

A fossil unicorn crestfish (Teleostei, Lampridiformes, Lophotidae) from the Eocene of Iran (#17364) 1

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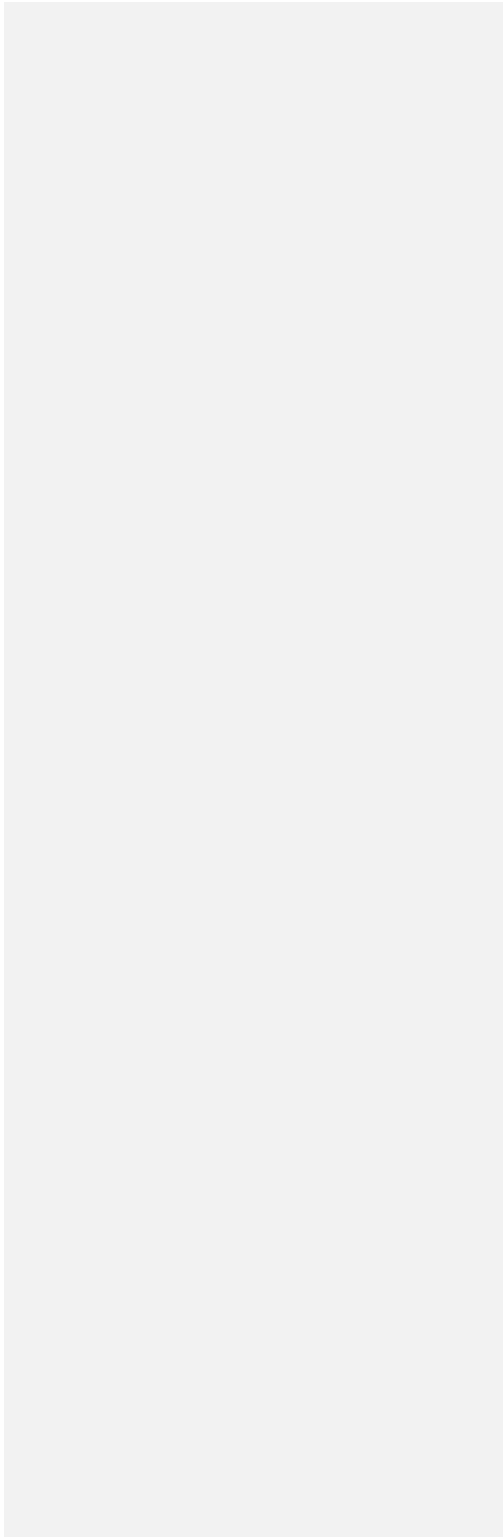
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A fossil unicorn crestfish (Teleostei, Lampridiformes, Lophotidae) from the Eocene of Iran

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Lophotidae, or crestfishes, is a family of rare deep-sea teleosts characterised by an enlarged horn-like crest on their 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, we argue that it represents 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 adds to the uniqueness of the deep-sea teleost fauna to which it belongs, improving our understanding of the taxonomic composition of the mesopelagic ecosystems in the early Cenozoic.

Commented [s1]: Why we?

1 A fossil unicorn crestfish (Teleostei, Lampridiformes, Lophotidae) from the

2 Eocene of Iran

3

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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, we argue that it represents a new genus and species. †Babelichthys
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15 projecting crest, suggesting a close relationship with the modern unicorn crestfish, Eumecichthys.
16 This new taxon adds to the uniqueness of the deep-sea teleost fauna to which it belongs,
17 improving our understanding of the taxonomic composition of the mesopelagic ecosystems in
18 the early Cenozoic.

19

Commented [s2]: How does it add to "the uniqueness?"

20 INTRODUCTION

21 Lampridiformes ~~is~~are a clade of strange spiny-rayed teleosts, found in mesopelagic environments in
22 every ocean of the world (Olney, Johnson & Baldwin, 1993; Olney, 2002). Their most famous
23 representatives are the endothermic opah (Lampris) and the gigantic, serpentine oarfish
24 (Regalecus), the longest known teleost. Along with these iconic taxa, Lampridiformes include
25 equally weird ribbon-like and elongate animals, characterized by a silver-coloured skin and long,
26 bright red fins: the taeniosomes. The 15 to 18 extant species of the clade Taeniosomi include
27 oarfishes (Regalecidae), ribbonfishes (Trachipteridae), the tapertail (Radiicephalidae) and
28 Lophotidae, the crestfishes (Regan, 1907; Walters & Fitch, 1960; Olney, 1984; Roberts, 2012).
29 Lophotids are characterized by unique structures, such as ~~their~~an ink gland (Walters & Fitch, 1960;
30 Honma, Ushiki & Takeda, 1999) not found anywhere else in teleosts (except in the closely
31 related radiicephalids; Harrisson & Palmer, 1968). ~~Their~~ most conspicuous osteological feature of
lophotids
32 is ~~their~~a well-developed ~~developed~~ horn-like crest, formed by an anteriorly projecting expansion of the
frontal and
33 supraoccipital bones of the cranium (Oelschläger, 1979, 1983; Olney, Johnson & Baldwin,
34 1993), ~~that is closely associated with the anterior pterygiophores supporting the dorsal fin. -This crest is~~
closely associated with the anterior pterygiophores supporting the dorsal fin, and ~~A~~ as a
35 result, ~~their~~ dorsal fin expands over, and sometimes anterior to the cranium. Lophotids are
36 represented in modern fauna by one to three Lophotus species and by the unicorn crestfish,
37 Eumecichthys fiski (Walters & Fitch, 1960; Craig, Hastings & Pondella, 2004).
38 The present article is a revision of an anatomically distinctive fossil specimen attributed to
39 Lophotidae. Arambourg (1943, 1967) first signalled the specimen from the rich late Eocene
40 fauna he described near Ilam, Zagros Basin, Iran. The Ilam fauna comprises numerous
41 representatives of teleost taxa such as Beryciformes, Gadiformes, Ophidiiformes and

Commented [s3]: What does this mean?

42 Stomiiformes, typical of the modern deep-sea pelagic environments (Arambourg, 1967; Afsari et
43 al., 2014; Příkryl, Brzobohatý & Gregorová, 2016).

44 The taxonomic status of the lophotid specimen studied here is currently unclear (Walters, 1957;
45 Oelschläger, 1979; Bannikov, 1999), and it lacks a proper anatomical description. Given the
46 rarity of fossil material attributed to taeniosome lampridiforms, a detailed description and revised
47 taxonomy of this material is needed in order to improve our understanding of the morphological
48 evolution and fossil record of this peculiar group.

49

50 MATERIAL AND METHODS

51 Taxonomic status of the material

52 The material described herein, MNHN.F.EIP11 (Figs. 1, 2), was discovered during excavations
53 near Ilam (Zagros Basin, Western Iran) by Camille Arambourg in 1938-1939. The specimen was
54 chosen to be the paratype of †*Lophotus elami* (Arambourg, 1943), along with the holotype

55 MNHN.F.EIP10 (Fig. 3). †*L. elami* was later ~~erected as a~~ assigned to a distinct new genus,
†*Protolophotus* (Fig. 3),

56 based on osteological differences ~~with~~ from extant lophotids, such as the well-ossified pelvic girdle ~~at~~ in
57 a ventral position ~~that is~~ observed ~~in~~ the holotype (Walters, 1957). Oelschläger (1979) proposed
58 that MNHN.F.EIP11 differs ~~enough~~ sufficiently from MNHN.F.EIP10 to be classified in a different
genus.

59 He related the specimen to the extant *Eumecichthys* and gave it the name †'*Protomecichthys*'.

60 However, the genus †'*Protomecichthys*' lacks both a designated type species and a formal
61 description. Thus, it fails to meet the requirements of Article 13.3 of the International Code of
62 Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) and
63 should be considered a nomen nudum (Bannikov, 1999).

64

65 Comparative material

66 †*Eolophotes lenis*, PIN 1413/86; *Eumecichthys fiski*, USNM 164170 (radiographs); *Lophotus*
67 *lacepede*, NHMUK 1863.8.27.1 (radiographs); †*Oligolophotes fragosus*, PIN 3363/121;
68 †*Protolophotus elami*, MNHN.F.EIP10.

69

70 Nomenclatural acts

71 The electronic version of this article in Portable Document Format (PDF) will represent a
72 published work according to the International Commission on Zoological Nomenclature (ICZN),
73 and hence the new names contained in the electronic version are effectively published under that
74 Code from the electronic edition alone. This published work and the nomenclatural acts it
75 contains have been registered in ZooBank, the online registration system for the ICZN. The
76 ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed
77 through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The
78 LSID for this publication is: urn:lsid:zoobank.org:pub:B677BA4F-CCF4-4678-A8A8-
79 502F059704D2. The online version of this work is archived and available from the following
80 digital repositories: PeerJ, PubMed Central and CLOCKSS.

81

82 Methods

83 The specimen was examined with a stereomicroscope equipped with a camera lucida drawing
84 arm. The interpretative drawing was produced with Adobe Illustrator CS6 from the camera
85 lucida drawings and from photographs. Measurements were taken with a compass or with the
86 software ImageJ 1.5 from radiographs; angles were also measured with ImageJ. The method for
87 estimating the degree of projection of the crest is modified from Craig, Hastings & Pondella

88 (2004): it is based on the angle between the straight line from the tip of the crest to the proximal
89 end of its anterior margin (instead of the tip of the upper jaw, due to varying jaw positions in
90 fossils) and the vertical line drawn perpendicular to the main axis of the parasphenoid ~~main axis~~ (instead
of the
91 vertebral column, not preserved in MNHN.F.EIP11). The relative length of the crest is the ratio
92 between the crest length (distance between the tip of the crest and the proximal end of its anterior
93 margin) and the head length without the crest (from the anterior margin of the ethmoid region to
94 the posterior margin of the neurocranium). All extinct taxa are indicated with a dagger (†).

95

96 RESULTS

97 Systematic palaeontology

98 TELEOSTEI Müller, 1845

99 ACANTHOMORPHA Rosen, 1973

100 Order LAMPRIDIFORMES Goodrich, 1909

101 Suborder TAENIOSOMI Gill, 1885

102 Family LOPHOTIDAE Bonaparte, 1845

103 Genus †Babelichthys gen. nov.

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

105 (Figs. 1, 2)

106

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

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

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

110 Type and only species. †Babelichthys olneyi, sp. nov.

111 Diagnosis. A Lophotid differing from †Eolophotes, Lophotus, †Oligolophotes and †Protolophotus
112 by the relatively longer, strongly projecting crest; and from Eumecichthys by the relatively
113 shorter, deeper and less strongly projecting crest, with strongly expanded anterior dorsal-fin
114 pterygiophores.

115

116 †Babelichthys olneyi sp. nov.

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

118 (Figs. 1, 2)

119

120 1943 †Lophotes elami Arambourg, p. 287, pl. X, fig. 1

121 1957 †Protolophotus elami Walters, p. 60

122 1967 †Protolophotes elami Arambourg, pl. VI, fig. 1

123 1979 †Protomecichthys sp. Oelschläger, p. 354, fig. 11 (nomen nudum)

124

125 Holotype. MNHN.F.EIP11d/g, almost complete articulated cranium and anterior portion of the
126 dorsal fin, in part and counterpart (Figs. 1, 2). This is the only specimen known for the genus and
127 species.

128 Etymology. Species named in honour of the late John E. Olney, in recognition of his work on the
129 anatomy and ontogeny of Lampridiformes.

130 Type locality and horizon. Near Ilam, Zagros Basin, Western Iran. This teleost fauna, part of
131 the Pabdeh Formation, was erroneously aged Cretaceous by Priem (1908), and Rupelian
132 (Oligocene) by Arambourg (1943, 1967). It is more accurately middle to late Eocene in age
133 (Afsari et al., 2014; and references therein).

134 Diagnosis. As for the genus.

135

136 Anatomical description

137 MNHN.F.EIP11 consists in only the head of the animal, along with the associated anterior
138 portion of the dorsal fin. The specimen is mostly articulated, except for the left ventral portion of
139 the hyoid arch that is upturned and preserved ventral to the rest of the cranium. The limits of
140 most bones are poorly preserved, probably due to their low degree of mineralization in life as is
141 the case in modern taeniosome lampridiforms.

142

143 Measurements

144 Total head length: 104 mm; head length (without the crest): 44 mm; crest length (anterior
145 margin): 51.5 mm; head depth: 25.5 mm; orbit diameter: 23 mm.

146

147 Neurocranium

148 The neurocranium of MNHN.F.EIP11 is highly modified. The frontal develops a dorsal lamina
149 that projects anterior to the jaws. Throughout approximately its anterior half, it is in contact with
150 an enlarged laminar process of the supraoccipital, delimited dorsally by a strong supraoccipital
151 spine. Together, they form a conspicuous "crest", long and strongly projecting anteriorly (at an
152 angle of 64.5°). Alone, the crest contributes to 58% of total head length.

153 The frontal makes up ~~for~~ approximately 60% of the anterior margin of the crest. Both the frontal
154 and the supraoccipital show radial ornamentation on the crest; it radiates from the posterior end
155 of the frontal and ~~but from~~ the distal tip of the supraoccipital. The supraoccipital spine borders the
156 dorsal margin of the bone, narrowing towards the tip.

157 The ethmoid region is poorly preserved, with an enlarged probable lateral ethmoid hiding the
158 mesethmoid. An enlarged lachrymal is nested in the antero-ventral corner of the orbit; it is
159 parallel to the parasphenoid ventrally, and curves dorsally along the edge of the lateral ethmoid.
160 The orbitosphenoid runs at along the dorsal margin of the orbit; ~~it shows~~ and has a conspicuous process
161 pointing ventrally. The posterior wall of the orbit is delimited ventrally by a robust and straight
162 basisphenoid. Otherwise, the sphenoid, otic and occipital regions are too poorly preserved to
163 distinguish the individual bones. The parasphenoid is robust and slightly curves dorsally at its
164 anterior end. The limit-junction between the parasphenoid and the vomer is not discernable. There is no
165 evidence of vomerine teeth.

166

167 Jaws

168 The premaxilla is relatively small, with a well-developed ascending process and a barely visible; ~~the~~
alveolar process ~~is~~

169 ~~barely visible~~. The maxilla bears a conspicuous and pointed ascending process. Its alveolar
170 process is expanded dorsoventrally at its posterior end, forming a rounded lamina. Neither the
171 premaxilla nor the maxilla bear visible teeth. There is no evidence of a supramaxilla. The
172 anterior margin of the dentary forms a strong angle with its ventral margin. It is slightly concave,
173 and bears no visible teeth. The posterior margin of the dentary forms a fenestra with the
174 anguloarticular, which is mostly hidden by overlaying bones.

175

176 Suspensorium and hyoid arch

177 Only the proximal, single-headed -articular of the hyomandibular r is clearly visible; its distal
178 end might be preserved, in close association with the metapterygoid. The latter is roughly
179 triangular and is one of the best preserved bones of the suspensorium. The symplectic is rod-like,

Commented [s4]: Not familiar with this term regarding maxilla

180 narrows slightly anteriorly and inserts in a notch on the postero-ventral margin of the quadrate.
181 The triangular quadrate bears an antero-ventral condyle that articulates with the angulo-articular.
182 The anterior portion of the suspensorium is poorly preserved, and it is difficult to outline the
183 limits of the endopterygoid, ectopterygoid and palatine bones. The dorsal and posterior portions
184 of the endopterygoid are preserved, suggesting that the bone forms two laminae, the dorsal one
185 along the parasphenoid, and the ventral one contacting both the quadrate and the metapterygoid.
186 Both the left and right ventral hyoid arches are visible. One is preserved in life position: its
187 posterior end overlaps with the operculum, but its dorsal margin is hidden by the lower jaw,
188 suggesting it corresponds to the right ventral hyoid arch. The left one is displaced and upturned,
189 and ~~lays lies~~ ventral to its counterpart. The posterior ceratohyal is triangular and articulates with the
190 anterior ceratohyal with an interdigitated suture. The anterior ceratohyal shows a strong ventral
191 concavity at midlength; its dorsal margin is much less concave. The anterior end of the anterior
192 ceratohyal forms a rounded condyle, over which the curved ventral hypohyal articulates. The
193 dorsal hypohyal lies dorsally over the anterior ceratohyal. There are six branchiostegals ~~rays~~: the
194 anterior two are shorter and articulate with the anterior ceratohyal at the level of its ventral
195 concavity; the four others articulate more posteriorly (due to the faint ~~limit-distinction~~ between both
196 ceratohyals, it is difficult to determine on which one they articulate); they are very long (the
197 posterior-most being the longest) and curved posteriorly over the ventral margin of the
198 interopercle. The branchiostegals of the left hyoid arch are disarticulated.

199

200 Opercular series

201 The preopercle is wide and angled at mid-length. The interopercle is an elongate bone rounded at
202 its extremity that forms the ventral margin of the opercular series. It has a smooth ventral margin,

203 closely associated with the posterior branchiostegals. The opercle seems to be missing, but its
204 anterior portion might be preserved in contact with the preopercle.

205

206 Dorsal fin and supports

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

208 fin rays ~~being~~ visible. Its most striking feature is the extremely elongated and enlarged first

209 dorsal-fin ray, ~~that~~ which is 10 times as wide as the more posterior fin rays (at their base and greatest

210 width). It does not bifurcate distally, lacks any visible segmentation and a groove runs

211 throughout its length. A rounded splint protrudes at its anterior base; it is unclear whether it

212 constitutes a separate dorsal-fin element or not. Fifteen other dorsal-fin rays are preserved

213 posteriorly. Their distal end is missing in most cases, but they all seem to be of a similar length,

214 except for the second and third dorsal-fin rays that are noticeably longer. They do not bifurcate

215 distally, and no segmentation is clearly visible.

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

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

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

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

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

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

222 the first pterygiophore throughout ~~at~~ its entire length. The third and fourth preserved pterygiophores

223 are in close contact with the second one throughout almost all of their lengths. The more

224 posterior pterygiophores have a mostly straight shaft that curves slightly at its distal extremity.

225 The most posterior ones are less inclined than the anterior ones. The proximal ends of all

226 preserved pterygiophores converge at the same point, ~~at~~ the base of the crest – thus they insert
227 anterior to the (not preserved) first neural spine. The elongated and enlarged first dorsal-fin ray
228 inserts on the first pterygiophore. It is unclear if the rays two to eight insert on pterygiophores
229 that are mostly hidden, or directly on the enlarged second pterygiophore. The rays 9-16 each
230 insert on a corresponding pterygiophore.

Commented [s5]: State whether the rays are in serially of supernumerary association with the referred pterygiophores

231

232 DISCUSSION

233 Taxonomic justification

234 Oelschläger (1979) proposed that MNHN.F. EIP11 is different enough anatomically from the
235 other lophotids, fossil and extant, to justify its attribution to a new genus. Indeed, it differs from
236 the holotype of †Protolophotus, found in the same geological levels, by the relative development
237 of the crest. In MNHN.F.EIP11, the crest is projecting anteriorly with an angle of 64.5°, and the
238 ratio between the lengths of the crest's anterior margin and of the head without the crest is of
239 1.17 to 1. In the holotype of †Protolophotus, MNHN .F.EIP10 (Fig. 3), the anterior margin of the
240 crest is almost vertical (degree of projection: 20°), and it is relatively shorter (margin of the
241 crest/head length without the crest: 0.67/1). MNHN.F.EIP11 also bears a much stronger first
242 dorsal-fin ray, and its two anterior dorsal-fin pterygiophores are considerably more developed.
243 Body size is known to affect crest size and degree of projection in extant Lophotus (Craig,
244 Hastings & Pondella, 2004), which could be misleading when trying to differentiate taxa based
245 on morphology. However, this bias can probably be ruled out in the case of MNHN.F.EIP11 and
246 MNHN.F.EIP10: both individuals have similar head lengths without the crest (42 and 44 mm,
247 respectively), suggesting that they are at a similar growth stage. It then seems that classifying

248 MNHN.F.EIP11 in a different genus and species, †*Babelichthys olneyi*, is justified from a
249 morphological point of view.

250

251 Systematic position

252 *Babelichthys* as a taeniosome lampridiform

253 The monophyly of Lampridiformes (excluding *Stylephorus*, sensu Nelson, Grande & Wilson,
254 2016) is well-supported by molecular phylogenetic analyses (Wiley, Johnson & Dimmick, 1998;
255 Miya et al., 2007; Betancur-R. et al., 2013; Near et al., 2013) and by numerous morphological
256 features (Olney, Johnson & Baldwin, 1993; Davesne et al., 2014, 2016; Delbarre, Davesne &
257 Friedman, 2016). Several of these character states are unambiguously found in †*Babelichthys*:
258 the premaxilla and dentary are toothless, the frontal and the supraoccipital are both involved in a
259 sagittal crest, the anterior ceratohyal forms a condyle that articulates with the ventral hypohyal,
260 and the first dorsal-fin pterygiophore inserts anterior to the neural spine of the first abdominal
261 vertebra.

262 The phylogenetic studies that explore lampridiform intrarelations with a sufficient sampling
263 all recover a monophyletic Taeniosomi ([Olney, Johnson & Baldwin, 1993](#); Wiley, Johnson & Dimmick,
1998; Grande, Borden &

264 Smith, 2013; Martin, 2015). The taeniosome character states found in †*Babelichthys* include the
265 absence of supraneurals, and anterior dorsal-fin pterygiophores that are enlarged and inclined
266 over the neurocranium (Olney, Johnson & Baldwin, 1993). †*Babelichthys* then clearly shows a
267 character state combination that confirms its identification as a taeniosome lampridiform.

268

269 Position within Lophotidae

270 Olney, Johnson & Baldwin (1993) proposed that the enlarged supraoccipital process, projecting
271 anteriorly over the frontals (forming the "crest" as described herein) and supporting the first
272 dorsal-fin pterygiophore, is a synapomorphy of Lophotidae. Since it is not observed elsewhere in
273 lampridiforms, this character confirms the attribution of †Babelichthys to Lophotidae. It has to
274 be noted that in the yet unpublished phylogenetic analysis of Martin (2015), the monophyly of
275 Lophotidae is ambiguous, with one parsimonious tree finding Lophotus more closely related to
276 the other taeniosomes than to Eumecichthys, while in the other both genera are sister groups.
277 Given this ambiguity, Lophotidae is kept as a monophyletic group in this discussion.
278 The distinction between an almost horizontal "crest" projecting anteriorly and a more vertical
279 and relatively shorter "crest" distinguishes †Babelichthys from †Protolophotus (see above,
280 Taxonomic justification), but also from the extant Lophotus and the other known lophotid fossil
281 taxa (Table 1). Conversely, in the Eumecichthys specimen that we examined, the crest is strongly
282 projected anteriorly (angle of 72.4°) and relatively very long (Table 1). Another element is the
283 apparent absence of vomerine fang-like teeth in †Babelichthys (it is however possible that they
284 were present, but not preserved in the fossil), like in Eumecichthys, while they are present in
285 Lophotus (Olney, Johnson & Baldwin, 1993). Since only one specimen is available, it is
286 impossible to perform a thorough comparison of head morphologies at various growth stages and
287 between individuals. Nevertheless, it seems based on available elements that head morphology in
288 †Babelichthys is closer to the one observed in Eumecichthys than in Lophotus, corroborating
289 Oelschläger's (1979) proposition that it represents a potential fossil sister group to Eumecichthys.
290 It would then be the first known fossil unicorn crestfish. Nevertheless, †Babelichthys also differs
291 from Eumecichthys: its crest is less strongly projecting and relatively shorter (Table 1).

292 Moreover, no other lophotid, fossil or extant, has such an extreme enlargement and expansion of
293 the dorsal-fin pterygiophores, in particular the second one.

294

295 The taeniosome fossil record

296 Taeniosome lampridiformes are known by several fossil representatives. The oldest
297 unquestionable occurrences are all attributed to Lophotidae: the diminutive †*Eolophotes lenis*
298 (Fig. 4A), from the Lutetian (Eocene) of Georgia (Daniltshenko, 1962, 1980) and
299 †*Protolophotus elami* (Fig. 3), found in the same middle-late Eocene formation as †*Babelichthys*
300 (see above). An additional, younger fossil lophotid is †*Oligolophotes fragosus* (Fig. 4B) from the
301 early Oligocene Pshekha Formation of Adygea, northern Caucasus, Russia (Bannikov, 1999).

302 The taeniosome fossil record also includes the trachipterid †*Trachipterus mauritanicus* from the
303 Messinian (late Miocene) of Algeria (Carnevale, 2004), and a fragmentary possible oarfish
304 (*Regalecus*) from the Pliocene of Italy (Bronzi, 2001; Roberts, 2012). There is no known fossil
305 Radiicephalidae. Finally, the small and distinctive †*Bajaichthys elegans*, from the Ypresian
306 (early Eocene) of Bolca, Italy, has been classified as a taeniosome or close relative due to its
307 mobile jaws, elongate body and reduced caudal fin (Sorbini & Bottura, 1988; Bannikov, 2014).
308 However, it can be confidently classified in Zeiformes, another teleost clade (Davesne,
309 Carnevale & Friedman, 2017). In total, five entirely fossil species of taeniosomes are currently
310 known (four Lophotidae, one Trachipteridae), a diversity expanded by the present description of
311 †*Babelichthys*.

312

313 CONCLUSION

314 In the present paper, †*Babelichthys olneyi*, a new genus and species of Lophotidae from the
315 Eocene of Iran is described. Few fossil representatives of Taeniosomi, an elusive group of deep-
316 sea teleosts, are known and only one of them has been previously described in details (Bannikov,
317 1999). †*Babelichthys* is potentially the only known fossil close relative of the unicorn crestfish
318 *Eumecichthys*. This discovery is also significant because it expands the diversity of the middle-
319 late Eocene Ilam fauna. Modern lophotids are found in mesopelagic environments (Olney, 2002),
320 so the presence of at least two representatives of the family in the fauna that is mostly composed
321 by relatives of modern deep-sea teleosts (Arambourg, 1967; Afsari et al., 2014; Prikryl,
322 Brzobohatý & Gregorová, 2016) reinforces the assumption that it represents a ~~precious-valuable~~ glimpse
323 ~~on-of~~ the poorly known early Cenozoic deep-water ecosystems.

324

325 Institutional Abbreviations

326 MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History
327 Museum, London, United Kingdom; PIN, Paleontological Institute of the Russian Academy of
328 Sciences, Moscow, Russia; USNM, National Museum of Natural History, Smithsonian
329 Institution, Washington D.C., United States.

330

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338

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452 molecular data. *Molecular Phylogenetics and Evolution* 10:417–425. DOI:
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454

455

456

457 Figure captions

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

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

460 FIGURE 2. †*Babelichthys olneyi*, gen. et sp. nov. holotype MNHN.F.EIP11d. Photograph (detail

461 of the head) and interpretative drawing. Legend: achy, anterior ceratohyal; bra, branchiostegal;

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

463 pterygiophore; enpt, endopterygoid; fr, frontal; hyo, hyomandibula; iop, interopercle; lac,

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

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

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

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

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

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

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

471 = 10 mm.

Figure 1

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

†*Babelichthys olneyi*, gen. et sp. nov., holotype. (A) MNHN.F.EIP11d. (B) counterpart MNHN.F.EIP11g. Scale bars = 20 mm.

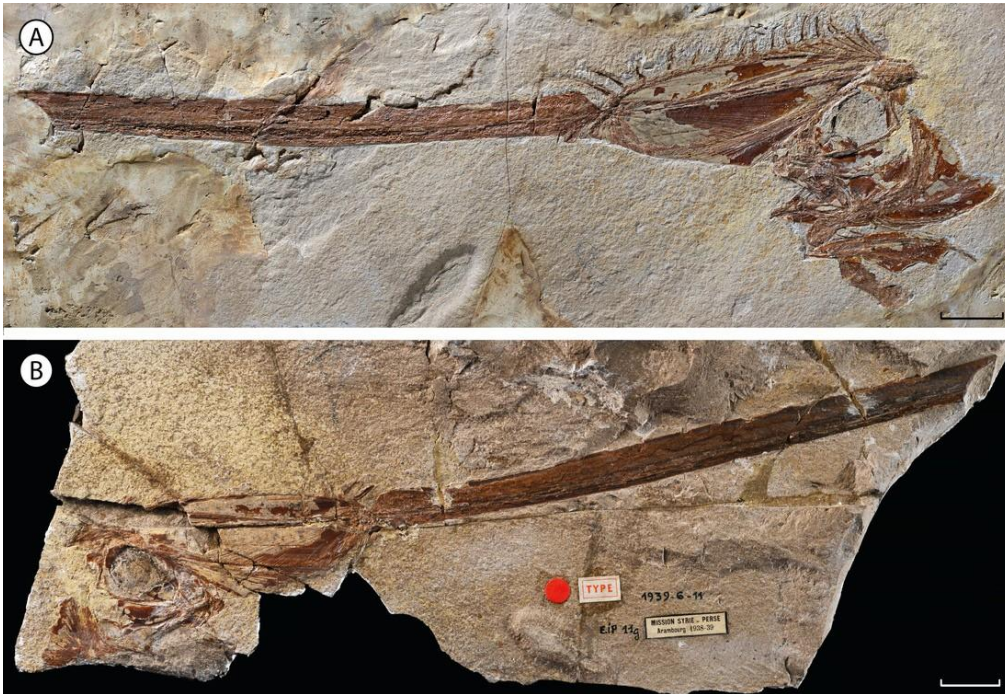
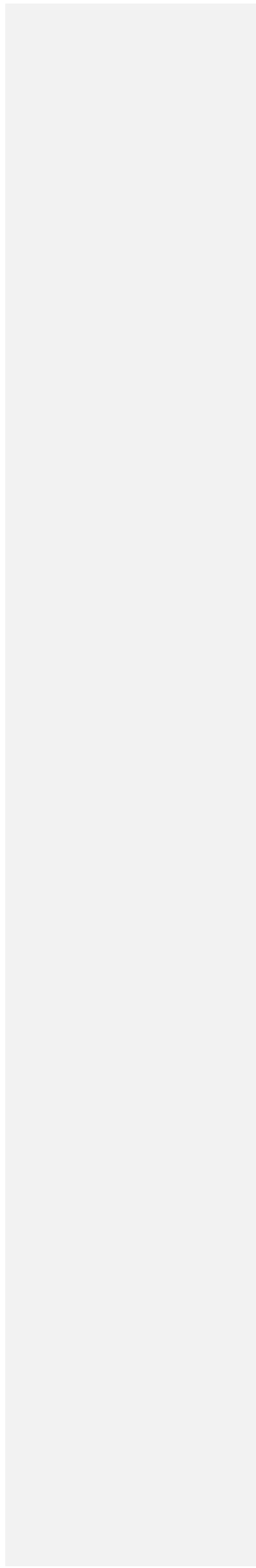


Figure 2 (on next page)

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

†*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.



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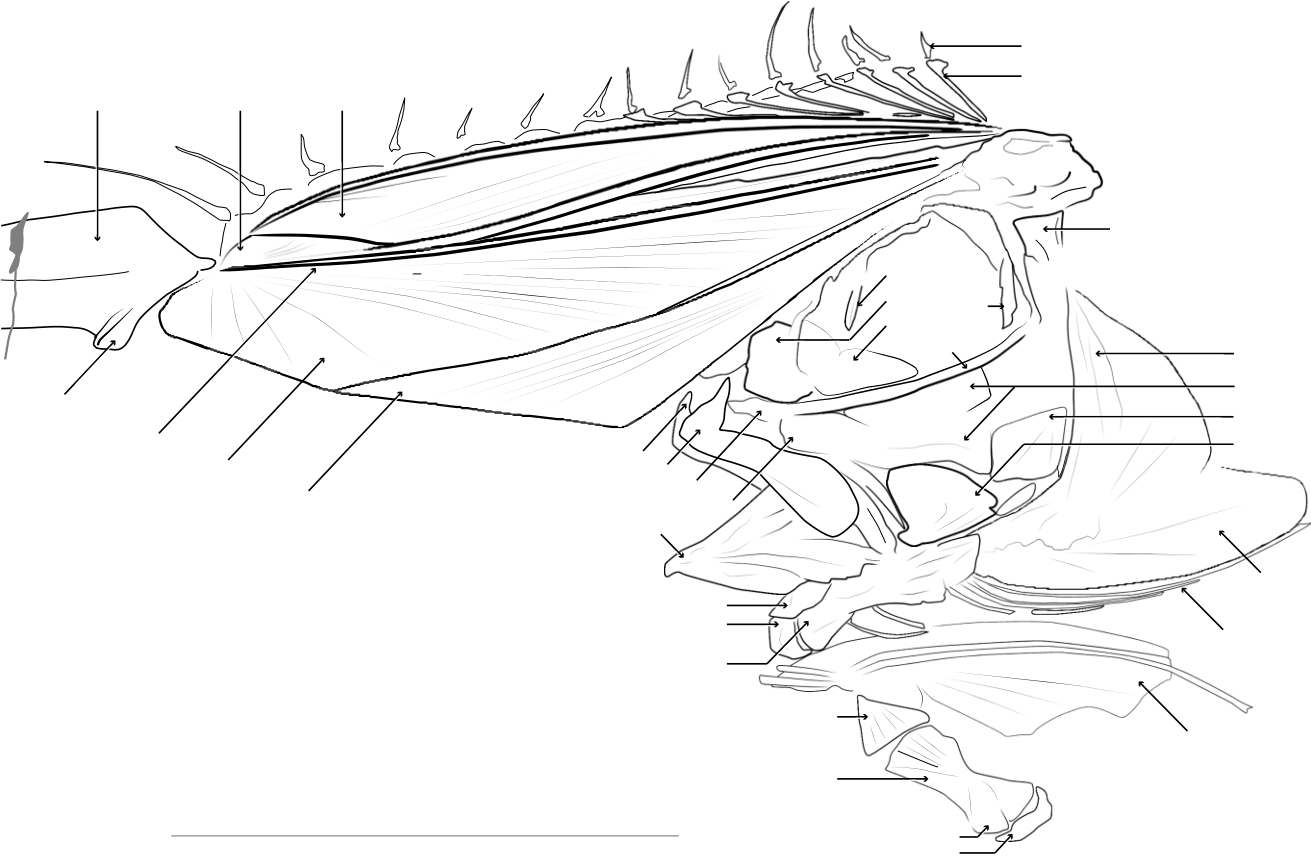


Figure 3

†*Protolophotus elami*, holotype.

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



Figure 4

Other fossil taxa attributed to family Lophotidae.

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.



Table 1 (on next page)

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

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

1
2 TABLE 1. Comparison between crest measurements in selected specimens of known lophotid
3 genera.
4
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