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†*Caruso*, a new genus of anglerfishes from the Eocene of Monte Bolca, Italy, with a comparative osteology and phylogeny of the family Lophiidae (Teleostei: Lophiiformes)

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Abstract

†*Caruso*, a new genus of lophiid anglerfishes, erected to contain †*Lophius brachysomus* Agassiz from the Eocene of Monte Bolca, Italy, is described and compared osteologically with all known representatives of the family, both extinct and extant. Together with †*Sharfia*, known from a single specimen also from Monte Bolca, †*Caruso* is the oldest member of the teleost family Lophiidae known to date, based on articulated skeletal remains. It possesses several autapomorphic features as well as a unique combination of character states that clearly separate it from all other known lophiiform fishes. Evidence is provided to show that †*Sharfia* is sister group of all other known lophiid taxa, that †*Caruso* is most closely related phylogenetically to the extant genus *Sladenia*, and that these two genera together form the

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sister group of all remaining members of the family. †*Caruso brachysomus* is the third valid extinct taxon of the Lophiidae known from articulated skeletal remains. Candidate developmental mechanisms that may have contributed to the origin of the lophiiform body plan are also suggested. The hypertrophic development of the jaws, suspensorium, hyoid apparatus and branchial arches typical of lophiiforms may be correlated, possibly under the influence of discrete sets of genes. The synapomorphic elongation of the pectoral-fin radials might be related to a heterochronic shift of the onset of the expression of the gene *sonic hedgehog*. Finally, the highly modified spinous dorsal fin may have arisen by submodularization and co-option of the first dorsal-fin module, whereas its forward shift over the neurocranium may represent an anterior shift of the stripes of competency for dorsal-fin formation along the dorsal midline.

Keywords: Teleostei; Lophiiformes; Lophiidae; comparative osteology; phylogenetic analysis; Eocene; Monte Bolca

Introduction

Anglerfishes of the family Lophiidae are the sole members of the Lophioidei, one of the five suborders of the order Lophiiformes (see Pietsch & Grobecker 1987; Pietsch & Orr 2007), a morphologically derived group of marine teleost fishes that includes some of the most bizarre and anatomically peculiar representatives of the animal kingdom. The Lophiidae consists of four extant genera with fewer than 30 described species (e.g., Regan 1903; Caruso & Bullis 1976; Caruso 1981; 1983) that inhabit tropical, subtropical and temperate waters of the Atlantic, Indian and Pacific oceans. These fishes, also known as monkfishes or goosefishes, are benthic on different substrates at depths ranging from the shoreline to greater than 1500 meters. They are characterized by having a dorsoventrally compressed head, a wide cavernous mouth and a luring apparatus, the latter primarily consisting of a highly modified anterior spine of the dorsal fin, commonly called the illicium. The angling behavior of lophiids was reported for the first time by Aristotle in his *Historia animalium* and subsequently by many naturalists in the eighteenth and nineteenth centuries (e.g., Parsons 1750; Hanow 1768; Montin 1779; Geoffroy St. Hilaire 1807; 1824; 1827; Bailly 1824). Lophiid anglerfishes are opportunistic feeders with a common feeding strategy; they are lie-and-wait predators settling on soft-bottom substrates and luring their prey by wriggling the illicium (e.g., Wilson 1937; Gudger 1945). Some species of this family, mostly belonging to the genus *Lophius*, support important commercial fisheries, and for this reason several aspects of their life history and reproductive biology are extremely well documented (see, e.g., Fariña *et al.* 2008). However, despite the economic relevance and abundance of these fishes, their osteological structure remains poorly known and almost totally restricted to species of the genus *Lophius* (Brühl 1856; Morrow 1882; Supino 1908; Regan 1912; Gregory 1933; Montcharmont 1950; Eaton *et al.* 1954; Monod 1960; Field 1966; Oliva *et al.* 1968; Le Danois 1974).

The family Lophiidae is scarcely represented in the fossil record, mostly by disarticulated fragmentary bones (Lawley 1876; De Stefano 1910; Leriche 1910; 1926; Ray *et al.* 1968; Landini 1977; Purdy *et al.* 2001; Schultz 2006), otoliths (see, e.g., Nolf 1985) and teeth (Leriche 1906; 1908; Hasegawa *et al.* 1988). Articulated skeletal remains are extremely rare. Eocene material is restricted to a few specimens from the localities of Monte Bolca, Italy (e.g., Agassiz 1833-1844; Zigno 1874) and Gornyi Luch, North Caucasus, Russia (Bannikov 2004); whereas Neogene fossils are known from Algeria (Arambourg 1927), Azerbaijan (Sychevskaya & Prokofiev 2010), and Italy (Sorbini 1988).

In this study we describe a new genus of the Lophiidae, including its anatomy, based on material from the Eocene of Monte Bolca, previously referred to the genus *Lophius* (Volta 1796; Agassiz 1833-1844; see synonymy below). Previous to this study, the family Lophiidae had never been carefully investigated osteologically and phylogenetically. We therefore set out to examine the comparative osteology of the Lophiidae phylogenetically. This work is another in a series of papers focused on the fossil record of lophiiform fishes (Carnevale & Pietsch 2006; 2009a; 2009b; 2010; in press; Carnevale *et al*. 2008; Pietsch & Carnevale, in press).

Materials and methods

Specimens were examined under binocular microscopes equipped with camera lucida drawing arms. Standard length (SL) is used throughout. Methods for taking counts and measurements mostly follow Caruso (1981), whereas osteological terminology follows Montcharmont (1950) and Pietsch (1981). Extant comparative material was cleared and double stained with alizarin red S and alcian blue following the trypsin digestion technique of Potthoff (1984). Fossil specimens were mechanically prepared whenever possible using mounting entomological needles. All extinct taxa are marked with daggers (†) preceding their names. The methodologies employed in the phylogenetic analysis are presented below.

Material examined is housed in the following institutions: Borysiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN); Burke Museum of Natural History and Culture, University of Washington, Seattle (UW); Commonwealth Scientific and Industrial Research Organization, Hobart, Tasmania (CSIRO); Museo Civico di Storia Naturale, Verona (MCSNV); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); National

Museum of Victoria, Melbourne (NMV); Natural History Museum, London (NHM); Queensland Museum, Brisbane (QM); Tulane University, New Orleans (TU).

Comparative lophiiform material is listed below, all but fossils were cleared and double stained:

Antennariidae: *Antennarius striatus*, UW 20768, 57 mm SL.

Brachionichthyidae: *Brachionichthys australis*, UW 116842, 38.7 mm SL; UW 116843, 55 mm SL; *Brachionichthys hirsutus*, NMV A.19954, 80 mm SL; †*Histionotophorus bassani*, MCSNV I.G.23163, 50.5 mm SL; NHM 19060, 16.4 mm SL; †*Orrichthys longimanus*, MCSNV T.160/161, 63 mm SL; *Sympterichthys unipennis*, UW 116844, 31.6 mm SL; UW 116845, 34 mm SL.

Chaunacidae: *Chaunax pictus*, UW 20770, 90 mm SL.

Lophichthyidae: *Lophichthys boschmai*, UW 20773, 47 mm SL.

Lophiidae: †*Eosladenia caucasica*, PIN 4425-72, 83 mm SL; *Lophiodes caulinaris*, MCZ 51260, 33.5 mm SL; TU 72942, 152 mm SL; *Lophiodes monodi*, MCZ 40928, 92 mm SL; *Lophiodes spilurus*, TU 78474, 71 mm SL; *Lophiomus setigerus*, TU 81104, 166 mm SL; *Lophius americanus*, MCZ 51259, 121 mm SL; †*Sharfia mirabilis*, MNHN Bol 38-39, 39.9 mm SL; *Sladenia remiger*, CSIRO H.2559-02, 133 mm SL.

Tetrabrachiidae: *Tetrabrachium ocellatum*, QM I.27988, 49 mm SL; QM I.30596, 56 mm SL.

Anatomical abbrevations: **alpmx**, alveolar process of the premaxilla; **ar**, articular; **aspmx**, ascending process of the premaxilla; **cl**, cleithrum; **co**, coracoid; **cs**, cleithral spine; **ctb**, ceratobranchial; **d**, dentary; **epi**, epioccipital; **epb**, epibranchial; **f**, frontal; **iop**, interopercle; **h**, hyomandibula; **hyb**, hypobranchial; **ih**, interhyal; **le**, lateral ethmoid; **mtp**, metapterygoid; **mx**, maxilla; **op**, opercle; **pa**, parietal; **pal**, palatine; **pas**, parasphenoid; **pcl**, postcleithrum; **phb**, pharyngobranchial; **pmx**, premaxilla; **pop**, preopercle; **pte**, pterygoid;

pto, pterotic; **ptt**, posttemporal; **q**, quadrate; **rad**, pectoral-fin radial; **sca**, scapula; **scl**, supracleithrum; **soc**, supraoccital; **sop**, subopercle; **sos**, supraocular spine of the frontal; **spo**, sphenotic; **sym**, symplectic; **tpc**, transverse process of the caudal centrum; **v**, vertebra; **vo**, vomer.

Systematic palaeontology

Subdivision **Teleostei** *sensu* Patterson & Rosen, 1977

Order **Lophiiformes** Garman, 1899

Suborder **Lophioidei** Regan, 1912

Family **Lophiidae** Rafinesque, 1810

Genus †*Caruso* nov.

(Figs. 1-8)

Diagnosis. A member of the Lophiidae with body moderately depressed, rounded, and relatively globose, and a compressed and moderately elongate tail; frontals heavily constricted in the interorbital region (distance between the lateral margins of the anteromedial extensions of the frontals is about 18% of that measured between the outer margins of the pterotics); dorsolateral ridge of the frontals smooth; elongate frontal fontanel; supraocular spines prominent, representing the anterolateral corners of the postorbital sector of the neurocranium; dorsal aspect of the parasphenoid narrow; symphysial process of the dentary absent; retroarticular process of the articular well developed; maxillary process of the palatine simple, with rounded profile; pterygoids (endo- + ecto-) greatly enlarged, ovoid in outline; subopercle with fimbriate posteroventral margin; 19 vertebrae; haemal spines of the abdominal vertebrae well developed and anteroposteriorly expanded; neural and haemal spines of the penultimate vertebra widely expanded; three post-cephalic dorsal-fin spines;

nine dorsal-fin rays; anterior pterygiophore of the soft dorsal fin shortened and anteroposteriorly expanded, bearing two rays, one in supernumerary association; posteriormost dorsal-fin pterygiophore bearing two rays; six anal-fin rays; anteriormost and posteriormost pterygiophores bearing two rays (one supernumerary on the anterior pterygiophore); distal end of the posteriormost anal-fin pterygiophore expanded, notably globose with rounded profile; cleithral spine short; pectoral-fin radials greatly elongate, the ventralmost measuring about 23% SL; pectoral fin paddle-shaped; 14-16 pectoral-fin rays.

Etymology. We are pleased to name this genus in honor of John H. Caruso of Tulane University for his years of service to the world ichthyological community and for his many published contributions to anglerfish systematics.

Included species. Monotypic.

†*Caruso brachysomus* (Agassiz, 1835)

1796 *Lophius piscatorius* Volta: pl. 42, fig. 3 (misidentification).

1818 *Lophius piscatorius* var. *Gonelli* Risso; De Blainville: 340, 342 (in part; misidentification based on *Lophius piscatorius* Volta).

1835 *Lophius brachysomus* Agassiz (name only): 292 (in part).

1844 *Lophius brachysomus* Agassiz; Agassiz: 114, vol. 5, pl. 1, figs 1-2.

1874 *Lophius brachysomus* Agassiz; Zigno: 105 (in part).

Non 1876 *Lophius brachyostomus* Agassiz; Lawley: 77, pl. 5, figs 2a-c.

1901 *Lophius brachysomus* Agassiz; Woodward: 591 (in part).

1905 *Lophius brachysomus* Agassiz; Eastman: 31 (in part).

1922 *Lophius brachysomus* Agassiz; D'Erasmo: 140-141 (in part).

1927 '*Lophius*' *brachysomus* Agassiz; Arambourg: 216.

1967 *Lophius brachysomus* Agassiz; Andrews, Gardiner, Miles & Patterson: 660.

Non 1972 *Lophius brachysomus* Agassiz; Sorbini; pl. 18 (misidentification).

1980 *Lophius brachysomus* Agassiz; Blot: 353-354 (in part).

1983 *Lophius brachysomus* Agassiz; Sorbini; pl. 9.

Non 1991 *Lophius brachysomus* Agassiz: Frickhinger: 694 (misidentification).

Non 1996 *Lophius brachysomus* Agassiz: Long: 157, fig. 2 (misidentification).

Diagnosis. As given for the genus.

Holotype. MNHN Bol42/43, a relatively complete skeleton in part and counterpart, 125.7 mm SL; late early Eocene, Ypresian; Monte Bolca, Pesciara cave site (Fig. 1).

Additional material. MCSNV T.978, a complete well-preserved skeleton, 136.5 mm SL, from the type locality (Fig. 2A); this specimen is part of the Baja's fossil collection of the Museo Civico di Storia Naturale, Verona, and was figured in a photographic catalogue published by Lorenzo Sorbini (1983; pl. 9). MCSNV B.13, a nearly complete skeleton, 92.1 mm SL, from the type locality (Fig. 3); not previously recognized.

Horizon and locality. Late early Eocene, Ypresian, *Alveolina dainelli* Zone; Monte Bolca, Pesciara cave site.

Biotope and palaeoecology. The finely laminated micritic limestone of the Pesciara cave site has provided a huge amount of fossils, including thousands of exceptionally well-preserved, fully articulated fish skeletons. The fish assemblage consists of more than 200 species of sharks, batoids, pycnodontiforms and teleosts, representing the earliest evidence of an acanthomorph dominated ichthyofauna, which also includes several representatives of the fish groups found on coral reefs today (Patterson 1993; Bellwood 1996; Landini & Sorbini 1996). The fish assemblage from Monte Bolca therefore marks the starting point in the known evolution of many reef fish groups and provides a reliable evidence of the morphological and compositional stability of tropical and subtropical marine ichthyofaunas throughout the Cenozoic (Bellwood & Wainwright 2002).

To date there is no consensus about the interpretation of the physiography and palaeoecological setting of the depositional environment during the sedimentation of the micritic limestone. Based on a wide comprehensive palaeocological analysis of the fish assemblage, Landini & Sorbini (1996) concluded that sedimentation of the fish-bearing limestone occurred at a short distance from the coast, many dozens of meters in depth in close proximity to coral reefs, seagrass beds and open ocean, under the seasonal influence of well-developed river systems. The fish carcasses possibly accumulated in a silled depression that occasionally favored restricted circulation and bottom anoxia. Sedimentological, palaeontological and taphonomic evidences, as well as the ecological spectrum of the fossil assemblage, concur to indicate that the Pesciara cave laminated micritic limestone represents an obrutionary stagnation deposit (Seilacher *et al*. 1985).

Remarks. †*Lophius brachysomus* was erected by Louis Agassiz (1835) to allocate the two lophiid anglerfish specimens from Monte Bolca, previously documented in the *Ittiolitologia Veronese*, the voluminous monograph by Abbot Giovanni Serafino Volta (1796), and referred to the extant species *Lophius piscatorius* and *Loricaria plecostomus* respectively. The two lophiid specimens, both in part and counterpart, were part of the Gazola collection of fossil fishes from Monte Bolca that was confiscated by the armies of Napoleon, and deposited in the Muséum National d'Histoire Naturelle in Paris (see Pietsch and Carnevale, in press). According to Agassiz (1844), the specimens represent different ontogenetic stages of a single species; the smaller one was formerly assigned to the catfish species *Loricaria plecostomus* by Volta (1796), while the larger one was considered as the lithified counterpart of the Atlantic-Mediterranean anglerfish species *Lophius piscatorius*. Several authors (see synonymy) followed the taxonomic interpretation of Agassiz up to the second half of the 1920s when Camille Arambourg (1927) questioned the generic identity of these fossils and, mainly based on their number of vertebrae, considered them to be related to the extant genus *Lophiomus*. Subsequently, Andrews *et al*. (1967) emphasized the necessity of a new detailed systematic study of these fossils in order to confirm their position. More recently, Blot (1980) cursorily discussed the generic identity of these specimens suggesting that a new generic name would be necessary to include them. A recent examination of the specimens in April 2010, however, has revealed the existence of two different taxa among the type material housed in the MNHN in Paris. The smaller specimen (MNHN Bol38/39) that was formerly assigned to *Loricaria plecostomus* by Volta (1796) has been described as a new genus and species (Pietsch & Carnevale in press). The morphology of the larger specimen is described herein together with that of additional specimens residing among the collections of the MCSNV.

Anatomical descriptions

Despite the small number of specimens (see Material section above), the available material of †*Caruso brachysomus* is relatively complete and reasonably well exposed from the matrix; therefore, although certain details are not evident, it has been possible to properly realize a morphological analysis of this taxon (see Fig. 2B).

Measurements are summarized in Table 1.

The body is moderately depressed with a large, rounded and relatively globose head, and a compressed and moderately elongate tail.

There is no evidence of dermal spinules so that the skin appears to be naked.

Neurocranium. The neurocranium (Fig. 4) appears to be greatly depressed dorso-ventrally and elongate, with its maximum width measured between the lateral extensions of the pterotics evidently less than its length (cranial width about 65% of the length). There is an evident regionalization of the neurocranium with a sharp differentiation into preorbital (rostral), orbital and postorbital sectors clearly related to a strong constriction at the level of the midlength of the frontals. The orbital-postorbital portion of the neurocranium is broadly expanded laterally with respect to the preorbital portion, which is narrow and linear; the distance between the lateral margins of the anteromedial extensions of the frontals equals about 18% of that measured between the outer margins of the pterotics. The dorsocranial architecture is recognizable, at least in part, in all the examined specimens; as a consequence, there is no evidence of the basicranial morphology. Because of the partial flattening of the bones due to the fossilization process, the presence of the spines that characterize the dorsal aspect of the neurocrania of extant lophiids cannot be observed. On the other hand, the original presence of prominent ridges that developed throughout the dorsal surface of the skull roof can be easily interpreted; in extant lophiids dorsocranial spines recurrently emerge in specific points of these ridges (see Caruso 1985), thereby suggesting that their presence in the fossils may be predicted, at least in certain cases (parietal, epioccipital, sphenotic). Another general morphological feature of the neurocranium is the presence of a moderately deep medial depression, developed throughout the neurocranial length; such a long concavity, which corresponds to the illicial trough of Waterman (1948), is more developed rostrally, in order to accommodate the ascending processes of the premaxillae. The posterior margin of the neurocranium is moderately concave on each side of the vertebral column, forming a large surface for the insertion of the epaxial muscles.

The frontals are the largest bones of the skull roof. These bones are greatly expanded laterally in their posterior half, becoming abruptly narrow anteriorly; such a marked difference in the lateral expansion in the two halves of the frontals occurs at the level of the supraocular spine (*sensu* Montcharmont 1950), which, as a consequence, forms the massive anterior corner of the orbital-postorbital sector of the neurocranium. The bony tissue of the frontals is cancellous in juveniles (MCSNV B.13), becoming dense and generally hard in adult specimens (MNHN Bol42/43; MCSNV T.9787). The two contralateral frontals are separated for most of their length by a large fontanel that apparently reduces in size during ontogeny. The lateral profile of the frontals is concave in their laterally expanded posterior portion, becoming more linear anteriorly, sometimes with reduced knobs and/or crenulations. Each frontal bears a dorsolateral longitudinal ridge, which represents the anterior part of a developed ridge system that originates posteriorly at the boundary between the first vertebra and the epioccipital. This smooth ridge can be divided into two portions, a supraorbital one that culminates with the prominent anterolaterally directed supraocular spine, and a preorbital-rostral portion that extends anteriorly to the lateral ethmoids. Each frontal articulates medially (before and behind the fontanel) with its opposite member, anterior and anterolaterally with the lateral ethmoid, which it partially overlies, posterolaterally with the sphenotic, posteriorly with the parietal and posteromedially with the supraoccipital.

The lateral ethmoids are large, crescent-shaped bones, with a gently rounded lateral profile. The medial sector of each is notably depressed, and the posterior portion lies ventral to the anteriormost extension of the respective frontal. Each lateral ethmoid articulates medially with the vomer, posteriorly with the frontals, and ventromedially with the parasphenoid.

The vomer is a flattened and anteriorly broadened bone, which makes contact posteriorly with the parasphenoid and posterolaterally with the lateral ethmoids. Like in other lophiids, the vomer appears to be characterized by having an anterior concave edge.

There is no evidence of an ossified mesethmoid. The reduced space between the two contralateral lateral ethmoids was probably occupied by the ethmoid cartilage in origin.

The parasphenoid is only partially exposed in the lectotype and MCSNV T.978. This median bone appears to be narrow, not expanded laterally.

The parietals are polygonal in shape. These bones lie lateral to the supraoccipital and articulate anteriorly with the frontals, laterally with the sphenotic, posterolaterally with the pterotic and posttemporal, and posteromedially with the epioccipital. A prominent ridge runs longitudinally through this bone; three additional ridges merge radially into the main longitudinal ridge; a spine probably was present at the intersection of all of these ridges.

The supraoccipital is a large median ovoid bone with a concave dorsal surface. This bone articulates anteriorly with the frontals, laterally with the parietals, and posteriorly and posterolaterally with the epioccipitals.

The sphenotic is a robust bone that forms a rounded flange culminating with a thick blunt spine, which extends outward in lateral direction, considerably beyond the width of the supraocular spine of the frontal. The dorsal surface of this bone bears a longitudinal ridge; a spine was possibly present on this ridge originally. Each sphenotic articulates anteriorly with the frontals, laterally with the parietal and posteriorly with the pterotic.

The pterotic is thickened and flange-like laterally and more massive medially; its lateral flange terminates with a blunt rounded spine. A prominent pterotic ridge radiates medially from that spine. The distance measured between the lateral ends of the pterotic spines coincides with the maximum width of the neurocranium. Each pterotic makes contact anteriorly with the sphenotic, laterally with the parietal, posteromedially with the epioccipital, and posteriorly with the posttemporal.

The epioccipitals are large and irregular bones that form the posteromedial border of the skull roof. There is a conspicuous longitudinal ridge, nearly sigmoid in shape, which is continuous with that of the parietal; a spine was possibly present along this ridge. Each epioccipital articulates medially through interdigitation with its opposite member in the midline of the neurocranium, anteromedially with the supraoccipital, anteriorly with the parietal, anterolaterally with the sphenotic and pterotic, and laterally with the posttemporal.

As in other lophiiforms the posttemporals are sutured to the neurocranium at its dorsolateral corner. A ridge, which terminates posteriorly with a blunt and thick process, radiates medially on the dorsolateral surface of this bone. Each posttemporal articulates medially and anteromedially with the epioccipital, and anteriorly with the pterotic.

Jaws, suspensorium and opercular series. As in other lophiids, the gape of the mouth is wide; the mandible length reaches more than 32% SL.

Each premaxilla (Figs. 5-6) has a long and distally spatulate alveolar process, an expanded and obliquely oriented articular process, a shallow postmaxillary process with a gently rounded dorsal profile, and a thick and labiolingually compressed autogenous ascending process. Two or three series of large conical and usually depressible teeth are visible along the anterior two thirds of the alveolar process. Fixed conical and recurved teeth insert along the alveolar surface of the distal portion of the premaxilla.

The maxillae (Fig. 5) consist of a wide posterior portion and an expanded anterior head; this bone is characterized by having a smooth external surface and, during the juvenile phase, by cancellous texture.

The mandibles (Fig. 5) are very large, characterized by having a cancellous texture in juveniles. The dentaries are strongly ossified and curved bones that bear a number of strong depressible conical teeth arranged in two or three rows. These bones are deeply forked posteriorly to accommodate the anterior pointed extensions of the articulars. The articular has a well developed retroarticular process (*sensu* Montcharmont 1950) that originates just posterior to the glenoid fossa (quadrate-articular joint). There is no evidence of spines along the external surface of the articular. The retroarticular is a small bone located posteromedially on the mandible.

The hyomandibulae (Fig. 5) are large and stout bones divided into three portions: the broad articular head, main vertical shaft, and anterior flange. The articular head has two condyles that articulates with the lateral otic region of the neurocranium, and the opercular process that articulates with the articulating condyle of the opercle. In the basal sector of the articular head is a stout anteriorly directed spine. The hyomandibular shaft tapers distally and articulates anteriorly with the posterior margin of the metapterygoid, anteroventrally with the dorsal and posterior margin of the symplectic and the dorsal margin of the quadrate, and posteriorly with the anterior margin of the preopercle. The anterior flange is a thin bony lamina that articulates ventrally with the process emerging from the posterodorsal corner of the metapterygoid.

The quadrates (Fig. 5) are stout and high bones, nearly triangular in outline, with a developed articular facet for the articular at their anteroventral corner. Each quadrate articulates at the anterodorsal corner with the pterygoids, and dorsally with the symplectic, hyomandibula and metapterygoid. Quadrate spines are not preserved.

The symplectics (Fig. 5) are long rod-like bones somewhat stouter posteriorly than anteriorly. Each symplectic articulates dorsally with hyomandibula, ventrally with the quadrate, and anteriorly with the metapterygoid.

The metapterygoids (Fig. 5) are relatively large and thin plates with an irregular outer margin. A posterodorsally directed process emerges from the posterodorsal corner of these bones. Each metapterygoid articulates dorsally and posteriorly with the hyomandibula, posteriorly with the symplectic, and ventrally with the quadrate.

The pterygoids (endo- + ecto-) (Fig. 5) are extremely large and ovoid in outline, connected with the palatine anteriorly and the quadrate posteriorly. The posterior sector of these bones is thick and slightly sculptured, becoming extremely thin, nearly translucent, anteriorly. A thick longitudinal ridge, which possibly represents the ontogenetic suture between the ectopterygoid and endopterygoid (see Morrow 1882; Matsuura & Yoneda 1987), extends from the posterior margin to the anterior tip of each of these bones.

The palatines (Fig. 5) are relatively large stout bones with an expanded maxillary process (*sensu* Montcharmont 1950) and a spatulate distal portion. Some strong depressible and slightly recurved teeth insert along the ventromedial margin of these bones. Each palatine articulates anteriorly with the maxilla, anteromedially with the lateral ethmoid, and posteriorly with the pterygoid.

The preopercles (Fig. 5) are long, subcylindrical and gently curved. Functionally, these bones are part of the suspensorium. Each preopercle articulates anterodorsally with the hyomandibula and anteroventrally with the quadrate.

The interopercles (Fig. 5) are large and flattened bones, subtriangular in outline, with an anteroventrally directed apex. Interopercular spines are not visible, possibly due to inadequate preservation.

The opercles (Fig. 5, 7) are deeply indented posteriorly making them notably bifurcate; the dorsal limb is filamentous and posteriorly directed, whereas the ventrolaterally directed lower limb is stout and characterized by having a strong thickening along the anterior margin.

Each subopercle (Fig. 5, 7) is a broad and morphologically complex bone that bears a stout and pointed process emerging from the dorsal margin, ventral and posterior flattened elongate fimbriations, and a spiny anterior process; the subopercle articulates with the opercle through the process that arise centrally from its dorsal margin.

Visceral arches. Of the hyoid apparatus, the elongate acinaciform branchiostegal rays can be observed in all the examined specimens. The interhyals (Fig. 5) are cylindrical and slightly curved.

The gill arches are only partially preserved. The bones are usually disarticulated and displaced from their original position. The first pharyngobranchial seems to be absent. The second pharyngobranchial is preserved in MCSNV B.13 (Fig. 8); this bone is moderately wide and bears a thick process emerging from its dorsal surface, and several strong and recurved teeth. What appears to be a large right third pharyngobranchial (Fig. 5) is preserved in MCSNV T.978. The epibranchials are thin and cylindrical (Fig. 5). The ceratobranchials (? I to IV) are long, stout and cyclindrical, gradually tapering and curved distally. The fifth ceratobrachial (Fig. 5) is massive and subtriangular in outline; the dorsal surface of this bone has a linear longitudinal ridge; strong recurved teeth appear to be restricted to the medial and lateral margins of the fifth ceratobranchial. Hypobranchials and basibranchials are not preserved in any of the available specimens.

Vertebral column. The vertebral column (Fig. 2B) is compact with the abdominal portion arcuate in a kyphotic curve, with the concave side toward the ventrum. There are 19 vertebrae (including the last hemicentrum fused to the hypural complex). As in other lophiiforms, the first vertebra is closely connected to the neurocranium (see, e.g., Rosen & Patterson 1969). The vertebral centra are massive and squared except for the second that is nearly rectangular, higher than long. The neural spines of the vertebrae three through eight incline posteriorly and are laterally flattened and anteroposteriorly expanded. More posteriorly, the neural spines are elongate and cylindrical but become progressively shorter and more inclined in the caudal region. Neural prezygapophyses are well-developed on all vertebrae. The first haemal spine occurs on the sixth vertebra. The first two haemal spines are poorly developed and remarkably inclined posteriorly, bent over the anteroventral sector of the succeeding vertebrae. Haemal arches and spines of the vertebrae eight through twelve are notably broad and laterally compressed, becoming considerably shorter more posteriorly.

Median fins and support. The caudal skeleton (Fig. 2B) is consistent with that of other lophiiforms. The neural and haemal arches and spines of the penultimate vertebra are strongly expanded anteroposteriorly and spatulate distally. The hypural complex consists of the fusion of the ural centra with the first preural centrum, hypurals and parhypural (see Rosen & Patterson 1969). The hypural plate is triangular with a slight notch along the posterior margin that continues on the plate as a shallow median furrow. A single well-developed and laterally compressed epural is also present. The caudal fin is slightly rounded and contains eight rays, of which the central six are bifurcated.

The cephalic portion of the spinous dorsal fin (including the illicial apparatus) is not preserved in any of the examined specimens. Like in †*Eosladenia*, *Lophiomus* and *Lophius*, the post-cephalic portion of the spinous dorsal fin (Fig. 2B) consists of three spines progressively decreasing in length posteriorly. The first spine is located over the fourth vertebral centrum, the second spine apparently inserts at the level of the fifth vertebral centrum, and the third post-cephalic spine is located above the seventh vertebral centrum.

The soft-rayed dorsal fin (Fig. 2B) inserts at the level of the tenth vertebra and contains nine distally bifurcated rays supported by seven pterygiophores. The first ray is in supernumerary association on the first dorsal-fin pterygiophore, and the posteriormost dorsal-fin pterygiophore supports two rays. The rays gradually increase in length from the first to the fourth, and succeeding elements are of progressively decreasing size. The first pterygiophore of the soft dorsal fin is massive, short and anteroposteriorly enlarged, whereas the succeeding elements are characterized by having dorsally rounded heads and elongate narrow vertical shafts interdigitating in the underlying interneural spaces. The posterior two dorsal-fin pterygiophores insert in the space between the neural spines of the vertebrae 12th and 13th. The head of the posteriormost pterygiophore has a hypertrophied rounded posterior flange.

The anal fin is not adequately preserved in the available material. It appears to be composed of six rays supported by four pterygiophores. The pterygiophores are subrectangular, stout and closely associated to the ventral margin of the overlying vertebral centra. The first anal-fin ray is in supernumerary association on the first anal-fin pterygiophore, and two rays are supported by the posterior pterygiophore.

Paired fins and support. The paddle-shaped pectoral fin (Figs. 1-3) comprises 14 to 16 simple rays. The fin is supported by two greatly elongate (22.8 – 23.3 % SL) and thick radials (Fig. 2B, 5). The dorsal radial is cylindrical, about two thirds the length of the ventral one. The ventral pectoral-fin radial is considerably expanded distally to form an articulatory surface for the pectoral-fin rays; the distal flat and dorsally convex expansion of the ventral radial shows some radial striae that possibly represent the traces of the ontogenetic fusion of additional radial elements. Scapulae and coracoids are poorly preserved in the examined material. The posttemporal, the dorsalmost element of the pectoral girdle, is firmly connected to the posterolateral corner of the neurocranium. The supracleithrum is approximately ovoid and laminar, closely associated with the lateral surface of the dorsal part of the ventral arm of the cleithrum. The cleithrum is the largest bone of the pectoral girdle. The horizontal and anteromedially directed arm is always nearly totally hidden by other cranial bones or partially covered by the sediment. The vertical arm is broad, laterally flattened and dorsomedially oriented; a short pointed and stout cleithral (=humeral) spine emerges in the basal portion of the vertical arm of the claithrum along its posterior margin. The lateral surface of this bone is slightly ornamented by small pits in the junction area between the vertical and horizontal arms. A single rod-like postcleithrum appears to be present.

The pelvic fins are not exposed in the examined material. A single displaced basipterygium can be observed in MCSNV T.978 (Fig. 2B); this bone is triradiate with a long cylindrical anterior limb and an expanded articular posterior part. The medial process is flattened with a straight profile and possibly served as a contact surface for its respective counterpart.

Phylogenetic relationships

The present analysis is based on an examination of seven lophioid genera (†*Caruso*, †*Eosladenia, Lophiodes, Lophiomus, Lophius,* †*Sharfia,* and *Sladenia*), representing all known members of the family Lophiidae (see Caruso 1985), plus two outgroup antennarioid genera *Antennarius* and *Brachonichthys* (Pietsch 2009:175−179, fig. 188). The purpose of this section is to place the extinct genera †*Caruso*, †*Eosladenia,* and †*Sharfia,* and the four extant lophiid genera in a phylogenetic framework of the family. A data matrix of nine taxa and 38 characters was constructed (Appendix 1). All characters were treated as unordered and unweighted. All characters except number 35 (see below) were binary. Characters states that could not be determined from the fossils because of inadequate preservation are coded as unknown, and indicated in the data matrix by a question mark. The matrix was analyzed with PAUP (Swofford 2002), using the branch and bound algorithm, with accelerated transformation (ACCTRAN) to optimize characters. To evaluate branch support, a heuristic bootstrap analysis of 1000 replicates was conducted, with simple addition sequence and TBR (tree bisection-reconnection) branch-swapping options. Bremer decay values (Bremer 1988) were calculated using TREEROT (Sorenson 1999).

Character descriptions. The descriptions of the phylogenetically relevant characters for the analyzed taxa are arranged below by discrete anatomical complexes. A description of each character is followed by a summary of the recognized character state of each character. Consistency and retention indices (CI and RI) were produced as a whole and for each character individually. Both CI and RI are given after each character description. The condition of the different features in the genera included in the phylogenetic analysis is briefly discussed. The numbered characters listed below correspond to the character numbers in the matrix. Some of the characters were previously included in the analysis generated by Caruso (1985). The intrageneric relationships hypothesized by Caruso (1985) were primarily based on external morphological features and spine distribution across the head, suspensorium, jaws and opercular apparatus; because of inadequate preservation, these characters are in many cases not observable in the fossil material and for this reason are not included in our analysis.

Cranium

1. *Mesethmoid: present (0); absent (1)* (CI 1.00, RI 1.00). Most lophiiforms, including both outgroups, possess an ossified mesethmoid lying between the lateral ethmoids and the anterior extensions of the frontals and above the parasphenoid (e.g., Regan & Trewavas 1932; Pietsch 1974; 1981). Regan (1912) and Le Danois (1974) described and figured an ossified mesethmoid in lophiids. The presence of the mesethmoid in extant and fossil lophiids has not been confirmed by our observations, which are consistent with those of Morrow (1882),

Supino (1908), and Montcharmont (1950). According to Supino (1908), a greatly reduced and thin cartilage located between the lateral ethmoids testifies to the presence of a mesethmoid in lophiid fishes. Based on functional considerations, Montcharmont (1950) suggested that the possible homolog of the mesethmoid should be searched among the tissues associated with the autogenous ascending processes of the premaxillae. The analysis of cleared and double stained specimens and dried skeletons of extant lophiids (Fig. 9), as well as the morphological study of fossil taxa have not revealed the presence of any trace of a mesethmoid either bony or cartilaginous.

2. *Interorbital width*: *greater than 30% of that measured between the outer margins of the pterotics (0); considerably less than 30% of that measured between the outer margins of the pterotics (1)* (CI 1.00, RI 1.00). The cranial width measured at the level of the medial extensions of the frontals anterior to the supraocular spine is unusually narrow, notably less than 30% of that measured between the outer margins of the pterotics in †*Caruso* (Fig. 4) and *Sladenia* (Fig. 9A), whereas it is always greater than 30% of that measured between the outer margins of the pterotics in both outgroups and other lophiids (Fig. 9; Bannikov 2004; Pietsch & Carnevale submitted).

3. *Dorsolateral ridge of the frontals: smooth and uninterrupted (0); rugose, bearing short conical spines or low rounded knobs (1)* (CI 0.50, RI 0.00). This character was originally described by Caruso (1985). The ornamented rugosities of the dorsolateral ridge of the frontal bones are unique to *Lophiomus* and *Lophius*, in which they increase during ontogeny. In both outgroups and other lophiids, including the fossil genera †*Caruso*, †*Eosladenia*, and †*Sharfia*, the dorsolateral ridge of the frontals is smooth (Fig. 9; Bannikov 2004; Pietsch & Carnevale submitted).

4. *Parasphenoid width: narrow (0); laterally expanded (1)* (CI 1.00, RI 1.00). The parasphenoid of most lophiiform fishes is elongate, narrow and well ossified; both outgroups

and the lophiid genera †*Caruso*, †*Eosladenia*, *Lophiodes*, †*Sharfia* and *Sladenia* display the typical lophiiform condition (Fig. 9A-B; Bannikov 2004; Pietsch & Carnevale submitted). The parasphenoid is characterized by having a remarkably wide lateral expansion in the extant genera *Lophiomus* and *Lophius* (Figs 9C-D).

Jaws

5. *Ascending process of the premaxilla: fused to the alveolar process (0); autogenous (1)* (CI 1.00, RI 0.00). The premaxilla of the vast majority of lophiiforms, including the outgroups, is characterized by having a narrow ascending process fused to an elongate alveolar process. All the lophiid genera exhibit an autogenous and highly mobile ascending process of the premaxilla (Fig. 10; Bannikov 2004; Carnevale & Pietsch submitted).

6. *External surface of the maxilla: smooth (0); ornamented (1)* (CI 1.00, RI 0.00). This character was described by Caruso (1985). A smooth outer surface of the maxilla is typical of the outgroups and all the lophiid genera (including the fossils), except for *Lophiomus* in which it is conspicuously ornamented with short conical spines (Fig. 10C).

7. *Symphysial spine: present (0); absent (1)* (CI 0.33, RI 0.33). The dentaries of *Antennarius* and the extant lophiid genera *Lophiomus*, *Lophius*, and *Sladenia* bear a prominent and often stout symphysial spine (Figs 11A, C-D). This spine is absent in *Brachionichthys* (Carnevale & Pietsch 2010) and in the lophiid genera †*Caruso*, †*Eosladenia*, *Lophiodes*, and †*Sharfia* (Figs. 5, 11B; Bannikov 2004; Pietsch & Carnevale submitted).

8. *External surface of the dentary: smooth (0); ornamented (1)* (CI 1.00, RI 0.00). This character was described by Caruso (1985). The dentary of *Lophiomus* is unique in having a dense covering of prominent rounded spines along its lateral surface (Fig. 11C). The outgroups and the other lophiid genera are characterized by having dentaries with smooth external surfaces.

9. *Retroarticular process of the articular: extremely short and high (0); well-developed and shallow (1)* (CI 0.50, RI 0.50). The lower jaw terminates posteriorly more or less at the articulation with the quadrate in both outgroups and *Sladenia* (Fig. 11A), but extends posteriorly well past the glenoid fossa in all other lophiids (Figs 5, 11B-D; Bannikov 2004; Pietsch & Carnevale submitted).

Suspensorium

10. *Maxillary process of the palatine: simple, with rounded profile (0); bifurcate (1)* (CI 1.00, RI 1.00). The maxillary process of the palatine is simple, often expanded with rounded profile, in *Antennarius*, *Brachionichthys*, †*Caruso*, †*Eosladenia*, *Lophiodes*, †*Sharfia* and *Sladenia* (Figs 5, 11A-B; Bannikov 2004; Pietsch & Carnevale submitted). In *Lophiomus* and *Lophius* this process bears a couple of divergent acute spines dorsally that make its dorsal aspect remarkably bifurcate (Figs 11C-D).

11. *Arrangement of ectopterygoid and endopterygoid: separate from each other (0); fused into a single element (1)* (CI 1.00, RI 1.00). In the vast majority of lophiiforms, including *Antennarius* (Pietsch 1981) and *Brachionichthys* (Carnevale & Pietsch 2010), the ectopterygoid and endopterygoid are distinctly separate elements. In all lophiids a large triangular, subrectangular or ovoid bony plate is always present in the region of the suspensorium usually occupied by the ectopterygoid and endopterygoid (Figs 5, 11; Bannikov 2004; Pietsch & Carnevale submitted); in all the lophiid genera, both extant and fossils, a longitudinal ridge emerges on the medial surface of this element. The anatomical identity of this bone is rather problematic. According to Morrow (1882), the single pterygoid element constitutes the product of the fusion between ectopterygoid and endopterygoid. Supino (1908) hypothesized that the ectopterygoid is absent in lophiids and that the single bone actually represents the endopterygoid. The structure of this bone was not clear in the

description and illustration provided by Gregory (1933). Montcharmont (1950) figured a single element (figs 11-14) formed by the fusion of the ectopterygoid and endopterygoid but surprisingly described two apparently separate bones. Le Danois (1974) proposed that the large bony plate is the homolog of the endopterygoid of other teleosts and that a small ectopterygoid is nearly fused to the proximal portion of the palatine. Such a controversial anatomical issue has been apparently resolved by Matsuura & Yoneda (1987) who, based on a complete ontogenetic series of *Lophius gastrophysus*, documented the existence of two bones recognizable as separate elements in specimens with notochord length of 20 mm. In summary, we tentatively consider the pterygoid plate of lophiids to be the result of an ontogenetic fusion of the ectopterygoid and endopterygoid.

Opercular series

12. *Opercular shape: subtriangular (0); strongly bifurcate (1)* (CI 1.00, RI 1.00). The possession of a fully ossified polygonal opercle is plesiomorphic for acanthomorphs and more generally for teleost fishes. The opercle is subtriangular in outline in the outgroups *Antennarius* and *Brachionichthys*, and the Eocene lophiid †*Sharfia* (Pietsch & Carnevale submitted). Such a condition has also been observed in lophichthyids, tetrabrachiids, ogcocephaloids and chaunacoids (see Pietsch 1981). In all other members of the Lophiidae the opercles are characterized by having a deep indentation along the posterior margin, which makes them strongly bifurcated (Figs 5, 7, 12; Bannikov 2004; Pietsch & Carnevale submitted). A bifurcated opercle also occurs in most ceratioids (see, e.g., Regan & Trewavas 1932; Pietsch 2009), possibly representing the result of an independent derivation.

13. *Posteroventral margin of the subopercle*: *simple (0); fimbriate (1)* (CI 0.50, RI 0.67). The subopercle of most lophiiform fishes is a morphologically heterogeneous bone with entire margins (e.g., Regan & Trewavas 1932; Pietsch 1974; 1981). In antennarioids

(including *Antennarius* and *Brachionichthys*), ceratioids, chaunacoids, and ogcocephaloids, the subopercle is relatively elongate, often broad, crescent-shaped and ovoid. The posteroventral margin of the subopercle is therefore linear and entire in the taxa of the lophiiform suborders Antennarioidei, Ceratioidei, Chaunacoidei and Ogcocephaloidei, as well as in the lophioid genera †*Sharfia* and *Sladenia* (Fig. 12A; Pietsch & Carnevale submitted). The posteroventral margin of the subopercle of the other lophioid genera is extremely fimbriated (Figs 5, 7, 12B-D; Bannikov 2004; Pietsch & Carnevale submitted), even in very small larvae (see Matsuura & Yoneda 1987).

14. *Anterodorsal process of the subopercle: short, reduced to a spine (0); prominent, articulating through connective tissue with the anteroventral margin of the opercle (1)* (CI 1.00, RI 1.00). The subopercles of a number of lophiiforms (including both the outgroups) bear a median spiny process on the anterodorsal margin. A stout prominent ascending process arising from the anterodorsal margin of the subopercle, making contact with the anterior margin of the opercle is unique to the Lophiidae (Figs 5, 7, 12; Bannikov 2004; Pietsch & Carnevale submitted).

Gill arches

15. *Distal end of the first epibranchial: simple (0); bifurcate (1)* (CI 1.00, RI 1.00). The distal tip of the first epibranchial has a single articular head in *Antennarius* and *Brachionichthys* (Pietsch 1981; Carnevale & Pietsch 2010), but two in the lophiid genera *Lophiodes*, *Lophiomus*, *Lophius*, and *Sladenia* (Fig. 13). The fossil genera †*Caruso*, †*Eosladenia*, and †*Sharfia* are coded as unknown.

16. *Third hypobranchial: present (0); absent (1)* (CI 1.00, RI 0.00). *Antennarius* has three hypobranchials, as do many other lophiiforms (see, e.g., Pietsch 1974; 1981). The third hypobranchial is absent in *Brachionichthys* (see Carnevale & Pietsch 2010), *Lophiodes*,

Lophiomus, *Lophius*, and *Sladenia* (Fig. 13). This character is unknown in †*Caruso*, †*Eosladenia*, and †*Sharfia*.

17. *Second hypobranchial: present (0); absent (1)* (CI 1.00, RI 0.00). The second hypobranchial is present in the outgroups *Antennarius* and *Brachionichthys* (Pietsch 1981; Carnevale & Pietsch 2010), and in the lophiids *Lophiodes*, *Lophiomus*, and *Sladenia* (Figs 13A-C), but absent in *Lophius* (Fig. 13D). The fossil genera are coded as unknown.

18. *Arrangement of teeth on the fifth ceratobranchial: dense cluster (0); restricted to discrete rows along the lateral and medial margins (1)* (CI 1.00, RI 1.00). In all lophiiform taxa except the lophiids, the teeth are arranged in a dense cluster on the inner surface of the fifth ceratobranchial (e.g., Pietsch 1981). The lophiid genera, including the fossils, are unique in having the fifth ceratobranchial teeth arranged in one or two rows along the outer margins of the bony plate (Figs 5, 13; Field 1966).

Axial skeleton and caudal fin

19. *Number of vertebrae: 18-22 (0); 26-31 (1)* (CI 1.00, RI 0.00). This character was described by Caruso (1985). The outgroups and the lophiid genera †*Caruso*, †*Eosladenia*, *Lophiodes*, *Lophiomus*, †*Sharfia*, and *Sladenia* usually have 22 or fewer vertebrae. *Lophius* has 26 to 31 vertebrae. The apomorphic high vertebral number of *Lophius* has been considered (Arambourg 1927) as further evidence of the so-called Jordan's rule (Jordan 1892), which states that number of vertebrae in fishes increase with latitude. The vertebral number in fishes, however, is subject to the influence of many different (often interacting) factors (see, e.g., McDowall 2008), which makes it very difficult to evaluate the plausibility of the possible effects of the Jordan's rule in anglerfishes of the genus *Lophius*.

20. *Haemal spines of abdominal vertebrae: well developed and anteroposteriorly expanded (0); reduced in size (1)* (CI 1.00, RI 1.00). The abdominal haemal spines are widely

expanded and well developed in *Antennarius*, *Brachionichthys* (Pietsch 1981; Carnevale & Pietsch 2010), and the lophiid genera †*Caruso*, †*Sharfia*, and *Sladenia* (Figs 2B, 14A; Pietsch & Carnevale submitted). The abdominal vertebrae of the other lophiid genera (†*Eosladenia*, *Lophiodes*, *Lophiomus*, *Lophius*) possess reduced haemal spines (Figs 14B-D; Bannikov 2004).

21. *Neural and haemal spines of the penultimate vertebra: well developed and anteroposteriorly expanded (0); narrow, reduced in size (1)* (CI 1.00, RI 1.00). In the vast majority of lophiiforms, including the outgroups *Antennarius* and *Brachionichthys* (Pietsch 1981; Carnevale & Pietsch 2010), and the lophiids †*Caruso*, †*Sharfia*, and *Sladenia*, the penultimate vertebra bears considerably enlarged and anteroposteriorly expanded neural and haemal spines (Figs 2B, 14A; Pietsch & Carnevale submitted). These spines are narrow and anteroposteriorly shortened in †*Eosladenia*, *Lophiodes*, *Lophiomus*, and *Lophius* (Figs 14B-D; Bannikov 2004).

22. *Caudal centrum: rounded in cross section (0); depressed with lateral transverse processes (1)* (CI 1.00, RI 1.00). This character was described and discussed by Caruso (1985). The caudal centrum of *Antennarius*, *Brachionichthys*, †*Caruso*, *Lophiodes*, †*Sharfia*, and *Sladenia* (Figs 2B, 14A-B; Pietsch 1981; Carnevale & Pietsch 2010; Pietsch & Carnevale submitted) is nearly circular in cross section. In †*Eosladenia*, *Lophiomus*, and *Lophius*, the caudal centrum is in some ways depressed and bears well-developed lateral transverse processes (Figs 14C-D; Bannikov 2004).

Median fins

23. *Number of caudal-fin rays: nine (0); eight (1)* (CI 1.00, RI 1.00). The caudal fin of antennarioids, chaunacoids, ogcocephaloids and most ceratioids contains nine rays. All members of the Lophiidae exhibit a caudal fin with eight rays.

24. *Cephalic dorsal-fin spines: three (0); two (1)* (CI 1.00, RI 0.00). This character was described by Caruso (1985). The two outgroups and the extant lophiid genera *Lophiodes*, *Lophiomus*, and *Lophius* are characterized by having three cephalic dorsal-fin spines. The third cephalic dorsal-fin spine is absent in *Sladenia*. This character could not be scored for any of the fossil taxa.

25. *Interdigitation between the anterior soft dorsal-fin pterygiophores and the underlying neural spines: absent (0); present (1)* (CI 1.00, RI 1.00). The anterior soft dorsal-fin pterygiophores of *Antennarius*, *Brachionichthys*, †*Caruso*, †*Sharfia* and *Sladenia* lie above the corresponding neural spines (Fig. 2B, 14A; Pietsch 1981; Carnevale & Pietsch 2010; Pietsch & Carnevale submitted), but interdigitate with the neural spines in †*Eosladenia*, *Lophiodes*, *Lophiomus*, and *Lophius* (Figs 14B-D; Bannikov 2004).

26. *Interdigitation between the anal-fin pterygiophores and the overlying haemal spines: present (0); absent (1)* (CI 0.50, RI 0.67). The anal-fin pterygiophores of *Antennarius*, *Brachionichthys*, *Lophius,* and †*Sharfia* are closely associated with the corresponding haemal spines and insert in the interhaemal spaces (Fig. 14D; Pietsch 1981; Carnevale & Pietsch 2010; Pietsch & Carnevale submitted). The anal-fin pterygiophores of the lophiid genera †*Caruso*, †*Eosladenia*, *Lophiodes*, *Lophiomus*, and *Sladenia* lie well below the corresponding haemal spines (Figs. 2B, 14A-C; Bannikov 2004).

27. *Proximal shaft of the soft dorsal-fin pterygiophores: slender and elongate (0); anteroposteriorly expanded (1)* (CI 1.00, RI 1.00). The soft dorsal-fin pterygiophores of the outgroups *Antennnarius* and *Brachionichthys* (Pietsch 1981; Carnevale & Pietsch 2010), and the lophiids †*Caruso*, *Lophiodes*, †*Sharfia* and *Sladenia* consist of a slender, elongate proximal shaft and an expanded articular distal portion (Figs 2B, 14A-B; Pietsch & Carnevale submitted). The proximal shaft of these pterygiophores is considerably expanded in *Lophiomus* and *Lophius* (Figs 14C-D). †*Eosladenia* is coded as unknown.

28. *Rays articulating with the anteriormost dorsal-fin pterygiophore: two, one supernumerary (0); one (1)* (CI 0.33, RI 0.00). The anterior dorsal-fin pterygiophore supports a supernumerary ray in *Antennarius*, †*Caruso*, *Lophiomus*, †*Sharfia*, and *Sladenia* (Fig. 2B, 14A, C; Pietsch 1981; Pietsch & Carnevale submitted). The supernumerary ray on the first dorsal-fin pterygiophore is absent in *Brachionichthys*, *Lophiodes*, and *Lophius* (Figs 14B, D; Carnevale & Pietsch 2010). This character is unknown in †*Eosladenia*.

29. *Rays articulating with the posteriormost dorsal-fin pterygiophore: one (0); two (1)* (CI 0.50, RI 0.50). The last dorsal-fin pterygiophore of *Antennarius*, *Brachionichthys*, and *Lophius* support a single ray (Fig. 14D; Pietsch 1981; Carnevale & Pietsch 2010). In the lophiid genera †*Caruso*, *Lophiodes*, *Lophiomus*, †*Sharfia*, and *Sladenia* two rays are associated with the posteriormost dorsal-fin pterygiophore (Figs 2B, 14A-C; Pietsch & Carnevale submitted). †*Eosladenia* is coded as unknown.

30. *Rays articulating with the anteriormost anal-fin pterygiophore: two, one supernumerary (0); one (1)* (CI 1.00, RI 0.00). The anterior anal-fin pterygiophore of the outgroups and of the lophiids †*Caruso*, *Lophiodes*, *Lophiomus*, and *Sladenia* supports two rays, one of which is in supernumerary association (Figs 2B, 14A-C; Pietsch 1981; Carnevale & Pietsch 2010). *Lophius* exhibits a single ray on the anteriormost anal-fin pterygiophore (Fig. 14D). This character is coded as unknown in †*Eosladenia* and †*Sharfia*.

31. *Rays articulating with the posteriormost dorsal-fin pterygiophore: one (0); two (1)* (CI 0.50, RI 0.50). The posteriormost anal-fin pterygiophore supports a single ray in *Antennarius*, *Brachionichthys*, and *Lophius* (Fig. 14D; Pietsch 1981; Carnevale & Pietsch 2010), but two rays are associated with this element in †*Caruso*, *Lophiodes*, *Lophiomus*, and *Sladenia* (Figs 2B, 14A-C). †*Eosladenia* and †*Sharfia* are coded as unknown.

32. *Posteriorly directed expansion of the distal end of the posteriormost dorsal-fin pterygiophore: absent (0); present (1)* (CI 1.00, RI 1.00). The distal portion of the

posteriormost dorsal-fin pterygiophore is similar to those of the preceding elements in both the outgroups, and in the lophiids †*Eosladenia*, *Lophiodes*, *Lophiomus*, *Lophius*, and †*Sharfia* (Figs 14B-D; Pietsch 1981; Bannikov 2004; Carnevale & Pietsch 2010; Pietsch & Carnevale submitted). In †*Caruso* and *Sladenia* the distal sector of the posteriormost dorsal-fin pterygiophore bears a broad posteriorly directed expansion with rounded profile (Figs 2B, 14A).

33. *Number of dorsal-fin rays: nine to nineteen (0); eight (1)* (CI 0.33, RI 0.33). This character was described by Caruso (1985) and partially incorporated into his phylogenetic study. The soft dorsal fin contains nine to nineteen rays in the outgroups *Antennarius* and *Brachionichthys*, and the lophiid genera †*Eosladenia*, *Lophius*, and †*Sharfia*. In the remaining lophiid genera (†*Caruso*, *Lophiodes*, *Lophiomus*, and *Sladenia*) the number of soft dorsal-fin rays is reduced to eight.

Pectoral fin and girdle

34. *Postcleithrum: rod-like (0); filamentous (1)* (CI 1.00, RI 0.00). The postcleithrum is a stout rod-like bone in antennarioids (e.g., Pietsch 1981), chaunacoids, ogcocephaloids, and many ceratioids (Regan & Trewavas 1932; Pietsch 1974; Bertelsen & Krefft 1988), and the lophioids (Figs 15A-C), except *Lophius*. The latter genus has a long filamentous postcleithrum (Fig. 15D).

35. *Cleithral spine (= humeral spine): absent (0); weakly developed (1); greatly reduced (2)* (CI 1.00, RI 1.00). This character was partially described by Caruso (1985). A cleithral spine is absent in the outgroups *Antennarius* and *Brachionichthys*. Lacking sufficient material for skeletal preparations, Caruso (1985) erroneously stated that this spine is absent also in *Sladenia*. *Sladenia*, as well as the extinct lophiids †*Caruso* and †*Sharfia*, possess a short, weakly developed cleithral spine (Figs 5, 15A; Pietsch & Carnevale submitted). The

cleithral spine is extremely well developed in †*Eosladenia*, *Lophiodes*, *Lophiomus*, and *Lophius* (Figs 15B-D; Bannikov 2004).

36. *Extent of ventralmost pectoral-fin radial: relatively short, measuring less than 20% SL (0); long, greater than 20% SL (1)* (CI 0.33, RI 0.33). The ventralmost pectoral-fin radial is relatively short in *Antennarius*, †*Eosladenia*, *Lophiomus*, *Lophius*, and †*Sharfia*, but remarkably elongate in *Brachionichthys* and the lophiids †*Caruso*, *Lophiodes*, and *Sladenia*.

37. *Shape of pectoral fin: paddle-like (0); fan-shaped (1)* (CI 1.00, RI 1.00). Distinctly paddle-like pectoral fins are characteristic of the outgroups *Antennarius* and *Brachionichthys* (e.g., Pietsch & Grobecker 1987), and the lophiid genera †*Caruso*, †*Eosladenia*, *Lophiodes*, †*Sharfia*, and *Sladenia* (Figs 1-3, 5; Caruo & Bullis 1976; Caruso 1981; Bannikov 2004; Pietsch & Carnevale submitted). *Lophiomus* and *Lophius* possess large fan-shaped pectoral fins (e.g., Caruso 1983).

Integument

38. *Skin: covered with dermal spinules (0); naked (1)* (CI 1.00, RI 1.00). The skin of the outgroups *Antennarius* and *Brachionichthys* is characterized by having a dense covering of close-set dermal spinules. All known lophiid genera exhibit a smooth naked skin.

Results

The phylogenetic analysis produced a single tree (Fig. 16), with a total length of 53, a consistency index of 0.7358, and a retention index of 0.7407 (Fig. 00). Monophyly of the extant genera of the Lophiidae was reconfirmed as recognized by Caruso (1985), as well as that of the family as a whole by the inclusion of the extinct genera †*Sharfia*, †*Caruso*, and †*Eosladenia* (with bootstrap support of 99.9% and a Bremer value of 9). Eight characters without homoplasy (unique and unreversed within the Lophiidae) support lophiid monophyly: mesethmoid absent (character 1, state 1); ascending process of premaxilla autogenous (5, 1); ectopterygoid and endopterygoid fused to form a single element (11, 1); anterodorsal process of subopercle prominent, articulating through connective tissue with anteroventral margin of opercle (14, 1); teeth on fifth ceratobranchial restricted to discrete rows along lateral and medial margins (18, 1); caudal-fin rays eight (23, 1); cleithral spine present (35, 1 and 2); and skin naked (38, 1). Monophyly of lophiid genera to the exclusion of †*Sharfia* was supported (with bootstrap support of 71.9% and a Bremer value of 2) by only a single unique and unreversed character: opercle strongly bifurcate (12, 1). A sister-group relationship between †*Caruso* and *Sladenia* and a sister group relationship of this clade relative to all remaining lophiids was supported (with bootstrap support of 62.8% and a Bremer value of 1) by two characters without homoplasy: interorbital width narrow, considerably less than distance between outer margins of pterotics (2, 1); and posteriorly directed expansion of distal end of posteriormost dorsal-fin pterygiophore present (32, 1). Monophyly of a clade containing †*Eosladenia* and the remaining extant lophiid genera was supported (with bootstrap support of 77.5% and a Bremer value of 2) by three characters: haemal spines of abdominal vertebrae reduced (20, 1); neural and haemal spines of penultimate vertebra narrow and reduced (21, 1); and interdigitation between anterior soft dorsal-fin pterygiophores and underlying neural spines present (25, 1). A clade containing †*Eosladenia*, *Lophiomus* and *Lophius*, to the exclusion of *Lophiodes*, was supported by only a single character: caudal centrum depressed, bearing lateral transverse processes (22, 1). Finally, a sister-group relationship between *Lophiomus* and *Lophius* was confirmed following Caruso (1985), supported by four unique and unreversed characters: dorsolateral ridge of frontals rugose, bearing short conical spines or low rounded knobs (3, 1); parasphenoid laterally expanded (4, 1); maxillary process of palatine bifurcate (10, 1); and proximal shaft of soft dorsal-fin pterygiophores anteroposteriorly expanded (27, 1).

Discussion

†*Caruso brachysomus* is the third valid extinct taxon of the family Lophiidae known from articulated skeletal remains. All of these fossils are characterized by having a modern body architecture, suggesting that the lophiid body plan was already established in the early Eocene. Based on an analysis of the fossil record and phylogenetic considerations, Patterson & Rosen (1989), and subsequently Carnevale & Pietsch (2006), concluded that all the lophiiform lineages (antennarioids, ceratioids, chaunacoids, lophioids, and ogcocephaloids) were already in existence in the early Eocene. Unfortunately, the fossil record does not provide precise data about the minimum age for the origin of the Lophiiformes in general and the lophiiform subgroups in particular, as well as the order of events in the phylogeny of the order. Two different hypotheses resulted from recent molecular-clock analyses of divergence times: according to Alfaro *et al*. (2009) and Santini *et al*. (2009), the origin of the lophiiform body plan should be searched for in the lower part of the Paleogene, thereby suggesting that the divergence of the lophiiform lineages occurred within a relatively short time interval; on the contrary, a Cretaceous origin, in an interval between 130 and 100 Myr ago, has been proposed by Miya *et al*. (2010).

The dramatic anatomical diversity of lophiiform subgroups, including the large number of morphological peculiarities make it very difficult to interpret the origin of these fishes, as well as to hypothesize the possible appearance of a primitive lophiiform. Apart for some synapomorphic features related to specific characters of the skeleton (cranial and caudal; Pietsch 1981; Pietsch & Grobecker 1987) or to reproductive biology (Rasquin 1958; Pietsch 1981), the lophiiform body plan may be defined by four relevant aspects that were documented and cursorily discussed by Gregory & Conrad (1936): (1) the enormous mouth and throat, and consequent macrophagous habits; (2) the gill opening restricted to a tube-like opening located close to the pectoral-fin base; (3) the elongation of pectoral-fin radials that results in their pediculate appearance; and (4) the cephalic spinous dorsal fin with the anterior element modified to serve as a luring apparatus. All but the tube-like gill opening refer to skeletal features, which can be also observed in the fossils.

The huge increase in size of the mouth and throat is related to the hypertrophic development of the jaws, suspensorium, hyoid apparatus, and branchial arches. As in other vertebrates, the development of these elements of the head in the fish embryo is characterized by having a hierarchy of cell movements and interactions between neural crest and mesodermal mesenchyme, and surrounding epithelia (see, e.g., Le Douarin *et al*. 1994). Several genes that function in the development of this region of the head have been identified. Recent studies (e.g., Neuhauss *et al*. 1996; Piotrowski *et al*. 1996; Schilling *et al*. 1996) have emphasized the existence of discrete sets of genes that influence the correlated diversification of both jaws and branchial arches (including the hyoid apparatus and suspensorium).

The elongation of the pectoral fins and girdles of lophiiforms and their resemblance to tetrapod limbs was evidenced by Cuvier (1829) who called these fishes “pediculate” (little feet), a term subsequently used to identify the whole group (see, e.g., Valenciennes 1837; Günther 1861; Gill 1883, 1909). The lophiiform pectoral girdle, or pseudobrachium (Monod 1960) is primarily characterized by having enlarged pectoral-fin radials, which in certain cases are employed in a tetrapod fashion to walk over the substrate (see Pietsch & Grobecker 1987; Edwards 1989). The elongation of the pectoral-fin radials exhibits considerable variation within lophiiforms, with the maximum lengths observed in certain lophioids (see above) and antennarioids (Carnevale & Pietsch 2010). In all vertebrates the embryonic development of paired appendages passes through three main phases, namely positioning, initiation, and outgrowth. During the first phase paired appendages arise from bud initials that originate in the lateral plate mesoderm at positions considered to be specified by *Hox* gene expression in somatic mesoderm (see Burke *et al*. 1995). The initiation phase of the pectoral fins (=forelimbs) follows the positioning phase. The transcription factor gene *Tbx5* is expressed in the pectoral-fin bud (Tamura *et al*. 1999), during both the initiation and outgrowth phases, mediated by interactions with *Wnt2b* and *Fgf10* (Takeuchi *et al*. 2003). Fibroblast growth factors (FGFs) are involved in both the initiation and the following outgrowth phases; the FGFs are expressed in the apical ectodermal ridge of the fin bud promoting fin outgrowth. The anteroposterior pattern is controlled by an equivalent of the zone of polarizing activity of the amniote limb, located at the posterior margin of the fin bud. The gene *Sonic hedgehog* (*Shh*) is a major upstream factor in development expressed in this sector of the fin bud. Neumann *et al*. (1999) demonstrated that *Shh* is required to establish some aspects of the anteroposterior polarity, for normal development of the fin bud, and formation of the fin endoskeleton. In a recent paper, Sakamoto *et al*. (2009) found that a temporal shift of *Shh* activity alters the size of the endoskeletal elements in paired fins. According to those authors, a heterochronic shift of the onset of *Shh* expression influences the proliferation of cells that contribute to the formation of the endoskeletal disk, with implications in the final size of the pectoral-fin radials. We may therefore hypothesize that the synapomorphic elongation of the pectoral-fin radials in lophiiforms could be related to a heterochronic shift of the onset of *Shh* expression. However, it is also interesting to note that the enlargement of jaws, suspensorium, hyoid apparatus, branchial arches and pectoral-fin endoskeleton may be linked together and that sets of genes that influence both cranial and appendicular skeletal morphology may also contribute to correlated fin and cranial enlargement (Neuhauss *et al*. 1996; Piotrowski *et al*. 1996; Schilling *et al*. 1996).

The highly modified spinous dorsal fin of lophiiforms certainly represents one of the most spectacular morphological characteristics of these fishes. The anterior elements of this fin are shifted anteriorly over the neurocranium and are modified to serve as a luring apparatus, involving a vast series of associated modifications of the general architecture of the neurocranium and of the musculature and innervations associated with the dorsal fin (see Bertelsen 1951; Bradbury 1967; Rosen & Patterson 1969). The anteriormost spine, or illicium, usually bears an esca at its tip, which exhibits considerable diversity and is extremely useful in alpha-level taxonomy; in female ceratioid anglerfishes the esca is unique in having bioluminescent bacteria and pheromone-producing secretory glands used to attract a conspecific male (e.g., Munk 1992; Pietsch 2009), while in ogcocephalids (and perhaps in some antennariids) it apparently produces a chemical attractant used to lure buried benthic preys (Pietsch & Grobecker 1987; Bradbury 1988; Nagareda & Shenker 2009). The anterior migration of the anterior (=cephalic) dorsal-fin spines occurs during the larval stage (e.g., Matsuura & Yoneda 1986), resulting from the forward extension of the cartilaginous basal pterygiophore inside the subepidermal space (Matsuura & Yoneda 1987). The forward migration of the dorsal-fin spines continues until the first two spines are well anterior to the eyes. The pterygiophores of the spinous dorsal fin develop from a single condensation of tissue that separates into independent pterygiophores during development (e.g., Everly 2002). In basal lophiiforms the spinous dorsal fin separates into two discrete units, comprising the cephalic and post-cephalic spines respectively (see Everly 2002). The spinous dorsal fin is a major innovation of acanthomorph fishes. Mabee *et al*. (2002) hypothesized that the spinous dorsal fin essentially is an anterior duplication of the soft-rayed fin typical of all the actinopterygians. In this context, the evolution of a discrete, anatomically regionalized and spatially separated structure is an example of duplication and divergence (*sensu* Raff 1996), enhanced by modular organization (Gilbert 2010). Such an hypothesis fits well with the configuration of the dorsal fins observed in lophiiforms. However, lophiiforms exhibit a really complex dorsal-fin structure; as documented above, the spinous dorsal fin becomes separated into discrete independent units during ontogeny, thereby resulting in a submodularization of the anterior dorsal fin. The cephalic unit of the submodularized dorsal fin includes the luring apparatus and associated muscles and nerves. The possibility of a further modularization of the first dorsal-fin module (*sensu* Mabee *et al*. 2002) in lophiiforms may be confirmed by the recurrent suppression of the post-cephalic unit of the spinous dorsal fin in antennarioids, ceratioids, chaunacoids, ogcocephaloids, and some lophioids (see, e.g., Pietsch 1981; 2009). The structural complexity of the luring apparatus of lophiiforms, with its vast array of highly derived characters and functions, may be envisaged as a remarkable case of co-option (*sensu* Raff 1996), involving both morphological and functional transformation of a pre-existing submodularized first dorsal-fin module. The forward shift of the cephalic unit of the submodularized spinous dorsal fin also represents a peculiarity of lophiiform fishes. A few other teleost groups are characterized by having an extensive anterior migration of the dorsal fin (see Nelson 2006; Bannikov & Carnevale 2011). The condition typical of lophiiforms, however, is extreme considering the broad rearrangements of cranial architecture observed in these fishes. Median fin development apparently involves the same genetic programs that operate in paired appendages, and expression of *Hoxd* and *Tbx18* genes (which specify paired limb position) defines the position of median fins (Freitas *et al*. 2006) along continuous stripes of competency on the midline of the body (Yonei-Tamura *et al*. 2008). Therefore, we may hypothesize that in lophiiforms, the forward migration of the dorsal fin over the neurocranium could be produced by an anterior shift of the stripes of competency for dorsal-fin formation along the dorsal midline.

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Captions of figures and tables

Figure 1. †*Caruso brachysomus* (Agassiz, 1835). A, B, lectotype, MNHN Bol 42/43. Scale bars = 20 mm. [planned for page width]

Figure 2. †*Caruso brachysomus* (Agassiz, 1835). A, MCSNV T.978; B, complete skeleton drawn from specimen in A. Scale bars = 20 mm. [planned for page width]

Figure 3. †*Caruso brachysomus* (Agassiz, 1835). MCSNV B.13. Scale bar = 20 mm. [planned for page width]

Figure 4. †*Caruso brachysomus* (Agassiz, 1835). Reconstruction of the dorsal view of the neurocranium mainly based on MCSNV T.978 and MNHN Bol42/43. [planned for page width]

Figure 5. †*Caruso brachysomus* (Agassiz, 1835). Skull drawn from specimen MCSNV T.978. Scale bar = 20 mm. [planned for page width]

Figure 6. †*Caruso brachysomus* (Agassiz, 1835). MNHN Bol 42, left lateral view of anterior portion of the premaxilla. Scale bar = 5 mm. [planned for column width]

Figure 7. †*Caruso brachysomus* (Agassiz, 1835). MCSNV B. 13, right lateral view of opercle and subopercle. Scale bar = 5 mm. [planned for column width]

Figure 8. †*Caruso brachysomus* (Agassiz, 1835). MCSNV B.13, left ceratobranchials and (?) second pharyngobranchial. Scale bar = 3 mm. [planned for column width]

Figure 9. Dorsal view of neurocrania of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Scale bars = 5 mm. [planned for page width]

Figure 10. Left lateral view of premaxillae and maxillae of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Scale bars = 5 mm. [planned for page width]

Figure 11. Left lateral view of lower jaws, suspensoria and part of opercular apparatuses of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Bone in stipple, cartilage in black. Scale bars = 5 mm. [planned for page width]

Figure 12. Left lateral view of opercles and subopercles of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Scale bars = 5 mm. [planned for page width]

Figure 13. Branchial arches of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Bone in stipple, cartilage in black. Scale bars = 5 mm. [planned for page width]

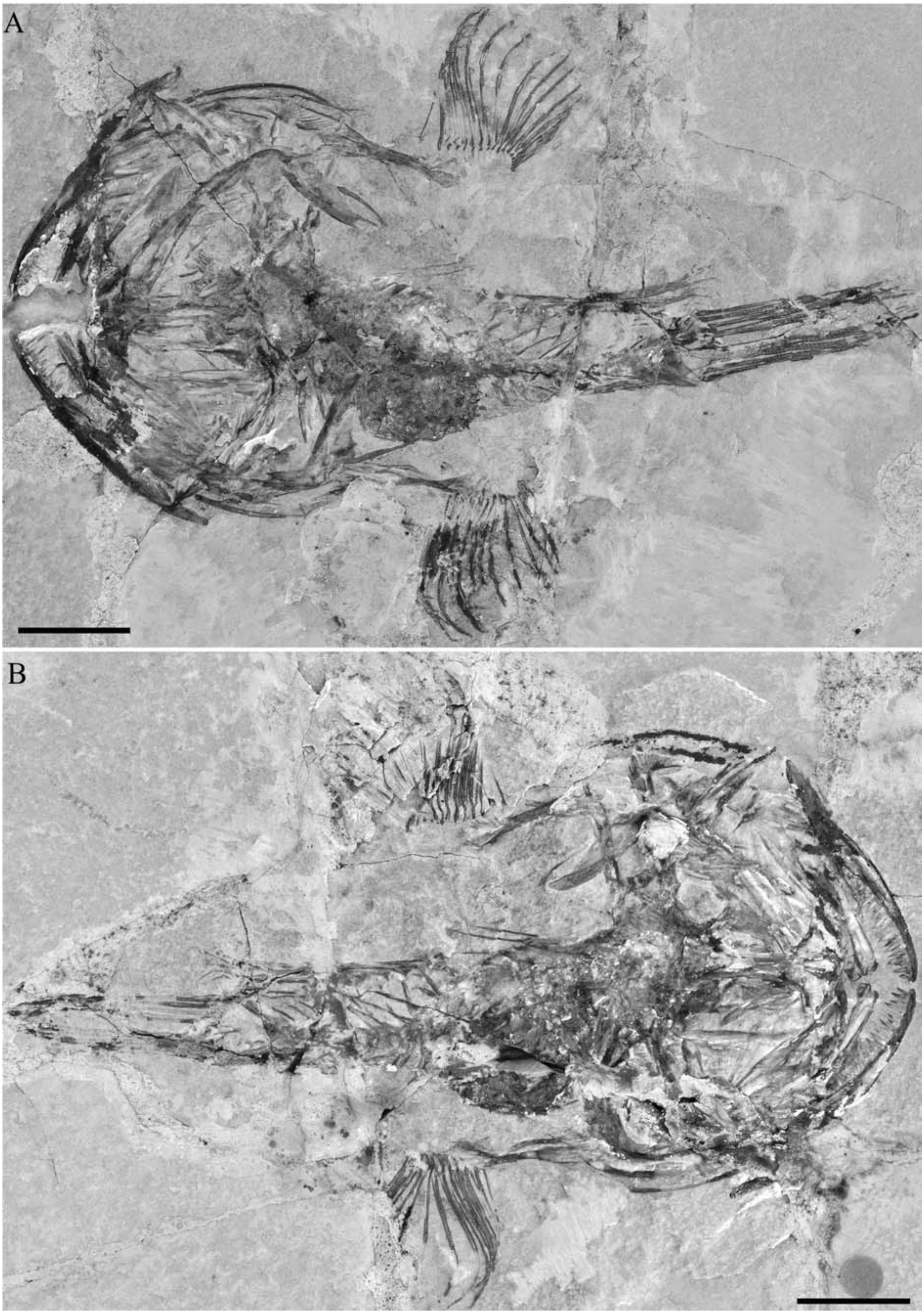
Figure 14. Left lateral view of vertebral columns, caudal skeletons, and median fins of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Bone in stipple, cartilage in black. Scale bars = 5 mm. [planned for page width]

Figure 15. Left lateral view of pectoral girdles of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Bone in stipple, cartilage in black. Scale bars = 5 mm. [planned for page width]

Figure 16. Cladogram of hypothesized relationships of the Lophiidae and two outgroups. The number above the base of a node is the Bremer value, and the number below the node indicates bootstrap support for the respective node. [planned for page width]

Table 1. Measurements (in percent standard length) of †*Caruso brachysomus* (Agassiz, 1835).

Appendix. Character matrix of 38 morphological characters for genera of the Lophiidae and two outgroups.



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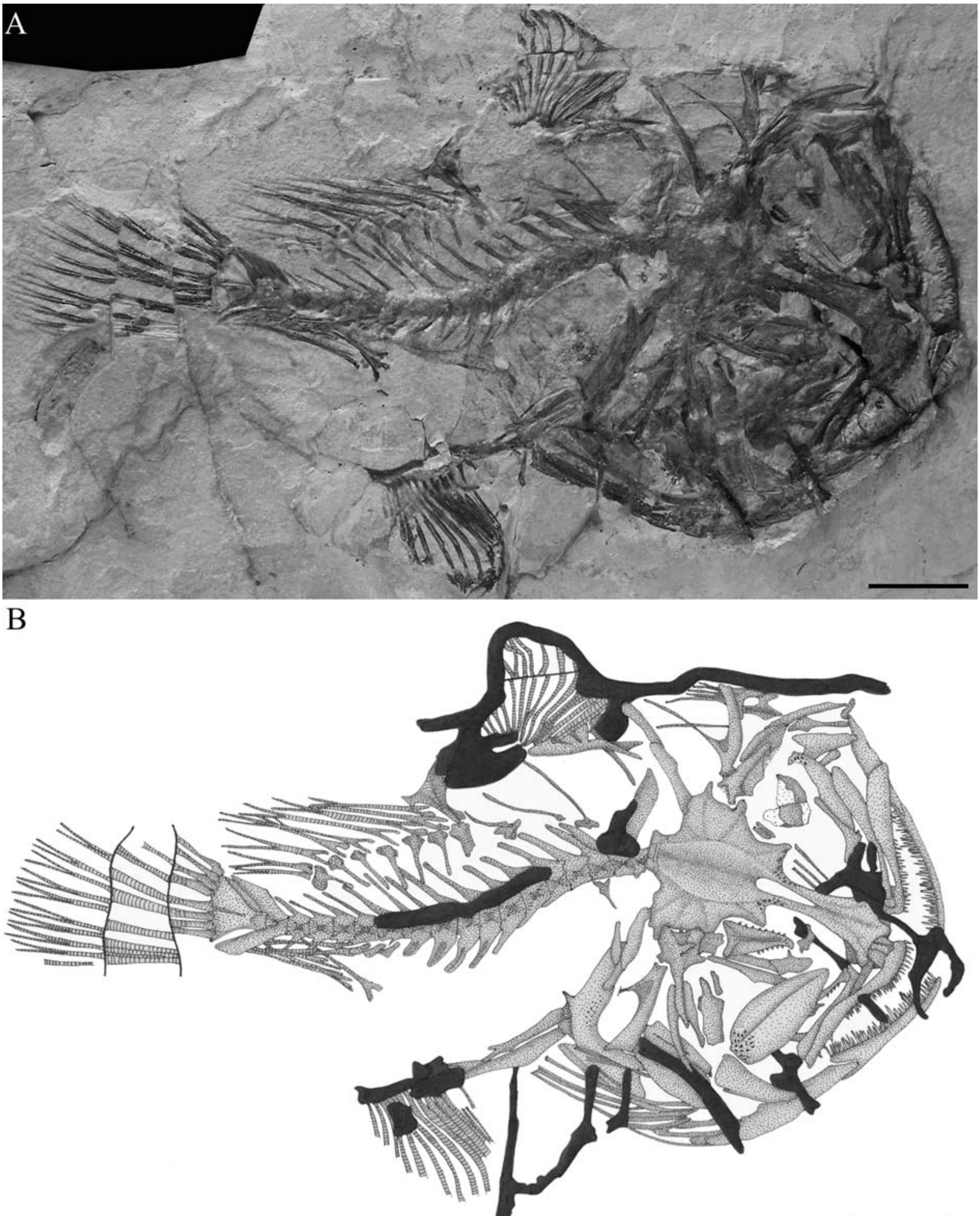
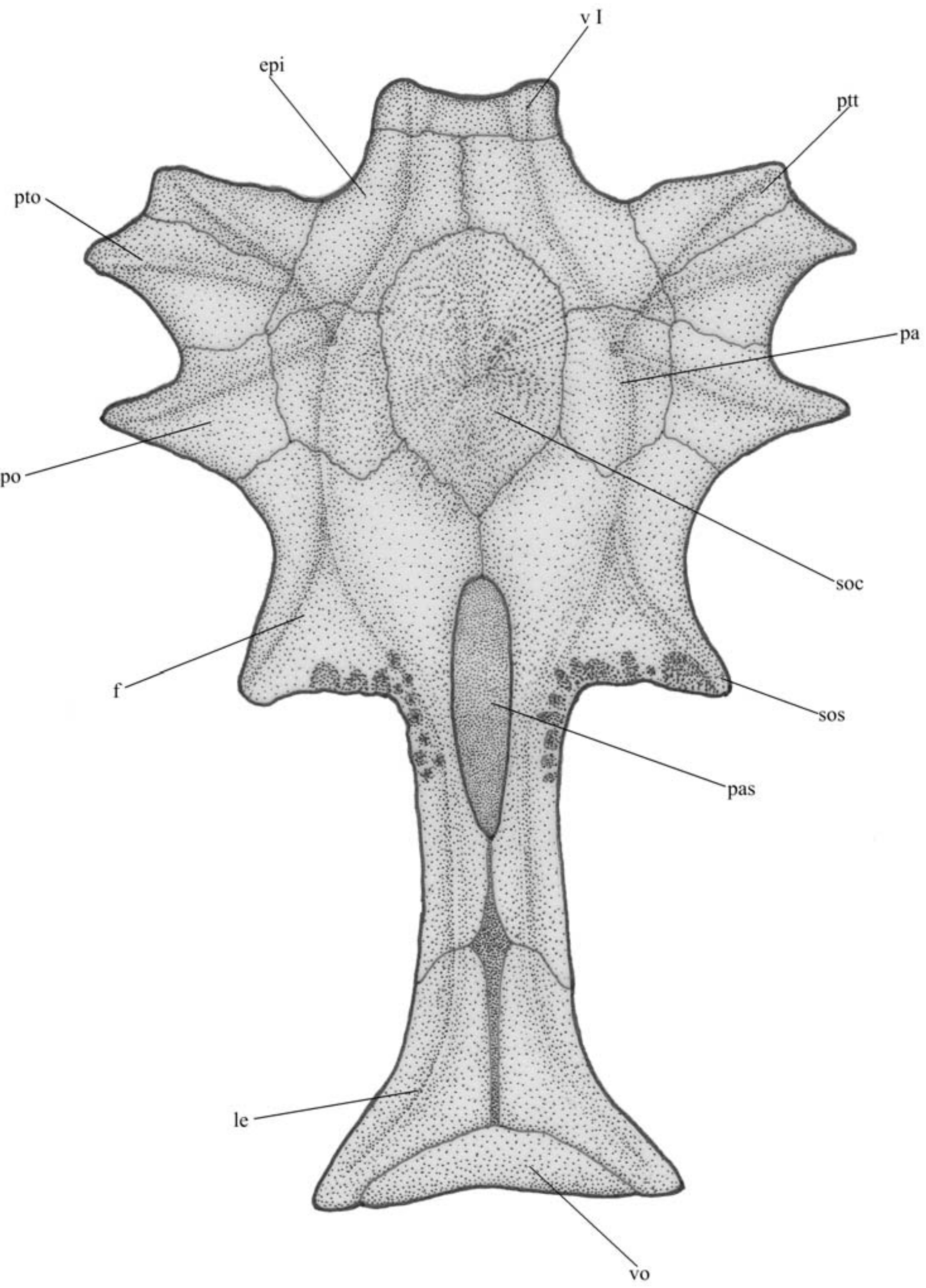


Figure 2.

Figure 3.



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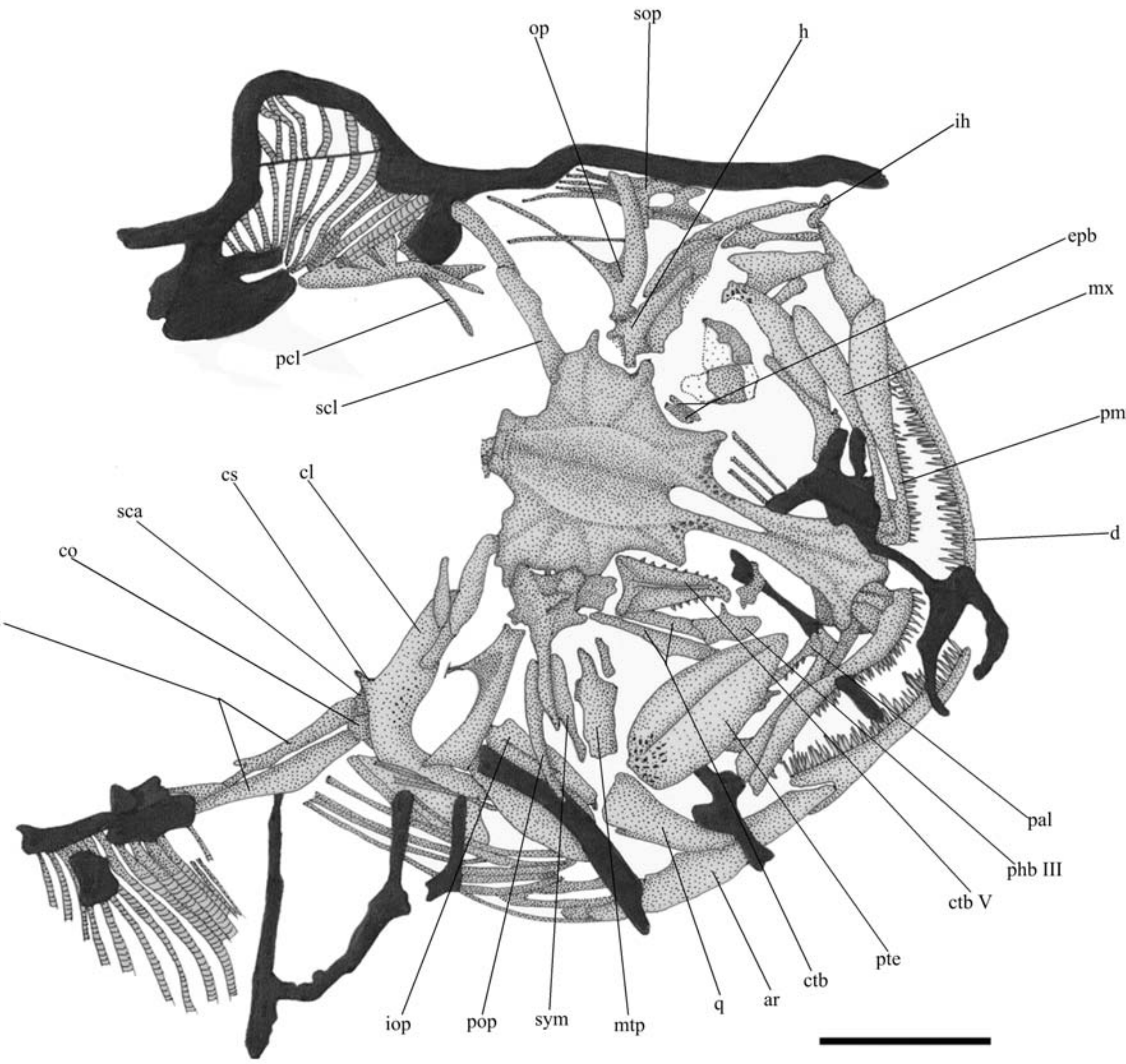
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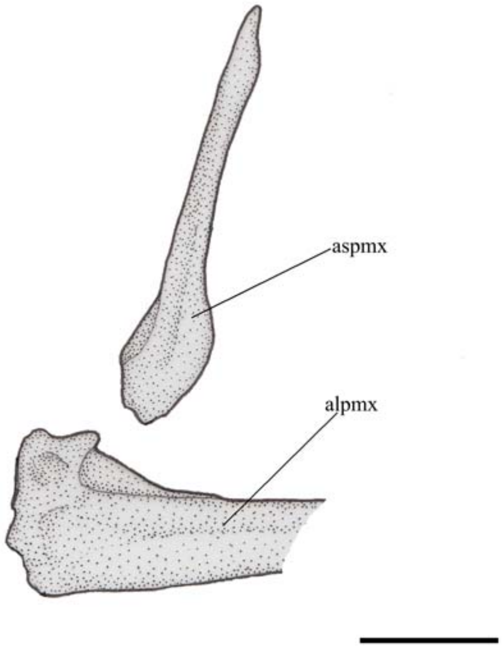
Figure 5.



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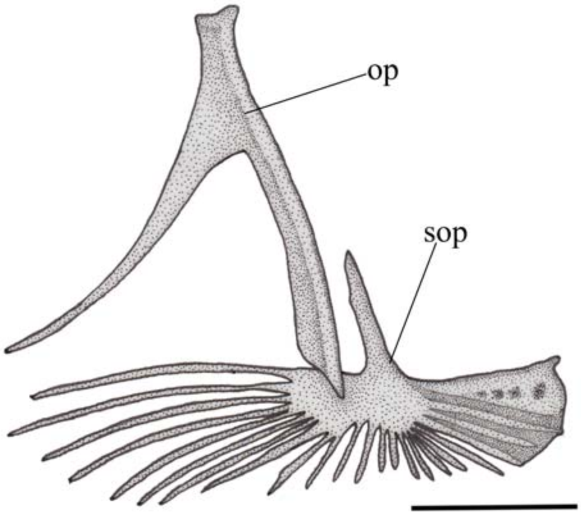

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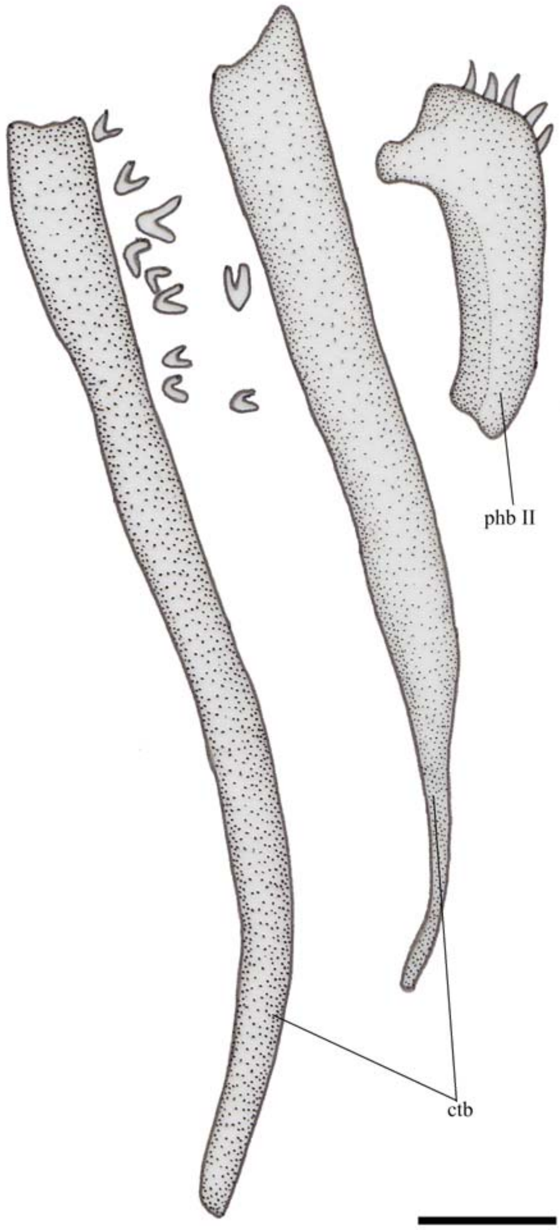

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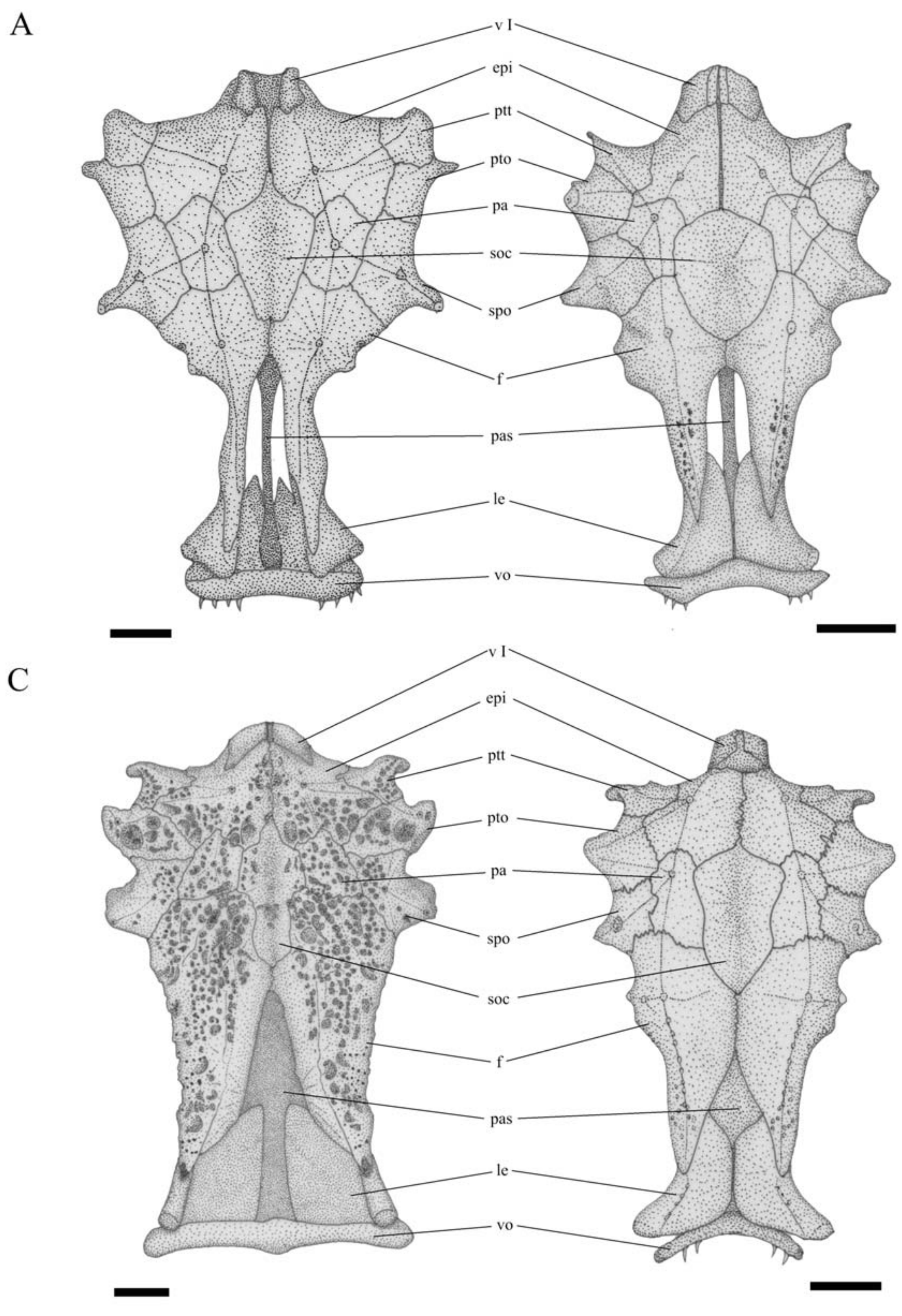
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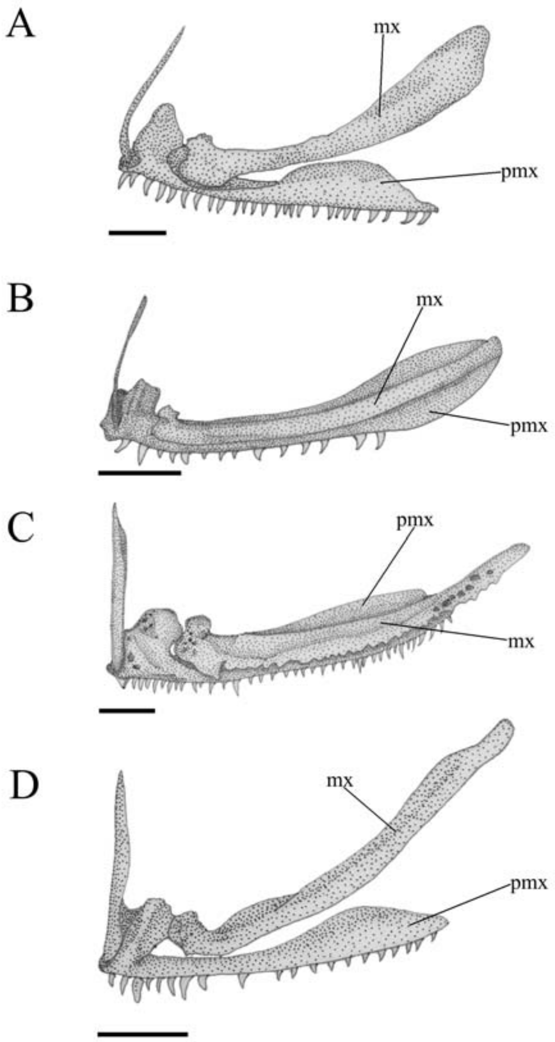
Figure 9.



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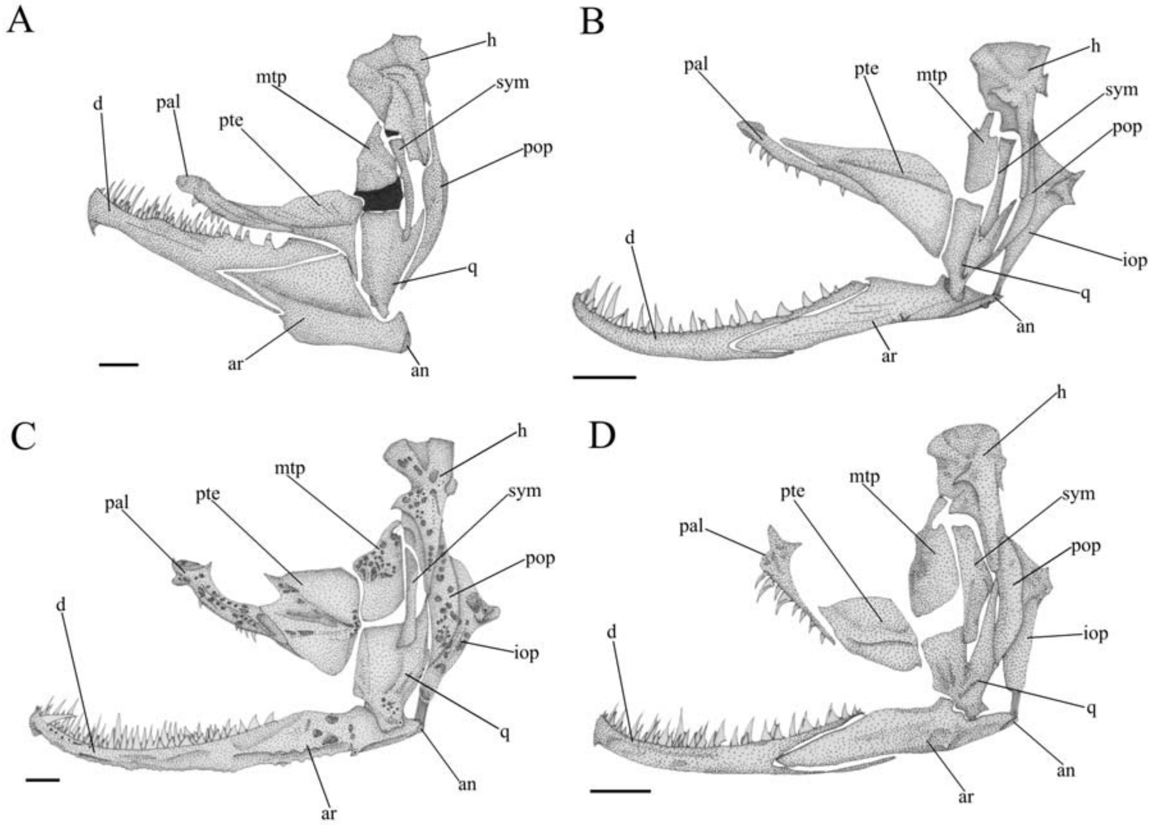

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1359 Figure 11.

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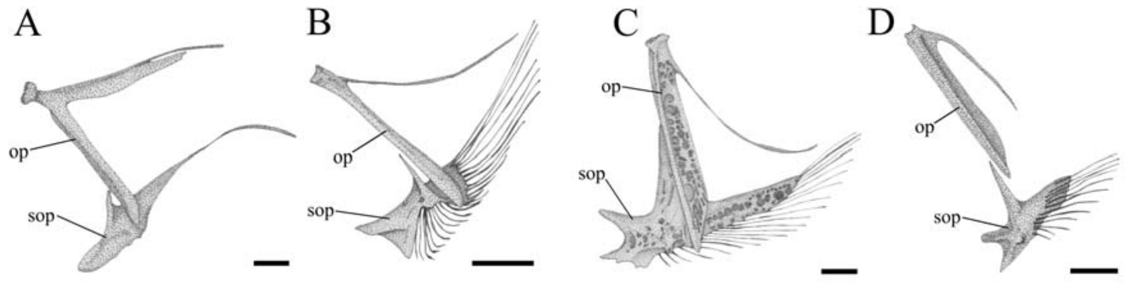

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1362 Figure 12.

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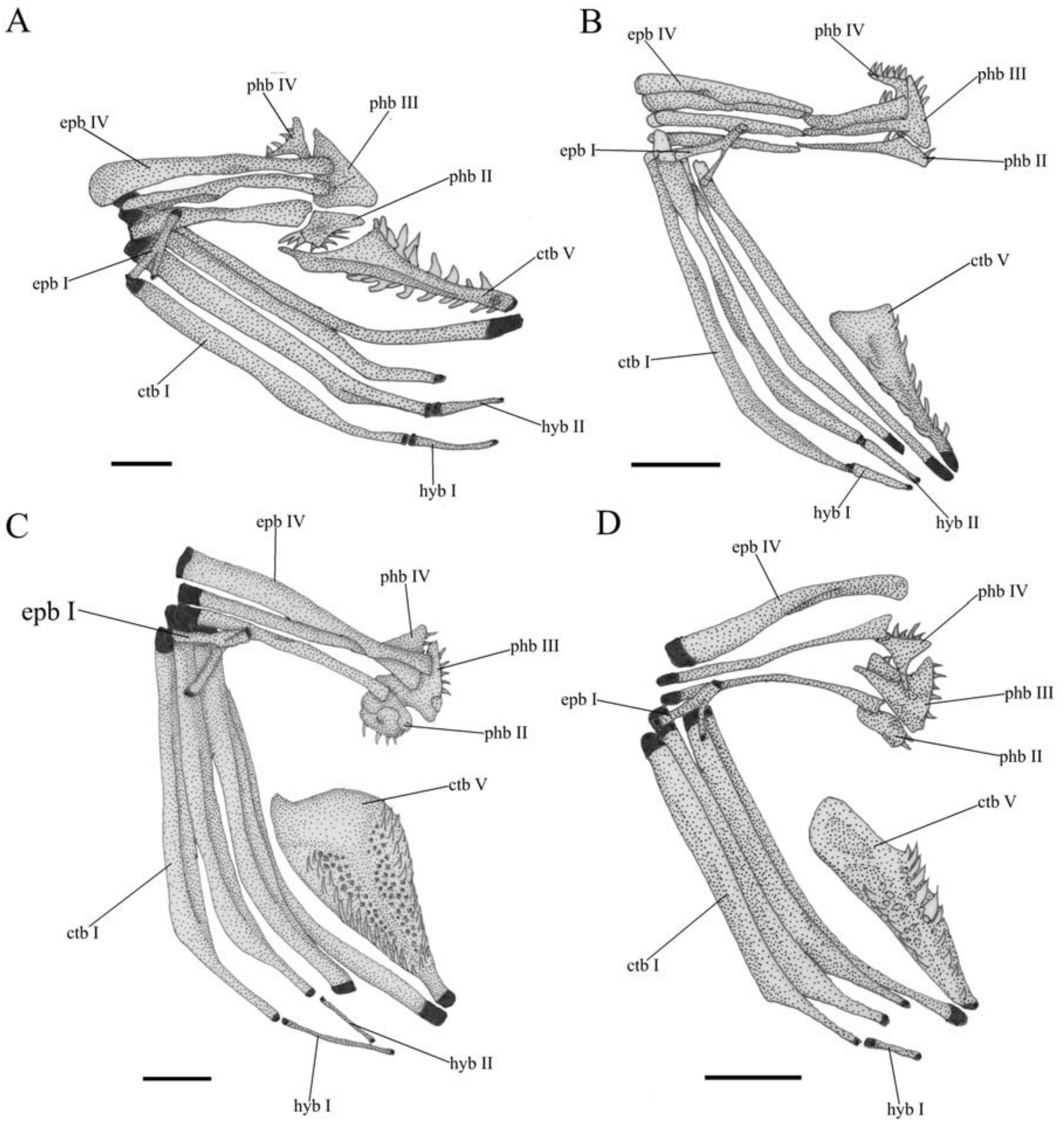
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Figure 13.

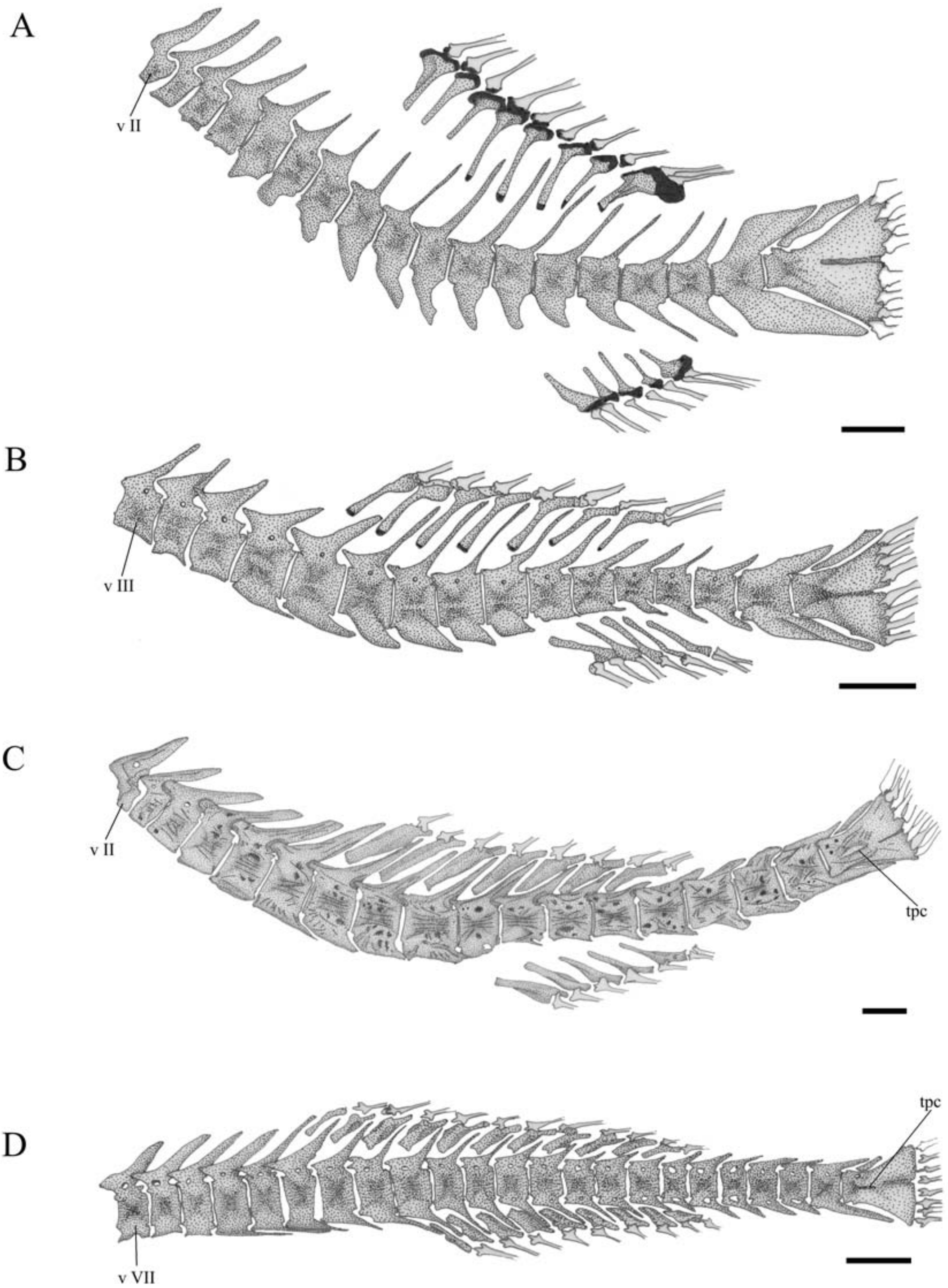

Figure 14.

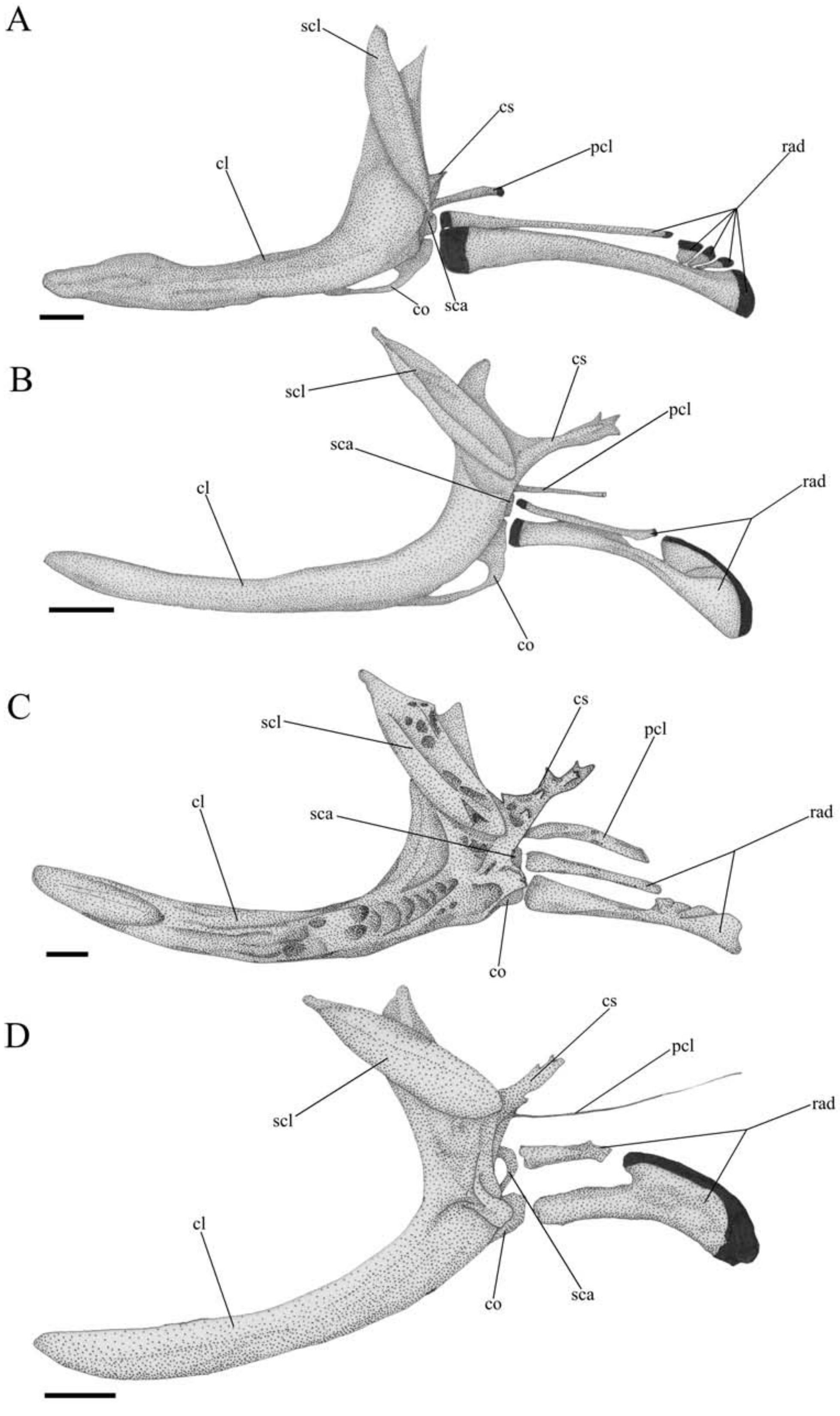
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Figure 15.

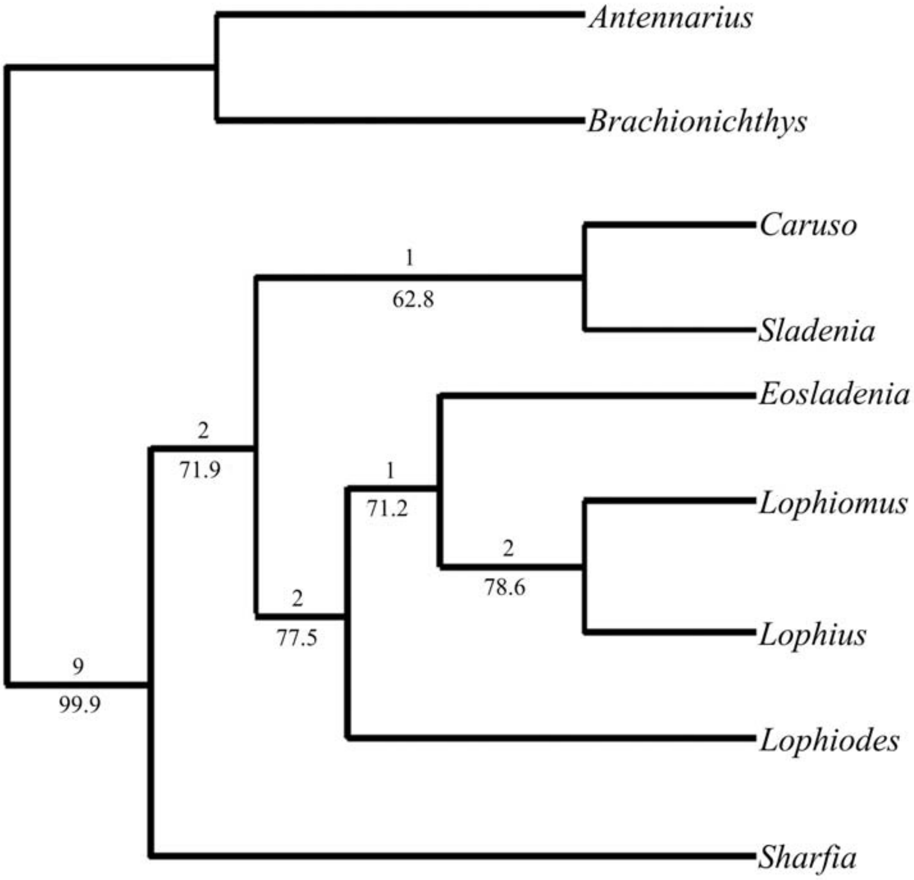

Figure 16.

	MNHN Bol. 42/43	MCSNV T.978	MCSNV B.13
Total length	165.0 mm	164.1 mm	113.7 mm
Standard length	125.7 mm	136.5 mm	92.1 mm
Head length	43.3	40.2	39.0
Head width	24.9	23.0	21.1
Snout length	21.0	24.5	26.2
Snout width	5.7	5.6	6.8
Tail length	37.7	36.0	46.7

Table 1.

	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	26	27	28	29	30	31	32	33
Antennarius	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	0	0	0	0	0	0	0
Brachionichthys	0	0	0	0	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	0	0	0
†*Caruso*	1	0	1	0	1	0	1	0	1	1	1	1	1	?	?	?	1	0	0	0	0	0	0	1	0	0	0	1	0	1	?	1	1
†*Eosladenia*	0	0	1	0	1	0	1	0	1	?	1	1	1	?	?	?	1	0	1	1	0	1	1	1	?	?	?	?	?	?	?	2	0
Lophiodes	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	1	0	2	1
Lophiomus	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	1	0	1	0	1	0	2	0
Lophius	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	2	0
†*Sharfia*	0	0	1	0	1	0	1	0	1	1	0	0	1	?	?	?	1	0	0	0	1	0	0	1	0	0	0	1	?	?	?	1	0
Sladenia	1	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1

Table 2.