A fossil unicorn crestfish (Teleostei, Lampridiformes, Lophotidae) from the Eocene of Iran

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Lophotidae, or crestfishes, is a family of rare deep-sea teleosts characterised by an enlarged horn-like crest on the forehead. They are poorly represented in the fossil record, by only three described taxa. One specimen attributed to Lophotidae has been described from the pelagic fauna of the middle-late Eocene Zagros Basin, Iran. Originally considered as a specimen of the fossil lophotid †*Protolophotus*, it is proposed hereby as a new genus and species. †*Babelichthys olneyi*, gen. et sp. nov., differs from the other fossil lophotids by its relatively long and strongly projecting crest, suggesting a close relationship with the modern unicorn crestfish, *Eumecichthys*. This new taxon increases the diversity of the deep-sea teleost fauna to which it belongs, improving our understanding of the taxonomic composition of the early Cenozoic mesopelagic ecosystems.

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2   **Eocene of Iran**

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8 ABSTRACT

9   Lophotidae, or crestfishes, is a family of rare deep-sea teleosts characterised by an enlarged

10   horn-like crest on the forehead. They are poorly represented in the fossil record, by only three

11   described taxa. One specimen attributed to Lophotidae has been described from the pelagic fauna

12   of the middle-late Eocene Zagros Basin, Iran. Originally considered as a specimen of the fossil

13   lophotid †*Protolophotus*, it is proposed hereby as a new genus and species. †*Babelichthys olneyi*,

14   gen. et sp. nov., differs from the other fossil lophotids by its relatively long and strongly

15   projecting crest, suggesting a close relationship with the modern unicorn crestfish, *Eumecichthys*.

16   This new taxon increases the diversity of the deep-sea teleost fauna to which it belongs,

17   improving our understanding of the taxonomic composition of the early Cenozoic mesopelagic

18   ecosystems.

INTRODUCTION

Lampridiforms are strange spiny-rayed teleosts, found in mesopelagic environments in every

ocean of the world (Olney, Johnson & Baldwin, 1993; Olney, 2002). Their most famous

representatives are the endothermic opah (*Lampris guttatus*) and the gigantic, serpentine oarfish

(*Regalecus glesne*), the longest known teleost. Along with these iconic taxa, lampridiforms

include equally weird ribbon-like and elongate animals, characterized by a silver-coloured skin

and long, bright red fins: the taeniosomes. The 15 to 18 extant species of the clade Taeniosomi

include oarfishes (Regalecidae), ribbonfishes (Trachipteridae), the tapertail (Radiicephalidae)

and Lophotidae, the crestfishes (Regan, 1907; Walters & Fitch, 1960; Olney, 1984; Roberts,

2012). Lophotids are characterized by unique structures, such as an ink gland (Walters & Fitch,

1960; Honma, Ushiki & Takeda, 1999) not found anywhere else in teleosts (except in the closely

related radiicephalids; Harrisson & Palmer, 1968). The most conspicuous osteological feature of

lophotids is a well-developed horn-like crest, formed by an anteriorly projecting expansion of the

frontal and supraoccipital bones of the cranium (Oelschläger, 1979, 1983; Olney, Johnson &

Baldwin, 1993). This crest is closely associated with the anterior pterygiophores supporting the

dorsal fin, and as a result, the dorsal fin expands over, and sometimes anterior to the cranium.

Lophotids are represented in modern fauna by one to three *Lophotus* species and by the unicorn

crestfish, *Eumecichthys fiski* (Walters & Fitch, 1960; Craig, Hastings & Pondella, 2004). Their

fossil record consists in at least three monotypic genera (Bannikov, 1999; Carnevale, 2004).

The present article is a revision of an anatomically distinctive fossil specimen attributed to

Lophotidae. Arambourg (1943, 1967) first described the specimen from a rich late Eocene fauna

located near Ilam, Zagros Basin, Iran. The Ilam fauna comprises numerous representatives of

teleost taxa such as Beryciformes, Gadiformes, Ophidiiformes and Stomiiformes, typical of the

43 modern deep-sea pelagic environments (Arambourg, 1967; Afsari et al., 2014; Přikryl,

44 Brzobohatý & Gregorová, 2016).

45 The taxonomic status of the lophotid specimen studied here is currently unclear (Walters, 1957;

46 Oelschläger, 1979; Bannikov, 1999), and it lacks a proper anatomical description. Given the

47 rarity of fossil material attributed to taeniosome lampridiforms, a detailed description and revised

48 taxonomy of this material is needed in order to improve our understanding of the morphological

49 evolution and fossil record of this peculiar group.

50

51 **MATERIAL AND METHODS**

52 **Taxonomic status of the material**

53 The material described herein, MNHN.F.EIP11 (Figs. 1, 2), was discovered during excavations

54 near Ilam (Zagros Basin, Western Iran) by Camille Arambourg in 1938-1939. The specimen was

55 chosen to be the paratype of †*Lophotes elami* (Arambourg, 1943), along with the holotype

56 MNHN.F.EIP10 (Fig. 3). On the basis of osteological differences from extant lophotids, such as

57 the well-ossified pelvic girdle in a ventral position observed in the holotype of †*Lophotes elami*,

58 Walters (1957) assigned it to a distinct new genus †*Protolophotus* (Fig. 3). Oelschläger (1979)

59 later proposed that MNHN.F.EIP11 differs sufficiently from MNHN.F.EIP10 to be classified in a

60 different genus. He related the specimen to the extant *Eumecichthys* and gave it the name

61 †'*Protomecichthys*'. However, the genus †'*Protomecichthys*' lacks both a designated type species

62 and a formal description. Thus, it fails to meet the requirements of Article 13.3 of the

63 *International Code of Zoological Nomenclature* (International Commission on Zoological

64 Nomenclature, 1999) and should be considered a *nomen nudum* (Bannikov, 1999).

65

66 **Comparative material**

67 †*Eolophotes lenis*, PIN 1413/86; *Eumecichthys fiski*, USNM 164170 (radiographs); *Lophotus*

68 *lacepede,* NHMUK 1863.8.27.1 (radiographs); †*Oligolophotes fragosus*, PIN 3363/121;

69 †*Protolophotus elami*, MNHN.F.EIP10.

70

71 **Nomenclatural acts**

72 The electronic version of this article in Portable Document Format (PDF) will represent a

73 published work according to the International Commission on Zoological Nomenclature (ICZN),

74 and hence the new names contained in the electronic version are effectively published under that

75 Code from the electronic edition alone. This published work and the nomenclatural acts it

76 contains have been registered in ZooBank, the online registration system for the ICZN. The

77 ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed

78 through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The

79 LSID for this publication is: urn:lsid:zoobank.org:pub:B677BA4F-CCF4-4678-A8A8-

80 502F059704D2. The online version of this work is archived and available from the following

81 digital repositories: PeerJ, PubMed Central and CLOCKSS.

82

83 **Methods**

84 The specimen was examined with a stereomicroscope equipped with a camera lucida drawing

85 arm. The interpretative drawing was produced with Adobe Illustrator CS6 from the camera

86 lucida drawings and from photographs. Measurements were taken with a compass or with the

87 software ImageJ 1.5 from radiographs; angles were also measured with ImageJ. The method for

88 estimating the degree of projection of the crest is modified from Craig, Hastings & Pondella

89 (2004): it is based on the angle between the straight line from the tip of the crest to the proximal

90 end of its anterior margin (instead of the tip of the upper jaw, due to varying jaw positions in

91 fossils) and the vertical line drawn perpendicular to the main axis of the parasphenoid (instead of

92 the vertebral column, not preserved in MNHN.F.EIP11). The relative length of the crest is the

93 ratio between the crest length (distance between the tip of the crest and the proximal end of its

94 anterior margin) and the head length without the crest (from the anterior margin of the ethmoid

95 region to the posterior margin of the neurocranium). All extinct taxa are indicated with a dagger

96 (†).

97

98 **RESULTS**

99 **Systematic palaeontology**

100 TELEOSTEI Müller, 1845

101 ACANTHOMORPHA Rosen, 1973

102 Order LAMPRIDIFORMES Goodrich, 1909

103 Suborder TAENIOSOMI Gill, 1885

104 Family LOPHOTIDAE Bonaparte, 1845

105 Genus †*Babelichthys* gen. nov.

106 urn:lsid:zoobank.org:act:86986E5E-5FFF-465D-A987-E475FBF02966

107 (Figs. 1, 2)

108

109 **Etymology.** Hellenization of the name of the "Babel fish", the teleost-like, ear-dwelling, polyglot

110 extra-terrestrial species from Douglas Adams' 1979 book *The Hitchhiker's Guide to the Galaxy*,

111 in reference to the very peculiar, almost alien-like, appearance of the genus.

112   **Type and only species**. †*Babelichthys olneyi*, sp. nov.

113   **Diagnosis.** A lophotid differing from †*Eolophotes*, *Lophotus*, †*Oligolophotes* and

114   †*Protolophotus* by the relatively longer, strongly projecting crest; and from *Eumecichthys* by the

115   relatively shorter, deeper and less strongly projecting crest, with strongly expanded anterior

116   dorsal-fin pterygiophores.

117

118   †***Babelichthys olneyi*** sp. nov.

119   urn:lsid:zoobank.org:act:D2540D1F-F169-40DE-B910-7302810615E7

120   (Figs. 1, 2)

121

122   1943 †*Lophotes elami* Arambourg, p. 287, pl. X, fig. 1

123   1957 †*Protolophotus elami* Walters, p. 60

124   1967 †*Protolophotes elami* Arambourg, pl. VI, fig. 1

125   1979 †*Protomecichthys* sp. Oelschläger, p. 354, fig. 11 (*nomen nudum*)

126

127   **Holotype.** MNHN.F.EIP11d/g, almost complete articulated cranium and anterior portion of the

128   dorsal fin, in part and counterpart (Figs. 1, 2). This is the only specimen known for the genus and

129   species.

130   **Etymology.** Species named in honour of the late John E. Olney, in recognition of his work on the

131   anatomy and ontogeny of Lampridiformes.

132   **Type locality and horizon**. Near Ilam, Zagros Basin, Western Iran. This teleost fauna, part of

133   the Pabdeh Formation, was erroneously aged Cretaceous by Priem (1908), and Rupelian

134   (Oligocene) by Arambourg (1943, 1967). It is more accurately middle to late Eocene in age

135   (Afsari et al., 2014; and references therein).

136   **Diagnosis**. As for the genus.

137

138   ## Anatomical description

139   MNHN.F.EIP11 consists only of the head of the animal, along with the associated anterior

140   portion of the dorsal fin. The specimen is mostly articulated, except for the left ventral portion of

141   the hyoid arch that is upturned and preserved ventral to the rest of the cranium. The limits of

142   most bones are poorly preserved, probably due to their low degree of mineralization in life as is

143   the case in modern taeniosome lampridiforms.

144

145   *Measurements*

146   Total head length: 104 mm; head length (without the crest): 44 mm; crest length (anterior

147   margin): 51.5 mm; head depth: 25.5 mm; orbit diameter: 23 mm.

148

149   *Neurocranium*

150   The neurocranium of MNHN.F.EIP11 is highly modified. The frontal develops a dorsal lamina

151   that projects anterior to the jaws. Throughout approximately its anterior half, it is in contact with

152   an enlarged laminar process of the supraoccipital, delimited dorsally by a strong supraoccipital

153   spine. Together, they form a conspicuous "crest", long and strongly projecting anteriorly (at an

154   angle of 64.5°). Alone, the crest contributes to 58% of total head length.

155   The frontal makes up approximately 60% of the anterior margin of the crest. Both the frontal and

156   the supraoccipital show radial ornamentation on the crest; it radiates from the posterior end of

157   the frontaland the distal tip of the supraoccipital. The supraoccipital spine borders the dorsal

158   margin of the bone, narrowing towards the tip.

159   The ethmoid region is poorly preserved, with an enlarged probable lateral ethmoid hiding the

160   mesethmoid. An enlarged lachrymal is nested in the antero-ventral corner of the orbit; it is

161   parallel to the parasphenoid ventrally, and curves dorsally along the edge of the lateral ethmoid.

162   The orbitosphenoid runs along the dorsal margin of the orbit and has a conspicuous process

163   pointing ventrally. The posterior wall of the orbit is delimited ventrally by a robust and straight

164   basisphenoid. Otherwise, the sphenoid, otic and occipital regions are too poorly preserved to

165   distinguish the individual bones. The parasphenoid is robust and slightly curves dorsally at its

166   anterior end. The junction between the parasphenoid and the vomer is not discernable. There is

167   no evidence of vomerine teeth.

168

169   *Jaws*

170   The premaxilla is relatively small, with a well-developed ascending process, and a barely visible

171   alveolar process. The maxilla bears a conspicuous and pointed process at its antero-dorsal end.

172   The posterior end is expanded dorsoventrally, forming a rounded lamina. Neither the premaxilla

173   nor the maxilla bear visible teeth. There is no evidence of a supramaxilla. The anterior margin of

174   the dentary, slightly concave and bearing no visible teeth, forms a strong angle with the ventral

175   margin. The posterior margin of the dentary forms an interosseous space with the

176   anguloarticular, which is mostly hidden by overlaying bones.

177

178   *Suspensorium and hyoid arch*

179 Only the proximal, single-headed articulation of the hyomandibula is clearly visible; the distal

180 end of the bone seems to be preserved in close association with the metapterygoid. The latter is

181 roughly triangular and is one of the best preserved bones of the suspensorium. The symplectic is

182 rod-like, narrows slightly anteriorly and inserts in a notch on the postero-ventral margin of the

183 quadrate. The triangular quadrate bears an antero-ventral condyle that articulates with the

184 anguloarticular. The anterior portion of the suspensorium is poorly preserved, and it is difficult to

185 outline the limits of the endopterygoid, ectopterygoid and palatine bones. The dorsal and

186 posterior portions of the endopterygoid are preserved, suggesting that the bone forms two

187 laminae, the dorsal one along the parasphenoid, and the ventral one contacting both the quadrate

188 and the metapterygoid.

189 Both the left and right ventral hyoid arches are visible. One is preserved in life position: its

190 posterior end overlaps the operculum, but its dorsal margin is hidden by the lower jaw,

191 suggesting it corresponds to the right ventral hyoid arch. The left one is displaced and upturned,

192 and lies ventral to its counterpart. The posterior ceratohyal is triangular and articulates with the

193 anterior ceratohyal with an interdigitated suture. The anterior ceratohyal shows a strong ventral

194 concavity at midlength; its dorsal margin is much less concave. The anterior end of the anterior

195 ceratohyal forms a rounded condyle, over which the curved ventral hypohyal articulates. The

196 dorsal hypohyal lies dorsally over the anterior ceratohyal. There are six branchiostegals: the

197 anterior two are shorter and articulate with the anterior ceratohyal at the level of its ventral

198 concavity; the four others articulate more posteriorly (due to the faint distinction between both

199 ceratohyals, it is difficult to determine on which one they articulate); they are very long (the

200 posteriormost being the longest) and curved posteriorly over the ventral margin of the

201 interopercle. The branchiostegals of the left hyoid arch are disarticulated.

202

Opercular series

204 The preopercle is wide and angled at mid-length. The interopercle is an elongate bone rounded at

205 its extremity that forms the ventral margin of the opercular series. It has a smooth ventral margin,

206 closely associated with the posterior branchiostegals. The possible presence of parts of the

207 opercle, in contact with the preopercle, is unclear.

208

Dorsal fin and supports

210 The dorsal fin is only partially preserved, with only the most anterior pterygiophores and dorsal-

211 fin rays visible. Its most striking feature is the extremely elongated and enlarged first dorsal-fin

212 ray, which is 10 times as wide as the more posterior fin rays (at their base and greatest width). It

213 does not bifurcate distally, lacks any visible segmentation, and a groove runs throughout its

214 length. A rounded splint protrudes at its anterior base; it is unclear whether it constitutes a

215 separate dorsal-fin element or not. Fifteen other dorsal-fin rays are preserved posteriorly. Their

216 distal end is missing in most cases, but they all seem to be of a similar length, except for the

217 second and third dorsal-fin rays that are noticeably longer. They do not bifurcate distally, and no

218 segmentation is clearly visible.

219 Ten dorsal-fin pterygiophores are clearly preserved. They are strongly inclined anteriorly, which

220 causes the dorsal fin to originate at the tip of the crest, and to run along the entire head of the

221 animal. The first two dorsal-fin pterygiophores are greatly enlarged and in close contact with the

222 crest. Both also show a conspicuous flange at their posterior margin. The first pterygiophore is

223 narrow posteriorly, where it does not contact the supraoccipital, and widens in its distal end. The

224 second one is much wider and slightly narrows at its distal extremity. It is in close contact with

225   the first pterygiophore throughout its entire length. The third and fourth preserved

226   pterygiophores are in close contact with the second one throughout almost all of their lengths.

227   The more posterior pterygiophores have a mostly straight shaft that curves slightly at its distal

228   extremity. The most posterior ones are less inclined than the anterior ones. The proximal ends of

229   all preserved pterygiophores converge at the same point: the base of the crest – thus they insert

230   anterior to the (not preserved) first neural spine. The elongated and enlarged first dorsal-fin ray

231   inserts on the first pterygiophore. It is unclear if the rays two to eight insert on pterygiophores

232   that are mostly hidden or not preserved, or in supernumerary association with the enlarged

233   second pterygiophore. The rays 9-16 each insert serially on a corresponding pterygiophore.

234

235   **DISCUSSION**

236   **Taxonomic justification**

237   Oelschläger (1979) proposed that MNHN.F. EIP11 is different enough anatomically from the

238   other lophotids, fossil and extant, to justify its attribution to a new genus. Indeed, it differs from

239   the holotype of †*Protolophotus*, found in the same geological levels, by the relative development

240   of the crest. In MNHN.F.EIP11, the crest is projecting anteriorly with an angle of 64.5°, and the

241   ratio between the lengths of the crest's anterior margin and of the head without the crest is of

242   1.17 to 1. In the holotype of †*Protolophotus*, MNHN .F.EIP10 (Fig. 3), the anterior margin of the

243   crest is almost vertical (degree of projection: 20°), and it is relatively shorter (margin of the

244   crest/head length without the crest: 0.67/1). MNHN.F.EIP11 also bears a much stronger first

245   dorsal-fin ray, and its two anterior dorsal-fin pterygiophores are considerably more developed.

246   Body size is known to affect crest size and degree of projection in extant *Lophotus* (Craig,

247   Hastings & Pondella, 2004), which could be misleading when trying to differentiate taxa based

248 on morphology. However, this bias can probably be ruled out in the case of MNHN.F.EIP11 and

249 MNHN.F.EIP10: both individuals have similar head lengths without the crest (42 and 44 mm,

250 respectively), suggesting that they are at a similar growth stage. It then seems that classifying

251 MNHN.F.EIP11in a different genus and species, †*Babelichthys olneyi*, is justified from a

252 morphological point of view.

253

254 **Systematic position**

255 **Babelichthys** *as a taeniosome lampridiform*

256 The monophyly of Lampridiformes (excluding *Stylephorus*, *sensu* Nelson, Grande & Wilson,

257 2016) is well-supported by molecular phylogenetic analyses (Wiley, Johnson & Dimmick, 1998;

258 Miya et al., 2007; Betancur-R. et al., 2013; Near et al., 2013) and by numerous morphological

259 features (Olney, Johnson & Baldwin, 1993; Davesne et al., 2014, 2016; Delbarre, Davesne &

260 Friedman, 2016). Several of these character states are unambiguously found in †*Babelichthys*:

261 the premaxilla and dentary are toothless, the frontal and the supraoccipital are both involved in a

262 sagittal crest, the anterior ceratohyal forms a condyle that articulates with the ventral hypohyal,

263 and the first dorsal-fin pterygiophore inserts anterior to the neural spine of the first abdominal

264 vertebra.

265 The phylogenetic studies that explore lampridiform intrarelationships with a sufficient sampling

266 all recover a monophyletic Taeniosomi (Wiley, Johnson & Dimmick, 1998; Grande, Borden &

267 Smith, 2013; Martin, 2015). The taeniosome character states found in †*Babelichthys* include the

268 absence of supraneurals, and anterior dorsal-fin pterygiophores that are enlarged and inclined

269 over the neurocranium (Olney, Johnson & Baldwin, 1993). †*Babelichthys* then clearly shows a

270 character state combination that confirms its identification as a taeniosome lampridiform.

271

272   ***Position within Lophotidae***

273   Olney, Johnson & Baldwin (1993) proposed that the enlarged supraoccipital process, projecting

274   anteriorly over the frontals (forming the "crest" as described herein) and supporting the first

275   dorsal-fin pterygiophore, is a synapomorphy of Lophotidae. Since it is not observed elsewhere in

276   lampridiforms, this character confirms the attribution of †*Babelichthys* to Lophotidae. It has to

277   be noted that in the yet unpublished phylogenetic analysis of Martin (2015), the monophyly of

278   Lophotidae is ambiguous, with one parsimonious tree finding *Lophotus* more closely related to

279   the other taeniosomes than to *Eumecichthys*, while in the other both genera are sister groups.

280   Given this ambiguity, Lophotidae is kept as a monophyletic group in this discussion.

281   The distinction between an almost horizontal "crest" projecting anteriorly and a more vertical

282   and relatively shorter "crest" distinguishes †*Babelichthys* from †*Protolophotus* (see above,

283   Taxonomic justification), but also from the extant *Lophotus* and the other known lophotid fossil

284   taxa (Table 1). Conversely, in the *Eumecichthys* specimen that is examined, the crest is strongly

285   projected anteriorly (angle of 72.4°) and relatively very long (Table 1). Another element is the

286   apparent absence of vomerine fang-like teeth in †*Babelichthys* (it is however possible that they

287   were present, but not preserved in the fossil), like in *Eumecichthys*, while they are present in

288   *Lophotus* (Olney, Johnson & Baldwin, 1993). Since only one specimen is available, it is

289   impossible to perform a thorough comparison of head morphologies at various growth stages and

290   between individuals. Nevertheless, it seems based on available elements that head morphology in

291   †*Babelichthys* is closer to the one observed in *Eumecichthys* than in *Lophotus*, corroborating

292   Oelschläger's (1979) proposition that it represents a potential fossil sister group to *Eumecichthys*.

293   It would then be the first known fossil unicorn crestfish. Nevertheless, †*Babelichthys* also differs

294   from *Eumecichthys*: its crest is less strongly projecting and relatively shorter (Table 1).

295   Moreover, no other lophotid, fossil or extant, has such an extreme enlargement and expansion of

296   the dorsal-fin pterygiophores, in particular the second one.

297

298   **The taeniosome fossil record**

299   Taeniosome lampridiforms are known by several fossil representatives. The oldest

300   unquestionable occurrences are all attributed to Lophotidae: the diminutive †*Eolophotes lenis*

301   (Fig. 4A), from the Lutetian (Eocene) of Georgia (Daniltshenko, 1962, 1980) and

302   †*Protolophotus elami* (Fig. 3), found in the same middle-late Eocene formation as †*Babelichthys*

303   (see above). An additional, younger fossil lophotid is †*Oligolophotes fragosus* (Fig. 4B) from the

304   early Oligocene Pshekha Formation of Adygea, northern Caucasus, Russia (Bannikov, 1999).

305   The taeniosome fossil record also includes the trachipterid †*Trachipterus mauritanicus* from the

306   Messinian (late Miocene) of Algeria (Carnevale, 2004), and a fragmentary possible oarfish

307   (*Regalecus*) from the Pliocene of Italy (Bronzi, 2001; Roberts, 2012). There is no known fossil

308   Radiicephalidae. Finally, the small and distinctive †*Bajaichthys elegans*, from the Ypresian

309   (early Eocene) of Bolca, Italy, has been classified as a taeniosome or close relative due to its

310   mobile jaws, elongate body and reduced caudal fin (Sorbini & Bottura, 1988; Bannikov, 2014).

311   However, it can be confidently classified in Zeiformes, another teleost clade (Davesne,

312   Carnevale & Friedman, 2017). In total, five entirely fossil species of taeniosomes are currently

313   known (four Lophotidae, one Trachipteridae), a diversity expanded by the present description of

314   †*Babelichthys*.

315

316   **CONCLUSION**

317   In the present paper, †*Babelichthys olneyi*, a new genus and species of Lophotidae from the

318   Eocene of Iran is described. Few fossil representatives of Taeniosomi, an elusive group of deep-

319   sea teleosts, are known and only one of them has been previously described in detail (Bannikov,

320   1999). †*Babelichthys* is potentially the only known fossil close relative of the unicorn crestfish

321   *Eumecichthys*. This discovery is also significant because it expands the diversity of the middle-

322   late Eocene Ilam fauna. Modern lophotids are found in mesopelagic environments (Olney, 2002),

323   so the presence of at least two representatives of the family in the fauna that is mostly composed

324   by relatives of modern deep-sea teleosts (Arambourg, 1967; Afsari et al., 2014; Přikryl,

325   Brzobohatý & Gregorová, 2016) reinforces the assumption that it represents a valuable glimpse

326   of the poorly known early Cenozoic deep-water ecosystems.

327

328   **Institutional Abbreviations**

329   **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, Natural History

330   Museum, London, United Kingdom; **PIN**, Borisyak Paleontological Institute of the Russian

331   Academy of Sciences, Moscow, Russia; **USNM**, National Museum of Natural History,

332   Smithsonian Institution, Washington D.C., United States.

333

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343

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462

463   **Figure captions**

464   FIGURE 1. †*Babelichthys olneyi*, gen. et sp. nov., holotype. **(A)** MNHN.F.EIP11d. **(B)**

465   counterpart MNHN.F.EIP11g. Scale bars = 20 mm.

466   FIGURE 2. †*Babelichthys olneyi*, gen. et sp. nov. holotype MNHN.F.EIP11d. **(A)** Photograph

467   (detail of the head) and **(B)** interpretative drawing. Legend: achy, anterior ceratohyal; bra,

468   branchiostegal; bsp, basisphenoid; den, dentary; dfr, dorsal-fin ray; dhhy, dorsal hypohyal; dpt,

469   dorsal-fin pterygiophore; enpt, endopterygoid; fr, frontal; hyo, hyomandibula; iop, interopercle;

470   lac, lachrymal; let, lateral ethmoid; mpt, metapterygoid; mx, maxilla; osp, orbitosphenoid; pal,

471   palatine; pchy, posterior ceratohyal; pmx, premaxilla; pop, preopercle; psp, parasphenoid; qu,

472   quadrate; soc, supraoccipital; soc-sp, spine of the supraoccipital; spl, splint of the first dorsal-fin

473   ray; vhhy, ventral hypohyal; vo, vomer. Scale bar = 10 mm.

474   FIGURE 3. †*Protolophotus elami*, holotype MNHN.F.EIP10d. Scale bar = 20 mm.

475   FIGURE 4. Other fossil taxa attributed to family Lophotidae. **(A)** †*Eolophotes lenis*, holotype

476   PIN 1413/86; scale bar = 5 mm. **(B)** †*Oligolophotes fragosus*, holotype PIN 3363/121; scale bars

477   = 10 mm.

Figure 1

†*Babelichthys olneyi*, gen. et sp. nov., holotype.

(A) MNHN.F.EIP11d. **(B)** counterpart MNHN.F.EIP11g. Scale bars = 20 mm.

†*Babelichthys olneyi*, gen. et sp. nov. holotype MNHN.F.EIP11d.

Photograph (detail of the head) and interpretative drawing. Legend: achy, anterior ceratohyal; bra, branchiostegal; bsp, basisphenoid; den, dentary; dfr, dorsal-fin ray; dhhy, dorsal hypohyal; dpt, dorsal-fin pterygiophore; enpt, endopterygoid; fr, frontal; hyo, hyomandibula; iop, interopercle; lac, lachrymal; let, lateral ethmoid; mpt, metapterygoid; mx, maxilla; osp, orbitosphenoid; pal, palatine; pchy, posterior ceratohyal; pmx, premaxilla; pop, preopercle; psp, parasphenoid; qu, quadrate; soc, supraoccipital; soc-sp, spine of the supraoccipital; spl, splint of the first dorsal-fin ray; vhhy, ventral hypohyal; vo, vomer. Scale bar = 10 mm.

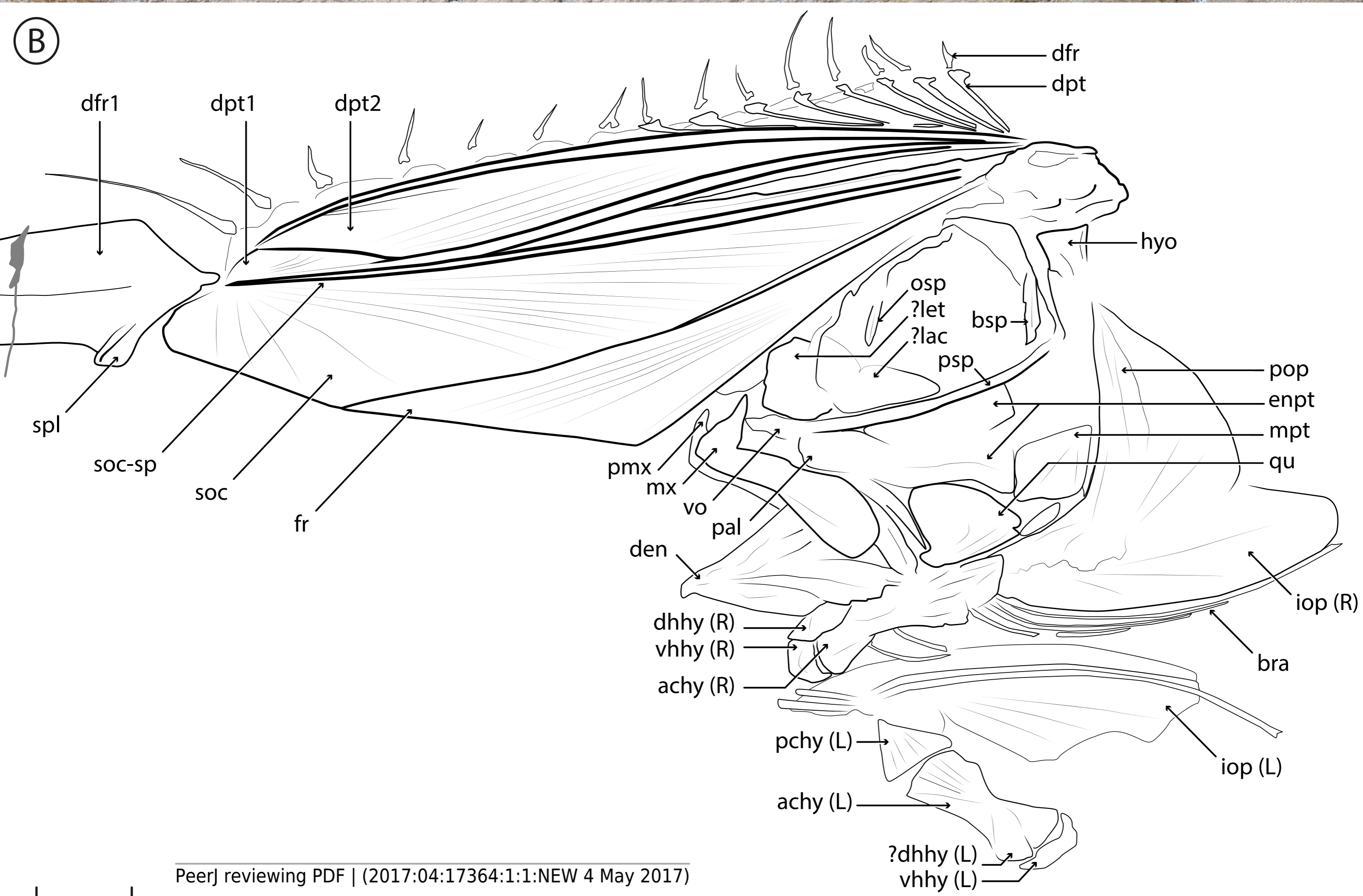



Figure 3

†*Protolophotus elami*, holotype MNHN.F.EIP10d.

Scale bar = 20 mm.

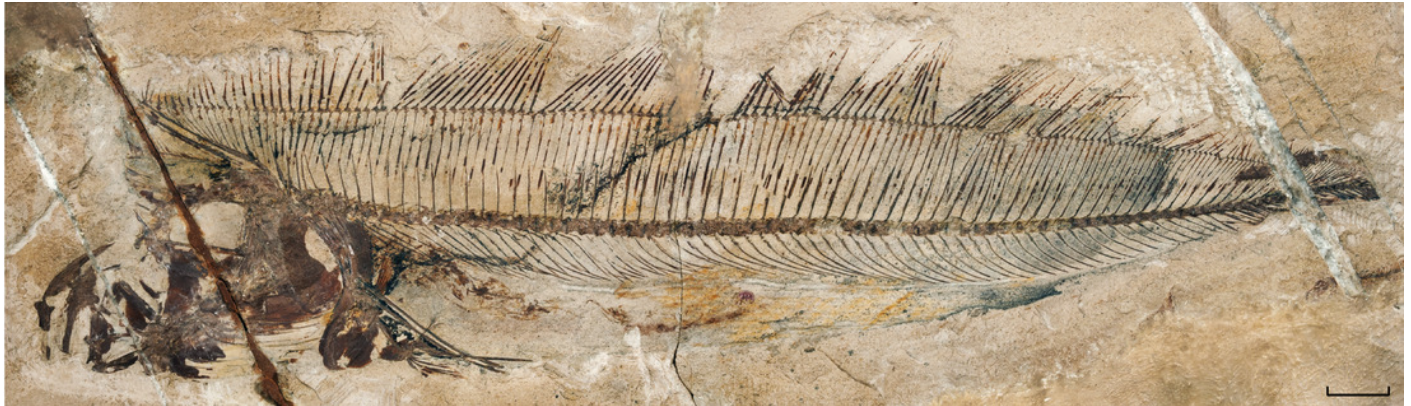
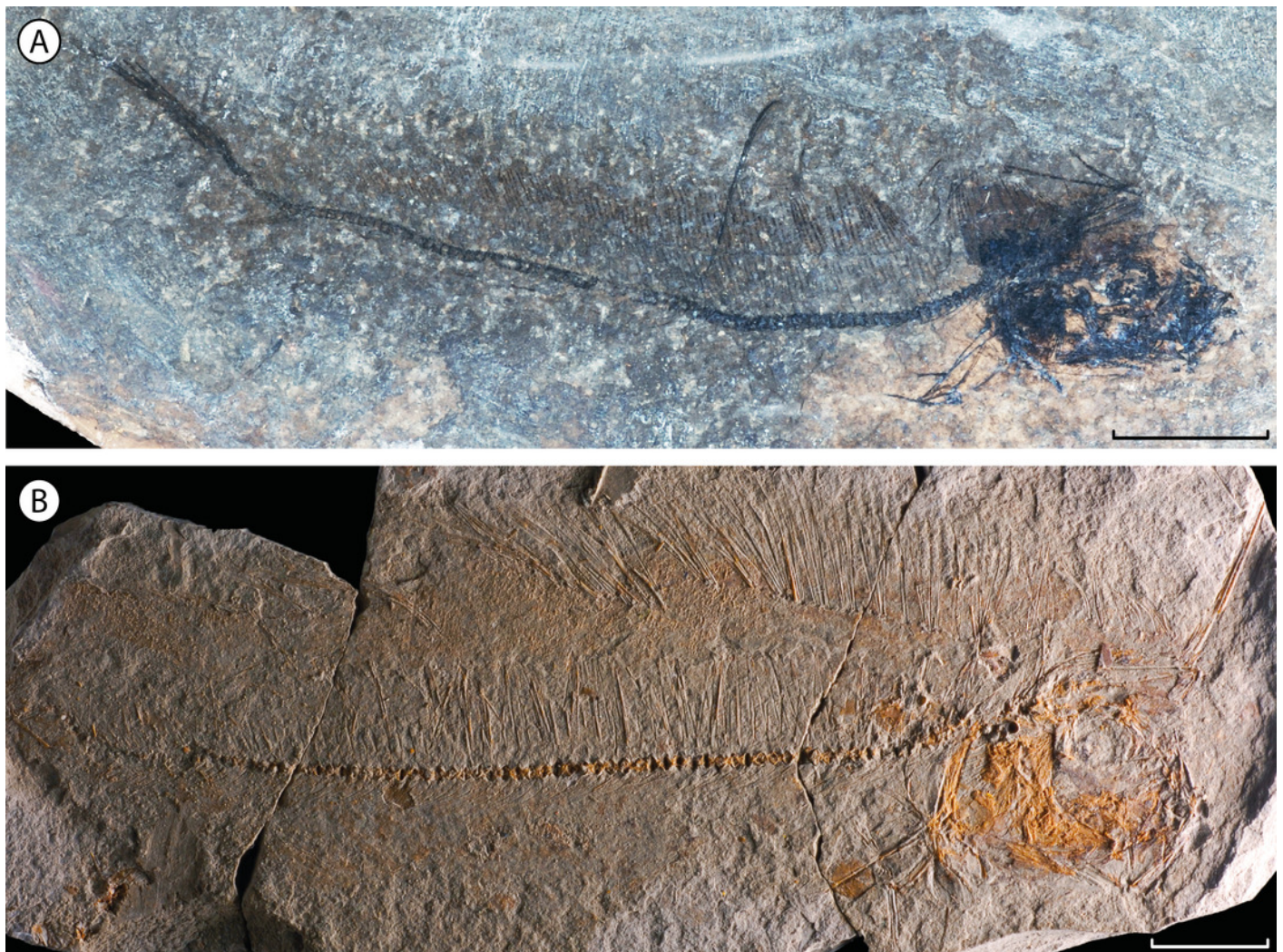



Figure 4

Other fossil taxa attributed to family Lophotidae.

(A) †*Eolophotes lenis*, holotype PIN 1413/86; scale bar = 5 mm. (B) †*Oligolophotes fragosus*, holotype PIN 3363/121; scale bars = 10 mm.

Comparison between crest measurements in selected specimens of known lophotid genera.

[1] Angle (°) between the straight line from the tip of the crest to the proximal end of its anterior margin, and the line drawn perpendicular to the main axis of the parasphenoid.

[2] Distance (mm) between the tip of the crest to the proximal end of its anterior margin.

[3] Distance (mm) between the anterior margin of the ethmoid and the posterior margin of the neurocranium

Species	Specimen studied	Projection of the crest [1]	Crest length [2]	Head length [3]	Crest length / head length
†*Babelichthys olneyi*, sp. nov.	MNHN.F.EIP11	64.5°	51.5 mm	44 mm	1.17/1
†*Protolophotus elami*	MNHN.F.EIP10	20°	28 mm	42 mm	0.67/1
†*Eolophotes lenis*	PIN 1413/86	-17°	1.1 mm	2.1 mm	0.52/1
†*Oligolophotes fragosus*	PIN 3363/121	6.7°	6.8 mm	12.7 mm	0.54/1
Lophotus lacepede	NHMUK 1863.8.27.1	25.7°	99.8 mm	108.6 mm	0.92/1
Eumecichthys fiski	USMN 164170	72.4°	26.8 mm	17.2 mm	1.55/1

2 TABLE 1. Comparison between crest measurements in selected specimens of known lophotid

3 genera.

5 [1] Angle (°) between the straight line from the tip of the crest to the proximal end of its anterior

6 margin and the line drawn perpendicular to the main axis of the parasphenoid.

7 [2] Distance (mm) between the tip of the crest to the proximal end of its anterior margin.

8 [3] Distance (mm) between the anterior margin of the ethmoid and the posterior margin of the

9 neurocranium