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†*Pavarottia astescalpone* sp. nov., a new percoid fish (Perciformes s.l.) from the Eocene of Bolca, northern Italy, representing a new extinct family

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ABSTRACT

A new species of the percoid fish genus †*Pavarottia* (Perciformes s.l.), †*P. astescalpone*, is described based on a single skeleton from the Eocene locality of Bolca (Monte Postale site) in northern Italy. This is the third species of the genus †*Pavarottia* Bannikov & Zorzin, 2011 recorded from Bolca. †*Pavarottia astescalpone* sp. nov. differs from the type species of the genus, †*P. lonardonii* Bannikov & Zorzin, 2011 (from the same Monte Postale site), in having: a less deep body with a shallower head; and somewhat shorter spines in both the unpaired and pelvic fins. At the same time, the new species differs from †*P. maiseyi* Bannikov, 2016 (from the Pesciara cave site), in having its fifth dorsal-fin spine longer than the last spine and by its shorter base length of the soft dorsal fin. Additionally, the new species has one more dorsal-fin spine and more numerous anal-fin rays than recorded for both †*P. lonardonii* and †*P. maiseyi*, and a smaller orbit. The new monotypic percoid family †Pavarottiidae is established to accommodate the genus †*Pavarottia*.

Key words: Perciformes, †*Pavarottia*, new species, new family, Eocene, northern Italy, Bolca locality.

RIASSUNTO

Una nuova specie di pesci percoidi del genere †*Pavarottia* (Perciformes s.l.), †*P. astescalpone*, è descritto sulla base di un unico scheletro proveniente dalla località eocenica di Bolca (giacimento di Monte Postale) nell'Italia settentrionale. Questa è la terza specie del genere †*Pavarottia* Bannikov & Zorzin, 2011 registrata a Bolca. *Pavarottia astescalpone* sp. nov. differisce dalla specie tipo del genere, †*P. lonardonii* Bannikov & Zorzin, 2011 (dallo stesso sito del Monte Postale), nell'avere un corpo meno alto con una testa più bassa, spine un po' più corte in entrambe le pinne spaiate e pelviche. Allo stesso tempo, la nuova specie differisce da †*P. maiseyi* Bannikov, 2016 (dal giacimento della Pesciara), nell'avere la quinta spina dorsale della pinna dorsale più lunga dell'ultima spina dorsale e per una più corta base della pinna dorsale morbida. Inoltre, la nuova specie ha una spina dorsale in più della pinna e raggi della pinna anale più numerosi di quelli registrati per entrambi i †*P. lonardonii* e †*P. maiseyi* e un'orbita più piccola. Viene istituita una nuova famiglia di percoidi monotipici †Pavarottiidae per accogliere il genere †*Pavarottia*.

Parole chiave: Perciformi, *Pavarottia*, nuova specie, nuova famiglia, Eocene, Italia settentrionale, Bolca.

INTRODUCTION

The Eocene marine fishes from Monte Bolca (northern Italy) have been known since the mid-sixteenth century for their extraordinary preservation. The latest lists of the Monte Bolca fishes (Bannikov, 2014; Carnevale et al., 2014) include 238 taxa, among which 222 represent actinopterygians. These numbers have increased subsequently, and now 237 species-level taxa of actinopterygians are recorded from Bolca (forthcoming revisions of certain higher taxa perhaps could reduce this number). The first comprehensive monographic work on these fishes, the "Ittiolitologia Veronese", was published by the Abbot G.S. Volta in 1796. Some years later, Agassiz (1833-1844) published his monumental treatise on comparative paleoichthyology, which was largely based on materials from Monte Bolca. Since that time a rather large number of papers have been devoted to the Monte Bolca fish fauna, based on the thousands of specimens extracted from this locality and now disseminated in museums and research institutes around the world. The fish fauna is strongly dominated by acanthomorphs (more than 190 species), with a diversity foreshadowing that of today (PATTERSON, 1993).

The Eocene acanthomorphs of Bolca were referred to both extant and extinct families (Bannikov, 2014; Carnevale *et al.*, 2014), whereas the systematic positions of 32 genera remain uncertain; most of the latter certainly belong to extinct families. One of these genera, †*Pavarottia* Bannikov & Zorzin, 2011, was recently established as a percoid of uncertain, but perhaps priacanthid, relationships (Bannikov and Zorzin, 2011). Its type species, †*P. lonardonii* Bannikov & Zorzin, 2011, was described based on a single specimen found in 2004 at the Monte Postale site (a few hundred meters across a ravine from the classic Pesciara site) of the Monte Bolca locality. Subsequently, the second species of †*Pavarottia*, †*P. maiseyi* Bannikov, 2016, was described based on five specimens from the Pesciara cave 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.

During the field excavations executed by the staff of the Museo Civico di Storia Naturale di Verona and the Cerato family (Bolca township) in 2021 at the Monte Postale site, among the other materials, the specimen (in part and counterpart) representing the genus †*Pavarottia* was discovered. This specimen is described below as a new species, †*Pavarottia astescalpone*. The morphological peculiarities of the genus †*Pavarottia* justify the establishment of a new monotypic percoid family for it.

Material and methods

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

All extinct taxa are marked with daggers (†) preceding their names.

Comparative material examined:

- †*Pavarottia lonardonii* Bannikov & Zorzin, 2011; MCSNV IGVR71259 (holotype), 48.5 mm SL; Monte Postale site.
- †*Pavarottia maiseyi* Bannikov, 2016; AMNH 9529 (holotype), 51 mm SL; MCSNV T99/T100 (paratype), 48 mm SL; MCSNV T101/T102, 47 mm SL; MCSNV T103/T104, 53 mm SL; MCSNV T105/T106, 57 mm SL; Pesciara cave site.

Abbreviations are as follows:

- *Institutional*:
  AMNH – American Museum of Natural History, New York;
  MCSNV – Museo Civico di Storia Naturale di Verona;
- *Anatomical*:
  cl – cleithrum;
  HL – head length;
  PU – preural vertebra;
  scl – supracleithrum;
  SL – standard length;
  U – ural vertebra.

Systematic description

Order Perciformes
Suborder Percoidei
Family †Pavarottiidae fam. nov.

Diagnosis

Body relatively deep, head rather large (head length 2.6 times in SL). Head length equal to or less than body depth. Supraoccipital crest thin and relatively low. Snout relatively short. Eye large, orbit diameter equal to or exceeds snout length. Mouth relatively wide, terminal. Ascending premaxillary process short. Jaw teeth small, conical. Lower jaw articulation at a level behind middle of orbit. Opercular region narrow. Vertebrae 28 (11 + 17); four posterior abdominal vertebrae with strong parapophyses. Pleural ribs moderately long. Hypurals unfused. Two supraneurals. Dorsal fin single, relatively long-based; soft part being as long as spinous part or slightly shorter. Dorsal fin with 11 to 12 strong spines and 15 to 16 soft rays. First dorsal-fin pterygiophore precedes neural spine of second vertebra. Anal fin with three spines and 12 to 14 soft rays. Anal fin base of moderate length. Dorsal and anal fins form rounded lobes posteriorly. Pectoral fins attached relatively low. Pelvic fins long, situated below pectorals or slightly anteriorly. Caudal fin truncate to slightly concave, with 17 principal rays. Scales moderately large, cycloid.

Type genus
†*Pavarottia* Bannikov & Zorzin, 2011, by monotypy and original designation.

Genus †*Pavarottia* Bannikov & Zorzin, 2011

†*Pavarottia*: Bannikov and Zorzin, 2011: 19; Bannikov, 2016: 6.

Diagnosis
Coincides with the diagnosis of the family.

Type species
†*Pavarottia lonardonii* Bannikov & Zorzin, 2011, by monotypy and original designation.

Composition
Type species, †*P. maiseyi* Bannikov, 2016 and †*P. astescalpone* sp. nov. from the Lower Eocene of Italy.

†*Pavarottia astescalpone* sp. nov.

Figures 1-3

Diagnosis
A species of the genus †*Pavarottia* which differs from both †*P. lonardonii* and †*P. maiseyi* in having: one more dorsal-fin spine and one less dorsal-fin soft ray than recorded for both †*P. lonardonii* and †*P. maiseyi*, more numerous anal-fin soft rays (14 rays vs. 12 rays in †*P. lonardonii* and 13 rays in †*P. maiseyi*), and smaller eye (orbit diameter 11.5% of SL vs. 14-15% of SL in †*P. maiseyi* and 17% of SL in †*P. lonardonii*). The new species also differs from †*P. lonardonii* in having a less deep body (maximum body depth 0.39 of SL vs. 0.51 of SL in †*P. lonardonii*) with shallower head and somewhat shorter spines in both the unpaired and pelvic fins. The new species differs from †*P. maiseyi* in its fifth dorsal-fin spine being longer than the last spine (vs. the last dorsal-fin spine longest in †*P. maiseyi*), larger lower jaw, and shorter base length of its soft dorsal fin (which is 19% SL vs. 25% SL in †*P. maiseyi*).

Etymology
The species is dedicated to the Associazione Temporanea di Scopo (AsTeSc) “Val d’Alpone – faune, flore e rocce del Cenozoico”, which in 2021 obtained the inclusion of the Eocene paleontological localities of the Alpone Valley and upper Chiampo Valley into the Italian UNESCO Tentative List.

Holotype
MCSNV 21.702/21.703, part and counterpart, complete articulated skeleton, 44 mm SL (Fig. 1).

Referred specimens
None.

Type locality and horizon
North-eastern Italy, Bolca locality, Monte Postale site; upper part of the Lower Eocene, upper Ypresian, about 50 Ma (Papazzoni *et al.*, 2014).

Description
The body is relatively deep, with a shallow and relatively short caudal peduncle. The caudal peduncle depth is ca. 25% of the body depth. The head is relatively large; its length equal to the body depth. The head length is contained 2.6 times in SL. The dorsal profile of the body is almost as equally convex as the ventral profile of the body.

Head. The length of the head only slightly exceeds its depth. The orbit is moderately large; the diameter of the orbit almost equals the snout length and is contained about 3.5 times in HL. There are sclerotic ossifications in the orbit. Traces of the eyeball are preserved as a thin carbonaceous film. The mouth is wide, oblique and terminal; the lower jaw articulation is situated at a level behind the middle of the orbit. The neurocranium depth is almost 1.7 times less than its length; the moderate ovoid otolith is outlined in the otic bulla region. The frontals form the upper margin of the orbit and overhang the ethmoids. The pterotic forms a longitudinal ridge in the upper portion of the neurocranium. The thin and low supraoccipital crest is only partially preserved. The ethmoid region is evidently short; the lateral ethmoids form the anterior border of the orbit, whereas the mesethmoid has a rounded anterior margin. The parasphenoid is exposed in the lowermost portion of the orbit as a slender, stout, only slightly curved shaft. The parasphenoid has a flattened dorsal surface and no prominent ventral flange. None of the infraorbital bones are preserved except for faint remains. The premaxilla has a very short pointed ascending process and a wide articular process. The premaxillary teeth are very poorly preserved in the material examined, but these are definitely very small and conical. The maxilla has a relatively narrow shaft and an expanded distal end.

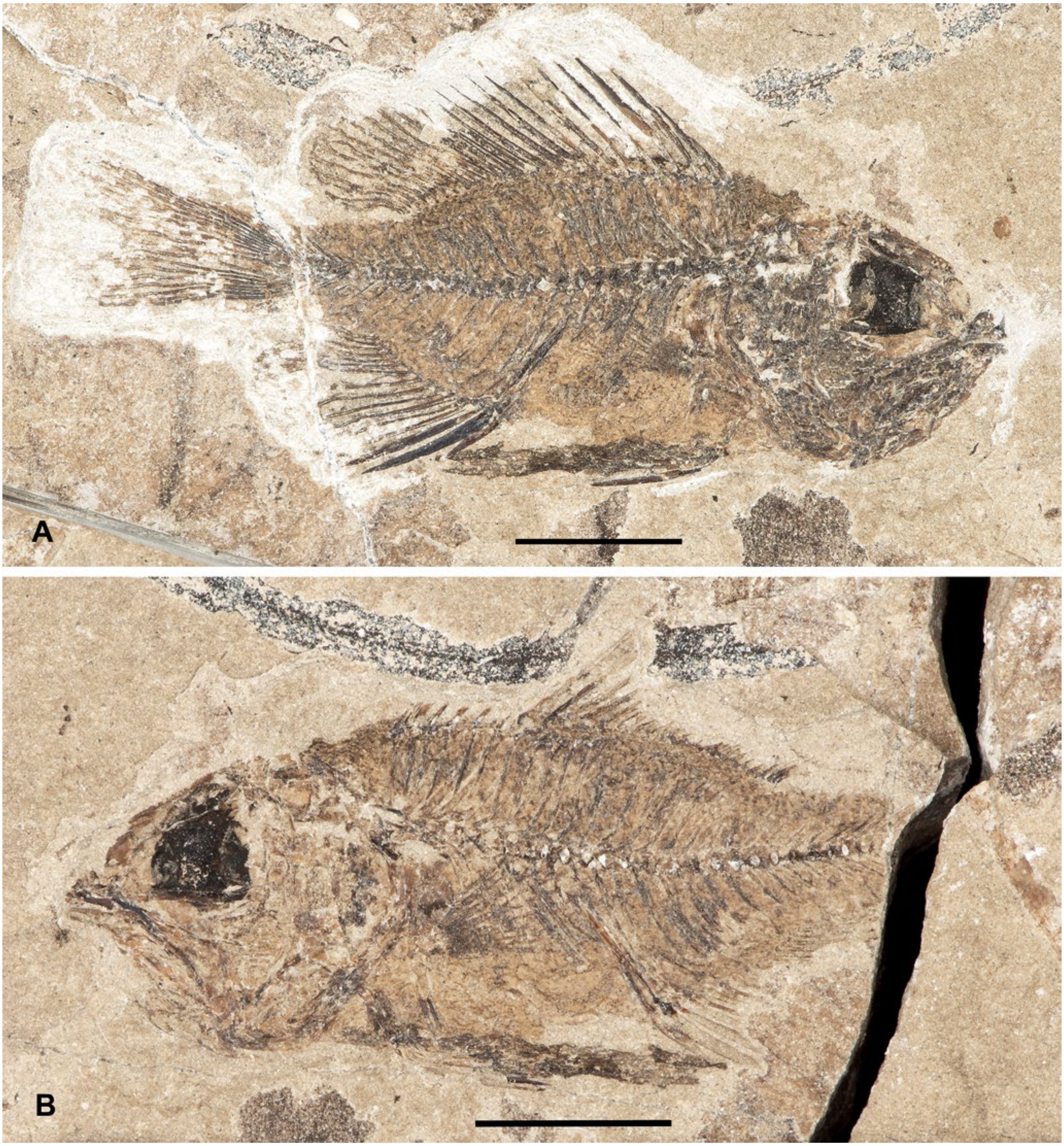

Fig. 1 – †*Pavarottia astescalpone* sp. nov., general view of holotype: **A** – MCSNV 21.702, **B** – MCSNV 21.703; Lower Eocene of Bolca in northern Italy, Monte Postale. Scale bar: 1 cm

No supramaxilla is evident. The lower jaw is relatively long; its length is about 69% of HL. The dentary occupies the anterior half of the lower jaw; it is remarkably shallow near its symphysis. Posteriorly the dentary is deeply notched. Only some of the lower jaw teeth are preserved; these are very small and conical. The angulo-articular is large; it fits tightly into the notch of the dentary. The hyomandibular shaft is almost vertical; the anterodorsal (for sphenotic) and extended dorsal (for pterotic) condyles of the hyomandibular head are recognizable in the MCSNV 21.702 counterpart. Among the pterygoids, the flat endopterygoid (mesopterygoid) is relatively well recognizable, extending below the orbit. The quadrate is evidently narrow and triangular in shape. The opercular region is relatively narrow. The preopercle is apparently slightly curved and bears short and flat serrations, as evidenced by MCSNV 21.703. The hyoid bar and branchial bones are mostly indistinguishable; although several relatively short branchiostegal rays are partially traceable; their total complement is unknown. Some pharyngeal teeth are recognizable in MCSNV 21.702; these are blunt and both big and smaller.

Axial skeleton. There are 28 vertebrae, eleven abdominal and seventeen caudal, including the urostyle. The vertebral column is slightly curved and elevated anteriorly. The vertebral centra are shortened anteroposteriorly, and bear a longitudinal ridge on the lateral surface. The length of the caudal portion of the vertebral column is 1.75 times greater than the length of the abdominal portion of the vertebral column. The neural spines of the anterior abdominal vertebrae are widened anteroposteriorly (especially those of the third to sixth vertebrae), whereas all the other neural spines are slender, both posteriorly in the abdominal region and in the caudal region. Among the thickened neural spines the fourth is the longest; subsequently, a few spines of the abdominal vertebrae decrease in length, and then increase in length again posteriorly in the series. In addition to the fourth spine, the longest neural spines are those of the anterior caudal vertebrae. The haemal spines of the caudal vertebrae are relatively long, slender and pointed. The neural spines of the anterior caudal vertebrae are shorter than the corresponding haemal spines. The last three or four abdominal vertebrae have prominent parapophyses which rapidly become longer posteriorly in the series. Most of the pleural ribs are moderately long and slender, and moderately inclined posteriorly; a few of the anterior ribs are stronger and attached high to the vertebral centra. As evidenced by the MCSNV 21.703 counterpart, the first pair of ribs is attached to the first vertebra; thus, there are a total of 11 pairs of ribs. The ribs occupy the upper half of the abdominal cavity. A few epineurals are distinguishable below the abdominal centra.

Pectoral fin and girdle. The pectoral-fin base is situated slightly closer to the vertebral column than to the ventral profile of the body, below the sixth vertebra. The pectoral fin is best seen in MCSNV 21.703; at least 12 moderately long pectoral-fin rays are recognizable. The posttemporal is evidently forked; its upper branch is easier to recognize than is the lower branch. The elongated supracleithrum bears two short retrorse spines, as evidenced by MCSNV 21.703 (Fig. 2). The cleithrum is large and mostly straight, being curved anteriorly in its upper portion; it has an extended posterodorsal projection above the pectoral-fin base. The ventral postcleithrum is robust, wedge-like in shape and pointed distally; it is oriented posteroventrally close to a vertical line. The dorsal postcleithrum seems to be recognizable in MCSNV 21.702 in the ventral portion of a posterodorsal projection of the cleithrum; it has a pointed anterodorsal process. The coracoid is relatively small; there is evidently a gap between the coracoid and cleithrum. The pectoral radials are poorly recognizable; these are slightly constricted in the middle.

Pelvic fin and girdle. The pelvic bones are relatively short and rather broad ventrally. The basipterygium extends anterodorsally to the cleithrum at an angle of ca. 57% to the body axis. The pelvic fin is very long; it is inserted anterior to the pectoral-fin base. There are five soft rays in each pelvic fin, in addition to the rather strong smooth pelvic-fin spine. The pelvic-fin spine is almost as long as the last dorsal-fin spine. The distal end of the pelvic fin reaches to far behind the anal-fin origin.

Supraneurals and dorsal fin. There are two relatively short and very slender supraneurals (predorsal bones); both supraneurals are situated behind the upper tip of the neural spine of the first vertebra.

The dorsal fin is relatively long-based and continuous, with no indentation or space between the spiny and soft parts. The origin of the dorsal fin is above the third vertebra. The spiny part of the dorsal fin consists of 12 smooth spines; the first spine is shortest and the fifth or sixth spine is longest. The second dorsal-fin spine is 2.5 times, and the last spine 1.1 times, shorter than the fifth spine. The dorsal-fin spines are relatively stout. The longest spine is 1.17 times shorter than the length of the base of the

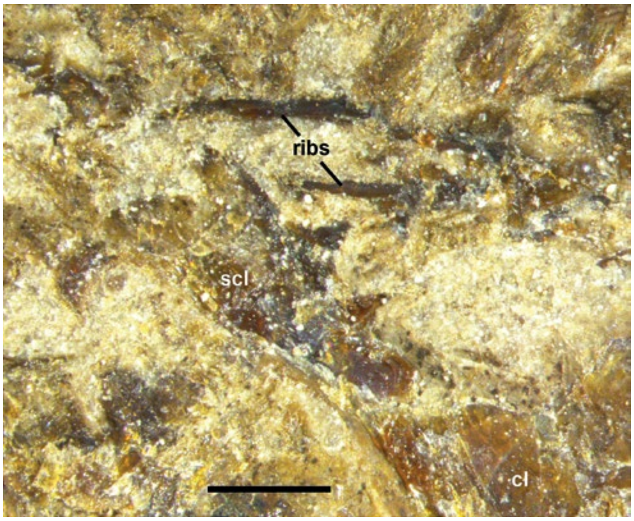

Fig. 2 – †*Pavarottia astescalpone* sp. nov., holotype MCSNV 21.703, supracleithrum and anterior ribs; Lower Eocene of Bolca in northern Italy, Monte Postale. Scale bar: 1 mm

spiny dorsal fin. The first two spines are in non-serial secondary association (supernumerary) with the first dorsal-fin pterygiophore, which precedes the neural spine of the second vertebra. The predorsal formula (Ahlstrom *et al.*, 1976; Johnson, 1984) is /0+0+2/1+1/. The soft part of the dorsal fin consists of 15 segmented rays. The dorsal-fin soft rays are branched and segmented distally. The anterior dorsal-fin soft rays are almost equal in length; after that the rays at first gradually, then more rapidly, decrease in length posteriorly in the series; thereby, the fin is rounded posteriorly. The length of the base of the soft dorsal fin is almost 1.3 times shorter than the length of the base of the spiny dorsal fin. The dorsal fin ends above the transition between the 10th and 11th caudal vertebrae. The pterygiophores of the dorsal fin penetrate down into the interneural spaces, with all the interneural spaces below the spiny dorsal fin having the ventral shaft of a single pterygiophore present, except for the second interneural space, which accommodates two pterygiophores. Few of the pterygiophores of the dorsal-fin soft rays are somewhat displaced post-mortem; however, it is clear that the interneural spaces below the soft dorsal fin have the ventral shafts of one or two pterygiophores present. The pterygiophores of the dorsal-fin spines are wide in lateral aspect whereas the pterygiophores of the dorsal-fin soft rays are narrower; the pterygiophores decrease in length posteriorly in the series. The dorsal-fin pterygiophores become more strongly inclined posteriorly in the series. The medial and proximal pterygiophores seem to be fused to one another, and each pterygiophore shaft bears a longitudinal strengthening ridge.

Anal fin. The anal fin originates below the fourth caudal vertebra; the length of the base of the anal fin slightly exceeds the length of the base of the soft part of the dorsal fin. The anal fin has three strong smooth spines and 14 soft rays. The second anal-fin spine is only slightly shorter than the third spine, which is the longest, almost 2.4 times longer than the shortest (first) spine. The first two anal-fin spines are supernumerary. The anterior anal-fin soft rays seem to slightly increase in length; after that the rays at first gradually, then more rapidly, decrease in length posteriorly in the series; thereby, the fin is rounded posteriorly. The anal fin ends under the 11th caudal vertebra. The first pterygiophore of the anal fin is strong and the longest; it is inclined obliquely posteriorly at an angle of ca. 55% to the body axis. The anterior border of the first anal-fin pterygiophore is very slightly curved. The distal ends of the anal-fin pterygiophores penetrate up into the interhaemal spaces. The pterygiophores are mostly somewhat displaced post-mortem; however, it is clear that most of the interhaemal spaces above the anal fin have the ventral shafts of two pterygiophores present.

Caudal fin and skeleton. The caudal skeleton is relatively poorly preserved because of a fracture of the matrix lying obliquely through it. The terminal centrum is composed of the fusion of PU1, U1 and U2. The neural spine of PU2 is evidently a short crest. All five hypurals, the parhypural, and the haemal spines of PU2 and PU3 seem to be autogenous. It is unclear if there are two or three epurals, as well as whether a second uroneural is present in addition to the stegural. The caudal fin is moderately long and either slightly concave or truncate posteriorly. There are 17 principal rays in the caudal fin (I,8-7,I) and about seven lower procurrent rays. The number of upper procurrent rays is unknown.

Squamation. The scales are moderately large and relatively thin. The scales appear to be cycloid; no indications of ctenii are evident. The limits of individual scales are scarcely recognizable; therefore the number of the scale rows on the body is unknown. There are both delicate concentric circuli on the scale surface and radii. The scale cover extends to the bases of the dorsal and anal fins, perhaps also to the base of the caudal fin. The lateral line is not evident.

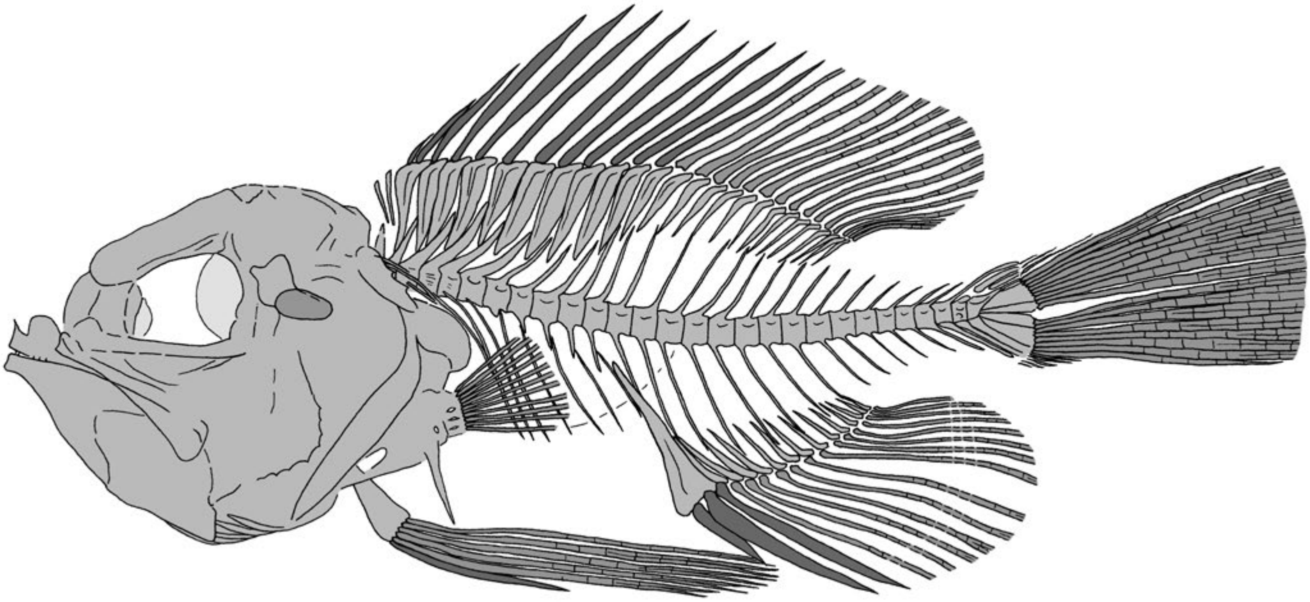

Fig. 3 – †*Pavarottia astescalpone* sp. nov., reconstruction of the skeleton based on holotype, scales omitted

Coloration. Traces of the original pigmentation pattern are preserved throughout the whole body, and on the dorsal, anal, and pelvic fins: these represent numerous small dark spots arranged more or less densely.

Measurements of the holotype, in percent of SL (44 mm) are as follows:

- Head length from tip of snout to anterior border of cleithrum: 39;
- Maximum body depth: 39;
- Depth of caudal peduncle: 9;
- Distance between tip of snout and first dorsal-fin spine: 42;
- Distance between tip of snout and first dorsal-fin soft ray: 67;
- Distance between tip of snout and anal fin: 70;
- Distance between pelvic fin and anal fin: 27.5;
- Length of base of dorsal fin: 44.5;
- Length of base of spiny dorsal fin: 25;
- Length of base of soft dorsal fin: 19;
- Length of base of anal fin: 21;
- Length of first spine of dorsal fin: 4.2;
- Length of second spine of dorsal fin: 8.7;
- Length of fifth spine of dorsal fin: 22;
- Length of last spine of dorsal fin: 20;
- Length of longest soft ray of dorsal fin: 20;
- Length of first spine of anal fin: 9.3;
- Length of longest (third) spine of anal fin: 22;
- Length of longest soft ray of anal fin: 23;
- Length of spine of pelvic fin: 19;
- Length of pelvic fin: 37;
- Length of caudal fin: ca. 28;
- Preorbital distance: 11;
- Horizontal diameter of orbit: 11.5;
- Length of lower jaw: 27.

Discussion

A general overview of the morphology of the new species described above clearly supports its alignment with the genus †*Pavarottia* Bannikov & Zorzin, 2011. The genus †*Pavarottia* was regarded as a percoid of uncertain, but perhaps priacanthid, relationships (Bannikov and Zorzin, 2011). Up to now the genus *Pavarottia* was known based on two Bolca species, †*P. lonardonii* Bannikov & Zorzin, 2011 from Monte Postale, and †*P. maiseyi* Bannikov, 2016 from the Pesciara. Because the genus †*Pavarottia* was represented by only a few relatively poorly preserved specimens, it was thought to be premature to either establish a new family for it or to modify the diagnoses of any of the known percoid families to accommodate this genus (Bannikov, 2016). The holotype of the new species described above is relatively better preserved than the material on which two other species of †*Pavarottia* were based; therefore, we believe that now there are enough data to establish a new monotypic percoid family for the genus †*Pavarottia* (see below).

Like the two previously described species of †*Pavarottia*, †*P. lonardonii* Bannikov & Zorzin, 2011 and †*P. maiseyi* Bannikov, 2016, †*P. astescalpone* sp. nov. has a relatively deep body, large eyes, oblique and wide mouth, small conical teeth, a relatively narrow opercular region, increased vertebral count with the vertebral formula typical for †*Pavarottia* (11+17=28), a caudal skeleton of the generalized percoid type, two small supraneurals, a relatively long-based and continuous dorsal fin with the similar formula (D XII, 15 vs. D XI, 16 in known species), and long pelvic fins. Also, in all three species the dorsal-fin origin is anterior in position, with the first dorsal-fin pterygiophore preceding the neural spine of the second rather than third vertebra. At the same time, †*P. astescalpone* sp. nov. differs from †*P. lonardonii* in a less deep body (maximum body depth 0.39 SL vs. 0.51 SL in †*P. lonardonii*) with a shallower head, a smaller eye (orbit diameter 11.5% SL vs. 17% SL in †*P. lonardonii*), and somewhat shorter spines in both the unpaired and pelvic fins. In these characters †*P. astescalpone* more closely resembles †*P. maiseyi* from the Pesciara than †*P. lonardonii* from the same Monte Postale locality. However, the new species differs from †*P. maiseyi* in some proportions (e.g., length of base of its soft dorsal fin is 19% SL vs. 25% SL in †*P. maiseyi*), larger lower jaw, and its fifth dorsal-fin spine is longer than the last spine (vs. the last dorsal-fin spine longest in †*P. maiseyi*). Additionally, the new species has one more dorsal-fin spine and one less dorsal-fin soft ray than recorded for both †*P. lonardonii* and †*P. maiseyi*, and more numerous anal-fin soft rays (14 rays vs. 12 rays in †*P. lonardonii* and 13 rays in †*P. maiseyi*). If it is not an artifact of preservation, the predorsal formula of †*P. astescalpone* (/0+0+2/1+1/) is different from both †*P. maiseyi* (0/0+2/1+1/) and †*P. lonardonii* (0+0/2/1+1/). The differences listed above strongly justify the establishment of a new species of the genus †*Pavarottia*, the second species of this genus for the Monte Postale site.

A general overview of the morphology of †*Pavarottia* clearly supports its alignment with percoid fishes in their traditional sense. Percoidei, the "largest and most diverse of the perciform suborders is undoubtedly polyphyletic..." (Johnson, 1993, p. 15) and is diagnosed by several features that are plesiomorphic for the Perciformes; this group includes those perciforms that cannot be placed in other suborders. More recently, citing molecular data, many families traditionally included in 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.

As previously mentioned (Bannikov and Zorzin, 2011), the genus †*Pavarottia* especially strongly resembles the percoid family Priacanthidae (catalufas) (see Fitch and Crooke, 1984; Starnes, 1988) in its general physiognomy and in a number of its morphological features. At the same time, †*Pavarottia* lacks such important priacanthid apomorphies (Starnes, 1988) as modified spiny scales (spinoid scales: Roberts, 1993), the reduction of the supraneurals to one or none, the reduction in the vertebral number to 23, the reduction in the principal caudal-fin rays number from the primitive complement of 9+8 to 8+8, and possession of spinules on the fin elements. Additionally, the genus †*Pavarottia* has one to two dorsal-fin spines more than recorded for priacanthids, and the first pair of ribs seem to be attached to the first vertebra rather than to the third as in priacanthids. Unlike the Priacanthidae (with their reduced number of vertebrae), the vertebral count of †*Pavarottia* is somewhat increased from the plesiomorphic percoid number of 24-25 (Gosline, 1968; Johnson, 1984) to 28 (11 + 17). Therefore, †*Pavarottia* cannot be accommodated in the family Priacanthidae.

Bannikov and Zorzin (2011) stated that perhaps †*Pavarottia* is a better candidate for the priacanthid sister group, according to its general appearance and multiple shared characters. However, it is at least equally probably that the Eocene genus is not related to the Priacanthidae and obtained a number of morphological conditions in parallel with catalufas because of the similar mode of life (nocturnal feeders). The earliest articulated skeletal remains of the Priacanthidae consist of a few specimens belonging to the species †*Pristigenys substriata* (Blainville), also from Bolca (see Starnes, 1988; Carnevale *et al.*, 2017).

The vertebral count of †*Pavarottia* gen. nov. is somewhat increased from the plesiomorphic percoid number of 24-25 and is rather unusual for the Percoidei (in its traditional sense). Among 92 extant percoid families and *incertae sedis* genera listed by Johnson (1984: Table 120), only a few acanthoclinids (now regarded as a subfamily of plesiopids: Smith-Vaniz and Johnson, 1990; Nelson, 2006), centrarchids, owstoniine cepolids, girellids, opistognathids, percichthyids and pseudochromids exhibit the vertebral formula of †*Pavarottia* (11+17=28). However, representatives of these families differ greatly from the Eocene genus in many other respects.

Dorsal- and anal-fin formulas of †*Pavarottia* (D XI-XII, 15-16; A III, 12-14) both lie within the ranges recorded in a relatively few percoid groups: families Caesionidae, Centrarchidae, Dinopercidae, Haemulidae, Opistognathidae, Oplegnathidae, Pentacerotidae, Percichthyidae, Plesiopidae, Serranidae, Sinipercidae, and the *incertae sedis* genus *Hapalogenys* (Johnson, 1984: Table 120). None of these groups exhibit such diagnostic features of †*Pavarottia* as, for example, extremely large eyes. Moreover, among these groups only a few pentacerotids and serranids have an anterior shift of the dorsal fin, with the first dorsal-fin pterygiophore present in the first (rather than second) interneural space.

The Eocene *incertae sedis* percoid fish genus †*Bradyurus* from Bolca has vertebral (11+16) and dorsal-fin (XII, 16-17) formulas similar to those of †*Pavarottia* (Bannikov and Zorzin, 2012). However, in other respects †*Bradyurus* differs greatly from †*Pavarottia*, having a longer body, short anal and pelvic fins, smaller mouth with bigger teeth, etc.

Therefore, although the genus †*Pavarottia* is represented by a relatively few specimens grouped into three species, we believe that the morphological peculiarities of this genus support the establishment of a new monotypic percoid family for it.

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