Bollettino della Società Paleontologica Italiana, 57 (3), 2018, 175-186. Modena

A sailfin velifer (Lampridiformes, Veliferidae) fish from the Eocene of Monte Bolca, Italy

Giorgio CARNEVALE & Alexandre F. BANNIKOV

G. Carnevale, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italia; giorgio.carnevale@unito.it
A.F. Bannikov, Borisyak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117647 Moscow, Russia; aban@paleo.ru

KEY WORDS - †Wettonius angeloi *n. gen. n. sp., new taxa, Teleostei, Ypresian, northern Italy.*

ABSTRACT - A new sailfin veliferid fish, †Wettonius angeloi *n. gen. n. sp., is described based on a single specimen from the Eocene locality of Monte Bolca in northern Italy.* †Wettonius angeloi *n. gen. n. sp. differs from the known Veliferidae by having a relatively short lower jaw, mandibular joint anterior to the orbit, reduced number of abdominal vertebrae, much advanced anal-fin insertion, with eight (vs six in other veliferids) anal-fin pterygiophores preceding the second haemal spine, first anal-fin ray considerably elongate, and pelvic fin with eight rays. Within the Veliferidae,* †Wettonius *n. gen. shares a number of morphological features with* Velifer. *However, despite these similarities it is not possible to determine the phylogenetic affinities of* †Wettonius *n. gen. for which additional comparative information would be necessary.*

RIASSUNTO - [Un veliferide (Lampridiformes, Veliferidae) dalle pinne a vela nell'Eocene di Monte Bolca, Italia] - †Wettonius angeloi *n. gen. n. sp., un nuovo veliferide dalle pinne a vela proveniente dai depositi eocenici di Monte Bolca, Italia settentrionale, viene descritto sulla base di un singolo reperto in buono stato di conservazione.* †Wettonius angeloi *n. gen. n. sp. differisce dagli altri membri della famiglia Veliferidae nel possedere una mandibola piuttosto breve, il giunto mandibolare anteriore al margine anteriore dell'orbita, un ridotto numero di vertebre addominali, origine della pinna anale molto avanzata, otto pterigiofori della pinna anale (vs sei negli altri veliferidi) anteriori alla seconda spina emale, primo raggio della pinna anale estremamente allungato, e pinna pelvica contenente otto raggi. Tra i veliferidi,* †Wettonius *n. gen. condivide una serie di caratteri morfologici con il genere* Velifer. *Tuttavia, nonostante queste somiglianze non è possibile definire le relazioni filogenetiche di* †Wettonius *n. gen. in assenza di informazioni maggiormente approfondite in merito alla morfologia scheletrica degli altri membri della famiglia Veliferidae.*

INTRODUCTION

The Eocene ichthyofauna of Monte Bolca represents one of the most important fossil fish assemblages known to date (Friedman & Carnevale, 2018). The fossiliferous deposits from this locality have been exploited since the XVI century due to the abundance of exquisitely preserved fishes, which have attracted the attention of palaeontologists and zoologists for several centuries. The ichthyofauna consists of more than 240 taxa of sharks, batoids, pycnodontiforms and teleosts (e.g., Carnevale et al., 2014; Cawley et al., 2018; Marramà et al., 2018), representing the earliest record of many reef-fish groups and providing strong evidence of the stability of the tropical and subtropical marine ichthyofaunas throughout the Cenozoic (Bellwood & Wainwright, 2002; Carnevale, 2006; Marramà et al., 2016b, c). Overall, the ichthyofauna is dominated by acanthomorphs, which comprise the vast majority of fishes from Monte Bolca, at least in terms of taxonomic diversity (e.g., Bannikov, 2014a; Carnevale et al., 2014). This ichthyofauna represents a peri-reefal assemblage, subject to the influence of a variety of coastal biotopes and the open sea (Marramà et al., 2016a).

In the past four decades, several dozens of studies have focused on the taxonomy and systematics of the bony fishes of Monte Bolca. As a result of these considerable efforts, the diversity of certain groups of teleosts is currently reasonably well known, including anguilliforms (Blot, 1978, 1984), aulopiforms (Marramà & Carnevale, 2017), atheriniforms (Bannikov, 2008), beryciforms (Sorbini, 1975, 1984; Sorbini & Tirapelle, 1975), clupeiforms (Marramà & Carnevale, 2015a, b, 2016, 2018; Marramà et al., in press), lophiiforms (Carnevale & Pietsch, 2009, 2010, 2011, 2012; Pietsch & Carnevale, 2011), pharyngognaths (e.g., Bannikov & Carnevale, 2010, 2012), pleuronectiforms (Chanet, 1999; Friedman, 2008, 2012), scombroids (Monsch, 2006), sparids (Day, 2003; Bannikov, 2006), syngnathiforms (Blot, 1980; Tyler, 2004; Bannikov & Carnevale, 2017), tetraodontiforms (e.g., Tyler & Santini, 2002), as well as of a number of other percomorphs (Blot, 1969; Bannikov & Carnevale, 2009, 2011, 2016; Carnevale et al., 2017). The diversity of some other fish groups, including the ostariophysans, lampridiforms, ophidiiforms and beloniforms, remains poorly known and would certainly benefit from a more detailed examination.

Lampridiforms are rarely found in the fossiliferous micritic limestone of Monte Bolca. Carnevale et al. (2014) recognized only four lampridiforms in the Monte Bolca ichthyofauna, the peculiar †*Bajaichthys elegans* Sorbini, 1983, the enigmatic †"*Pegasus*" *volans* Volta, 1796, the veliferid †*Veronavelifer sorbinii* Bannikov, 1991, plus another veliferid, this latter still awaiting a formal descriptive analysis. †*Bajaichthys elegans* was originally referred to the Zeiformes (Sorbini, 1983), subsequently redescribed as an incertae sedis lampridiform (Sorbini & Bottura, 1988), and finally assigned to the Zeiformes based on a detailed analysis of its skeletal structure

ISSN 0375-7633 doi:10.4435/BSPI.2018.11

(Davesne et al., 2017). The elongate †"*Pegasus*" *volans* (Volta, 1796: pl. XLII, fig. 2) is known by two incomplete specimens and seems to be a taeniosomous lampridiform; a detailed morphological analysis of the available material would be desirable to properly interpret its phylogenetic relationships. The family Veliferidae is represented by the species †*Veronavelifer sorbinii*, interpreted by Bannikov (1991) as closely related to the extant genus *Metavelifer*, as well as by an undescribed taxon known from a single specimen tentatively referred to by Bannikov (2014) as a new species of the extant genus *Velifer*. The goal of this paper is therefore to describe this new Eocene veliferid from Monte Bolca and to discuss its affinities within the Veliferidae.

MATERIALS AND METHODS

The present study is based on a single specimen in part and counterpart, separately housed in the collections of the Museo Civico di Storia Naturale, Verona and the Museo di Geologia e Paleontologia dell'Università degli Studi di Padova. These counterparts were studied using stereomicroscopes Leica MZ6, Leica M80, and WILD Heerbrugg with attached camera lucida drawing arms. During examination, the counterparts were moistened with alcohol to enhance some details of their skeletal anatomy. Measurements were taken with a dial caliper to the nearest 0.1 mm. Standard length (SL) is used throughout. Extinct taxa are marked with a dagger (†) preceding their name.

Institutional abbreviations

AMNH: American Museum of Natural History, New York; AMS: Australian Museum, Sidney; MCSNV: Museo Civico di Storia Naturale, Verona; MGPUP: Museo di Geologia e Paleontologia dell'Università degli Studi di Padova; MNHN: Muséum National d'Histoire Naturelle, Paris; NMFS: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Honululu laboratory, Hawaii; USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Comparative materials examined

Metavelifer multiradiatus (Regan, 1907), AMNH 219280 SD; NMFS field no. TC-59-S; USNM 39440; †*Nardovelifer altipinnis* Sorbini & Sorbini, 1999, holotype, MCSNV Na518+519; *Velifer hypselopterus* Bleeker, 1879, AMS 21840020, MNHN IC.1982-0025, USNM 306618; †*Veronavelifer sorbinii* Bannikov, 1991, holotype, MCSNV I.G.37576+I.G.37577, and paratype, MCSNV I.G.1336.

Anatomical abbreviations

aa: anguloarticular; br: branchiostegal rays; bsp: basisphenoid; cl: cleithrum; cor: coracoid; d: dentary; ect: ectopterygoid; enp: endopterygoid; ep: epural; f: frontal; h: hyomandibula; hyp: hypural; io: infraorbital bone; iop: interopercle; lac: lachrymal; le: lateral ethmoid; me: mesethmoid; mtp: metapterygoid; mx: maxilla; op: opercle; osp: orbitosphenoid; pal: palatine; pas: parasphenoid; pcl: postcleithrum; ph: parhypural; pmx: premaxilla; pop: preopercle; ptt: posttemporal; pu: preural centrum; q: quadrate; ra: pectoral-fin radials; sca: scapula; scl: supracleithrum; sn: supraneural; soc: supraoccipital; sop: subopercle; sym: symplectic; u: ural centrum; un: uroneural; v: vomer.

SYSTEMATICS

Order Lampridiformes Goodrich, 1909
Family Veliferidae Bleeker, 1859

Genus †*Wettonius* n. gen.

Type species - †*Wettonius angeloi* n. gen. n. sp.

Diagnosis - Body deep and laterally compressed, body depth slightly more than 55% SL; head length 25.8% SL; lower jaw relatively short, its length measuring about 10% SL; mandibular joint anterior to the orbit; 31 (13+18) vertebrae; two supraneurals; anterior portion of the dorsal and anal fins considerably elevated; dorsal fin with 35 soft rays; anal fin with 26 soft rays, the first being the longest; anal-fin origin remarkably advanced, preanal length slightly more than 44% SL; eight anal-fin pterygiophores precede the second haemal spine; pelvic fin with eight rays; pelvic-fin insertion slightly anterior to that of the pectoral fin; caudal fin large and forked, with 19 principal rays plus seven upper and six lower procurrent rays.

Composition - Type species only.

Etymology - It is our pleasure to name this genus after the late British musician John Wetton. Gender, masculine.

†*Wettonius angeloi* n. sp.
(Figs 1-4)

2014a *Velifer carosii* (nomen nudum) - Bannikov, p. 26.

Holotype - MCSNV V.D.110 and MGPUP 6852, a complete and relatively well-preserved articulated skeleton, in part and counterpart; 149 mm SL (Fig. 1).

Referred specimens - None.

Occurrence - Pesciara site, Bolca Lagerstätte, northeastern Italy; late early Eocene, late Ypresian, Middle Cuisian, slightly less than 49 Ma (see Papazzoni et al., 2014).

Diagnosis - As for the genus.

Etymology - Species named for Angelo Sebastiano Carnevale, who was born and turned one year old during the long lasting preparation of this paper.

Measurements (as percentage of SL) - Body depth: 55.3; head length: 25.8; head depth: 40.2; snout length: 9.1; orbit diameter: 8.9; mandible length: 10.1; caudal

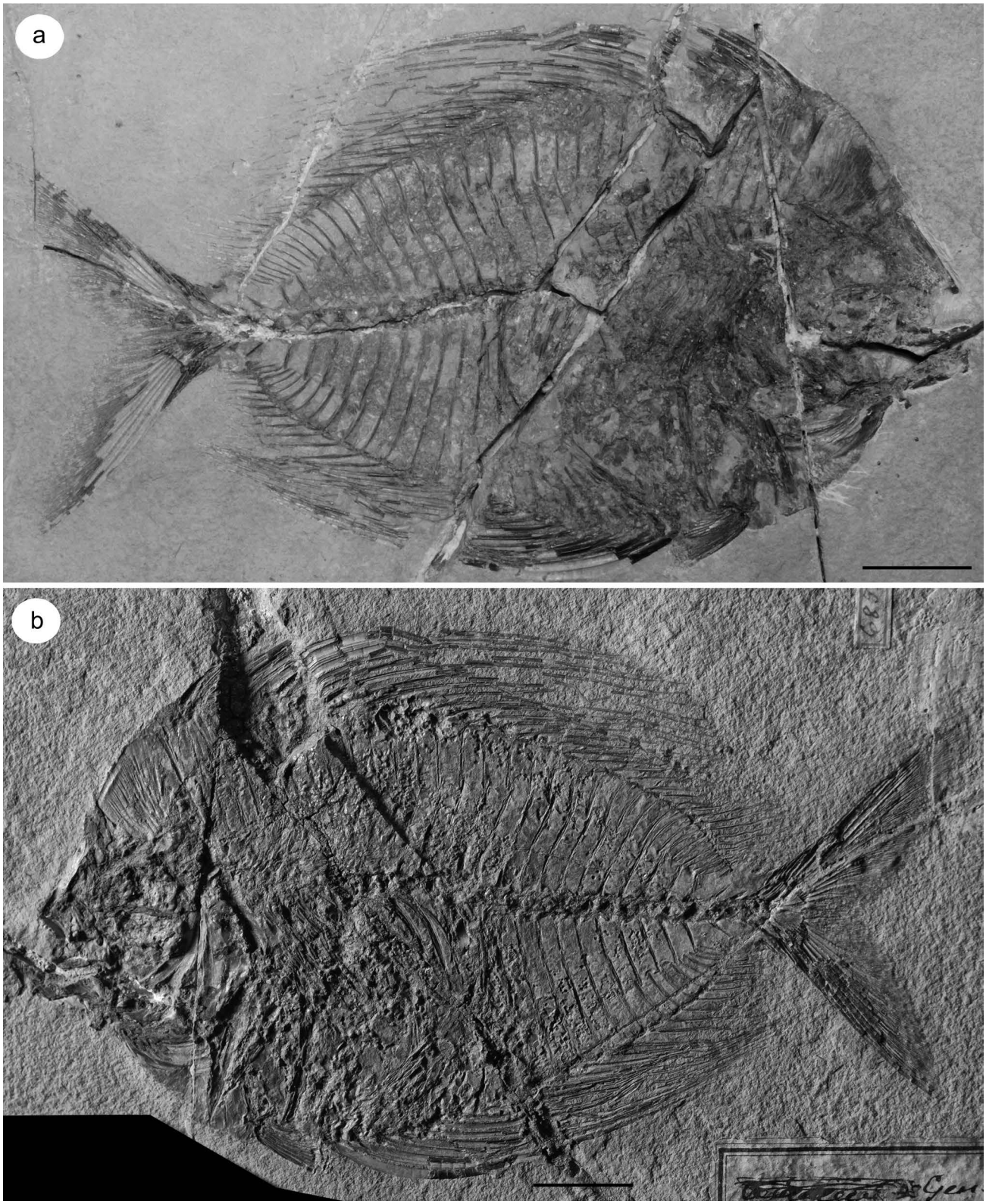
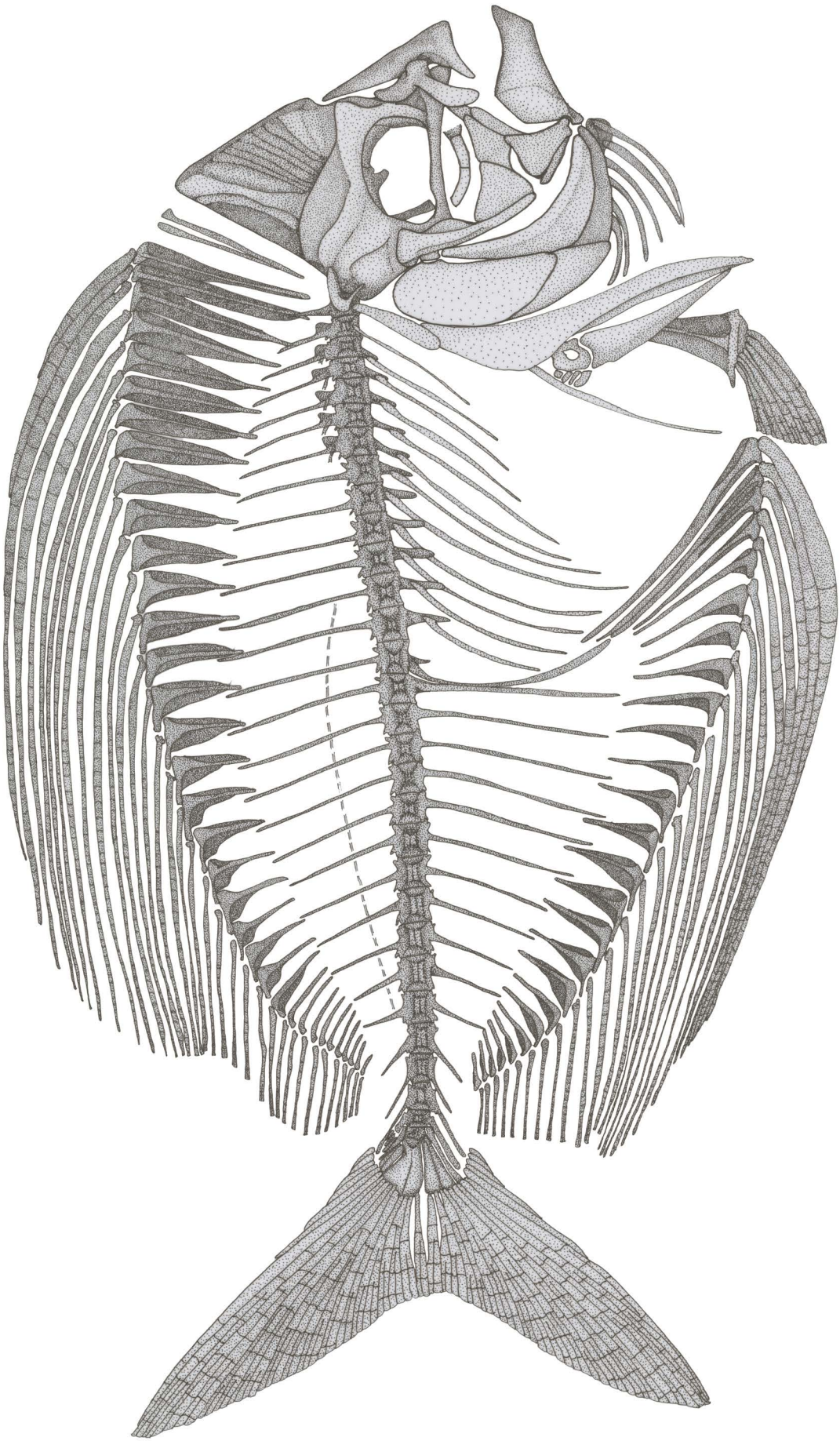


Fig. 1 - †*Wettonius angeloi* n. gen. n. sp. from the Eocene of Monte Bolca. a) Holotype, MCSNV V.D.110, right lateral view; b) holotype, MGPUP 6852 (counterpart of specimen in a), left lateral view. Scale bars: 20 mm.

peduncle length: 5.0; caudal peduncle depth: 8.9; predorsal length: 33.1; preanal length: 44.3; prepectoral length: 31.8; prepelvic length: 33.9; dorsal-fin base length: 76.8; anal-fin base length: 62.7; pelvic-fin length: 11.7.

Description - The body is deep, ovoid, and laterally compressed, with a short and slender caudal peduncle. The body depth is contained slightly less than two times in SL. The caudal peduncle length is about 56% of its depth. The



head is antero-posteriorly compressed and considerably deep; the head length is contained about 1.5 times in its depth and slightly less than four times in SL. The orbit is moderately small and placed in the upper half of the head. The snout length is slightly greater than the orbit diameter. The dorsal and ventral profiles of the body are almost equally convex. Part of the body is covered with small and globular skin nodules similar to those documented by Petit (2010) in a number of fish specimens from Monte Bolca and interpreted as cutaneous lesions likely produced by unidentified pathogens.

The neurocranium is large and moderately robust. The supraoccipital crest is broad, considerably high and almost triangular in shape; its lateral surface bears several anterodorsally directed ridges. The supraoccipital crest articulates anteroventrally with the dorsally elevated frontals that are arched anteromedially to form a large vault for the insertion of the ascending process of the premaxilla (see Olney et al., 1993). The ethmoid region is short. The lateral ethmoid is columnar and strongly ossified. The mesethmoid is posterior to the lateral ethmoid and is well exposed through the orbit in its anterodorsal sector; the mesethmoid contacts posteriorly the orbitosphenoid and possibly forms at least part of the floor of the frontal vault. The vomer is stout, toothless and almost triangular in lateral view. The parasphenoid is slightly curved and well exposed through the lower half of the orbit. The orbitosphenoid bears a compact and stout anteroventrally directed process. The basisphenoid is rod-like and obliquely oriented. The limits of most of the bones of the otic and occipital regions are difficult to recognize.

The infraorbital series is represented by the posteriormost portion of the lachrymal and by tubular and slightly curved second and third infraorbitals. There is no evidence of a subocular shelf.

The mouth is terminal, with the lower jaw articulation located approximately under the anterior edge of the orbit. The premaxilla has a considerably elongate and strong ascending process, measuring about 48% of head length; the postmaxillary process of the premaxilla seems to be absent. The maxilla is rather robust and almost L-shaped, with a large and dorsally-oriented articular process and distally spatulate main shaft. There is no supramaxilla. The mandible is relatively short; its length is contained about 10 times in SL and 2.5 times in head length. The posterior limits of the dentary are not clearly recognizable; the symphyseal region of the dentary is oblique. There is no evidence of jaw teeth.

Of the suspensorium, the palatine, pterygoid bones, quadrate and hyomandibula are recognizable. The overall configuration of the suspensorial bones fits well with that characteristic of the extant veliferid genera *Metavelifer* and *Velifer* (e.g., Oelschläger, 1983). There are no teeth on the endopterygoid. The anterior palatine process (palatine prong, see Olney et al., 1993) seems to be absent. The hyomandibula is nearly vertically oriented; it has a single articular head and bears a compact anterior flange with a rounded profile.

The opercular region is relatively narrow. The bones of the opercular series are of appropriate veliferid size and shape: the preopercle is crescent shaped with a smooth posterior profile; the vertical arm of the preopercle is nearly perpendicular to the horizontal arm; the opercle is thin and laminar, with gently rounded dorsal and posterior margins; the interopercle and subopercle are consistent with those of extant veliferids (e.g., Rosen, 1973; Oelschläger, 1983).

At least six sabre-like branchiostegal rays are present. A small part of the hyoid bar and of what appears to be the urohyal are also recognizable.

The vertebral column consists of 31 (13+18) vertebrae, including the second ural centrum. The axis of the vertebral column is almost straight and slightly elevated anteriorly. The length of the caudal portion of the vertebral column is 1.7 times greater than the length of the abdominal portion. Most of the vertebral centra are almost squared, while some of the anterior abdominal centra are anteroposteriorly compressed. Dorsal and ventral pre- and post-zygapophyses are usually easily recognizable. The neural and haemal spines of the caudal vertebrae are slender and almost straight. The neural spines of the anterior caudal vertebrae are the longest of the series. Most of the haemal spines of the caudal vertebrae are longer than the opposite neural spines. The haemal spine of the anteriormost caudal vertebra is notably curved so that it contacts the succeeding spine at its mid-length, whereas they are clearly divergent distally. Parapophyses of gradually increasing size emerge from the ventral portion of the abdominal vertebrae 3rd through 13th. Twelve pairs of strong ribs occupying the upper two-thirds of the abdominal cavity occur from the second vertebra posteriorly; except for the most anterior rib that articulates with the ventral portion of the second abdominal centrum, the succeeding ribs insert on the lateral surface of the parapophyses. A few incomplete epineurals are visible in the anterior half of the abdominal region of the body where they articulate with the neural arches of the abdominal vertebrae.

The caudal skeleton is consistent with that of other veliferid fishes (e.g., Rosen, 1973; Oelschläger, 1974, 1983; Bannikov, 1991). The terminal (second) ural centrum is fused with the third and fourth hypurals. The first ural centrum is fused with the first preural centrum. The first and second hypurals seem to be fused to each other. The fifth and sixth hypurals are autogenous and separated from each other. The parhypural is slightly weaker than the haemal spine of the second preural centrum. There are two uroneurals and three rod-like epurals. The haemal spines of the second and third preural vertebrae seem to be fused with their respective centra. The neural spine of the second preural vertebra is reduced to a low crest.

The caudal fin is large and forked; it comprises 19 principal rays (I,9-8,I) and at least seven upper and (possibly) six lower procurrent rays.

There are two supraneurals, of which the anterior is longer and slender. The supraneurals are closely spaced and insert in the preneural space. The long-based dorsal fin originates just above the occiput. The length of the dorsal-fin base is slightly less than 77% SL. The specimen

Fig. 2 - †*Wettonius angeloi* n. gen. n. sp. from the Eocene of Monte Bolca. Reconstruction of the skeleton, right lateral view. Scales omitted.

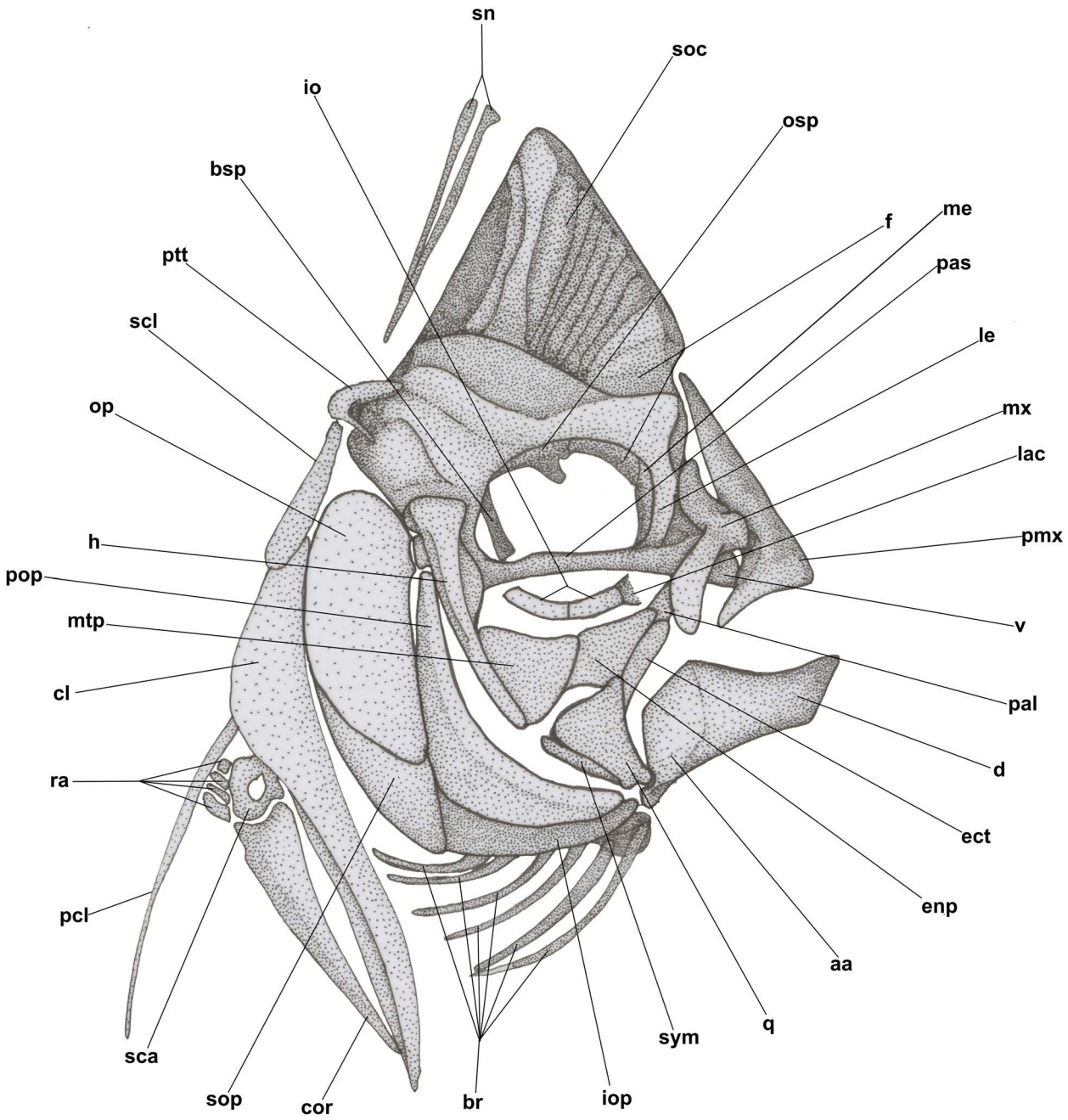


Fig. 3 - †*Wettonius angeloi* n. gen. n. sp. from the Eocene of Monte Bolca. Reconstruction of the skull and pectoral girdle, right lateral view.

seems to lack true spines in the dorsal, anal, and pelvic fins. As far as the dorsal fin is concerned, all the elements, including the most anterior, are segmented and, in many cases, apparently not completely bilaterally fused and, for this reason, should be considered rays. Overall, the dorsal fin consists of 35 rays, of which the first is supernumerary on the first dorsal-fin pterygiophore. The majority of these rays are considerably elongate and unbranched, although segmented distally. The posterior rays are shorter and branched. The longest dorsal-fin rays (the third and several succeeding ones) are almost as long as the maximum body depth. The long and slender first dorsal-fin pterygiophore inserts in the preneural space. The succeeding pterygiophores become gradually shorter in the series. Each interneural space underlying most of the dorsal fin accommodates the proximal end of a single dorsal-fin pterygiophore; however, each of the posterior five interneural spaces just below the dorsal fin accommodates two or three dorsal-fin pterygiophores. The longitudinal axes of the anteriormost dorsal-fin pterygiophores are anteriorly inclined, whereas the succeeding pterygiophore shafts become subvertically oriented and then increasingly inclined posteriorly.

The anal fin insertion is located just behind the pectoral-fin origin, and its posterior end is located approximately at the same level as that of the dorsal fin. The length of

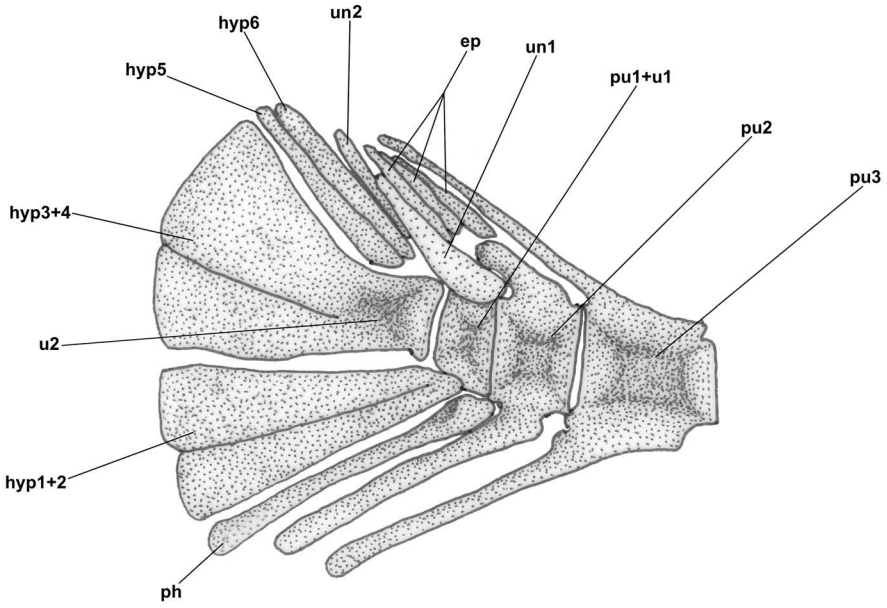


Fig. 4 - †*Wettonius angeloi* n. gen. n. sp. from the Eocene of Monte Bolca. Reconstruction of the caudal skeleton, right lateral view.

the anal-fin base is slightly less than 63% SL. The anal fin consists of 26 rays, of which the first is the longest and supernumerary on the first anal-fin pterygiophore. The overall shape of the anal fin is similar to that of the dorsal fin, with the majority of the anal-fin rays very long and unbranched, although segmented distally. As in the dorsal fin, the posterior anal-fin rays are short and distally branched. The first anal-fin pterygiophore is the longest of the series. The proximal shaft of this pterygiophore is bent backward over the adjacent four pterygiophores. The succeeding pterygiophore shafts are gradually shorter and less strongly inclined, becoming subvertically oriented in the middle part of the series, and then increasingly inclined posteriorly. Three anal-fin pterygiophores insert in the abdominal cavity anteriorly to the first haemal spine and the five succeeding anal-fin pterygiophores insert in the first interhaemal space. Most of the anal-fin pterygiophores are similar to the opposite dorsal-fin pterygiophores in size and shape. The second to ninth interhaemal spaces above the anal fin usually accommodate a single anal-fin pterygiophore, whereas each of the succeeding interhaemal spaces accommodate two or three anal-fin pterygiophores.

Most of the bones of the pectoral girdle can be recognized, while the morphology and composition of the pectoral fin is unclear. The posttemporal has two well-developed arms, of which the upper one is thicker and characterized by a gently curved dorsal profile. The supracleithrum is oblong. The cleithrum is the largest bone of the pectoral girdle; it is feebly sigmoid in shape and terminates ventrally in a pointed process. The coracoid is narrow. The scapula is subquadrangular and centrally pierced by a relatively large scapular foramen. The postcleithrum is strong and long, terminating ventrally just behind the pelvic-fin base. Four pectoral-fin radials appear to be present. The pectoral-fin base is located approximately at midlength between the vertebral column and the ventral profile of the body.

The basipterygia are massive and vertically oriented. The pelvic-fin origin is located slightly anterior to the pectoral-fin base. The pelvic fin is short and consists of eight soft rays, of which the outer is unbranched. The distal ends of the pelvic-fin rays extend posteriorly up to the anal-fin origin. The length of the pelvic fin equals slightly less than 12% SL.

The body, most of the head and a large part of the caudal fin are covered by thin and relatively large cycloid scales. Radii are not evident in the basal field. Each scale bears tiny concentric striation. A thick scaly sheath is present at the base of both the dorsal and anal fins. The lateral line is exposed only in the posterior part of the body, where it is very slightly arched and low in position, just above the vertebral column. No pigment is evident on the scales.

DISCUSSION

Lampridiformes is a group of exclusively marine fishes that comprises about 20 extant species included in six families. These fishes are characterized by an extreme morphological and ecological disparity, and comprise some of the most bizarre vertebrate species. Because of their considerable morphological diversity, lampridiforms were not recognized as a natural group until 1907, when Regan provided the first comprehensive analysis of this group that he called Allotriognathi. Regan (1907b) divided the lampridiforms into two groups: the Bathysomi, which included the families Lamprididae (the so-called Selenichthyes) and Veliferidae (the so-called Histichthyes), and the Taeniosomi, the elongate lampridiforms, which currently include the

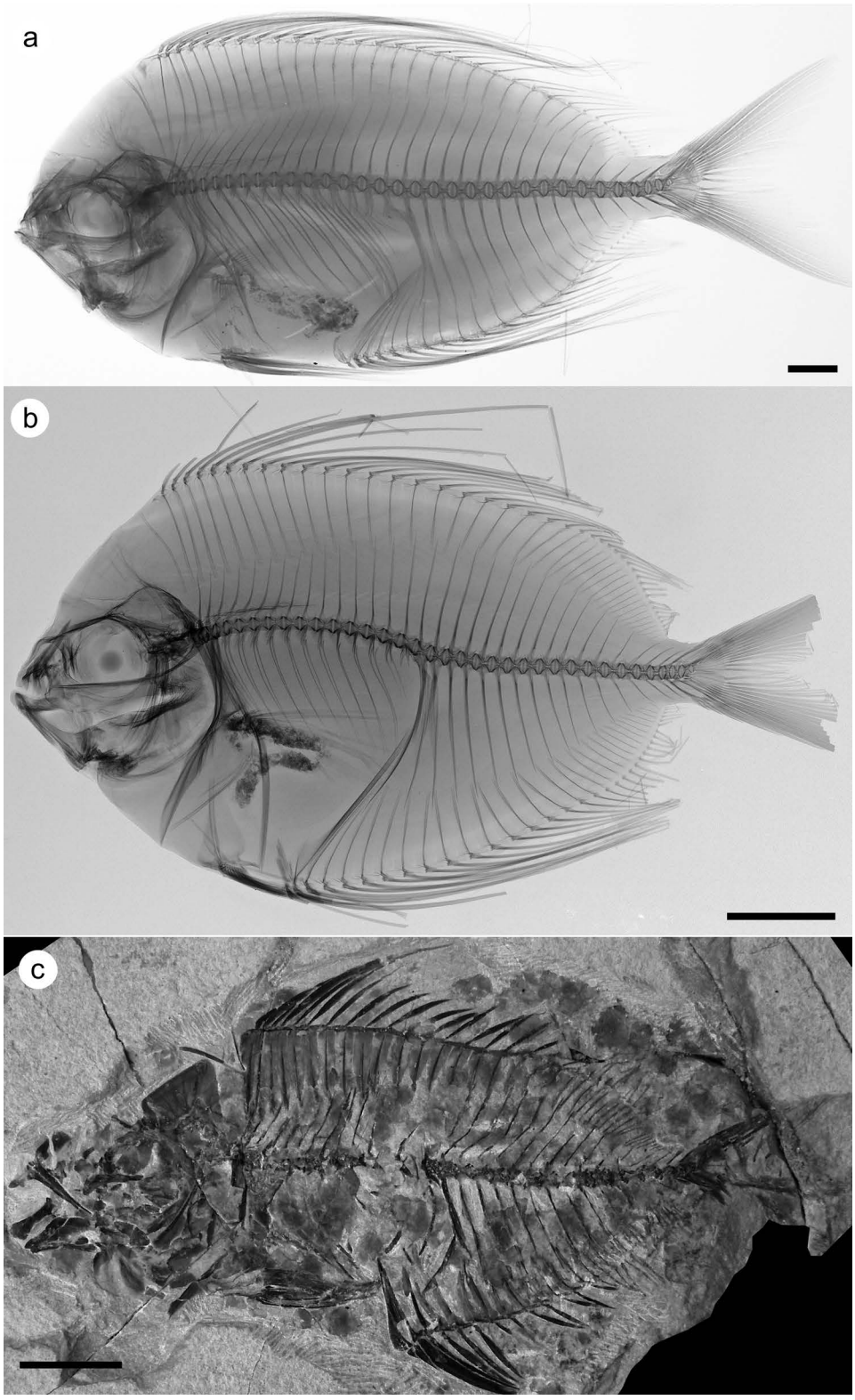


Fig. 5 - Representatives of extant and fossil veliferids. a) *Velifer hypselopterus* Bleeker, 1879, USNM 306618, radiograph, left lateral view; b) *Metavelifer multiradiatus* (Regan, 1907), USNM 39440, radiograph, left lateral view; c) †*Veronavelifer sorbinii* Bannikov, 1991 from the Eocene of Monte Bolca, Italy, holotype, MCSNV I.G. 37576, left lateral view. Scale bars: 10 mm. a) and b) courtesy of Sandra J. Raredon (USNM).

families Lophotidae, Radiicephalidae, Regalecidae and Trachipteridae (see Oelschläger, 1983; Olney et al., 1993; Roberts, 2012). Together with a series of Cretaceous taxa (aipichthyoids, pharmacichthyids, pycnosteroidids), lampridiforms form the clade Lampridomorpha, which represents the sister group of all the other acanthomorphs (Davesne et al., 2014). The monophyletic status of the Lampridiformes and the family-level relationships within the group have been extensively discussed from both a morphological (Oelschläger, 1976; Olney et al., 1993) and

	†*Wettonius angeloi* n. gen. n. sp.	†*Veronavelifer sorbinii*	*Velifer hypselopterus*	*Metavelifer multiradiatus*
Morphometrics (%SL)				
Body depth	55.3	45.4	46.3	60.5
Head length	25.8	29.8	24.7	27.8
Mandible length	10.1	12.3	16.4	14.8
Predorsal length	33.1	38.8	31.8	34.5
Preanal length	44.3	58.9	51.9	48.1
Prepectoral length	31.8	33.7	24.5	28.8
Prepelvic length	33.9	37.1	35.7	32.8
Caudal peduncle length	5.0	4.8	8.2	5.0
Caudal peduncle depth	8.9	8.9	9.9	9.0
Meristics				
Vertebrae	13+18	15+19	16+17-18	16+17-18
Dorsal-fin formula	35	XIX+19-20	I-II+33-34	XXI-XXII+20-23
Anal-fin formula	26	XIV+16	I+24-25	XVII-XVIII+16-18
Pelvic fin rays	8	11	7-8	9
Supraneurals	2	2	2	1

Tab. 1 - Summary of selected morphometric and meristic features of fossil and extant species of the family Veliferidae. Includes new data and data from Regan (1907a), Smith (1951), Walters (1960), Stephenson (1977), Olney (1984), Heemstra (1986), Bannikov (1991). Morphometric data of *Metavelifer multiradiatus* and *Velifer hypselopterus* based on USNM 39440 and USNM 306618, respectively.

molecular (Wiley et al., 1998; Miya et al., 2007) point of view, with the Veliferidae recognized as the sister group to all the other lampridiforms.

The detailed morphological analysis of the single available specimen of †*Wettonius angeloi* n. gen. n. sp. revealed a set of features that unquestionably support its recognition as a lampridiform fish (see, e.g., Olney et al., 1993; Davesne et al., 2014), including: absence of anterior palatine process, mesethmoid entirely posterior to the lateral ethmoids, ascending process of the premaxilla considerably elongate, frontals elevated and arched anteriorly to form a vault that accommodates the ascending processes of the premaxillae, supramaxillae absent, two supraneurals, epineurals absent on caudal vertebrae, first dorsal-fin pterygiophore inserting in the preneural space, hypurals 3 and 4 fused together and to the second ural centrum (see Patterson, 1968; Wiley & Johnson, 2010), and first and second postcleithra fused together.

Within lampridiform fishes, †*Wettonius* exhibits a number of osteological characters that justify its assignment to the family Veliferidae (Walters, 1960; Olney et al., 1993), including: body deep and laterally compressed, dorsal- and anal-fin bases covered with scaly sheaths, pelvic fins thoracic, orbitosphenoid projecting anteroventrally into the orbit with a stout and laterally flattened process, jaws and palate toothless, six branchiostegal rays, general structure of the caudal skeleton (see Rosen, 1973; Bannikov, 1991), caudal fin forked and approximately symmetrical, four pectoral-fin radials (see Regan, 1907b; Delbarre et al., 2016), and ribs strong.

The family Veliferidae includes two extant taxa, *Metavelifer multiradiatus* and *Velifer hypselopterus*, rarely collected but widely distributed in the Indo-Pacific region in depths between 40 and 100 m (e.g., Heemstra, 1986), plus the fossil †*Veronavelifer sorbinii* from the Eocene of Monte Bolca (e.g., Smith, 1951; Bannikov, 1991). The Cretaceous †*Nardovelifer altipinnis* from Nardò, southern Italy is usually considered as a member of the Veliferidae (Sorbini & Sorbini, 1999; Carnevale, 2004), although Delbarre et al. (2016) identified a series of morphological features (dentition on jaws and endopterygoid, ural centra clearly separated from the autogenous hypurals, two postcleithra) that suggests that it should be regarded as a stem lampridiform.

†*Wettonius* differs from the other members of the family Veliferidae by having a number of unique morphological and meristic features (see Tab. 1 and Fig. 5), which clearly support its recognition as a new genus. In particular, it has a remarkably deep body; mandibular joint at the level of the anterior edge of the orbit; mandible considerably shortened, reaching about 10% of SL; reduced number of abdominal vertebrae (13 vs 15-16); no spines in both the dorsal and anal fins; anal-fin insertion much advanced, with the preanal distance measuring about 44% SL; and eight (vs six in other veliferids) anal-fin pterygiophores preceding the second haemal spine (Figs 2 and 5). Sorbini & Sorbini (1999) evidenced the morphological variability of the anterior haemal spines and anterior portion of the anal-fin skeleton, and more generally of the anterior portion of the so-called haemaxanal complex, within the Veliferidae (see also Figs 2 and 5). As far as the configuration of the anterior haemal spines is concerned,

†*Wettonius* resembles †*Veronavelifer* in having a strongly curved first haemal spine that solely contacts the second haemal spine, whereas in the extant genera *Metavelifer* and *Velifer* the anterior three haemal spines are closely associated to each other in their middle regions. On the other hand, the morphology and orientation of the anterior anal-fin pterygiophores of †*Wettonius* is consistent with that of *Velifer* and *Metavelifer* in having the shafts that are directed posterodorsally; moreover, as in *Metavelifer*, †*Wettonius* has three (rather than four as in *Velifer* and †*Veronavelifer*) anal-fin pterygiophores that are placed anterior to the first haemal spine. As described above, however, the second haemal spine of †*Wettonius* is preceded by eight anal-fin pterygiophores, whereas in all the other veliferids six anal-fin pterygiophores are placed anterior to the second haemal spine (see Figs 2 and 5).

Unlike other veliferids, †*Wettonius* has no spines in both the dorsal and anal fins, representing a relevant diagnostic character for this taxon. The nature of the median-fin spines of veliferids has been commented upon in several papers (e.g., Walters, 1960; Rosen, 1973; Lauder & Liem, 1983; Bannikov, 1991; Olney et al., 1993). The anterior elements of the median fins of *Metavelifer*, *Velifer* and †*Veronavelifer* are bilaterally fused at their proximal ends and not segmented and for this reason should be regarded as true spines (Bannikov, 1991; Olney et al., 1993). According to Bannikov (1991), at least in the genus *Metavelifer*, the anterior rays of both the dorsal and anal fins transform into spines ontogenetically and some of them show traces of distal segmentation (see also Regan, 1907a; McCulloch, 1914). In any case, as also pointed out by Olney et al. (1993), although those of veliferids (and more generally of lampridiforms) should be considered as true spines, they certainly differ from those of percomorphs in having open bases that embrace most of the serially corresponding distal radial, not showing the typical chain-link support (Bridge, 1896; Johnson & Patterson, 1993). A further evidence of the peculiar nature of median-fin spines of veliferids (and more generally of lampridiforms) can be provided by the pattern characteristic of the members of the Paleogene "veliferoid" family †Palaeocentrotidae, which exhibit dorsal-fin spines preceded by several segmented and branched soft rays (Bonde, 1966; Bannikov, 2014b), a condition unique within acanthomorphs.

As described above (see also Tab. 1), the vast majority of the characters that are used to discriminate between veliferid taxa refer to morphometric or meristic features that are of limited relevance for phylogenetic interpretations. The general physiognomy and skeletal structure of †*Wettonius* is consistent with that of *Metavelifer* and *Velifer*, whereas that of †*Veronavelifer* appears to be more generalized (Fig. 5). More particularly, †*Wettonius* shows a certain degree of similarity to *Velifer*, indicated by a series of shared features (see Tab. 1), such as posterior end of the maxilla just below the anterior margin of the orbit, similar number of dorsal- and anal-fin elements, eight pelvic fin rays (seven or eight in *Velifer*), median fins remarkably elevated with no lobe anteriorly in the dorsal fin, entire dorsal fin with basal scaly sheath (scaly sheath restricted to the spinous portion of the fin in *Metavelifer* and †*Veronavelifer*; see Walters, 1960; Bannikov, 1991), and preopercle with vertical arm perpendicular to the horizontal arm. In any case, despite these similarities it is not possible to conclusively define the actual affinities of †*Wettonius* and, more generally, to properly interpret the intrafamilial relationships of the Veliferidae without additional comparative information. A more detailed knowledge of veliferid anatomy would also be necessary to resolve the phylogenetic relationships between extant and fossil veliferids, Paleogene "veliferoids" (the genera of the families †Palaeocentrotidae and †Turkmenidae plus the *incertae sedis* genus †*Bathysoma*; Patterson, 1964; Bannikov, 1999, 2014b), and the putative stem-lampridiform †*Nardovelifer altipinnis*.

ACKNOWLEDGEMENTS

We are particularly obliged to Roberto Zorzin and late Anna Vaccari (MCSNV), Mariagabriella Fornasiero and Letizia Del Favero (MGPUP) and G. David Johnson (USNM) for access to material in their care and logistic support. We are grateful to Francesco Sorbini (Verona), Anna Vaccari (MCSNV) and Stefano Castelli (MGPUP) for the excellent photographs. For reviewing the manuscript and providing many constructive suggestions for its improvement, we are particularly grateful to Tomáš Příkryl (Institute of Geology, Czech Academy of Sciences, Prague), James C. Tyler (National Museum of Natural History, Smithsonian Institution, Washington), and the Editor Johannes Pignatti (Dipartimento di Scienze della Terra, Università degli Studi di Roma "La Sapienza", Roma). We are grateful to Dr. Giuseppe Minciotti, former Director of the Museo Civico di Storia Naturale, Verona, for providing funding for the travel of AFB in 2014 to Verona. The research of GC was supported by grants (ex-60% 2017 and 2018) from the Università degli Studi di Torino.

REFERENCES

Bannikov A.F. (1991). An Eocene veliferoid (Teleostei, Lampridiformes) from Bolca. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 161-174.

Bannikov A.F. (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 A.F. (2006). Fishes from the Eocene of Bolca, northern Italy, previously classified in the Sparidae, Serranidae and Haemulidae (Perciformes). *Geodiversitas*, 28: 249-275.

Bannikov A.F. (2008). Revision of the atheriniform fish genera *Rhamphognathus* Agassiz and *Mesogaster* Agassiz (Teleostei) from the Eocene of Bolca, northern Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 12: 77-97.

Bannikov A.F. (2014a). The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 15: 23-34.

Bannikov A.F. (2014b). A new genus of the family Palaeocentrotidae (Teleostei, Lampridiformes) from the Oligocene of the Northern Caucasus and comments on other Veliferoidei. *Paleontological Journal*, 48: 624-632.

Bannikov A.F. & Carnevale G. (2009). A new percoid fish from the Eocene of Monte Bolca, Italy: *Hendrixella grandei* gen. & sp. nov. *Swiss Journal of Geosciences*, 102: 481-488.

Bannikov A.F. & Carnevale G. (2010). *Bellwoodilabrus landinii* n. gen., n. sp., a new genus and species of labrid fish (Teleostei, Perciformes) from the Eocene of Monte Bolca. *Geodiversitas*, 32: 201-220.

Bannikov A.F. & Carnevale G. (2011). Enigmatic spiny-rayed fish from the Eocene of Monte Bolca. *Geological Journal*, 46: 52-62.

Bannikov A.F. & Carnevale G. (2012). *Frippia labroiformis* gen. et sp. nov., a new perciform fish from the Eocene of Pesciara di Bolca, Italy. *Bollettino della Società Paleontologica Italiana*, 51: 155-165.

Bannikov A.F. & Carnevale G. (2016). †*Carlomonnius quasigobius* gen. et sp. nov.: the first gobioid fish from the Eocene of Monte Bolca, Italy. *Bulletin of Geosciences*, 91: 13-22.

Bannikov A.F. & Carnevale G. (2017). Eocene ghost pipefishes (Teleostei, Solenostomidae) from Monte Bolca, Italy. *Bollettino della Società Paleontologica Italiana*, 56: 319-331.

Bellwood D.R. & Wainwright P.C. (2002). The history and biogeography of fishes on coral reefs. *In* Sale P.F. (ed.), Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego: 5-32.

Bleeker P. (1859). Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societas Scientarum Indo-Neerlandaises*, 6: 1-276.

Bleeker P. (1879). Énumerátion des espèces de poissons actuellement connue au Japon et description de trois espèces inédites. *Verhandlingen der K. Akademie van Wetenschappen (Amsterdam)*, 18: 1-33.

Blot J. (1969). Les poissons fossiles du Monte Bolca classés jusqu'ici dans les familles des Carangidae, Menidae, Ephippidae, Scatophagidae. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 1: 1-525.

Blot J. (1978). Les Apodes fossiles du Monte Bolca. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 3: 1-260.

Blot J. (1980). La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e série, 2, section C, 4: 339-396.

Blot J. (1984). Les Apodes fossiles du Monte Bolca. II. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 4: 61-264.

Bonde N. (1966). The fishes of the Mo-Clay Formation (Lower Eocene). *Meddelelser fra Dansk Geologisk Forening*, 16: 198-202.

Bridge T.W. (1896). The mesial fins of ganoids and teleosts. *Journal of the Linnean Society of London, Zoology*, 25: 530-602.

Carnevale G. (2004). The first fossil ribbonfish (Teleostei, Lampridiformes, Trachipteridae). *Geological Magazine*, 141: 573-582.

Carnevale G. (2006). Morphology and biology of the Miocene butterflyfish *Chaetodon ficheuri* (Teleostei: Chaetodontidae). *Zoological Journal of the Linnean Society*, 146: 251-267.

Carnevale G., Bannikov A.F., Marramà G., Tyler J.C. & Zorzin R. (2014). The Pesciara-Monte Postale Fossil-Lagerstätte: 2. Fishes and other vertebrates. *In* Papazzoni C.A., Giusberti L., Carnevale G., Roghi G., Bassi D. & Zorzin R. (eds), The Bolca Fossil-Lagerstätten: A window into the Eocene World. *Rendiconti della Società Paleontologica Italiana*, 4: 37-63.

Carnevale G., Johnson G.D., Marramà G. & Bannikov A.F. (2017). A reappraisal of the Eocene priacanthid fish *Pristigenys substriata* (Blainville, 1818) from Monte Bolca, Italy. *Journal of Paleontology*, 91: 554-565.

Carnevale G. & Pietsch T.W. (2009). An Eocene frogfish from Monte Bolca, Italy: the earliest known skeletal record for the family. *Palaeontology*, 52: 745-752.

Carnevale G. & Pietsch T.W. (2010). Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family Brachionichthyidae. *Zoological Journal of the Linnean Society*, 160: 621-647.

Carnevale G. & Pietsch T.W. (2011). Batfishes from the Eocene of Monte Bolca. *Geological Magazine*, 148: 461-472.

Carnevale G. & Pietsch T.W. (2012). †*Caruso*, a new genus of anglerfishes from the Eocene of Monte Bolca, Italy, with a comparative osteology and phylogeny of the teleost family Lophiidae. *Journal of Systematic Palaeontology*, 10: 47-72.

Cawley J.J., Marramà G., Carnevale G. & Kriwet J. (2018). A quantitative approach to determine the taxonomic identity and ontogeny of the pycnodontiform fish *Pycnodus* (Neopterygii, Actinopterygii) from Eocene of Bolca Lagerstätte, Italy. *PeerJ*, 6: e4809.

Chanet B. (1999). Supposed and true flatfishes [Teleostei: Pleuronectiformes] from the Eocene of Monte Bolca, Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 8: 219-243.

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.

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.

Day J.J. (2003). Evolutionary relationships of the Sparidae (Teleostei: Percoidei): integrating fossil and recent data. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 93: 333-353.

Delbarre D.J., 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.

Friedman M. (2008). The evolutionary origin of flatfish asymmetry. *Nature*, 454: 209-212.

Friedman M. (2012). Osteology of †*Heteronectes chaneti* (Acanthomorpha, Pleuronectiformes), an Eocene stem flatfish, with a discussion of flatfish sister-group relationships. *Journal of Vertebrate Paleontology*, 32: 735-756.

Friedman M. & Carnevale G. (2018). The Bolca *Lagerstätten*: shallow marine life in the Eocene. *Journal of the Geological Society*, 175: 569-579.

Goodrich E.S. (1909). Vertebrata Craniata, first fascicle, cyclostomes and fishes. Part 9. *In* Lankester E.R. (ed.), A Treatise on Zoology. A. and C. Black, Edinburgh: 1-518.

Heemstra P.C. (1986). Family No. 118: Veliferidae. *In* Smith M.M. & Heemstra P.C. (eds), Smith's Sea Fishes. Springer-Verlag, Berlin-Heidelberg: 398-399.

Johnson G.D. & Patterson C. (1993). Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, 52: 554-625.

Lauder G.V. & Liem K.F. (1983). The evolution and interrelationships of the actinopterygian fishes. *Bulletin of the Museum of Comparative Zoology*, 150: 95-197.

Marramà G., Bannikov A.F., Kriwet J. & Carnevale G. (in press). An Eocene paraclupeid fish (Teleostei: Ellimmichthyiformes) from Bolca, Italy: The youngest marine record of double-armoured herrings. *Papers in Palaeontology*. doi: 10.1002/spp2.1230

Marramà G., Bannikov A.F., Tyler J.C., Zorzin R. & Carnevale G. (2016a). Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the paleoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 454: 228-245.

Marramà G. & Carnevale G. (2015). Eocene round herring from Monte Bolca, Italy. *Acta Palaeontologica Polonica*, 60: 701-710.

Marramà G. & Carnevale G. (2016a). The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Monte Bolca, Italy: osteology, taxonomy and paleobiology. *Journal of Vertebrate Paleontology*, 35: e1014490.

Marramà G. & Carnevale G. (2016b). An Eocene anchovy from Monte Bolca, Italy: The earliest known record for the family Engraulidae. *Geological Magazine*, 153: 84-94.

Marramà G. & Carnevale G. (2017). Morphology, relationships and palaeobiology of the Eocene barracudina †*Holosteus esocinus* (Aulopiformes, Paralepididae) from Monte Bolca, Italy. *Zoological Journal of the Linnean Society*, 181: 209-228.

Marramà G. & Carnevale G. (2018). *Eoalosa janvieri* gen. et sp. nov., a new clupeid fish (Teleostei, Clupeiformes) from the Eocene of Monte Bolca. *Paläontologische Zeitschrift*, 92: 107-120.

Marramà G., Carnevale G., Engelbrecht A., Claeson K.M., Zorzin R., Fornasiero M. & Kriwet J. (2018). A synoptic review of the Eocene (Ypresian) cartilaginous fishes (Chondrichthyes: Holocephali, Elasmobranchii) of the Bolca Konservat-Lagerstätte, Italy. *Paläontologische Zeitschrift*, 92: 283-313.

Marramà G., Garbelli C. & Carnevale G. (2016b). A morphospace for the Eocene fish assemblage of Bolca, Italy: A window into the diversification and ecological rise to dominance of modern tropical marine fishes. *Bollettino della Società Paleontologica Italiana*, 55: 11-21.

Marramà G., Garbelli C. & Carnevale G. (2016c). A clade-level morphospace for the Eocene fishes of Bolca: Patterns and relationships with modern tropical marine fish assemblages. *Bollettino della Società Paleontologica Italiana*, 55: 139-156.

McCulloch A.R. (1914). Report on some fishes obtained by the F.I.S. "Endeavour" on the coasts of Queensland, New South Wales, Victoria, Tasmania. South and South Western Australia. Part 2. *Zoological Results of the Fishing Experiments carried on by F.I.S. "Endeavour" 1909-10*, 2: 77-165.

Miya M., Holcroft N.I., Satoh T.P., Yamaguchi M., Nishida M. & Wiley E.O. (2007). Mitochondrial genome and a nuclear gene indicate a novel phylogenetic position of deep-sea tube-eye fish (Stylephoridae). *Ichthyological Research*, 54: 323-332.

Monsch K.A. (2006). A revision of scombrid fishes (Scombroidei, Perciformes) from the Middle Eocene of Monte Bolca, Italy. *Palaeontology*, 49: 873-888.

Oelschläger H. (1974). Das Caudalskelett von *Lampris regius* und seine Ableitung von *Velifer hypselopterus* (Teleostei: Allotriognathi). *Senckenbergiana biologica*, 55: 77-85.

Oelschläger H. (1976). On the evolution and ecological adaptations of the Allotriognathi. *Revue des Travaux de l'Institut des Pêches Maritimes*, 40: 691-694.

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

Olney J.E. (1984). Lampridiformes: Development and Relationships. *In* Moser H.G., Richard W.J., Cohen D.M., Fahay M.P., Kendall Jr. A.W. & Richardson S.L. (eds), Ontogeny and Systematics of Fishes. *American Society of Ichthyologists and Herpetologists, Special Publication*, 1: 464-498.

Olney J.E., Johnson G.D. & Baldwin C.C. (1993). Phylogeny of lampridiform fishes. *Bulletin of Marine Science*, 52: 137-169.

Papazzoni C.A., Carnevale G., Fornaciari E., Giusberti L. & Trevisani E. (2014). The Pesciara-Monte Postale Fossil-Lagerstätte: 1. Biostratigraphy, sedimentology and depositional model. *In* Papazzoni C.A., Giusberti L., Carnevale G., Roghi G., Bassi D. & Zorzin R. (eds), The Bolca Fossil-Lagerstätten: A window into the Eocene World. *Rendiconti della Società Paleontologica Italiana*, 4: 29-36.

Patterson C. (1964). A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, 247: 213-482.

Patterson C. (1968). The caudal skeleton of Mesozoic acanthopterygian fishes. *Bulletin of the British Museum (Natural History) Geology*, 17: 29-59.

Petit G. (2010). Skin nodules in fossil fishes from Monte Bolca (Eocene, Northern Italy). *Geodiversitas*, 32: 157-163.

Pietsch T.W. & Carnevale G. (2011). A new genus and species of anglerfish (Teleostei: Lophiiformes: Lophiidae) from the Eocene of Monte Bolca, Italy. *Copeia*, 2011: 64-71.

Regan C.T. (1907a). Descriptions of the teleostean fish *Velifer hypselopterus* and of a new species of the genus *Velifer*. *Proceedings of the Zoological Society of London*, 1907: 633-634.

Regan C.T. (1907b). 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 T.R. (2012). Systematics, biology and distribution of the species of the oceanic oarfish genus *Regalecus* (Teleostei, Lampridiformes, Regalecidae). *Memoires du Muséum National d'Histoire Naturelle*, 202: 1-268.

Rosen D.E. (1973). Interrelationships of higher euteleostean fishes. *In* Greenwood P.H., Miles R.S. & Patterson C. (eds), Interrelationships of Fishes. *Zoological Journal of the Linnean Society of London*, 53 (Supplement 1): 397-513.

Smith J.L.B. (1951). The fishes of the family Veliferidae from South East Africa. *Annals and Magazine of Natural History*, Ser. 12, 4: 497-510.

Sorbini C. & Sorbini L. (1999). The Cretaceous fishes of Nardò. 10°. *Nardovelifer altipinnis*, gen. nov. et sp. nov. (Teleostei, Lampridiformes, Veliferidae). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 8: 11-27.

Sorbini L. (1975). Gli Holocentridae di M. Bolca, II: *Tenuicentrum pattersoni* (nov. gen., nov. sp.). Nuovi dati a favore dell'origine monofiletica dei Beryciformi (Pisces). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2: 455-472.

Sorbini L. (1983). La collezione Baja di pesci e piante fossili di Bolca. 117 pp. Museo Civico di Storia Naturale, Verona.

Sorbini L. (1984). Les Holocentridae du Monte Bolca. III: *Berybolcensis leptacanthus* (Agassiz). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 4: 19-35.

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.

Sorbini L. & Tirapelle R. (1975). Gli Holocentridae di M. Bolca, I: *Eoholocentrum* (nov. gen.), *Eoholocentrum macrocephalum* (de Blainville) (Pisces, Actinopterygii). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2: 206-228.

Stephenson A.B. (1977). *Metavelifer multiradiatus* (Regan, 1907) (Pisces: Veliferidae), a new record from New Zealand waters. *Records of the Auckland Institute and Museum*, 14: 143-144.

Tyler J.C. (2004). Review of the species of the Eocene of Monte Bolca, Italy, fish family Aulorhamphidae, new, related to Gasterosteiformes. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 10: 37-54.

Tyler J.C. & Santini F. (2002). Review and reconstructions of the tetraodontiform fishes from the Eocene of Monte Bolca, Italy, with comments on related Tertiary taxa. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 9: 47-119.

Volta G.S. (1796). Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti di fossili veronesi. 172 pp. Stamperia Giuliari, Verona.

Walters V. (1960). Synopsis of the lampridiform suborder Veliferoidei. *Copeia*, 1960: 245-247.

Wiley E.O. & Johnson G.D. (2010). A teleost classification based on monophyletic groups. *In* Nelson J.S., Schultze H.-P. & Wilson M.V.H. (eds), Origin and phylogenetic interrelationships of teleosts. Verlag Dr. Friedrich Pfeil, München: 123-182.

Wiley E.O., Johnson G.D. & Dimmick W.W. (1998). The phylogenetic relationships of lampridiform fishes (Teleostei: Acanthomorpha), based on total-evidence analysis of morphological and molecular data. *Molecular Phylogenetics and Evolution*, 10: 417-425.

Manuscript received 27 August 2018
Revised manuscript accepted 29 September 2018
Online publication 17 November 2018
Editor Johannes Pignatti