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

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ABSTRACT

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 taxonomical composition of the mesopelagic ecosystems in the early Cenozoic.

INTRODUCTION

Lampridiformes is a clade of 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*) and the gigantic, serpentine oarfish (*Regalecus*), the longest known teleost. Along with these iconic taxa, Lampridiformes 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 their ink gland (Walters & Fitch, 1960; Honma, Ushiki & Takeda, 1999) not found anywhere else in teleosts (except in the closely related radiicephalids; Harrisson & Palmer, 1968). Their most conspicuous osteological feature is their developed horn-like crest, formed by a anteriorly projecting expansion of the frontal and supraoccipital bones of the cranium (Oelschläger, 1979, 1983; Olney, Johnson & Baldwin, 1993), that is closely associated with the anterior pterygiophores supporting the dorsal fin. As a result, their 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).

The present article is a revision of an anatomically distinctive fossil specimen attributed to Lophotidae. Arambourg (1943, 1967) first signalled the specimen from the rich late Eocene fauna he described near Ilam, Zagros Basin, Iran. The Ilam fauna comprises numerous representatives of teleost taxa such as Beryciformes, Gadiformes, Ophidiiformes and Stomiiformes, typical of the modern deep-sea pelagic environments (Arambourg, 1967; Afsari et al., 2014; Přikryl, Brzobohatý & Gregorová, 2016).

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

MATERIAL AND METHODS

Taxonomic status of the material

The material described herein, MNHN.F.EIP11 (Figs. 1, 2), was discovered during excavations near Ilam (Zagros Basin, Western Iran) by Camille Arambourg in 1938-1939. The specimen was chosen to be the paratype of †*Lophotus elami* (Arambourg, 1943), along with the holotype MNHN.F.EIP10 (Fig. 3). †*L. elami* was later erected as a new genus, †*Protolophotus* (Fig. 3), based on osteological differences with extant lophotids, such as the well-ossified pelvic girdle at a ventral position that is observed on the holotype (Walters, 1957). Oelschläger (1979) proposed that MNHN.F.EIP11 differs enough from MNHN.F.EIP10 to be classified in a different genus. He related the specimen to the extant *Eumecichthys* and gave it the name †'*Protomecichthys*'. However, the genus †'*Protomecichthys*' lacks both a designated type species and a formal description. Thus, it fails to meet the requirements of Article 13.3 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 1999) and should be considered a *nomen nudum* (Bannikov, 1999).

Comparative material

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

Nomenclatural acts

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

Methods

The specimen was examined with a stereomicroscope equipped with a camera lucida drawing arm. The interpretative drawing was produced with Adobe Illustrator CS6 from the camera lucida drawings and from photographs. Measurements were taken with a compass or with the software ImageJ 1.5 from radiographs; angles were also measured with ImageJ. The method for estimating the degree of projection of the crest is modified from Craig, Hastings & Pondella (2004): it is based on the angle between the straight line from the tip of the crest to the proximal end of its anterior margin (instead of the tip of the upper jaw, due to varying jaw positions in fossils) and the vertical line drawn perpendicular to the parasphenoid main axis (instead of the vertebral column, not preserved in MNHN.F.EIP11). The relative length of the crest is the ratio between the crest length (distance between the tip of the crest and the proximal end of its anterior margin) and the head length without the crest (from the anterior margin of the ethmoid region to the posterior margin of the neurocranium). All extinct taxa are indicated with a dagger (†).

RESULTS

Systematic palaeontology

TELEOSTEI Müller, 1845

ACANTHOMORPHA Rosen, 1973

Order LAMPRIDIFORMES Goodrich, 1909

Suborder TAENIOSOMI Gill, 1885

Family LOPHOTIDAE Bonaparte, 1845

Genus †***Babelichthys*** gen. nov.

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

(Figs. 1, 2)

Etymology. Hellenization of the name of the "Babel fish", the teleost-like, ear-dwelling, polyglot extra-terrestrial species from Douglas Adams' 1979 book *The Hitchhiker's Guide to the Galaxy*, in reference to the very peculiar, almost alien-like, appearance of the genus.

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

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

†***Babelichthys olneyi*** sp. nov.

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

(Figs. 1, 2)

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

1957 †*Protolophotus elami* Walters, p. 60

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

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

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

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

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

Diagnosis. As for the genus.

Anatomical description

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

Measurements

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

Neurocranium

The neurocranium of MNHN.F.EIP11 is highly modified. The frontal develops a dorsal lamina that projects anterior to the jaws. Throughout approximately its anterior half, it is in contact with an enlarged laminar process of the supraoccipital, delimited dorsally by a strong supraoccipital spine. Together, they form a conspicuous "crest", long and strongly projecting anteriorly (at an angle of 64.5°). Alone, the crest contributes to 58% of total head length. The frontal makes up for approximately 60% of the anterior margin of the crest. Both the frontal and the supraoccipital show radial ornamentation on the crest; it radiates from the posterior end of the frontal, but from the distal tip of the supraoccipital. The supraoccipital spine borders the dorsal margin of the bone, narrowing towards the tip. Unclear in fig. The ethmoid region is poorly preserved, with an enlarged probable lateral ethmoid hiding the mesethmoid. An enlarged lachrymal is nested in the antero-ventral corner of the orbit; it is parallel to the parasphenoid ventrally, and curves dorsally along the edge of the lateral ethmoid. The orbitosphenoid runs at the dorsal margin of the orbit; it shows a conspicuous process pointing ventrally. The posterior wall of the orbit is delimited ventrally by a robust and straight basisphenoid. Otherwise, the sphenoid, otic and occipital regions are too poorly preserved to distinguish the individual bones. The parasphenoid is robust and slightly curves dorsally at its anterior end. The limit between the parasphenoid and the vomer is not discernable. There is no evidence of vomerine teeth.

Jaws

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

Suspensorium and hyoid arch

Only the proximal, single-headed, articulation of the hyomandibula is clearly visible; its distal end might be preserved, in close association with the metapterygoid. The latter is roughly triangular and is one of the best preserved bones of the suspensorium. The symplectic is rod-like, narrows slightly anteriorly and inserts in a notch on the postero-ventral margin of the quadrate. The triangular quadrate bears an anterio-ventral condyle that articulates with the angulo-articular. The anterior portion of the suspensorium is poorly preserved and it is difficult to outline the limits of the endopterygoid, ectopterygoid and palatine bones. The dorsal and posterior portions of the endopterygoid are preserved, suggesting that the bone forms two laminae, the dorsal one along the parasphenoid, and the ventral one contacting both the quadrate and the metapterygoid.

Both the left and right ventral hyoid arches are visible. One is preserved in life position: its posterior end overlaps with the operculum, but its dorsal margin is hidden by the lower jaw, suggesting it corresponds to the right ventral hyoid arch. The left one is displaced and upturned, and lays ventral to its counterpart. The posterior ceratohyal is triangular and articulates with the anterior ceratohyal with an interdigitated suture. The anterior ceratohyal shows a strong ventral concavity at midlength; its dorsal margin is much less concave. The anterior end of the anterior ceratohyal forms a rounded condyle, over which the curved ventral hypohyal articulates. The dorsal hypohyal lies dorsally over the anterior ceratohyal. There are six branchiostegal rays: the anterior two are shorter and articulate with the anterior ceratohyal at the level of its ventral concavity; the four others articulate more posteriorly (due to the faint limit between both ceratohyals, it is difficult to determine on which one they articulate), they are very long (the posterior-most being the longest) and curved posteriorly over the ventral margin of the interopercle. The branchiostegals of the left hyoid arch are disarticulated.

Opercular series

The preopercle is wide and angled at mid-length. The interopercle is an elongate bone rounded at its extremity that forms the ventral margin of the opercular series. It has a smooth ventral margin, closely associated with the posterior branchiostegals. The opercle seems to be missing, but its anterior portion might be preserved in contact with the preopercle.

Dorsal fin and supports

The dorsal fin is only partially preserved, with only the most anterior pterygiophores and dorsal-fin rays being visible. Its most striking feature is the extremely elongated and enlarged first dorsal-fin ray, that is 10 times as wide as the more posterior fin rays (at their base and greatest width). It does not bifurcate distally, lacks any visible segmentation and a groove runs throughout its length. A rounded splint protrudes at its anterior base; it is unclear whether it constitutes a separate dorsal-fin element or not. Fifteen other dorsal-fin rays are preserved posteriorly. Their distal end is missing in most cases, but they all seem to be of a similar length, except for the second and third dorsal-fin rays that are noticeably longer. They do not bifurcate distally, and no segmentation is clearly visible.

Ten dorsal-fin pterygiophores are clearly preserved. They are strongly inclined anteriorly, which causes the dorsal fin to originate at the tip of the crest, and to run along the entire head of the animal. The first two dorsal-fin pterygiophores are greatly enlarged and in close contact with the crest. Both also show a conspicuous flange at their posterior margin. The first pterygiophore is narrow posteriorly, where it does not contact the supraoccipital, and widens in its distal end. The second one is much wider and slightly narrows at its distal extremity. It is in close contact with the first pterygiophore throughout all its length. The third and fourth preserved pterygiophores are in close contact with the second one throughout almost all of their lengths. The more posterior pterygiophores have a mostly straight shaft that curves slightly at its distal extremity. The most posterior ones are less inclined than the anterior ones. The proximal ends of all preserved pterygiophores converge at the same point, at the base of the crest – thus they insert anterior to the (not preserved) first neural spine. The elongated and enlarged first dorsal-fin ray inserts on the first pterygiophore. It is unclear if the rays two to eight insert on pterygiophores that are mostly hidden, or directly on the enlarged second pterygiophore. The rays 9-16 each insert on a corresponding pterygiophore.

DISCUSSION

Taxonomic justification

Oelschläger (1979) proposed that MNHN.F. EIP11 is different enough anatomically from the other lophotids, fossil and extant, to justify its attribution to a new genus. Indeed, it differs from the holotype of †*Protolophotus*, found in the same geological levels, by the relative development of the crest. In MNHN.F.EIP11, the crest is projecting anteriorly with an angle of 64.5°, and the ratio between the lengths of the crest's anterior margin and of the head without the crest is of 1.17 to 1. In the holotype of †*Protolophotus*, MNHN .F.EIP10 (Fig. 3), the anterior margin of the crest is almost vertical (degree of projection: 20°) and it is relatively shorter (margin of the crest/head length without the crest: 0.67/1). MNHN.F.EIP11 also bears a much stronger first dorsal-fin ray, and its two anterior dorsal-fin pterygiophores are considerably more developed. Body size is known to affect crest size and degree of projection in extant *Lophotus* (Craig, Hastings & Pondella, 2004), which could be misleading when trying to differentiate taxa based on morphology. However, this bias can probably be ruled out in the case of MNHN.F.EIP11 and MNHN.F.EIP10: both individuals have similar head lengths without the crest (42 and 44 mm, respectively), suggesting that they are at a similar growth stage. It then seems that classifying MNHN.F.EIP11in a different genus and species, †*Babelichthys olneyi*, is justified from a morphological point of view.

Systematic position

Babelichthys *as a taeniosome lampridiform*

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

The phylogenetic studies that explore lampridiform intrarelationships with a sufficient sampling all recover a monophyletic Taeniosomi (Wiley, Johnson & Dimmick, 1998; Grande, Borden & Smith, 2013; Martin, 2015). The taeniosome character states found in †*Babelichthys* include the absence of supraneurals, and anterior dorsal-fin pterygiophores that are enlarged and inclined over the neurocranium (Olney, Johnson & Baldwin, 1993). †*Babelichthys* then clearly shows a character state combination that confirms its identification as a taeniosome lampridiform.

Position within Lophotidae

Olney, Johnson & Baldwin (1993) proposed that the enlarged supraoccipital process, projecting anteriorly over the frontals (forming the "crest" as described herein) and supporting the first dorsal-fin pterygiophore, is a synapomorphy of Lophotidae. Since it is not observed elsewhere in lampridiforms, this character confirms the attribution of †*Babelichthys* to Lophotidae. It has to be noted that in the yet unpublished phylogenetic analysis of Martin (2015), the monophyly of Lophotidae is ambiguous, with one parsimonious tree finding *Lophotus* more closely related to the other taeniosomes than to *Eumecichthys*, while in the other both genera are sister groups. Given this ambiguity, Lophotidae is kept as a monophyletic group in this discussion.

The distinction between an almost horizontal "crest" projecting anteriorly and a more vertical and relatively shorter "crest" distinguishes †*Babelichthys* from †*Protolophotus* (see above, Taxonomic justification), but also from the extant *Lophotus* and the other known lophotid fossil taxa (Table 1). Conversely, in the *Eumecichthys* specimen that we examined, the crest is strongly projected anteriorly (angle of 72.4°) and relatively very long (Table 1). Another element is the apparent absence of vomerine fang-like teeth in †*Babelichthys* (it is however possible that they were present, but not preserved in the fossil), like in *Eumecichthys*, while they are present in *Lophotus* (Olney, Johnson & Baldwin, 1993). Since only one specimen is available, it is impossible to perform a thorough comparison of head morphologies at various growth stages and between individuals. Nevertheless, it seems based on available elements that head morphology in †*Babelichthys* is closer to the one observed in *Eumecichthys* than in *Lophotus*, corroborating Oelschläger's (1979) proposition that it represents a potential fossil sister group to *Eumecichthys*. It would then be the first known fossil unicorn crestfish. Nevertheless, †*Babelichthys* also differs from *Eumecichthys*: its crest is less strongly projecting and relatively shorter (Table 1). Moreover, no other lophotid, fossil or extant, has such an extreme enlargement and expansion of the dorsal-fin pterygiophores, in particular the second one.

The taeniosome fossil record

Taeniosome lampridiformes are known by several fossil representatives. The oldest unquestionable occurrences are all attributed to Lophotidae: the diminutive †*Eolophotes lenis* (Fig. 4A), from the Lutetian (Eocene) of Georgia (Daniltshenko, 1962, 1980) and †*Protolophotus elami* (Fig. 3), found in the same middle-late Eocene formation as †*Babelichthys* (see above). An additional, younger fossil lophotid is †*Oligolophotes fragosus* (Fig. 4B) from the early Oligocene Pshekha Formation of Adygea, northern Caucasus, Russia (Bannikov, 1999). The taeniosome fossil record also includes the trachipterid †*Trachipterus mauritanicus* from the Messinian (late Miocene) of Algeria (Carnevale, 2004), and a fragmentary possible oarfish (*Regalecus*) from the Pliocene of Italy (Bronzi, 2001; Roberts, 2012). There is no known fossil Radiicephalidae. Finally, the small and distinctive †*Bajaichthys elegans*, from the Ypresian (early Eocene) of Bolca, Italy, has been classified as a taeniosome or close relative due to its mobile jaws, elongate body and reduced caudal fin (Sorbini & Bottura, 1988; Bannikov, 2014). However, it can be confidently classified in Zeiformes, another teleost clade (Davesne, Carnevale & Friedman, 2017). In total, five entirely fossil species of taeniosomes are currently known (four Lophotidae, one Trachipteridae), a diversity expanded by the present description of †*Babelichthys*.

CONCLUSION

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

Institutional Abbreviations

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

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REFERENCES

Afsari S., Yazdi M., Bahrami A., Carnevale G. 2014. A new deep-sea hatchetfish (Teleostei: Stomiiformes: Sternoptychidae) from the Eocene of Ilam, Zagros Basin, Iran. *Bollettino della Società Paleontologica Italiana* 53:27–37. DOI: 10.4435/BSPI.2014.03.

Arambourg C. 1943. Note préliminaire sur quelques Poissons fossiles nouveaux. *Bulletin de la Société Géologique de France* 5:281–288.

Arambourg C. 1967. Résultats Scientifiques de la Mission C. Arambourg en Syrie et en Iran (1938-1939). II. Les Poissons Oligocènes de l'Iran. *Notes et Mémoires sur le Moyen-Orient* 8:1–210.

Bannikov AF. 1999. A review of fossil Lampridiformes (Teleostei) finds with a description of a new Lophotidae genus and species from the Oligocene of the Northern Caucasus. *Paleontological Journal* 33:68–76.

Bannikov AF. 2014. A new genus of the family Palaeocentrotidae (Teleostei, Lampridiformes) from the Oligocene of the Northern Caucasus and comments on other fossil Veliferoidei. *Paleontological Journal* 48:624–632. DOI: 10.1134/S0031030114060021.

Betancur-R. R., Broughton RE., Wiley EO., Carpenter K., López JA., Li C., Holcroft NI., Arcila D., Sanciangco M., Cureton JC., Zhang F., Buser T., Campbell MA., Ballesteros JA., Roa-Varón A., Willis S., Borden WC., Rowley T., Reneau PC., Hough DJ., Lu G., Grande T., Arratia G., Ortí G. 2013. The tree of life and a new classification of bony fishes. *PLoS Currents Tree of Life* 2013 Apr 1. DOI: 10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288

Bonaparte CL. 1845. Specchio generale del sistema ittiologico. *Atti della sesta Riunione degli Scienziati Italiani* 6:386–390.

Bronzi P. 2001. *Regalecus* cf. *glesne*, prima segnalazione dal Pliocene marchigiano. *Fossili & Fossili, Centro studi e ricerche geopaleontologici di Sigillo* 2:39–42.

Carnevale G. 2004. The first fossil ribbonfish (Teleostei, Lampridiformes, Trachipteridae). *Geological Magazine* 141:573–582. DOI: 10.1017/S0016756804009598.

Craig MT., Hastings PA., Pondella DJ. 2004. Notes on the systematics of the crestfish genus *Lophotus* (Lampridiformes: Lophotidae), with a new record from California. *Bulletin - Southern California Academy of Sciences* 103:57–65.

Daniltshenko PG. 1962. Fishes from the Dabhakan Formation of Georgia. *Paleontologicheskii Zhurnal* 1:111–126.

Daniltshenko PG. 1980. Order Lampridiformes. Pp. 91–96 *in*: Iskopayemyye kostistyye ryby SSSR [Fossil bony fishes of the USSR]. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk CCCP* 178.

Davesne D., Carnevale G., Friedman M. 2017. *Bajaichthys elegans* from the Eocene of Bolca (Italy) and the overlooked morphological diversity of Zeiformes (Teleostei, Acanthomorpha). *Palaeontology* 60:255–268. DOI: 10.1111/pala.12280.

Davesne D., Friedman M., Barriel V., Lecointre G., Janvier P., Gallut C., Otero O. 2014. Early fossils illuminate character evolution and interrelationships of Lampridiformes (Teleostei, Acanthomorpha). *Zoological Journal of the Linnean Society* 172:475–498.

DOI: 10.1111/zoj.12166.

Davesne D., Gallut C., Barriel V., Janvier P., Lecointre G., Otero O. 2016. The phylogenetic intrarelationships of spiny-rayed fishes (Acanthomorpha, Teleostei, Actinopterygii): fossil taxa increase the congruence of morphology with molecular data. *Frontiers in Ecology and Evolution* 4:129. DOI: 10.3389/fevo.2016.00129.

Delbarre DJ., Davesne D., Friedman M. 2016. Anatomy and relationships of †*Aipichthys pretiosus* and †“*Aipichthys*” *nuchalis* (Acanthomorpha: Lampridomorpha), with a review of Late Cretaceous relatives of oarfishes and their allies. *Journal of Systematic Palaeontology* 14:545–567. DOI: 10.1080/14772019.2015.1078538.

Gill T. 1885. Sub-order XII - Taeniosomi. In: Kingsley JS ed. *The Standard Natural History*. Boston: S. E. Cassino and Co., 265–267.

Goodrich ES. 1909. *Part IX. Vertebrata Craniata (First Fascicle: Cyclostomes and Fishes).* In: *A Treatise on Zoology*. London: Adam and Charles Black.

Grande T., Borden WC., Smith WL. 2013. Limits and relationships of Paracanthopterygii: A molecular framework for evaluating past morphological hypotheses. In: Arratia G, Schultze H-P, Wilson MVH eds. *Mesozoic Fishes 5 - Global Diversity and Evolution*. Munich: Verlag Dr. Friedriech Pfeil, 385–418.

Harrisson CMH., Palmer G. 1968. On the neotype of *Radiicephalus elongatus* Osório with remarks on its biology. *Bulletin of the British Museum (Natural History) Zoology* 16:187–211.

Honma Y., Ushiki T., Takeda M. 1999. Histology of the ink tube and its associated organs in a unicornfish, *Eumecichthys fiskii* (Lampridiformes). *Ichthyological Research* 46:19–25.

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. 4th Edition.

Martin JM. 2015. Phylogeny, ontogeny and distribution of the ribbonfishes (Lampridiformes:

Trachipteridae). PhD thesis, College of William & Mary, Williamsburg, Virginia, USA.

Miya M., Holcroft NI., Satoh TP., Yamaguchi M., Nishida M., Wiley EO. 2007. Mitochondrial genome and a nuclear gene indicate a novel phylogenetic position of deep-sea tube-eye fish (Stylephoridae). *Ichthyological Research* 54:323–332. DOI: 10.1007/s10228-007-0408-0.

Müller J. 1845. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* 1844:117–216.

Near TJ., Dornburg A., Eytan RI., Keck BP., Smith WL., Kuhn KL., Moore JA., Price SA., Burbrink FT., Friedman M., Wainwright PC. 2013. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings of the National Academy of Sciences* 110:12738–12743. DOI: 10.5061/dryad.d3mb4.

Nelson JS., Grande TC., Wilson MVH. 2016. *Fishes of the World, Fifth Edition*. Hoboken, New Jersey: John Wiley & Sons.

Oelschläger HA. 1979. Zur funktionellen Osteologie der Lophotidae (Pisces: Teleostei). *Zoologische Jahrbücher* 102:336–360.

Oelschläger HA. 1983. Vergleichende und funktionelle Anatomie der Allotriognathi (= Lampridiformes), ein Beitrag zur Evolutionsmorphologie der Knochenfische. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 541:1–127.

Olney JE. 1984. Lampriformes: development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL eds. *Ontogeny and Systematics of Fishes, Special Publication Number 1, American Society of Ichthyologists and Herpetologists*. Lawrence, Kansas: Allen Press, 368–379.

Olney JE. 2002. Lophotidae, Radiicephalidae, Trachipteridae, Regalecidae. In: Carpenter KE ed. *The Living Marine Resources of the Western Central Atlantic. Volume 2: Bony*

Fishes part 1 (Acipenseridae to Grammatidae). Rome: Food and Agriculture Organization of the United Nations, 954–959.

Olney JE., Johnson GD., Baldwin CC. 1993. Phylogeny of lampridiform fishes. *Bulletin of Marine Science* 52:137–169.

Priem F. 1908. Poissons fossiles de Perse. *Annales d'Histoire Naturelle, Paléontologie* 1:1–25.

Přikryl T., Brzobohatý R., Gregorová R. 2016. Diversity and distribution of fossil codlets (Teleostei, Gadiformes, Bregmacerotidae): review and commentary. *Palaeobiodiversity and Palaeoenvironments* 96:13–39. DOI: 10.1007/s12549-015-0222-z.

Regan CT. 1907. On the anatomy, classification, and systematic position of the teleostean fishes of the suborder Allotriognathi. *Proceedings of the Zoological Society of London* 1907:634–643.

Roberts TR. 2012. *Systematics, Biology and Distribution of the Species of the Oceanic Oarfish Genus* Regalecus *(Teleostei, Lampridiformes, Regalecidae)*. Paris: Publications Scientifiques du Muséum.

Rosen DE. 1973. Interrelationships of higher euteleostean fishes. In: Greenwood PH, Miles RS, Patterson C eds. *Interrelationships of Fishes*. London: Academic Press, 397–513.

Sorbini L., Bottura C. 1988. *Bajaichthys elegans*, an Eocene lampridiform from Bolca (Italy). *Bollettino del Museo Civico di Storia Naturale di Verona* 14:369–380.

Walters V. 1957. *Protolophotus*, a new genus of allotriognath fish from the Oligocene of Iran. *Copeia* 1:60–61.

Walters V., Fitch JE. 1960. The families and genera of the Lampridiform (Allotriognath) suborder Trachipteroidei. *California Fish and Games* 46:441–451.

Wiley EO., Johnson GD., Dimmick WW. 1998. The phylogenetic relationships of lampridiform fishes (Teleostei: Acanthomorpha), based on a total-evidence analysis of morphological and molecular data. *Molecular Phylogenetics and Evolution* 10:417–425. DOI: 10.1006/mpev.1998.0532.

Figure captions

FIGURE 1. †*Babelichthys olneyi*, gen. et sp. nov., holotype. **(A)** MNHN.F.EIP11d. **(B)** counterpart MNHN.F.EIP11g. Scale bars = 20 mm.

FIGURE 2. †*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.