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New generic name for a small Triassic ray-finned fish from Perledo (Italy)

Adriana López-Arbarello^{1,2*} and Rainer Broccke³

Abstract

Our new study of the species originally included in the genus *Allolepidotus* led to the taxonomic revision of the halecomorph species from the Triassic of Perledo, Italy. The morphological variation revealed by the analysis of the type material is sufficient to confirm four different taxa represented in the Perledo Formation. We correct the misunderstanding about the type species of *Allolepidotus*, which is *A. ruppelii* and not "*A. bellottii*" as considered in the literature over the past two decades. The latter species was originally placed in the genus *Semionotus*. Fossils from the Kalkschieferzone of Besnasca/Ca' del Frate (Viggiù-Varese, Italy) and Meride (Ticino, Switzerland) which were referred to *Allolepidotus*, rather represent a species of *Eoeugnathus*. Therefore, we transfer the species *Semionotus bellottii* to that genus and propose the new combination *E. bellottii*. The second and only other species originally included in the genus *Allolepidotus* is transferred here to the new genus *Perledovatus*. The holotype of *P. nothosomoides* new comb. has been mechanically prepared, revealing additional anatomical information that allows to place this taxon in the halecomorph family Subortichthyidae. The other halecomorph species named from the Perledo Formation, *Pholidophorus oblongus* and *Pholidophorus curionii*, have been treated as junior synonyms of *E. bellottii*, but our analysis indicates that they represent distinct separate taxa. However, due to the loss of the type specimens, it is not possible to decide whether they might have been conspecific with other ray-finned fishes from the Middle Triassic of the Alps.

Keywords Middle Triassic, Perledo, Ray-finned fish, Taxonomy

Introduction

The famous black shales of Perledo, Italy, have yielded one of the first known fossil assemblages from the Middle Triassic of the Alps. The first report on Triassic fishes from Perledo is found in Balsamo-Crivelli (1839), including the description of only two fish specimens. From that

very modest beginning, a total of 30 fish species, mostly ray-finned fishes except for one shark and one coelacanth, had been named over the following hundred years (Balsamo-Crivelli, 1839; Bassani, 1886; Bellotti, 1857; De Alessandri, 1910; Deecke, 1889). Unfortunately, most of the type specimens were lost during World War II and many of those taxa remain dubious or placed under synonymy.

The main collection of fishes from the Triassic of Perledo was housed at the Natural History Museum in Milan (MSNM), Italy, but it is completely lost (Lombardo, pers. comm. April 26, 2023). However, a smaller collection of the Perledo fish fauna was brought to Frankfurt am Main, Germany, and is conserved in the fossil vertebrate collection of the Senckenberg Research Institute and Natural History Museum (SMF). The Frankfurt collection ("Rüppel collection") was studied by Deecke (1889) and included 37 specimens, 28 of them survived

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World War II. Within the original collection, Deecke identified several of the species published by Bellotti (1857). However, Deecke referred most of these species to different genera, some of which were newly proposed. Additionally, he described four new taxa.

According to Deecke (1889) and Tintori et al. (1985), specimens collected at Perledo have gone to several museums and private collections. However, only the main collection of the MSNM—which has been completely lost, and the smaller collection of the SMF, have been studied scientifically. The present contribution was triggered by the need to revise the taxonomy of the species of *Allolepidotus* Deecke, 1889, and resulted in the erection of a new genus and the clarification of the taxonomic status of all the halecomorph species from Perledo.

Material and methods

Specimen SMF P1237a was recently mechanically re-prepared at Senckenberg. The specimen was studied under a Leica Wild M3 binocular microscope. At the same time, drawings were made on top of high-quality photographs using an iPad and the Affinity Designer (v. 1.10.24) software.

The relative position of the fins is expressed in a pterygial formula (Westoll, 1944), in which the numbers indicate the number of scale rows between the first complete row behind the pectoral girdle and the insertion of the dorsal (D), pelvic (P), anal (A), and caudal (C) fins respectively, and the caudal inversion (T). The systematic and anatomical nomenclature follows López-Arbarello and Sferco (2018).

Measurements have been taken using the software ImageJ from photographs, as distances between landmarks projected on the longitudinal or sagittal planes as indicated in López-Arbarello (2004).

Institutional abbreviations

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MSNM, Museo di Storia Naturale di Milano, Milan, Italy; PIMUZ, Paleontological Institute and Museum at the University of Zürich, Zürich, Switzerland; SMF, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany.

Morphometric abbreviations

BD, maximal body depth; HL, maximal head length; PreA, preanal length; PreD, predorsal length; PreV, pre-pelvic length; SL, standard length.

Systematic paleontology

Subclass Actinopterygii Cope, 1887

Superdivision Neopterygii Regan, 1923

Subdivision Halecomorphi Cope, 1872

Halecomorphi incertae sedis

Genus *Allolepidotus* Deecke, 1889

1889 *Allolepidotus*—Deecke: p. 113, in part.

1910 *Allolepidotus* Deecke—De Alessandri: p. 115–116, in part.

2001 *Allolepidotus* Deecke, 1889—Lombardo: p. 347–348, in part.

Type species

Pholidophorus ruppelii Bellotti, 1857, fixed by Woodward (1895: p. 315).

Remarks The genus *Allolepidotus* was erected by Deecke (1889) including two species: *Pholidophorus ruppelii* Bellotti, 1857, and *Allolepidotus nothosomoides* Deecke, 1889. Woodward (1895) locked *A. ruppelii* (Bellotti, 1857) as the type species of the genus.

Species *Allolepidotus ruppelii* (Bellotti, 1857)

1857 *Pholidophorus ruppelii* nob.—Bellotti: p. 428.

1886 *Pholidophorus Rüppeli* Bell.—Bassani: p. 63.

1889 *Allolepidotus Rüppeli* Bell. sp.—Deecke: p. 117–118, pl. 6: Fig. 5.

1910 *Allolepidotus Rüppeli* Bell. sp.—De Alessandri, p. 118–120, pl. 8: Fig. 4.

2001 *Pholidophorus rueppelli*—Lombardo: p. 350.

Lectotype

SMF P.1266 (Fig. 1), plaster copy described by Bellotti (1857).

Diagnosis

Although there is little anatomical information preserved in the lectotype, the following combination of features distinguishes the species: BD/SL=0.31; HL/SL=0.24; HL/BD=0.79; PreV/SL=0.48; PreD/SL=0.60; PreA/SL=0.69; (PreD-PreV)/SL=0.11; (PreA-PreD)/SL=0.10; 37 scales along the lateral line; posterior border of scales serrated. Pterygial formula: (D20 / V8 A19 C32) T37.

Remarks According to The Code (ICZN Art. 32.5), the original spelling of the species *Pholidophorus ruppelii* is correct and posterior emendations are unjustified.

Bellotti (1857) named this species for two specimens. The whereabouts of one of them are unknown. The other specimen, which he described, was represented in a plaster

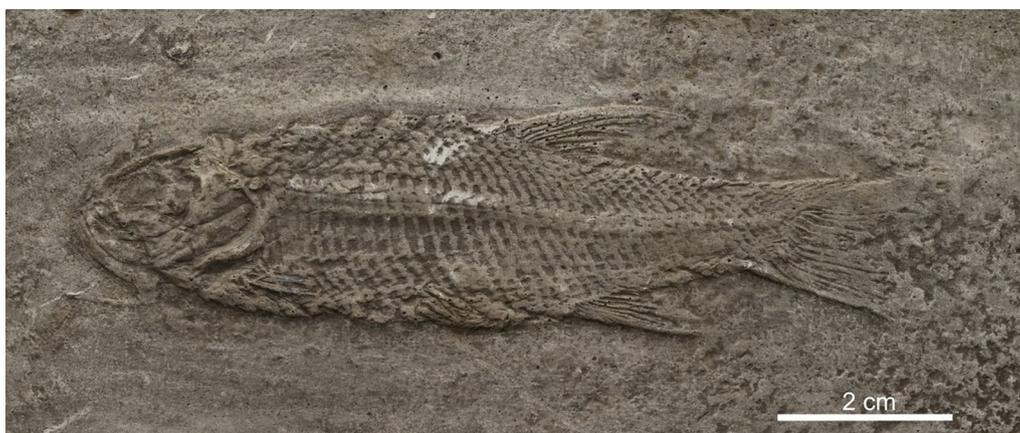


Fig. 1 *Allelepidotus ruppelii* (Bellotti, 1857). Photograph of the lectotype SMF P.1266, a plaster copy described by Bellotti (1857)

copy at the MSNM, which is currently housed in the SMF collection, and is designated here as the lectotype.

Detailed examination of SMF P.1266 does not allow for confirmation of the values given by Bellotti for the numbers of rays and fulcra in the fins. The peculiar shape of the dorsal fin might be an artifact due to incomplete preservation of the original fossil or imperfect replication in the plaster copy. However, the few general features preserved in SMF P.1266 such as the body proportions and relative position of the fins are sufficient to validate the species.

It should be noted that Deecke's description of this species is not based on the cast, but on another specimen that has not been located. Nevertheless, according to the description of this unknown specimen, it is likely that it is a different species than SMF P.1266.

Family Subortichthyidae Feng et al., 2023

Genus *Perledovatus* gen. nov.

Zoobank LSID: urn:lsid:zoobank.org:pub:D861D4F8-89EB-4193-B6A9-598A5EDDA6E2

1889 *Allelepidotus*—Deecke: p. 113, in part.

1910 *Allelepidotus* Deecke—De Alessandri: p. 115–116, in part.

2001 *Allelepidotus* Deecke, 1889—Lombardo: p. 347–348, in part.

Type species

Allelepidotus nothosomoides Deecke, 1889.

Etymology

The generic name *Perledovatus* is formed by 'Perledo', the name of the famous type locality and stratigraphic unit, and 'ovatus' recalling the characteristically oval shape of the body of this fish, especially noticed by Deecke (1889).

Species *Perledovatus nothosomoides* (Deecke, 1889) new comb.

1889 *Allelepidotus nothosomoides* n. sp.—Deecke: p. 118–119, pl. 6: Fig. 9.

1910 *Allelepidotus nothosomoides* Deecke—De Alessandri: p. 116–118, pl. 8: Fig. 7.

2001 *Allelepidotus nothosomoides*—Lombardo: p. 350.

Holotype

SMF P1237a, b. (Fig. 2). The holotype is a complete and rather well-preserved specimen in right lateral view. Unfortunately, it has been damaged and the squamation in the second half of the body and parts of the caudal fin are now lost (compare Fig. 2 with pl. 6, Fig. 9 in Deecke, 1889).

Type locality and horizon

Perledo, Italy. Perledo Member of the Perledo-Varenna Formation; upper Ladinian, Middle Triassic (Gaetani et al., 1992).

Diagnosis

Small neopterygian fish characterized by the following combination of characters: bones of the skull and pectoral girdle densely ornamented with tubercles; small parietals contacting at midline; large dermopterotic, almost twice the size of the parietal, approximately trapezoidal, deepest posteriorly; supraorbital bones present; suborbital bones present; maxilla long, almost reaching posterior end of lower jaw; maxilla with almost straight ventral border, fully garnished with small conical teeth, and concave posterior border, but without postmaxillary process; moderately large median gular, also strongly ornamented; quadratomandibular articulation well behind the orbit; comma-shaped preopercle almost vertically oriented; very inclined interopercle; opercle much larger than subopercle; oval body shape with large, nearly circular head;



Fig. 2 *Perledovatus nothosomoides* (Deecke, 1889). Complete view of the holotype SMF P1237a

BD/SL = 0.44; HL/SL = 0.35; OL/HL = 0.29; dorsal fin emarginate with distinctly long marginal ray; caudal fin deeply forked with equally large dorsal and ventral lobes, with broadly acute distal ends; dorsal fin originates slightly behind insertion of pelvic fins and ends approximately at origin of anal fin; PreD/SL = 0.56, PreV/SL = 0.52, PreA/SL = 0.70; (PreD-PreV)/SL = 0.04; (PreA-PreD)/SL = 0.15; complete series of distinctly large scutes between dorsal and caudal fins, and between anal and caudal fins; scales in anterior two thirds of the body with serrated posterior borders; middle flank scales deeper than long, up to 2.3 depth/length ratio; ventral flank scales between pectoral and pelvic fins quadrangular; 38 scales along the lateral line, vertical row at dorsal fin origin with 17 scales (7 + 1 + 9); 9 scales in marginal row of axial lobe. Pterygial formula: (D18 / V5 A15 C33) T38.

Remarks The original description of SMF P1237 by Deecke (1889) is quite complete, and after direct study of the specimen, the senior author (ALA) has been able to verify most of the characters described by him. Deecke was not able to trace the boundaries of the individual cranial bones and did not describe them, but he did describe details of the postcranium, which are now lost but appear to be accurate given the remains still in the rock. Recent preparation of the specimen has revealed more detailed anatomical information, making it possible to complete the description.

Description

Specimen SMF P1237 is a medium-sized fish with oval body shape, broad caudal peduncle and deeply forked

and evenly lobed caudal fin (Fig. 2). Although large, the head is relatively short. Its length represents ~35% of the standard length, but its depth is larger than its length, equal to the body depth close to the end of the dorsal fin and represents ~83% of the maximal body depth approximately midway between the skull and the dorsal fin. The maximal body depth is close to half of the standard length. The profile of the head is strongly curved, and the round orbit is large and very close to the forehead edge. The longitudinal diameter of the orbit reaches almost a third of the head length and the preorbital distance is only ~18% of the head length.

The exposed dermal bones in the skull and pectoral girdle are strongly ornamented with densely arranged fine tubercles; there is no evidence of ganoin on them (Fig. 3). This ornamentation extends on a few scales around the dorsal midline immediately behind the skull. The bones in the snout are imperfectly preserved, but a small rectangular rostral is visible; it is traversed by a median groove corresponding to the ethmoidal commissure. The presence of a post rostral is unlikely, but it cannot be excluded with certainty. The nasals seem to be long and slender, but are poorly preserved. The frontal broadens in posterior direction, following the curvature of the orbit, and narrows towards the midline at the suture with the dermopterotic. The proportions of the bone can be estimated only roughly, the maximal length to width ratio being approximately three. The parietal is relatively small and almost quadrangular, with a width to length ratio of 0.85; the ratio between the parietal length and the frontal length is ~0.27. The trapezoidal dermopterotic is large,

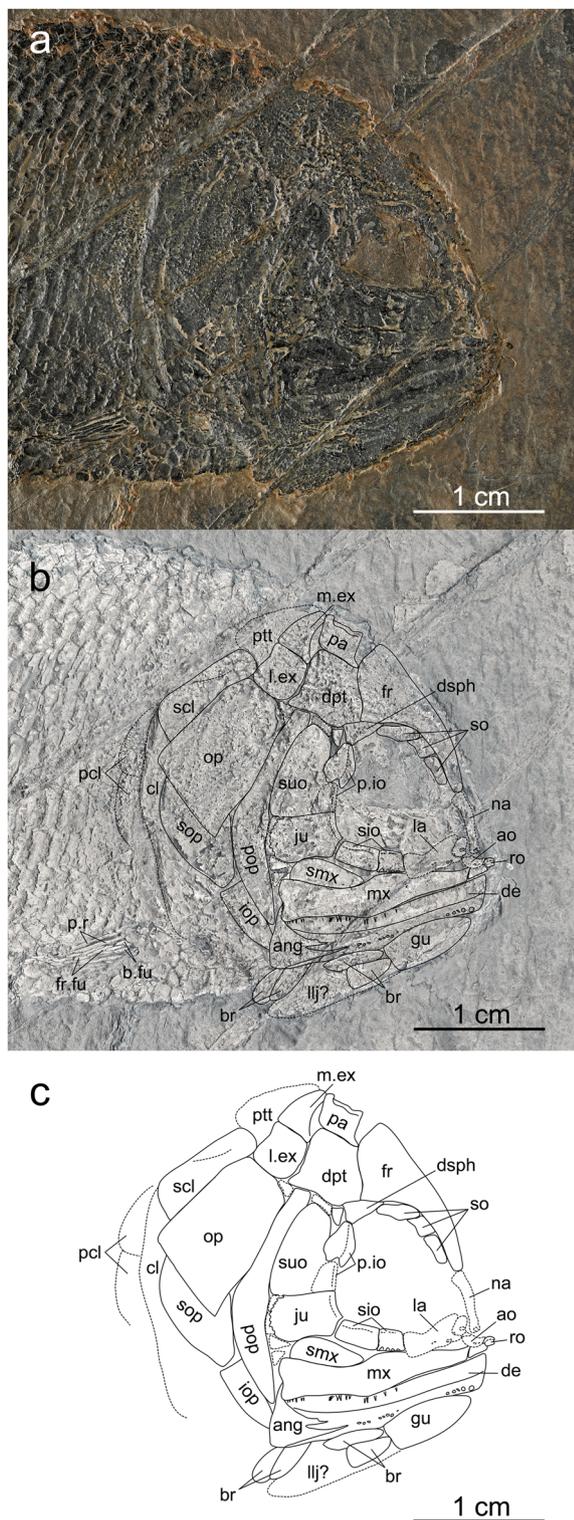


Fig. 3 Skull and pectoral fin of *Perledovatus nothosomoides* (Deecke, 1889). Anatomical abbreviations: **a** Photograph; **b** line drawing over imposed to the digitally modified photograph; **c** line drawing. *ang* angular, *ao* antorbital, *b.fu* basal fulcra, *cl* cleithrum, *de* dentary, *dpt* dermopterotic, *dsph* dermosphenotic, *br* branchiostegal rays, *fr* frontal, *fr.fu* fringing fulcra, *gu* gular plate, *iop* interopercle, *ju* jugal, *la* lacrimal, *llj?* left lower jaw?, *l.ex* lateral extrascapular, *m.ex* median extrascapular, *mx* maxilla, *na* nasal, *op* opercle, *pa* parietal, *pcl* postcleithra, *pmx* premaxilla, *p.io* posterior infraorbitals, *pop* preopercle, *p.r* pectoral fin rays, *ptt* posttemporal, *ro* rostral, *scl* supracleithrum, *sio* subinfraorbitals, *smx* supramaxilla, *so* supraorbitals, *sop* subopercle, *suo* suborbital

approximately as long as it is wide, with almost parallel medial and lateral borders, perpendicular posterior border, and posteriorly inclined anterior border. Its posterior and ventral borders are nearly equally long and perpendicular; they form a small, posteriorly directed posteroventral process. The lateral border of the dermopterotic is ~1.5 times the length of the dorsal border or the length of the parietal. In the back of the skull are two extrascapular bones. The lateral extrascapular is almost quadrangular and the medial extrascapular is subtriangular, narrowing towards and reaching the dorsal midline. The posterior limits of the posttemporal are unclear, but the bone is relatively large and reaches the dorsal midline.

The circumorbital series includes the antorbital, lacrimal, two subinfraorbitals, the jugal, two postinfraorbitals, the dermosphenotic, and three supraorbitals (Fig. 3). The antorbital and lacrimal are very poorly preserved and their shape is only roughly estimated. The antorbital apparently has approximately equally large vertical and horizontal portions. The lacrimal is larger than the subinfraorbitals, but smaller than the jugal. It is almost rectangular, more than twice as long as it is high, with an excavated concave dorsal border. The subinfraorbitals are rectangular, with the anterior one slightly longer than deep, and the posterior subinfraorbital nearly twice as long as it is high, and twice as long as the length of the anterior subinfraorbital. The jugal is quite large, and subtrapezoidal in shape, expanding posteriorly, almost reaching the preopercle. It has almost straight dorsal and anterior borders, irregularly convex posterior border, and slightly concave ventral and orbital borders. Numerous ridges on the surface of the jugal and irregular indentations of its posterior border indicate intensive branching of the infraorbital canal. The ventral postinfraorbital is very badly preserved and its shape can be reconstructed only roughly. The dorsal postinfraorbital is trapezoidal, narrowing dorsally, somewhat deeper than it is long. The

infraorbital sensory canal is indicated close to the orbital border of the infraorbital bones, except in the lacrimal and antorbital, and several ridges and pores indicate the presence of numerous branches, especially in the jugal and subinfraorbitals. Sensory lines are not clearly discernible in the lacrimal and antorbital, except for a portion of the infraorbital canal in the posterior part of the lacrimal and several large openings in the lacrimal and antorbital.

The dermosphenotic is tightly bound to the dermopteroic and frontal and rigidly incorporated into the skull roof (Fig. 3). Its shape is subtriangular, narrowest ventrally, with divergent posterior and anterior borders; the latter is longer than the former and follows the curvature of the orbit. The dorsal and orbital borders are approximately equally long. Anterior to the dermosphenotic, three supraorbitals complete the dorsal rim of the orbit. The posterior supraorbital is the largest in the series. The dermosphenotic and supraorbitals show the same ornamentation of densely arranged tubercles as present in the skull roofing bones.

The area between the postinfraorbitals, jugal and opercle is covered by what appears to be a single large suborbital bone, which covers the anterior margin of the dorsal portion of the preopercle (Fig. 3). Dorsal and ventral to this large suborbital, several partially preserved bones are interpreted as additional suborbitals; their precise number and shape cannot be determined. Between the large suborbital and the dermosphenotic is a small bone which might represent a dermal sphenotic ossification or, more likely, an additional small suborbital.

The preopercle is comma shaped and almost vertically oriented; its precise shape cannot be reconstructed (Fig. 3). The opercle is approximately rectangular with oblique ventral border. It is deeper than it is long, and much larger than the subopercle. The maximal length of the opercle, at its ventral border, is ~60% of its maximal depth at the anterior border. The maximal depth of the subopercle, excluding the ascending process, is ~25% of that of the opercle. The interopercle is elongated in a posterodorsal to anteroventral direction at an angle of approximately -55° to the longitudinal axis of the fish. There appears to be a separate small bone, an anteopercle or a dermohyal, between the anterodorsal corner of the opercle and the dorsal end of the preopercle, but this should be confirmed with better preserved specimens.

The gape is large (Fig. 3). The quadrato-mandibular articulation is well behind the orbit and both jaws are long and robust. The premaxilla is only partially exposed, anterior to the maxilla and medioventral to the antorbital and rostral. The long maxilla extends far beyond the posterior rim of the orbit, its length represents ~57% of the head length and ~64% of the lower jaw length. The

shape of the maxillary blade in lateral view is quite irregular. The ratio between the maxillary maximal depth, at its posterior border, and the maxillary length is ~0.20. The ventral border is almost straight in the anterior third, convex in the middle and slightly concave in the posterior third. Tiny conical teeth are scattered along the ventral margin of the maxilla, which was probably completely toothed. The maxillary posterior border is gently sinuous, concave in the middle, but there is no postmaxillary process. The dorsal border is almost straight in the anterior half, and it is concave in the posterior half, where it accommodates the relatively large supramaxilla. The supramaxilla is approximately oval, slightly narrowing anteriorly, with a depth to length ratio of ~0.33. The length of the supramaxilla represents ~38% of the length of the maxilla.

The lower jaw is incompletely exposed in lateral view; the dentary, angular and surangular are visible (Fig. 3). The dentary is very long, approximately as long as the maxilla, with a more or less rectangular, uniformly deep anterior half. The dentary symphysis is rather deep. As exposed, the depth of the anterior end of the dentary represents ~15% of the lower jaw length. The ascending ramus of the dentary forming the coronoid process is hidden by the maxilla. The posterior border of the dentary, which sutures to the angular, is irregularly zigzag. The dorsal half of the dentary is smooth, but the ventral portion is strongly ornamented with densely arranged short ridges and small tubercles. The mandibular sensory canal is indicated by a series of relatively large openings aligned parallel and close to the ventral border of the dentary. Dentary teeth are not preserved, but their presence cannot be excluded. The angular completes the lower jaw posteroventrally. Its surface is ornamented with densely arranged tubercles. The surangular is only little exposed, mostly hidden by the maxilla.

There is a moderately large median gular, which is also strongly ornamented with densely arranged tubercles (Fig. 3). The shape of the bone is somewhat ovoid, with maximal width at midlength, narrowing anteriorly to a deeply convex anterior border. The posterior border is straight. The length of the gular is ~38% of the length of the lower jaw. As preserved, the width to length ratio of the gular is 0.41, but the actual bone was probably somewhat wider. As usual, the gular is followed posteriorly, at both sides of the skull, by the series of branchiostegal bones. Although the most anterior branchiostegals are certainly plate-like and relatively broad, the preservation is not sufficient to establish their precise shape or number.

The dermal bones of the pectoral girdle, supraclithrum, cleithrum and postcleithra, present the same ornamentation of densely arranged tubercles as in most

of the skull bones (Fig. 3). The supracleithrum is dorsoventrally elongated; its exposed surface has a depth to length ratio of ~ 3 . The lateral line enters the bone at approximately the middle of the posterior border. A series of short longitudinal ridges arranged parallel to each other along the posterior margin of the bone projects beyond the bony plate so that the posterior border of the supracleithrum is serrated, as is the case of the scales. The cleithrum is relatively large, but it is poorly preserved, and no details can be described. Similarly, the presence of at least two postcleithra is evident, but they are badly preserved. The only well-preserved feature is their posterior borders, which show an ornamentation similar to the one described for the posterior border of the supracleithrum.

The pectoral fins are incompletely preserved, but they were likely small and placed low in the flank, almost at the same level of the pelvic fins (Fig. 2). The leading edge is garnished with fringing fulcra. At least one pair of small basal fulcra is present. The pelvic fins are also incompletely preserved, only the presence of basal (two or three pairs) and fringing fulcra like those on the pectoral fin can be described (Fig. 4).

The dorsal fin is deeply emarginate and has a distinctly long anterior marginal ray (Fig. 4a). The fin starts almost directly above the pelvics and reaches to the beginning of the anal fin, which has the appearance of the dorsal except for the unusual length of the first ray and its posterior profile is only slightly concave. Deecke

counted 12 dorsal and anal fin rays, but he did not distinguish between fin rays and fulcra, so at least some of the basal fulcra are probably included in his counts. As preserved today, there are only nine dorsal and anal fin rays. The dorsal fin has five basal fulcra, the first of them is tiny and unpaired, and numerous (more than 20) fringing fulcra. The first fringing fulcra have very broad bases and following fulcra become very slender distally. The anal fin has three basal fulcra and the most posterior one is comparatively smaller than the last dorsal basal fulcrum (Fig. 4b). The fringing fulcra on the anal fin also become slenderer distally, but the anterior elements are not as large as the corresponding elements on the dorsal fin. Sixteen fringing fulcra are preserved on the marginal anal fin ray, but they were certainly a few more.

Deecke reported a total of 20 caudal fin rays. The caudal fin was better preserved at that time (Deecke, 1889: pl. 35, Fig. 9; Fig. 2). Presently, there is evidence for 11 rays below and probably nine rays above the lateral line, corresponding to the ventral and dorsal lobes, respectively. The dorsal margin of the fin is not preserved, the ventral margin is incomplete, but a group of small but relatively strong fringing fulcra are preserved. The series of dorsal caudal fulcra is also incomplete; the preserved elements are relatively large. Three ventral basal fulcra are poorly preserved, but seem to be the complete set of these elements.

The squamation consists of 38 (Deecke counted 35) vertical rows of scales along the lateral line (Fig. 2). The scales immediately behind the opercle are higher than long; those of the lateral line have a height to length ratio of 2.2–2.3. The scales become shallower in dorsal, posterior and ventral direction, but only in the posterior caudal peduncle and in the ventrum, between the pectoral and pelvic fins, both masses are equal and the scales are square. The posterior margin of all scales is serrated, all over the body, but the serrations are more numerous in the anterior half of the body and are restricted to the ventral half of the scale towards the caudal peduncle. Deecke described a complete series of median strong hexagonal shields between the dorsal and caudal fins and in front of the anal fin. However, only imperfect remains of these scutes are left in the specimen today. The lateral line runs from the middle posterior edge of the supracleithrum, descending from the upper third of the body to the middle of the tail. The lateral line scales are characterized by a round bulge in the middle of the posterior margin. Some of them are pierced by relatively large foramina. There are 17 scales in the vertical row at the origin of the dorsal fin, with one scale pierced by the lateral line, seven above and nine below it. The axial lobe is relatively large,

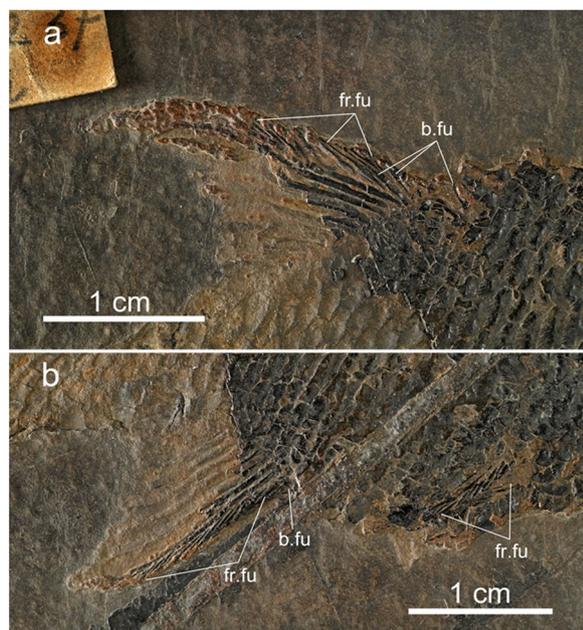


Fig. 4 Dorsal (a), anal (b, left) and pelvic (b, right) fins of *Perledovatus nothosomoides* (Deecke, 1889). b.fu basal fulcra, fr.fu fringing fulcra

including nine quadrangular scales forming its single marginal row and four inverted rows of scales.

Discussion

Perledovatus nothosomoides has been considered a valid species (De Alessandri, 1910; Deecke, 1889) until Lombardo (2001) claimed that its holotype was conspecific with the type of *Semionotus bellottii* Rüppel, 1857 (in Bellotti, 1857). Moreover, in the same work, Lombardo (2001) put all halecomorph species from Perledo under synonymy. The first two sections of this discussion deal with the taxonomy of these species. The systematic position of *P. nothosomoides* is discussed in the third section.

Taxonomic status of *Semionotus bellottii*

In a review article about the Middle Triassic ray-finned fishes from the Swiss and Italian Alps, Lombardo (2001) proposed the synonymy of several species under the name *Allolepidotus bellottii* (Rüppel), which was mistakenly considered as the type species of *Allolepidotus*. As a consequence, Lombardo's work has been taken as a reference to represent this genus in several studies (e.g., Feng et al., 2023).

The genus *Allolepidotus* was erected by Deecke (1889) including two species: *Pholidophorus ruppelii* Bellotti, 1857, and *Allolepidotus nothosomoides* Deecke, 1889. *Semionotus bellottii* Rüppel is not among the species originally included in the genus and, thus, it is not eligible as the type species (ICZN Article 69.1.1). Moreover, at the time of Lombardo (2001), *A. ruppelii* (Bellotti, 1857) had been designated the type species of *Allolepidotus* by Woodward (1895).

The species recognized by Lombardo (2001) was originally published by Bellotti (1857) under the name *Semionotus bellottii* acknowledging Rüppel as its author. Later on, De Alessandri (1910) transferred the species to the genus *Allolepidotus* and provided the first complete description of the type specimen, which is stored at the Servizio Geologico d'Italia in Rome under the catalogue number 'P 4431'. Lombardo's revised description of the species is based on the holotype and several specimens from the Kalkschieferzone of Besnasca/Ca' del Frate (Viggù, Varese, Italy) and Meride (Ticino, Switzerland). Hence, the validity of the species is well supported. Nevertheless, due to significant morphological differences with the type species *A. ruppelii* (see below), the referral to *Allolepidotus* Deecke, 1889, cannot be maintained.

Following a comprehensive morphological analysis of *Eoeugnathus megalepis* Brough, 1939, and in light of Lombardo's (2001) detailed description and illustrations of the specimens from Besnasca/Ca' del Frate, Herzog (2003) proposed that the Italian specimens might

represent a species of the genus *Eoeugnathus*. The senior author had the opportunity to examine additional specimens of this same species, sourced from the Kalkschieferzone of Val Mara Site D near Meride (Monte San Giorgio, Mendrisio, Canton Ticino, Switzerland). The morphology of this fish, particularly the anatomy of the skull, is strikingly similar to that of *E. megalepis* (ALA, pers. obs.), which lends support to the hypothesis put forth by Herzog (2003) that *S. bellotti* may be a species of the genus *Eoeugnathus*. Nevertheless, a comprehensive examination of the holotype specimen and the entire collection is essential to resolve the taxonomic status of *Semionotus bellottii*. Pending such a study, the species is tentatively considered to be *Eoeugnathus bellottii* (Rüppel in Bellotti, 1857).

Neither De Alessandri (1910) nor Lombardo (2001) provide body measurements for any specimen of "*S.* *bellottii*". However, some measurements can be taken from the photograph of MSCNIO P669 (Lombardo, 2001: pl. 1, fig. B). In this specimen, the body proportions and relative position of the fins plot close to the range of variation of specimens attributed to *E. megalepis* (Figs. 5, 6). Figure 5a shows that the anal fin is slightly more posteriorly placed in the body of *E. megalepis* ($PreA/SL=0.75-0.82$) than in any other potentially closely related species ($PreA/SL=0.69-0.72$). The specimens of *E. megalepis* show a clear pattern of ontogenetic variation: the body growths in length anterior to the dorsal and anal fins, which maintain their position relative to each other (Figs. 5a, 6a). Based on its photograph, the small individual MSCNIO P669, with more anteriorly placed dorsal and anal fins, roughly follows the trend revealed by the specimens of *E. megalepis*, although it is significantly smaller than the smallest of them.

Taxonomic status of *Pholidophorus oblongus* and *Pholidophorus curionii*

In addition to the question of the generic identity of this species, Lombardo (2001) treated *Pholidophorus oblongus* Bellotti, 1857, and *Pholidophorus curionii* Haeckel, 1910 (in De Alessandri, 1910), as junior synonyms of *Eoeugnathus bellottii*. This view contradicts the opinion of previous reviewers who considered these nominal species as valid taxa (De Alessandri, 1910; Deecke, 1889).

It is important to note that Haeckel (1849) proposed the name *Palaeoniscus curioni* for a taxon he intended to create, but this mention alone does not satisfy the requirements of the Code (ICZN Article 12.1) and, thus, the name is not available. In an unpublished work, Bellotti (1873) transferred the nominal species to the genus *Pholidophorus*, and Bassani (1886) listed the taxon as *Pholidophorus curioni*. The first description and illustration of this species was published by De Alessandri

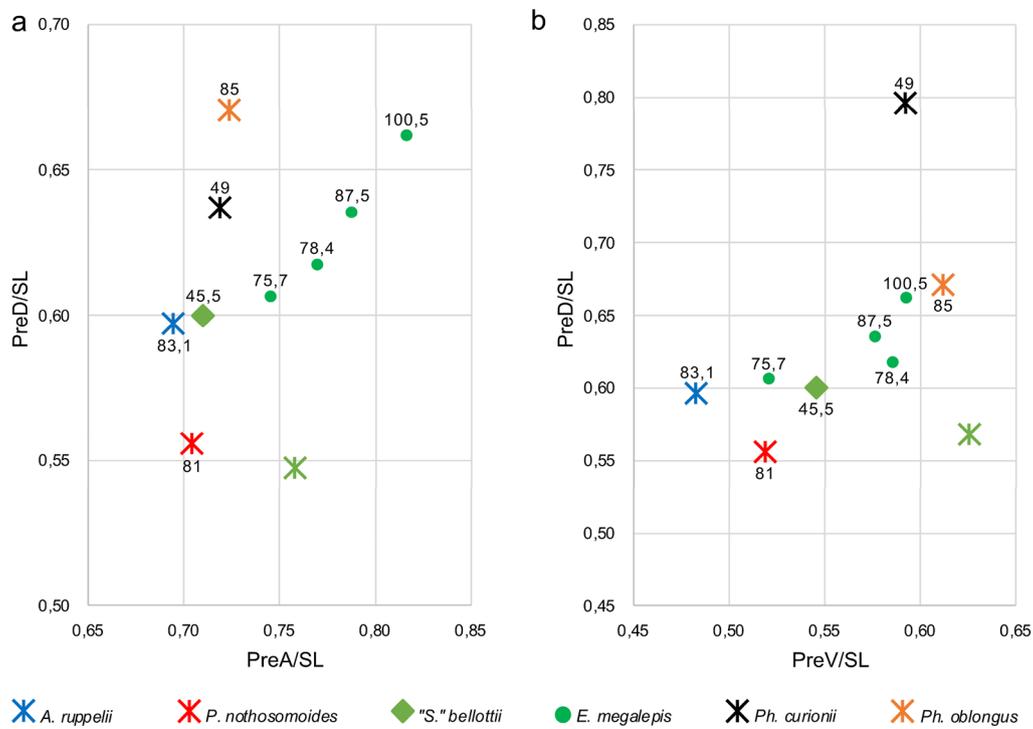


Fig. 5 Relative position of the fins respect to the body length in the studied taxa. Scatter plots of the ratios reflecting the position of the dorsal and anal fins relative to the standard length (a), and the position of the dorsal and pelvic fins relative to the standard length (b). The numbers accompanying the symbols correspond to the standard length values of each specimen

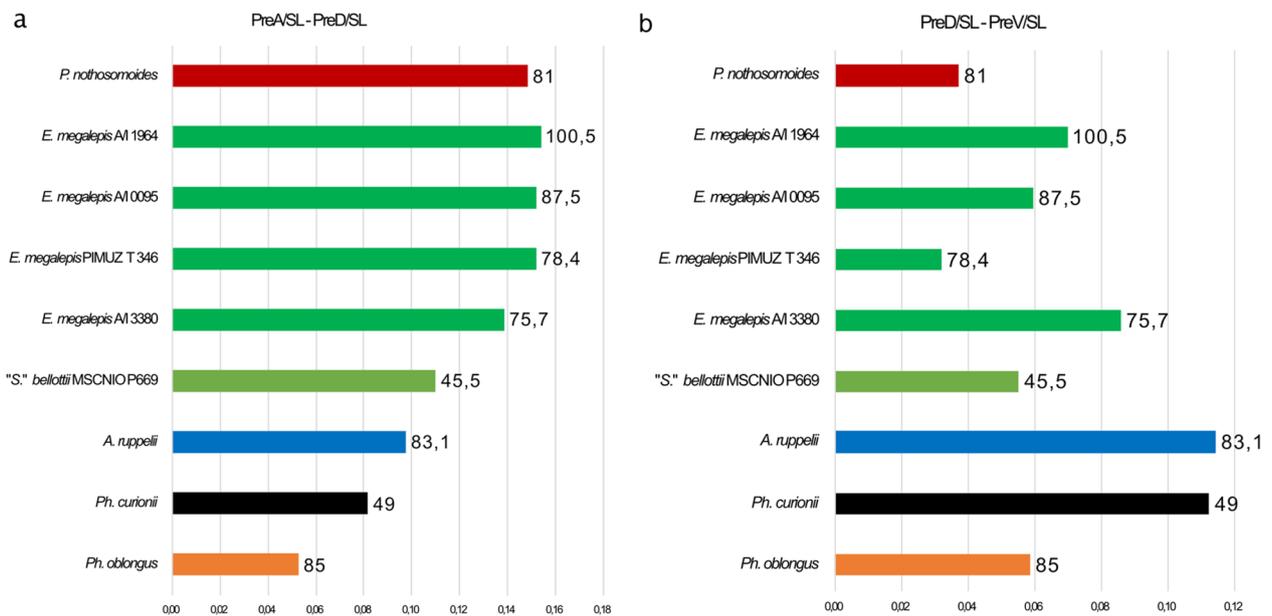


Fig. 6 Relative position of the fins respect to each other. Bar charts representing the distance between the dorsal and anal fins as a ratio to the standard length (PreA/SL - PreD/SL) (a), and the distance between the dorsal and pelvic fins as a ratio to the standard length (PreD/SL - PreV/SL) (b) in the studied taxa. The numbers at the end of each bar correspond to the standard length values of each specimen

(1910) and, since he explicitly acknowledges Heckel as the author of the species, according to the Code (ICZN Article 50.1.1), the nominal taxon takes authorship and date *Pholidophorus curionii* Heckel in De Alessandri, 1910. De Alessandri's description of this species is based on a plaster copy of the holotype and a few other specimens, including the only exemplar in Rüppel's collection (SMF) that Deecke (1889) referred to *Ph. oblongus*.

The species *Pholidophorus oblongus* was first described but not figured by Bellotti (1857), based on a single specimen. Deecke's (1889) contribution to the knowledge of this species is not based on the holotype, but a different specimen that De Alessandri later considered to be *Ph. curionii* (see previous paragraph). The most complete description of *Ph. oblongus* and the first illustration of its holotype is found in De Alessandri (1910). However, this latter description is not based solely on the holotype and differs from Bellotti's description in the number of fin rays in all fins, and the number of scales along the lateral line. It is not known whether these differences are due to a different evaluation of the holotype or to variations among the specimens De Alessandri referred to this species.

The type specimens of *Ph. curionii* and *Ph. oblongus* were part of the Perledo collection of the Natural History Museum in Milan and were lost during World War II. Based on the measurements of the type specimens reported by De Alessandri (1910), the body proportions and relative position of the fins indicate that they probably represented different taxa (Fig. 5). However, since the holotypes cannot be examined, it is impossible to confirm or reject the synonymy between these species and *E. bellottii* proposed by Lombardo (2001). Therefore, *Pholidophorus oblongus* Bellotti, 1857, and *Pholidophorus curionii* Haeckel, 1910 (in De Alessandri, 1910), are regarded here as nomina dubia.

Taxonomic status of *Perledovatus nothosomoides*

The combination of characters given in the above diagnosis distinguishes *Perledovatus* from any other Triassic neopterygian. In particular, the morphology of the holotype and only known specimen of this species, is clearly different from the morphology of the holotype and only specimen of the type species of *Allolepidotus*, *A. ruppelii*. The two specimens are of comparable size, but their general body shape and proportions are noticeably different (Figs. 2, 3). The relative position of the fins is very different in the two species (Figs. 5, 6). The anal fin is approximately in the same position in *A. ruppelii* and *P. nothosomoides* (PreA/SL=0.69 and 0.70, respectively). The dorsal fin is more posteriorly placed in *A. ruppelii* than in *P. nothosomoides* (PreD/SL=0.60 and 0.56, respectively), while the opposite is true for the position of the pelvic fins (PreD/SL=0.48 and 0.52, respectively). As

a result, the distance between the dorsal and anal fins is larger in *P. nothosomoides* than in *A. ruppelii*, but the distance between the dorsal and pelvic fins is smaller in the first than in the second species (Fig. 6). More obviously, the head is much smaller and the body much shallower in *A. ruppelii* than in *P. nothosomoides* (HL/SL=0.24 and 0.35, and BD/SL=0.31 and 0.44, respectively). Based on these data, and although the anatomical information is limited, we conclude that each of the two species should be treated as separate genera.

Lombardo (2001) proposed that the small halecomorphs from the Kalkschieferzone at Besnasca/Ca' del Frate are conspecific with *P. nothosomoides* and "*S.* *bellottii*". However, as discussed above, the referral of the halecomorphs from the Kalkschieferzone to "*S.* *bellottii*" is doubtful and a comprehensive evaluation of these fishes is necessary to clarify their taxonomy. In agreement with Herzog (2003) the Kalkschieferzone species is regarded as *Eoegnathus bellottii*. On the other hand, *Perledovatus nothosomoides* differs from *E. megalepis* and *E. bellottii* in several features.

The pelvic fins are more anteriorly placed in *P. nothosomoides* than in *E. megalepis* individuals of comparable size or in the small *E. bellottii* specimen that could be measured for comparison. According to the measurements given by De Alessandri (1910) for the position of the pelvic fins in the holotype of "*S.* *bellottii*", these fins are placed much more posterior than in any of the other specimens compared. However, according to De Alessandri's illustration of the specimen, the insertion of the pelvic fins is not well preserved in the fossil and, thus, his measurement should be taken with caution. The pterygial formula of *P. nothosomoides* does not fit within the range of variation of *E. megalepis* (Herzog, 2003: Table 4). The number of fin rays is uncertain for all these species, but the dorsal and anal fins are of equivalent size in *P. nothosomoides* (Deecke, 1889; this work), and the dorsal fin is larger than the anal fin in the species of *Eoegnathus* (Herzog, 2003; Lombardo, 2001). Besides these features, *P. nothosomoides* differs from the species of *Eoegnathus* in the presence of two extrascapular bones and the large dermopterotic that is at least double the size of the parietal.

Systematic position of *Perledovatus* gen. nov.

According to the cladistic analysis of López-Arbarello and Sferco (2018: Supplementary File S4), *Perledovatus nothosomoides* is referred to Crown-Neopterygii based on the presence of the following neopterygian synapomorphies: maxilla detached from preopercle, elongate and shallow; presence of supramaxilla; subopercle with ascending process; presence of interopercle. Unfortunately, SMF P1237 does not preserve any of the

synapomorphies supporting any of the neopterygian clades.

One of the best preserved and most noticeable features in the skull of *Perledovatus nothosomoides* is the very large gape. Among Triassic crown neopterygians, only teleosts and a few halecomorphs have comparably large gapes. Triassic teleosts differ from *P. nothosomoides* in the presence of relatively short and broad nasals, small antorbitals, two supramaxillae, and the dermosphenotic is not tightly sutured to the skull roofing bones (e.g., Arratia, 2013). Among Triassic halecomorphs, only *E. megalepis* and *E. bellottii*, denoted *Eoegnathus* and “*Allolepidotus*” in previous work, *Subortichthys triassicus* Ma & Xu, 2017, from the Guanling Formation at Luoping (Anisian, China), and *Sinoegnathus kueichowensis* Su, 1959, from the Falang Formation (Ladinian, China) have similarly large gapes. In the recently published phylogenetic hypothesis of Fang et al. (2023), these taxa form a monophyletic clade for which they proposed the new family name Subortichthyidae.

Except for the somewhat higher number of lateral line scales (38 vs. 30–35), *P. nothosomoides* preserves six (indicated with asterisks) out of nine diagnostic features of Subortichthyidae: frontal about four times as long as parietal; two or three supraorbitals*; one to three suborbitals*; quadrate almost fully covered by posterior portion of maxilla*^S; elongate maxilla extending posterior to coronoid process of lower jaw*^S; supramaxillary process of maxilla relatively small*; 12 pairs of branchiostegal rays; 30–35 lateral line scales; and complete row of elongate scales between last lateral line scale and uppermost caudal fin ray*^S (Feng et al., 2023). Among the three diagnostic features of Subortichthyidae that cannot be confirmed in *P. nothosomoides*, the proportion between the lengths of the frontal and parietal and the number of branchiostegal rays, are not preserved in SMF P1237 which is the only specimen of this species. Consequently, the sole morphological feature that diverges from the diagnosis of Subortichthyidae is the total number of lateral line scales.

Furthermore, in the phylogenetic hypothesis of Feng et al. (2023), the clade Subortichthyidae is supported by five unambiguous synapomorphies, three of which are indicated with a superscript ‘S’ after the asterisks in the previous paragraph (Feng et al., 2023: chs. 94[1], 120[2], 223[1]). The posterior end of the maxilla located posterior to the orbit is another synapomorphy of Subortichthyidae also found in *P. nothosomoides* (Feng et al., 2023: chs. 121[0]). The remaining synapomorphy of this clade is the presence of up to 35 lateral line scales (Feng et al., 2023: ch. 225[1]), the number of lateral line scales is 38 in *P. nothosomoides*.

Additionally, *P. nothosomoides* share with *Su. triassicus* and *Si. kueichowensis* the presence of large dermopterotic bones. Although there is some intraspecific variation at least in *Si. kueichowensis*, in the three species, the parietals are small and roughly quadrangular, and the dermopterotics are notably larger than the parietals. In *P. nothosomoides* and *Su. triassicus* the dermopterotics are anteroposteriorly short, but mediolaterally broad, whereas in *Si. kueichowensis* the dermopterotics are not only broad, but also longer than the parietals.

Conclusions

The revision of the type material of the species originally included in the genus *Allolepidotus* Deecke, 1889, led to the taxonomic revision of all halecomorph species from the Triassic of Perledo, Italy. Contrary to Lombardo (2001), the morphological variation between these taxa is sufficient to confirm the existence of four different taxa represented in the Perledo Formation.

First of all, we are able to correct the misunderstanding about the type species of *Allolepidotus*, which is not *Allolepidotus bellottii*. The type species of *Allolepidotus* is *A. ruppelii*, which is a valid species, with holotype SMF P1266 in the Senckenberg Research Institute and Natural History Museum in Frankfurt am Main, Germany. The fossil material from the Kalkschieferzone at Besnasca/Ca’ del Frate studied by Lombardo (2001) does not represent a species of *Allolepidotus*, but rather a species of the genus *Eoegnathus*, resulting in the new combination *E. bellottii*.

The second and only other species originally included in *Allolepidotus* is classified in its own genus *Perledovatus* gen. nov. The holotype of *P. nothosomoides* has been mechanically prepared revealing additional anatomical information which allows the referral of this taxon to the clade Subortichthyidae of Feng et al. (2023).

The species *Pholidophorus oblongus* Bellotti, 1857, and *Pholidophorus curionii* Haeckel, 1910 (in De Alessandri, 1910), which Lombardo (2001) considered to be junior synonyms of *Eoegnathus bellottii*, are shown to represent different taxa. However, the type specimens are lost and it is not possible to decide whether the nominal species proposed by Bellotti and Haeckel are valid, or if their holotypes might be conspecific with other established ray-finned fish species from the Middle Triassic of the Alps. Therefore, *Ph. oblongus* Bellotti, 1857, and *Ph. curionii* Haeckel, 1910 (in De Alessandri, 1910), are considered here as nomina dubia.

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Author contributions

A.L.A. conceived, designed and carried out the study. A.L.A. wrote the manuscript with support from R.B. R.B. contributed data and revised the work critically by means of important scientific content.

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Declarations

Ethics approval and consent to participate

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