† *Bolcaperca craccorum*, a new genus and species of *incertae sedis* percoid fish (Perciformes s.l.) from the Eocene of Bolca in northern Italy

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ABSTRACT

A new genus and species of percomorph fish, †*Bolcaperca craccorum* gen. et sp. nov., is described based upon at least 15 skeletons from the Pesciara site of the early Eocene locality Bolca in northern Italy. The new taxon is retained *incertae sedis* within the generalized Percoidei. †*Bolcaperca craccorum* gen. et sp. nov. is easily recognizable among the other generalized percoids of Bolca in having the following combination of characters: stronger dorsal-fin spines, the second anal-fin spine being the longest, larger mouth and very typical strong serrations on the preopercle. Additionally, the new taxon is characterized by cycloid or feebly ctenoid scales, nine dorsal-fin spines, seven anal-fin soft rays and weak dentition.
Key words: Perciformes, Percoidei, new genus and species, Eocene, northern Italy, Bolca locality, Pesciara site.

RIASSUNTO

Un nuovo genere e specie di pesce percomorfo, †*Bolcaperca craccorum* gen. e sp. nov., è descritto sulla base di almeno 15 scheletri provenienti dal sito della Pesciara di Bolca dell'Eocene inferiore, nell'Italia settentrionale. Il nuovo taxon viene descritto come Percioidei *incertae sedis*. †*Bolcaperca craccorum* gen. e sp. nov. è facilmente distinguibile daglialtri percoidi di Bolca per avere la seguente combinazione di caratteri: spine dorsali più robuste, la seconda spina della pinna anale più lunga delle altre, bocca più grande e una tipica forte dentellatura sul preopercolo. Inoltre, il nuovo taxon è caratterizzato da scaglie cicloidi o debolmente ctenoidi, nove spine della pinna dorsale, sette raggi molli della pinna anale e una debole dentatura.
Parole chiave: Perciformes, Percoidei, nuovo genere e nuova specie, Eocene, Italia settentrionale, località Bolca, sito della Pesciara.

INTRODUCTION

The Early Eocene fish fauna of the famous locality of Bolca, to the north of Verona in northern Italy, known since the mid-sixteenth century (Sorbini, 1981), 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 perciform fishes (*sensu* Nelson, 2006) are the most variable among the Bolca

fishes, and percoids predominate among the perciforms, being represented by more than 50 species. According to the latest Bolca fishes lists (Bannikov, 2014; Carnevale *et al.*, 2014, with additions), the Bolca percoids are represented by a number of extant (Latidae, Percichthyidae, Acropomatidae, Priacanthidae, Apogonidae, Pomatomidae, Carangidae, etc.) and extinct (Ductoridae, Exelliidae, Quasimullidae, Carangodidae, Eocottidae, Robertanniidae, Pavarottiidae) families; in addition, at least 14 genera cannot yet be attributed to any family, they are left *incertae sedis* within the Percoidei. This does not exhaust the variety of Bolca percoids. As demonstrated by the considerable number of papers published in

the last decade (see, e.g., Bannikov, 2014; Carnevale *et al.*, 2014; Bannikov and Zorzin, 2020, etc.), the possibility to recognize new taxa is not uncommon during the examination of the historical and more recent collections of Bolca fishes. Among the fossil fishes housed in the collections of the three different museums (but mostly in the Verona museum) there are not less than 15 specimens from Bolca (Pesciara cave site), which can be interpreted as belonging to a new genus and species of percoid fish. This fish is described below as the new genus and species †*Bolcaperca craccorum*.

The order Perciformes has traditionally been considered (Berg, 1940; Greenwood *et al.*, 1966; Nelson, 2006; etc.) the most diverse order of evolutionarily advanced bony fish, 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 the taxa of higher rank (Li *et al.*, 2009; Wiley and Johnson, 2010; Near *et al.*, 2012, 2013; Betancur-R. *et al.*, 2013, 2017; Lautredou *et al.*, 2013; Nelson *et al.*, 2016; Hughes *et al.*, 2018; Ghezelayagh *et al.*, 2022; 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. In molecular taxonomy, many percomorph families and genera do not have a fixed position and transfer from one to another clade (or to the *incertae sedis* position) in different publications. This encourages us to use traditional, natural taxonomy herein (as did, e.g., Heemstra *et al.*, 2022), with the order Perciformes *sensu lato*, and suborder Percoidei, the "largest and most diverse of the perciform suborders … undoubtedly polyphyletic..." (Johnson, 1993: 15) which is diagnosed by several plesiomorphic for the Perciformes features; this group includes those of perciforms that cannot be placed in other suborders. Citing molecular data, many families traditionally included into the Percoidei are removed from this suborder (e.g., Nelson *et al.*, 2016), or its composition 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.

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*: FMNH – Field Museum of Natural History, Chicago; MCSNV – Museo Civico di Storia Naturale di Verona; MGPUP – Museo di Geologia e Paleontologia dell'Università degli Studi di Padova; *Anatomical*: I – outermost, unbranched principal caudal-fin ray; an – angulo-articular; bh – basihyal; bpt – basipterygium; ch – ceratohyal; cl – cleithrum; cor – coracoid; d – dentary; e – epural; fr – frontal; h – hypural; HL – head length; hpu – haemal spine of preural vertebra; hyo – hyomandibular; iop – interopercle; mx – maxilla; npu – neural spine of preural vertebra; op – opercle; orb – orbit; pas – parasphenoid; pmx – premaxilla; pop – preopercle; PU – preural vertebra; qu – quadrate; rbr – branchiostegal ray; SL – standard length; soc – supraoccipital; sop – subopercle; U – ural vertebra; uh – urohyal.

The dagger symbol (†) indicates extinct taxa.

SYSTEMATIC DESCRIPTION

Order Perciformes *sensu* Nelson, 2006
Suborder Percoidei *sensu* Nelson, 2006
Percoidei *incertae familiae*
Genus †*Bolcaperca* gen. nov.

Diagnosis
Moderately elongate teardrop-shaped fish with a relatively long and deep caudal peduncle. Dorsal profile of body almost equally convex to ventral profile. Head relatively big. Head length slightly exceeds maximum body depth. Eye moderate. Mouth large; lower jaw articulation under middle to posterior border of orbit. Jaws with small sharp conical teeth,

without canines. Preopercle serrated posteriorly, ventrally bears 3 strong spines directed anteriorly. 10+14 vertebrae. Hypurals autogenous; 3 epurals, 2 uroneurals. 3 supraneurals. Dorsal fin single, but notched between spiny and soft portions. There are 9 very strong robust spines and (9) 10 soft rays in dorsal fin; fourth spine is longest. Anal fin with 3 strong spines (of which second thickest and longest) and 7 (8) soft rays. Pelvics inserted under pectorals. Caudal fin slightly emarginate, with 17 principal rays. Scales relatively large, cycloid or feebly ctenoid, cover entire body and bases of unpaired fins. Lateral line very gently arched in parallel to dorsal body profile.

Type Species
†*Bolcaperca craccorum* sp. nov., by monotypy and designation herein.

Etymology
The genus is named after the Bolca locality and the generic name *Perca*; gender feminine.

Composition
Type species only.

†*Bolcaperca craccorum* sp. nov.
Figures 1–5

†*Acropoma lepidotus* (Agassiz): Sorbini, 1975b: pl. V, fig. 2 (misidentification).

Diagnosis
As for the genus.

Etymology
The species is named in favor of Battista and Paolo Cracco, who collaborated with the second listed author in the excavations at the Bolca locality.

Holotype
MCSNV IG135659/IG135667, part and counterpart, complete skeleton, 36 mm SL (Fig. 1).

Paratypes
MCSNV IG142556, single specimen, complete skeleton, 32 mm SL (Fig. 2A); MCSNV IG43360/IG43404, part and counterpart, complete skeleton, 28 mm SL (Fig. 2D, 4A); MCSNV 440/441, part and counterpart, complete skeleton, 31 mm SL.

Referred Specimens
MCSNV IG145089, single specimen, complete skeleton; MCSNV IG135666, single specimen, complete skeleton (Fig. 3); MCSNV 444, single specimen, complete skeleton; MCSNV 463, single specimen, complete skeleton; MCSNV IG43432, single specimen, skeleton somewhat incomplete anteriorly (Fig. 2B); MCSNV IG129688, single specimen, complete skeleton; MCSNV IG129715, single specimen, complete skeleton; MCSNV IG129695, single specimen, complete skeleton (Fig. 4B); MCSNV IG43429/IG43430, part and counterpart, complete skeleton (Fig. 2C); FMNH PF3222, single specimen, complete skeleton. More questionably, MCSNV IG129671, single specimen, complete skeleton relatively poorly preserved; and MGPUP 6926/6927, part and counterpart, complete skeleton relatively poorly preserved (figured by Sorbini, 1975b: pl. V, fig. 2 as *Acropoma lepidotus*).

Type Locality and Horizon
Monte 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 and relatively long caudal peduncle. The caudal peduncle depth is 0.41–0.53 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 2.6 to 3 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 1.2–1.3 times less than its length. The orbit is moderate; its horizontal diameter is about one-fourth of HL. Ossifications of the sclerotic are relatively small. Traces of the eyeball are preserved as a thin carbonaceous film. The snout length roughly equals diameter of the orbit. The mouth is large and terminal. The lower jaw articulation is situated approximately under the middle to posterior border of the orbit. The infraorbital bones are poorly recognizable; the second suborbital forms a short flat spine in its ventral border, as evidenced by MCSNV 440. The neurocranium is moderately deep, with the supraoccipital crest evidently small and triangular. The frontals are extended above the orbit. The ethmoid region is relatively short; the lateral ethmoid forms most of anterior wall of the orbit. The unclear outline of a recrystallized rather large otolith is traceable in the otic region of several specimens. The parasphenoid is relatively slender and almost

Fig. 1 – †*Bolcaperca craccorum* gen. et sp. nov., holotype; Lower Eocene of Bolca in northern Italy, Pesciara: A – general view of MCSNV IG135659, B – counterpart MCSNV IG135667. Scale bar: 1 cm.

straight; it is exposed in the lowermost portion of the orbit. The premaxilla has a long and very slender ascending process and massive articular process. The postmaxillary process is well developed. The premaxilla bears small conical teeth better recognizable in MCSNV 440/441. The maxilla is curved near its head; it is flat and expanded distally. The supramaxilla is present; it is very narrow and tapered anteriorly. The lower jaw is moderately deep; its length is 53–61% HL. The dentary is notched posteriorly and almost does not project ventrally near the low sym-

physis. 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. Some specimens reveal a narrow space between the anterodorsal border of the angulo-articular and the posterodorsal process of the dentary. The retroarticular process of the angulo-articular is robust. The hyomandibular shaft is sub-vertical, at least in larger specimens. The quadrate is relatively small, triangular in shape, thickened along its posterior border; its articular condyle is moderate. The
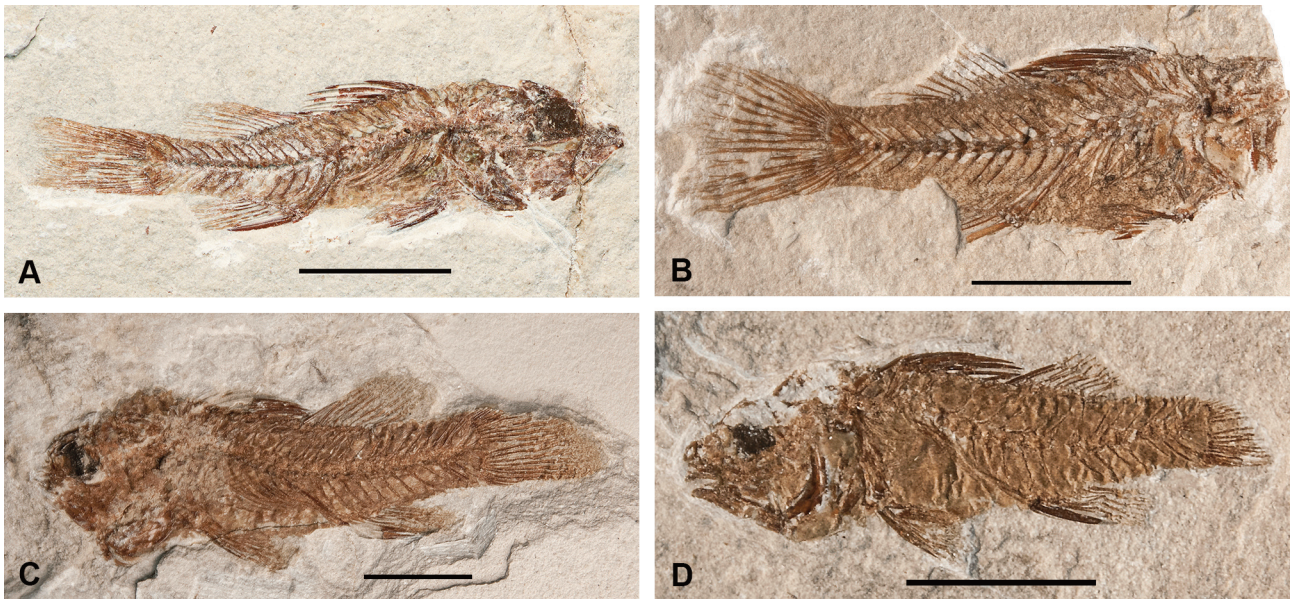
Fig. 2 – †*Bolcaperca craccorum* gen. et sp. nov., Lower Eocene of Bolca in northern Italy, Pesciara: A – paratype MCSNV IG142556, B – referred specimen MCSNV IG43432, C – referred specimen MCSNV IG43429, D – paratype MCSNV IG43360. Scale bar: 1 cm.

symplectic is narrow and wedge-shaped. The ectopterygoid is a narrow bone consisting of the tapered ventral arm and longer anterior shank, also tapered. The entopterygoid is moderately wide and lamellar. The palatine is poorly preserved, its posterior end is tapered. The preopercle is a strong, moderately wide and slightly curved bone serrated posteriorly; ventrally it bears three strong spines directed anteriorly (Fig. 4A). The opercle is flat, broad and subtriangular in shape, thickened along the anterior border. It bears a ridge extended posteriorly from the articular facet, which terminates in a spine (Fig. 3). The subopercle is relatively narrow; it seems to have a prong on its anterior corner and no serrations. The shape of the interopercle is unclear. The ceratohyal is broadest at the posterior end, and with a concave ventral margin; it seems to have a "beryciform foramen" (McAllister, 1968). There are seven sabre-like branchiostegal rays; the anterior three are slender, and the posterior four are more robust (Fig. 3). Anterior six branchiostegals are attached to the ceratohyal, and the last one to the epihyal. The basihyal (glossohyal) is a thin elongate rod. The urohyal is incompletely preserved; it is thickened along its ventral margin. Neither the branchial bones nor pharyngeal teeth are recognizable; some specimens reveal ossified gill filaments.

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 the lateral view and bear a longitudinal ridge on the lateral surface. The length of the caudal portion of the vertebral column is 1.4 times greater than the length of the abdominal portion of the vertebral column. The vertebral spines are relatively short, straight or only slightly curved. The neural spines of the anterior four vertebrae are expanded in relation to those of the succeeding vertebrae. The haemal spines of the anterior caudal vertebrae are longer than the corresponding neural spines. Short parapophyses are recognizable in at least two posterior abdominal vertebrae. The pleural ribs are moderately long and relatively slender; these are rather strongly inclined posteroventrally. Slender epineurals sometimes are recognizable just below the middle abdominal vertebrae (e.g., in paratype MCSNV IG142556).

Pectoral fin and girdle. The pectoral girdle is usually poorly preserved. The posttemporal is forked; it seems to be not serrated along its distal margin. The supracleithrum seems to be a moderately large, elongate bone. The cleithrum is strong and moderately curved in C-shape. The moderately
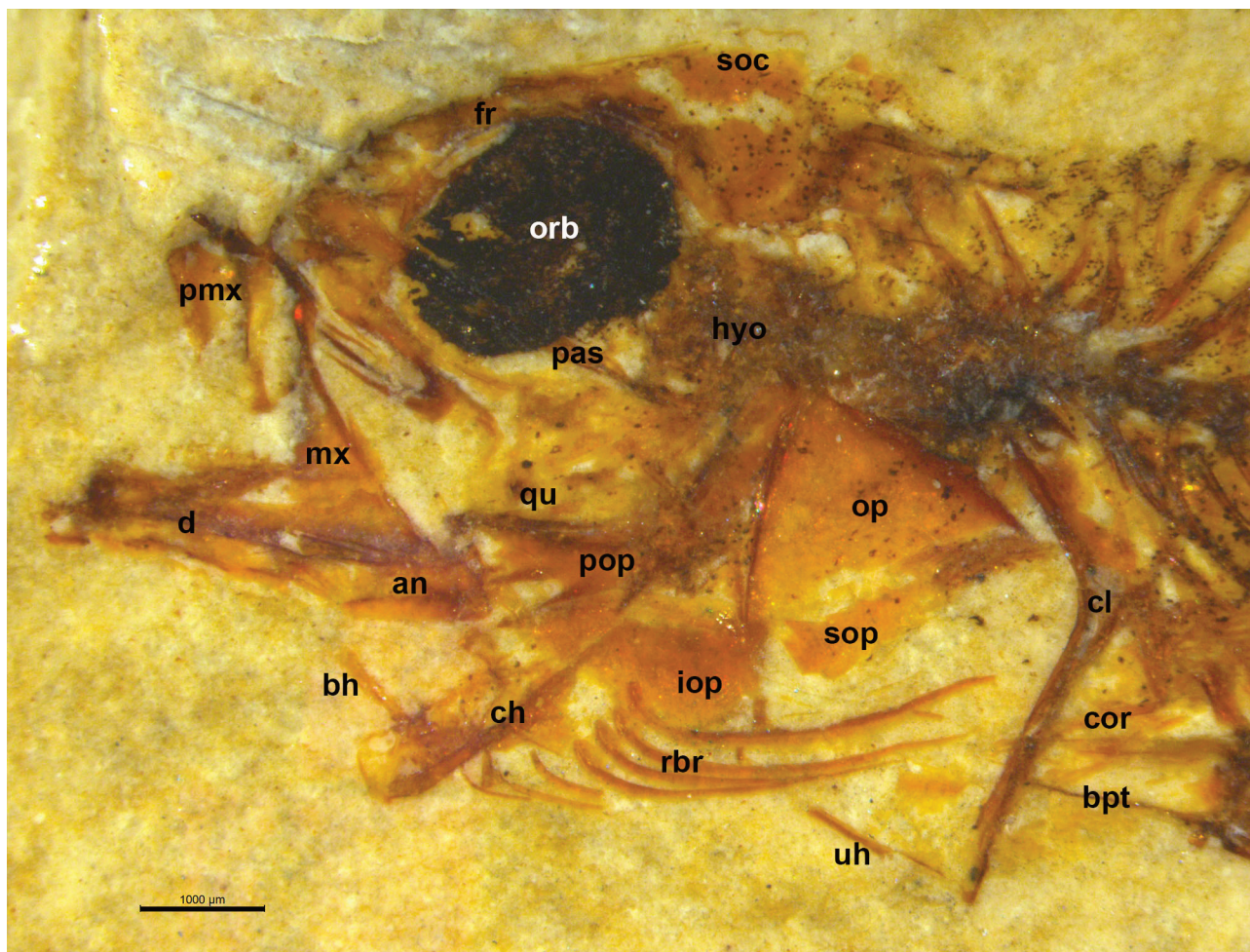
Fig. 3 – †*Bolcaperca craccorum* gen. et sp. nov., referred specimen MCSNV IG135666, head and anterior part of body (moistened with alcohol); Lower Eocene of Bolca in northern Italy, Pesciara. Scale bar: 1 mm.

wide posterodorsal plate of the cleithrum, which is situated over the pectoral-fin base, is located under the third and beginning of the fourth vertebrae. The ventral postcleithrum is relatively short and wedge-shaped. The coracoid is short and narrow; it extends to the attachment of the basipterygium, far from the lower end of the cleithrum. The scapula is poorly recognizable. The three pectoral radials are hour-glass-shaped; these increase in length ventrally in the series. There are not less than 11 pectoral-fin rays. The pectoral fins are moderately long. The pectoral-fin base is situated relatively low, close to the mid-point between the vertebral column and the ventral body margin.

Pelvic fin and girdle. The pelvic bone is moderately long and wedge-shaped; it is oriented almost horizontally. The pelvic fins contain a slender spine and five soft, branched rays each. The pelvic fin is inserted roughly under the pectoral-fin base. The pelvic fin is relatively long and seems to be longer that the pectoral fin; the pelvic-fin spine is 1.3–1.5 times shorter than the longest anal-fin spine.

Supraneurals and dorsal fin. There are three rather small supraneurals; these lack detectable apical projections and become slightly longer posteriorly in the series. The predorsal formula (Ahlstrom *et al*., 1976; Johnson, 1984) is variable because of taphonomic reasons (displacement of the anterior pterygiophores and supraneurals from their original position – e.g., 0//0+0+2/1+1+1/1 in MCSNV IG135666); we regard its most frequent pattern of 0/0/0+2/1+1/1 as apparently natural and character-
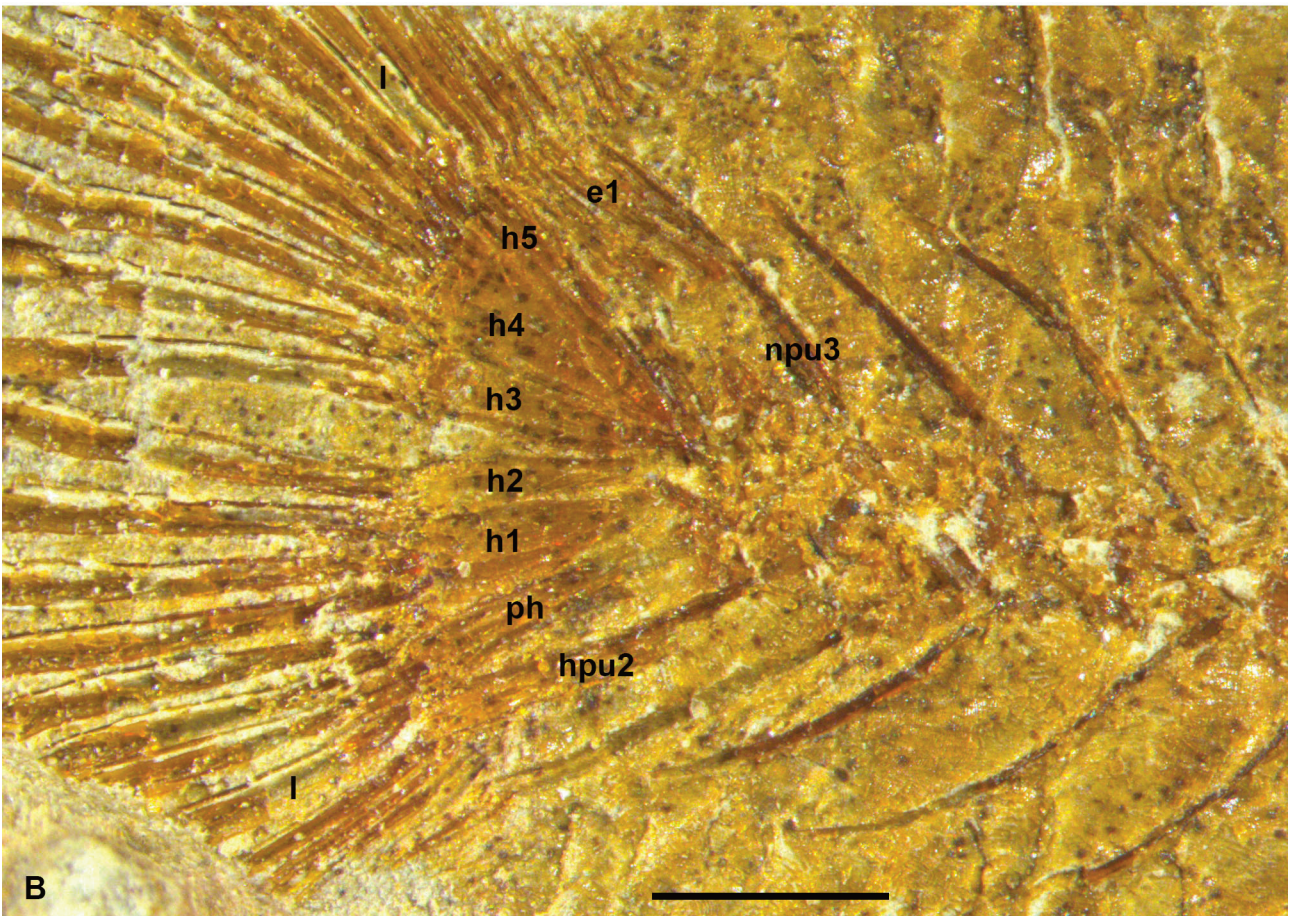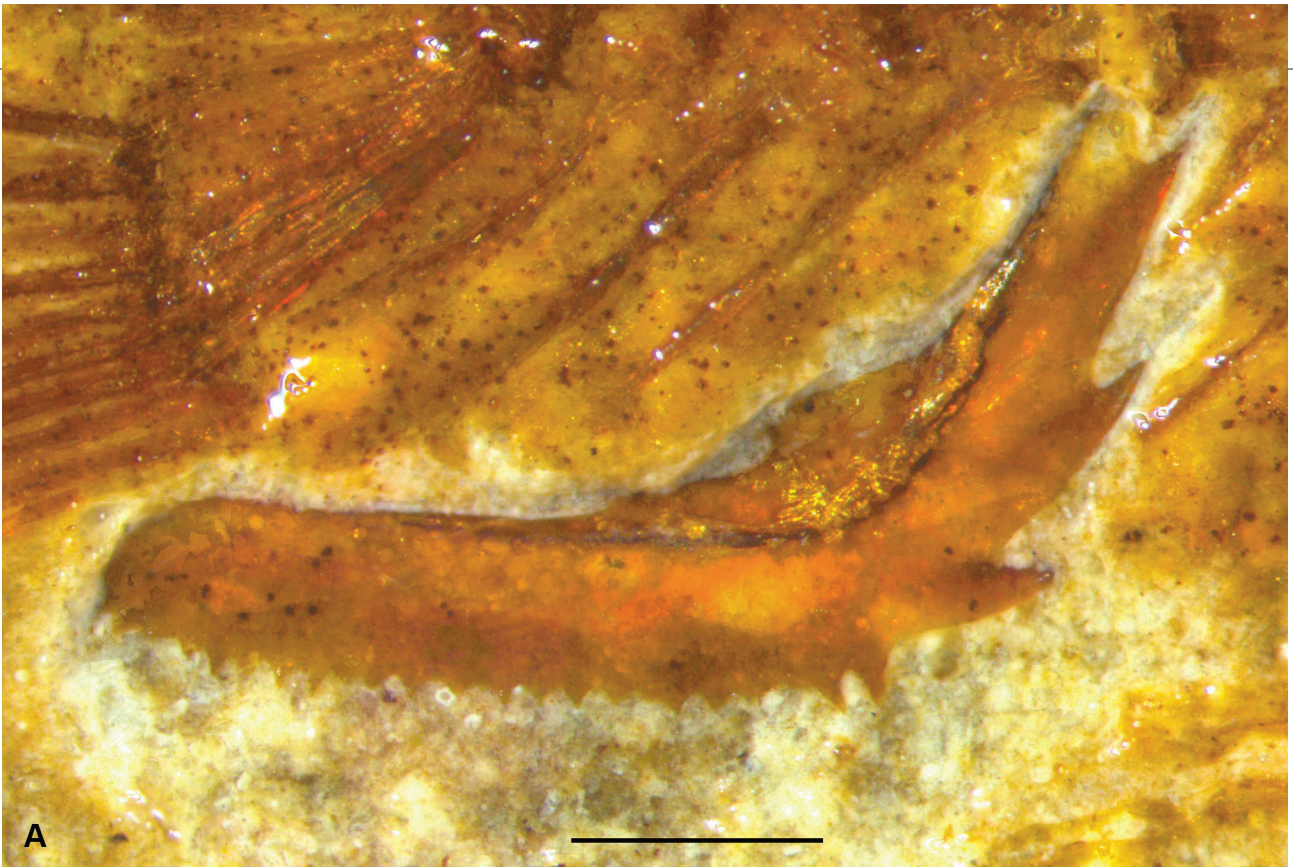
Fig. 4 – †*Bolcaperca craccorum* gen. et sp. nov., Lower Eocene of Bolca in northern Italy, Pesciara: A – paratype MCSNV IG43404, detached preopercle (moistened with alcohol); B – referred specimen MCSNV IG129695, caudal skeleton. Scale bar: 1 mm.
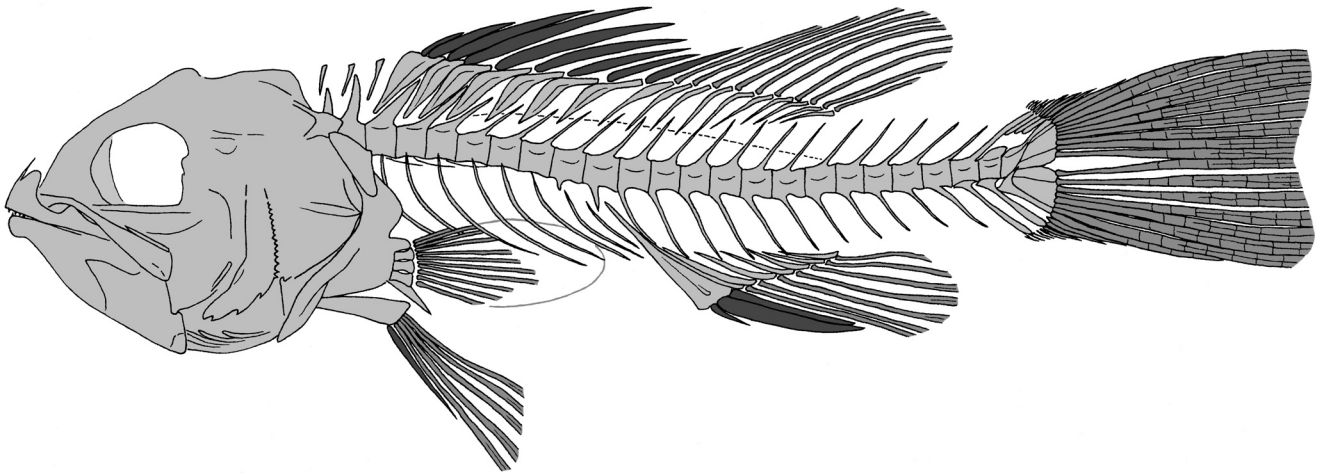
Fig. 5 – †*Bolcaperca craccorum* gen. et sp. nov., reconstruction of the skeleton based mostly on the holotype.

istic for the species. The dorsal fin is continuous but somewhat notched, with its pterygiophores forming a continuous series. The dorsal fin is moderately long-based; it originates over the fourth vertebra and ends above the seventh or eighth caudal vertebra. There are nine very strong robust smooth spines and ten (occasionly nine) soft rays in the dorsal fin. The fourth dorsal-fin spine is longest; it is 4.1–4.2 times longer than the first spine and 2.05–2.2 times longer than the penultimate spine. The last spine is slightly longer than the penultimate spine. The first two dorsal-fin spines are supernumerary on the first dorsal-fin pterygiophore; these are closely spaced. The dorsal-fin spines are close-set anteriorly, becoming more widely spaced posteriorly (the space between the penultimate and ultimate spines almost equals to the space between the last spine and the first soft ray). The longest soft rays of the dorsal fin are very slightly longer than the longest dorsal-fin spine. The soft portion of the dorsal fin forms a rounded lobe; it is higher than long. The length of the base of the soft portion of the dorsal fin is 1.35–1.4 times shorter than the base length of the spiny portion. There are a total of 17 dorsal-fin pterygiophores; the interneural spaces below the dorsal fin have the ventral shafts of one or two pterygiophores present. Several anterior pterygiophores are wedge-shaped; posteriorly in the series the pterygiophores become narrower. 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 the last spine of the dor-

sal fin. The pterygiophores of the soft dorsal-fin rays decrease in length posteriorly in the series and become more strongly inclined posteriorly.

Anal fin. The anal fin is short-based; it originates usually under the beginning of the fourth caudal vertebra and ends roughly opposite to the end of the dorsal fin. There are three smooth spines and seven (occasionally eight) soft segmented and branched rays in the anal fin. The first anal-fin spine is small and slender, whereas two others are strong and robust. The second anal-fin spine is thickest and longest, similar in length with the third dorsal-fin spine and 1.1–1.25 times longer than the third anal-fin spine. The anal-fin spines are close-set to each other; the first two spines are supernumerary on the first anal pterygiophore. The longest anal-fin soft rays are usually slightly shorter than the longest dorsal-fin soft rays and also form a rounded lobe. There are seven anal-fin pterygiophores; the first pterygiophore is longest, robust and wedge-shaped; the succeeding pterygiophores are narrow, become more strongly inclined and decrease in length posteriorly in the series. The last anal-fin pterygiophore lies almost horizontally, in parallel to the body axis. The one (usually) or two anal-fin pterygiophores only slightly enter up into the each of the interhaemal spaces.

Caudal fin and skeleton. The caudal skeleton is of the generalized percoid type, showing the fusion of PU1, U1, and U2 in the terminal centrum[1]. The hy-

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[1] The diural terminology is used. Schultze and Arratia (2013) have shown that the two ural centra are not homologous in different Teleostei.

purals, parhypural, haemal spines of PU2 and PU3 are autogenous (Fig. 4B). There is a small hypural diastema between the epaxial and hypaxial hypurals. The neural and haemal spines of PU3 are stronger than those of the preceding vertebra. The PU2 centrum is shortened, and its neural spine is evidently a short crest. There are three epurals; the first is longest. There are two uroneurals, the first of which seems to form a stegural. Both the parhypural and haemal spine of PU2 are plate-like broadened anteriorly at their proximal portion. The caudal fin is moderately large and slightly emarginated. 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, with no procurrent spur (Johnson, 1975).

Squamation. Scales are large but not especially thick, covering the entire body and bases of the unpaired fins. Ctenii are not recognizable in most of the specimens, although perhaps due to inadequate preservation: two of examined specimens (MCSNV IG129671 and MCSNV 463) seem to reveal unclear ctenii, mostly in the abdominal region of the trunk and in the caudal peduncle, respectively. Each of the body scales bears several (usually five to seven) radii in the basal field. The scales are covered by tiny striations. The limits of individual scales are hardly recognizable; therefore, the number of the 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 18th vertebra.

Coloration. Traces of the original pigmentation pattern are preserved throughout the whole body and fins; these represent small dark spots arranged more or less densely.

Measurements (in percent of SL), are as follows (in parentheses are those of the holotype):
- Head length from tip of snout to posterior border of opercle: 33–39 (34)
- Maximum body depth: 26–33.5 (26.5)
- Depth of caudal peduncle: 11–17 (13)
- Distance between tip of snout and dorsal fin: 39.5–44 (42)
- Distance between tip of snout and first soft ray of dorsal fin: 62–66 (65)
- Distance between tip of snout and anal fin: 66–73 (67.5)
- Distance between pelvic fin and anal fin: 22–29 (29)
- Length of base of dorsal fin: 36–42 (40)
- Length of base of anal fin: 11–14 (13)
- Length of longest (fourth) spine of dorsal fin: 16–19.5 (18.5)
- Length of last spine of dorsal fin: 8.5–10 (9.7)
- Length of longest soft ray of dorsal fin: 17–20 (19.5)
- Length of longest spine of anal fin: 14–18 (14)
- Length of longest soft ray of anal fin: 14.5–21 (14.5)
- Length of spine of pelvic fin: 11–12 (11)
- Length of longest soft ray of pelvic fin: 17–18 (17.5)
- Length of pectoral fin: ca. 15 (ca. 17)
- Length of caudal fin: 23.5–28 (?)
- Preorbital distance: 7–10.5 (8.5)
- Horizontal diameter of orbit: 8–11 (9)
- Length of lower jaw: 17–23 (21)

Remarks. Most of the material of †*Bolcaperca craccorum* gen. et sp. nov. represent relatively small fishes, usually 20–45 mm SL. However, the specimen MGPUP 6926/6927, although similar to the hypodigm in the available characters, is distinguished by a larger size (182 mm SL; see Sorbini, 1975b: pl. V, fig. 2). Therefore, this specimen is only tentatively regarded here as †*Bolcaperca craccorum* gen. et sp. nov.; we cannot exclude the possibility that it belongs to another species of the same genus.
In ontogenesis, with an increase in the size of the fish, the relative length of the head and the body depth decrease and the distance between the pelvic and anal fins as well as the relative length of the lower jaw increase.

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 a single, although notched, dorsal fin, †*Bolcaperca* gen. nov. differs from those percoids which have more or less divided dorsal fins, such as, for example, the early Eocene *incertae sedis* Percoidei †*Voltamulloides* and †*Stefanichthys* (Table 1), also from Bolca (Bannikov, 2008; Bannikov and Zorzin, 2020), as well as the Bolca percoids attributed to their own families, †Quasimullidae (Bannikov, 1999) and †Robertanniidae (Bannikov, 2011).

Taxon	Vertebral formula	D formula	D spines	A formula	A spines	Mouth, teeth	Scales	Preopercle peripheral border	Caudal fin
†*Veronabrax*	10+14	X, 8	Relatively strong, 4th longest	III, 6	Weak, graduated	Small, edentulous	Cycloid	Not serrated	Forked
†*Voltamulloides*	10+14	VIII – I, 10	Slender, 4th longest	II, 8	Weak, 2d longest	Small; teeth small, sharp	Ctenoid	Not serrated	Forked
†*Jimtylerius*	10+14	X, 9	Relatively strong, 4th longest	III, 7	Moderately strong, 2d and 3rd almost equal	Relatively large; teeth small, rounded	Cycloid	No data	Emarginated
†*Stefanichthys*	10+14	VIII – I, 9	Slender, 4th longest	III, 7	Weak, graduated	Small; teeth moderate, bluntly cylindrical	Cycloid	Not serrated except small serrations dorsally	Notched
†*"Acropoma" lepidotum*	10+14	IX, 9	Relatively strong, 3rd and 4th longest	III, 8	Moderately strong, graduated	Small; teeth moderate, cylindrical	Ctenoid	Serrated posteriorly, even ventrally	Notched
†*Cyclopoma*	10+14	IX, 9-10	Relatively strong, 3rd and 4th longest	III, 8	Moderately strong, 2d thicker but slightly shorter than 3rd	Relatively large; teeth small, conical	Both ctenoid and cycloid	Strongly serrated, with ventral spines strongest and anteriorly directed	Truncated to slightly rounded
†*Eolates*	11+14	VIII, 11-13	Strong, 3rd longest	III, 8	Strong, 2d and 3rd equal	Relatively large; teeth very small, conical	Ctenoid	Serrated posteriorly, ventrally bears 4 strong spines directed both anteriorly and posteriorly	Rounded
†*Bolcaperca* gen. nov.	10+14	IX, (9)10	Very strong, 4th longest	III, 7(8)	Strong, 2d thickest and longest	Large; teeth small, conical	Ctenoid (?)	Serrated posteriorly, ventrally bears 3 strong spines directed anteriorly	Slightly emarginated

Table 1 – Some characters of generalized percoids from the Lower Eocene of Bolca (after: Sorbini, 1975a, b; Sorbini Frigo and Sorbini, 1975; Bannikov and Carnevale, 2007; Bannikov, 2008; Bannikov and Zorzin, 2020).

In addition to the generalized percoids from Bolca attributed to extant families – †*Eolates gracilis* (Agassiz, 1833) (Latidae), †*Cyclopoma gigas* Agassiz, 1833 (Percichthyidae) and †*"Acropoma" lepidotum* (Agassiz, 1836) (questionable Acropomatidae) – there are about 15 percoid genera from Bolca left *incertae sedis* (Bannikov, 2014; Carnevale et al., 2014).

Most of them are easily distinguishable from †*Bolcaperca* gen. nov. in their general appearance, meristics and specialisations: e.g., genera †*Blotichthys* Sorbini, 1984, †*Pygaeus* Agassiz, 1838, †*Frigoichthys* Bannikov, 2004 and †*Squamibolcoides* Bannikov et Zorzin, 2013 are deep-bodied; †*Parapelates* Bannikov, 2008 has an unusually high number of dorsal-fin spines

(15); †*Montepostalia* Bannikov et Zorzin, 2004 has long-based soft dorsal and anal fins with 14 segmented rays each; †*Bradyurus* Gill, 1904 and †*Frippia* Bannikov et Carnevale, 2012 have a labroid general appearance with an enlarged to 26–27 number of vertebrae and a single dorsal fin with numerous (14 to 17) soft rays.

However, such genera of the Bolca percoids as †*Veronabrax* Bannikov, 2008 and †*Jimtylerius* Bannikov et Carnevale, 2007 are not easily distinguishable from †*Bolcaperca* gen. nov., especially if the material examined is not perfectly preserved. Therefore, we recommend use the combination of characters for identifying the generalized percoids from Bolca (see Table 1). The new genus has a larger mouth and thicker dorsal-fin spines than any other Bolca generalized percoid, but these are hardly quantified. †*Bolcaperca* gen. nov. is the only taxon among the genera in question which has the second anal-fin spine longer and thicker than the third spine: usually the anal-fin spines are either graduated or the second and third spines are equal in length (although the second spine is thickest in †*Cyclopoma*). Also, †*Bolcaperca* gen. nov. has a characteristic preopercle, which is serrated posteriorly and bears three strong (but not long) spines directed anteriorly along the ventral margin. Only †*Cyclopoma* and †*Eolates* have somewhat similar armoring of the preoprcle, but their lower spines are longer than in †*Bolcaperca* gen. nov. Thus, when both the anal fin and the preopercle are recognizable in the fossil material, †*Bolcaperca craccorum* gen. et sp. nov. can be easily identified. Some other characters could be also used for its identification: 10+14 vertebrae (vs. 11+14 in †*Eolates*); a total of nine dosal-fin spines (vs. 10 spines in †*Veronabrax* and †*Jimtylerius* and eight spines in †*Eolates*); seven (occasionally eight) anal-fin soft rays (vs. six rays in †*Veronabrax*); weak oral teeth (vs. stronger dentition in †*Stefanichthys* and †*"Acropoma" lepidotum* and absence of teeth in †*Veronabrax*); not forked caudal fin (vs. forked in †*Veronabrax* and †*Voltamulloides*) (Table 1). Sorbini (1975b) in his revision of †*"Acropoma" lepidotum* indicated rather significant differences between †*A. lepidotum* and extant species of *Acropoma*, but accommodated the former in this genus. This allocation should be verified further.

As well as from the Bolca percoids, the new genus is easily distinguished from other fossil genera of Percoidei *incertae sedis*. One of these, †*Oliganodon* Bannikov, 2010, was established for the two Oligocene species from the Parathethys basin; it is somewhat similar to †*Bolcaperca* gen. nov. in meristic characters.

Prokofiev, familiar with the manuscript of the monograph of Bannikov (2010), nevertheless decided to describe, among other new taxa, a new genus analogous to †*Oliganodon*, having the same species composition (Prokofiev, 2009). However, the generic name †*"Oligoserranoides"* introduced by Prokofiev in order to obtain priority over †*Oliganodon* can hardly be considered available or valid, since the paper in which the name is published does not meet the publication criteria (ICZN, 1999, Articles 8.1.2, 8.1.3): the non-referred journal "Actual Problems of Modern Science" is not an edition containing simultaneously obtainable copies by a method that ensures numerous identical copies distributed in the form of numerous copies. The journal is absent even in the main libraries of Russia. In the same publication, Prokofiev described a new taxon of Oligocene percoids based on a specimen from the Moravian Museum of the Earth (Brno, Czech Republic), without obtaining the necessary permission from the Museum curators.

†*Bolcaperca* gen. nov. differs from †*Oliganodon* by the notched dorsal fin with nine stronger spines (vs. dorsal fin not notched with 10 weaker spines in †*Oliganodon*), shorter pectoral fins, strongest and longest second anal-fin spine (vs. graduated spines in †*Oliganodon*), different pattern of armoring of the preopercle, and posttemporal not serrated (vs. serrated in †*Oliganodon*).

Since the new genus is characterized mostly by plesiomorphic characters, we suppose that it is premature at present to either establish a new family for †*Bolcaperca* gen. nov. or modify the diagnoses of any of the known percoid families to accommodate the new taxon. We prefer to retain †*Bolcaperca craccorum* gen. et sp. nov. *incertae sedis* within the generalized Percoidei.

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