

***Stefanichthys mariannae*, a new genus and species of percoid fish (Perciformes s.l.) from the Eocene of Bolca in northern Italy**

ALEXANDRE F. BANNIKOV* - ROBERTO ZORZIN**

(*Borisyak Paleontological Institute of the Russian Academy of Sciences, Moscow)

(**Museo Civico di Storia Naturale, Verona)

ABSTRACT

A new genus and species of percomorph fish, †*Stefanichthys mariannae* gen. et sp. nov., is described based upon four skeletons from the Pesciara site of the Eocene locality of Bolca in northern Italy. Resembling the Eocene Bolca species †*Acropoma lepidotum* (AGASSIZ), the new taxon differs from it in having cycloid scales, a smaller orbit, weaker dorsal- and anal-fin spines, seven rather than eight anal-fin soft rays and more robust dentition. The apparent supernumerary association of the all three anal-fin spines on the first anal pterygiophore is a quite unusual character of †*Stefanichthys mariannae* gen. et sp. nov. and probably can be regarded as an autapomorphy. The taxon is placed *incertae sedis* within the generalized Percoidei.

Key words: Perciformes, Percoidei, new genus and species, Eocene, northern Italy, Bolca locality, Pesciara site.

RIASSUNTO

†*Stefanichthys mariannae*, un nuovo genere e specie di pesce percomorfo, viene descritto sulla base di quattro scheletri provenienti dal sito della Pesciara, località eocenica di Bolca, in Italia settentrionale. †*Stefanichthys mariannae* presenta numerose caratteristiche in comune con la specie †*Acropoma lepidotum* (AGASSIZ), anch'essa proveniente dall'Eocene di Bolca, dalla quale differisce per avere squame cicloidi, orbite più piccole, spine dorsali e pinne anali più delicate, sette anziché otto raggi molli della pinna anale e dentatura più robusta. L'apparente associazione soprannumeraria di tutte e tre le spine della pinna anale sul primo pterigioforo anale rappresenta un carattere abbastanza insolito di †*Stefanichthys mariannae* e, probabilmente, può essere considerato una sua autapomorfia. Il nuovo taxon descritto nel presente articolo viene considerato come *incertae sedis* all'interno dei Percoidei.

Parole chiave: Perciformi, Percoidei, nuovo genere e nuova specie, Eocene, Italia settentrionale, Bolca, sito della Pesciara.

INTRODUCTION

The Early Eocene fish fauna of the famous Pesciara site of the Bolca locality, to the north of Verona in northern Italy, has been known since the mid-sixteenth century (SORBINI, 1981), and is exceptionally rich in marine fishes, especially of the acanthomorphs (e.g., FRIEDMAN and CARNEVALE, 2018). Fish remains have long been collected from two approximately coeval sites (Pesciara and Monte Postale) of the Bolca locality that are close by one another but which have different fish assemblages and different depositional contexts (MARRAMÀ *et al.*, 2016). The Pesciara site marks the first fossil record of many groups of fishes found on modern coral reefs (BELLWOOD, 1996). Some groups of Recent coral reef fishes (e.g., butterflyfishes and gobies) first appeared only in the Oligocene or later in the Eocene (COW-

MAN and BELLWOOD 2011; NEAR *et al.*, 2013); these are represented in the Pesciara assemblage by their extinct ecological analogues (BANNIKOV, 2004a, b). True gobioids are represented there only by a single specimen of a diminutive species (BANNIKOV and CARNEVALE, 2016; BANNIKOV, 2019).

The perciform fishes (*sensu* NELSON, 2006) are the most various among the Pesciara fishes, and percoids predominate among the perciforms. The order of perch-like fishes (Perciformes) has traditionally been considered (BERG, 1940; GREENWOOD *et al.*, 1966; NELSON, 2006; etc.) the most diverse order of evolutionarily advanced bony fishes, the largest of the orders not only of fishes, but of vertebrates in general. Recently, however, the traditional classification of organisms is often replaced by a

formal cladistic systematics, built on computer processing of molecular data and often contradicting morphological evidence. In cladistic taxonomy, the order Perciformes is divided into numerous orders, bizarrely grouped into taxa of higher rank (WILEY and JOHNSON, 2010; NEAR *et al.*, 2012, 2013; BETANCUR-R. *et al.*, 2013, 2017; NELSON *et al.*, 2016; etc.). The higher taxa of the cladistic hierarchy are morphologically heterogeneous, which is recognized by the cladists themselves (MIYA *et al.*, 2013); usually these taxa cannot be diagnosed by morphological features. This encourages us to use traditional, natural taxonomy herein.

Percoidei, the “largest and most diverse of the perciform suborders is undoubtedly polyphyletic...” (JOHNSON, 1993, p. 15) and is diagnosed by several plesiomorphic for the Perciformes features; this group includes those perciforms that cannot be placed in other suborders. More recently, citing molecular data, many families traditionally included into the Percoidei are removed from this suborder (e.g., NELSON *et al.*, 2016), or its composition is even limited to two or three families (BETANCUR-R. *et al.*, 2017). According to the more traditional view of NELSON (2006), the suborder Percoidei includes 79 Recent families.

The latest lists of Bolca fishes (BANNIKOV, 2014; CARNEVALE *et al.*, 2014, with additions) include 24 families, 44 genera and 49 species of percoids. Additionally, 17 species and 14 genera of Bolca percoids have not attributed to any family and are left as *incertae sedis* within the Percoidei.

As demonstrated by the considerable number of papers published in the last decade (see, e.g., BANNIKOV, 2014; CARNEVALE *et al.*, 2014), the possibility to recognize new taxa is not uncommon during the examination of both the historical and more recent collections of Bolca fishes. Among the fossil fishes housed in the collections of four different museums are four specimens from the Pesciara which we herein interpret as belonging to a new genus and species of percoid fish. This fish is described below as the new genus and species †*Stefanichthys mariannae*.

METHODS

The specimens were examined using a WILD Heerbrugg stereomicroscope with an attached camera lucida drawing arm. Some details of the specimens examined were best seen when the specimens were

moistened with alcohol. The specimens were prepared by needles. Measurements were taken with a dial caliper, to the nearest 0.1 mm.

Interneural and interhaemal spaces are numbered based on the vertebra whose neural or haemal spine forms the anterior border of the space, with the first space being between the first and second neural or haemal spines (following BALDWIN and JOHNSON, 1993; BANNIKOV and TYLER, 1995; TYLER and BANNIKOV, 1997; etc.).

Abbreviations are as follows: *Institutional*: CMNH – Carnegie Museum of Natural History; GMLM – Green Museum, Le Mans; MCSNV – Museo Civico di Storia Naturale di Verona; MFB – Museo dei Fossili di Bolca; *Anatomical*: HL – head length; lac – lachrymal; mx – maxilla; pal – palatine; pmx – premaxilla; PU – preural vertebra; SL – standard length; U – ural vertebra.

The dagger symbol (†) indicates extinct taxa.

SYSTEMATIC DESCRIPTION

Order Perciformes s.l.
Suborder Percoidei s.l.
Percoidei *incertae familiae*
Genus †*Stefanichthys* gen. nov.

Diagnosis

Moderately elongate fusiform fish with a long and deep caudal peduncle. Dorsal profile of body as equally convex as ventral profile. Head relatively big. Head length slightly exceeds maximum body depth. Eye small. Lachrymal large. Mouth small; lower jaw articulation under anterior border of orbit. Jaws with moderately large bluntly cylindrical to conical teeth, without canines. Preopercle with even ventral border, finely serrated posterodorsally. 10+14 vertebrae. Hypurals autogenous; 3 epurals, 2 uroneurals. 3 supraneurals. Dorsal fin divided, but with pterygiophores forming continuous series. First dorsal with 8 slender spines; second dorsal with a spine and 9 soft rays. Anal fin with 3 weak spines (anterior two minute) and 7 rays. Pelvics inserted behind pectorals. Caudal fin notched, with 17 principal rays. Scales large, thick, and cycloid, cover entire body and bases of unpaired fins. Lateral line very gently arched and poorly traceable.

Type Species

†*Stefanichthys mariannae* sp. nov., by monotypy and designation herein.

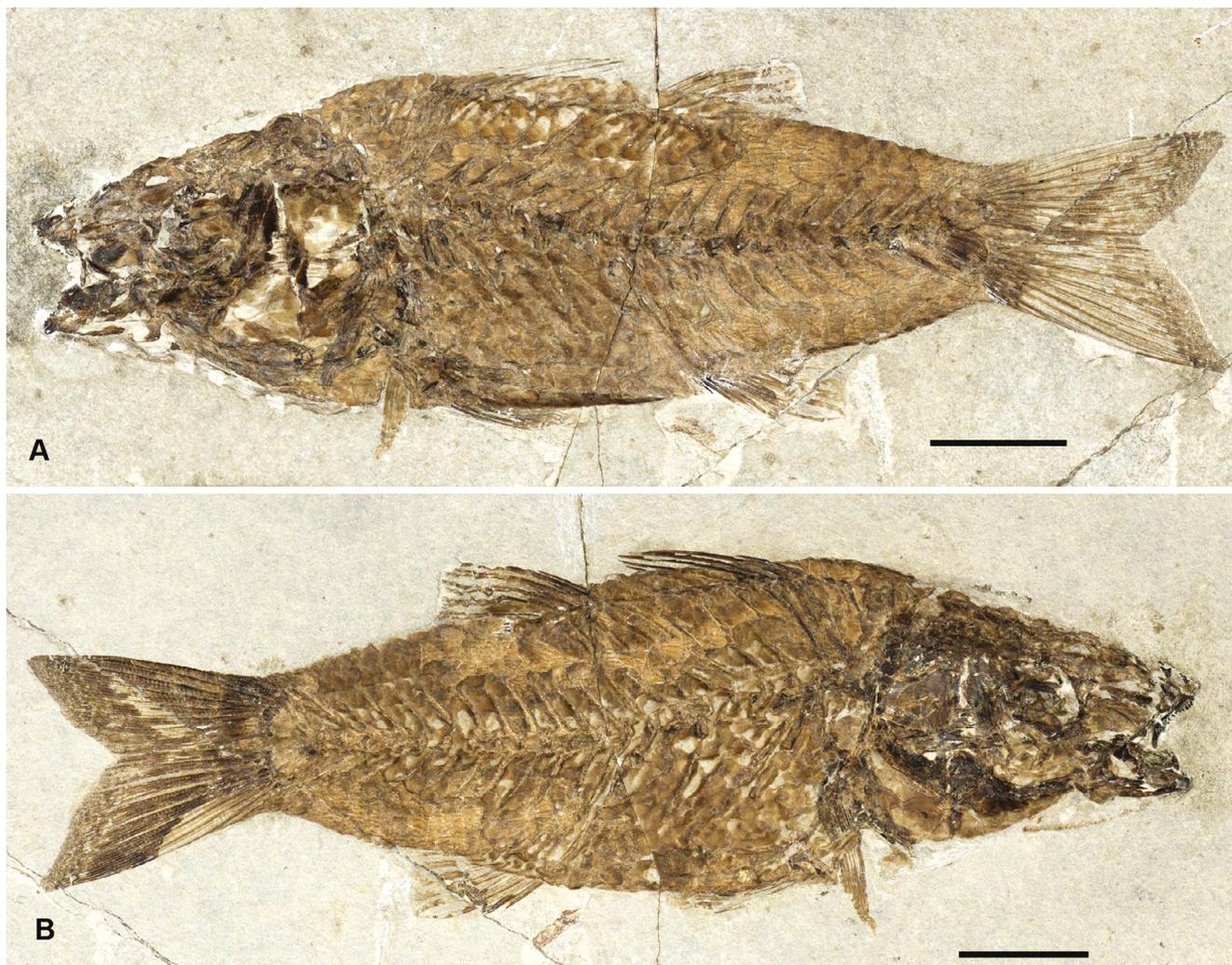


Fig. 1 – †*Stefanichtys mariannae* gen. et sp. nov., holotype; Lower Eocene of Bolca in northern Italy, Pesciara: **A** – general view of MFB IG186671, **B** – counterpart MFB IG186670. Scale bar: 2 cm

Etymology

The genus is named after the daughter of the second listed author (RZ), Stefania, and from the Greek word *ichthys* for fish; gender masculine.

Composition

Type species only.

†*Stefanichtys mariannae* sp. nov.

Figures 1-5

Diagnosis

As for the genus.

Etymology

The species is named after the daughter of the first listed author (AFB), Marianna.

Holotype

MFB IG186670/IG186671, part and counterpart, complete skeleton, 142 mm SL (Fig. 1).

Paratype

CMNH 4356, single specimen, complete skeleton, 127.5 mm SL (Fig. 2A).

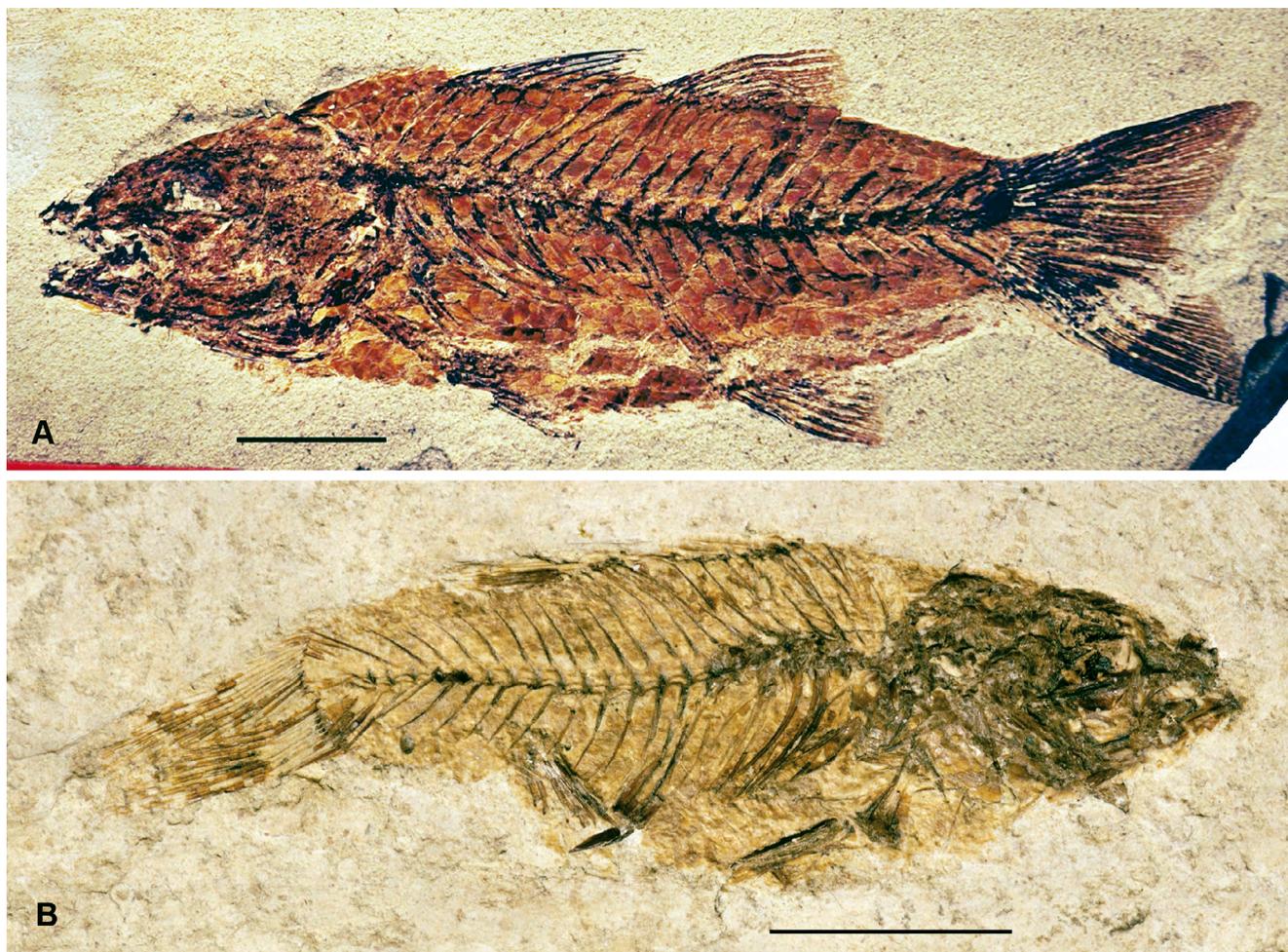


Fig. 2 – †*Stefanichthys mariannae* gen. et sp. nov., Lower Eocene of Bolca in northern Italy, Pesciara: **A** – paratype CMNH 4356, **B** – referred specimen MCSNV VR 27624. Scale bar: **A** – 2 cm, **B** – 1 cm

Referred Specimens

GMLM uncatalogued, single specimen, complete skeleton, 140 mm SL; MCSNV II D.202/II D.208, part and counterpart, complete skeleton, 37.5 mm SL (Fig. 2B).

Type Locality and Horizon

Bolca locality, Pesciara cave site; Early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone (see PAPAZZONI and TREVISANI, 2006; PAPAZZONI *et al.*, 2014).

Description

The body is moderately elongate, with a rather deep, long caudal peduncle. The caudal peduncle depth is about 0.44 of the body depth. The head is relatively large; its length (tip of snout to posterior edge of

opercle) slightly exceeds the body depth. The head length is contained approximately 2.8 times in SL. The dorsal and ventral profiles of the body are almost equally convex.

Head. The head is moderately deep, conical, with its depth 1.3-1.4 times less than its length. The orbit is small; its horizontal diameter is about 18% HL. The snout is almost twice as long as the orbit; its length is about 36-37% HL. The mouth is small and terminal. The lower jaw articulation is situated approximately under the anterior border of the orbit. The lachrymal is large and relatively deep, covering laterally significant portion of the snout; the other infraorbital bones are poorly recognizable. The neurocranium is relatively low, with the supraoccipital crest evidently small and triangular. The frontals are broad and extended. The ethmoid

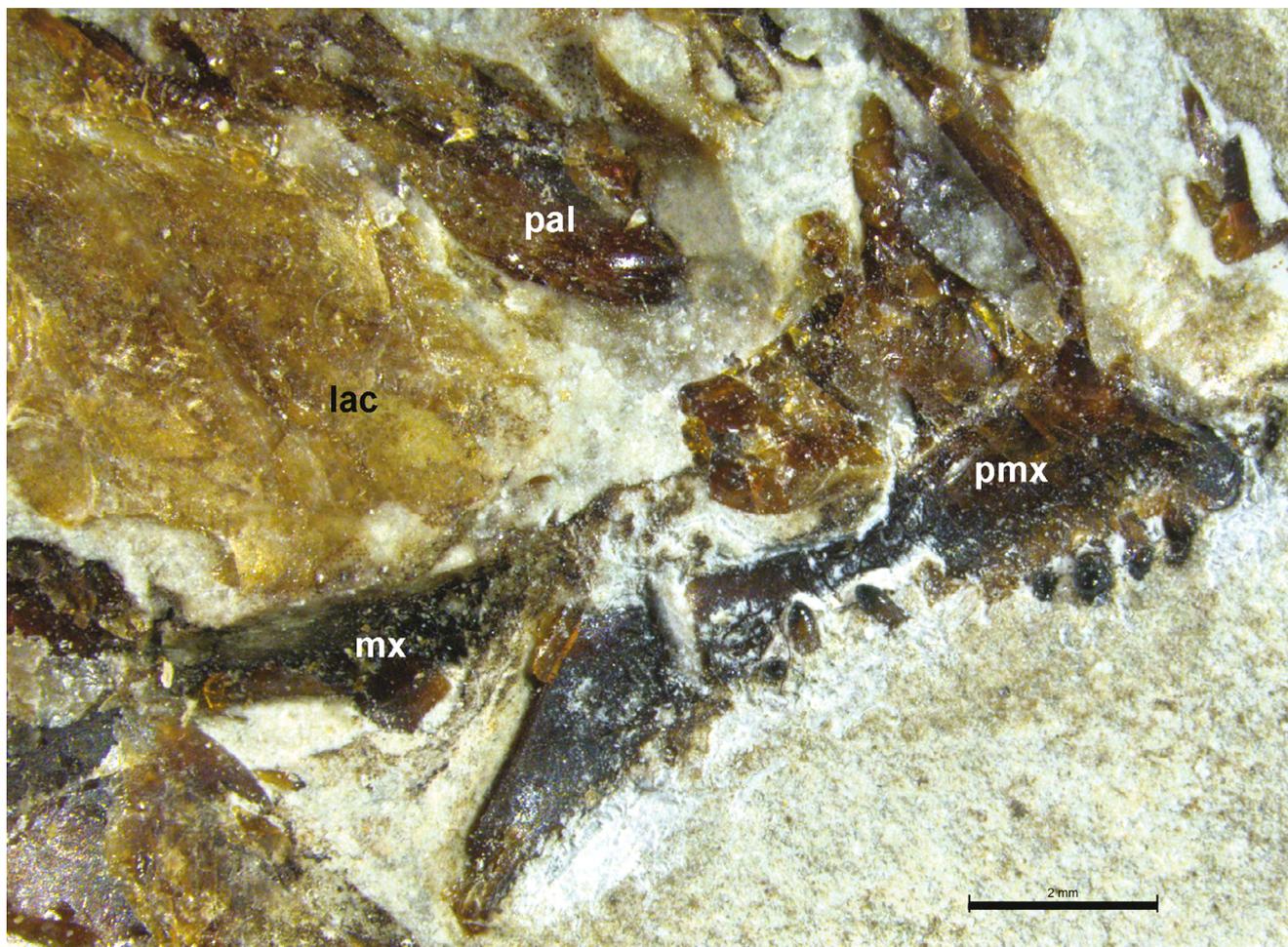


Fig. 3 – †*Stefanicthys mariannae* gen. et sp. nov., holotype MFB IG186670, upper jaw; Lower Eocene of Bolca in northern Italy, Pesciara. Scale bar: 2 mm

region is rather long; the lateral ethmoid forms most of anterior wall of the orbit and bears a pit dorsally. The parasphenoid is relatively slender and almost straight; it is exposed in the lower portion of the orbit. The nasals seem to be relatively small and elongate. The premaxilla has distinct and moderately long ascending and articular processes. The premaxilla bears uniserial, moderately large bluntly cylindrical to conical teeth (Fig. 3). No canines are present. The maxilla is somewhat curved near its head; it is slightly expanded distally. No supramaxilla is evident. The lower jaw is relatively deep; its length is about 34% HL. The dentary is notched posteriorly and does not project ventrally near the low symphysis. The oral border of the dentary bears teeth equal to those of the upper jaw in size and shape. The angulo-articular is inserted

deeply into the dentary notch. There seems to be a narrow space between the anterodorsal border of the angulo-articular and the posterodorsal process of the dentary. The hyomandibular shaft is slightly inclined from a vertical line. The quadrate seems to be relatively small. The symplectic is robust, as evidenced by the referred specimen MCSNV II D.202. The palatine has a strong anterior process. The preopercle is relatively strongly curved; its posterior border is serrated in the smallest specimen (MCSNV II D.202/208). The other specimens do not reveal any preopercular serrations other than in the upper portion of the posterior border of the bone. The opercle is flat and subtriangular in shape; it bears a triangular posterior spine, as evidenced by the referred specimen MCSNV II D.202. The opercular spine is strengthened by a ridge in the inner

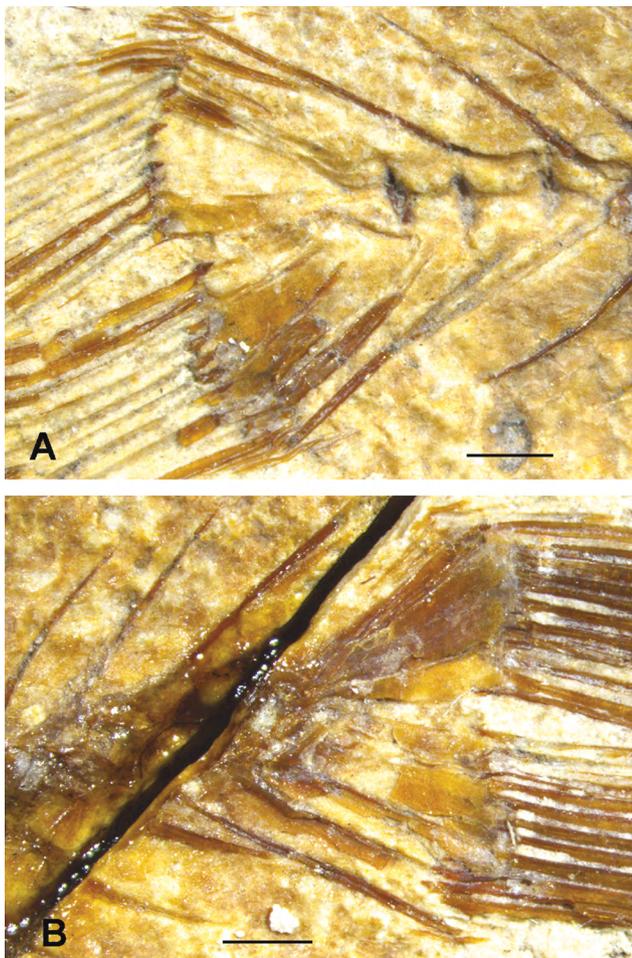


Fig. 4 – †*Stefaniaichthys mariannae* gen. et sp. nov., referred specimen, caudal skeleton; Lower Eocene of Bolca in northern Italy, Pesciara: **A** – MCSNV II D.202; **B** – MCSNV II D.208. Scale bar: 1 mm

surface. The subopercle has a distinct prong on its anterior corner; the bone has no serrations. Neither the hyoid bar nor branchial arch bones are preserved completely enough to be described. The exact number of sabre-like branchiostegal rays is not evident in any of the specimens. Some specimens reveal numerous ossified gill filaments; only a few of the small pharyngeal teeth are recognizable.

Axial skeleton. There are 24 vertebrae, including the urostyle: ten abdominal and fourteen caudal. The axis of the vertebral column is very slightly sigmoid, being elevated anteriorly. The vertebral centra are almost rectangular in lateral view. The length of the caudal portion of the vertebral column is 1.5 times greater than the length of the abdominal portion of the vertebral column. The vertebral spines

are relatively short and straight, or only slightly curved. The neural spines of the anterior vertebrae are only slightly expanded in relation to those of the succeeding vertebrae. The haemal spines of the two anterior caudal vertebrae of the large specimens are more closely spaced to each other than the other haemal spines. Short parapophyses are recognizable in a few of the posterior abdominal vertebrae. The pleural ribs are moderately long and relatively slender; these are rather strongly inclined posteroventrally. Slender epineurals are recognizable above the middle abdominal vertebrae in MCSNV II D.202/208.

Pectoral fin and girdle. The pectoral girdle is only poorly preserved. The posttemporal is forked; it is unclear if its distal margin is serrated or not. The supracleithrum seems to be moderately elongated. The cleithrum is strong and almost straight in its ventral portion; its upper part is curved anteriorly. The posterodorsal plate of the cleithrum, which is situated over the pectoral-fin base, is located under the third and fourth vertebrae. The ventral postcleithrum is moderately long and rib-like. The coracoid seems to be narrow; this bone, as well as the scapula and pectoral radials, is poorly recognizable. There are no fewer than 10 pectoral-fin rays. The pectoral fins are relatively short and narrow. The pectoral-fin base is situated relatively low, just above the midpoint between the vertebral column and the ventral body margin.

Pelvic fin and girdle. The pelvic bone is moderately long and wedge-shaped. The pelvic fins have a slender spine and probably five soft, branched rays each. The pelvic fin is inserted posterior to the pectoral-fin base. The pelvic fin is moderately long, only slightly shorter than the pectoral fin; the pelvic-fin spine is much longer than the longest anal-fin spine but about 1.4 times shorter than the longest dorsal-fin spine.

Supraneurals and dorsal fin. There are three rather short supraneurals; the first supraneural bears a strong apical projection directed rostrad and is usually inclined anteriorly (except for MCSNV II D.202/208), whereas the two other supraneurals lack such a projection and are inclined posteriorly. The predorsal formula (AHLSTROM *et al.*, 1976; JOHNSON, 1984) is usually poorly recognizable because of taphonomic reasons. There are two dorsal fins, but their pterygiophores form a continuous series. The first dorsal fin is moderately short-based; it originates over the fifth vertebra. There are eight slender spines in the first dorsal fin. The fourth dorsal-

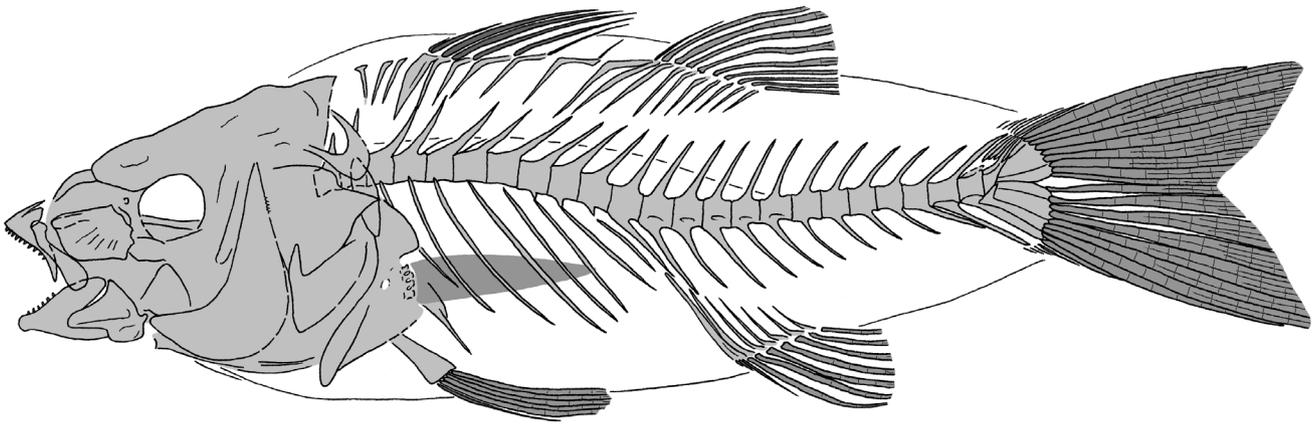


Fig. 5 – †*Stefanchthys mariannae* gen. et sp. nov., reconstruction of the skeleton based mostly on the holotype; scales omitted

fin spine is longest; it is 2.3 times longer than the second spine and 1.08 times longer than the third spine in the holotype. The first two dorsal-fin spines are supernumerary on the first dorsal-fin pterygiophore; these are closely spaced. The first spine is relatively well developed in the smallest specimen, MCSNV II D.202/208, whereas it becomes minute in the larger specimens. The dorsal-fin spines are close-set anteriorly, becoming more widely spaced posteriorly (the space between the penultimate and ultimate spines of the first dorsal fin almost equals the space between the two dorsal fins). The second dorsal fin is relatively short-based; usually it originates over the second caudal vertebra. The second dorsal fin consists of a slender spine (which is 2.2 times shorter than the longest spine of the first dorsal fin) and nine soft rays. The longest soft ray in the second dorsal fin of the holotype is 1.1 times shorter than the longest spine of the first dorsal fin. Posteriorly in the series the rays decrease in length. The length of the base of the soft dorsal fin is 1.4-1.5 times shorter than the base length of the spiny dorsal fin. There are a total of 16 dorsal-fin pterygiophores; the anterior six pterygiophores belong to the first dorsal fin. The medio-distal parts (concurrent to the dorsal profile of body) of the dorsal-fin pterygiophores become longer progressively from the first to the seventh pterygiophore, which bears a spine of the second dorsal fin. The pterygiophores of the second dorsal fin decrease in length posteriorly in the series. In the large specimens most of the ventral shafts of the dorsal-fin pterygiophores do not enter down into the in-

terneural spaces, terminating above the upper tips of the neural spines. In the small referred specimen MCSNV II D.202/208 the interneural spaces below the dorsal fins have the ventral shafts of one or two pterygiophores present.

Anal fin. In the large specimens the anal fin originates more posteriorly than does the second dorsal fin, usually under the fifth caudal vertebra; in the small referred specimen MCSNV II D.202/208 the position of the anal fin is less posterior. There are three weak graduated spines and seven soft segmented and branched rays in the anal fin, and not more than seven anal-fin pterygiophores are recognizable in any of the specimens. The first two anal-fin spines are minute in the large specimens (but stronger in the small referred specimen MCSNV II D.202/208) and evidently do not protrude to the exterior. The anal-fin spines are exceptionally close-set to each other and to the first soft anal-fin ray, as seen in the holotypic counterpart MFB IG186671; it seems likely that all three anal-fin spines are supernumerary on the first anal pterygiophore. The longest, third anal-fin spine is shorter than the spines of the pelvic and second dorsal fins, and is 2.6 times shorter than the longest spine of the first dorsal fin. The longest anal-fin soft rays are slightly shorter than the longest dorsal-fin soft rays. The first anal-fin pterygiophore is longest; the succeeding pterygiophores decrease in length posteriorly in the series. Except for the smallest specimen (MCSNV II D.202/208), the anal-fin pterygiophores do not enter up into the interhaemal spaces, terminating below the lower tips of the haemal spines.

Caudal fin and skeleton. The terminal centrum is composed of the fusion of PU1, U1 and U2¹. The hypurals, parhypural, and haemal spines of PU2 and PU3 are autogenous (Fig. 4). There is a small hypural diastema between the epaxial and hypaxial hypurals. The neural and haemal spines of PU3 are longer than those of the preceding vertebra. The neural spine of PU2 is evidently a short crest. There are three epurals; the first is longest. There are two slender uroneurals. The caudal fin is moderately large and notched. There are 17 principal rays in the caudal fin (I,8-7,I), about 10 procurrent rays above and not less than nine rays below.

Squamation. Scales are large, thick, and cycloid, covering the entire body and bases of the unpaired fins. Each of the body scales bears several (up to nine) radii in the basal field. The scales are covered by striations and minute tubercles. The limits of individual scales are scarcely recognizable; therefore, the number of scale rows on the body is unknown. The lateral line is poorly traceable; it is very gently arched anteriorly and descends to the level of the vertebral column near the 16th vertebra.

Coloration. No pigmentation is unambiguously traceable.

Measurements of the holotype, in percent of SL (142 mm), are as follows:

- Head length from tip of snout to posterior border of opercle: 35
- Maximum body depth: 32
- Depth of caudal peduncle: 14
- Distance between tip of snout and first dorsal fin: 43
- Distance between tip of snout and second dorsal fin: 64
- Distance between tip of snout and anal fin: 71
- Distance between pelvic fin and anal fin: 27
- Length of base of first plus second dorsal fins: 32
- Length of base of anal fin: 9
- Length of longest spine of first dorsal fin: 17
- Length of spine of second dorsal fin: 8
- Length of longest soft ray of second dorsal fin: 15
- Length of third spine of anal fin: 6
- Length of longest soft ray of anal fin: 14
- Length of spine of pelvic fin: 12
- Length of longest soft ray of pelvic fin: ca. 16
- Length of pectoral fin: ca. 17
- Length of caudal fin: 27

- Preorbital distance: 13
- Horizontal diameter of orbit: 6
- Length of lower jaw: 12

Remarks. The referred specimen MCSNV II D.202/208 is only tentatively regarded as †*Stefanichthys mariannae* gen. et sp. nov., because it differs in some respects from the other three specimens of this species: it has stronger anal-fin spines, serrations throughout the whole posterior border of the preopercle (vs. only upper portion of this border serrated), and probably a less thick scale cover. However, since this specimen is more than 3 times smaller than the other specimens of †*S. mariannae*, one can suppose that these differences are ontogenetically based, because in their body shape, proportions, meristics, and dentition all the specimens are quite similar. Probably during the ontogeny of †*S. mariannae* the anal fin somewhat shafts posteriorly, its spines become weaker, the scales become thicker, and most of the preopercular serrations fade.

DISCUSSION

The new genus definitely represents a generalized percoid fish (Percoidei *sensu* NELSON, 2006); however, its precise relationships are unclear. The incomplete knowledge of percoid anatomy and unstable modern systematics of percoids (see above) create many difficulties in classifying fossils with extant members of this heterogeneous group (BANNIKOV and CARNEVALE, 2007). When the fossil taxa are only imperfectly known and when their allocation in a Recent monophyletic group cannot be evaluated without ambiguity, the use of *incertae sedis* category should be applied (see PATTERSON and ROSEN, 1977).

Having obviously two dorsal fins, †*Stefanichthys* differs from those percoids which have a single, although notched, dorsal fin, such as, for example, the early Eocene *incertae sedis* Percoidei †*Jimtylerius temnopterus* (AGASSIZ) (see BANNIKOV and CARNEVALE, 2007), †*Veronabrax schizurus* (see BANNIKOV, 2008) and †*Asianthus celebratus* (DANILTSHENKO). The latter taxon was divided by SYTCHEVSKAYA and PROKOFIEV (2003, 2011) into the four species of two genera and a special family was created for them. It was shown, however, that these taxonomic novelties were based

1. The diurnal terminology is used. SCHULTZE and ARRATIA (2013) have shown that the two ural centra are not homologous in different Teleostei.

either on the characters of poor taxonomic significance or upon multiple misinterpretations (BANNIKOV and CARNEVALE, 2007; BANNIKOV, 2010).

†*Stefanichthys* resembles a number of Recent percoid families in having relatively widely divided dorsal fins, i.e., the Acropomatidae, Ambassidae, Apogonidae, Dinolestidae, Epigonidae, Moronidae, Mullidae, Scombroptidae. Some of these have a number of vertebrae greater than 24 (as in †*Stefanichthys*) – 25 (Epigonidae, Moronidae and most Acropomatidae), 26 (Scombroptidae and some Acropomatidae), or 27 (Dinolestidae). The Moronidae and Mullidae also differ from the new genus in always having ctenoid rather than cycloid scales on the body. Although only one anal-fin spine is evident in the large specimens of †*Stefanichthys mariannae*, additional preparing reveals the presence of two more minute anterior anal-fin spines not protruding to the exterior. Reduction of the number of the anal-fin spines to two differentiates the Mullidae, Apogonidae, Scombroptidae, some Epigonidae and Acropomatidae from †*Stefanichthys*, resembling the latter with the Ambassidae and Moronidae in that character. The dinolestids have only one anal-fin spine. Like most of the listed families, the new genus has the plesiomorphic number of principal caudal-fin rays (17) and an unconsolidated caudal skeleton, whereas the Mullidae have two fewer principal caudal-fin rays, and hypurals 1+2 and 3+4 are fused (hypural fusion occurs also in ambassids and some apogonids).

The new genus shares the vertebral formula, cycloid scales and divided dorsal fins with the Eocene genus †*Quasimullus* from the same locality of Bolca, which represents the distinctive family †Quasimullidae of percoid fishes (BANNIKOV, 1999). However, such autapomorphies of †*Quasimullus*, as the edentulous mouth, extremely long ascending process of the premaxilla and presence of a spineless pterygiophore between the more widely divided dorsal fins strongly differentiates that genus from †*Stefanichthys*. †*Quasimullus* also differs from the new genus by the hypural fusion, more slender neural and haemal spines and greater number of soft dorsal- and anal-fin soft rays.

Another extinct family of Eocene percoids, †Robertanniidae, includes two monotypic genera from Bolca (BANNIKOV and CARNEVALE, 2009; BANNIKOV, 2011). Representatives of this family are easily distinguishable from †*Stefanichthys* in having a more elongated body, larger mouth with sharp teeth, much more widely divided dorsal fins, only

two anal-fin spines, and ctenoid scales. Therefore, †*Stefanichthys* cannot be related to the †Robertanniidae.

The new genus resembles the Eocene *incertae sedis* percoid genus †*Voltamulloid*, also from Bolca (BANNIKOV, 2008), by body proportions, vertebral formula, and divided dorsal fins with similar meristic counts. However, †*Stefanichthys* differs from †*Voltamulloid* by its deeper body, smaller mouth, serrations at least at the upper portion of the posterior preopercular margin, three rather than two anal-fin spines and cycloid rather than ctenoid scales.

Finally, †*Stefanichthys mariannae*, especially its smaller referred specimen (MCSNV II D.202/208), is similar in many respects to the Eocene Bolca species †*Acropoma lepidotum* (AGASSIZ). SORBINI (1975), in his revision of this species, indicated rather significant differences between †*A. lepidotum* and the extant species of *Acropoma*, but accommodated the former in this genus. Both †*Stefanichthys mariannae* and †*Acropoma lepidotum* share similar body depth, small mouth, similar degree of division of the dorsal fins and the same dorsal fin counts, vertebral formula, the plesiomorphic number of the principal caudal-fin rays (17), and an unconsolidated caudal skeleton. However, †*Stefanichthys mariannae* has cycloid scales (vs. ctenoid scales in †*Acropoma lepidotum*), smaller orbits, weaker dorsal- and anal-fin spines, seven (vs. eight) anal-fin soft rays, more robust dentition, no serrations on the subopercle, and evidently lacks supramaxilla. †*Stefanichthys* obviously cannot be regarded as an acropomatid (see above); however, strong similarities indicate the possible relationship of this genus with †*Acropoma lepidotum*. Perhaps future investigations may remove the latter species from the Acropomatidae.

The apparent supernumerary association of all three anal-fin spines on the first anal pterygiophore is a very unusual character of †*Stefanichthys mariannae* and probably can be regarded as its autapomorphy. JOHNSON (1984) did not indicate such a condition in any of the extant percoids. The robust dentition of the new taxon also represents a character not usually found among the Percoidei. Somewhat similar dentition (see BERKOVITZ and SHELLIS, 2017) is characteristic for some labroids and such percoids as Sparidae and †*Jimtylerius*.

Because the new genus is characterized mostly by plesiomorphic characters, we suppose that it is premature at present to either establish a new family for †*Stefanichthys* or modify the diagnoses of any

of the known percoid families to accommodate the new taxon. We prefer to retain †*Stefanichthys mariannae* gen. et sp. nov. *incertae sedis* within the generalized Percoidae.

ACKNOWLEDGEMENTS

We are very grateful to Mrs. Francesca Rossi, Director of the Museo Civico di Storia Naturale di Verona, for providing funding for the travel of AFB in 2020 to Verona to engage in this and other studies. We are much indebted for the photographs to Mr. Francesco Sorbini (Verona) (Fig. 1, 2B), Dr. Leonardo Latella (MCSNV) (Fig. 3, 4) and Dr. Matt Friedman (University of Michigan) (Fig. 2A). Dr. James C. Tyler of the Smithsonian Institution kindly reviewed the manuscript and improved the English.

LITERATURE CITED

- AHLSTROM E.H., BUTLER J.L., SUMIDA B.Y., 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. *Bulletin of Marine Science*, 26: 285-402.
- BALDWIN C.C., JOHNSON G.D., 1993. Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bulletin of Marine Science*, 52 (1): 240-283.
- BANNIKOV A.F., 1999. Unusual new percoid fish from the Eocene of Bolca. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 8: 117-128.
- BANNIKOV A.F., 2004a. Eocottidae, a new family of perciform fishes (Teleostei) from the Eocene of northern Italy (Bolca). *Miscellanea Paleontologica n. 7. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 10: 17-35.
- BANNIKOV A.F., 2004b. Fishes from the Eocene of Bolca, northern Italy, previously classified with the Chaetodontidae (Perciformes). *Miscellanea Paleontologica n. 7. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 10: 55-74.
- BANNIKOV A.F., 2008. Two new genera for long known percoid fishes (Perciformes) from the Eocene of Bolca, Italy. *Miscellanea Paleontologica n. 9. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 12: 29-44.
- BANNIKOV A.F., 2010. *Fossil Vertebrates of Russia and Adjacent Countries. Fossil Acanthopterygian Fishes (Teleostei, Acanthopterygii)*. GEOS, Moscow: LXI+244 pp. [In Russian].
- BANNIKOV A.F., 2011. A new percoid fish (Perciformes) related to *Hendrixella* from the Eocene of Bolca, Italy. *Miscellanea Paleontologica n. 10. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 13: 7-16.
- BANNIKOV A.F., 2014. The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *Miscellanea Paleontologica n. 12. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 15: 23-33.
- BANNIKOV A.F., 2019. A revision of “*Gobius*” *microcephalus* Ag. (Teleostei) from the early Eocene locality of Monte Bolca (Pesciara site, northern Italy). *Miscellanea Paleontologica n. 16. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 19: 17-28.
- BANNIKOV A.F., CARNEVALE G., 2007 (2005). The Eocene “*Dules*” *temnopterus* Agassiz, 1836 from Monte Bolca, and the problem of classifying fossil percoid fishes. *Palaeontographia Italica*, 91: 69-84.
- 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., 2016. †*Carlomonnus quasigobius* gen. et sp. nov.: the first gobioid fish from the Eocene of Monte Bolca, Italy. *Bulletin of Geosciences*, 91 (1): 13-22.
- BANNIKOV A.F., TYLER J.C., 1995. Phylogenetic revision of the fish families Luvaridae and †Kushlukidae (Acanthuroidei), with a new genus and two new species of Eocene luvarids. *Smithsonian Contributions to Paleobiology*, 81: 1-45.
- BELLWOOD D.R., 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs*, 15: 11-19.
- BERG L.S., 1940. Classification of fishes, both recent and fossil. *Travaux de l'Institut Zoologique, Academie de la Science de l'URSS*, 5: 87-517.
- BERKOVITZ B., SHELLIS R.P., 2017. *The Teeth of Non-Mammalian Vertebrates*. Academic Press, London, 342 pp.
- BETANCUR-R. R., BROUGHTON R.E., WILEY E.O., CARPENTER K., LOPEZ J.A., LI C., HOLCROFT N.I., ARCILA D., SANCIANGCO M., CURETON II J.C., ZHANG F., BUSER T., CAMPBELL M.A., BALLESTEROS J.A., ROA-VARON A., WILLIS S., BORDEN W.C., ROWLEY T., RENEAU P.C., HOUGH D.J., LU G., GRANDE T.C., ARRATIA G., ORTI G., 2013. The tree of life and a new classification of bony fishes. *PLOS Currents Tree of Life*: 1-41.
- BETANCUR-R. R., WILEY E.O., ARRATIA G., ACERO A., BAILLY N., MIYA M., LECOINTRE G., ORTI G., 2017.

Phylogenetic classification of bony fishes, *BMC Evolutionary Biology*, 17: 162, pp. 1-40. DOI 10.1186/s12862-017-0958-3.

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

COWMAN P.F., BELLWOOD D.R., 2011. Coral reefs as drivers of cladogenesis: expanding coral reefs, cryptic extinction events, and the development of biodiversity hotspots. *Journal of Evolutionary Biology*, 24: 2543-2562.

FRIEDMAN M., CARNEVALE G., 2018. The Bolca Lagerstätten: shallow marine life in the Eocene. *Journal of the Geological Society*, 175 (4): jgs2017-164.

GREENWOOD P.H., ROSEN D.E., WIETZMAN S.H., MYERS G.S., 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, 131 (4): 339-455.

JOHNSON G.D., 1984. Percoidei: development and relationships: 464-498. In: Moser H.G., Richards W.J., Cohen D.M., Fahay M.P., Kendall Jr. A.W., Richardson S.L. (Editors). *Ontogeny and systematics of fishes*. American Society of Ichthyologists and Herpetologists. Special Publication no.1.

JOHNSON G.D., 1993. Percomorph phylogeny: progress and problems. *Bulletin of Marine Science*, 52 (1): 3-28.

MARRAMÀ G., BANNIKOV A.F., TYLER J.C., ZORZIN R., CARNEVALE G., 2016. Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 454: 228-245.

MIYA M., FRIEDMAN M., SATOH T.P., TAKESHIMA H., SADO T., IWASAKI W., YAMANOUÉ Y., NAKATAMI M., MABUCHI K., INOUE J.G., POULSEN J.Y., FUKUNAGA T., SATO Y., NISHIDA M., 2013. Evolutionary origin of the Scombridae (tunas and mackerels): Members of a Paleogene adaptive radiation with 14 other pelagic fish families. *PLOS One*, 8 (9): e73535: 1-19.

NEAR T.J., DORNBURG A., EYTAN R.I., KECK B.P., SMITH W.L., KUHN K.L., MOORE J.A., PRICE S.A., BURBRINK F.T., FRIEDMAN M., WAINWRIGHT P.C., 2013. Phylogeny and tempo of diversification in the super-radiation of spiny-rayed fishes. *Proceedings of the*

National Academy of Sciences of the United States of America, 110: 12738-12743.

NEAR T.J., EYTAN R.I., DORNBURG A., KUHN K.L., MOORE J.A., DAVIS M.P., WAINWRIGHT P.C., FRIEDMAN M., SMITH W.L., 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences of the United States of America*, 109: 13698-13703.

NELSON J.S., 2006. *Fishes of the World*. 4th edn. John Wiley & Sons, Hoboken, New Jersey, 601 pp.

NELSON J.S., GRANDE T.C., WILSON M.V.H., 2016. *Fishes of the World*. 5th edn. John Wiley & Sons, Hoboken, New Jersey, 707 pp.

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

PAPAZZONI C.A., TREVISANI E., 2006. Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the "Pesciara di Bolca" (Verona, northern Italy): An early Eocene *Fossil-Lagerstätte*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242: 21-35.

PATTERSON C., ROSEN D.E., 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History*, 158: 81-172.

SCHULTZE H.-P., ARRATIA G., 2013. The caudal skeleton of basal teleosts, its conventions, and some of its major evolutionary novelties in a temporal dimension: 187-246. In: Arratia G., Schultze H.-P., Wilson M.V.H. (Editors), *Mesozoic Fishes 5: Global Diversity and Evolution*. Verlag Dr. Friedrich Pfeil, München.

SORBINI L., 1975 (1974). Studio paleontologico di *Acropoma lepidotus* (Agassiz). Pisces; Acropomatidae. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2: 177-203.

SORBINI L., 1981. *I fossili di Bolca, II ed.* "La Grafica", Vago di Lavagno (VR), 134 pp.

SYTCHEVSKAYA E.K., PROKOFIEV A.M., 2003. A new acanthopterygian family, Asiantidae (Perciformes) from the Upper Paleocene of Turkmenistan. *Journal of Ichthyology*, 43: 1-15.

SYTCHEVSKAYA E.K., PROKOFIEV A.M., 2011. On the status and volume of the late Paleocene family of

the spiny-rayed fishes Asianthidae (Percoidei). *Voprosy Ikhtiologii*, 51: 5-18. [In Russian].

TYLER J.C., BANNIKOV A.F., 1997. Relationships of the fossil and Recent genera of rabbitfishes (Acanthuroidei: Siganidae). *Smithsonian Contributions to Paleobiology*, 84: 1-35.

WILEY E.O., JOHNSON G.D., 2010. A teleost classification based on monophyletic groups: 123-182. In: Nelson J.S., Schultze H.-P., Wilson M. V. H. (Editors), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. Friedrich Pfeil, München.

INDIRIZZI DEGLI AUTORI

ALEXANDRE F. BANNIKOV
Borisyak Paleontological Institute
of the Russian Academy of Sciences
Profsoyuznaya 123
Moscow 117647 - Russia
e-mail: aban@paleo.ru

ROBERTO ZORZIN
Museo Civico di Storia Naturale di Verona
Lungadige Porta Vittoria 9
37129 Verona - Italia
e-mail: roberto.zorzin@comune.verona.it