

***Paralabrus rossiae*, a new genus and species of putative labroid fish (Perciformes) from the Eocene of Bolca in northern Italy**

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ABSTRACT

A new genus and species of percomorph fish, *Paralabrus rossiae*, is described based upon a single skeleton of a small fish from the Pesciara site of the Eocene locality Bolca in northern Italy. Although most of the skeleton is perfectly articulated, the specimen has a displaced pelvic fin and girdle. *Paralabrus* gen. nov. has a general appearance similar to that of labrid fishes, including relatively strong oral teeth, deep caudal peduncle, rounded caudal fin, etc., and is characterized by such labrid synapomorphies as oligomerization of the caudal skeleton and pharyngognathy. However, the most useful labrid synapomorphy, a single supraneural, can only be presumed to be present based on our interpretation of its anterior displacement in the single specimen. Therefore, *Paralabrus* gen. nov. is only tentatively accommodated in the family Labridae, and thus becomes the sixth wrasse taxon in the rich Eocene fish fauna of Bolca.

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

RIASSUNTO

Un nuovo genere e specie di pesce percomorfo, *Paralabrus rossiae*, è descritto sulla base di un unico scheletro di un piccolo pesce proveniente dal giacimento della Pesciara, località eocenica di Bolca (Italia settentrionale). Sebbene la maggior parte dello scheletro sia perfettamente articolata, l'esemplare ha una cintura pelvica e una pinna pelvica spostata. Il nuovo genere *Paralabrus* ha un aspetto complessivo simile a quello dei labridi, compresi i denti relativamente forti, il profondo peduncolo caudale, la pinna caudale arrotondata, ecc., ed è caratterizzato da tali sinapomorfie ibride come l'oligomineralizzazione dello scheletro caudale, e dei Faringognati. Tuttavia, si può presumere che la sinapomorfia labiale più utile, unico supraneurale, sia presente sulla base della nostra interpretazione del suo spostamento anteriore nel singolo esemplare. Pertanto, *Paralabrus* gen. nov. è solo provvisoriamente ospitato nella famiglia Labridae, e diventa così il sesto taxon nella ricca fauna ittica di Bolca.

Parole chiave: Perciformes, Labroidei, nuovo genere e specie, Eocene, Italia settentrionale, Bolca, Pesciara.

INTRODUCTION

The Early Eocene fish fauna of the famous locality Monte Bolca, to the north of Verona in northern Italy, is exceptionally rich in marine fishes, especially of the acanthomorphs (e.g., FRIEDMAN and CARNEVALE, 2018). Monte Bolca 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 (COWMAN and BELLWOOD 2011; NEAR *et al.*, 2013); these are represented in the Bolca assemblage by their extinct ecological analogues (BANNIKOV, 2004a, b). True gobioids are represented there only by a single specimen of diminutive species (BANNIKOV and

CARNEVALE, 2016). Except for discoveries of fragmentary remains (pharyngeal jaws) elsewhere, the Bolca fish fauna establishes the earliest known record of the Pharyngognathi or Labroidei. After the extensive study of the Bolca pharyngognath fishes (BELLWOOD, 1991, 1995, 1999; SORBINI *et al.*, 1991; BANNIKOV and SORBINI, 1991; BELLWOOD and SORBINI, 1996; BANNIKOV, 2004b; BANNIKOV and CARNEVALE, 2010, 2012; BANNIKOV and BELLWOOD, 2014, 2015) (see overview in BANNIKOV and BELLWOOD, 2017), the latest lists of the Monte Bolca fishes (BANNIKOV, 2014; CARNEVALE *et al.*, 2014, with additions) include eleven monotypic pharyngognath taxa: five Labridae (*Phyllopharyngodon* BELLWOOD, 1991, *Eocoris* BANNIKOV et SORBINI, 1991, *Bellwoodilabrus* BANNIKOV et CARNEVALE, 2010, *Labrobolcus* BANNIKOV et BELLWOOD, 2015 and *Zorzi-*

nilabrus BANNIKOV et BELLWOOD, 2017), three Pomacentridae (*Palaeopomacentrus* BELLWOOD et SORBINI, 1996, *Lorenzichthys* BELLWOOD, 1999 and *Sorbinichromis* BANNIKOV et BELLWOOD, 2014), as well as three genera of uncertain relationships (*Tortonesia* SORBINI, 1983, *Sorbinia* BELLWOOD, 1995, and *Quasicichla* BANNIKOV, 2004). BANNIKOV (2019) added one more genus, *Guus*, to the family Tortonesidae; the labroid affinities of this family are only tentative and it was placed *incertae sedis* within the order Perciformes.

Each Bolca taxon of labrids and pomacentrids is represented by one (usually) to three specimens. *Zorzinilabrus furcatus* was described recently based upon the holotype only (BANNIKOV and BELLWOOD, 2017); however, one more specimen from the type locality, MCSNV VB66, probably belongs to the same species. All the Bolca pharyngognath fishes were collected at the Pesciara cave site rather than at the Monte Postale site. The quantitative and taphonomic analyses of the Pesciara and Monte Postale fish assemblages performed recently (MARRAMÀ *et al.*, 2016) clearly defined two distinctive paleocommunities and two different depositional settings.

Among the fossil fishes housed in the collection of the MCSNV there is one more specimen from Monte Bolca, collected in 1988, which can be interpreted as belonging to a new genus and species of pharyngognath fish related to the Labridae. This fish is described below as the new genus and species *Paralabrus rossiae*.

METHODS

The specimen was examined using a WILD Heerbrugg stereomicroscope with an attached camera lucida drawing arm. Some details of the specimen examined were best seen when the specimen was moistened with alcohol. The specimen was prepared by needle. 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*: MCSNV – Museo Civico di Storia Naturale di Verona; *Anatomical*: HL – head length; PU – preural vertebra; SL – standard length; U – ural vertebra.

SYSTEMATIC DESCRIPTION

Family gap Labridae Cuvier, 1817 Genus *Paralabrus* gen. nov.

Diagnosis

Relatively elongated fish of diminutive size with a relatively long caudal peduncle. Head relatively small, 3.4 times in SL. Maximum body depth only slightly less than head length. Supraoccipital crest poorly developed. Lower jaw articulation under anterior portion of orbit. Mouth relatively small. Jaw teeth conical, arranged in a single row; enlarged premaxillary canines absent. Posterior preopercular margin even. 26 (9+17) vertebrae. Supraneural single (?). Dorsal fin continuous, with 8 spines (1 supernumerary) and at least 7 soft rays. Anal fin with 3 spines and 7 rays. Unpaired-fin spines very slender. Two anal-fin pterygiophores placed anterior to second haemal spine. Nine or more pectoral-fin rays. Caudal fin rounded, with 15 principal rays; 5 procurrent rays above.

Type species

Paralabrus rossiae sp. nov., by monotypy and designation herein.

Etymology

The genus is named after παρά (Greek) as near, and the genus *Labrus*; gender masculine.

Composition

Type species only.

***Paralabrus rossiae* sp. nov.**

Figures 1-3

Diagnosis

As for the genus.

Etymology

The species is named in honour of Mrs. Francesca Rossi, Director of the Museo Civico di Storia Naturale di Verona, who recognizes the international importance of the fossils from the Monte Bolca locality that have been assembled over a long period of time at the Verona natural history museum, and she has the wisdom to encourage the study of these organisms.

Holotype

MCSNV VR 27624, single plate, complete skeleton, 16.2 mm SL. The pelvic fin and girdle are displaced.

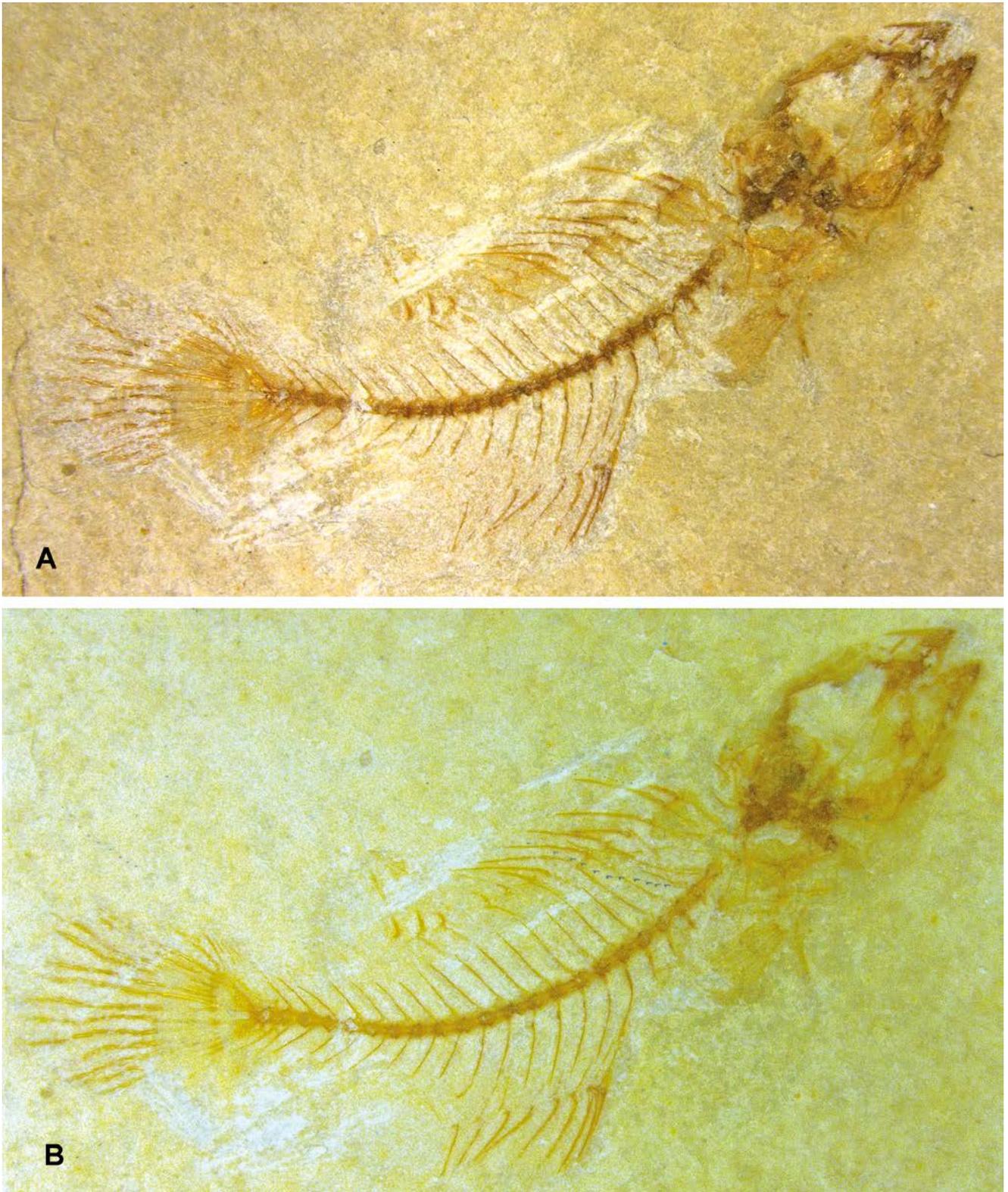


Fig. 1 – *Paralabrus rossiae* gen. et sp. nov., holotype MCSNV VR 27624, SL 16.2 mm; Lower Eocene of Bolca in northern Italy, Pesciara: **A** – general view, **B** – specimen moistened with alcohol to improve contrast

Referred Specimens

None.

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).

Description

The body is relatively elongate and perhaps somewhat laterally compressed, with a moderately deep and relatively long caudal peduncle. The dorsal and ventral profiles of the body are almost equally convex. The body depth is contained 3.98 times in SL. The caudal peduncle depth is about 0.43 of the body depth. The head is moderately large, contained 3.2 times in SL. The head is relatively deep, its maximum depth is only somewhat less than its length; the snout is moderately elongate and contained 2.9 times in HL. The mouth is terminal, probably nearly horizontal, with a relatively small gape. The lower jaw articulation is situated under the anterior portion of the orbit.

Head. The neurocranium is moderately deep; the supraoccipital crest is poorly developed. The details of the ethmoid region are not recognizable; the ethmoid region is relatively short. It is unclear if the ethmoid-frontal depression (=frontal recess; see GOMON, 1997) is developed or not. The frontals occupy most of the braincase roof above the orbit. The parasphenoid is an almost straight rod; its apophyses are not recognizable. The vomer seems to be toothed (if it is not an artifact of preservation). The nasals are slender and elongate. Only faint remains of some infraorbital bones can be recognized. The premaxilla has a moderately high ascending process apparently coalescent with the articular process. The premaxillary ascending process is very strong; it seems to be almost as long as the alveolar ramus. Only a few of the premaxillary teeth are preserved anteriorly, these being relatively strong and conical, with no canines. The maxilla is only partially preserved. The lower jaw is moderately deep; its length is 2.3 times shorter than HL. The dentary is V-shaped and has a deep indentation for the insertion of the angulo-articular. The symphysis of the dentaries is oblique and not deep. The oral border of the dentary bears moderately small sharp conical teeth apparently arranged in a single row; the anterior teeth are not stronger than the others. The tips of the tooth crowns are darkened. The angulo-articular is an elongate relatively strong bone. The lateral line

sensory canal is traceable through both the angulo-articular and dentary. The bones of the suspensorium are only fragmentarily preserved. The quadrate is subtriangular in outline and very wide, it is thickened from the condyle along the postero-ventral margin. The symplectic is narrow and elongate. The limits of the pterygoid bones are unclear. The opercular region is relatively wide; its bones are not clearly recognizable. The preopercle is only slightly curved, with the lower branch longer than the upper one; there is no evidence of serrations along the posterior and lower margins of this bone. The hyoid bar seems to be relatively short, but it is indistinctly outlined. The branchiostegal rays are not recognizable other than by their unclear imprints on the matrix. The branchial skeleton is completely hidden by the opercular bones. The pharyngeal jaws are certainly hypertrophied; the pharyngeal teeth are large, blunt, and conical.

Axial skeleton. The vertebral column consists of 26 (9+17) vertebrae, including the urostyle. The axis of the vertebral column of the holotype is curved for taphonomic reasons, being convex ventrally. The vertebral centra are longer than high in lateral view and constricted in the middle. The length of the caudal portion of the vertebral column is twice as long as that of the abdominal portion of the vertebral column. The vertebral spines are moderately long, straight or slightly curved, and usually slender (anterior three neural spines somewhat thickened). The neural spine of the first vertebra seems to be reduced, as in many labrid taxa (see RUSSELL, 1988; GOMON, 1997). Well-developed parapophyses are clearly recognizable in the six posterior abdominal vertebrae; they increase in length posteriorly in the series. The haemal spines of the several anterior caudal vertebrae are longer than the opposite neural spines. There are probably seven pairs of pleural ribs. The posterior ribs are slender and relatively short; these are incompletely preserved. The first pair of pleural ribs is the strongest and associated with the third vertebra. Epineurals are not preserved.

Caudal fin and skeleton. The caudal skeleton has the typical labrid structure. The urostyle is characterized by the fusion of the centrum PU1 to the centra U1 and U2; it is completely fused to the uroneural, forming a solid block ankylosed to the fused hypurals 3 and 4. Hypurals 1 and 2 are fused into a roughly triangular hypaxial hypural plate. The reduced fifth hypural seems to be autogenous. There is a deep hypural diastema between the epaxial and hypaxial plates. The parhypural is autogenous; it apparently

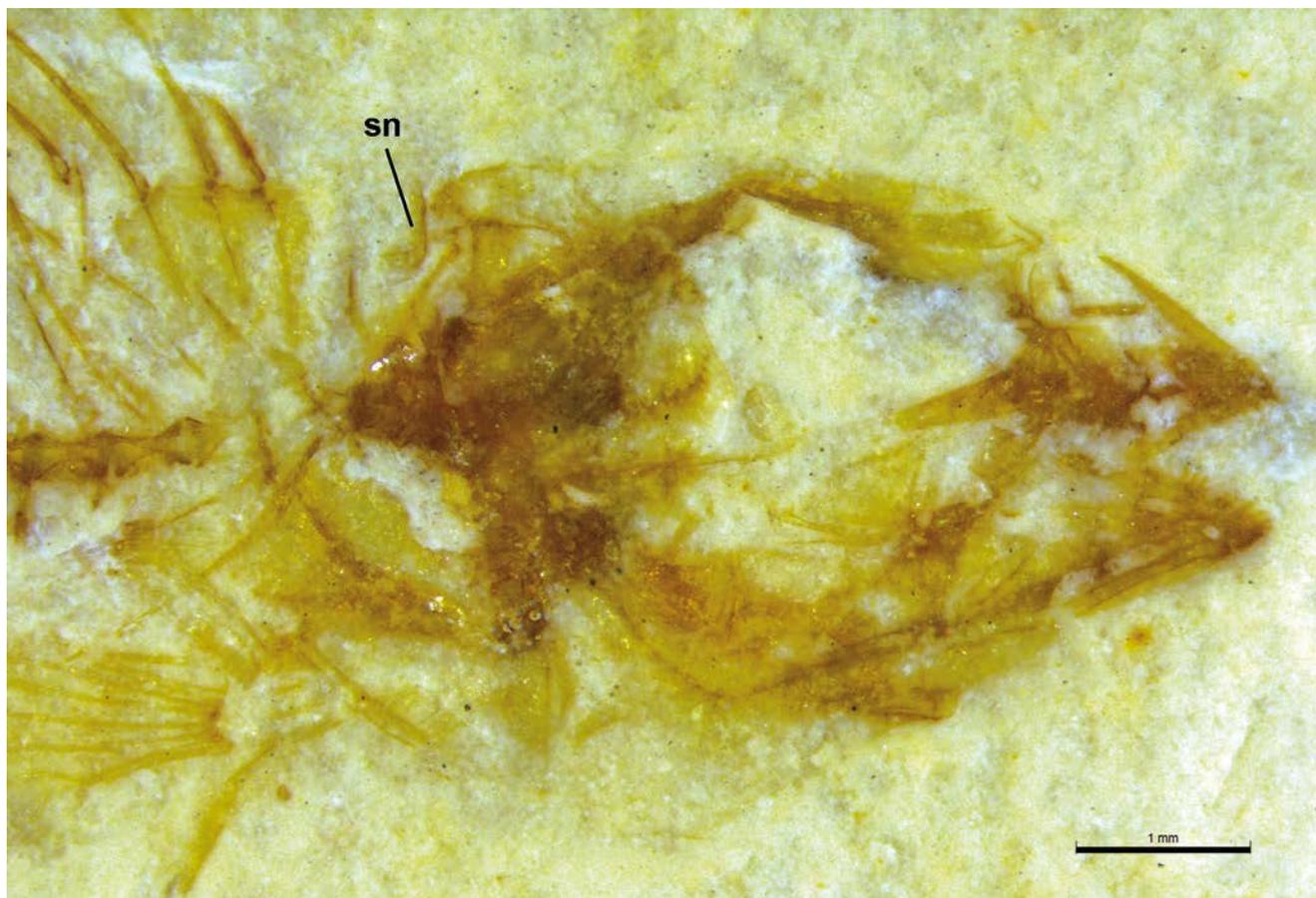


Fig. 2 – *Paralabrus rossiae* gen. et sp. nov., head and anterior portion of body of holotype MCSNV VR 27624, specimen moistened with alcohol to improve contrast; Lower Eocene of Bolca in northern Italy, Pesciara: **sn** – putative supraneural

lacks a parhypurapophysis. The haemal spine of the penultimate vertebra is autogenous, while that of the antepenultimate vertebra seems to be fused to the centrum. The neural spine of the PU2 vertebra has a short rhomboid crest. There seem to be two epurals, the first of which is longest. The caudal fin is moderately large and rounded; it consists of 15 principal rays (I,7-6,I), plus five upper procurrent rays (total complement of lower procurrent rays unknown). The caudal-fin length is about 24% SL.

Supraneural and dorsal fin. The supraneural is not present in its natural position antero-dorsally in front of the distal tip of the second neural spine. However, one can presume that a small slender curved bone situated at the occiput of the holotype (Fig. 2) could represent a supraneural displaced from its natural position. The dorsal fin is relatively short-based; its extension is about 36% of the body length. The dorsal fin is continuous and originates above the posterior portion of the third vertebra.

The first and second dorsal-fin pterygiophores are located between the neural spines of the second and third vertebrae, i.e., in the second interneural space. The dorsal fin has eight very slender spines and seven soft segmented rays, supported by 14 pterygiophores. The 12th pterygiophore and a supernumerary ray associated with it are displaced post-mortem into the anterior portion of the dorsal fin (Fig. 1); these are not shown in the reconstruction of the skeleton (Fig. 3). The first dorsal-fin spine is in supernumerary association on the first dorsal-fin pterygiophore; the first spine is incomplete apically. The completely preserved dorsal-fin spines have approximately the same length, being about 1.6 times shorter than the base length of the dorsal fin. It remains unknown if the dorsal-fin soft rays are longer than the spines or not. The first three dorsal-fin pterygiophores are broad and wedge-shaped, with a longitudinal strengthening ridge laterally; the succeeding pterygiophores of the dorsal

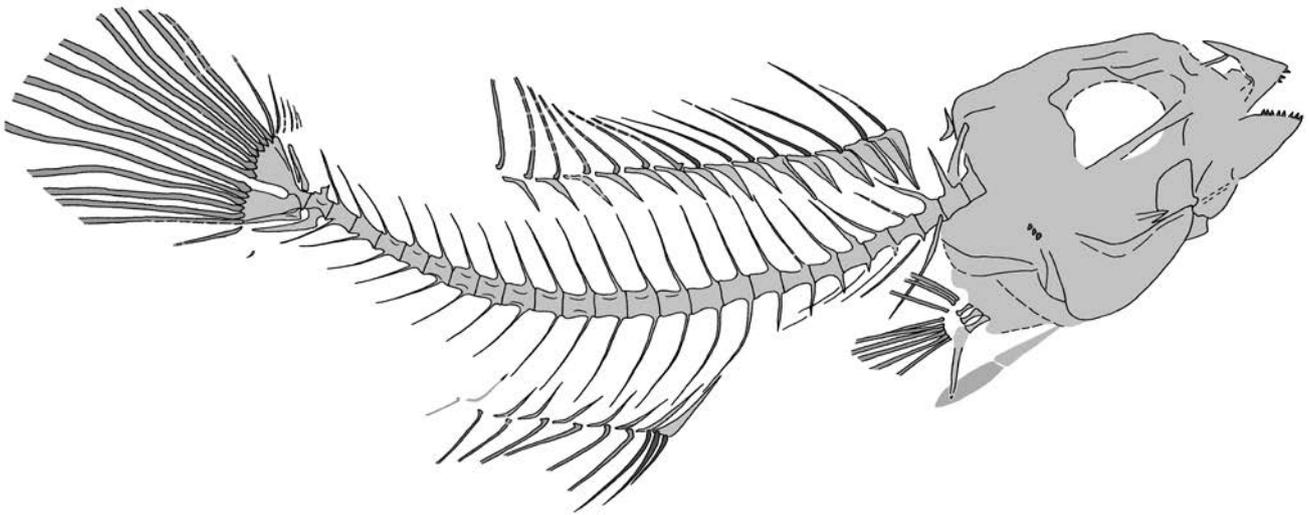


Fig. 3 – *Paralabrus rossiae* gen. et sp. nov., reconstruction of the skeleton based on the holotype

fin are narrower. Each of the eight dorsal-fin pterygiophores bears a spine in supernumerary association, and eighth pterygiophore additionally bears a serially associated first soft ray. The pterygiophores of the soft portion of the dorsal fin seem to be narrower than those of the spiny portion of the dorsal fin. The number of dorsal-fin pterygiophores corresponds to the number of neural spines below them. The dorsal fin terminates above the ninth or 10th caudal vertebra.

Anal fin. The anal fin originates just below the third caudal vertebra; it is relatively short-based. The anal fin consists of three graduated spines and evidently seven segmented rays, supported by eight pterygiophores; the first two anal-fin spines are supernumerary. The last anal-fin ray is not preserved in its natural position; however, the preserved proximal end of the eighth anal pterygiophore makes it possible to restore the presence of the seventh anal-fin ray in its natural position. The longest anal-fin spine is only slightly shorter than the longest dorsal-fin spine. The anal-fin spines are slender, with the third spine 1.8 times longer than the first spine. The longest anal-fin rays seem to be shorter than the third anal-fin spine, but they are probably incomplete distally. The first anal-fin pterygiophore is moderately long, narrow and wedge-shaped; its shaft is strongly inclined to the body axis and precedes the first haemal spine. The succeeding anal-fin pterygiophores are even narrower. The interhaemal spaces above the anal fin have the ventral shafts of one pterygiophores present.

Pectoral fin and girdle. The pectoral girdle is somewhat displaced from its natural position; most of its bones are scarcely recognizable, partly because they are obscured by the displaced pelvic bones. The posttemporal has a strong and long upper branch. The cleithrum is large and elongate. The ventral postcleithrum is slender and rib-like. The limits of the coracoid and scapula are scarcely recognizable. The pectoral radials are hourglass-shaped and elongate; these are oriented posteriorly. The three preserved pectoral radials increase in length downward in the series. The base of the pectoral fin is relatively narrow, located under the fifth vertebra. The pectoral fin contains not less than nine relatively short rays. Perhaps several more pectoral-fin rays were not preserved.

Pelvic fin and girdle. The basypterygium and the pelvic fin are displaced dorsally and poorly distinguishable, being partly obscured by the pectoral fins and girdles.

Squamation. The scales and lateral line are scarcely recognizable.

No pigmentation is traceable.

Measurements. The skeleton of the holotype is somewhat curved; its restored SL is 16.2 mm.

DISCUSSION

Paralabrus gen. nov. is characterized by a unique mosaic of characters, including labrid synapomorphies [such as oligomerization of the caudal skele-

ton and pharyngognathy (STIASSNY and JENSEN, 1987), and the first dorsal-fin pterygiophore located in the second rather than third interneural space]. However, the most useful labrid synapomorphy, a single supraneural, is only presumed to be present: we regard a small slender curved bone situated at the occiput as a putative supraneural displaced from its natural position (there are also some displacements within the dorsal and pelvic fins). All of the other characters of *Paralabrus* gen. nov. are within the norms present in the Labridae, although a combination of its meristic features is unique and justifies the establishment of a new genus. According to a list of meristic features of the genera within the Labridae (BANNIKOV and BELLWOOD, 2015, Table 1), wrasses very rarely have the 26 vertebrae that characterize *Paralabrus* gen. nov. However, the genera *Oxyjulis* and *Ophthalmolepis* (with 26 vertebrae) strongly differ from *Paralabrus* in other respects and cannot be regarded as related to the new genus. The possession of eight dorsal-fin spines is also unusual for the Labridae, which usually have nine or more dorsal-fin spines. Among the known wrasses eight dorsal-fin spines is the characteristic of only three genera of the tribe Julidini: *Gomphosus*, *Minilabrus* and *Thalassoma*. (The Eocene Bolca wrasse *Zorzinilabrus furcatus* has even fewer, with only seven dorsal-fin spines: BANNIKOV and BELLWOOD, 2017). The soft dorsal- and anal-fin ray counts (seven in both fins) are also among the minimal recorded for the Labridae. Such counts can be found as a variation in several genera of the tribe Labrini (BANNIKOV and BELLWOOD, 2015, Table 1). Finally, the dorsal- and anal-fin spines of *Paralabrus* gen. nov. are weaker than in most other labrids, although they are relatively stronger than flexible spines of *Zorzinilabrus furcatus* (BANNIKOV and BELLWOOD, 2017).

BELLWOOD *et al.* (2019) recently published an important comprehensive review of the fossil record of the Labridae, but they did not include (overlooked?) the mid-Miocene *Symphodus salvus* from northern Moldova (BANNIKOV, 1986, 2010). BELLWOOD *et al.* (2019) noted that the fossils of the labrid tribe Hypsi- genyini are particularly abundant, having its earliest record in the Ypresian of Bolca (*Phyllopharyngodon*), "... followed by the major expansion in the Miocene and pan-tropical distributions today" (BELLWOOD *et al.*, 2019: 178). Unlike *Phyllopharyngodon*, all the other genera of Bolca wrasses cannot be unambiguously placed in any of the presently recognized labrid tribes (BANNIKOV and BELLWOOD, 2015; BELLWOOD *et al.*, 2019), although *Eocoris* resembles

certain Julidini in many respects (BANNIKOV and SORBINI, 1991). *Paralabrus* gen. nov. is also somewhat similar to certain julidines, except for its low soft dorsal- and anal-fin ray counts.

The diminutive size of the holotype of *Paralabrus rossiae* gen. et sp. nov. indicates that it represents a not completely adult fish. We regard it as a young adult, because it lacks any larval characters: e.g., its head is not enlarged as would be expected in a larva.

Labroid fishes usually have been regarded as a suborder in the order Perciformes based on a single complex of functionally related characters, mostly in the pharyngeal region. The limits and composition of this group have been relatively unstable (see discussion in BANNIKOV, 2019; this volume). In the latest publications, the Labroidei tends to be regarded as the order Labriformes (WILEY and JOHNSON, 2010; NELSON *et al.*, 2016).

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LITERATURE CITED

- BALDWIN C.C., JOHNSON G.D., 1993. Phylogeny of the Epinephelidae (Teleostei: Serranidae). *Bulletin of Marine Science*, 52 (1): 240-283.
- BANNIKOV A.F., 1986. The first discovery of fossil wrasses (Teleostei) in the Sarmatian deposits of Moldavia. *Paleontological Journal*, 20 (1): 57-62.
- 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., 2010. *Fossil Vertebrates of Russia and Adjacent Countries. Fossil Acanthopterygians Fishes (Teleostei, Acanthopterygii)*. GEOS, Moscow: LXI+244 pp. [In Russian].

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: 19-30; this volume.

BANNIKOV A.F., BELLWOOD D.R., 2014. A new genus and species of pomacentrid fish (Perciformes) from the Eocene of Bolca in northern Italy. *Miscellanea Paleontologica n. 12. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 15: 7-14.

BANNIKOV A.F., BELLWOOD D.R., 2015. A new genus and species of labrid fish (Perciformes) from the Eocene of Bolca in northern Italy. *Miscellanea Paleontologica n. 13. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 16: 5-16.

BANNIKOV A.F., BELLWOOD D.R., 2017. *Zorzinilabrus furcatus*, a new genus and species of labrid fish (Perciformes) from the Eocene of Bolca in northern Italy. *Miscellanea Paleontologica n. 15. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 18: 5-14.

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 (2): 201-220.

BANNIKOV A.F., CARNEVALE G., 2012. *Frippia labroiformis* n. gen. n. sp., a new perciform fish from the Eocene of Pesciara di Bolca, Italy. *Bollettino della Società Paleontologica Italiana*, 51 (3): 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 (1): 13-22.

BANNIKOV A.F., SORBINI L., 1990 (1991). *Eocoris bloti*, a new genus and species of labrid fish (Perciformes, Labroidei) from the Eocene of Monte Bolca, Italy. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 133-148.

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., 1990 (1991). A new fossil fish *Phyllopharyngodon longipinnis* gen. et sp. nov. (family Labridae) from the Eocene, Monte Bolca, Italy. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 149-160.

BELLWOOD D.R., 1992 (1995). A new Eocene fossil fish, *Sorbinia caudopunctata* gen. et sp. nov., from Monte Bolca, Italy. *Bollettino del Museo Civico di Storia Naturale di Verona*, 19: 461-474.

BELLWOOD D.R., 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs*, 15: 11-19.

BELLWOOD D.R., 1999. Fossil pharyngognath fishes from Monte Bolca, Italy, with a description of a new pomacentrid genus and species. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 8: 207-217.

BELLWOOD D.R., SCHULTZ O., SIQUEIRA A.C., COWMAN P.F., 2019. A review of the fossil record of the Labridae. *Annalen des Naturhistorischen Museums in Wien, Serie A*, 121: 125-193.

BELLWOOD D.R., SORBINI L., 1996. A review of the fossil record of the Pomacentridae (Pisces: Labroidae) with a description of a new genus and species from the Eocene of Monte Bolca, Italy. *Zoological Journal of the Linnean Society*, 117: 159-174.

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. *et al.* (Editors), *The Bolca Fossil-Lagerstätten: A window into the Eocene World. Rendiconti della Società Paleontologica Italiana*, 4: 37-63.

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.

GOMON M.F., 1997. Relationships of fishes of the labrid tribe Hypsigenyini. *Bulletin of Marine Science*, 60 (3): 789-871.

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.

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.

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., 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.

RUSSELL B.C., 1988. Revision of the fish genus *Pseudolabrus* and allied genera. *Records of the Australian Museum*, Suppl. 9: 1-72.

SORBINI L., BOSCAINI E., BANNIKOV A.F., 1990 (1991). On the morphology and systematics of the Eocene fish genus *Tortonesia* Sorbini from Bolca. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 115-132.

STIASSNY M.L.J., JENSEN J.S., 1987. Labroid interrelationships revisited: morphological complexity, key

innovations, and the study of comparative diversity. *Bulletin of the Museum of Comparative Zoology*, 151: 269-319.

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. In: Nelson J. S., Schultze H.-P., Wilson M. V. H. (Editors), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. Friedrich Pfeil, München: 123-182.

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