

This article will be submitted to PCI-Paleo.
Please carefully note that subsequent
versions of this manuscript may have
different content.

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

López-Arbarello Adriana^{1,2,*}, and Brocke Rainer³

¹Department of Earth and Environmental Sciences, Paleontology and Geobiology, Ludwig-Maximilians-Universität München – Munich, Germany

²GeoBio-Center, Ludwig-Maximilians-Universität München – Munich, Germany

³Abteilung Paläontologie and Historische Geologie, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt – Frankfurt am Main, Germany

*Corresponding author: Adriana López-Arbarello

Correspondence: a.lopez-arbarello@lrz.uni-muenchen.de

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 genotype of *Allolepidotus*, which is *A. rueppelli* and not "*A.*" *bellottii* as considered in the literature over the past two decades. Fossil material from the calcareous zone of Ca' del Frate (Viggiù-Varese, Italy) which ~~has been~~ referred to *Allolepidotus*, rather represent a species of *Eoeugnathus*. There, 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 [REDACTED]. The holotype of [REDACTED] *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

40 The famous black shales of Perledo, Italy, have yielded one of the first known fossil assemblages from
41 the Middle Triassic of the Alps. The first report on Triassic fishes from Perledo is found in Balsamo-Crivelli
42 (1839), including the description of only two fish specimens. From that very modest beginning, a total of
43 30 fish species, mostly ray-finned fishes except of one shark and one coelacanth, had been named over the
44 following hundred years (Balsamo-Crivelli 1839; Bellotti 1857; Bassani 1886; Deecke 1889; De Alessandri
45 1910). Unfortunately, most of the type specimens were lost during World War II and many of those taxa
46 remain dubious or placed under synonymy.

47 The main collection of fishes from the Triassic of Perledo was housed at the Natural History Museum
48 in Milan (MCSM), Italy, but it is completely lost (Lombardo, pers. comm. April 26, 2023). However, a smaller
49 collection of the Perledo fish fauna was brought to Frankfurt am Main, Germany, and is conserved in the
50 fossil vertebrate collection of the Senckenberg Research Institute and Natural History Museum (SMF). The
51 Frankfurt collection (“Rüppel collection”) was studied by Deecke (1889) and included 37 specimens, 28 of
52 them survived World War II. Within the original collection, Deecke identified several of the species
53 published by Bellotti (1857). However, Deecke referred most of these species to different genera, some of
54 which were newly proposed. Additionally, he described four new taxa.

55 According to Deecke (1889) and Tintori et al. (1985), specimens collected at Perledo have gone to
56 several museums and private collections. However, only the main collection of the MCSM - which has been
57 completely lost, and the smaller collection of the SMF, have been studied scientifically. The present
58 contribution was triggered by the need to revise the taxonomy of the species of *Allolepidotus* Deecke,
59 1889, and resulted in the erection of a new genus and the clarification of the taxonomic status of all the
60 halecomorph species from Perledo.

61

Material and methods

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

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

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

71 *Institutional abbreviations*

72 IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences,
73 Beijing, China; PIMUZ, Paleontological Institute and Museum at the University of Zürich, Zürich,
74 Switzerland; SMF, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main,
75 Germany.

76 *Morphometric abbreviations*

77 BD, maximal body depth; HL, maximal head length; PreA, preanal length; PreD, predorsal length; PreV,
78 prepelvic length; SL, standard length.

79

Systematic Paleontology

80 Subclass Actinopterygii Cope, 1887

81 Superdivision Neopterygii Regan, 1923

82 Subdivision Halecomorphi Cope, 1872

83 Halecomorphi incertae sedis

84

85 Genus *Allolepidotus* Deecke, 1889

86

87 1889 *Allolepidotus*—Deecke: p. 113, in part.

88 1910 *Allolepidotus* Deecke—De Alessandri: p. 115–116, in part.

89 2001 *Allolepidotus* Deecke, 1889—Lombardo: p. 347–348, in part.

90

91 Type species

92 *Pholidophorus rueppelli* Bellotti, 1857, fixed by Woodward (1895: p. 315).

93 Remarks

94 The genus *Allolepidotus* was erected by Deecke (1889) including two species: *Pholidophorus rueppelli*
95 Bellotti, 1857, and *Allolepidotus nothosomoides* Deecke, 1889. Woodward (1895) locked *A. rueppelli*
96 (Bellotti 1857) as the genotype.

97

98 Species *Allolepidotus rueppelli* (Bellotti 1857)

99

100 1857 *Pholidophorus ruppelli* nob.—Bellotti: p. 428.

101 1886 *Pholidophorus Rüppelli* Bell.—Bassani: p. 63

102 1889 *Allolepidotus Rüppelli* Bell. sp.—Deecke: p. 117–118, pl. 6: fig. 5.

103 1910 *Allolepidotus Rüppelli* Bell. sp.—De Alessandri, p. 118–120, pl. 8: fig. 4.

104 2001 *Pholidophorus rueppelli*—Lombardo: p. 350.

105

106 Lectotype

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



108

109 **Figure 1** - *Allolepidotus rueppelli* (Bellotti, 1857). Photograph of the lectotype SMF P.1266, a plaster
110 copy described by Bellotti (1857).

111 **Diagnosis**

112 Although there is little anatomical information preserved in the lectotype, the following combination
113 of features distinguishes the species: BD/SL = 0,31; HL/SL = 0,24; HL/BD = 0,79; PreV/SL = 0,48; PreD/SL=
114 0,60; PreA/SL = 0,69; (PreD-PreV)/SL = 0,11; (PreA-PreD)/SL = 0,10; 37 scales along the lateral line; posterior
115 border of scales serrated. Pterygial formula: (D20 / V8 A19 C32) T37.

116 **Remarks**

117 Bellotti (1857) named this species for two specimens. The whereabouts of one of them are unknown.
118 The other specimen, which he described, was represented in a plaster copy at the MCSM, which is currently
119 housed in the SMF collection, and is designated here the lectotype.

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

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

128

129 Family Subortichthyidae Feng, Xu, Ma, and Ren, 2023

130 Genus ██████████ gen. nov.

131

132 1889 *Allolepidotus*—Deecke: p. 113, in part.

133 1910 *Allolepidotus* Deecke—De Alessandri: p. 115–116, in part.

134 2001 *Allolepidotus* Deecke, 1889—Lombardo: p. 347–348, in part.

135 **Type species**

136 *Allolepidotus nothosomoides* Deecke, 1889.

137 **Etymology**

138 The generic name ██████████ is formed by '████████', the name of the famous type locality and
139 stratigraphic unit, and '████████' recalling the characteristically oval shape of the body of this fish, especially
140 noticed by Deecke (1889).

141

142 Species ██████████ *nothosomoides* (Deecke 1889) new comb.

143

144 1889 *Allolepidotus nothosomoides* n. sp.—Deecke: p. 118–119, pl. 6: fig. 9.

145 1910 *Allolepidotus nothosomoides* Deecke—De Alessandri: p. 116–118, pl. 8: fig. 7.

146 2001 *Allolepidotus nothosomoides*—Lombardo: p. 350.

147

148 **Holotype**

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

152 **Type locality and horizon**

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

155 **Diagnosis**

156 Small neopterygian fish characterized by the following combination of characters: bones of the skull
157 and pectoral girdle densely ornamented with ganoin tubercles; small parietals contacting at midline; large
158 dermopterotic, almost twice the size of the parietal, approximately trapezoidal, deepest posteriorly;

159 supraorbital bones present; suborbital bones present; maxilla long, almost reaching posterior end of lower
160 jaw; maxilla with almost straight ventral border, fully garnished with small conical teeth, and concave
161 posterior border, but without postmaxillary process; moderately large median gular, also strongly
162 ornamented; quadratomandibular articulation well behind the orbit; comma-shaped preopercle almost
163 vertically oriented; very inclined interopercle; opercle much larger than subopercle; oval body shape with
164 large, nearly circular head; BD/SL 0,44; HL/SL 0,35; OL/HL 0,29; dorsal fin emarginate with distinctly long
165 marginal ray; caudal fin deeply forked with equally large dorsal and ventral lobes, with broadly acute distal
166 ends; dorsal fin originates slightly behind insertion of pelvic fins and ends approximately at origin of anal
167 fin; PreD/SL = 0.56, PreV/SL = 0.52, PreA/SL = 0.70; (PreD-PreV)/SL = 0,04; (PreA-PreD)/SL = 0,15; complete
168 series of distinctly large scutes between dorsal and caudal fins, and between anal and caudal fins; scales in
169 anterior two thirds of the body with serrated posterior borders; middle flank scales deeper than long, up
170 to 2.3 depth/length ratio; ventral flank scales between pectoral and pelvic fins quadrangular; 38 scales
171 along the lateral line, vertical row at dorsal fin origin with 17 scales (7+1+9); 9 scales in marginal row of
172 axial lobe. Pterygial formula: (D18 / V5 A15 C33) T38.



173

174

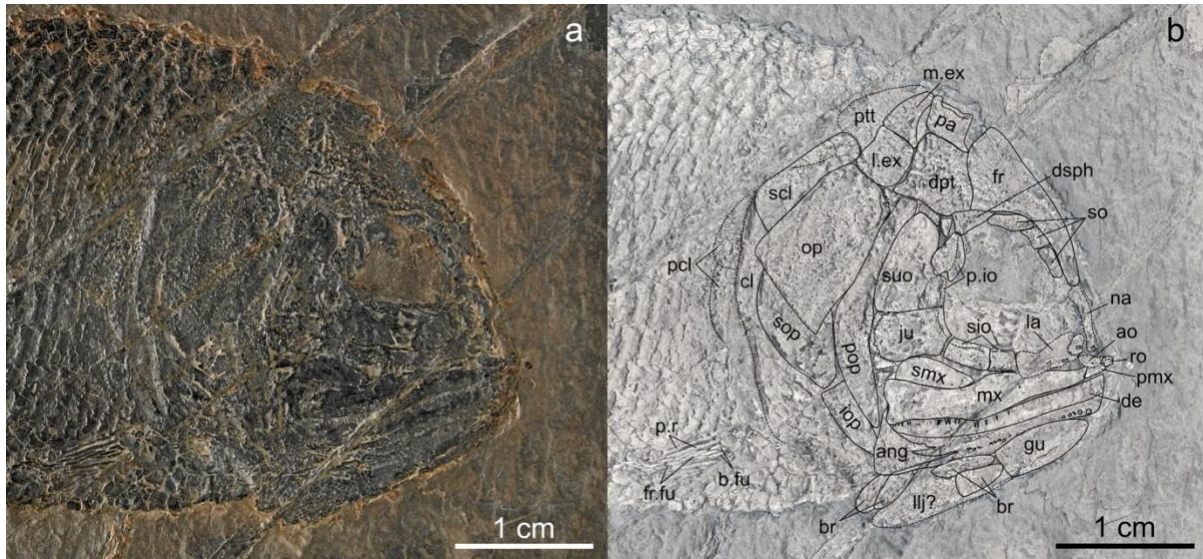
Figure 2: [REDACTED] *nothosomoides* (Deecke, 1889). Complete view of the holotype SMF P1237a.

175 **Remarks**

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

182 **Description**

183 Specimen SMF P1237 is a medium-sized fish with oval body shape, broad caudal peduncle and deeply
184 forked and evenly lobed caudal fin (Fig. 2). Although large, the head is relatively short. Its length represents
185 ~35% of the standard length, but its depth is larger than its length, equal to the body depth close to the
186 end of the dorsal fin and represents ~83% of the maximal body depth approximately midway between the
187 skull and the dorsal fin. The maximal body depth is close to half of the standard length. The profile of the
188 head is strongly curved, and the round orbit is large and very close to the forehead edge. The longitudinal
189 diameter of the orbit reaches almost a third of the head length and the preorbital distance is only ~18% of
190 the head length.



191

192

193

194

195

196

197

198

199

200

Figure 3: Skull and pectoral fin of [REDACTED] *nothosomoides* (Deecke, 1889). a, photograph; b, line drawing over imposed to the digitally modified photograph. Anatomical abbreviations: 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, interoperculum; ju, jugal; la, lacrima; llj?, left lower jaw?; l.ex, lateral extrascapular; m.ex, median extrascapular; mx, maxilla; na, nasal; op, operculum; pa, parietal; pcl, postcleithra; pmx, premaxillae; p.io, posterior infraorbitals; pop, preoperculum; p.r, pectoral fin rays; ptt, Posttemporal; ro, rostral; scl, supracleithrum; sio, subinfraorbitals; smx, supramaxilla; so, supraorbitals; sop, suboperculum; suo, suborbital.

201

202

203

204

205

206

207

208

209

210

211

212

213

214

215

216

217

218

219

220

221

222

223

224

225

226

227

228

The 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 width to length 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, 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 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 reaches 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 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, approximately as large as the lacrimal, but with a different shape. The Jugal is subtrapezoidal, expanding posteriorly, almost reaching the preopercle. It has an 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

229 border indicate intensive branching of the infraorbital canal. The ventral postinfraorbital is very badly
230 preserved and its shape can be reconstructed only roughly. The dorsal postinfraorbital is trapezoidal,
231 narrowing dorsally, somewhat deeper than it is long. The infraorbital sensory canal is indicated close to the
232 orbital border of the infraorbital bones, except in the lacrimal and antorbital, and several ridges and pores
233 indicate the presence of numerous branches, especially in the jugal and subinfraorbitals. Sensory lines are
234 not clearly discernible in the lacrimal and antorbital, except for a portion of the infraorbital canal in the
235 posterior part half of the lacrimal and several large openings in the lacrimal and antorbital.

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

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

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

258 The gape is large (Fig. 3). The quadrato-mandibular articulation is well behind the orbit and both jaws
259 are long and robust. The premaxilla is only partially exposed, anterior to the maxilla and medioventral to
260 the antorbital and rostral. The long maxilla extends far beyond the posterior rim of the orbit, its length
261 represents ~57% of the head length and ~64% of the lower jaw length. The shape of the maxillary blade in
262 lateral view is quite irregular. The maximal depth, at its posterior border, to length ratio of the maxilla is
263 ~0.20. The ventral border is almost straight in the anterior third, convex in the middle and slightly concave
264 in the posterior third. Tiny conical teeth are scattered along the ventral margin of the maxilla, which was
265 probably completely toothed. The maxillary posterior border is gently sinuous, concave in the middle, but
266 there is no postmaxillary process. The dorsal border is almost straight in the anterior half and concave in
267 the posterior half, where it accommodates the relatively large supramaxilla. The supramaxilla is
268 approximately oval, slightly narrowing anteriorly, with a depth to length ratio of ~0.33. The length of the
269 supramaxilla represents ~38 % of the length of the maxilla.

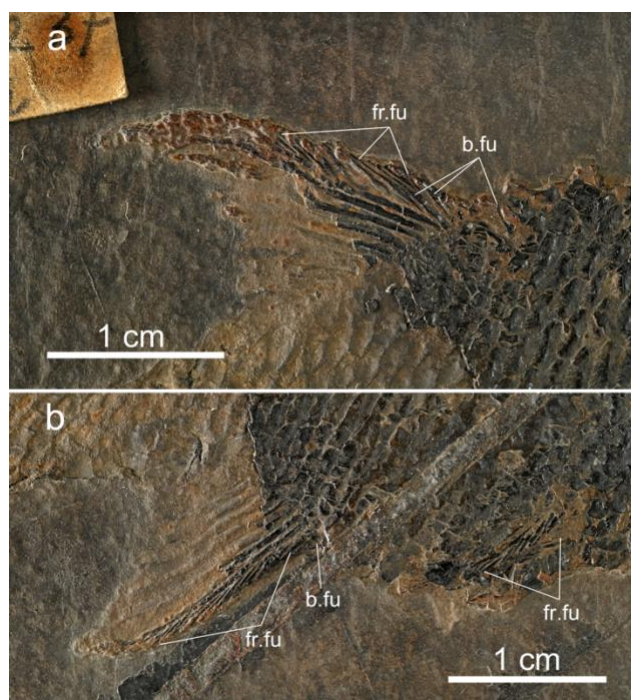
270 The lower jaw is incompletely exposed in lateral view; the dentary, angular and surangular are visible
271 (Fig. 3). The dentary is very long, approximately as long as the maxilla, with a more or less rectangular,
272 uniformly deep anterior half. The dentary symphysis is rather deep. As exposed,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

281 There is moderately large median gular, which is also strongly ornamented with densely arranged
282 tubercles (Fig. 3). The shape of the bone is somewhat ovoid, with maximal width at midlength, narrowing

283 anteriorly to a deeply convex anterior border. The posterior border is straight. Its length is ~38% of the
284 length of the lower jaw. As preserved, the width to length ratio of the gular is 0,41, but the actual bone
285 was probably somewhat wider. As usual, the gular is followed posteriorly, at both sides of the skull, by the
286 series of branchiostegal bones. Although the most anterior branchiostegals are certainly plate-like and
287 relatively broad, the preservation is not good enough to establish their precise shape or number.

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

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



302
303 Figure 4: Dorsal (a), anal (b, left) and pelvic (b, right) fins of [REDACTED] *nothosomoides* (Deecke,
304 1889). Anatomical abbreviations: b.fu, basal fulcra; fr.fu, fringing fulcra.

305 The dorsal fin is deeply emarginate and has a distinctly long anterior marginal ray (Fig. 4a). The fin starts
306 almost directly above the pelvis and reaches to the beginning of the anal fin, which has the appearance
307 of the dorsal except for the unusual length of the first ray and its posterior profile is only slightly concave.
308 Deecke counted 12 dorsal and anal fin rays, but he did not distinguish between fin rays and fulcra, so at
309 least some of the basal fulcra are probably included in his counts. As preserved today, there are only nine
310 dorsal and anal fin rays. The dorsal fin has five basal fulcra, the first of them is tiny and unpaired, and
311 numerous (more than 20) fringing fulcra. The first fringing fulcra have very broad bases and following fulcra
312 become very slender distally. The anal fin has three basal fulcra, the most posterior one is comparatively
313 smaller than the last dorsal basal fulcrum (Fig. 4b). The fringing fulcra on the anal fin also become slenderer

314 distally, but the first elements are not as large as the corresponding elements on the dorsal fin. Sixteen
315 fringing fulcra are preserved on the marginal anal fin ray, but they were certainly a few more.

316 Deecke reported a total of 20 caudal fin rays. The caudal fin was better preserved at that time (Deecke,
317 1889: pl. 35, fig. 9; Fig. 2). Presently, there is evidence for 11 rays below and probably nine rays above the
318 lateral line, corresponding to the ventral and dorsal lobes, respectively. The dorsal margin of the fin is not
319 preserved, the ventral margin is incomplete, but a group of small but relatively strong fringing fulcra are
320 preserved. The series of dorsal caudal fulcra is also incomplete; the preserved elements are relatively large.
321 Three ventral basal fulcra are poorly preserved, but seem to be the complete set of these elements.

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

336

Discussion

337 [REDACTED] *nothosomoides* has been considered a valid species (Deecke 1889; De Alessandri 1910)
338 until Lombardo (2001) claimed that its holotype was conspecific with the type of *Semionotus bellottii*
339 Rueppel, 1857 (in Bellotti 1857). Moreover, in the same work, Lombardo (2001) put all halecomorph
340 species from Perledo under synonymy. The first part of this discussion deals with the taxonomy of these
341 species. The systematic position of [REDACTED] *nothosomoides* is discussed in the second part.

342 Taxonomic status of *Semionotus bellottii*

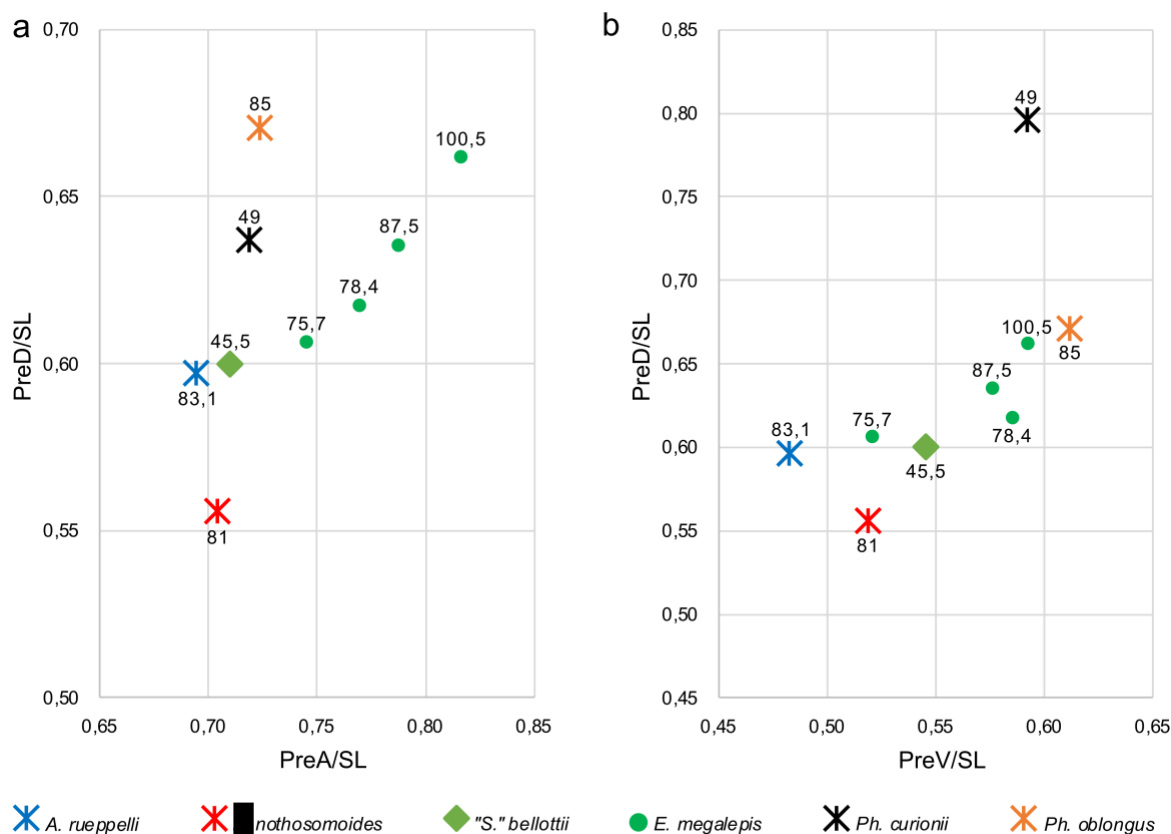
343 In a review article about the Middle Triassic ray-finned fishes from the Swiss and Italian Alps, Lombardo
344 (2001) proposed the synonymy of several species under the name *Allolepidotus bellottii* (Rüppel), which
345 was mistakenly considered the genotype of *Allolepidotus*. As a consequence, Lombardo's work has been
346 taken as a reference to represent this genus in several studies (e.g., Feng et al. 2023).

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

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

360 Herzog (2003) studied *Eoeugnathus megalepis* Dee, 1939, and concluded that the taxon studied by
361 Lombardo (2001) could represent a species of *Eoeugnathus*, a hypothesis adhered to here by the senior
362 author (ALA pers. obs.). Neither De Alessandri (1910) nor Lombardo (2001) provide body measurements for
363 any specimen of "*S.*" *bellottii*. However, some measurements can be taken from the photograph of MSCNIO
364 P669 (Lombardo 2001 : pl. 1, fig. B). In this specimen, the body proportions and relative position of the fins

365 plot close to the range of variation of specimens attributed to *E. megalepis* (Figs. 5–6). This is in particular
 366 true, when individuals of similar size are compared. Figure 5a shows that the anal fin is slightly more
 367 posteriorly placed in the body of *E. megalepis* ($PreA/SL = 0,75–0,82$) than in any other potentially closely
 368 related species ($PreA/SL = 0,69–0,72$). However, the specimens of *E. megalepis* show a clear pattern of
 369 ontogenetic variation: the body growths in length anterior to the dorsal and anal fins, which maintain their
 370 position relative to each other (Fig. 5b). Based on its photograph, the small individual MSCNIO P669, with
 371 more anteriorly placed dorsal and anal fins, would fit the trend revealed by the specimens of *E. megalepis*
 372 (Fig. 5a). New material recently recovered from the Kalkschieferzone of the Monte San Giorgio is currently
 373 under study and will help to clarify the alpha taxonomy and systematic position of these fishes. Pending
 374 the final results of this latter study, the species is tentatively considered to be *Eoegnathus bellottii* (Rüppel
 375 in Bellotti 1857).



376

377 Figure 5: Relative position of the fins respect to the body length. Scatter plots of the ratios reflecting
 378 the position of the dorsal and anal fins (a), and the position of the dorsal and pelvic fins (b). The
 379 numbers accompanying the symbols correspond to the SL values of each specimen.

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

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

385 It is important to note that Haeckel (1849) proposed the name *Palaeoniscus curionii* for a taxon he
 386 intended to create, but this mention alone does not satisfy the requirements of the Code (ICZN Article 12.1)
 387 and, thus, the name is not available. In an unpublished work, Bellotti (1873) transferred the nominal species
 388 to the genus *Pholidophorus*, and subsequent authors listed the taxon as *Pholidophorus curioni*. The first
 389 description and illustration of this species was published by De Alessandri (1910) and, since he explicitly
 390 acknowledges Heckel as the author of the species, according to the Code (ICZN Article 50.1.1), the nominal
 391 taxon takes authorship and date *Pholidophorus curionii* Heckel in De Alessandri, 1910. De Alessandri's

392 description of this species is based on a plaster copy of the holotype and a few other specimens, including
393 the only exemplar in Rüppel's collection (SMF) that Deecke (1889) referred to *Ph. oblongus*.

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

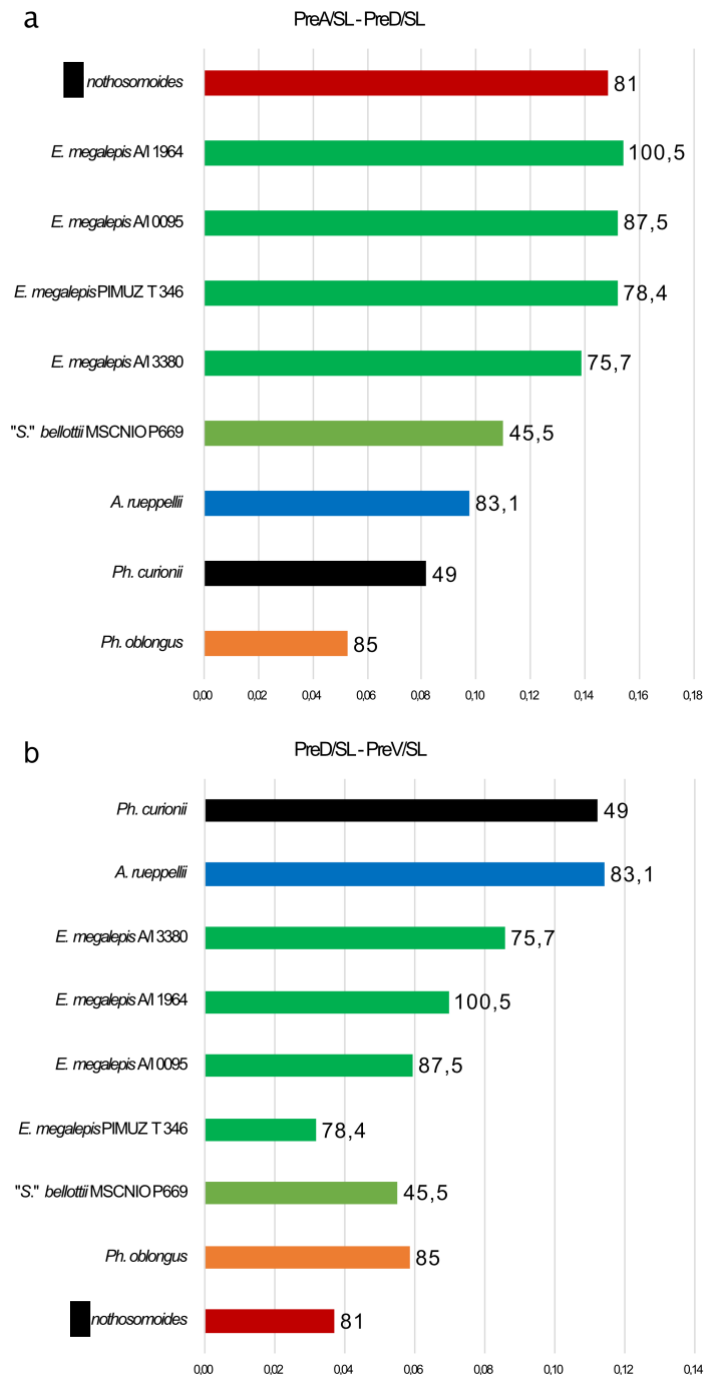
402 The type specimens of *Ph. curionii* and *Ph. oblongus* were part of the Perledo collection of the Natural
403 History Museum in Milan and were lost during World War II. Based on the measurements of the type
404 specimens reported by De Alessandri (1910), the body proportions and relative position of the fins indicate
405 that they probably represented different taxa (Fig. 5). However, since the holotypes cannot be examined,
406 it is impossible to confirm or reject the synonymy between these species and *E. bellottii* proposed by
407 Lombardo (2001). Therefore, *Pholidophorus oblongus* Bellotti, 1857, and *Pholidophorus curionii* Haeckel,
408 1910 (in De Alessandri, 1910), are regarded here as nomina dubia.

409 **Taxonomic status of *Perledovatus nothosomoides***

410 The combination of characters given in the above diagnosis allows to distinguish [REDACTED] from any
411 other Triassic neopterygian. In particular, the holotype and only known specimen of this species, strongly
412 mismatch the morphology of the holotype and only specimen of the type species of *Allolepidotus*, *A.*
413 *rueppelli*. The two specimens are of comparable size, but their general body shape and proportions are
414 noticeably different (Figs. 2–3). The relative position of the fins is very different in the two species (Figs. 5–
415 6). The anal fin is approximately in the same position in *A. rueppelli* and [REDACTED] *nothosomoides* (PreA/SL = 0,69
416 and 0,70, respectively). The dorsal fin is more posteriorly placed in *A. rueppelli* than in [REDACTED] *nothosomoides*
417 (PreD/SL = 0,60 and 0,56, respectively), while the opposite is true for the position of the pelvic fins (PreD/SL
418 = 0,48 and 0,52, respectively). As a result, the distance between the dorsal and anal fins is larger in [REDACTED]
419 *nothosomoides* than in *A. rueppelli*, but the distance between the dorsal and pelvic fins is smaller in the
420 first than in the second species (Fig. 6). More obviously, the head is much smaller and the body much
421 shallower in *A. rueppelli* than in [REDACTED] *nothosomoides* (HL/SL = 0,24 and 0,35, and BD/SL = 0,31 and 0,44,
422 respectively). Based on these data, and although the anatomical information is limited, we conclude that
423 each of the two species should be treated as separate genera.

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

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



442

443

444

445

446

Figure 6: Relative position of the fins respect to each other. Bar chart representing the distance between the dorsal and anal fins PreA/SL – PreD/SL (a), and the distance between the dorsal and pelvic fins PreD/SL – PreV/SL (b). The numbers at the end of each bar correspond to the SL values of each specimen.

447

Systematic position of *Perledovatus* gen. nov.

448

449

450

451

452

453

454

According to the cladistic analysis of López-Arbarello and Sferco (2018: Supplementary File S4), *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 *nothosomoides* is the very large gape. Among Triassic crown neopterygians, only teleosts and a few halecomorphs have

455 comparably large gapes. Triassic teleosts differ from *nothosomoides* in the presence of relatively short
456 and broad nasals, small antorbitals, two supramaxillae, and the dermosphenotic is not tightly sutured to
457 the skull roofing bones (e.g., Arratia 2013). Among Triassic halecomorphs, only *E. megalepis* and *E. bellottii*,
458 denoted *Eoeugnathus* and “*Allolepidotus*” in that work, *Subortichthys triassicus* Ma and Xu, 2017, from the
459 Guanling Formation at Luoping (Anisian, China), and *Sinoeugnathus kueichowensis* Su, 1959, from the
460 Falang Formation (Ladinian, China). In the recently published phylogenetic hypothesis of Fang et al. (2023),
461 these taxa form a monophyletic clade for which they proposed the new family name Subortichthyidae.

462 Except for the somewhat higher number of lateral line scales (38 vs. 30–35), *nothosomoides*
463 preserves six out of nine diagnostic features of Subortichthyidae: three supraorbitals; one suborbital;
464 quadrate almost fully covered by posterior portion of maxilla*; elongate maxilla extending posterior to
465 coronoid process of lower jaw*; supramaxillary process of maxilla relatively small; and complete row of
466 elongate scales between last lateral line scale and uppermost caudal fin ray*. Two of the remaining
467 diagnostic features, the proportion between the lengths of the frontal and parietal and the number of
468 branchiostegal rays, are not preserved in SMF P1237 which is the only specimen of *nothosomoides*.

469 The clade Subortichthyidae is supported by five unambiguous synapomorphies, three of which are
470 indicated with asterisks in the previous paragraph (Feng et al. 2023: chs. 94[1], 120[2], 223[1]). The
471 posterior end of the maxilla located posterior to the orbit (Feng et al. 2023: chs. 121[0]) is another
472 synapomorphy of Subortichthyidae also found in *nothosomoides*. The remaining two synapomorphies
473 of this clade, the presence of up to 35 lateral line scales (Feng et al. 2023: ch. 225[1]) is absent in
474 *nothosomoides*.

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

481

Conclusions

482 The revision of the type material of the species originally included in the genus *Allolepidotus* Deecke,
483 1889, led to the taxonomic revision of all halecomorph species from the Triassic of Perledo, Italy. Contrary
484 to Lombardo (2001), the morphological variation between these taxa is sufficient to confirm the existence
485 of four different taxa represented in the Perledo Formation.

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

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

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

503

Acknowledgements

504 Our very special thanks go to the preparator Olaf Vogel from Senckenberg, who performed the fine
505 preparation of SMF P1237. High quality photographs of the studied specimens were made by Lena Kraus
506 (SMF P1266) and Michael Ricker (SMF P1237), both technical assistants at Senckenberg in Frankfurt. We
507 are thankful to reviewer A, reviewer B, and the editor for their constructive comments and suggestions.

508

Funding

509 The research leading to these results received funding from the Deutsche Forschungsgemeinschaft
510 (DFG) through grant LO1405/8-1 to ALA.

511

Conflict of interest disclosure

512 The authors declare that they comply with the PCI rule of having no financial or non-financial conflicts
513 of interest in relation to the content of the article.

514 *Adriana López-Arbarello is recommender for one Peer Community (PCI Paleo).*

515

References

- 516 Arratia G, (2013) Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii,
517 Teleostei). *Journal of Vertebrate Paleontology*, **33**, 1–138.
518 <https://doi.org/10.1080/02724634.2013.835642>
- 519 Balsamo-Crivelli, G (1839) Descrizione di un nuovo rettile fossile, della famiglia dei Paleosauri, e di due pesci
520 fossili, trovati nel calcare nero, sopra Varenna sul lago di Como, dal nobile sig. Ludovico Trotti, con
521 alcune riflessioni geologiche. *Il politecnico repertorio mensile di studj applicati alla prosperita e coltura*
522 *sociale* **1**, 421–431.
- 523 Bassani, F (1886) Sui fossili e sull'eta` degli scisti bituminosi triassici di Besano in Lombardia. *Atti della*
524 *Societa` Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **29**, 15–72.
- 525 Bellotti, C (1857) Descrizione di alcune nuove specie di pesci fossili di Perledo e di altre localita` lombarde.
526 In: *Studii geologici e paleontologici sulla Lombardia*, ed. Stoppani, A, 491–438. Milano: Biblioteca
527 Politecnica.
- 528 Bellotti, C (1873) Osservazioni alla collezione dei pesci fossili del Museo civico. Dal catalogo manoscritto
529 del 1873, 27–30. Reprinted in Pinna, G (1991) I primi studi sui pesci fossili triassici della Lombardia al
530 Museo di Storia Naturale di Milano. *Natura: Rivista di Scienze Naturali*, **82**, 1–41.
- 531 Brough, J (1939) The triassic fishes of Besano, Lombardy. British Museum (N. H.), 117 pp., London.
- 532 Cope, ED (1872) Observations on the Systematic Relations of the Fishes. *The American Naturalist*, **5**, 579–
533 593. <https://doi.org/10.1080/00222937208696555>
- 534 Cope, ED (1887) Zittel's manual of palaeontology. *American Naturalist*, **21**, 1014–1019.
- 535 De Alessandri, G (1910) Studii sui Pesci Triasici della Lombardia. Memorie della Societa` Italiana di Scienze
536 Naturali e Museo Civico di Storia Naturale di Milano, *Societa` italiana di scienze naturali*, **7**, 1–145.
- 537 Deecke, W (1889) Uber Fische aus verschiedenen Horizonten der Trias. *Palaeontographica*, **35**, 13–138.
- 538 Feng, DH, Xu, GH, Ma, XY, Ren, Y (2023) Taxonomic revision of *Sinoeugnathus kueichowensis*
539 (Halecomorphi, Holostei) from the Middle Triassic of Guizhou and Yunnan, China. *Vertebrata*
540 *PalAsiatica*, **61**, 161–168.
- 541 Gaetani, M, Gnacolini, M, Poliani, G, Grignani, D, Gorza, M, Martellini, L (1992) An anoxic intraplateform
542 basin in the Middle Triassic of Lombardy (Southern Alps, Italy): Anatomy of a hydrocarbon source.
543 *Rivista Italiana di Paleontologia e Stratigrafia*, **97**, 329–354.
- 544 Haeckel, J (1849) Untersuchung der fossilen Fische des osterreichischen Kaiser-Staates. In *Neues Jahrbuch*
545 *für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 499–500.
- 546 Herzog, A (2003) A revision of the genus *Eoeugnathus* Brough, 1939 (Actinopterygii Halecomorphi) from
547 the Alpine Middle Triassic of Grisons (Switzerland). *Paläontologische Zeitschrift*, **77**, 223–240.
548 <https://doi.org/10.1007/BF03004570>

549 Lombardo, C (2001) Actinopterygians from the Middle Triassic of northern Italy and Canton Ticino
550 (Switzerland): anatomical descriptions and nomenclatural problems. *Rivista Italiana di Paleontologia e*
551 *Stratigrafia*, **107**, 345–369. <https://doi.org/10.13130/2039-4942/5439>
552 López-Arbarello, A (2004) Taxonomy of the genus *Percichthys* (Perciformes: Percichthyidae). *Ichthyological*
553 *Exploration of Freshwaters*, **15**, 331-350.
554 López-Arbarello, A, Sferco, E (2018) Neopterygian phylogeny: The merger assay. *Royal Society Open*
555 *Science*, **5**, 172337. <http://dx.doi.org/10.1098/rsos.172337>
556 Ma, XY, Xu, GH (2017) A new ionoscopiform fish (Holostei: Halecomorphi) from the Middle Triassic (Anisian)
557 of Yunnan, China. *Vertebrata Palasiatica*, **55**, 162–176.
558 Pinna, G (1991) I primi studi sui pesci fossili triassici della Lombardia al Museo di Storia Naturale di Milano.
559 *Natura*, **82**, 1–43.
560 Regan, CT (1923) The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower
561 neopterygian fishes. *Proceedings of the Zoological Society of London* 1923, 445–461.
562 <https://doi.org/10.1111/j.1096-3642.1923.tb02191.x>
563 Tintori, A, Muscio, G, Nardon, S (1985) The Triassic fossil fishes localities in Italy. *Rivista Italiana di*
564 *Paleontologia e Stratigrafia*, **91**, 197–209. <https://doi.org/10.54103/2039-4942/13312>
565 Woodward, AS (1895) Catalogue of the Fossil Fishes in the British Museum (Natural History), Volume 3.
566 British Museum (Natural History), London, 544 pp. <https://doi.org/10.5962/bhl.title.61854>
567