxie); (B) *Chirophryne xenolophus*, 22 mm SL, SIO 70-306, with well-developed sphenotic (ss) and quadrate spines (qs). Drawn by P. Chaudhuri.

19. The preopercle is large and distinctly crescent shaped in nearly all lophiiforms (0), straight in both genera of the Thaumatchthyidae (Bertelsen and Struhsaker, 1977:12, figs. 5A, 18) (1); strongly bowed at mid-length and extending posteriorly in the linophrynid genera *Haplophryne*, *Borophryne*, and *Linophryne*, leaving a large space between it and the remaining elements of the suspensorium (Regan and Trewavas, 1932:44, figs. 61, 66; Fig. 9) (2); and very much reduced to a small strut of bone in the Gigantactinidae (Bertelsen et al., 1981:11, fig. 13) (3) (1.00).

20. The posterior margin of the preopercle is smooth and spineless in nearly all lophiiforms (0), but bears a series of four to six short spines along its anterior, lateral, and posterior margins in the linophrynid genus *Photocorynus* (Regan and Trewavas, 1932:44, fig. 59); and a single, large, posteriorly directed spine in the linophrynid genera *Haplophryne*, *Borophryne*, and *Linophryne* (the preopercular spine of *Haplophryne* terminating in three to five radiating cusps; Regan and Trewavas, 1932: 44, figs. 61, 66; Bertelsen, 1951:172, figs. 115, 118, 126; Fig. 9) (1) (1.00).

21. The upper arm of the opercle is simple in nearly all lophiiforms (0), but divided into three

or more radiating ribs or branches in the Thaumatchthyidae (Bertelsen, 1951:118, figs. 77, 78; Bertelsen and Struhsaker, 1977:32-33, figs. 1, 4, 5, 18) (1) (1.00).

22. The anterodorsal margin of the subopercle bears a distinct anteriorly directed spine in most of the outgroups and in the Centrophrynidae, the ceratiid genus *Cryptopsaras*, the Diceratiidae, Melanocetidae, and the genus *Thaumatchthys* (Bertelsen and Struhsaker, 1977:14, figs. 4, 5A), and (Bertelsen, 1951:139, figs. 88B, 89A, C) (0); a small subopercular spine or projection is present in some specimens of several oneirodid genera (*Chaenophryne*; Bertelsen, 1951:109, figs. 66, 67), but absent in ogocephaloids, the antennarioid families Tetrabrachiidae and Brachionichthyidae, and all other lophiiforms (1) (0.20, 0.43).

23. The interopercle of nearly all lophiiforms is long and slender (0), but extremely reduced to a small triangular bone in the Neoceratiidae and Gigantactinidae (Bertelsen, 1951:156, fig. 105; Bertelsen et al., 1981:11, fig. 13; Fig. 9-11) (1) (1.00).

24. An interopercular-mandibular ligament is present in nearly all lophiiforms (0), but absent in both genera of the Gigantactinidae (Bertelsen et al., 1981:11, fig. 13) (1) (1.00).

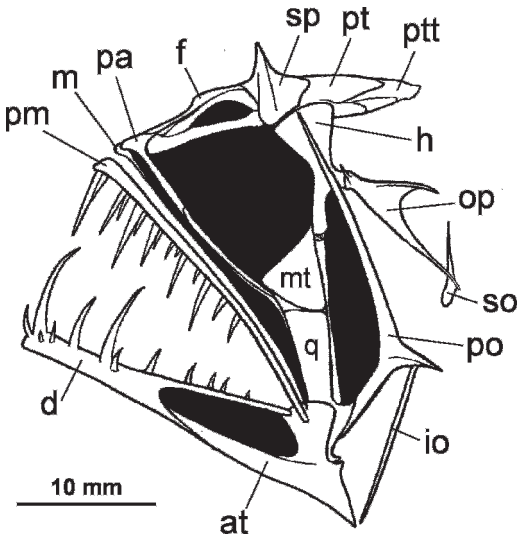


Fig. 9. Head skeleton of *Linophryne racemifera*, left lateral view, 52 mm SL, ZMUC P92146, showing large open space (rendered in solid black) between preopercle (po) and remaining elements of the suspensorium. Pectoral girdle and hyoid apparatus not shown. at = articular; d = dentary; f = frontal; h = hyomandibular; io = interopercle; m = maxilla; mt = metapterygoid; op = opercle; pa = palatine; pm = premaxilla; pt = pterotic; ptt = posttemporal; q = quadrate; so = subopercle; sp = sphenotic. Modified after Regan and Trewavas (1932).

25. The upper and lower jaws are more or less equal in length in nearly all lophiiforms (0); in sharp contrast, the upper jaw extends anteriorly far beyond the lower in the *Thaumatichthyidae*, the distal ends of the premaxillae widely separated from each other and connected only by membranous connective tissue (Bertelsen and Struhsaker, 1977:11, 29, 31, figs. 1, 2, 17, 18; Fig. 10) (1) (1.00).

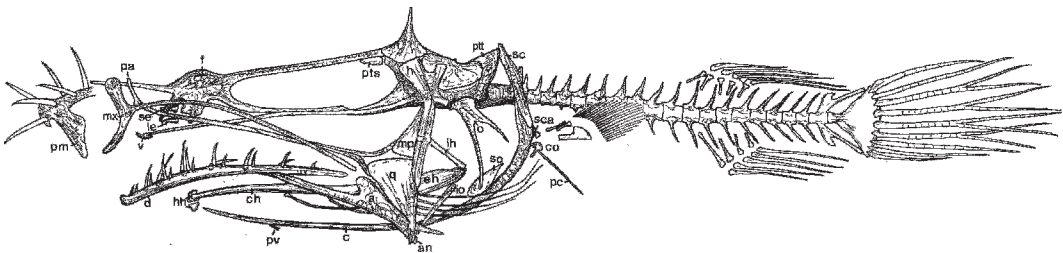


Fig. 10. Skeleton of *Lasiognathus* sp., left lateral view, 40 mm SL, SIO 73-305, showing elements of upper jaw extending anteriorly far beyond lower jaw. an = angular; c = cleithrum; ch = ceratohyal; co = coracoid; d = dentary; eh = epihyal; f = frontal; h = hyomandibular; hh = hypohyal; ih = interhyal; io = interopercle; le = lateral ethmoid; mp = metapterygoid; mx = maxilla; o = opercle; pa = palatine; pc = postcleithrum; pm = premaxilla; pt = posttemporal; pts = pterosphenoid; pv = pelvic bone; q = quadrate; sca = supracleithrum; sca = scapula; se = supraethmoid; sp = subopercle; v = vomer. After Bertelsen and Struhsaker (1977).

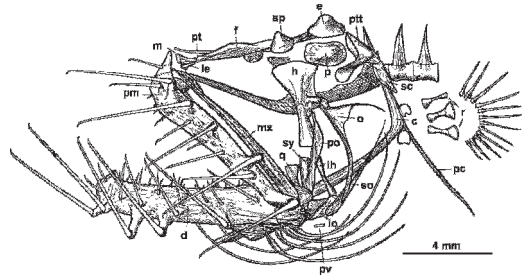


Fig. 11. Head skeleton of *Neoceratias spinifer*, left lateral view, 52 mm SL, ZMUC P921726, showing teeth attached to the lateral surface of the dentary and premaxilla. pt = pterygiophore of illicium; all other abbreviations as in Figures 9 and 10. Modified after Bertelsen (1951).

26. A rostral cartilage (symphyseal cartilage of Bertelsen and Pietsch) of the upper jaw is present in nearly all lophiiforms (0), but absent in the genus *Thaumatichthys*, the *Gigantactinidae*, and the linophrynid genera *Haplophryne*, *Borophryne*, and *Linophryne* (Bertelsen and Struhsaker, 1977:11, figs. 1, 2; Bertelsen et al., 1981:11, figs. 11, 13) (1) (0.33, 0.60).

27. The ascending process of the premaxilla of lophioids (as well as all batrachoidiform genera; Monod, 1960:665, figs. 47–49; Field, 1966:51, fig. 3; David W. Greenfield, pers. comm., 23 March 2006) articulates with the toothed portion of this bone (i.e., autogenous; capable of considerable independent lateral movement) (0), but fused to the latter in all other lophiiforms (Pietsch, 1981:399, fig. 20) (1) (1.00).

28. A postmaxillary process of the premaxilla is present in all the outgroups (Pietsch, 1981:399, fig. 20) and in the *Ceratiidae* (Lütken, 1878:334, fig. 7; Regan and Trewavas, 1932:39, fig. 53; Bertelsen, 1951:128, fig. 88) (0); it is absent in all other lophiiforms (1) (0.50, 0.80).

29. The maxillae are well developed in nearly all lophiiforms (0); considerably reduced in the Caulophrynidae, Neoceratiidae, the genus *Gigantactis*, and the linophrynid genus *Photocorynus* (1); and further reduced to a fine thread of bone or absent in the gigantactinid genus *Rhynchactis* and the linophrynid genera *Haplophryne*, *Borophryne*, and *Linophryne* (Bertelsen et al., 1981:10, fig. 13; Figs. 9, 11) (2) (0.67, 0.83).

30. A thick anterior-maxillomandibular ligament (labial cartilage of Le Danois, 1964; Pietsch, 1972) is present in most lophiiforms (Pietsch, 1978:4, fig. 3) (0), but very much reduced or absent in the Melanocetidae, Thaumathichthyidae, Caulophrynidae, Neoceratiidae, Gigantactinidae, and Linophrynidae (1) (0.50, 0.90).

31. The dentaries of nearly all lophiiforms are strongly bifurcated posteriorly (0), but simple in the Neoceratiidae and Gigantactinidae (Bertelsen, 1951:156, fig. 105; Bertelsen et al., 1981:11, fig. 13; Figs. 9, 11) (1) (1.00).

32. Jaw teeth vary considerably in size among the outgroups and most all ceratioids (0), but never become as large and fang-like in proportion to the head and mouth as those of the linophrynid genera *Borophryne* and *Linophryne* (as well as those of the linophrynid genus *Acentrophryne*, unavailable for analysis; Regan, 1926:23, pl. 2, figs. 1–3, pl. 3, fig. 1; Bertelsen, 1951:172, 193, figs. 118, 126; Fig. 9) (1) (1.00).

33. The outermost lower-jaw teeth are smaller than the inner and mounted on the dorsal edge of the dentaries in nearly all lophiiforms (0), but considerably larger than the inner and conspicuously attached to the lateral surface of the dentaries in the Neoceratiidae and the genus *Gigantactis* (jaw teeth are minute or absent in metamorphosed specimens of the gigantactinid genus *Rhynchactis*; Bertelsen, 1951:156, fig. 105; Bertelsen et al., 1981:11, figs. 5, 19, 23; Fig. 11) (1) (1.00).

34. The posterior end of the lower jaw (articular and angular) extends posteriorly considerably beyond its articulation with the quadrate in nearly all lophiiforms (0), but terminates at the articular-quadrate joint in the Thaumathichthyidae, Neoceratiidae, and Gigantactinidae (Bertelsen and Struhsaker, 1977:11, figs. 1, 9; Bertelsen et al., 1981:11, fig. 13; Figs. 9–11) (1) (0.50, 0.75).

35. The posteroventral margin of the articular is rounded in nearly all lophiiforms (0), but greatly expanded and squared off in chaunacooids (Pietsch, 1981:403, fig. 24) and in the Ceratiidae (Regan and Trewavas, 1932:40, fig. 52; Bertelsen, 1951:128, fig. 88) (1) (0.50, 0.50).

36. The interhyal bears a medial, posterolaterally directed process in lophioids and antennarioids (0), but this element is simple and

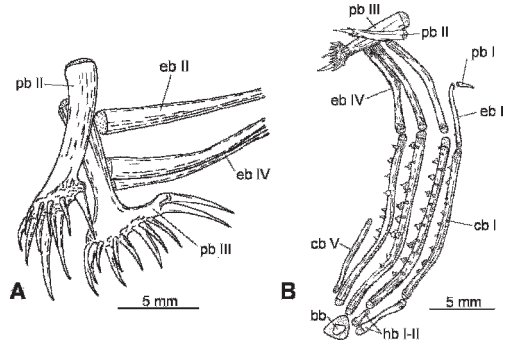


Fig. 12. Portions of gill arches of ceratioids: (A) Upper pharyngobranchials of *Gigantactis longicirra*, 209 mm SL, ISH 973/71, showing hypertrophied and distally expanded third pharyngobranchial (modified after Bertelsen et al., 1981); (B) Gill arches of *Himantolophus groenlandicus*, 53.5 mm SL, ISH 2056/71, showing teeth on all four ceratobranchials (modified after Bertelsen and Krefft, 1988). bb = basibranchial; cb = ceratobranchial; eb = epibranchial; hb = hypobranchial; pb = pharyngobranchial.

cylindrical in all other lophiiforms (Pietsch, 1981:400, fig. 26) (1) (1.00).

37. Nearly all lophiiforms have six branchiostegal rays (0); this number is reduced in some taxa, the anteriormost element dropping out in some specimens of the Caulophrynidae and Neoceratiidae, and in all members of the Linophrynidae (1) (1.00).

38. A basihyal is present in most of the outgroups (0), but absent in some antennarioids (i.e., Brachionichthyidae), at least some ogocephaloids, and all ceratioids (Pietsch, 1981:394, 400, fig. 10) (1) (1.00).

39. The first pharyngobranchial is present in most of the outgroup taxa and many ceratioids (0), but present or absent in ogocephaloids (0/1), and absent in lophioids, the Melanocetidae, Thaumathichthyidae, all oneirodid genera except *Spiniphryne* and *Oneirodes*, the Caulophrynidae, Neoceratiidae, Gigantactinidae, and Linophrynidae (Pietsch, 1979:8, fig. 10; Pietsch and Van Duzer, 1980:66, fig. 13; Bertelsen et al., 1981:11, fig. 16) (1) (0.25, 0.67).

40. The third pharyngobranchial is large and well-toothed in the outgroups and most ceratioid taxa (0), but greatly hypertrophied and expanded distally in the Neoceratiidae and Gigantactinidae (Bertelsen, 1951:156, fig. 105A; Bertelsen et al., 1981:11, 17, figs. 9, 16; Fig. 12) (1) (1.00).

41. A fourth pharyngobranchial tooth-plate is present and well developed in lophioids (Field, 1966:58, figs. 8, 9) (0), but absent in all other lophiiforms (Pietsch, 1981:401, figs. 11, 28–32) (1) (1.00).

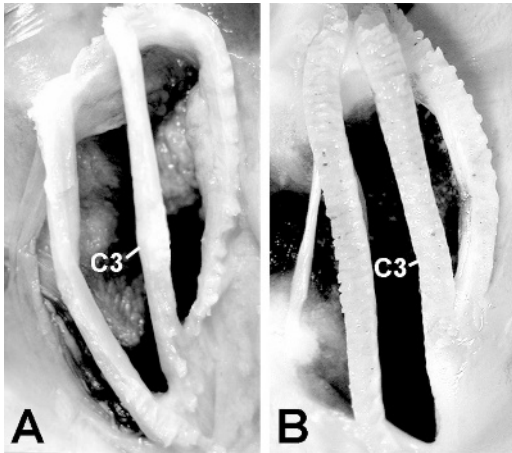


Fig. 13. Gill arches of ceratioids, left posterior view, showing the extent to which the dorsal and ventral ends of the third (C3) and fourth ceratobranchials are bound together by connective tissue: (A) *Oneirodes thompsoni*, 143 mm SL, UW 43825; (B) *Gigantactis vanhoeffeni*, 290 mm SL, UW 46040, showing greatly restricted space behind the third ceratobranchial. Gill filaments removed for better clarity.

42. The first epibranchial is present in nearly all lophiiforms (0), but absent in the genus *Thaumatichthys* and in the Gigantactinidae (Bertelsen and Struhsaker, 1977:14, fig. 5; Bertelsen et al., 1981:17, fig. 16; Fig. 12) (1) (0.50, 0.50).

43. The first epibranchial of lophioids, antennarioids, and chaunacoids bears a medial process ligamentously attached to the proximal tip of the second epibranchial (0); this element is simple and without ligamentous connection to the second epibranchial in ogocephaloids and ceratioids (Pietsch, 1981:401, figs. 28–32) (1). The first epibranchial is absent in the genus *Thaumatichthys* and in the Gigantactinidae (Fig. 12A) (1.00).

44. The dorsal and ventral ends of the third and fourth ceratobranchials are more or less free of each other in nearly all lophiiforms (0), but bound tightly to one another by connective tissue in the Neoceratiidae, Gigantactinidae, and Linophrynidae, greatly restricting the space between these two elements (Fig. 13) (1) (1.00).

45. The third hypobranchial is present in most lophiiforms (0), but absent in the Himantolophidae, Caulophrynidae, Neoceratiidae, Gigantactinidae, and Linophrynidae (Bertelsen et al., 1981:12, fig. 16; Bertelsen and Krefft, 1988:16, fig. 4C) (1) (0.50, 0.88).

46. Among the outgroups, branchial teeth are present on the first three ceratobranchials (and usually the fourth) of chaunacoids, ogocephal-

oids, some antennarioids, and the ceratioid families Centrophrynidae and Himantolophidae (Pietsch, 1972:35, fig. 15; Bertelsen and Krefft, 1988:16, fig. 4C; Fig. 12B) (0); they are absent in all other lophiiforms (1) (0.33, 0.33).

47. Gill filaments are present on the first gill arch of lophioids and antennarioids (0) but absent on this element in all other lophiiforms (present, however, on the ventralmost tip of the first ceratobranchial of some ceratioids; Bradbury, 1967:408; Pietsch, 1981:415) (1) (1.00).

48. Vertebral centra are short in nearly all lophiiforms, their greatest diameter approximately equal to their length (Pietsch, 1972:37, figs. 16, 18; 1974:12, fig. 12) (0), but elongate in the *Thaumatichthyidae*, *Neoceratiidae*, and *Gigantactinidae*, their greatest diameter only about half their length (Bertelsen and Struhsaker, 1977:13, figs. 5, 18; Bertelsen et al., 1981:12, fig. 17; Fig. 10) (1) (0.50, 0.75).

49. The caudal peduncle is relatively short in nearly all lophiiforms (0), but exceptionally long and narrow in the *Thaumatichthyidae*, *Neoceratiidae*, and *Gigantactinidae*, the posterior insertion of the dorsal and anal fins well separated from the posterior margin of the hypural plate (Figs. 2H, I, 3D, E, 10) (1) (0.50, 0.67).

50. A single epural is present in all outgroup taxa and in the *Caulophrynidae* (Pietsch, 1979:9, fig. 11) (0); epurals are absent in all other lophiiforms (1) (0.50, 0.75). Bertelsen's (1984:326) report of an epural in the linophrynid genus *Photocorynus* could not be confirmed by reexamination of all available material.

51. The caudal fin is rounded in nearly all lophiiforms (0), but emarginate in females of both genera of the *Gigantactinidae* (Bertelsen et al., 1981:5, figs. 4, 63; Fig. 3E) (1) (1.00).

52. The caudal fin of lophiiforms nearly always contains nine rays (0), but the ninth or lowermost ray is reduced to less than one-half the length of the eighth ray in the genus *Ceratias*, the *Gigantactinidae*, and *Linophrynidae* (1); there are only eight caudal-fin rays in lophioids, the ceratiid genus *Cryptopsaras*, and in the *Caulophrynidae* (2) (0.33, 0.50).

53. The innermost six caudal-fin rays are bifurcated in nearly all the outgroups (seven or all nine caudal rays bifurcated in antennarioids) as well as in the ceratioid families *Himantolophidae*, *Diceratiidae*, and *Melanocetidae* (0); the innermost four are bifurcated in all remaining ceratioid taxa (1), except for females of the genus *Gigantactis* in which all nine caudal-fin rays are simple (Bertelsen et al., 1981:5, fig. 4) (2) (0.67, 0.86).

54. There are primitively six dorsal-fin spines in lophioids (0), but three or fewer in all other

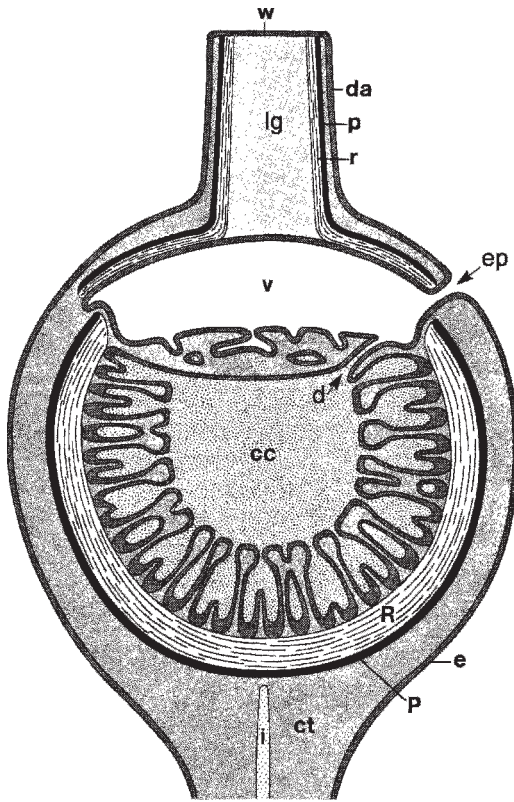


Fig. 14. Diagrammatic medial section of a ceratioid esca, left lateral view. The light gland is enclosed within a lightproof capsule consisting of an inner reflecting layer (R) and an outer pigmented layer (P). A duct (d) connects the bacteria-filled central cavity (cc) of the light gland with the vestibule (v), which opens to the outside by way of an esca pore (ep) positioned on the posterior margin of the distal surface of the esca. The distal esca appendage (da) contains a single light guide (lg), with a terminal window (w). ct = connective tissue; e = epidermis; i = illicial bone; p = pigmented layer of light-guide wall; r = reflecting layer of light-guide wall. Modified after Munk (1999).

lophiiforms (Pietsch, 1981:409, figs. 36–38) (1) (1.00).

55. The pterygiophore of the illicium is relatively small in nearly all lophiiforms (0), but exceptionally well developed in the Gigantactinidae (Bertelsen et al., 1981:14, fig. 13) (1) (1.00).

56. The esca is non-luminescent in all the outgroups, and in the Caulophryniidae (Pietsch, 1979:12, figs. 15, 17, 19–22) and gigantactinid genus *Rhynchactis* (Bertelsen et al., 1981:3, figs. 2, 3; Bertelsen and Pietsch, 1998:586, figs. 2–6) (0); in all other ceratioids (except the Neoceratiidae, in which the illicium and esca have been lost; Bertelsen, 1951:156, fig. 105) the esca encloses

an expanded central cavity containing bioluminescent bacteria (O'Day, 1974:4, figs. 3–6; Munk and Bertelsen, 1980:111, figs. 3–9; Munk, 1999:266, fig. 2; Fig. 14) (1) (0.33, 0.60).

57. The esca is a solid structure, with no central cavity or opening to the outside, in lophioids, antennarioids, chaunacoids, Caulophryniidae, and the gigantactinid genus *Rhynchactis* (0); a tiny opening (the esca pore of Bertelsen, 1951:16) leading from a central cavity to the outside is present in ogcocephaloids (Bradbury, 1988:20) and in all other ceratioids (except the Neoceratiidae in which the illicium and esca have been lost; Brauer, 1904:18, fig. 1; Munk, 1999:266, fig. 2; Fig. 14) (1) (0.33, 0.50).

58. Large, tooth-like dermal denticles embedded in the esca are absent in nearly all lophiiforms (0), but present in both genera of the Thaumachthyidae (Bertelsen and Struhsaker, 1977:21, figs. 10, 11; Bertelsen and Pietsch, 1996:402, figs. 2–5; Pietsch, 2005:78, figs. 1–3) (1) (1.00).

59. The cephalic second dorsal-fin spine is simple in nearly all lophiiforms (0), but bears a more or less concealed (within a pore on the head just behind the base of the illicium) distal light organ in larvae of the Ceratiidae, and in larvae and juvenile females of the Diceratiidae (Bertelsen, 1951:16, 67, 127, figs. 28, 90G–I, 93C–E; Fig. 15) (1) (0.50, 0.67).

60. A third cephalic dorsal-fin spine and pterygiophore are present in lophioids, antennarioids, and chaunacoids (0), but absent in ogcocephaloids and ceratioids (Bertelsen, 1951:17; Bradbury, 1967:401; Pietsch, 1981:410, fig. 38) (1) (1.00).

61. The rays of the dorsal and anal fins are relatively short in nearly all metamorphosed lophiiforms (0), but extremely long in both genera of the Caulophryniidae, in extreme cases exceeding 160% standard length (Pietsch, 1979:9, figs. 14, 20; Fig. 3C) (1) (1.00).

62. Caruncles (light organs associated with dorsal-fin rays), absent in nearly all lophiiforms (0), are present in both genera of the Ceratiidae (Brauer, 1908:103, pl. 32, fig. 17; Bertelsen, 1951:16, figs. 90, 93; Munk and Herring, 1996:517, figs. 1–4; Fig. 15A, B) (1) (1.00).

63. The posttemporal of lophioids, antennarioids, and chaunacoids is attached to the cranium in such a way that considerable movement in an anterodorsal-posteroventral plane is possible (0); this element is fused to the cranium in ogcocephaloids and all ceratioids (Pietsch, 1981:411, figs. 3–5, 15–19) (1) (1.00).

64. The pectoral lobe of nearly all lophiiforms is relatively short, shorter than the longest pectoral-fin rays (0), but considerably longer

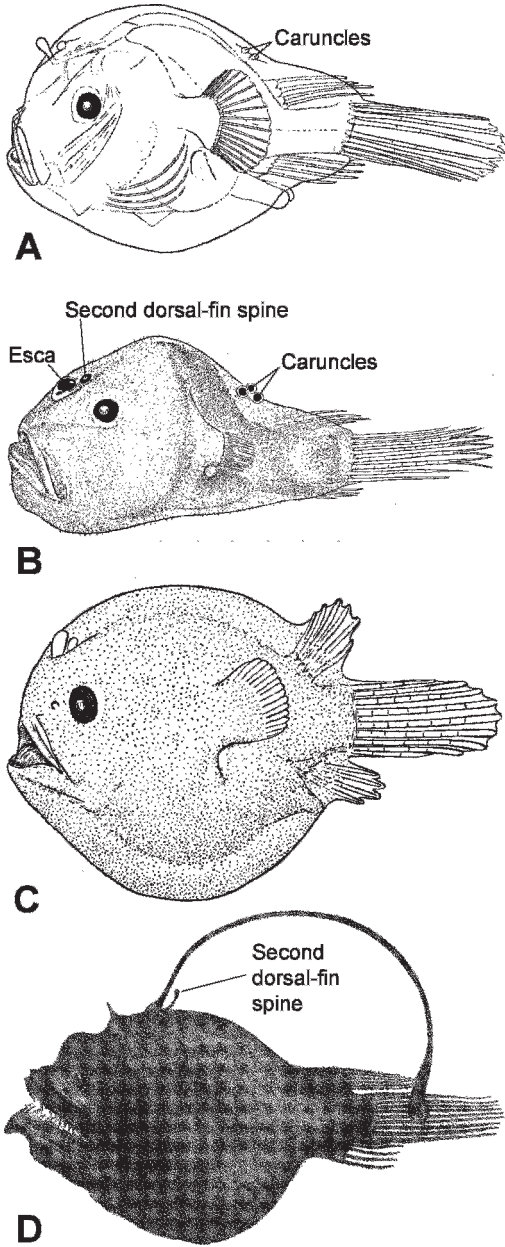


Fig. 15. Female larvae and juveniles of ceratiids and diceratiids showing development of second cephalic spine, bearing distal esca-like light organ: (A) *Ceratias* sp., 7.6 mm SL, ZMUC P921133; (B) *Cryptopsaras couesii*, 9.6 mm SL, ZMUC P921291; (C) Diceratiidae sp., 10.5 mm SL, ZMUC P92676; (D) *Bufoceratias wedli*, 35 mm SL, NMW 3524. After Bertelsen (1951) and Pietschmann (1930).

than the longest pectoral-fin rays in the oneirodid genera *Puck*, *Leptacanthichthys*, *Chirophryne*, and *Ctenochirichthys* (Pietsch, 1978:7, figs. 8, 9, 11, 14, 16) (1) (1.00).

65. Most lophiiforms, including most outgroup taxa, have three pectoral radials (0), but the Centrophrynidae, Ceratiidae, and Melanocetidae have four (1); lophioids (small juveniles) and gigantactinids have five (2) (0.50, 0.60). Fusion of pectoral radials with increasing standard length is common in lophiiforms (the five radials present in juvenile lophioids fuse to two in adults; Pietsch, 1972:41, fig. 23; Bertelsen and Struhsaker, 1977:14, fig. 6; Pietsch, 1979:11, fig. 13).

66. The pelvic bones of all the outgroups are well developed and expanded distally to form two heads, one bearing the spine and rays of the pelvic fin, the other making contact with its counterpart on the opposite side (0); these bones are considerably reduced in ceratioids, lacking the pelvic spine and rays and ranging from triradiate in the Himantolophidae (Bertelsen and Krefft, 1988:19, fig. 5C) and some females of the oneirodid genus *Chaenophryne* (Pietsch, 1975:79, fig. 2) to somewhat expanded distally, or slender and cylindrical throughout their length (1); they are rudimentary or absent in the Neoceratiidae and Gigantactinidae, and absent in the Linophrynidae (Bertelsen, 1951:156, fig. 105A; Bertelsen et al., 1981:14, fig. 13; Figs. 10, 11) (2) (1.00).

67. Pelvic fins are present in all the outgroups (0), but absent in all juvenile and adult ceratioids of both sexes (1) (1.00).

68. The skin is covered with numerous, close-set, dermal spines or spinules in most of the outgroups (except lophioids and some antennarioids), and in the Centrophrynidae, Ceratiidae, Himantolophidae, Diceratiidae, the genus *Thaummatichthys*, the oneirodid genus *Spiniphryne*, and the Gigantactinidae (Regan, 1926:12, figs. 1, 3; Bertelsen and Krefft, 1988:21, figs. 1, 15) (0); although tiny dermal spinules may be present in some specimens (detectable only microscopically in cleared and stained material; Pietsch, 1974:29; Pietsch and Van Duzer, 1980:67), the skin is everywhere smooth and naked in all other lophiiforms (1) (0.20, 0.64).

69. In contrast to those of all other lophiiforms (0), females of the genus *Thaummatichthys*, the Neoceratiidae, and Gigantactinidae have a large elongate nasal papilla (Bertelsen, 1951:160, fig. 106D) (1) (0.50, 0.67).

70. The opercular opening is primitively large in lophioids, extending not only behind the base of the pectoral fin, but in front of it as well (Caruso, 1985:873) (0); the opercular opening is considerably more restricted and fully situated behind the base of the pectoral fin in all other lophiiforms (Pietsch and Grobecker, 1987:34, 349, pl. 16A) (1) (1.00).

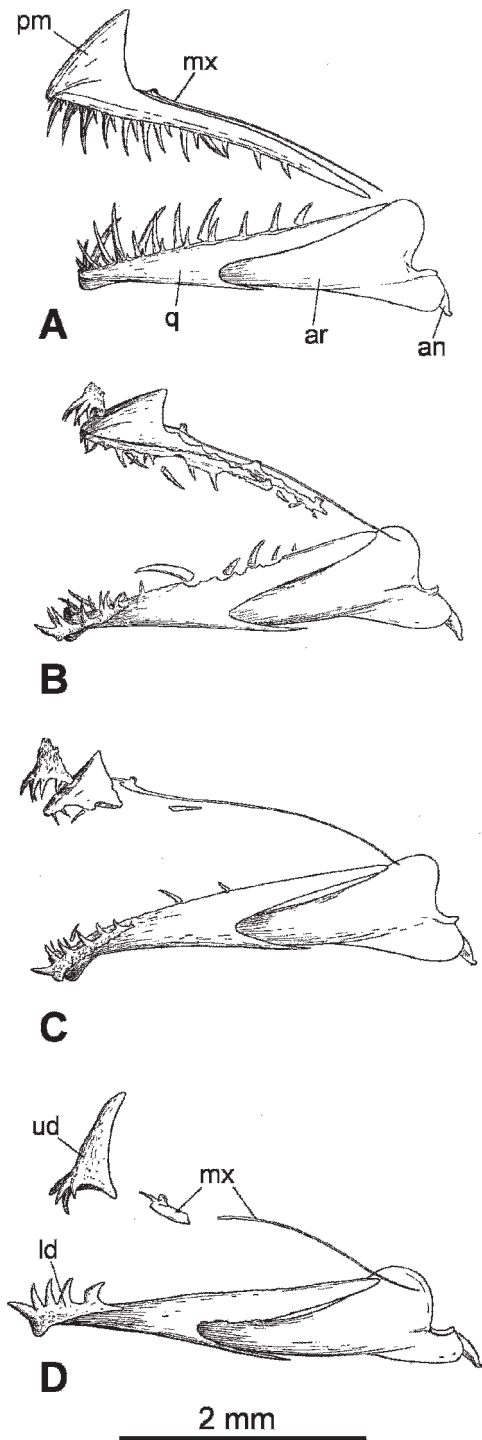


Fig. 16. Jaws of free-living males of *Linophryne arborifera*-group showing development of upper (ud) and lower denticular bones (ld), and simultaneous loss of jaw teeth, reduction of the maxilla (mx), and reduction and final loss of the premaxilla (pm): (A) Larval stage, 13.0 mm SL, ZMUC P921801; (B) Early

71. The anal opening is situated on the ventral midline in nearly all lophiiforms (0), but skewed to the left of the midline (i.e., sinistral) in all members of the Linophrynidae (males and larvae as well as females; Bertelsen, 1951:161, figs. 112, 115–117; Figs. 3H, 4O, P, 6H–J) (1) (1.00).

Characters restricted to metamorphosed males.—72. Adult males and females of all outgroup taxa are similar in size (0), whereas metamorphosed males of all ceratioids are dwarfed, reaching only a small fraction of the size of the females (Regan, 1925a:395, figs. 1–9; Parr, 1930a:129, figs. 1–7; Bertelsen, 1951:15; Fig. 4) (1) (1.00).

73. The eyes of metamorphosed males of all outgroup taxa as well as those of nearly all metamorphosed ceratioid males are large, their diameters ranging between approximately 9.1–20.0% head length (Bertelsen, 1951:24) (0); those of the Ceratiidae are relatively huge, with diameters greater than 28% head length (Fig. 4B, C) (1); while those of the Centrophrynidae, Neoceratiidae, and Gigantactinidae are very much reduced, with diameters of 5.9–7.1% head length (Bertelsen, 1984:326, table 89; Fig. 4A, L–N) (2) (0.67, 0.75).

74. The eyes of males of all the outgroups and most ceratioids are spherical (0), but oval and bowl-shaped in the Ceratiidae (Munk, 1964:5, 9, figs. 1A, B, 2A, B, D–G; 1966:22, fig. 10; Fig. 4B, C) (1) and tubular (described as “telescopic” by Bertelsen, 1951:25) in the Linophrynidae (Munk, 1964:10, figs. 1C, 2C; 1966:31, figs. 17, 18; Fig. 4O, P) (2) (1.00).

75. The olfactory organs of males of all the outgroups are small relative to head length (0); those of nearly all metamorphosed ceratioid males are large, their greatest diameter ranging between approximately 12.5–21.7% head length (Bertelsen, 1951:25; Marshall, 1967a, 1967b) (1); those of the Gigantactinidae are relatively huge, diameters greater than 30% head length (Fig. 4M, N) (2); but those of the Ceratiidae and Neoceratiidae are very much reduced and probably non-functional (Fig. 4B, C, L) (Bertelsen, 1984:326, table 89) (3) (0.75, 0.83).

76. The paired nostrils of males of all the outgroups and many ceratioids are similarly directed, either both laterally or both anteriorly (0); in the Centrophrynidae, Thaumatoichthyidae,

metamorphosis, 15.1 mm SL, ZMUC P921789; (C) Late metamorphosis, 13.9 mm SL, ZMUC P921788; (D) Metamorphosed specimen, 17.2 mm SL, ZMUC P921787. Modified after Bertelsen (1951), all drawn to the same scale.

Oneirodidae, Caulophrynidae, Gigantactinidae, and Linophryniidae the posterior nostrils are directed laterally, but the anterior nostrils are directed anteriorly (Bertelsen, 1984:326, table 89) (1) (0.33, 0.78).

77. The premaxillae of metamorphosed males of all outgroup taxa as well as those of nearly all ceratioids are well-developed (0); those of the linophrynid genera *Borophryne* and *Linophryne* are extremely reduced or absent (Bertelsen, 1951:161, 164, fig. 108; Fig. 16) (1) (1.00).

78. Jaw teeth are retained in adult males of all the outgroups and in those of the linophrynid genera *Photocorynus* and *Haplophryne* (Bertelsen, 1951:21, fig. 5) (0); they are lost during metamorphosis in those of all other ceratioids (Fig. 16) (1) (0.33, 0.60).

79. Denticular bones, a unique set of pincer-like denticles at the anterior tips of the jaws used for grasping and holding fast to a prospective mate (originating during metamorphosis by fusion of modified dermal spinules anterior to the toothed symphysis of the premaxillae and dentaries; Bertelsen, 1951:21, figs. 5, 6; Munk, 2000:315), are absent in all the outgroups (0), but present in all metamorphosed ceratioid males (Bertelsen, 1984:326, table 89; Figs. 4, 16) (1) (1.00).

80. An anterior medial ridge of consolidated dermal spinules is absent in nearly all Lophiiforms (0); a series of fused dermal spinules form a conspicuous medial ridge on the snout of metamorphosed males of the Himantolophidae, Melanocetidae, and the oneirodid genus *Microlophichthys* (Bertelsen, 1951:22, 39, 93, figs. 14, 47; Bertelsen and Krefft, 1988:26, fig. 10A, C) (1) (0.50, 0.50).

81. An upper denticular bone is absent or limited to the distal tip of the snout in nearly all lophiiforms (0); the upper denticular bone makes contact with the anterior tip of the pterygiophore of the illicium of metamorphosed males of the Ceratiidae, Himantolophidae, and Melanocetidae (Parr, 1930a:132, fig. 6; Parr, 1930b:7, figs. 2, 3; Bertelsen, 1951:22, fig. 6; Bertelsen and Krefft, 1988:26, fig. 10A, C) (1) (0.50, 0.67).

Characters that extend only to larvae.—82. The eggs and larvae of lophioids are relatively large (0), but small in all other lophiiforms (at all stages the eggs are considerably less than 50% the diameter of those of lophioids; the smallest larvae are certainly less than 50%, and probably less than 30%, the size of those of lophioids; size at transformation to the prejuvenile stage is less than 60% that of lophioids (Bertelsen, 1984:327, figs. 167–170; Pietsch, 1984:323, fig. 164; Figs. 5, 6) (1) (1.00).

83. The head of the larvae of lophioids is small relative to the body (less than 30% SL) (0), but proportionately large in all other lophiiforms, always greater than 45% SL (Bertelsen, 1984:327, figs. 167–170; Pietsch, 1984:324, fig. 164; Figs. 5, 6) (1) (1.00).

84. Larvae are short and deep, nearly spherical in most outgroups and most ceratioids (0), but elongate and slender in lophioids, most oneirodid genera (except *Lophodolos*), the Neoceratiidae, and the linophrynid genera *Haplophryne*, *Borophryne*, and *Linophryne* (larvae of *Photocorynus* and *Acentrophryne* are unknown; Bertelsen, 1984:327, figs. 167B–G, 170, table 89; Figs. 5I, J; 6A–C, E, H–J) (1); the larvae are distinctly “hump-backed” in the Ceratiidae (Bertelsen, 1984:327, fig. 168C–E, table 89; Fig. 5B, C) (2) (0.40, 0.73).

85. The skin of the larvae of most of the outgroups as well as those of the Himantolophidae, Thaumatchthyidae, Caulophrynidae, and Gigantactinidae is highly inflated (Bertelsen and Struhsaker, 1977:27, fig. 15; Bertelsen, 1984:327, figs. 167A, 168A, B, 169A, B, table 89; Fig. 5D, E, H; 6D, F, G) (0), but only moderately inflated in antennarioids and all other ceratioids (1) (0.17, 0.38).

86. Sexual dimorphism in the illicial apparatus is absent in all the outgroups and in the larvae of the ceratioid families Caulophrynidae and Neoceratiidae (Bertelsen, 1984:328, fig. 167A, B, table 89) (0), but present in all other ceratioids (1) (0.33, 0.60).

87. The pectoral fins of larvae are large (the rays extending well beyond the origin of the dorsal and anal fins) in most outgroup taxa and in the ceratioid families Caulophrynidae and Gigantactinidae (Bertelsen, 1984:327, figs. 167A, 168A, B, table 89; Fig. 6D, F, G) (0); they are relatively small in antennarioids and in all other ceratioids (1) (0.20, 0.33).

88. Pelvic-fin rays are present in the larvae of all the outgroups and in the ceratioid family Caulophrynidae (Bertelsen, 1984:327, fig. 167A, table 89; Fig. 6D) (0), but absent in those of all other ceratioids (1) (0.50, 0.75).

Tree based on characters applicable to metamorphosed females.—The phylogenetic analysis produced five equally parsimonious trees, with a total length of 153, a consistency index of 0.5560, and a retention index of 0.7952. Differences between the trees were restricted to a single family, the relatively poorly understood Oneirodidae, which contains 16 genera and 65 species, nearly 40% of all recognized ceratioids. The strict consensus tree is presented in Figure 17. Monophyly of the Ceratioidei was confirmed and all ceratioid

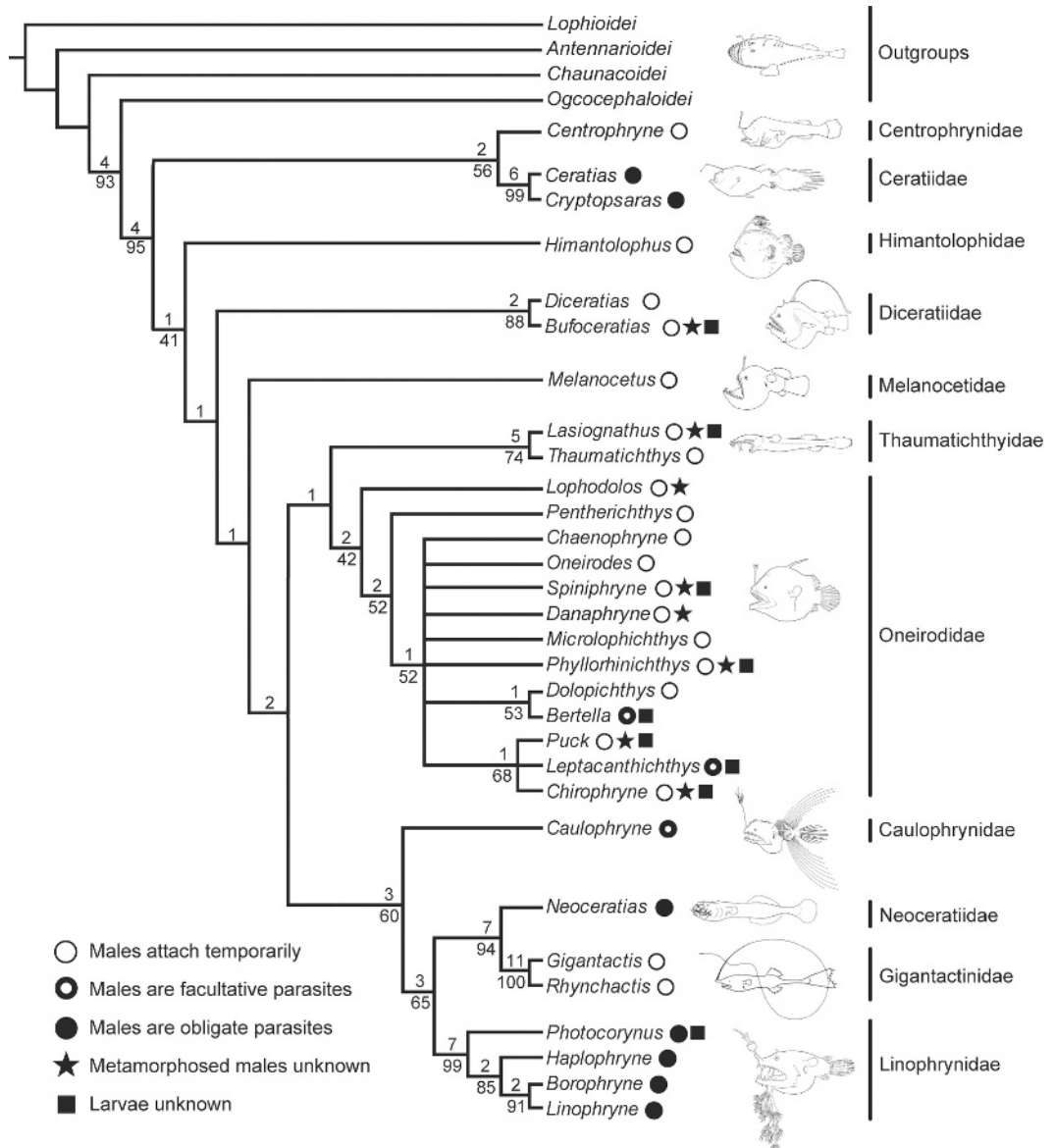


Fig. 17. Strict consensus of five trees from a parsimony analysis of 71 morphological characters applicable to metamorphosed females for the genera of the Ceratioidei and four lophiiform outgroups. The number above the base of a node is the Bremer value, and the number below the node indicates bootstrap support greater than 40% for the respective node. Reproductive modes are plotted and those genera for which metamorphosed males and/or larvae are unknown are indicated.

genera were placed in currently recognized monophyletic families (i.e., as presented by Bertelsen, 1984). Characters without homoplasy (unique and unreversed within ceratioids) that support monophyly of the Ceratioidei, however, are surprisingly few: palatines reduced and toothless (character 17, state 1), basihyal absent (38, 1), and pelvic fins absent in metamorphosed specimens (67, 1). A clade comprising the Centrophrynidae (containing only *Centrophryne*)

and Ceratiidae (with two genera, *Ceratias* and *Cryptopsaras*) is represented as the sister group of all other ceratioids. The sister-group relationship of the Centrophrynidae and Ceratiidae is supported by one non-homoplastic character: parietals enlarged (9, 2). Monophyly of the Ceratiidae is supported by a single non-homoplastic character: caruncles present (62, 1).

The Himantolophidae (containing only *Himantolophus*), Diceratiidae (*Diceratias* and *Bufoceratias*),

and Melanocetidae (*Melanocetus*) diverge next in sequential step-wise fashion, the latter family forming the sister group of all remaining ceratioids. No non-homoplastic character supports the relationships of each of these clades as basal to other ceratioids, and bootstrap and Bremer support is very low for each node. Members of the Diceratiidae share one non-homoplastic character: pterospheonid reduced (10, 1).

Two relatively large clades remain: one containing the Thaumatchthyidae (*Lasiognathus* and *Thaumatchthys*) and the Oneirodidae (only 13 of 16 genera available for analysis), and the other containing the Caulophrynidae (*Caulophryne*; a second genus, *Robia*, unavailable for analysis), Neoceratiidae (*Neoceratias*), Gigantactinidae (*Gigantactis* and *Rhynchactis*), and Linophrynidae (*Photocorynus*, *Haplophryne*, *Borophryne*, and *Linophryne*; a fifth genus, *Acentrophryne*, unavailable for analysis). Monophyly of the Thaumatchthyidae–Oneirodidae clade was poorly supported, having very low bootstrap support and a Bremer value of one. Monophyly of the Thaumatchthyidae (*Lasiognathus* and *Thaumatchthys*), however, is supported by four synapomorphies: preopercle straight (19, 1), upper arm of opercle with three or more radiating branches (21, 1), upper jaw extending anteriorly far beyond the lower jaw (25, 1), and esca with dermal denticles (58, 1). Monophyly of the Oneirodidae has low bootstrap and Bremer support, primarily because of homoplasy among character states of *Lophodolos*, the basal member of the family. All oneirodids share a narrow pterotic process that overlaps the respective sphenotic (13, 1), while all oneirodids except *Lophodolos* share one non-homoplastic character: parasphenoid with a pair of antero-dorsal extensions that approach or overlap the posterior ventromedial extensions of the respective frontal (11, 1). *Pentherichthys* diverges next, leaving the most derived clade among oneirodids as an unresolved polytomy comprising *Chaenophryne*, *Oneirodes*, *Spiniphryne*, *Danaphryne*, *Microlophichthys*, *Phyllorhynchichthys*, a monophyletic *Dolopichthys* plus *Bertella* (supported by the ontogenetic loss of vomerine teeth; 3, 1), and an unresolved monophyletic triplet containing *Puck*, *Leptacanthichthys*, and *Chirophryne* (which share an elongate pectoral-fin lobe; 63, 1). In all five of the most parsimonious trees, the clades *Dolopichthys* plus *Bertella* and *Puck*, *Leptacanthichthys*, and *Chirophryne*, as well as the genera *Danaphryne*, *Microlophichthys*, and *Phyllorhynchichthys* formed a single large polytomy because of the absence of, as opposed to conflict between, characters to support any other relationship. However, *Chaenophryne*, *Spiniphryne*, and *Oneirodes* were always basal relative to other derived

oneirodids, and *Chaenophryne* was basalmost in three of the five resolutions. In two of five resolutions, *Chaenophryne* formed a polytomy with *Spiniphryne* or a clade containing *Spiniphryne* plus *Oneirodes*.

Support for monophyly of the clade containing the Caulophrynidae, Neoceratiidae, Gigantactinidae, and Linophrynidae is moderate, having bootstrap support of 64% and a Bremer value of three. No non-homoplastic character supports monophyly of the Caulophrynidae, Neoceratiidae, Gigantactinidae, and Linophrynidae clade. The Caulophrynidae (*Caulophryne* and *Robia*) is the sister group of the remaining three families. The Neoceratiidae (*Neoceratias*) and Gigantactinidae (*Gigantactis* and *Rhynchactis*) are sister groups that together form the sister group of the Linophrynidae (only four of five genera available). The latter clade of three families is supported by three characters: endopterygoids absent (16, 1), dorsal and ventral ends of the third and fourth ceratobranchials tightly bound together by connective tissue (44, 1), and pelvic bones rudimentary or absent (66, 2). The clade comprising the Neoceratiidae and Gigantactinidae is strongly supported by four characters: interopercle extremely reduced (23, 1), dentary simple posteriorly (31, 1), outermost lower-jaw teeth large (33, 1), and the third pharyngobranchial enlarged and expanded distally (40, 1). Monophyly of the Gigantactinidae is the most strongly supported clade in this analysis, with bootstrap support at 100%, and seven synapomorphies: vomer absent (2, 1), supraoccipital anterior with dorsal surface in vertical plane (14, 1), preopercle reduced to a small strut (19, 3), interopercular-mandibular ligament absent (24, 1), caudal fin emarginate (51, 1), and pterygiophore of illicium exceptionally well developed (55, 1). Monophyly of the Linophrynidae is also well supported, with a bootstrap value of 99%. Among linophrynids, *Photocorynus* and *Haplophryne* diverge sequentially in step-wise fashion, the latter genus forming the sister group of *Borophryne* plus *Linophryne*, each clade with high bootstrap values and supported by non-homoplastic characters. Monophyly of the Linophrynidae is supported by five characters: pterotic with tapered pointed process (13, 2), preopercle with a large posteriorly directed spine (20, 1), and anteriormost branchiostegal ray lost (37, 1). Monophyly of *Haplophryne*, *Borophryne*, and *Linophryne* is supported by one synapomorphy: preopercle bowed and extending posteriorly (19, 2). *Borophryne* and *Linophryne* share three characters: a conspicuous, rounded, laterally compressed frontal protuberance (4, 1), and greatly enlarged jaw teeth (32, 1).

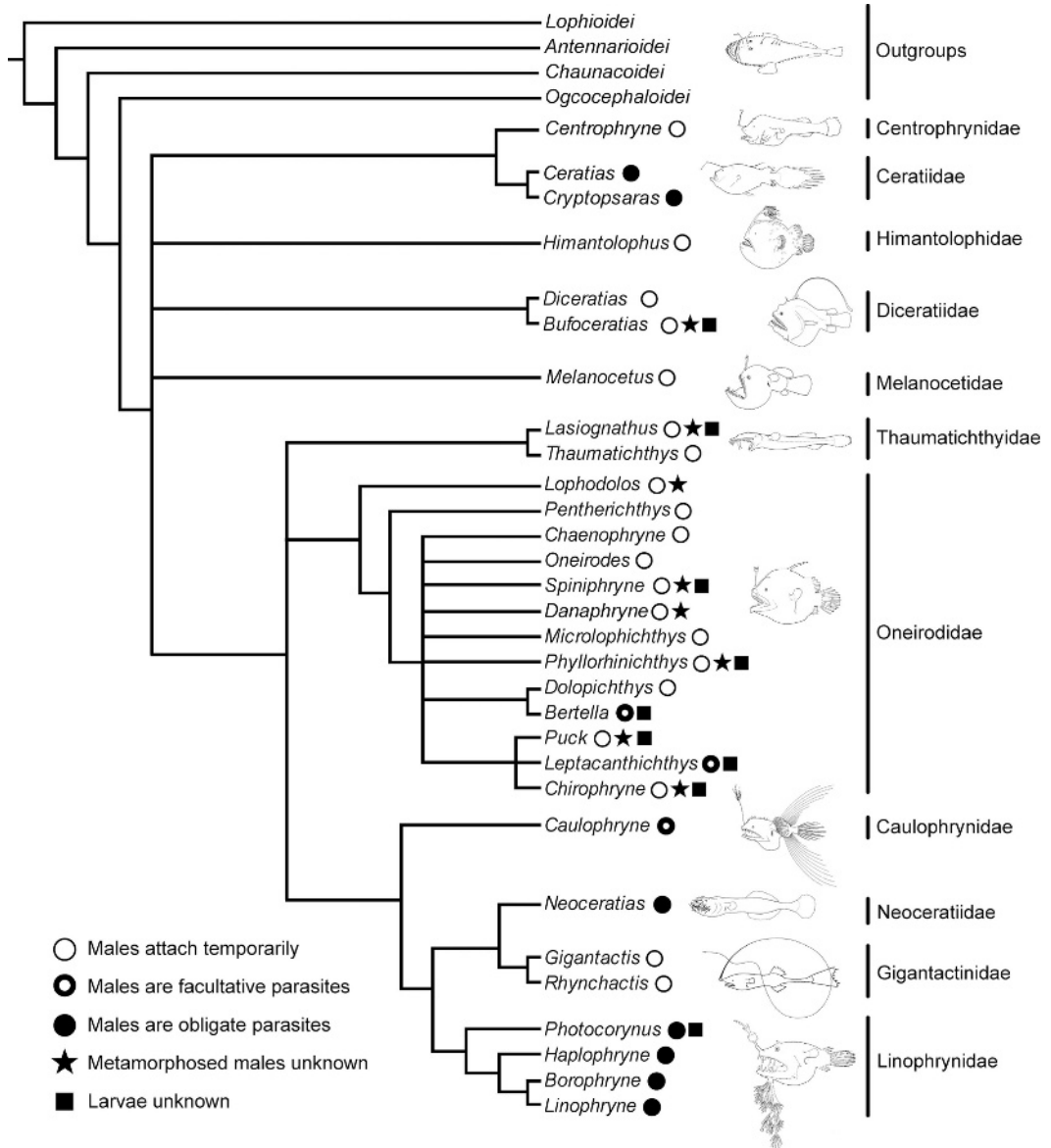


Fig. 18. Strict consensus of 292 trees from a parsimony analysis of 88 morphological characters, applicable to metamorphosed females, metamorphosed males, and larvae, for the genera of the Ceratioidei and four lophiiform outgroups. Reproductive modes are plotted and those genera for which metamorphosed males and/or larvae are unknown are indicated.

Tree based on characters of metamorphosed females, males, and larvae.—This analysis produced 352 equally parsimonious trees, with a total length of 202, a consistency index of 0.5680, and a retention index of 0.7723. The strict consensus tree is presented in Figure 18. Differences between the trees were found among the deeper nodes and among derived oneirodid genera. Lack of resolution was present at the basal position of the tree where the Himantolophidae, Diceratiidae,

and Melanocetidae, and a monophyletic Centrophrynidae and Ceratiidae formed a polytomy, as well as in the position of the Thaumatichthyidae in a polytomy with the Oneirodidae and the Caulophrynidae through Linophrynidae. The polytomies are the result of the lack of data rather than conflict among characters. Metamorphosed male and larval characters offered some support for monophyly of the Ceratioidei as a whole, as well as monophyly of some

terminal taxa. Two characters of males supported monophyly of the Ceratioidae: an extreme sexual dimorphism in which males are dwarfed relative to females (character 72, 1), and denticular bones present (character 79, 1). Characters of males and larvae supported monophyly of the Ceratiidae: eyes of males huge (73, 1), eyes of males bowl-shaped (74, 1), and larvae "hump-backed" (84, 1). Monophyly of the Gigantactinidae was supported by one additional male character: olfactory organs huge (75, 2). One character provided additional evidence for monophyly of the Linophryinidae, eyes of males tubular (74, 2), while within the Linophryinidae, *Borophryne* and *Linophryne* shared one male character: premaxillae greatly reduced or absent (77, 1).

DISCUSSION

Comparisons with previous hypotheses.—In some ways the relationships proposed here corroborate the findings of earlier studies of ceratioid evolution, but in more ways they are vastly different. Some of the similarities and more significant differences are summarized below, along with additional pertinent comments.

Centrophrynidae and Ceratiidae (Figs. 2A, B, 4A–C, 5A–C): Despite Bertelsen's (1951:28) conclusion that the Centrophrynidae "shows no obviously close relationship to any other family," Pietsch (1972:43, fig. 25) argued in support of a lineage containing the Centrophrynidae and Ceratiidae, listing 11 shared character states, most of which are incorporated here in this study. A sister-group relationship between these two families, however, was later challenged by both Pietsch (1979:23, figs. 25, 26) and Bertelsen (1984:333, fig. 171). A basal position among ceratioid families for either of these two families, as proposed here, has never been suggested before. Both taxa are deeply nested within the suborder in all earlier phylogenetic hypotheses.

Himantolophidae, Diceratiidae, Melanocetidae, Thaumatchthyidae, and Oneirodidae (Figs. 2C–J, 3A, B, 4D–J, 5D–J, 6A–C): The sequential step-wise divergence of these five families is not too surprising given that a similar arrangement has been proposed in nearly all previously published discussions of ceratioid relationships. In contrast to the present findings, however, all earlier proposals suggest that the Melanocetidae diverged first, followed in order by the Diceratiidae, Himantolophidae, and Oneirodidae (including the Thaumatchthyidae), according to Regan and Trewavas (1932); and the Himantolophidae, Diceratiidae, and Oneirodidae (including the Thaumatchthyi-

dae), according to Bertelsen (1951, 1984) and Pietsch (1979). A monophyletic Himantolophidae, Melanocetidae, and Diceratiidae is supported by one character, ventromedial extensions of the frontal that make no contact with the parasphenoid (8, 1). No other non-homoplastic character supports any other alternative resolution.

Thaumatchthyidae (Figs. 2H, I, 4G, 5H): Regan (1925b, 1926), followed by Regan and Trewavas (1932), Bertelsen (1951), and Maul (1961, 1962), chose not to recognize Smith and Radcliffe's (1912) Thaumatchthyidae, placing the two relevant genera *Thaumatchthys* and *Lasiognathus* in the family Oneirodidae. Pietsch (1972:18) resurrected the Thaumatchthyidae to include both genera, stating that these two taxa "possess several important and unique characters that justify familial status." Bertelsen and Struhsaker (1977), however, compared the osteology of *Thaumatchthys* and *Lasiognathus*, pointing out that the latter appears more closely related to the Oneirodidae in several of the characters in which it differs most from *Thaumatchthys*. They (1977:34) concluded that "it becomes a subjective choice whether the genera *Lasiognathus* and *Thaumatchthys* both should be included in the Oneirodidae as Regan (1926) did, or placed together in Thaumatchthyidae as proposed by Pietsch (1972), or whether each of them should be referred to a family of its own." At the same time, however, they cited the two unique features used by Pietsch (1972) to diagnose the Thaumatchthyidae (premaxillae extending anteriorly far beyond lower jaw, and enlarged dermal denticles associated with the esca) and added a third (dorsal portion of opercle divided into two or more branches). In the end, they chose to retain the Thaumatchthyidae in the enlarged sense as proposed by Pietsch (1972) and supported in the present analysis. It should be noted, however, that preliminary results of a molecular analysis of ceratioid evolution place *Lasiognathus* deep within the Oneirodidae, leaving *Thaumatchthys* as the only known genus of the Thaumatchthyidae (Masaki Miya, pers. comm., 20 December 2005; see below).

No character in this analysis unequivocally supports a sister-group relationship of a Thaumatchthyidae composed of *Lasiognathus* and *Thaumatchthys* and the Oneirodidae. However, two characters show convergence between *Lasiognathus* (to the exclusion of *Thaumatchthys*) and most members of the Oneirodidae, and two other characters are convergent also with the Linophryinidae and Ceratiidae or both. Three of these characters are associated with the frontal

bones: frontals with anterior bifurcation (6, 1; convergent also with the Ceratiidae and Linophryniidae), frontal overlapping the full length of the lateral ethmoid (7, 1; convergent also with the Linophryniidae), and ventromedial extension of the frontals bifurcate (8, 1); the fourth is the conspicuous, laterally directed quadrate spine (18, 1) found in *Lasiognathus* and most oneirodids. In contrast, four characters that are lost in the Caulophryniidae and Linophryniidae also support a close relationship of the Thaumatchthyidae with the Neoceratiidae and Gigantactinidae: articular and angular extending posteriorly (34, 1), vertebral centra elongate (48, 1), and caudal peduncle elongate (49, 1). In addition, one character, nasal papillae elongate (69, 1), is reversed in *Lasiognathus* as well as in the Caulophryniidae and Linophryniidae. Given the strength of the evidence for monophyly of the Thaumatchthyidae and absence of non-homoplastic characters that unite *Lasiognathus* and the Oneirodidae to the exclusion of *Thaumatchthys*, the relationships described here are those best supported by the data.

Oneirodidae (Figs. 2J, 3A, B, 4H–J, 5I, J, 6A–C): With 16 genera and 63 species, nearly 40% of all recognized ceratioids, the Oneirodidae is by far the largest, most complex, and certainly the least understood family of the suborder. Of the 16 genera, five are currently represented by only one, two, or three juvenile or adult females; only eight are represented by more than a dozen females. Males have been described for only seven genera, while larvae are known for only eight. Despite the rareness of most recognized taxa, however, new oneirodids are being discovered on a regular basis. The results of the present study provide the first evidence of monophyly for the family, although its more derived members remain in a large unresolved polytomy. In many ways, the relationships proposed here are remarkably similar to those suggested in a phenetic analysis of oneirodid genera published by Pietsch (1974:86, fig. 103), but bear almost no resemblance to a cladistic attempt described in that same study (1974:87, fig. 104).

Caulophryniidae (Figs. 3C, 4K, 6D): Although the relationship is not supported by any non-homoplastic characters, another surprising result of this study is the derived position of the Caulophryniidae. Bertelsen (1951, 1984) was convinced that this family is isolated from all other ceratioids, based primarily on three larval characters: (1) the presence of pelvic fins (lost in caulophryniids during metamorphosis; well developed in larvae and adults of all the outgroups, but absent in all other ceratioids); (2) the apparent absence of sexual dimorphism in

rudiments of the illicium (all 16 known larval caulophryniids bear the beginnings of an illicial apparatus, a peculiarity also apparently found in neoceratiids; Bertelsen, 1984:328); and (3) the absence of a distal swelling of the illicial rudiments that would indicate the early development of a bioluminescent esca (the esca of adult caulophryniids is not a bulbous, bacteria-filled light organ as in other ceratioids, but a tuft of filaments like those found in the outgroups; Pietsch, 1979:12, figs. 15, 17, 19, 21). With respect to the ontogenetic implications of the latter two character states, Bertelsen (1984) held that the absence of an escal light organ in all life-history stages of caulophryniids is not due to secondary loss or reduction. All remaining ceratioids, being derived in these characters, thus cluster to the exclusion of the Caulophryniidae leaving it in the most basal position in the suborder. The only prior suggestion that caulophryniids may be derived (aside from an unexplained juxtaposition of caulophryniids and linophryniids by Greenwood et al., 1966:397) was made by Pietsch (1979:22, fig. 25) who proposed an alignment with the Neoceratiidae and Gigantactinidae (see below). The results of this work indicate that the absence of these characters in the Caulophryniidae reflects a secondary loss.

Neoceratiidae, Gigantactinidae, and Linophryniidae (Figs. 3D–I, 4L–P, 6E–J): In proposing the family Neoceratiidae to contain Pappenheim's (1914) *Neoceratias spinifer*, Regan (1926:39) wrote that it "may be related to the Gigantactinidae, because *Gigantactis* differs from other ceratioids in having the outer teeth larger than the inner, and moreover placed on the outer side of the jaws and inserted in muscular pads, a type of dentition from which that of *Neoceratias* might readily have been derived." Agreeing with this notion, Regan and Trewavas (1932:95), emphasizing the importance of the lack of an illicium, went a step further in considering that it might be "a male of some unknown gigantactinid." While quickly dismissing the latter proposal, Bertelsen (1951:28) concluded that the Neoceratiidae and Gigantactinidae "seem related and show a few approaches . . . to the linophryniids . . ." That these three families form a clade was subsequently supported by Pietsch (1972:44, fig. 25; 1979:23, fig. 26), but Bertelsen (1984:334, fig. 171), impressed with the apparent lack of sexual dimorphism in the illicium of neoceratiid larvae (a feature shared with caulophryniids; see above), tentatively proposed an unresolved trichotomy in which the Caulophryniidae and Neoceratiidae are basal to all remaining ceratioids.

The results described here include the first explicit demonstration of monophyly for the

Linophrynidae as currently recognized (Bertelsen, 1951, 1984). Since Regan (1926) laid the foundation for the present classification of ceratioids, *Haplophryne*, *Borophryne*, and *Linophryne* have all been readily accepted as linophrynids, but the inclusion of *Photocorynus* has been more recent. When Regan (1925a, 1926:16) first described *Photocorynus*, he saw no affinity with linophrynids, placing the genus in a family of its own, the Photocorynidae, and describing its cranium as "less specialized than that of any other ceratioid, and more nearly approaching that of *Lophius* in essentials." While citing a number of features that seem to unite *Photocorynus* with the linophrynids, and which distinguish them from all other ceratioids, Regan and Trewavas (1932) continued to recognize the Photocorynidae. It was not until Bertelsen's (1951) in-depth comparative study of the Ceratioidei that a close relationship between *Photocorynus* and linophrynids was established. While no longer recognizing the Photocorynidae, Bertelsen placed *Photocorynus* basal to the other linophrynid genera, thus predicting the results described here. In further corroboration of the present findings, Bertelsen entered *Haplophryne* next in the sequence, thus implying a closer relationship between the terminal genera *Borophryne* and *Linophryne*.

Characters restricted to metamorphosed males.—As mentioned above, sexual dimorphism is so strongly developed in ceratioids that separate taxonomic treatment of females and males is required (Fig. 4). While some distinguishing meristic and osteological characters are shared with the males, such as fin-ray counts, families and genera are defined primarily on the basis of characters present only in females. Those few structures unique to the males, such as denticular teeth and nostril morphology, show distinct intergeneric differences (in full agreement with separations based on characters of the females), but most features, like those of the females, are autapomorphic and thus provide no evidence for reconstructing evolutionary history. In addition, ceratioid males are generally rare in collections, poorly described anatomically, and unknown for 13 of the 35 recognized genera (Figs. 17, 18). A thorough review of what is known about males produced only ten characters that seemed useful to this study (most identified by Bertelsen, 1984:326, table 89). The addition of these features to the analysis provided support primarily for the monophyly of ceratioid families, including the Gigantactinidae, Ceratiidae, and Linophrynidae. While support for monophyly of the Ceratioidei as a whole is also provided, none

of these characters is useful in resolving other deep nodes.

Characters restricted to larvae.—Larvae as well as relatively poorly known anatomically and available for only 24 of the 35 recognized ceratioid genera (Figs. 5, 6). Like metamorphosed males, they present few characters that can be used in phylogenetic studies (only seven; Pietsch, 1984). While providing additional support for monophyly of the Ceratioidei as a whole, larval characters offer no support for relationships within the suborder and the absence of data for some taxa leads to a lack of resolution in basal clades.

Conflicting molecular evidence.—The results of a molecular study, still in its preliminary stages (Miya et al., unpubl. data), based on a partitioned Bayesian analysis of whole mitochondrial genome sequences of 47 lophiiform species, including representatives of all 11 ceratioid families, show very little resemblance to the hypothesis presented here. While characters for ceratioids are here polarized by outgroup comparison with non-ceratioid lophiiforms, and those in turn by batrachoidiform fishes (Pietsch, 1981), the molecular results indicate that lophiiforms are deeply nested within the Perciformes, showing a close alignment with tetraodontiforms (Miya et al., 2003, 2005; Holcroft, 2004, 2005; Simmons and Miya, 2004). While linophrynids hold a terminal position in the present proposal, the unpublished molecular findings show them basal to all other ceratioids. In further contrast to the hypothesis presented here, caulophrynids plus ceratiids diverge next, followed in step-wise fashion by gigantactinids, neoceratiids plus thaumatchthyids, centrophrynids, and oneirodids, the latter forming the sister-group of a monophyletic assemblage that includes himantolophids, diceratiids, and melanocetids. Among these proposed relationships, only the clade containing the himantolophids, diceratiids, and melanocetids can be supported by aspects of our morphological data (i.e., the condition of the ventromedial extensions of the frontals, character 8). Clearly, considerably more work will be required to reconcile these two competing hypotheses.

Sexual parasitism.—Bertelsen (1951:28) was the first to reject the idea that those ceratioids in which males become permanently and parasitically attached to females form a natural assemblage, and every study since then has corroborated this assumption (Pietsch 1976, 2005; Bertelsen, 1984; Shedlock et al., 2004). As

currently understood, reproductive modes in lophiiform fishes exist in four states: (1) males never attach themselves to females; (2) males attach temporarily to females but never become parasitic; (3) parasitism is facultative in some taxa; and (4) parasitism is obligate in other taxa (Pietsch, 1976, 2005). Obviously, the latter three states are derived relative to the first, but the results of this study provide no basis for further character-state transformation. While Character state 1 describes the outgroup taxa identified in this study, all ingroup taxa (i.e., ceratioids) are characterized by males that become attached to females (Pietsch, 2005): those of the Centrophrynidae, Himantolophidae, Diceratiidae, Melanocetidae, Thaumatchthyidae, Gigantactinidae, and all the better known oneirodid genera except *Bertella* and *Leptacanthichthys* apparently attach themselves temporarily (Character state 2); those of the Caulophrynidae and oneirodid genera *Bertella* and *Leptacanthichthys* are facultative parasites (state 3); and those of the Ceratiidae, Neoceratiidae, and Linophrynidae are obligate sexual parasites (state 4). When mapped on the strict consensus trees proposed here (Figs. 17, 18), these character states appear more or less scattered throughout the branches. In the most basal ceratioid clade proposed here, attached males have never been found in the Centrophrynidae (despite more than 40 known females, 18–247 mm SL), yet numerous examples of parasitized females are known for both genera of its sister-family, the Ceratiidae (Pietsch, 2005:223, table 1). On the other hand, the himantolophid-diceratiid-melanocetid lineages, all thought to reproduce by way of temporary non-parasitic attachment, are deeply nested within the suborder, while the thaumatchthyid-oneirodid clade contains primarily non-parasitic forms, but also at least two genera that employ facultative parasitism. Finally, the terminal assemblage containing the Caulophrynidae through Linophrynidae displays a mosaic of all three derived reproductive modes. Whether temporary attachment and facultative parasitism are precursors to obligate parasitism, or the former are more derived states of the latter, is thus still unknown.

The disjunct pattern of occurrence of sexual parasitism within ceratioids appears to be the result of independent acquisition among the various lineages rather than a repeated loss of this attribute within the suborder. Evidence to support this notion comes from the many differences in the precise nature of male–female attachment among the various taxa (Pietsch, 2005): nearly always single males attached invariably on the belly in *Ceratiidae*, but multiple

males (as many as eight) found almost anywhere on the body in *Cryptopsaras*; males fused to the tip of a cylindrical stalk of female tissue in the oneirodid genera *Bertella* and *Leptacanthichthys*; attached to the apex of an unpigmented conical growth from the female in *Caulophryne*; broadly attached males, with fully occluded mouths in *Neoceratiidae*; multiple males common in *Haplophryne*, attached anywhere on the head and body, and always involving a papilla of female tissue that fills the mouth of the male; and, finally, single males are always the rule in *Linophryne*, almost always attached upside down at nearly the same spot on the ventral mid-line of the female. Having been established independently at least three and possibly as many as seven times within the suborder, it seems evident that sexual parasitism in ceratioid anglerfishes, with all its extreme complexity of morphological, physiological, and behavioral adaptations, is a considerably less drastic evolutionary event than might be supposed. When viewed in this light, it is perhaps surprising that this remarkably successful reproductive strategy has not evolved in other vertebrate taxa that have come to occupy the deep-sea.

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APPENDIX 1. CHARACTER STATES FOR EACH TAXON. Character matrix of 88 characters for the genera of the Ceratioidei and outgroup lophiiforms. Character numbers correspond to those given in the text.

Taxon	Character																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Lophioidei	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antennarioidei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0/1	0	0	0	0	0	0	0	0	0
Chaunacoidei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ogcocephaloidei	0	0	0/2	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0
Centrophryne	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ceratias	0	0	0/1	0	0	1	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Cryptoparas	0	0	0	0	1	0	0	2	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Himantolophus	0	0	2	0	1	0	0	1	1	0	0	1	0	2	0	0	1	0	0	0	0	0	1	0	0	0
Melanocetus	0	0	0	0	1	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0
Diceratias	0	0	0	0	1	0	0	1	0	1	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0
Bufoeratias	0	0	0	0	1	0	0	1	0	1	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0
Lophodolos	0	0	2	0	1	1	1	0	0	2	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0
Penherichthys	0	0	0	0	1	1	1	2	0	0	1	1	0	2	0	0	1	0	0	0	0	1	0	0	0	0
Chaenophryne	0	0	0	0	1	1	1	2	0	0	1	0	1	2	0	0	1	0	0	0	0	1	0	0	0	0
Onerodes	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	1	0	0	0	1	0	0	0	0
Spiniphryne	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	0	0	0	0	1	0	0	0	0
Danaphryne	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	0	0	0	0	1	0	0	0	0
Microlophichthys	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	1	0	0	0	1	0	0	0	0
Phyllorhynchichthys	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	1	0	0	0	1	0	0	0	0
Dolopichthys	0	0	1	0	1	1	1	2	0	0	1	1	1	2	0	0	1	1	0	0	0	1	0	0	0	0
Bertella	0	0	1	0	1	1	1	2	0	0	1	1	1	2	1	0	1	1	0	0	0	1	0	0	0	0
Puck	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	1	0	0	0	1	0	0	0	0
Leptacanthichthys	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	1	0	0	0	1	0	0	0	0
Chirophryne	0	0	0	0	1	1	1	2	0	0	1	1	1	2	0	0	1	1	0	0	0	1	0	0	0	0
Lasiognathus	1	0	2	0	1	1	1	2	0	0	1	1	0	0	0	0	1	1	1	0	1	1	0	0	1	1
Thaumatichthys	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1
Gaulophryne	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Neoceratias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0
Gigantactis	1	1	?	0	1	0	0	0	0	2	0	0	0	1	1	1	1	0	3	0	0	1	1	1	1	0
Rhynchactis	1	1	?	0	1	0	0	0	1	2	0	0	0	1	1	1	1	0	3	0	0	1	1	1	1	0
Photocorynus	0	0	2	2	0	1	1	0	0	2	0	1	2	0	1	1	1	0	0	1	0	1	0	0	0	0
Haplophryne	0	0	2	2	1	1	1	0	0	2	0	1	2	0	1	1	1	0	2	1	0	1	0	0	0	0
Borophryne	0	0	0	1	1	1	1	0	0	2	0	1	2	0	1	1	1	0	2	1	0	1	0	0	0	0
Linophryne	0	0	0	1	1	1	1	0	0	2	0	1	2	0	1	1	1	0	2	1	0	1	0	0	0	0

APPENDIX 1. CONTINUED.

Taxon	Character																									
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	
Lophioidei	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	
Antennarioidei	0	1	0	0	0	0	0	0	0	0	0	0	0/1	0	0	1	0	0	0	0	0	0/1	0	0	0	
Chaunacoidei	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	
Ogcocephaloidei	0	1	0	0	0	0	0	0	0	0	1	0	0/1	0/1	0	1	0	1	0	0	0	0	1	0	0	
Centrophryne	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	0	1	
Centrias	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	1	
Cryptosaras	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	1	
Himantolophus	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	0	1	0	0	1	
Melanocetus	0	1	1	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Diceratias	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	0	0	1	
Bufoeratias	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	0	0	1	
Lophodolos	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Pentherichthys	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Chaenophryne	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Onerades	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	0	0	1	
Spiriphryne	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	0	0	1	
Danaphryne	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Microlophichthys	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Phyllorhynchichthys	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Dolopichthys	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Bertella	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Puck	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Leptacanthichthys	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Chirophryne	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	
Lasiognathus	0	1	1	0	1	0	0	0	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	
Thaumatichthys	1	1	1	0	1	0	0	0	1	0	1	0	1	1	0	1	1	?	0	0	1	1	1	1	1	
Caulophryne	0	1	1	1	1	0	0	0	0	0	1	0/1	1	1	0	1	0	1	0	1	1	1	0	0	0	
Neoceratias	0	1	1	1	1	0	1	1	1	0	0/1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	
Gigantactis	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	
Rhynchactis	1	1	1	2	1	1	0	?	1	0	1	0	1	1	1	1	1	?	1	1	1	1	1	1	1	
Photocoelus	0	1	1	1	1	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	0	0	1	
Haplophryne	1	1	1	2	1	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	0	0	1
Borophryne	1	1	1	2	1	0	1	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	0	0	1
Linophryne	1	1	1	2	1	0	1	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	0	0	1

APPENDIX 1. CONTINUED.

Taxon	Character																									
	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	
Lophioidei	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	
Antennarioidei	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	1	0	0	0	0	0	
Chaunacoidei	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Ogcocephaloidei	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	
Centrophryne	0	0	1	1	0	1	1	0	0	1	0	0	1	0	1	1	1	0	0	1	0	1	2	0	1	
Ceratias	0	1	1	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	1	3	
Cryptosaras	0	2	1	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	1	3	
Himantolophus	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	1	
Melanocetus	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1	0	1	0	0	1	
Diceratias	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	
Bufoeratias	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	1	1	0	0	1	0	?	?	?	?	
Lophodolos	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	?	?	?	?	
Pentherichthys	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Chaenophryne	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Oneirodes	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Spiniphryne	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Danaphryne	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Microlophichthys	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Phyllorhynchichthys	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	?	?	?	
Dolopichthys	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Bertella	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Puck	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	?	?	?	
Leptacanthichthys	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Chirophryne	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	?	?	?	
Lasiognathus	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	?	?	?	
Thaumatichthys	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	
Caulophryne	0	2	1	1	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	1	0	1	0	1	
Nooceratias	0	0	1	1	0	?	?	?	0	1	0	0	1	0	0	2	1	1	1	1	1	0	1	2	0	3
Gigantactis	1	1	2	1	1	1	1	0	0	1	0	0	1	0	2	2	1	0	1	1	0	1	2	0	2	
Rhynchactis	1	1	1	1	1	0	0	0	0	1	0	0	1	0	2	2	1	0	1	1	0	1	2	0	2	
Photocorynus	0	1	1	1	0	1	1	0	0	1	0	0	1	0	0	2	1	1	1	0	1	1	0	2	1	
Hapliphryne	0	1	1	1	0	1	1	0	0	1	0	0	1	0	0	2	1	1	1	0	1	1	0	2	1	
Borophryne	0	1	1	1	0	1	1	0	0	1	0	0	1	0	0	2	1	1	1	0	1	1	0	2	1	
Linophryne	0	1	1	1	0	1	1	0	0	1	0	0	1	0	0	2	1	1	1	0	1	1	0	2	1	

APPENDIX 1. CONTINUED.

Taxon	Character												
	76	77	78	79	80	81	82	83	84	85	86	87	88
Lophioidei	0	0	0	0	0	0	0	0	1	0	0	0	0
Antennarioidei	0	0	0	0	0	0	1	1	0	1	0	1	0
Chaunacoidei	0	0	0	0	0	0	1	1	0	0	0	0	0
Ogcocephaloidei	0	0	0	0	0	0	1	1	0	0	0	0	0
Centrophryne	1	0	1	1	0	0	1	1	0	0	1	1	1
Ceratias	0	0	1	1	0	1	1	1	2	1	1	1	1
Cryptosaras	0	0	1	1	0	1	1	1	2	1	1	1	1
Himantolophus	0	0	1	1	1	1	1	1	0	0	1	1	1
Melanocetus	0	0	1	1	1	1	1	1	0	1	1	1	1
Diceratias	0	0	1	1	0	0	1	1	0	1	1	1	1
Bufoeratias	?	?	?	?	?	?	?	?	?	?	?	?	?
Lophodolos	?	?	?	?	?	?	?	?	?	?	?	?	?
Pentherichthys	1	0	1	1	0	0	1	1	1	1	1	1	1
Chaenophryne	1	0	1	1	0	0	1	1	1	1	1	1	1
Oncirodes	1	0	1	1	0	0	1	1	1	1	1	1	1
Spiniphryne	?	?	?	?	?	?	?	?	?	?	?	?	?
Danaphryne	?	?	?	?	?	?	?	?	?	?	?	?	?
Microlophichthys	1	0	1	1	1	0	1	1	1	1	1	1	1
Phyllorhynchichthys	?	?	?	?	?	?	?	?	?	?	?	?	?
Dolopichthys	1	0	1	1	0	0	1	1	1	1	1	1	1
Bertella	1	0	1	1	0	0	?	?	?	?	?	?	?
Puck	?	?	?	?	?	?	?	?	?	?	?	?	?
Leptacanthichthys	1	0	1	1	0	0	?	?	?	?	?	?	?
Chirophryne	?	?	?	?	?	?	?	?	?	?	?	?	?
Lasiognathus	?	?	?	?	?	?	?	?	?	?	?	?	?
Thaumatichthys	1	0	1	1	0	0	1	1	0	0	1	1	1
Caulophryne	1	0	1	1	0	0	1	1	0	0	0	0	0
Neoceratias	0	0	1	1	0	0	1	1	1	1	0	1	1
Gigantactis	1	0	1	1	0	0	1	1	0	0	1	0	1
Rhynchactis	1	0	1	1	0	0	1	1	0	0	1	0	1
Photocorynus	1	0	0	1	0	0	?	?	?	?	?	?	?
Haplopleryne	1	0	0	1	0	0	1	1	1	1	1	1	1
Borophryne	1	1	1	1	0	0	1	1	1	1	1	1	1
Linophryne	1	1	1	1	0	0	1	1	1	1	1	1	1