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This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/101141> since

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This is an author version of the contribution published on:

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JOURNAL OF SYSTEMATIC PALAEONTOLOGY (2012) 10

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

35
36 **Keywords:** Teleostei; Lophiiformes; Lophiidae; comparative osteology; phylogenetic
37 analysis; Eocene; Monte Bolca

40 **Introduction**

41 Anglerfishes of the family Lophiidae are the sole members of the Lophioidei, one of the five
42 suborders of the order Lophiiformes (see Pietsch & Grobecker 1987; Pietsch & Orr 2007), a
43 morphologically derived group of marine teleost fishes that includes some of the most bizarre
44 and anatomically peculiar representatives of the animal kingdom. The Lophiidae consists of
45 four extant genera with fewer than 30 described species (e.g., Regan 1903; Caruso & Bullis
46 1976; Caruso 1981; 1983) that inhabit tropical, subtropical and temperate waters of the
47 Atlantic, Indian and Pacific oceans. These fishes, also known as monkfishes or goosefishes,
48 are benthic on different substrates at depths ranging from the shoreline to greater than 1500

49 meters. They are characterized by having a dorsoventrally compressed head, a wide
50 cavernous mouth and a luring apparatus, the latter primarily consisting of a highly modified
51 anterior spine of the dorsal fin, commonly called the illicium. The angling behavior of
52 lophiids was reported for the first time by Aristotle in his *Historia animalium* and
53 subsequently by many naturalists in the eighteenth and nineteenth centuries (e.g., Parsons
54 1750; Hanow 1768; Montin 1779; Geoffroy St. Hilaire 1807; 1824; 1827; Bailly 1824).
55 Lophiid anglerfishes are opportunistic feeders with a common feeding strategy; they are lie-
56 and-wait predators settling on soft-bottom substrates and luring their prey by wriggling the
57 illicium (e.g., Wilson 1937; Gudger 1945). Some species of this family, mostly belonging to
58 the genus *Lophius*, support important commercial fisheries, and for this reason several
59 aspects of their life history and reproductive biology are extremely well documented (see,
60 e.g., Fariña *et al.* 2008). However, despite the economic relevance and abundance of these
61 fishes, their osteological structure remains poorly known and almost totally restricted to
62 species of the genus *Lophius* (Brühl 1856; Morrow 1882; Supino 1908; Regan 1912; Gregory
63 1933; Montcharmont 1950; Eaton *et al.* 1954; Monod 1960; Field 1966; Oliva *et al.* 1968; Le
64 Danois 1974).

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

73 In this study we describe a new genus of the Lophiidae, including its anatomy, based on
74 material from the Eocene of Monte Bolca, previously referred to the genus *Lophius* (Volta
75 1796; Agassiz 1833-1844; see synonymy below). Previous to this study, the family Lophiidae
76 had never been carefully investigated osteologically and phylogenetically. We therefore set
77 out to examine the comparative osteology of the Lophiidae phylogenetically. This work is
78 another in a series of papers focused on the fossil record of lophiiform fishes (Carnevale &
79 Pietsch 2006; 2009a; 2009b; 2010; in press; Carnevale *et al.* 2008; Pietsch & Carnevale, in
80 press).

81

82 **Materials and methods**

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

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

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

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

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

102 Brachionichthyidae: *Brachionichthys australis*, UW 116842, 38.7 mm SL; UW 116843,
103 55 mm SL; *Brachionichthys hirsutus*, NMV A.19954, 80 mm SL; †*Histionotophorus*
104 *bassani*, MCSNV I.G.23163, 50.5 mm SL; NHM 19060, 16.4 mm SL; †*Orrichthys*
105 *longimanus*, MCSNV T.160/161, 63 mm SL; *Sympterichthys unipennis*, UW 116844, 31.6
106 mm SL; UW 116845, 34 mm SL.

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

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

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

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

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

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

126

127 **Systematic palaeontology**

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

129 Order **Lophiiformes** Garman, 1899

130 Suborder **Lophioidei** Regan, 1912

131 Family **Lophiidae** Rafinesque, 1810

132 Genus †*Caruso* nov.

133 (Figs. 1-8)

134

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

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

154

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

158

159 **Included species.** Monotypic.

160

161 †*Caruso brachysomus* (Agassiz, 1835)

162

163 1796 *Lophius piscatorius* Volta: pl. 42, fig. 3 (misidentification).

164 1818 *Lophius piscatorius* var. *Gonelli* Risso; De Blainville: 340, 342 (in part;

165 misidentification based on *Lophius piscatorius* Volta).

166 1835 *Lophius brachysomus* Agassiz (name only): 292 (in part).

167 1844 *Lophius brachysomus* Agassiz; Agassiz: 114, vol. 5, pl. 1, figs 1-2.

168 1874 *Lophius brachysomus* Agassiz; Zigno: 105 (in part).

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

170 1901 *Lophius brachysomus* Agassiz; Woodward: 591 (in part).

171 1905 *Lophius brachysomus* Agassiz; Eastman: 31 (in part).

172 1922 *Lophius brachysomus* Agassiz; D'Erasmus: 140-141 (in part).
173 1927 '*Lophius*' *brachysomus* Agassiz; Arambourg: 216.
174 1967 *Lophius brachysomus* Agassiz; Andrews, Gardiner, Miles & Patterson: 660.
175 Non 1972 *Lophius brachysomus* Agassiz; Sorbini; pl. 18 (misidentification).
176 1980 *Lophius brachysomus* Agassiz; Blot: 353-354 (in part).
177 1983 *Lophius brachysomus* Agassiz; Sorbini; pl. 9.
178 Non 1991 *Lophius brachysomus* Agassiz; Frickhinger: 694 (misidentification).
179 Non 1996 *Lophius brachysomus* Agassiz; Long: 157, fig. 2 (misidentification).

180

181 **Diagnosis.** As given for the genus.

182

183 **Holotype.** MNHN Bo142/43, a relatively complete skeleton in part and counterpart, 125.7
184 mm SL; late early Eocene, Ypresian; Monte Bolca, Pesciara cave site (Fig. 1).

185

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

191

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

194

195 **Biotope and palaeoecology.** The finely laminated micritic limestone of the Pesciara cave site
196 has provided a huge amount of fossils, including thousands of exceptionally well-preserved,

197 fully articulated fish skeletons. The fish assemblage consists of more than 200 species of
198 sharks, batoids, pycnodontiforms and teleosts, representing the earliest evidence of an
199 acanthomorph dominated ichthyofauna, which also includes several representatives of the
200 fish groups found on coral reefs today (Patterson 1993; Bellwood 1996; Landini & Sorbini
201 1996). The fish assemblage from Monte Bolca therefore marks the starting point in the
202 known evolution of many reef fish groups and provides a reliable evidence of the
203 morphological and compositional stability of tropical and subtropical marine ichthyofaunas
204 throughout the Cenozoic (Bellwood & Wainwright 2002).

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

216

217 **Remarks.** †*Lophius brachysomus* was erected by Louis Agassiz (1835) to allocate the two
218 lophiid anglerfish specimens from Monte Bolca, previously documented in the *Ittiolitologia*
219 *Veronese*, the voluminous monograph by Abbot Giovanni Serafino Volta (1796), and referred
220 to the extant species *Lophius piscatorius* and *Loricaria plecostomus* respectively. The two
221 lophiid specimens, both in part and counterpart, were part of the Gazola collection of fossil

222 fishes from Monte Bolca that was confiscated by the armies of Napoleon, and deposited in
223 the Muséum National d'Histoire Naturelle in Paris (see Pietsch and Carnevale, in press).
224 According to Agassiz (1844), the specimens represent different ontogenetic stages of a single
225 species; the smaller one was formerly assigned to the catfish species *Loricaria plecostomus*
226 by Volta (1796), while the larger one was considered as the lithified counterpart of the
227 Atlantic-Mediterranean anglerfish species *Lophius piscatorius*. Several authors (see
228 synonymy) followed the taxonomic interpretation of Agassiz up to the second half of the
229 1920s when Camille Arambourg (1927) questioned the generic identity of these fossils and,
230 mainly based on their number of vertebrae, considered them to be related to the extant genus
231 *Lophiomus*. Subsequently, Andrews *et al.* (1967) emphasized the necessity of a new detailed
232 systematic study of these fossils in order to confirm their position. More recently, Blot (1980)
233 cursorily discussed the generic identity of these specimens suggesting that a new generic
234 name would be necessary to include them. A recent examination of the specimens in April
235 2010, however, has revealed the existence of two different taxa among the type material
236 housed in the MNHN in Paris. The smaller specimen (MNHN Bol38/39) that was formerly
237 assigned to *Loricaria plecostomus* by Volta (1796) has been described as a new genus and
238 species (Pietsch & Carnevale in press). The morphology of the larger specimen is described
239 herein together with that of additional specimens residing among the collections of the
240 MCSNV.

241

242 **Anatomical descriptions**

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

247 Measurements are summarized in Table 1.

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

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

251

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

272 order to accommodate the ascending processes of the premaxillae. The posterior margin of
273 the neurocranium is moderately concave on each side of the vertebral column, forming a
274 large surface for the insertion of the epaxial muscles.

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

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

296 medially with the vomer, posteriorly with the frontals, and ventromedially with the
297 parasphenoid.

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

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

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

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

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

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

318 The pterotic is thickened and flange-like laterally and more massive medially; its lateral
319 flange terminates with a blunt rounded spine. A prominent pterotic ridge radiates medially
320 from that spine. The distance measured between the lateral ends of the pterotic spines

321 coincides with the maximum width of the neurocranium. Each pterotic makes contact
322 anteriorly with the sphenotic, laterally with the parietal, posteromedially with the epioccipital,
323 and posteriorly with the posttemporal.

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

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

334

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

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

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

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

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

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

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

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

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

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

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

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

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

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

399

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

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

414

415 **Vertebral column.** The vertebral column (Fig. 2B) is compact with the abdominal portion
416 arcuate in a kyphotic curve, with the concave side toward the ventrum. There are 19 vertebrae
417 (including the last hemicentrum fused to the hypural complex). As in other lophiiforms, the
418 first vertebra is closely connected to the neurocranium (see, e.g., Rosen & Patterson 1969).
419 The vertebral centra are massive and squared except for the second that is nearly rectangular,

420 higher than long. The neural spines of the vertebrae three through eight incline posteriorly
421 and are laterally flattened and anteroposteriorly expanded. More posteriorly, the neural
422 spines are elongate and cylindrical but become progressively shorter and more inclined in the
423 caudal region. Neural prezygapophyses are well-developed on all vertebrae. The first haemal
424 spine occurs on the sixth vertebra. The first two haemal spines are poorly developed and
425 remarkably inclined posteriorly, bent over the anteroventral sector of the succeeding
426 vertebrae. Haemal arches and spines of the vertebrae eight through twelve are notably broad
427 and laterally compressed, becoming considerably shorter more posteriorly.

428

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

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

443 The soft-rayed dorsal fin (Fig. 2B) inserts at the level of the tenth vertebra and contains
444 nine distally bifurcated rays supported by seven pterygiophores. The first ray is in

445 supernumerary association on the first dorsal-fin pterygiophore, and the posteriormost dorsal-
446 fin pterygiophore supports two rays. The rays gradually increase in length from the first to the
447 fourth, and succeeding elements are of progressively decreasing size. The first pterygiophore
448 of the soft dorsal fin is massive, short and anteroposteriorly enlarged, whereas the succeeding
449 elements are characterized by having dorsally rounded heads and elongate narrow vertical
450 shafts interdigitating in the underlying interneural spaces. The posterior two dorsal-fin
451 pterygiophores insert in the space between the neural spines of the vertebrae 12th and 13th.
452 The head of the posteriormost pterygiophore has a hypertrophied rounded posterior flange.

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

458

459 **Paired fins and support.** The paddle-shaped pectoral fin (Figs. 1-3) comprises 14 to 16
460 simple rays. The fin is supported by two greatly elongate (22.8 – 23.3 % SL) and thick radials
461 (Fig. 2B, 5). The dorsal radial is cylindrical, about two thirds the length of the ventral one.
462 The ventral pectoral-fin radial is considerably expanded distally to form an articulatory
463 surface for the pectoral-fin rays; the distal flat and dorsally convex expansion of the ventral
464 radial shows some radial striae that possibly represent the traces of the ontogenetic fusion of
465 additional radial elements. Scapulae and coracoids are poorly preserved in the examined
466 material. The posttemporal, the dorsalmost element of the pectoral girdle, is firmly connected
467 to the posterolateral corner of the neurocranium. The supraclithrum is approximately ovoid
468 and laminar, closely associated with the lateral surface of the dorsal part of the ventral arm of
469 the cleithrum. The cleithrum is the largest bone of the pectoral girdle. The horizontal and

470 anteromedially directed arm is always nearly totally hidden by other cranial bones or partially
471 covered by the sediment. The vertical arm is broad, laterally flattened and dorsomedially
472 oriented; a short pointed and stout cleithral (=humeral) spine emerges in the basal portion of
473 the vertical arm of the clathrum along its posterior margin. The lateral surface of this bone is
474 slightly ornamented by small pits in the junction area between the vertical and horizontal
475 arms. A single rod-like postcleithrum appears to be present.

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

481

482 **Phylogenetic relationships**

483 The present analysis is based on an examination of seven lophioid genera (†*Caruso*,
484 †*Eosladenia*, *Lophiodes*, *Lophiomus*, *Lophius*, †*Sharfia*, and *Sladenia*), representing all
485 known members of the family Lophiidae (see Caruso 1985), plus two outgroup antennarioid
486 genera *Antennarius* and *Brachonichthys* (Pietsch 2009:175–179, fig. 188). The purpose of
487 this section is to place the extinct genera †*Caruso*, †*Eosladenia*, and †*Sharfia*, and the four
488 extant lophiid genera in a phylogenetic framework of the family. A data matrix of nine taxa
489 and 38 characters was constructed (Appendix 1). All characters were treated as unordered and
490 unweighted. All characters except number 35 (see below) were binary. Characters states that
491 could not be determined from the fossils because of inadequate preservation are coded as
492 unknown, and indicated in the data matrix by a question mark. The matrix was analyzed with
493 PAUP (Swofford 2002), using the branch and bound algorithm, with accelerated
494 transformation (ACCTRAN) to optimize characters. To evaluate branch support, a heuristic

495 bootstrap analysis of 1000 replicates was conducted, with simple addition sequence and TBR
496 (tree bisection-reconnection) branch-swapping options. Bremer decay values (Bremer 1988)
497 were calculated using TREEROT (Sorenson 1999).

498

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

512

513 **Cranium**

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

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

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

536 3. *Dorsolateral ridge of the frontals: smooth and uninterrupted (0); rugose, bearing*
537 *short conical spines or low rounded knobs (1)* (CI 0.50, RI 0.00). This character was
538 originally described by Caruso (1985). The ornamented rugosities of the dorsolateral ridge of
539 the frontal bones are unique to *Lophiomus* and *Lophius*, in which they increase during
540 ontogeny. In both outgroups and other lophiids, including the fossil genera †*Caruso*,
541 †*Eosladenia*, and †*Sharfia*, the dorsolateral ridge of the frontals is smooth (Fig. 9; Bannikov
542 2004; Pietsch & Carnevale submitted).

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

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

549

550 **Jaws**

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

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

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

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

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

575

576 **Suspensorium**

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

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

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

605

606 **Opercular series**

607 12. *Opercular shape: subtriangular (0); strongly bifurcate (1)* (CI 1.00, RI 1.00). The
608 possession of a fully ossified polygonal opercle is plesiomorphic for acanthomorphs and
609 more generally for teleost fishes. The opercle is subtriangular in outline in the outgroups
610 *Antennarius* and *Brachionichthys*, and the Eocene lophiid †*Sharfia* (Pietsch & Carnevale
611 submitted). Such a condition has also been observed in lophichthyids, tetrabrachiids,
612 ogocephaloids and chaunacoids (see Pietsch 1981). In all other members of the Lophiidae
613 the opercles are characterized by having a deep indentation along the posterior margin, which
614 makes them strongly bifurcated (Figs 5, 7, 12; Bannikov 2004; Pietsch & Carnevale
615 submitted). A bifurcated opercle also occurs in most ceratioids (see, e.g., Regan & Trewavas
616 1932; Pietsch 2009), possibly representing the result of an independent derivation.

617 13. *Posteroventral margin of the subopercle: simple (0); fimbriate (1)* (CI 0.50, RI
618 0.67). The subopercle of most lophiiform fishes is a morphologically heterogeneous bone
619 with entire margins (e.g., Regan & Trewavas 1932; Pietsch 1974; 1981). In antennarioids

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

628 14. *Anterodorsal process of the subopercle: short, reduced to a spine (0); prominent,*
629 *articulating through connective tissue with the anteroventral margin of the opercle (1)* (CI
630 1.00, RI 1.00). The subopercles of a number of lophiiforms (including both the outgroups)
631 bear a median spiny process on the anterodorsal margin. A stout prominent ascending process
632 arising from the anterodorsal margin of the subopercle, making contact with the anterior
633 margin of the opercle is unique to the Lophiidae (Figs 5, 7, 12; Bannikov 2004; Pietsch &
634 Carnevale submitted).

635

636 **Gill arches**

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

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

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

647 17. *Second hypobranchial: present (0); absent (1)* (CI 1.00, RI 0.00). The second
648 hypobranchial is present in the outgroups *Antennarius* and *Brachionichthys* (Pietsch 1981;
649 Carnevale & Pietsch 2010), and in the lophiids *Lophiodes*, *Lophiomus*, and *Sladenia* (Figs
650 13A-C), but absent in *Lophius* (Fig. 13D). The fossil genera are coded as unknown.

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

657

658 **Axial skeleton and caudal fin**

659 19. *Number of vertebrae: 18-22 (0); 26-31 (1)* (CI 1.00, RI 0.00). This character was
660 described by Caruso (1985). The outgroups and the lophiid genera †*Caruso*, †*Eosladenia*,
661 *Lophiodes*, *Lophiomus*, †*Sharfia*, and *Sladenia* usually have 22 or fewer vertebrae. *Lophius*
662 has 26 to 31 vertebrae. The apomorphic high vertebral number of *Lophius* has been
663 considered (Arambourg 1927) as further evidence of the so-called Jordan's rule (Jordan
664 1892), which states that number of vertebrae in fishes increase with latitude. The vertebral
665 number in fishes, however, is subject to the influence of many different (often interacting)
666 factors (see, e.g., McDowall 2008), which makes it very difficult to evaluate the plausibility
667 of the possible effects of the Jordan's rule in anglerfishes of the genus *Lophius*.

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

670 expanded and well developed in *Antennarius*, *Brachionichthys* (Pietsch 1981; Carnevale &
671 Pietsch 2010), and the lophiid genera †*Caruso*, †*Sharfia*, and *Sladenia* (Figs 2B, 14A; Pietsch
672 & Carnevale submitted). The abdominal vertebrae of the other lophiid genera (†*Eosladenia*,
673 *Lophiodes*, *Lophiomus*, *Lophius*) possess reduced haemal spines (Figs 14B-D; Bannikov
674 2004).

675 21. *Neural and haemal spines of the penultimate vertebra: well developed and*
676 *anteroposteriorly expanded (0); narrow, reduced in size (1)* (CI 1.00, RI 1.00). In the vast
677 majority of lophiiforms, including the outgroups *Antennarius* and *Brachionichthys* (Pietsch
678 1981; Carnevale & Pietsch 2010), and the lophiids †*Caruso*, †*Sharfia*, and *Sladenia*, the
679 penultimate vertebra bears considerably enlarged and anteroposteriorly expanded neural and
680 haemal spines (Figs 2B, 14A; Pietsch & Carnevale submitted). These spines are narrow and
681 anteroposteriorly shortened in †*Eosladenia*, *Lophiodes*, *Lophiomus*, and *Lophius* (Figs 14B-
682 D; Bannikov 2004).

683 22. *Caudal centrum: rounded in cross section (0); depressed with lateral transverse*
684 *processes (1)* (CI 1.00, RI 1.00). This character was described and discussed by Caruso
685 (1985). The caudal centrum of *Antennarius*, *Brachionichthys*, †*Caruso*, *Lophiodes*, †*Sharfia*,
686 and *Sladenia* (Figs 2B, 14A-B; Pietsch 1981; Carnevale & Pietsch 2010; Pietsch & Carnevale
687 submitted) is nearly circular in cross section. In †*Eosladenia*, *Lophiomus*, and *Lophius*, the
688 caudal centrum is in some ways depressed and bears well-developed lateral transverse
689 processes (Figs 14C-D; Bannikov 2004).

690

691 **Median fins**

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

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

700 25. *Interdigitation between the anterior soft dorsal-fin pterygiophores and the*
701 *underlying neural spines: absent (0); present (1)* (CI 1.00, RI 1.00). The anterior soft dorsal-
702 fin pterygiophores of *Antennarius*, *Brachionichthys*, †*Caruso*, †*Sharfia* and *Sladenia* lie
703 above the corresponding neural spines (Fig. 2B, 14A; Pietsch 1981; Carnevale & Pietsch
704 2010; Pietsch & Carnevale submitted), but interdigitate with the neural spines in
705 †*Eosladenia*, *Lophiodes*, *Lophiomus*, and *Lophius* (Figs 14B-D; Bannikov 2004).

706 26. *Interdigitation between the anal-fin pterygiophores and the overlying haemal*
707 *spines: present (0); absent (1)* (CI 0.50, RI 0.67). The anal-fin pterygiophores of *Antennarius*,
708 *Brachionichthys*, *Lophius*, and †*Sharfia* are closely associated with the corresponding haemal
709 spines and insert in the interhaemal spaces (Fig. 14D; Pietsch 1981; Carnevale & Pietsch
710 2010; Pietsch & Carnevale submitted). The anal-fin pterygiophores of the lophiid genera
711 †*Caruso*, †*Eosladenia*, *Lophiodes*, *Lophiomus*, and *Sladenia* lie well below the corresponding
712 haemal spines (Figs. 2B, 14A-C; Bannikov 2004).

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

720 28. *Rays articulating with the anteriormost dorsal-fin pterygiophore: two, one*
721 *supernumerary (0); one (1)* (CI 0.33, RI 0.00). The anterior dorsal-fin pterygiophore supports
722 a supernumerary ray in *Antennarius*, †*Caruso*, *Lophiomus*, †*Sharfia*, and *Sladenia* (Fig. 2B,
723 14A, C; Pietsch 1981; Pietsch & Carnevale submitted). The supernumerary ray on the first
724 dorsal-fin pterygiophore is absent in *Brachionichthys*, *Lophiodes*, and *Lophius* (Figs 14B, D;
725 Carnevale & Pietsch 2010). This character is unknown in †*Eosladenia*.

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

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

738 31. *Rays articulating with the posteriormost dorsal-fin pterygiophore: one (0); two (1)*
739 (CI 0.50, RI 0.50). The posteriormost anal-fin pterygiophore supports a single ray in
740 *Antennarius*, *Brachionichthys*, and *Lophius* (Fig. 14D; Pietsch 1981; Carnevale & Pietsch
741 2010), but two rays are associated with this element in †*Caruso*, *Lophiodes*, *Lophiomus*, and
742 *Sladenia* (Figs 2B, 14A-C). †*Eosladenia* and †*Sharfia* are coded as unknown.

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

745 posteriormost dorsal-fin pterygiophore is similar to those of the preceding elements in both
746 the outgroups, and in the lophiids †*Eosladenia*, *Lophiodes*, *Lophiomus*, *Lophius*, and
747 †*Sharfia* (Figs 14B-D; Pietsch 1981; Bannikov 2004; Carnevale & Pietsch 2010; Pietsch &
748 Carnevale submitted). In †*Caruso* and *Sladenia* the distal sector of the posteriormost dorsal-
749 fin pterygiophore bears a broad posteriorly directed expansion with rounded profile (Figs 2B,
750 14A).

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

757

758 **Pectoral fin and girdle**

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

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

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

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

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

782

783 **Integument**

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

787

788 **Results**

789 The phylogenetic analysis produced a single tree (Fig. 16), with a total length of 53, a
790 consistency index of 0.7358, and a retention index of 0.7407 (Fig. 00). Monophyly of the
791 extant genera of the Lophiidae was reconfirmed as recognized by Caruso (1985), as well as
792 that of the family as a whole by the inclusion of the extinct genera †*Sharfia*, †*Caruso*, and
793 †*Eosladenia* (with bootstrap support of 99.9% and a Bremer value of 9). Eight characters
794 without homoplasy (unique and unreversed within the Lophiidae) support lophiid

795 monophyly: mesethmoid absent (character 1, state 1); ascending process of premaxilla
796 autogenous (5, 1); ectopterygoid and endopterygoid fused to form a single element (11, 1);
797 anterodorsal process of subopercle prominent, articulating through connective tissue with
798 anteroventral margin of opercle (14, 1); teeth on fifth ceratobranchial restricted to discrete
799 rows along lateral and medial margins (18, 1); caudal-fin rays eight (23, 1); cleithral spine
800 present (35, 1 and 2); and skin naked (38, 1). Monophyly of lophiid genera to the exclusion of
801 †*Sharfia* was supported (with bootstrap support of 71.9% and a Bremer value of 2) by only a
802 single unique and unreversed character: opercle strongly bifurcate (12, 1). A sister-group
803 relationship between †*Caruso* and *Sladenia* and a sister group relationship of this clade
804 relative to all remaining lophiids was supported (with bootstrap support of 62.8% and a
805 Bremer value of 1) by two characters without homoplasy: interorbital width narrow,
806 considerably less than distance between outer margins of pterotics (2, 1); and posteriorly
807 directed expansion of distal end of posteriormost dorsal-fin pterygiophore present (32, 1).
808 Monophyly of a clade containing †*Eosladenia* and the remaining extant lophiid genera was
809 supported (with bootstrap support of 77.5% and a Bremer value of 2) by three characters:
810 haemal spines of abdominal vertebrae reduced (20, 1); neural and haemal spines of
811 penultimate vertebra narrow and reduced (21, 1); and interdigitation between anterior soft
812 dorsal-fin pterygiophores and underlying neural spines present (25, 1). A clade containing
813 †*Eosladenia*, *Lophiomus* and *Lophius*, to the exclusion of *Lophiodes*, was supported by only
814 a single character: caudal centrum depressed, bearing lateral transverse processes (22, 1).
815 Finally, a sister-group relationship between *Lophiomus* and *Lophius* was confirmed following
816 Caruso (1985), supported by four unique and unreversed characters: dorsolateral ridge of
817 frontals rugose, bearing short conical spines or low rounded knobs (3, 1); parasphenoid
818 laterally expanded (4, 1); maxillary process of palatine bifurcate (10, 1); and proximal shaft
819 of soft dorsal-fin pterygiophores anteroposteriorly expanded (27, 1).

820

821 **Discussion**

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

837 The dramatic anatomical diversity of lophiiform subgroups, including the large number
838 of morphological peculiarities make it very difficult to interpret the origin of these fishes, as
839 well as to hypothesize the possible appearance of a primitive lophiiform. Apart for some
840 synapomorphic features related to specific characters of the skeleton (cranial and caudal;
841 Pietsch 1981; Pietsch & Grobecker 1987) or to reproductive biology (Rasquin 1958; Pietsch
842 1981), the lophiiform body plan may be defined by four relevant aspects that were
843 documented and cursorily discussed by Gregory & Conrad (1936): (1) the enormous mouth
844 and throat, and consequent macrophagous habits; (2) the gill opening restricted to a tube-like

845 opening located close to the pectoral-fin base; (3) the elongation of pectoral-fin radials that
846 results in their pediculate appearance; and (4) the cephalic spinous dorsal fin with the anterior
847 element modified to serve as a luring apparatus. All but the tube-like gill opening refer to
848 skeletal features, which can be also observed in the fossils.

849 The huge increase in size of the mouth and throat is related to the hypertrophic
850 development of the jaws, suspensorium, hyoid apparatus, and branchial arches. As in other
851 vertebrates, the development of these elements of the head in the fish embryo is characterized
852 by having a hierarchy of cell movements and interactions between neural crest and
853 mesodermal mesenchyme, and surrounding epithelia (see, e.g., Le Douarin *et al.* 1994).
854 Several genes that function in the development of this region of the head have been
855 identified. Recent studies (e.g., Neuhauss *et al.* 1996; Piotrowski *et al.* 1996; Schilling *et al.*
856 1996) have emphasized the existence of discrete sets of genes that influence the correlated
857 diversification of both jaws and branchial arches (including the hyoid apparatus and
858 suspensorium).

859 The elongation of the pectoral fins and girdles of lophiiforms and their resemblance to
860 tetrapod limbs was evidenced by Cuvier (1829) who called these fishes “pediculate” (little
861 feet), a term subsequently used to identify the whole group (see, e.g., Valenciennes 1837;
862 Günther 1861; Gill 1883, 1909). The lophiiform pectoral girdle, or pseudobranchium (Monod
863 1960) is primarily characterized by having enlarged pectoral-fin radials, which in certain
864 cases are employed in a tetrapod fashion to walk over the substrate (see Pietsch & Grobecker
865 1987; Edwards 1989). The elongation of the pectoral-fin radials exhibits considerable
866 variation within lophiiforms, with the maximum lengths observed in certain lophioids (see
867 above) and antennarioids (Carnevale & Pietsch 2010). In all vertebrates the embryonic
868 development of paired appendages passes through three main phases, namely positioning,
869 initiation, and outgrowth. During the first phase paired appendages arise from bud initials that

870 originate in the lateral plate mesoderm at positions considered to be specified by *Hox* gene
871 expression in somatic mesoderm (see Burke *et al.* 1995). The initiation phase of the pectoral
872 fins (=forelimbs) follows the positioning phase. The transcription factor gene *Tbx5* is
873 expressed in the pectoral-fin bud (Tamura *et al.* 1999), during both the initiation and
874 outgrowth phases, mediated by interactions with *Wnt2b* and *Fgf10* (Takeuchi *et al.* 2003).
875 Fibroblast growth factors (FGFs) are involved in both the initiation and the following
876 outgrowth phases; the FGFs are expressed in the apical ectodermal ridge of the fin bud
877 promoting fin outgrowth. The anteroposterior pattern is controlled by an equivalent of the
878 zone of polarizing activity of the amniote limb, located at the posterior margin of the fin bud.
879 The gene *Sonic hedgehog* (*Shh*) is a major upstream factor in development expressed in this
880 sector of the fin bud. Neumann *et al.* (1999) demonstrated that *Shh* is required to establish
881 some aspects of the anteroposterior polarity, for normal development of the fin bud, and
882 formation of the fin endoskeleton. In a recent paper, Sakamoto *et al.* (2009) found that a
883 temporal shift of *Shh* activity alters the size of the endoskeletal elements in paired fins.
884 According to those authors, a heterochronic shift of the onset of *Shh* expression influences
885 the proliferation of cells that contribute to the formation of the endoskeletal disk, with
886 implications in the final size of the pectoral-fin radials. We may therefore hypothesize that
887 the synapomorphic elongation of the pectoral-fin radials in lophiiforms could be related to a
888 heterochronic shift of the onset of *Shh* expression. However, it is also interesting to note that
889 the enlargement of jaws, suspensorium, hyoid apparatus, branchial arches and pectoral-fin
890 endoskeleton may be linked together and that sets of genes that influence both cranial and
891 appendicular skeletal morphology may also contribute to correlated fin and cranial
892 enlargement (Neuhauss *et al.* 1996; Piotrowski *et al.* 1996; Schilling *et al.* 1996).

893 The highly modified spinous dorsal fin of lophiiforms certainly represents one of the
894 most spectacular morphological characteristics of these fishes. The anterior elements of this

895 fin are shifted anteriorly over the neurocranium and are modified to serve as a luring
896 apparatus, involving a vast series of associated modifications of the general architecture of
897 the neurocranium and of the musculature and innervations associated with the dorsal fin (see
898 Bertelsen 1951; Bradbury 1967; Rosen & Patterson 1969). The anteriormost spine, or
899 illicium, usually bears an esca at its tip, which exhibits considerable diversity and is
900 extremely useful in alpha-level taxonomy; in female ceratioid anglerfishes the esca is unique
901 in having bioluminescent bacteria and pheromone-producing secretory glands used to attract
902 a conspecific male (e.g., Munk 1992; Pietsch 2009), while in ogocephalids (and perhaps in
903 some antennariids) it apparently produces a chemical attractant used to lure buried benthic
904 preys (Pietsch & Grobecker 1987; Bradbury 1988; Nagareda & Shenker 2009). The anterior
905 migration of the anterior (=cephalic) dorsal-fin spines occurs during the larval stage (e.g.,
906 Matsuura & Yoneda 1986), resulting from the forward extension of the cartilaginous basal
907 pterygiophore inside the subepidermal space (Matsuura & Yoneda 1987). The forward
908 migration of the dorsal-fin spines continues until the first two spines are well anterior to the
909 eyes. The pterygiophores of the spinous dorsal fin develop from a single condensation of
910 tissue that separates into independent pterygiophores during development (e.g., Everly 2002).
911 In basal lophiiforms the spinous dorsal fin separates into two discrete units, comprising the
912 cephalic and post-cephalic spines respectively (see Everly 2002). The spinous dorsal fin is a
913 major innovation of acanthomorph fishes. Mabee *et al.* (2002) hypothesized that the spinous
914 dorsal fin essentially is an anterior duplication of the soft-rayed fin typical of all the
915 actinopterygians. In this context, the evolution of a discrete, anatomically regionalized and
916 spatially separated structure is an example of duplication and divergence (*sensu* Raff 1996),
917 enhanced by modular organization (Gilbert 2010). Such an hypothesis fits well with the
918 configuration of the dorsal fins observed in lophiiforms. However, lophiiforms exhibit a
919 really complex dorsal-fin structure; as documented above, the spinous dorsal fin becomes

920 separated into discrete independent units during ontogeny, thereby resulting in a
921 submodularization of the anterior dorsal fin. The cephalic unit of the submodularized dorsal
922 fin includes the luring apparatus and associated muscles and nerves. The possibility of a
923 further modularization of the first dorsal-fin module (*sensu* Mabee *et al.* 2002) in lophiiforms
924 may be confirmed by the recurrent suppression of the post-cephalic unit of the spinous dorsal
925 fin in antennarioids, ceratioids, chaunacoids, ogocephaloids, and some lophioids (see, e.g.,
926 Pietsch 1981; 2009). The structural complexity of the luring apparatus of lophiiforms, with its
927 vast array of highly derived characters and functions, may be envisaged as a remarkable case
928 of co-option (*sensu* Raff 1996), involving both morphological and functional transformation
929 of a pre-existing submodularized first dorsal-fin module. The forward shift of the cephalic
930 unit of the submodularized spinous dorsal fin also represents a peculiarity of lophiiform
931 fishes. A few other teleost groups are characterized by having an extensive anterior migration
932 of the dorsal fin (see Nelson 2006; Bannikov & Carnevale 2011). The condition typical of
933 lophiiforms, however, is extreme considering the broad rearrangements of cranial architecture
934 observed in these fishes. Median fin development apparently involves the same genetic
935 programs that operate in paired appendages, and expression of *Hoxd* and *Tbx18* genes (which
936 specify paired limb position) defines the position of median fins (Freitas *et al.* 2006) along
937 continuous stripes of competency on the midline of the body (Yonei-Tamura *et al.* 2008).
938 Therefore, we may hypothesize that in lophiiforms, the forward migration of the dorsal fin
939 over the neurocranium could be produced by an anterior shift of the stripes of competency for
940 dorsal-fin formation along the dorsal midline.

941

942 **Acknowledgements**

943 We wish to thank Walter Landini, Università di Pisa, Pisa, for suggestions and a critical
944 review of an early draft of the text. Presubmission reviews of the manuscript were also

945 provided by James W. Orr and Duane E. Stevenson, both of NOAA Fisheries, Seattle. We are
946 particularly obliged to Gaël Clement and Monette Veran, Muséum National d'Histoire
947 Naturelle, Paris, and Roberto Zorzini and Anna Vaccari, Museo Civico di Storia Naturale di
948 Verona, for access to fossil material under their care and for hospitality during our visits to
949 Paris and Verona in April and February 2010 respectively. Loans of additional fossil material
950 were kindly provided by Zerina Johanson, Natural History Museum, London and Alexandre
951 F. Bannikov, Borysiak Paleontological Institute, Russian Academy of Sciences, Moscow.
952 Thanks are also due to the following individuals for providing access to extant comparative
953 material, and permission to clear and stain specimens for osteological study: Katherine P.
954 Maslenikov, University of Washington, Seattle; Karsten Hartel, Museum of Comparative
955 Zoology, Harvard University, Cambridge; John H. Caruso, Tulane University, New Orleans;
956 Dianne J. Bray, Museum of Victoria, Melbourne; Jeffrey Johnson, Queensland Museum,
957 South Brisbane. Many thanks go to Anna Vaccari, Museo Civico di Storia Naturale di
958 Verona, and Philippe Loubry, Muséum National d'Histoire Naturelle, Paris for photographs.
959 The work was supported in part by U.S. National Science Foundation Grant DEB-0314637,
960 T. W. Pietsch, principal investigator. Visit to Paris of the senior author was supported by the
961 SYNTHESYS grants of the Muséum National d'Histoire Naturelle, Paris.

962

963

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1283 **Captions of figures and tables**

1284

1285 **Figure 1.** †*Caruso brachysomus* (Agassiz, 1835). A, B, lectotype, MNHN Bol 42/43. Scale
1286 bars = 20 mm. [planned for page width]

1287 **Figure 2.** †*Caruso brachysomus* (Agassiz, 1835). A, MCSNV T.978; B, complete skeleton
1288 drawn from specimen in A. Scale bars = 20 mm. [planned for page width]

1289 **Figure 3.** †*Caruso brachysomus* (Agassiz, 1835). MCSNV B.13. Scale bar = 20 mm.
1290 [planned for page width]

1291 **Figure 4.** †*Caruso brachysomus* (Agassiz, 1835). Reconstruction of the dorsal view of the
1292 neurocranium mainly based on MCSNV T.978 and MNHN Bol42/43. [planned for
1293 page width]

1294 **Figure 5.** †*Caruso brachysomus* (Agassiz, 1835). Skull drawn from specimen MCSNV
1295 T.978. Scale bar = 20 mm. [planned for page width]

1296 **Figure 6.** †*Caruso brachysomus* (Agassiz, 1835). MNHN Bol 42, left lateral view of anterior
1297 portion of the premaxilla. Scale bar = 5 mm. [planned for column width]

1298 **Figure 7.** †*Caruso brachysomus* (Agassiz, 1835). MCSNV B. 13, right lateral view of
1299 opercle and subopercle. Scale bar = 5 mm. [planned for column width]

1300 **Figure 8.** †*Caruso brachysomus* (Agassiz, 1835). MCSNV B.13, left ceratobranchials and (?)
1301 second pharyngobranchial. Scale bar = 3 mm. [planned for column width]

1302 **Figure 9.** Dorsal view of neurocrania of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes*
1303 *monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*,
1304 MCZ 51259. Scale bars = 5 mm. [planned for page width]

1305 **Figure 10.** Left lateral view of premaxillae and maxillae of (A) *Sladenia remiger*, CSIRO
1306 H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D)
1307 *Lophius americanus*, MCZ 51259. Scale bars = 5 mm. [planned for page width]

1308 **Figure 11.** Left lateral view of lower jaws, suspensoria and part of opercular apparatuses of
1309 (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C)
1310 *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Bone in
1311 stipple, cartilage in black. Scale bars = 5 mm. [planned for page width]

1312 **Figure 12.** Left lateral view of opercles and subopercles of (A) *Sladenia remiger*, CSIRO
1313 H.2559-02; *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D)
1314 *Lophius americanus*, MCZ 51259. Scale bars = 5 mm. [planned for page width]

1315 **Figure 13.** Branchial arches of (A) *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*,
1316 MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ
1317 51259. Bone in stipple, cartilage in black. Scale bars = 5 mm. [planned for page
1318 width]

1319 **Figure 14.** Left lateral view of vertebral columns, caudal skeletons, and median fins of (A)
1320 *Sladenia remiger*, CSIRO H.2559-02; *Lophiodes monodi*, MCZ 40928; (C)
1321 *Lophiomus setigerus*, TU 81104; (D) *Lophius americanus*, MCZ 51259. Bone in
1322 stipple, cartilage in black. Scale bars = 5 mm. [planned for page width]

1323 **Figure 15.** Left lateral view of pectoral girdles of (A) *Sladenia remiger*, CSIRO H.2559-02;
1324 *Lophiodes monodi*, MCZ 40928; (C) *Lophiomus setigerus*, TU 81104; (D) *Lophius*
1325 *americanus*, MCZ 51259. Bone in stipple, cartilage in black. Scale bars = 5 mm.
1326 [planned for page width]

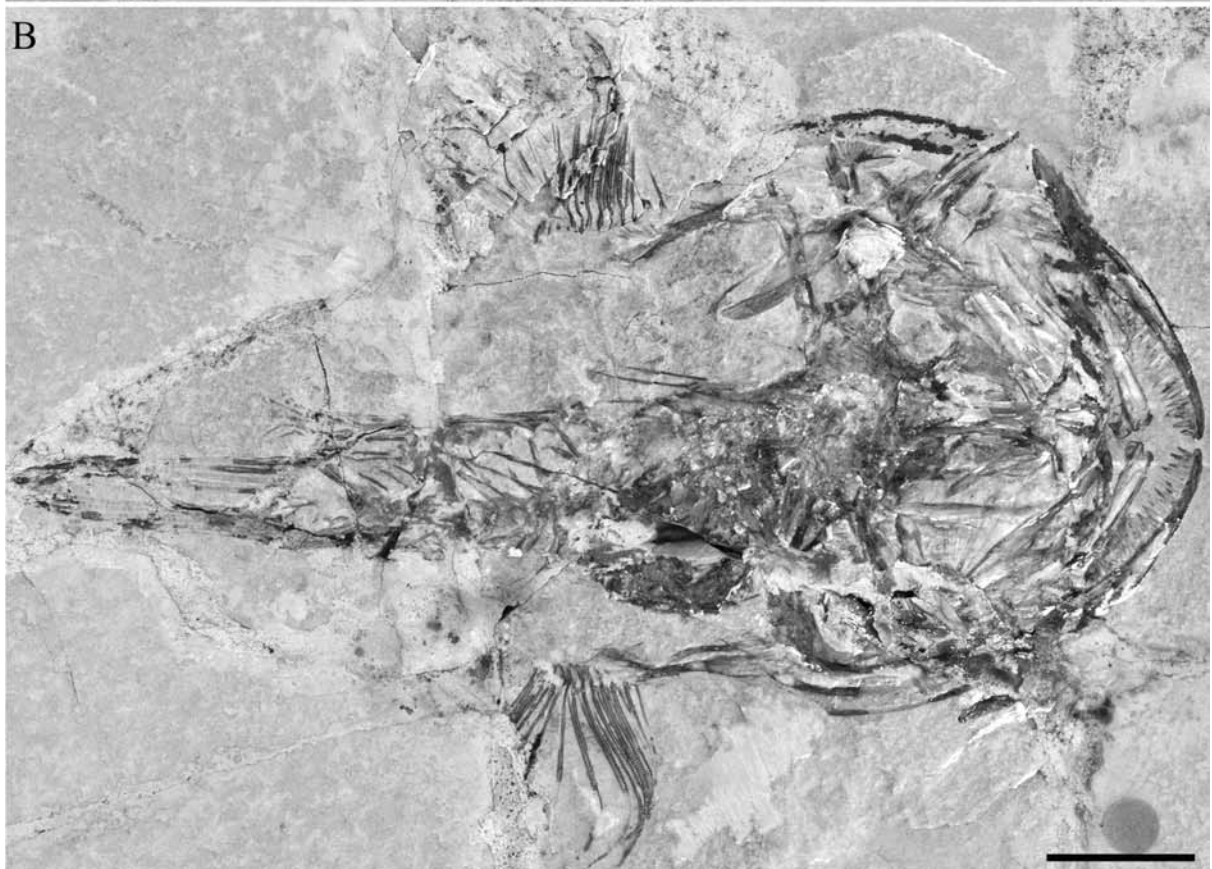
1327 **Figure 16.** Cladogram of hypothesized relationships of the Lophiidae and two outgroups. The
1328 number above the base of a node is the Bremer value, and the number below the node
1329 indicates bootstrap support for the respective node. [planned for page width]

1330 **Table 1.** Measurements (in percent standard length) of †*Caruso brachysomus* (Agassiz,
1331 1835).

1332 **Appendix.** Character matrix of 38 morphological characters for genera of the Lophiidae and

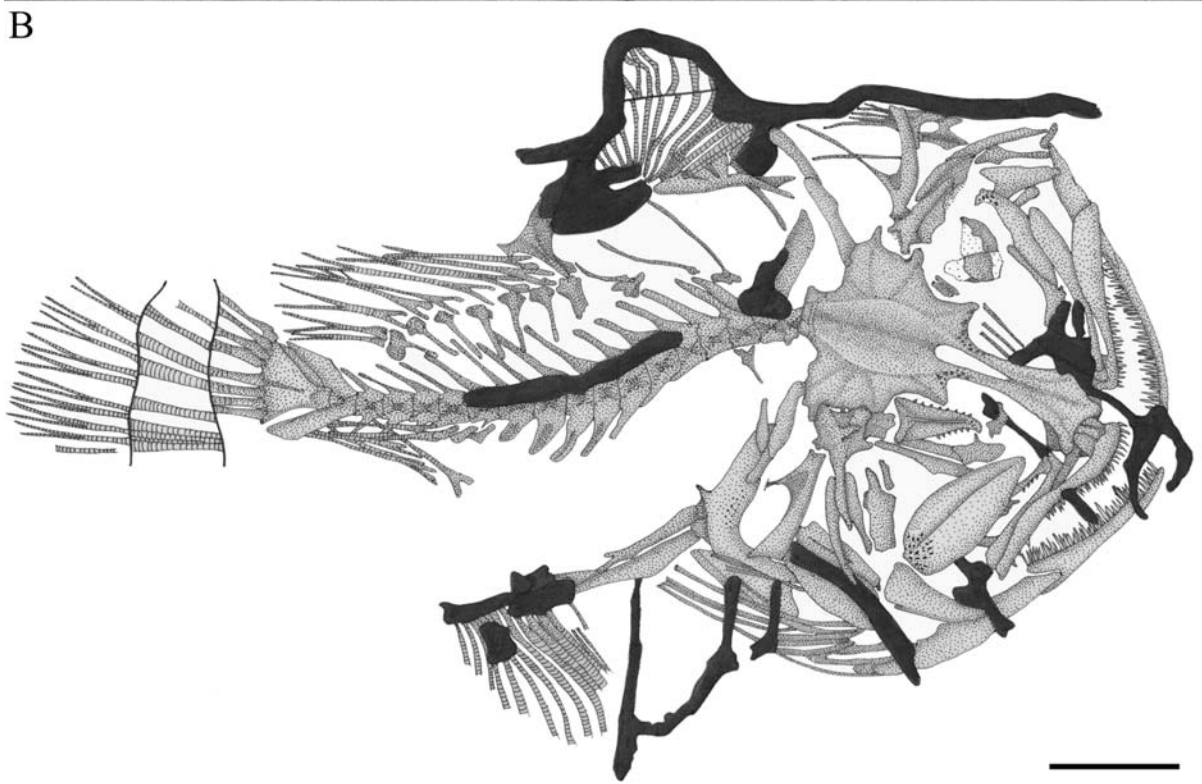
1333 two outgroups.

1334



1335

1336 Figure 1.



1337

1338 Figure 2.

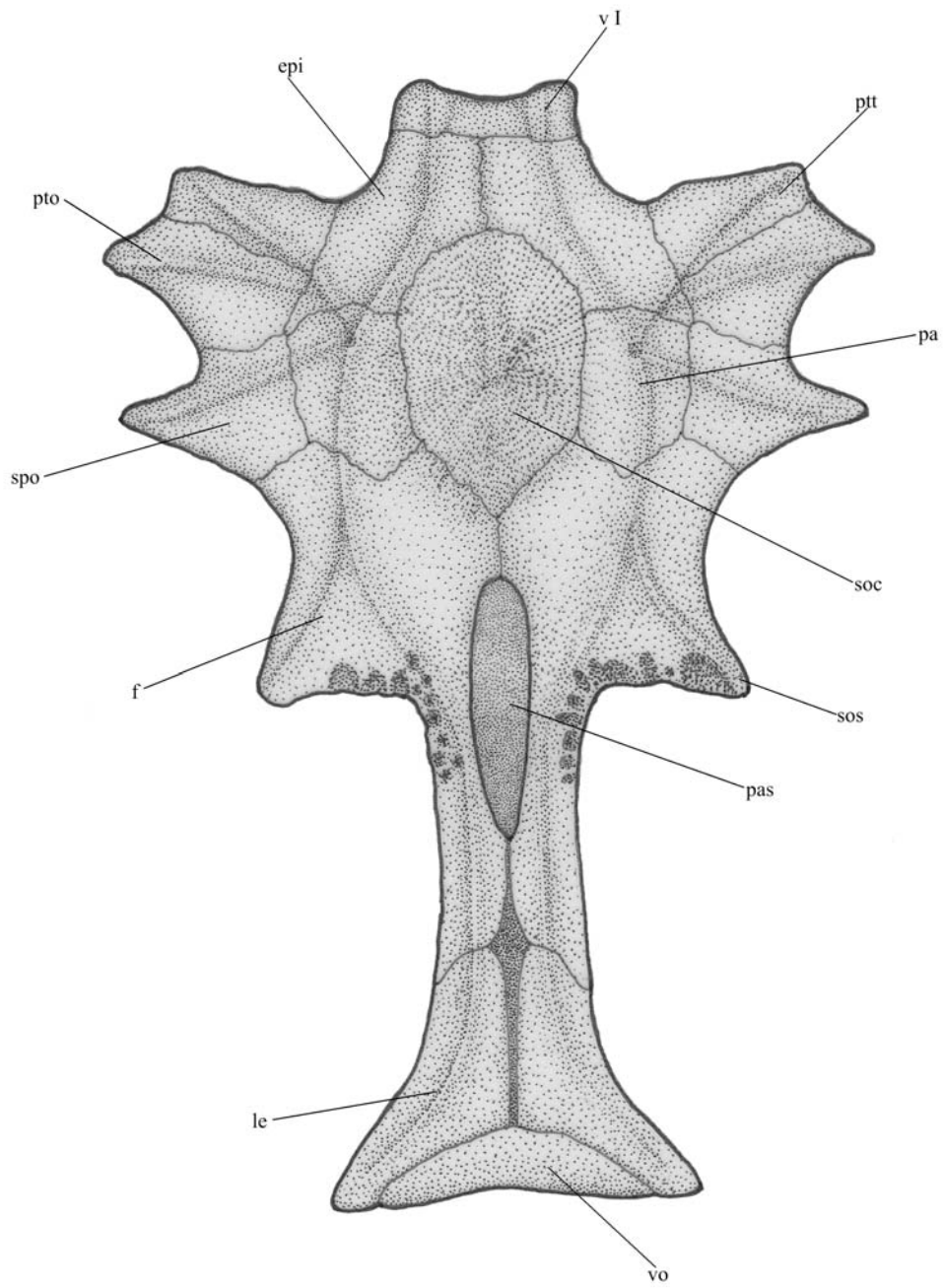
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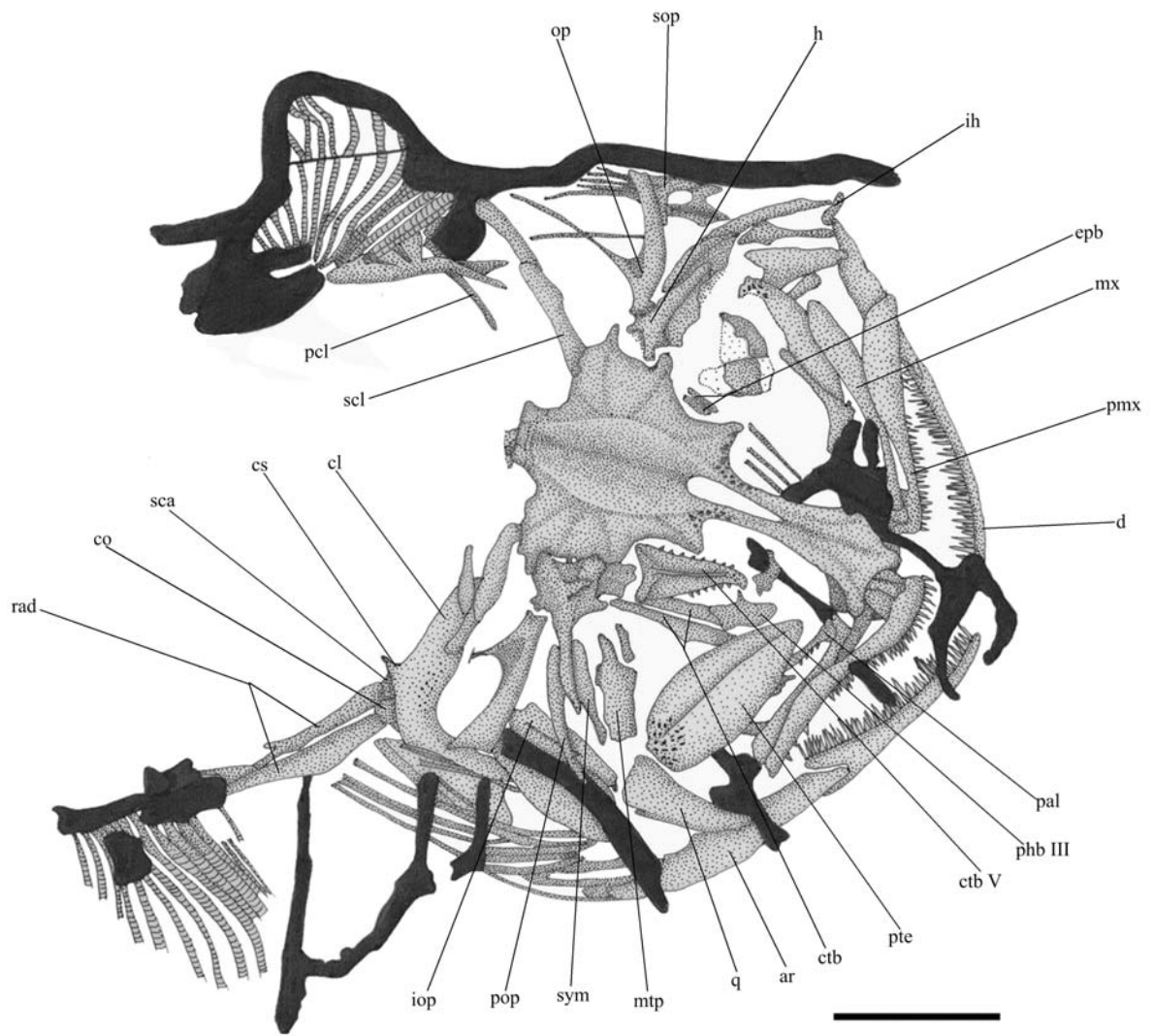
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1342 Figure 3.



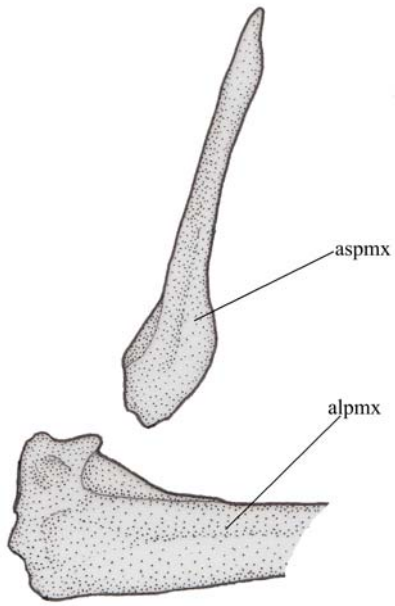
1343

1344 Figure 4.



1345

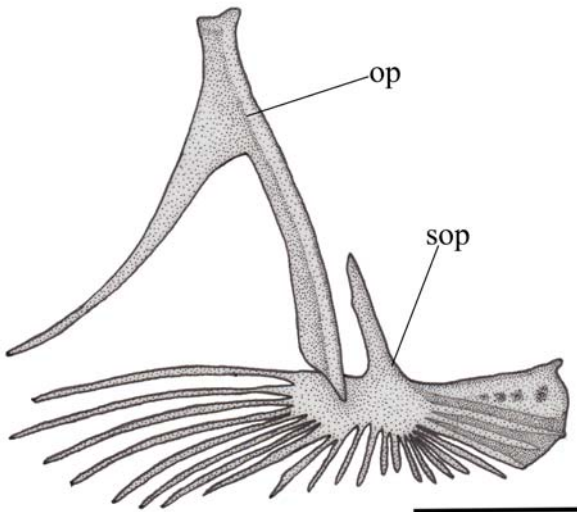
1346 Figure 5.



1347

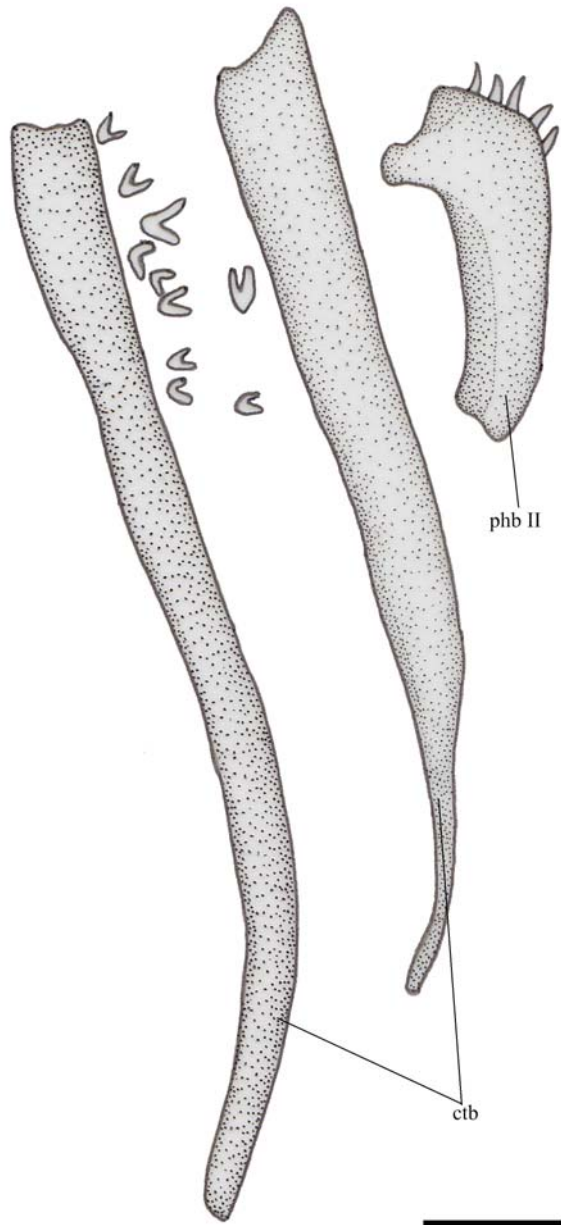
1348 Figure 6.

1349



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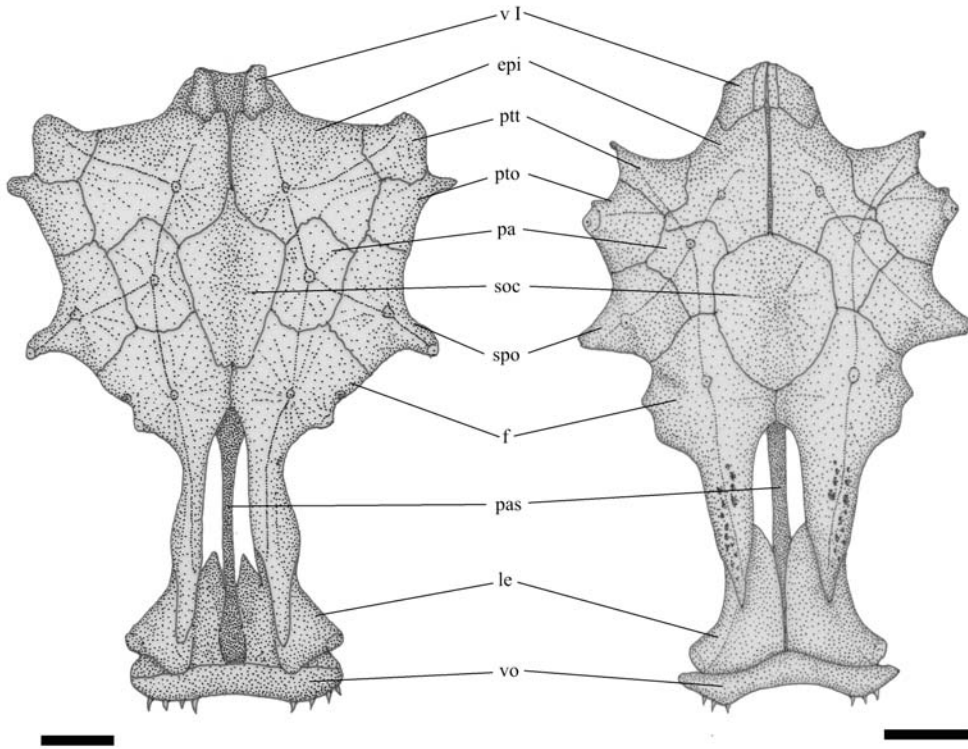
1351 Figure 7.



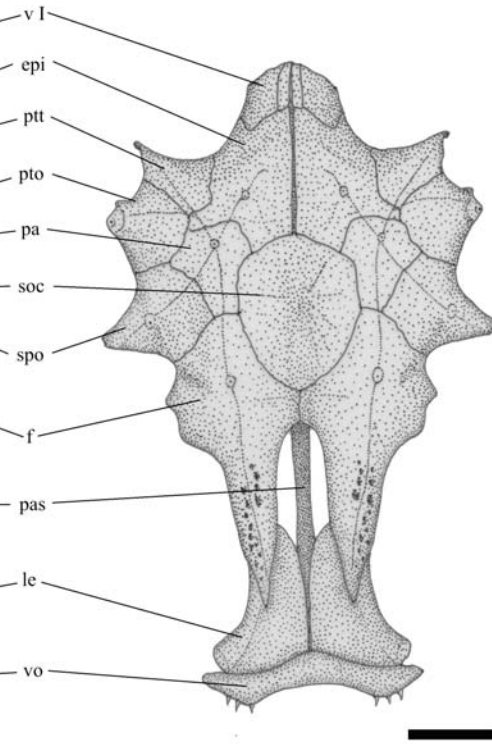
1352

1353 Figure 8.

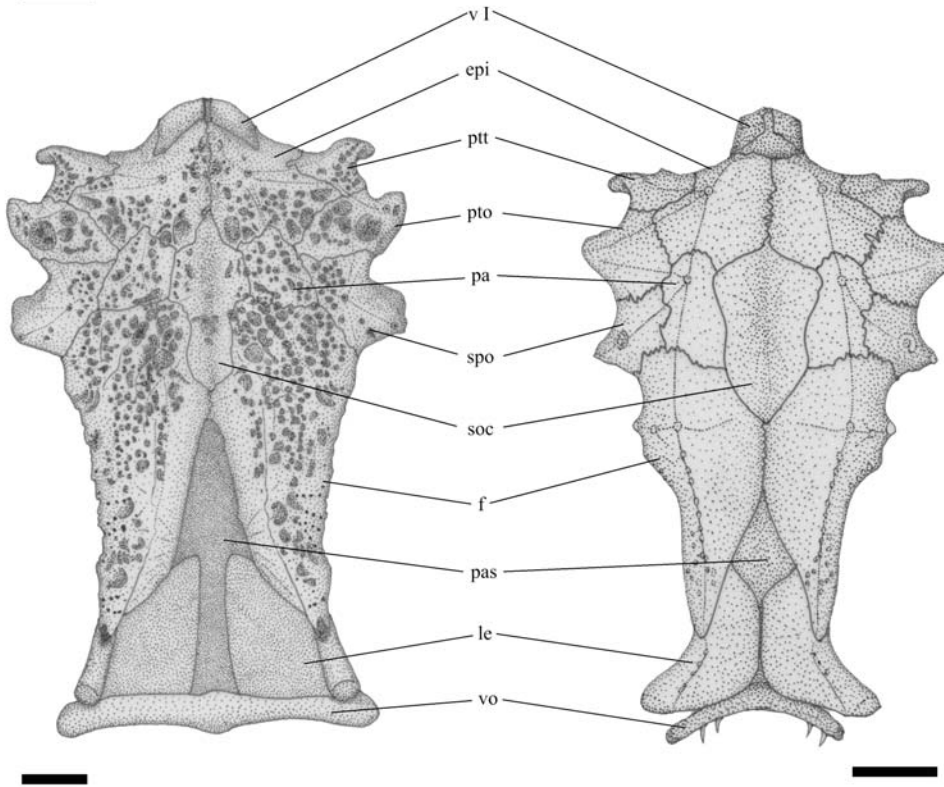
A



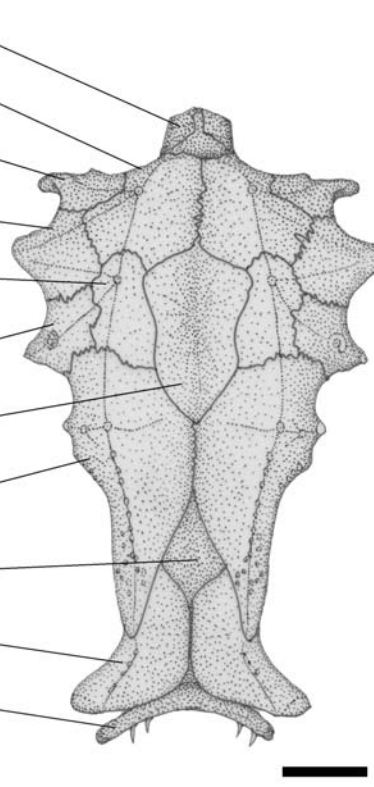
B



C

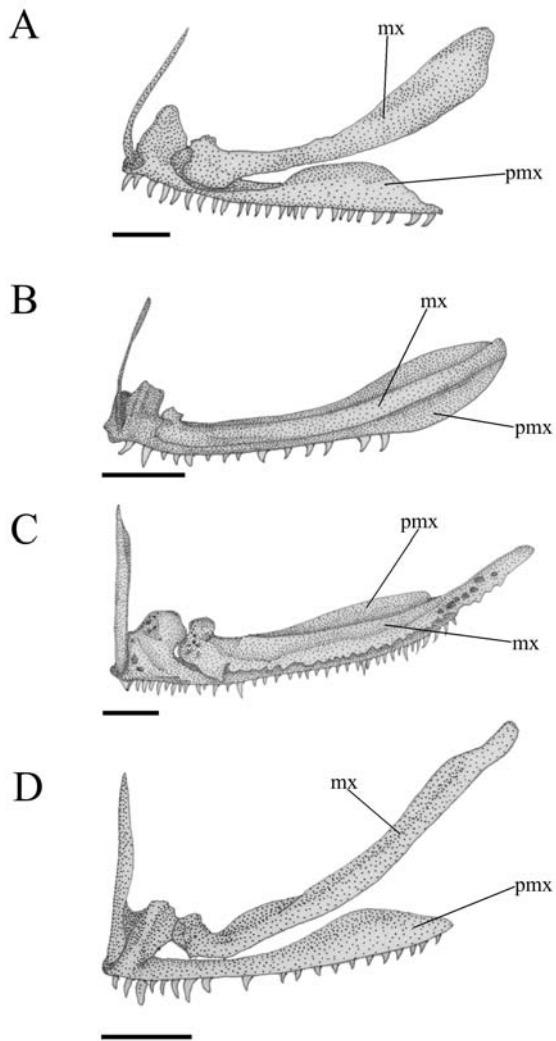


D



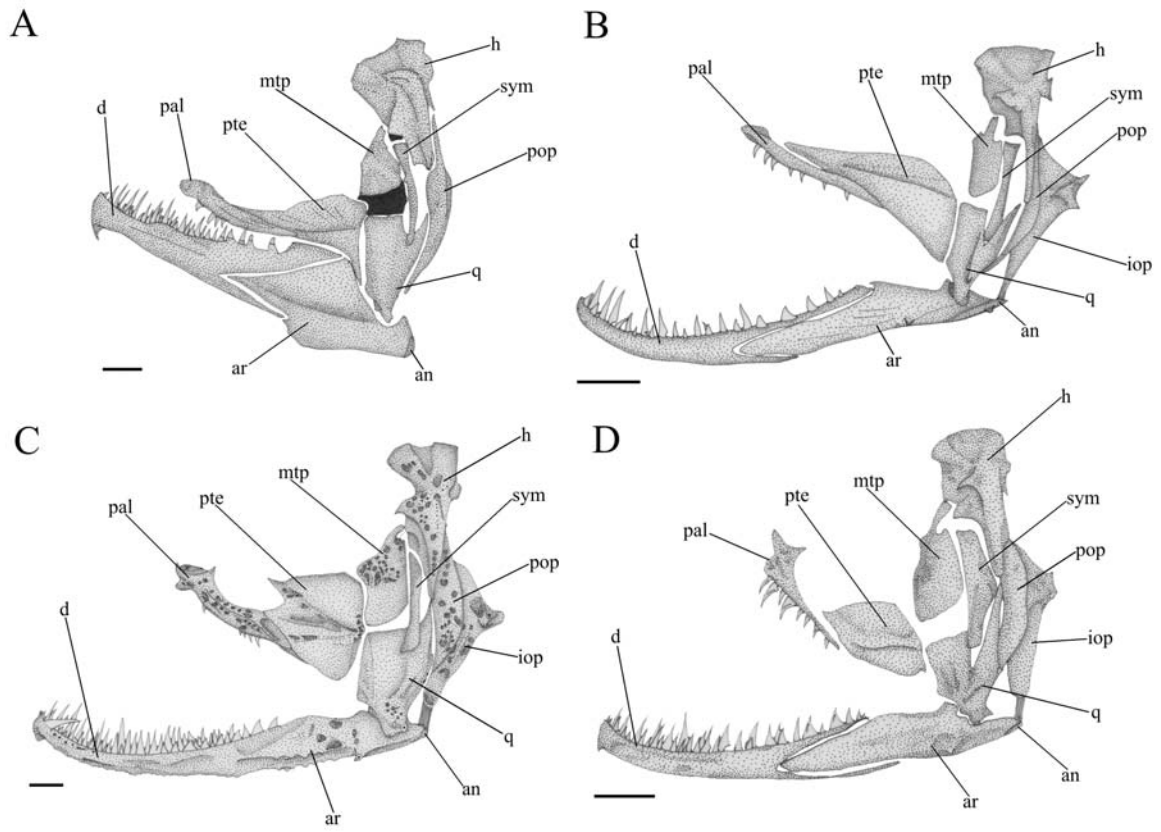
1354

1355 Figure 9.



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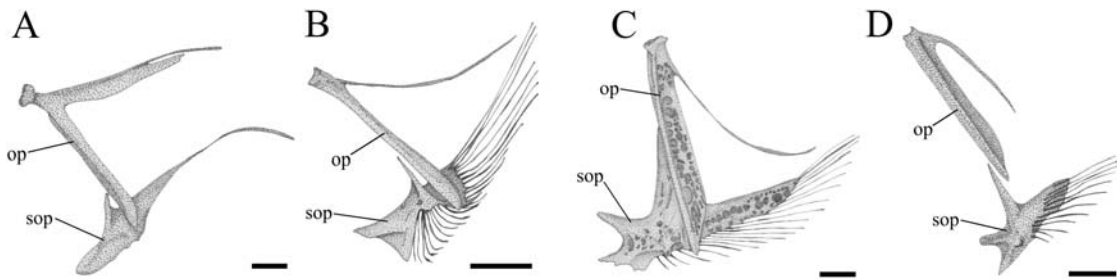
1357 Figure 10.



1358

1359 Figure 11.

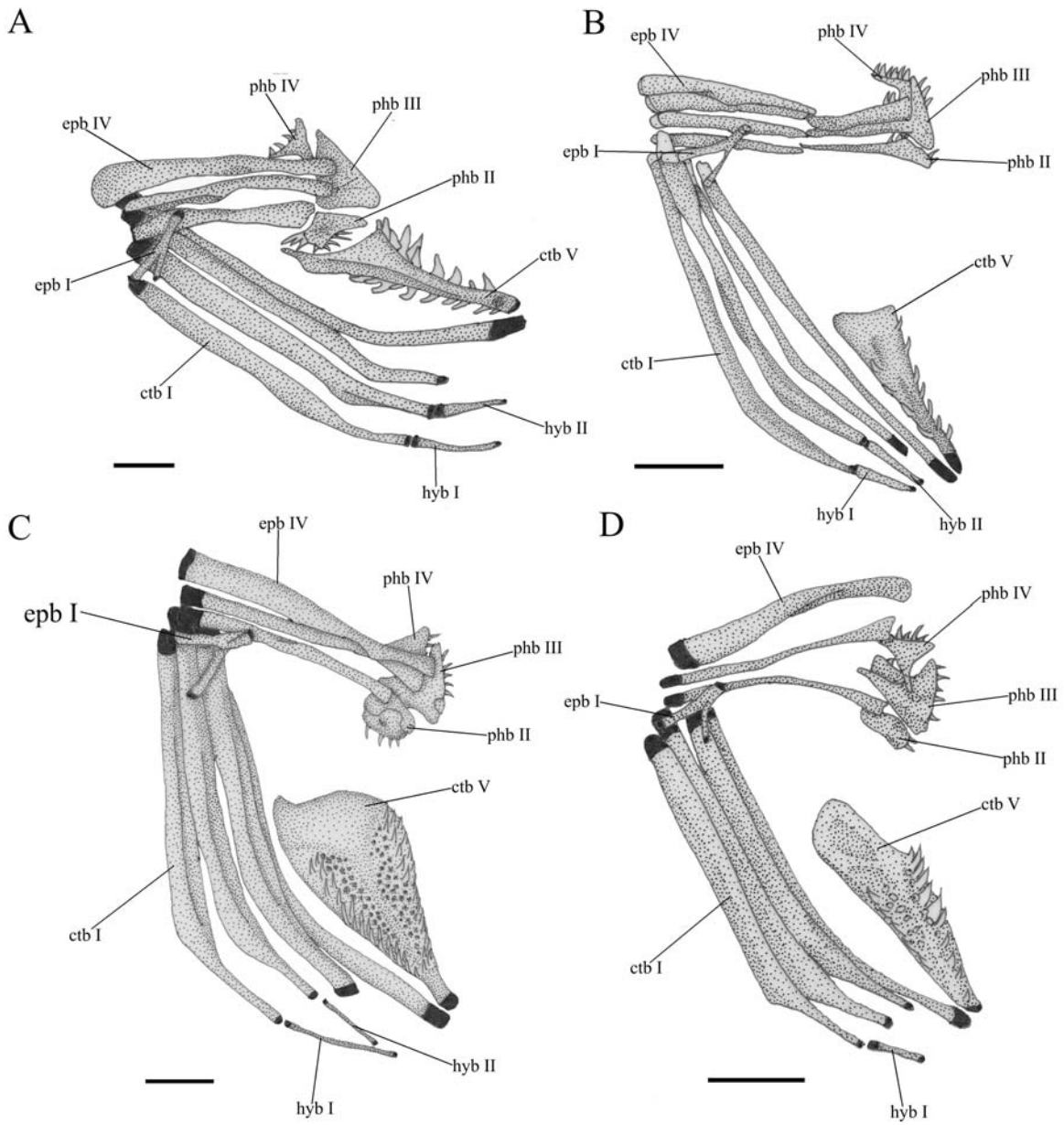
1360



1361

1362 Figure 12.

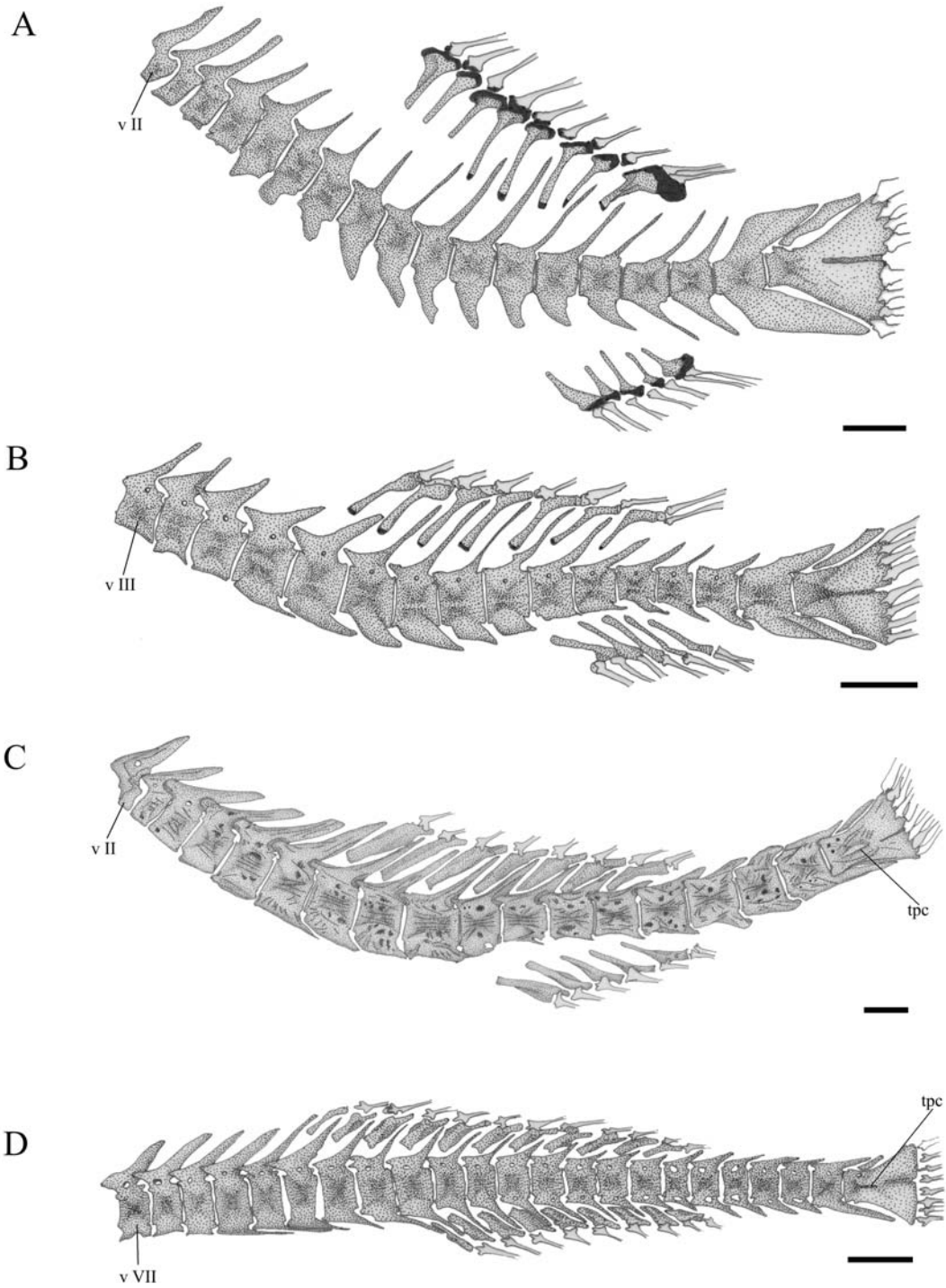
1363



1364

1365 Figure 13.

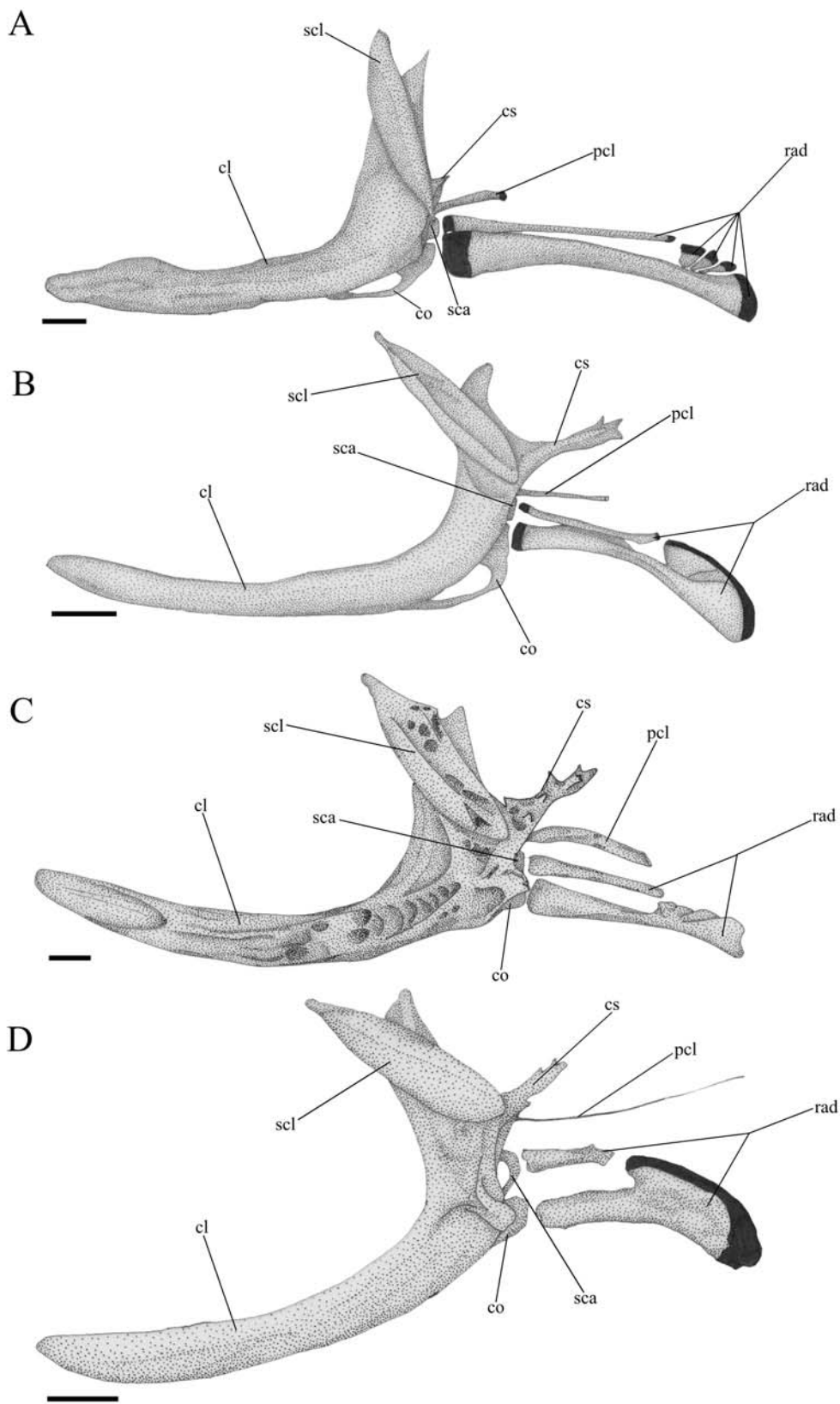
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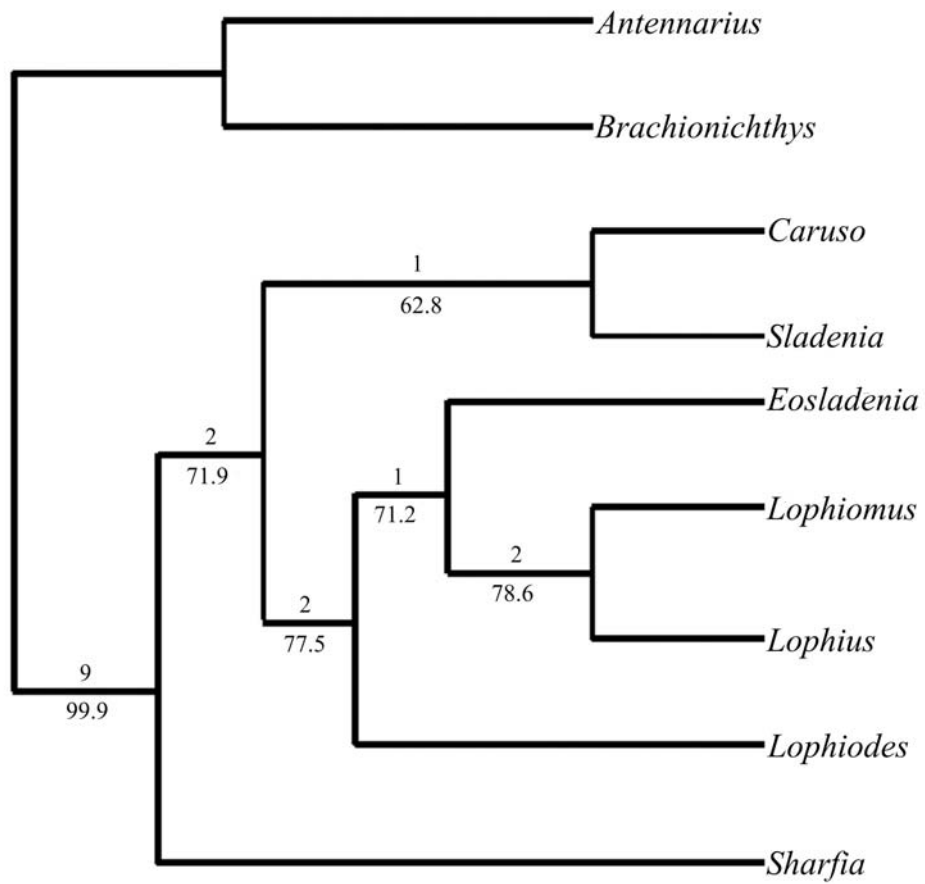
1368 Figure 14.

1369



1371 Figure 15.

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1373

1374 Figure 16.

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	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

1382

1383 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	
<i>Antennarius</i>	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	
<i>Brachionichthys</i>	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	
† <i>Caruso</i>	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	
† <i>Eosladenia</i>	0	0	1	0	1	0	1	0	1	?	1	1	1	?	?	?	1	0	1	1	0	1	1	1	?	?	?	?	?	?	?	2	0	
<i>Lophiodes</i>	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	
<i>Lophiomus</i>	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	1	0	1	0	1	0	2	0
<i>Lophius</i>	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	1	0	1	0	0	2	0
† <i>Sharfia</i>	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	
<i>Sladenia</i>	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	

1384

1385 Table 2.