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Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy

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25 **Abstract**

26

27 The Eocene Konservat-Lagerstätte of Bolca, Italy, is famous for the abundance and exquisite  
28 preservation of its fossils. Although the Bolca sites have provided one of the most studied  
29 ichthyofaunistic fossil assemblages of the world, several aspects about the community  
30 structure and the biostratigraphic processes that led to the accumulation of its fish remains have  
31 been neglected or underestimated. In order to improve our knowledge concerning the  
32 palaeoecology and palaeoenvironment of Bolca, a quantitative palaeoecological and  
33 taphonomic analysis of the fish remains collected during controlled excavations at the  
34 Pesciara and Monte Postale sites is presented herein. The results of these analyses concur to  
35 suggest that these two sites have different speciose fish assemblages and different  
36 depositional contexts. The high-quality preservation of the fishes from the Pesciara site has  
37 allowed for the species level identification of most of its specimens, providing a good  
38 resolution of its palaeoecological spectrum. The Pesciara fish assemblage is defined by a  
39 sharp oligarchic structure clearly dominated by planktivorous taxa. The taphonomic features  
40 confirm that the sediments were deposited in an intraplatform basin in which anoxic conditions  
41 at the bottom and the development of the biofilm acted as promoters of high-quality fossil  
42 preservation. On the other hand, the moderate preservation quality of the fishes from Monte  
43 Postale does not allow for most of the specimens to be identified at the genus or species level,  
44 making it difficult to interpret the ecological and trophic relationships within this assemblage.  
45 Nevertheless, the abundance of marine and terrestrial plants, coupled with the large number of  
46 invertebrates (including abundant corals), concur to suggest that the sediments of Monte  
47 Postale were likely deposited close to an emerged coastal area characterized by mangroves,  
48 seagrass, and coral reefs. The prominent disgregation of fish skeletons, coupled with the  
49 unimodal dispersion of the elements and bioturbations, clearly indicate a high degree of

50 disturbance in the Monte Postale palaeoenvironment, suggesting at least periodic aerobic  
51 conditions at the bottom.

52

53 *Key words:* Palaeoichthyocenosis; quantitative palaeoecology; taphonomy; Eocene; Bolca  
54 Konservat-Lagerstätte.

55

56

## 57 **1. Introduction**

58

59 The Eocene locality of Bolca, northern Italy, has one of the most important and well  
60 known ichthyofaunistic fossil assemblages. The study of these fossils started in 1550 when  
61 the Italian botanist and physician Pietro Andrea Mattioli reported the existence of exquisitely  
62 preserved petrified fishes in the limestone of Bolca in the third edition of the translation of his  
63 “Dioscorides De Materia Medicinale” (see Sorbini, 1972; Carnevale et al., 2014).

64 In the last four decades, studies of the large number of specimens from Bolca housed  
65 in many museums, institutions and private collections around the world have allowed for  
66 extensive taxonomic revision of the fishes from this Eocene locality. This has resulted in a  
67 vast exploration of the diversity of the main teleost lineages, including anguilliforms,  
68 atheriniforms, beryciforms, clupeiforms, lophiiforms, pleuronectiforms, tetraodontiforms and  
69 several other percomorph groups, such as acanthuroids (e.g., Blot, 1969, 1978; Sorbini, 1984;  
70 Blot and Tyler, 1990; Tyler and Santini, 2002; Bannikov, 2004a, b, 2006, 2008; Bannikov and  
71 Zorzin, 2004; Monsch, 2006; Friedman, 2008; Bannikov and Carnevale, 2010; Carnevale and  
72 Pietsch, 2009, 2010, 2011, 2012; Marramà and Carnevale, 2015a, 2016).

73 Although more than 100,000 fish specimens have been collected from the two main  
74 sites of Bolca, the Pesciara and Monte Postale, during the last four centuries (Blot, 1969) and

75 more than 230 species representing at least 190 genera have been created (Bannikov, 2014;  
76 Carnevale et al., 2014), several aspects of the fish community structure, as well as of the  
77 depositional context of the Pesciara-Monte Postale system, remain elusive. Several studies  
78 concur to suggest that the Pesciara carbonates originated in a moderately depressed coastal  
79 tropical setting strongly influenced by the open sea (Landini and Sorbini, 1996), or originated  
80 in a shallow-water intraplatform basin (Papazzoni and Trevisani, 2006) with periodic unstable  
81 conditions (Petit, 2010). Recently, Trevisani (2015) proposed a unique model for the  
82 Pesciara-Monte Postale system, in which the Pesciara depositional context was considered  
83 substantially valid as well as for the Monte Postale site. In this context, the differences in  
84 preservation of the fishes between the two deposits are due to differential proximity to the  
85 open environment; this was considered to be less favorable to fossilization.

86 Coral bioconstructions have recently been reported in the area of Monte Postale  
87 (Papazzoni et al., 2014), but no direct evidence of coral bioherms has been reported for the  
88 Pesciara site. Although the abundances of reef fish families at Bolca is very different from  
89 those observed in modern reef contexts (Bellwood, 1996) and no representatives of fish  
90 groups exclusively associated with coral reefs have been found at Bolca, the entire  
91 ichthyofauna traditionally has been regarded as the oldest evidence of a coral reef fish  
92 assemblage of modern type (Blot, 1969, 1980; Sorbini, 1972; Choat and Bellwood, 1991;  
93 Bellwood, 1996). Moreover, the overall structure of the Pesciara and Monte Postale fish  
94 assemblages has in some cases been considered to be similar (Sorbini, 1972), or, in other  
95 cases, the latter was considered to be characterized by a larger component of pelagic taxa with  
96 respect to that of the Pesciara (Bannikov and Tyler, 1999; Bannikov and Zorzin, 2004).

97 Despite the fish diversity of the Bolca ichthyofauna having been extensively explored  
98 in the last several decades, a complete quantitative palaeoecological analysis and a  
99 taphonomic study are still lacking. Such studies could clarify several aspects of the

100 community structure and palaeoenvironment of this famous Konservat-Lagerstätte. From  
101 1999 to 2011 the Museo Civico di Storia Naturale di Verona, Italy, conducted controlled  
102 excavations at the Pesciara and Monte Postale sites. About 3000 fossils were extracted,  
103 including fishes, plants, invertebrates and coprolites. In this paper we present the first  
104 quantitative palaeoecological study and a taphonomic analysis of the fish assemblages of the  
105 two main sites of Bolca. The aim of this work is to contribute to the reconstruction of the  
106 structure of the fish assemblages of the Pesciara and Monte Postale sites based on their  
107 taxonomic composition and diversity. We also provide a comprehensive analysis of the  
108 preservation patterns (e.g., disarticulation and displacement of the skeletal elements, tetany  
109 features, etc.) in order to interpret the biostratinomic processes that led to the remarkable  
110 accumulation of fish skeletons at Bolca.

111

## 112 **2. Geological setting**

113

114 The specimens from the 1999-2011 controlled excavations were extracted from the  
115 fossiliferous layers of the Pesciara and Monte Postale sites, located in the eastern part of the  
116 Lessini Mountains (Southern Alps), about 2 km north-east of the village of Bolca, Verona  
117 Province, northeastern Italy (Fig. 1A). The two localities are about 300 m from each other and  
118 share some sedimentological features, such as the presence of finely laminated micritic  
119 limestone with fish and plant remains. However, the volcanic and volcanoclastic rocks  
120 surrounding the isolated block of the Pesciara site make it difficult to interpret the mutual  
121 stratigraphic relationships between the two fossiliferous layers, and clarification of these  
122 matters is still needed.

123 During the 1999-2011 excavations, specimens from the Pesciara site were quarried  
124 from a less than 2 m thick sequence with 13 fish-bearing strata corresponding to the L2 fine-

125 grained laminated micritic level of Papazzoni and Trevisani (2006) (Fig. 1B). The  
126 stratigraphic sequence of the Pesciara site has been investigated by several authors who  
127 referred the fossiliferous layers to the “Calcari Nummulitici”, an informal unit of Eocene age  
128 widely distributed in northeastern Italy (e.g., Fabiani, 1914; Sorbini, 1968; Barbieri and  
129 Medizza, 1969; Dal Degan and Barbieri, 2005; Papazzoni and Trevisani, 2006). The entire  
130 succession of the Pesciara site consists of a less than 20 m thick cyclic alternation of finely  
131 laminated micritic limestone, rich in exquisitely well-preserved fishes, plants and  
132 invertebrates, and coarse-grained biocalcarene/biocalcirudite with a benthic fauna (Fig. 1B).  
133 Based on their larger benthic foraminiferan content, the fish-bearing limestone of the Pesciara  
134 site has been referred to the *Alveolina dainelli* Zone (Papazzoni and Trevisani, 2006), or to  
135 the SBZ 11 Biozone (Serra-Kiel et al., 1998), corresponding to the late Cuisian (late Ypresian,  
136 slightly less than 50 Ma).

137         The entire Monte Postale succession includes the Cretaceous Scaglia Rossa Formation  
138 up to the Ypresian-?Lutetian limestone. The first detailed stratigraphic study of the Monte  
139 Postale site was carried out by Fabiani (1914, 1915), who assigned the entire succession to the  
140 Lutetian. More recently, a preliminary report by Papazzoni and Trevisani (2009) considered  
141 the lower-middle strata of the Monte Postale site to be Ypresian. At present, there are no  
142 detailed biozonal assignments for the uppermost sequence of the Monte Postale section,  
143 where the specimens of the 1999-2011 excavations were extracted. The fossils of the Monte  
144 Postale site, discussed herein, were collected from 36 fine-grained laminated micritic layers  
145 pertaining to the uppermost part of the succession (Fig. 1B); based on their benthic fauna,  
146 these strata were interpreted to be Lutetian in age by Fabiani (1914, 1915) and Malaroda  
147 (1954), or Ypresian by Hottinger (1960). Recently, Trevisani (2015) referred the fish-bearing  
148 layers of the uppermost part of the Monte Postale succession to the microfacies M of  
149 Papazzoni and Trevisani (2006), consisting of pale to dark finely laminated mudstone

150 containing abundant plants, small foraminiferans, invertebrates and fish remains. Although  
151 coral bioconstructions were reported only for the Monte Postale succession (Papazzoni et al.,  
152 2014), and the overall preservational features of the skeletal remains differ from those of the  
153 Pesciara site, Trevisani (2015) proposed a unique model for the Pesciara-Monte Postale  
154 system, in which the two successions are considered coeval, being part of a tropical coastal  
155 lagoon bordered by a volcanic archipelago and a carbonate buildup. According to Trevisani  
156 (2015), the different preservational quality of the fossil remains between these two sites is  
157 related to differences in proximity to the offshore environment, which is considered less  
158 favorable to high-quality preservation.

159

### 160 **3. Material and methods**

161

162 The present analysis is based on 1188 fish remains that were collected during the  
163 systematic quarrying of the fossiliferous layers of the Pesciara and Monte Postale site from  
164 1999 to 2011. All the specimens are currently housed in the collections of the Museo Civico  
165 di Storia Naturale di Verona (MCSNV). The material was examined using a Leica M80  
166 stereomicroscope and measurements were made to the nearest 0.1 mm using a dial caliper.

167 For quantitative palaeoecology, the standard length (SL) of fishes is used throughout.  
168 Orientation data were also assessed. In order to detect sampling quality, individual-based  
169 taxon accumulation curves were obtained for each site (Gotelli and Colwell, 2001). The curve  
170 rises quickly as more taxa are recorded, whereas it arises slowly if few taxa are recognized in  
171 a large sample. Therefore, the taxon accumulation curve can also be indicative of species  
172 richness. The taxonomic diversity of the two fish assemblages was computed by selecting  
173 different diversity indices: we used the Dominance, Berger-Parker, Simpson and Shannon  
174 indices that are insensitive to sample size and describe different patterns of taxonomic



175 diversity such as the abundance of taxa, species richness and evenness (Magurran, 2004). The  
176 Shannon *t*-test was used in order to detect if the two fish assemblages exhibit different species  
177 diversity. The relative abundance of each species in its own assemblage was evaluated using  
178 the semi-quantitative ACFOR approach, ranking the species as abundant (>50%), common  
179 (50–26%), frequent (25–6%), occasional (5–1%) and rare (<1%). Detailed content of the two  
180 samplings with the relative abundance of species is provided in Tables 1 and 2. Since the  
181 preservation of most of the specimens from Monte Postale did not allow for the identification  
182 of many taxa of fishes at the species level, the overall composition of the Pesciara and Monte  
183 Postale fish assemblages was computed in terms of percentage at high taxonomic level,  
184 following, e.g., Bieńkowska-Wasiluk (2010) and Iserbyt and De Schutter (2012).

185         The taphonomy of the Pesciara and Monte Postale sites was measured in terms of the  
186 completeness of specimens, 3D orientation of the body with respect to the bedding plane, and  
187 analysis of tetany features. Completeness was based on the degree of articulation of the  
188 skeletons (Fig. 2). Four degrees of completeness were distinguished, as follows. “Fully  
189 articulated” for specimens in which the skeletal elements are completely articulated and in  
190 anatomical connection without remarkable signs of disgregation; and the scales are all firmly  
191 attached and the body outline is well-defined (Figs. 2A–B). “Partially articulated” for  
192 specimens with recognizable body outline (Figs. 2C–D) and articulated vertebral centra, even  
193 if some skeletal elements are unjoined or disarticulated (e.g., ribs, jaws, fins); and most of the  
194 scales are still attached but some of them may be scattered and lie around the skeleton.  
195 “Disarticulated” for specimens with unclear body outline (Figs. 2E–F) and dislodged or  
196 unjoined vertebral centra; and most of the skeletal elements are fully disarticulated, spread out  
197 and sometimes lost. Fragmentary or isolated elements (scales, vertebral centra, teeth, isolated  
198 bones) represent a separate degree of completeness (Figs. 2G–I).

199           The 3D orientation of the body was documented with respect to the bedding plane. A  
200 “lateral” orientation was determined when the dorso-ventral axis of the specimen is parallel to  
201 the bedding plane, with the fish laying on its side (Figs. 3A, D, F, H). By contrast, “dorso-  
202 ventral” refers to specimens with the dorso-ventral axis perpendicular to the bedding plan,  
203 thereby exhibiting their dorsal or ventral side (Fig. 3B, G).

204           Tetany is a postmortem contraction of the muscles of the fish caused by traumatic  
205 environmental conditions (e.g., Schaeffer and Mangus, 1976; Ferber and Wells, 1995). In  
206 order to define the degree of tetany, three features were recorded: jaw aperture with closed  
207 (Figs. 3D, F) or open mouth (Figs. 2A–B, 3A, C); backbone curvature showing concave (Figs.  
208 2A, 3A), convex (Fig. 3E), S-shaped (Fig. 3C) or straight vertebral column (Figs. 3D, F, H);  
209 fin disposition pattern including flabellate (Figs. 2C, 3F, G), closed (Figs. 2A, 3D) or  
210 disordered fin elements (Fig. 3H). Of these features, gaping jaw, dorsally concave backbone  
211 (i.e., opisthotonic posture) and flabellate fins can be referred to as tetany features (Faux and  
212 Padian, 2007; Anderson and Woods, 2013; Pan et al., 2015), whereas a S-shaped vertebral  
213 column and disordered fin elements may be indicative of weak currents acting when the fish  
214 was already partially decomposed (Hecker and Merklin, 1946; Jerzmańska, 1960;  
215 Bieńkowska, 2004; Pan et al., 2015). Incomplete specimens were taken into account when the  
216 features used in the taphonomy were recognizable (see Bieńkowska-Wasiluk, 2010).

217           In order to identify the overall taphonomic state of each fish assemblage, a cluster  
218 analysis was performed using the Ward’s method on the nine standardized attributes  
219 described above and summarized in Table 3. Then, a combination of principal component  
220 analysis (PCA) and canonical variate analysis (CVA) was performed in order to have a visual  
221 image of the degree of separation between taphonomic states. Obviously, the analysis was  
222 performed only for those specimens having all nine of the standardized attributes; incomplete

223 specimens, fragments and isolated elements cannot be included because of the lack of most of  
224 the features.

225 Further considerations were also formulated based on the presence of other features,  
226 including signs of currents at the bottom, predation, bioturbations and coprolites.

227 All methods follow the schemes applied in recent studies of quantitative  
228 palaeoecology and taphonomy of extinct palaeoichthyocenoses, mainly Fara et al. (2005),  
229 Chellouche et al. (2012), Mancuso (2012), Anderson and Woods (2013) and Pan et al. (2015).  
230 It is often assumed that standard statistics that directly compare abundance distribution (e.g.,  
231 Chi-square) or parametric tests (e.g., ANOVA) may not be useful for palaeontological data. In  
232 this study the non-parametric test for multivariate analysis of similarities (ANOSIM, Clarke,  
233 1993) was used in order to recognize significant differences in content, preservation or tetany  
234 features between levels or localities. The Bray-Curtis index was chosen as the distance  
235 measure because it places emphasis on the difference between the common taxa (Bray and  
236 Curtis, 1957; Etter, 1999). Alpha was set at 0.05. All analyses were performed using the  
237 software package PAST 3.08 (Hammer et al., 2001). Additional details are in the  
238 Supplementary Material.

239

## 240 **4. Results**

241

### 242 *4.1. Quantitative palaeoecology*

243

#### 244 *4.1.1. Size-frequency analysis and rose diagram*

245 Fishes from the Pesciara site range from 10 to 530 mm SL; 95% of the specimens are  
246 less than 130 mm (Fig. 4). The plot has a bimodal pattern, with a first peak at about 20–30  
247 mm reflecting the abundance of small-sized fishes, mostly apogonids and holocentrids; the

248 second distinct peak is around 50–70 mm and reflects the abundance of the epipelagic sardine  
249 *Bolcaichthys catopygopterus*, whose individuals reached their maturity at about this size  
250 (Marramà and Carnevale, 2015b). There is no apparent relationship between the SL of the  
251 fishes and their stratigraphic position as shown in the box plots whose medians range from 30  
252 to 60 mm in all levels of the Pesciara section (Fig. S1A). The ANOSIM suggests the same  
253 trend, indicating no significant difference in size-frequency between layers ( $R=-0.02$ ,  $p=0.56$ ).

254 Fishes from the Monte Postale site range from 10 to 900 mm SL; 95% of the  
255 specimens are less than 180 mm (Fig. 4). The size-frequency distribution has a polymodal  
256 pattern, with a main distinct peak around 10–30 mm reflecting the abundance of small-sized  
257 fishes, mainly perciforms and clupeids. The ANOSIM detected no significant difference in  
258 size ranges between the productive layers of the Monte Postale succession (Fig. S1B;  $R=0.18$ ,  
259  $p=0.08$ ).

260 Based on size-frequency analysis, the Pesciara and Monte Postale assemblages have  
261 different variances and high dissimilarity (ANOSIM:  $R=0.49$ ,  $p=0.0001$ ); this suggests that  
262 the specimens belong to two different populations. Both of the assemblages also have a  
263 leptokurtosis right-skewed distribution (Kurtosis  $\gg 0$ ; Skewness  $\gg 0$ ) indicative of high  
264 mortality for small-sized individuals.

265 Limited data on orientation are available only for the Pesciara fish assemblage (Fig.  
266 5). Directionality tests do not indicate any preferential orientation pattern (all  $p>0.05$ ); this  
267 suggests that there are no significant agents affecting the orientation of the carcasses before  
268 burial.

269

#### 270 4.1.2. Taxonomic composition

271 The overall composition of the two assemblages is very different in terms of category  
272 percentages (Fig. 6). Although fishes are the most studied component of the Bolca Konservat-

273 Lagerstätte, plant remains, invertebrates and coprolites are well-represented in both deposits  
274 (Fig. 7). Terrestrial vertebrates were not found during the controlled excavations.

275         Fishes represent more than 55% of the specimens at the Pesciara site, whereas about  
276 38% of the sample is composed of plant remains, mainly macroalgae and seagrasses  
277 (*Delessertes* and *Halochloris*), some dicotyledonous angiosperms, and amber. Crustaceans,  
278 mollusks and insects are less than 6% of the sample, and coprolites represent about 1%. By  
279 contrast, macroalgae, seagrasses, and terrestrial plants are the main component of the Monte  
280 Postale assemblage (about 50%), and fishes represent about one third of the sample.  
281 Invertebrates (15.6%) and coprolites (3.4%) from Monte Postale are more abundant with  
282 respect to those of the Pesciara site. One of the most distinctive features that differentiate the  
283 two sites is the exclusive presence of coral remains in all the fish-bearing strata of Monte  
284 Postale (Fig. 7F).

285         The Pesciara and Monte Postale sites are characterized by notably diverse fish  
286 assemblages containing several species each. Although in terms of presence/absence, Pesciara  
287 and Monte Postale share most of the main fish groups, but their relative abundances are very  
288 different (Figs. 8A–B). A total of 595 specimens collected from the 13 fossiliferous layers at  
289 the Pesciara site yielded at least 40 species belonging to 27 families and nine orders (Table 1).  
290 The most striking feature of the taxonomic composition of the Pesciara fish assemblage is the  
291 overwhelming abundance of clupeids, with the sardine *Bolcaichthys catopygopterus* being the  
292 dominant species in all layers (about 60% of the specimens, Fig. 8A). The size-frequency  
293 distribution for this taxon and the survivorship curve approximating a Type I convex-up curve  
294 (Fig. S2A–B) clearly indicate increasing mortality with age, suggesting that juvenile *B.*  
295 *catopygopterus* are not well-represented. Perciforms are the second most abundant lineage,  
296 with apogonids, menids, percichthyids and sparids together representing about 27% of the  
297 sample. Squirrelfishes (Holocentridae) represent the third most abundant lineage, and the

298 second most abundant family after clupeids (about 6% of the specimens). Representatives of  
299 anguilliforms, atheriniforms, anotoophysans, syngnathiforms, tetraodontiforms and  
300 dactylopteriform-like fishes together account for the remaining 7% of the sample. There are  
301 no significant differences in relative abundance of the fish lineages in any of the sampled  
302 fossiliferous layers (Fig. S3; ANOSIM:  $R=0.16$ ,  $p=0.30$ ); this suggests that the structure of  
303 the fish assemblage was very similar throughout the stratigraphic sequence of the Pesciara  
304 site.

305 A total of 593 specimens from the 36 fossiliferous levels at Monte Postale yielded 34  
306 identifiable species belonging to 25 families and 8 orders (Table 2). Perciforms are dominant,  
307 with scombrids, acropomatids, menids, putative labroids and sparids together accounting for  
308 about 60% of the sample (Fig. 8B). Clupeids constitute about 30% of the specimens, with the  
309 round herring *Trollichthys bolcensis* being the most common species. The size-frequency  
310 distribution and the survivorship curve of this taxon approximate a sigmoid-shape curve (Fig.  
311 S2C–D), suggesting an increasing mortality in young individuals. Another interesting feature  
312 of the Monte Postale assemblage is the relative abundance of isolated shark teeth that,  
313 together with the large numbfish, *Titanonarke molini*, represent 5% of the specimens, making  
314 elasmobranchs the third most common lineage. Anguilliforms, beloniforms, beryciforms,  
315 lophiiforms and syngnathiforms account for about 7% of the sample. The ANOSIM did not  
316 indicate significant difference in relative abundance of the lineages in the 36 fossiliferous  
317 layers sampled (Fig. S3;  $R=0.11$ ,  $p=0.12$ ), suggesting that the abundance of taxa was similar  
318 in the Monte Postale sequence.

319 As expected, there are significant differences in taxonomic composition between the  
320 Pesciara and Monte Postale fish faunas (ANOSIM:  $R=0.26$ ,  $p=0.002$ ).

321

322 *4.1.3. Sampling and taxonomic diversity*

323           The sampling quality in both deposits was tested by analyzing the respective  
324 rarefaction curves (Fig. 9). The abundance of the sardine *Bolcaichthys catopygopterus* at the  
325 Pesciara site (293 individuals out of 466 specimens identifiable at the species level) produced  
326 a curve that rises slowly, whereas the more even distribution of the Monte Postale site  
327 produced a curve that rises more steeply. Nevertheless, neither curve reaches an asymptotic  
328 trend, suggesting that sampling was not sufficient to explain the full diversity of the Bolca  
329 fish assemblage.

330           Diversity indices clearly suggest different taxonomic diversity for the two assemblages  
331 (Table 4). The overwhelming abundance of the sardine *B. catopygopterus* results in the  
332 highest values of Dominance and Berger-Parker indices and the lowest scores for the Simpson  
333 and Shannon indices in the Pesciara fish assemblage. On the other hand, the absence of  
334 dominant species in the Monte Postale assemblage produces low values of Dominance and  
335 Berger-Parker, as well as the highest scores of the Simpson and Shannon indices. The  
336 different taxonomic diversity of the two assemblages is corroborated by the Shannon *t*-test  
337 ( $p < 0.001$ ).

338

## 339 4.2. Taphonomy

340

### 341 4.2.1. Completeness and 3D orientation patterns

342           The degree of completeness of the fish remains is clearly different at the two sites.  
343 About 80% of the specimens of the Pesciara fish assemblage have a moderately high to  
344 excellent degree of preservation of the skeletons (Fig. 10). More than one quarter of the  
345 specimens are fully articulated, without evident traces of disarticulation of the skeletal  
346 elements; the scales are firmly attached to the body and all the lepidotrichia are articulated.  
347 About half of the specimens are partially articulated; although the centra of the vertebral

348 column are articulated without evidence of rotation, the specimens have partial disarticulation  
349 of some elements of the cranium. In particular, the upper and lower jaws are often displaced  
350 (mostly in clupeids), and the hyoid apparatus is sometimes disarticulated. The fins may be  
351 distally disordered and some lepidotrichia lost. A few scales appear to be detached from the  
352 body. About 20% of the specimens are disarticulated and only 3% of the examined material is  
353 represented by isolated skeletal elements. The specimens usually lie on the lateral surface of  
354 the body. Therefore, the “lateral” orientation of the body with respect to the bedding plane  
355 sharply dominates (94.5%) relative to the scarce number of fishes showing their dorsal or  
356 ventral side (5.5%). The various degrees of completeness and 3D orientation patterns are  
357 similar in all the sampled layers of the Pesciara quarry (Figs. S4A–S5A), suggesting a  
358 substantial homogeneity of preservational features (ANOSIM:  $R=0.20$ ,  $p=0.23$ ).

359 By contrast, more than 85% of the specimens of the Monte Postale assemblage have a  
360 low degree of completeness of the skeletal remains (Fig. 10), resulting in a reduced number of  
361 specimens identifiable at the species level (see Table 2). Very few specimens are fully  
362 articulated (4.2%) or partially articulated (13.2%). It is interesting to note that more than 60%  
363 of the fully or partially articulated specimens are small-sized fishes of less than 40 mm SL.  
364 About 50% of the specimens appear disarticulated and more than one third are represented by  
365 isolated skeletal remains. Similar to the Pesciara assemblage, more than 92% of the  
366 specimens of the Monte Postale site are preserved in “lateral” 3D orientation, whereas about  
367 8% of the fishes are “dorso-ventrally” oriented. No significant differences in the degree of  
368 completeness and 3D orientation pattern were detected between the strata of the Monte  
369 Postale sequence (Figs. S4B–S5B; ANOSIM:  $R=0.02$ ,  $p=0.37$ ). As expected, the test  
370 demonstrates remarkable differences between the two sites concerning the degree of  
371 articulation and 3D orientation of the specimens ( $R=0.62$ ,  $p=0.0001$ ).

372



373 4.2.2. *Tetany features*

374 Fishes from the Pesciara and Monte Postale sites show different degrees of tetany (Fig.  
375 11). In both of the assemblages most of the specimens have widely gaping jaws, and no  
376 significant difference has been observed in terms of individuals having this pattern between  
377 the Pesciara (67.5%) and Monte Postale (80.2%) sites. More remarkable is the presence of a  
378 large number of individuals with concave bending of the backbone in the Pesciara assemblage  
379 (44.2%) compared to that characteristic of the Monte Postale assemblage (24.8%). Some  
380 individual of the Pesciara site, especially the relatively uncommon juvenile clupeids, have  
381 vertebral columns that are fractured in one or more places due to the extreme postmortem  
382 contraction of muscles (e.g., Fig. 3A). More than 80% of the fish with concave distortion of  
383 the vertebral column from the Pesciara site are clupeids. Specimens with S-shape deformation  
384 of the vertebral column are much more abundant in the Monte Postale assemblage (29.4%)  
385 than in the Pesciara assemblage (7.9%). The percentage of individuals without deformation of  
386 the backbone appears to be similar in both assemblages (about 50% of specimens). The most  
387 common fin pattern observed in the Pesciara specimens is the flabellate disposition, present in  
388 more than 45% of the examined specimens. By contrast, this pattern was found in about 20%  
389 of the specimens from the Monte Postale site. On the other hand, more than 70% of the  
390 specimens from Monte Postale have disordered fins; this feature was found in only about 18%  
391 of the specimens from the Pesciara site.

392 The ANOSIM indicated no significant differences in the degree of tetany of the  
393 specimens from the fossiliferous layers of both the Pesciara ( $R=0.20$ ,  $p=0.26$ ) and Monte  
394 Postale sites ( $R=0.12$ ,  $p=0.08$ ), suggesting that biostratigraphic processes are consistent  
395 throughout the stratigraphic sequences in both sites (see also Figs. S6–S8). However, as  
396 expected, the test detected highly significant differences in degree of tetany between the  
397 Pesciara and Monte Postale sites ( $R=0.50$ ,  $p=0.0001$ ).

398           Although articulated individuals of similar size on a single bedding plane found in  
399 some museum specimens (see, e.g., Marramà and Carnevale, 2015b) document mass  
400 mortality events (see, e.g., Martill et al., 2008), the number of fishes per square meter is  
401 generally too low in both sites to be able to identify catastrophic events as one of the main  
402 causes of fish accumulation. Localized and small concentrations of fishes recognized in some  
403 levels of the Monte Postale site were probably in some way related to the action of currents.  
404 Therefore, it is reasonable to suggest that time-averaging may have represented the main  
405 factor for the concentration of individuals in the productive layers of both sites, as reported  
406 also for other Konservat-Lagerstätten (e.g., Grande, 1984).

407

#### 408 *4.2.3. Cluster analysis*

409           A cluster analysis based on the nine standardized taphonomic features discussed above  
410 and reported in Table 3 was performed on 194 specimens from the two assemblages. The  
411 analysis divides the specimens into three well-separated groups representing the combinations  
412 of different identifiable taphonomic states (Fig. 12). Cluster 1 contains almost exclusively  
413 poorly-preserved specimens from the Monte Postale assemblage having mainly disarticulated  
414 bones and disordered disposition of the fin elements. Cluster 2 contains mainly taxa from the  
415 Pesciara site that are fully or partially articulated, with a concave bending of the vertebral  
416 column, open mouth and flabellate fins; this particular combination of features typically  
417 characterizes tetany, involving mainly the sardine *Bolcaichthys catopygopterus*, which is the  
418 dominant species in the Pesciara fish assemblage. Cluster 3 includes specimens with a more  
419 variable combination of taphonomic features that are common in both the Pesciara and Monte  
420 Postale assemblages. The specimens of cluster 3 are fully or partially articulated, primarily  
421 with straight backbone, and flabellate, closed or disordered fins. This latter combination of

422 features is typical of perciforms, which only rarely have the backbone bent, unlike clupeids  
423 which tend to undergo a concave curvature of the vertebral column (Bieńkowska, 2004).

424         The PCA made on the nine standardized taphonomic features produced nine PC axes,  
425 with the first three explaining about 87% of the variance (Table 5). All PC axes were used to  
426 perform the CVA, producing a scatterplot of the specimens along the first two canonical axes,  
427 and yielding a visual image of the maximal separation between the groups (Fig. 13). The  
428 polygons do not show significant overlap. The specimens belonging to cluster 1 are clearly  
429 separated from the others and lie on the opposite side from cluster 2. There is only weak  
430 overlap between clusters 2 and 3.

431

#### 432 *4.2.4. Additional biostratinomic features*

433         Other taphonomic characters observed in the examined fossils include the so-called  
434 “half-and-half” fishes, current marks, evidence of predator-prey relationships, and  
435 bioturbation. Some specimens from the Pesciara site have a particular pattern of preservation  
436 in which the posterior part of the body is well-preserved and articulated whereas its anterior  
437 part is totally or partially disgregated (Fig. 14A). This particular pattern is typical of the so  
438 called “half-and-half” fishes and is regarded as possible evidence of the presence of a  
439 microbial mat (e.g., Hellowell and Orr, 2012; see Discussion). Several fishes from the Monte  
440 Postale site have an unimodal distribution of scales, orientated along a preferential direction  
441 (Fig. 14B, I), that has been interpreted as clear evidence of biological or hydrodynamic  
442 disturbance (e.g., Tintori, 1992; Chellouche et al., 2012). Specimens from the Pesciara site  
443 never exhibit this kind of taphonomic feature.

444         Although rare, some evidence of direct predation can be recognized in both of the fish  
445 assemblages. Because of the abundance of clupeids, the most evident sign of predator-prey  
446 relationships in the Pesciara quarry is the presence of cololites (i.e., intestinal content) lying in

447 the abdominal region of *Bolcaichthys catopygopterus* specimens. The cololites are not coiled  
448 and are relatively short in relation to the zooplanktivorous diet of these fishes (see Marramà  
449 and Carnevale, 2015b). Further evidence of predation is exclusive to the Monte Postale site  
450 and is represented by regurgitates entirely composed by fish bones (Fig. 14F). An exquisite  
451 direct evidence of predator-prey relationships from the Monte Postale site is represented by a  
452 single specimen of *Pseudaxides speciosus* (Scombridae) having at least two articulated small  
453 prey fishes as stomach content, likely representing the round herring *Trollichthys bolcensis*  
454 (Fig. 14G–H). Evidence of bioturbation appears to be not present in the slabs extracted from  
455 the Pesciara site, whereas these are common in the material from the Monte Postale site (Fig.  
456 14E).

457

## 458 **5. Discussion**

459

460 Although more than 1000 fish remains were collected from the Pesciara and Monte  
461 Postale sites, only a small part of the overall taxonomic diversity of the Bolca fish assemblage  
462 has been revealed in the 12 (1999-2011) years of controlled excavations (see Carnevale et al.,  
463 2014). As expected, the excavations yielded the most common species as well as some rare  
464 taxa. As a consequence, the results of the excavations define two different diverse fish  
465 communities pertaining to two different depositional contexts. Although both sites need  
466 further sedimentological and geochemical investigations before a comprehensive  
467 palaeoenvironmental scenario can be outlined, the recent controlled excavations revealed new  
468 details that confirm and improve upon previous palaeoenvironmental hypotheses.

469

### 470 *5.1. The Pesciara fish assemblage*

471

472           The high quality preservation of the fishes from the Pesciara allowed the identification  
473 of about 80% of the collected specimens, providing a good resolution for the interpretation of  
474 their palaeoecological significance. The palaeoecology of the most common taxa appears to  
475 be consistent with the interpretation proposed by Landini and Sorbini (1996) for the Pesciara  
476 palaeobiotope. Clupeids, atheriniforms, ductorids, carangids, menids and blochiids were the  
477 most common representatives of the peri-reefal/pelagic assemblage defined by Landini and  
478 Sorbini (1996), whereas anguilliforms, labroids, siganids, syngnathiforms and  
479 tetraodontiforms represent the most common taxa of the so-called sand/seagrass bed  
480 assemblage. Representatives exclusively associated with coral reefs were not detected.

481           From a trophodynamic point of view, the taxonomic composition concurs to suggest  
482 that the Pesciara assemblage was dominated by zooplanktivorous fishes. The overwhelming  
483 abundance of the sardine *Bolcaichthys catopygopterus* results in the lower diversity of the  
484 Pesciara fish assemblage with respect to that of Monte Postale. The analyses of the size  
485 frequency and the survivorship curve of this taxon (Fig. S2A-B) indicate that juveniles were  
486 not well-represented, contrary to what would be expected in a population in which young  
487 individuals should be the most abundant (see Newbrey and Bozek, 2003). Modern juvenile  
488 clupeids primarily inhabit very shallow bays and inlets (e.g., Blaxter and Hunter, 1982;  
489 Munroe, 2000); consequently, the presence of a large number of adult *B. catopygopterus* in  
490 the Pesciara assemblage seems to exclude these kinds of biotopes as possible modern  
491 analogues of the Pesciara palaeoenvironment (see Marramà and Carnevale, 2015b). Genner et  
492 al. (2004) demonstrated that in inshore marine fish assemblages, environmental fluctuations  
493 may have a negative effect on the abundance of the dominant species. Since commonness and  
494 rarity of taxa can be related to their permanence in the assemblage (Magurran and Henderson,  
495 2003), it is possible to hypothesize that the dominance of *B. catopygopterus* in the Pesciara  
496 assemblage can be related to the permanent presence of this taxon in a stable environment,

497 remarkably influenced by the open sea. In particular, the very large number of sardine  
498 specimens could be related to the abundance of zooplankton in a nutrient-rich environment.  
499 According to Schwark et al. (2009), molecular biomarkers measured in the fossiliferous  
500 limestone of the Pesciara site suggest that the primary production was dominated by diatoms.  
501 Therefore, diatoms possibly constituted a large part of the base of the trophic chain of the  
502 Pesciara assemblage, sustaining zooplankton, which in turn represented the main food  
503 resource of sardines. Extant clupeids represent a fundamental prey for higher trophic level  
504 fishes, playing a central role in the ecology of modern tropical coastal marine environments  
505 (e.g., Longhurst and Pauly, 1987). These fishes possibly represented the trophic nucleus in the  
506 Pesciara palaeobiotope, being extensively exploited by the diverse assemblage of piscivorous  
507 fishes. Nocturnal invertebrativedores, represented by squirrelfishes (Holocentridae) and  
508 cardinalfishes (Apogonidae), are also relatively common in the Pesciara palaeobiotope, where  
509 they probably occupied the role of commuters of energy from adjacent habitats feeding on  
510 invertebrates living around seagrass beds and mangroves (see Parrish, 1989). The abundance  
511 of clupeids and nocturnal feeders is therefore consistent with the hypothesis that the Pesciara  
512 palaeobiotope was not directly associated with a coral reef system, but, rather, most likely  
513 represented a peri-reefal system, strongly subject to the ecological influence of both the  
514 coastal environment and the open sea (Landini and Sorbini, 1996).

515         The most striking taphonomic feature of the Pesciara site is the remarkable large  
516 number of well-preserved complete and partially complete fish specimens that constitute  
517 about 80% of the collected fishes. The good preservation of the fishes and, in particular, the  
518 complete squamation, clearly indicates an early interruption of the decay processes (e.g.,  
519 Weiler, 1929; Bieńkowska-Wasiluk, 2010). Taphonomic studies conducted on fossil fish  
520 assemblages (e.g., Elder, 1985; Elder and Smith, 1988; Wilson and Barton, 1996; Barton and  
521 Wilson, 2005; Pan et al., 2015) suggested that high-quality preservation in Konservat-

522 Lagerstätten is the result of a combination of several factors. The overall completeness of the  
523 specimens indicates that carcasses were not subject to prolonged floating after death, likely  
524 being rapidly accumulated on the bottom. The presence over an extended period of time of  
525 fishes in the water column after their death may also be excluded because all the skeletal  
526 elements (lower jaw, fins, ribs) of the disarticulated or partially disarticulated specimens are  
527 concentrated around the carcasses, thereby suggesting that decay processes took place on the  
528 bottom (see Chellouche et al., 2012). The possibility of a prolonged floatation of the carcasses  
529 may also be excluded because of the presence of only a few “dorso-ventrally” oriented  
530 specimens. Although the dorso-ventral orientation of the specimens could be also related to  
531 the anatomy of fish, or, alternatively, the result of sinking of the carcasses into a soft substrate  
532 (Schäfer, 1972), these fishes are usually indicative of prolonged floating due to the  
533 considerable amount of gases that expand the abdominal cavity and lead to the fish floating  
534 with its belly up, and subsequently to be deposited with its dorso-ventral axis perpendicular to  
535 the bedding plane (see, e.g., Pan et al., 2015).

536         Experimental studies have suggested that the high pressure of deep water  
537 environments may suppress the production of decay gas and prevent the disarticulation of  
538 carcasses (e.g., Elder, 1985; Elder and Smith, 1988). It is unlikely that hydrostatic pressure  
539 was sufficient to prevent floating and refloating in the Pesciara palaeobiotope because  
540 sedimentological and stratigraphic evidence concur to suggest that the fossiliferous sediments  
541 originated at some dozen of meters in a coastal setting (Landini and Sorbini, 1996) or, more  
542 generally, in a shallow-water intraplatform basin (Papazzoni and Trevisani, 2006).

543         Several studies have demonstrated that high temperatures over 20°C contribute to  
544 accelerate decomposition (e.g., Swift et al., 1979), whereas low temperatures may promote  
545 good preservation of fossil fishes (e.g., Pan et al., 2015). The possibility of cold temperature  
546 as a major cause for the good preservation of specimens in the Pesciara deposit can be

547 excluded because of the very high mean annual palaeotemperature estimated for this region of  
548 the northwestern Tethys (see Giusberti et al., 2014). Moreover, the occurrence of the  
549 specialized marine water strider *Halobates* (Fig. 7H) suggests a sea surface  
550 palaeotemperatures exceeding 20°C, the latter representing the lower value tolerated by the  
551 extant species of this genus (Andersen et al., 1994; Cheng et al., 2012).

552         Papazzoni and Trevisani (2006) demonstrated that the main feature of the Pesciara  
553 fish-bearing microfacies is the regular or slightly wavy, varve-like lamination with a nearly  
554 complete absence of bioturbation. These kinds of structures are also typical of other  
555 Konservat-Lagerstätten, including the Jurassic Solnhofen (Viohl, 1990) and the Eocene Green  
556 River Formation (Fischer and Roberts, 1991). The alternation of light and dark laminae has  
557 been traditionally interpreted as the product of seasonal changes (e.g., Bradley, 1929, 1948;  
558 McGrew, 1975; Crowley et al., 1986). More recently, the origin of the varved deposits has  
559 been reinterpreted and considered to be the result of the development of conspicuous  
560 microbial mats at the sediment-water interface (Fischer and Roberts, 1991; Schieber, 1999,  
561 2007; Papazzoni and Trevisani, 2006; Hellowell and Orr, 2012). Several studies concur to  
562 demonstrate that microbial mats are implicated in the high quality preservation of fossils by  
563 delaying their decomposition, inhibiting floating and disarticulation, protecting the carcasses  
564 from scavengers and bottom currents, preventing contact with the oxygenated water column,  
565 and promoting the formation of a calcium-rich film that protects the remains from the oxygen  
566 produced by cyanobacteria (e.g., Briggs, 2003; Hellowell and Orr, 2012; Iniesto et al., 2012,  
567 2015). The substrate of the Pesciara site was probably further stabilized by the accumulation  
568 of diatoms that were probably directly implicated in the high-quality preservation of the  
569 fossils (Schwark et al., 2009); diatoms with their gelatinous extracellular exudates also  
570 represent a substrate for development of microbial mats (see Westall and Rincé, 1994;  
571 Carnevale, 2004). Additional indirect evidence of the presence of a microbial biofilm in the



572 fossiliferous laminated micritic limestone of the Pesciara site appears to be the presence of the  
573 so called “half-and-half” fishes (Fig. 14A). This particular type of preservation is also  
574 commonly observed in the Eocene fishes of the Green River Formation and has been  
575 experimentally replicated in the laboratory (Hellowell and Orr, 2012). Subsequent to an early  
576 envelopment of the body within the microbial mat, muscle contraction in certain cases caused  
577 a lateral bending of the anterior part of the body of the fish. Consequently, the anterior portion  
578 of the body partially protruded from the mat and underwent a progressive decay of the soft  
579 and skeletal parts. The biofilm is also likely responsible for the preferential splitting surfaces  
580 (Hagadorn and Bottjer, 1999) of the Pesciara fish-bearing slabs that can be easily separated  
581 along individual laminations. By preventing the action of currents, the presence of a microbial  
582 biofilm can also explain the absence of unimodal dispersion of skeletal elements around  
583 disarticulated carcasses (Briggs, 2003). The rose diagram and directionality tests indicate a  
584 random orientation of fish bodies (Fig. 5), therefore suggesting the absence of significant  
585 unidirectional palaeocurrents.

586 Tetany is rather common in the Pesciara fish assemblage, with most of the examined  
587 specimens having opisthotonic posture, gaping mouth and flabellate fins. Tetany is  
588 traditionally considered an indicator of traumatic stress due to anoxic or hypoxic conditions at  
589 the bottom (Elder, 1985; Elder and Smith, 1988; Barton and Wilson, 2005; Anderson and  
590 Woods, 2013), temperature or salinity variations, or toxic algal blooms (e.g., Schaeffer and  
591 Mangus, 1976; Granéli et al., 1989; Nixon, 1989; Barthel et al., 1990). Since there is no  
592 evidence of abnormal salinity suggested by the taxonomic composition of the fish  
593 assemblage, nor by molecular indicators (Schwark et al., 2009), the possibility of enhanced  
594 salinity could be excluded as representing the main factor responsible for the tetany. Some  
595 studies have indicated that bending of the backbone may be produced by currents acting  
596 perpendicular to the vertebral column (e.g., Chellouche et al., 2012). In this case, the

597 sedimentological features of the Pesciara fossiliferous sediments and the absence of evidence  
598 of significant bottom currents indicate that the distortion of the vertebral column is more  
599 likely due to the peri- or post-mortem contraction of the muscles.

600 Despite several factors that concur in suggesting that the bottom of the Pesciara  
601 palaeobiotope was characterized by dysoxic or anoxic conditions (see Papazzoni and  
602 Trevisani, 2006), the tetany features exhibited by numerous specimens cannot be directly  
603 related to asphyxia because the upper part of the water column was certainly well oxygenated.  
604 In any case, the possible role of toxic algal blooms cannot be ruled out even if these events  
605 usually result in huge accumulations of specimens in mass mortality layers; the latter are  
606 uncommon in the Pesciara sequence (see Marramà and Carnevale, 2015b), and were not  
607 discovered during the controlled excavations.

608 The abundance of fishes with concave appearance of the backbone in the Pesciara fish  
609 assemblage is due, in large part, to the dominance of clupeids, which represent more than  
610 90% of the specimens with opisthotonic posture. Several studies demonstrated that some  
611 types of deformation are strictly dependent on the osteological structure of the skeletons  
612 (Weiler, 1929; Hecker and Merklin, 1946; Bieńkowska, 2004). In particular, clupeiforms are  
613 more susceptible to have the concave curvature with respect to other groups, including  
614 perciforms that do not have such distortion and tend to keep the original conformation of the  
615 vertebral column (e.g., Bieńkowska, 2004). In any case, although the Pesciara perciforms  
616 always exhibit a straight backbone, they often have flabellate fins and gaping mouths,  
617 suggesting that tetany was involved uniformly in most of the fish specimens of the Pesciara  
618 site.

619 Bieńkowska-Wasiluk (2010) suggested that if one group has a predominant  
620 preservational pattern, it is possible to assume stable conditions at the bottom. The Pesciara  
621 clupeids share a similar type of preservation, in most cases exhibiting tetany features, thereby

622 supporting the hypothesis of permanent dysoxic or anoxic conditions at the bottom, as also  
623 proposed by Papazzoni and Trevisani (2006).

624

## 625 *5.2. The Monte Postale fish assemblage*

626

627         The inadequate preservation of most of the specimens from Monte Postale greatly  
628 reduced the percentage of fishes identifiable at the species level (about 20%), with negative  
629 implications on the interpretation of the original palaeoecological spectrum. The quantitative  
630 analysis presented herein clearly demonstrates the high taxonomic diversity of this  
631 assemblage, as well as the presence of a large number of small-sized individuals (more than  
632 50% of the specimens are less than 40 mm SL). In general, it seems evident that there is a  
633 correlation between body size and preservation quality of the fishes from Monte Postale, in  
634 which the well-preserved fishes are primarily of small-size. Although the large number of  
635 small individuals might reflect their effective original abundance in the Monte Postale  
636 palaeobiotope, it is likely that taphonomic biases selectively prevented the preservation of  
637 large-sized individuals. For example, large fishes are able to more easily escape  
638 environmentally stressed conditions, and small-sized individuals are more likely to become  
639 quickly buried or covered by biofilm than are large fishes, preventing decomposition and the  
640 action of scavengers or predators (e.g., Grogan and Lund, 2002).

641         The abundance and high taxonomic diversity of small-sized fishes possibly reflects the  
642 original structure of the ichthyofauna. Most of these small-sized taxa were certainly benthic,  
643 more particularly epibenthic and cryptobenthic (see Miller, 1979). Small-sized epibenthic and  
644 cryptobenthic fishes play a relevant ecological role in the trophodynamics of tropical shallow  
645 water biotopes, particularly in coral reef systems (e.g., Ackerman and Bellwood, 2002).  
646 Therefore, the abundance of small-sized fishes appears to be consistent with the presence of

647 coral bioherms in the Monte Postale palaeobiotope; this is also revealed by the presence of  
648 coral remains in all of its fossiliferous strata (Fig. 7F), as well as by the presence of a  
649 bioconstructed coral threshold (already indicated by Papazzoni et al., 2014). The analysis  
650 herein of the overall fossil content demonstrates the overwhelming abundance of plant  
651 remains, mainly macroalgae, seagrasses and terrestrial angiosperms. Seagrass beds and  
652 mangroves form part of the modern coral reef ecosystems and have high fish diversity,  
653 particularly of small-sized and juveniles individuals (e.g., Parrish, 1989; Laegdsgaard and  
654 Johnson, 1995; Beck et al., 2001; Sichum and Tantichodok, 2013), whereas the density of  
655 adults and large-sized fishes is generally low (Blaber, 1980, 1986). Several studies focused on  
656 the role of shallow-water habitats in modern tropical seas demonstrated that seagrass beds and  
657 mangroves provide protective cover for many species of fishes and invertebrates, acting as  
658 nurseries and safe havens for many families living on coral reefs (Parrish, 1989; Laegdsgaard  
659 and Johnson, 1995; Nagelkerken et al., 2002; Verweij et al., 2006). The abundance of fossil  
660 macroalgae and seagrasses, and the ecological affinities of the fish taxa of the Monte Postale  
661 assemblage, might indicate that seagrass beds and mangroves (primarily constituted by the  
662 mangrove palm *Nypa*; see Wilde et al., 2014) surrounding a coral reef system characterized  
663 the Monte Postale palaeobiotope. Anguilliforms, lophiiforms, holocentrids, syngnathiforms,  
664 ephippids, labroids, apogonids, sparids, carangids, acanthurids and siganids possibly inhabited  
665 both the densely vegetated peri-reefal areas and the reefs (see Landini and Sorbini, 1996).  
666 Round herrings are abundant in modern mangrove fish assemblages of tropical regions  
667 associated with coral reefs (e.g., Castellanos-Galindo et al., 2013). Large-size pelagic fishes  
668 such as scombrids, carangids, and sharks possibly occupied the role of top predators in the  
669 Monte Postale palaeobiotope.

670           The most striking taphonomic feature exhibited by the fish specimens from Monte  
671 Postale is the remarkably large number of disarticulated and fragmented specimens (about

672 88% of the sample). The inadequate preservation of most of the fish remains is clearly  
673 indicative of a rapid decay of the soft tissues (e.g., Weiler, 1929; Tintori, 1992; Bieńkowska-  
674 Wasiluk, 2010). The extended floatation of dead fishes over a long period of time might be  
675 plausible because of the abundance of disarticulated specimens, and fragmentary and isolated  
676 bones, suggesting that the decomposition of the carcasses began in the water column (Fürsich  
677 et al., 2007; Chellouche et al., 2012). About 70% of the fishes have disordered disposition of  
678 the fins, whereas about 60% of specimens with deformed backbones have a S-shaped  
679 disposition of the vertebral column. These characters likely represent the result of the action  
680 of weak bottom currents acting on the skeleton when the tissues were partially decomposed  
681 (Hecker and Merklin, 1946; Jerzmańska, 1960; Bieńkowska, 2004). The presence of  
682 palaeocurrents at the bottom may also be supported by the unidirectional dispersion of the  
683 scales around the bodies of fishes (Figs. 13B, I). Several studies (Elder and Smith, 1988;  
684 Tintori, 1992; Chellouche et al., 2012) have suggested that the arrangement of the skeletal  
685 elements along a preferential direction may be indicative of the presence of bottom currents.  
686 Therefore, the high degree of fragmentation and disarticulation of carcasses, S-shaped  
687 backbones, disordered fin elements, and unimodal dispersion of skeletal elements clearly  
688 indicate episodic hydrodynamic disturbance at the sediment-water interface. Bottom currents  
689 in shallow-water basins produce a temporary mixing of water, bringing oxygen to the bottom  
690 (Tintori, 1992; Barton and Wilson, 2005; Mancuso, 2012). The clear evidence of bioturbation  
691 tracks (Fig. 14E) suggest that normal aerobic conditions that allowed for a moderately  
692 abundant invertebrate fauna (mainly worms, crustaceans and mollusks) often characterized  
693 the Monte Postale palaeoenvironment. Periodic changes of environmental conditions can also  
694 be inferred by the different degrees of preservation of specimens belonging to a single fish  
695 taxon. Unlike at the Pesciara site, in which specimens belonging to a specific lineage (i.e.,  
696 clupeids) have a unique degree of preservation pattern (i.e., mostly articulated), the fishes

697 belonging to a specific lineage have different degrees of preservation at the Monte Postale  
698 site. Bieńkowska-Wasiluk (2010) suggested that the presence of several fishes of a single  
699 specific lineage in at least three different stages of disarticulation may be indicative of highly  
700 variable bottom conditions. Therefore, we can hypothesize that stable environmental  
701 conditions were interrupted by periodic disturbance events. In any case, traumatic conditions  
702 at the bottom can be inferred by the moderate degree of tetany in well-preserved specimens.  
703 Moodie (1918) suggested that the abundance of specimens with a straight backbone may be  
704 indicative of the absence or remarkable reduction of the factors that can produce the  
705 opisthotonic posture in death throes. However, the reduced number of specimens  
706 characterized by a deformed vertebral column in the Monte Postale fish assemblage (with  
707 respect to that of the Pesciara) is probably due to the relative scarcity of fish taxa (i.e.,  
708 clupeids) that are potentially more prone to have this kind of deformation. Moreover, the  
709 specimens that do not have backbone distortion (e.g., perciforms) in some cases exhibit  
710 gaping mouths and flabellate fins, two signs of tetany (Anderson and Woods, 2013; Pan et al.,  
711 2015).

712

## 713 **6. Conclusions**

714

715 Although the controlled excavations of 1999-2011 did not include the full diversity of  
716 the Bolca ichthyofauna, the analysis of the extracted material helps us to confirm and better  
717 define some palaeoecological and palaeoenvironmental aspects of the two most important  
718 productive sites of the Bolca Konservat-Lagerstätte. The quantitative and taphonomic  
719 analyses of the Pesciara and Monte Postale fish assemblages clearly defined two distinctive  
720 palaeocommunities and two different depositional settings.

721           The ecological and trophic relationships hypothesized by Landini and Sorbini (1996)  
722 for the Pesciara site were substantially confirmed, supporting the hypothesis of a peri-reefal  
723 coastal setting strongly influenced both by emerged areas and the pelagic environment. The  
724 taphonomic analysis confirmed that the fossiliferous sediment was deposited in a relatively  
725 shallow basin with persistent dysoxic or anoxic conditions at the bottom, corroborating the  
726 hypothesis of a stagnation deposit with low hydrodynamic energy (Papazzoni and Trevisani,  
727 2006).

728           The Monte Postale fish assemblage, by contrast, was characterized by a low degree of  
729 preservation of fish skeletons that resulted in a reduced number of specimens identifiable at  
730 the generic or species level. Therefore, because of the inadequate knowledge of fish diversity  
731 in the Monte Postale assemblage, it was not possible to properly define the ecological and  
732 trophic relationships characteristic of this site. Nevertheless, the abundance of macroalgae,  
733 seagrasses, terrestrial plants, invertebrates and coral remains concur in suggesting that the  
734 Monte Postale sediments were deposited close to an emerged coastal area, in a setting  
735 characterized by seagrass beds, mangroves and coral reefs, a context remarkably different  
736 from the open environment suggested by Trevisani (2015). The high degree of disgregation of  
737 fish carcasses, the disordered disposition of fins, the unimodal dispersion of skeletal elements,  
738 and the relative abundance of benthic invertebrates and bioturbation tracks clearly suggest a  
739 moderately high degree of disturbance of the environment, and that normal aerobic conditions  
740 at the bottom episodically characterized the Monte Postale palaeobiotope.

741           Unfortunately, the detailed reconstruction of the actual trophic and ecological  
742 relationships within of the Bolca fish fauna cannot be hypothesized solely using museum  
743 collections because these fossils usually do not have precise stratigraphic data and their  
744 abundance was surely biased by artificial selection of well-preserved specimens. For example,  
745 very common taxa like clupeids are not proportionally well represented in collections,

746 whereas rare species are far more likely become part of a museum collection. Further  
747 systematic excavations in these two deposits are therefore necessary to expand our knowledge  
748 about this extraordinary Eocene Konservat-Lagerstätte.

749

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751

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761

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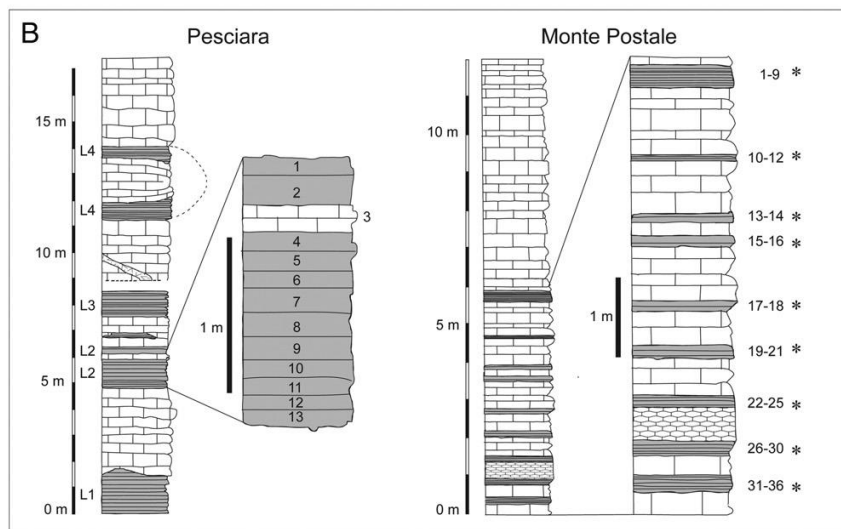
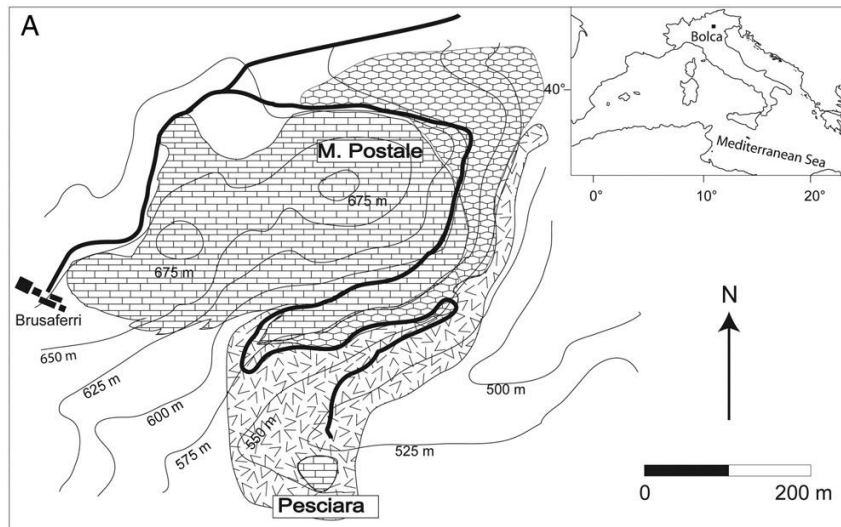
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


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-  Fine-grained laminated micritic limestone with fish and plant remains (Microfacies M of Papazzoni and Trevisani 2006; Lithofacies 3 of Trevisani 2015)
-  Coarse-grained biocalcarenite-biocalcirudite limestone with benthic fauna (Microfacies F of Papazzoni and Trevisani 2006; Lithofacies 2 of Trevisani 2015)
-  Massive nodular limestone with benthic fossils (Lithofacies 1 of Trevisani 2015; only at M. Postale)
-  Volcanic and basaltic rocks
- \* Coral remains

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1089 **Fig. 1.** A, Location and geological map of the Bolca area. B, Stratigraphic sections of the

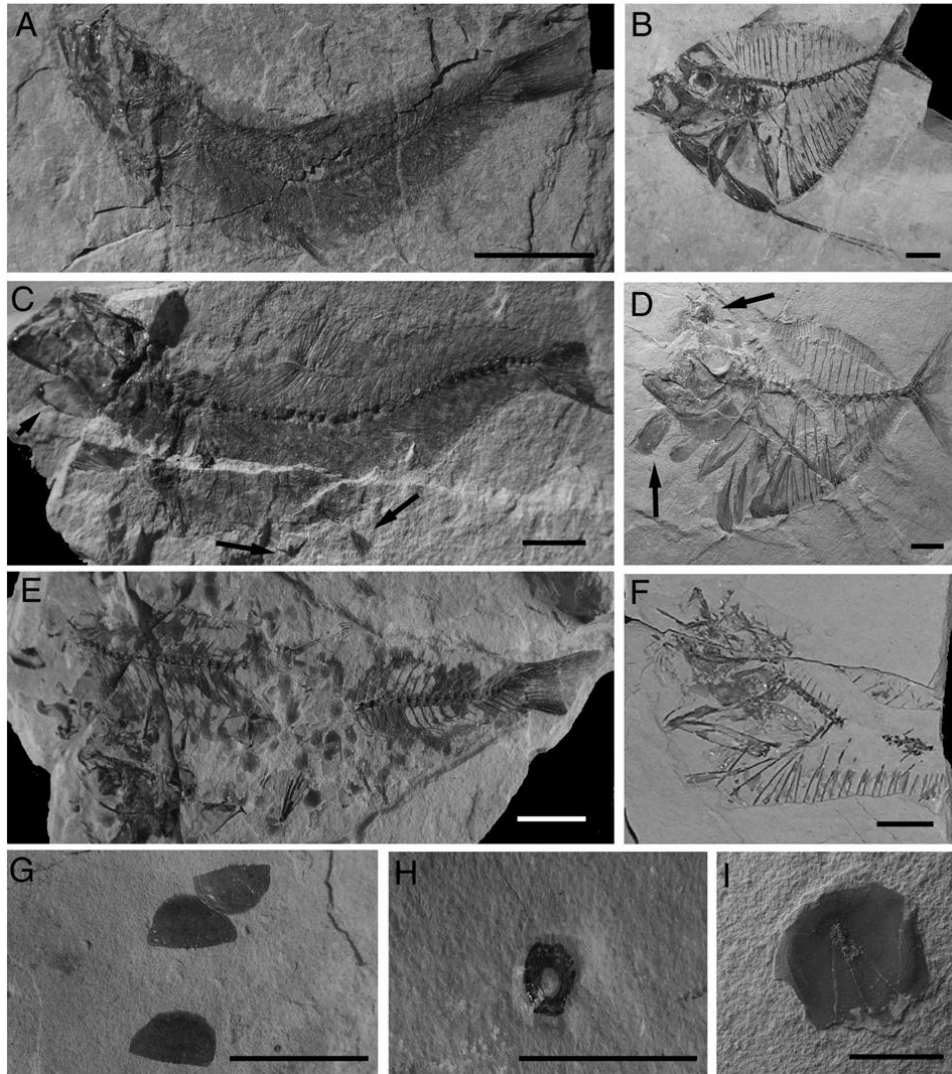
1090 Pesciara and uppermost part of the Monte Postale sequences; the 13 productive levels of

1091 Pesciara and the 36 productive levels of Monte Postale from which all specimens were

1092 extracted are also indicated. Modified from Papazzoni and Trevisani (2006) and Trevisani

1093 (2015).

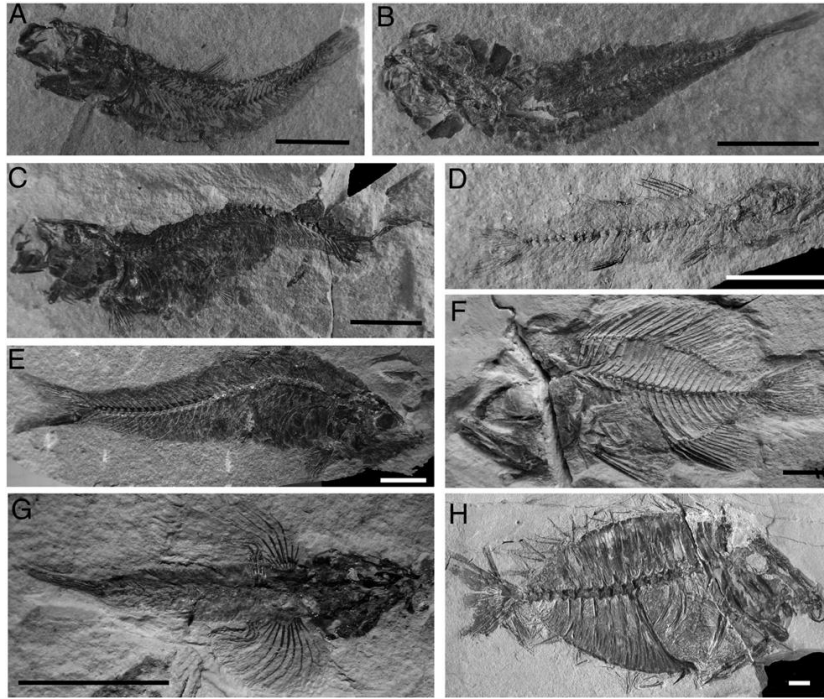
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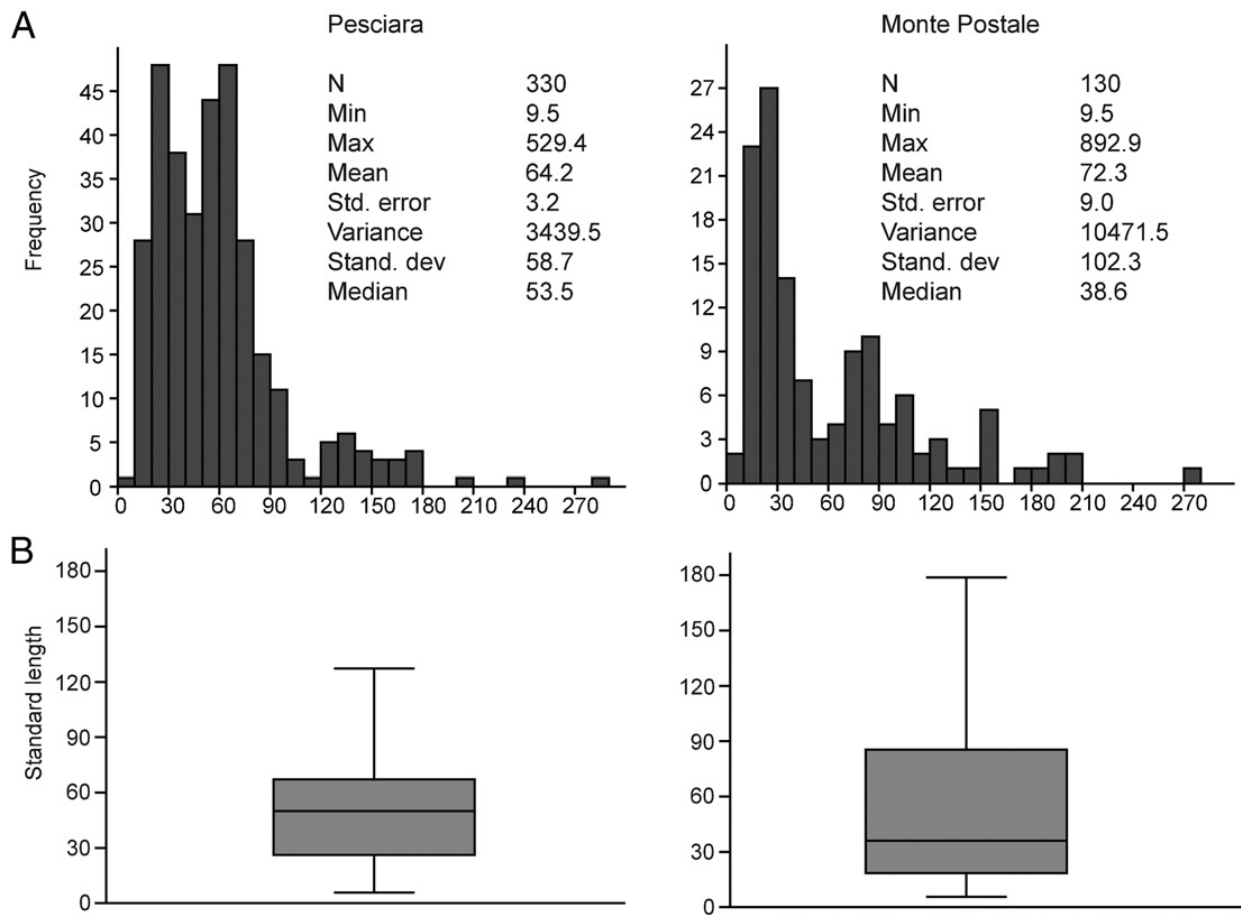
1097 **Fig. 2.** Biostratinomic features showing the different preservation patterns in the sardine  
 1098 *Bolcaichthys catopygopterus* (left) and the moonfish *Mene rhombea* (right): A, B, complete  
 1099 and fully articulated specimens; C, D, partially articulated fishes (arrows indicate some  
 1100 dislodged elements); E, F, disarticulated skeletons, the body outline is not recognizable. G, H,  
 1101 I, isolated elements such as scales (G, I) and a vertebral centrum (H) of indeterminate fishes.  
 1102 (A) MCSNV IG.VR.69576; (B) MCNSV IG.VR.69600; (C) MCSNV IG.VR.69549; (D)  
 1103 MCSNV IG.VR.69374; (E) MCSNV IG.VR.71374; (F) MCSNV IG.VR.69275; (G) MCSNV  
 1104 IG.VR.82166; (H) MCSNV IG.VR.82177; (I) MCSNV IG.VR.69472. Scale bars represent 10  
 1105 mm.



1106

1107 **Fig. 3.** Taphonomic features observed in Bolca fishes. A, the sardine *Bolcaichthys*  
 1108 *catopygopterus* (MCSNV IG.VR.71407) in “lateral” 3D orientation (with dorso-ventral axis  
 1109 of the body parallel with respect to the bedding plan), with concave backbone curvature and  
 1110 open mouth, Pesciara site. B, *B. catopygopterus* (MCSNV IG.VR. 71571) showing dorso-  
 1111 ventrally orientated body, Pesciara site. C, *B. catopygopterus* (MCSNV IG.VR.81852) with  
 1112 S-shaped vertebral column, Pesciara site. D, the percoid *Voltamulloides ceratorum* (MCSNV  
 1113 IG.VR.69585) showing “lateral” 3D orientation, no deformed backbone (straight) and closed  
 1114 mouth and fins, Pesciara site. E, *B. catopygopterus* (MCSNV IG.VR.71956) with convex  
 1115 curvature of the vertebral column and closed dorsal fin, Pesciara site. F, the percoid  
 1116 *Pavarottia lonardonii* (MCNSV IG.VR.71259) in “lateral” 3D orientation, with straight  
 1117 vertebral column and closed mouth, Monte Postale site. G, the dactylopteriform  
 1118 *Pterygocephalus paradoxus* (MCSNV IG.VR.70029) in “dorso-ventral” orientation with  
 1119 respect to the bedding plan, showing flabellate pectoral fins, Pesciara site. H, the acanthurid  
 1120 *Tylerichthys nuchalis* (MCSNV IG.VR.67382) in “lateral” 3D orientation, straight backbone  
 1121 and disordered disposition of the fins, Monte Postale site. Scale bars represent 10 mm.

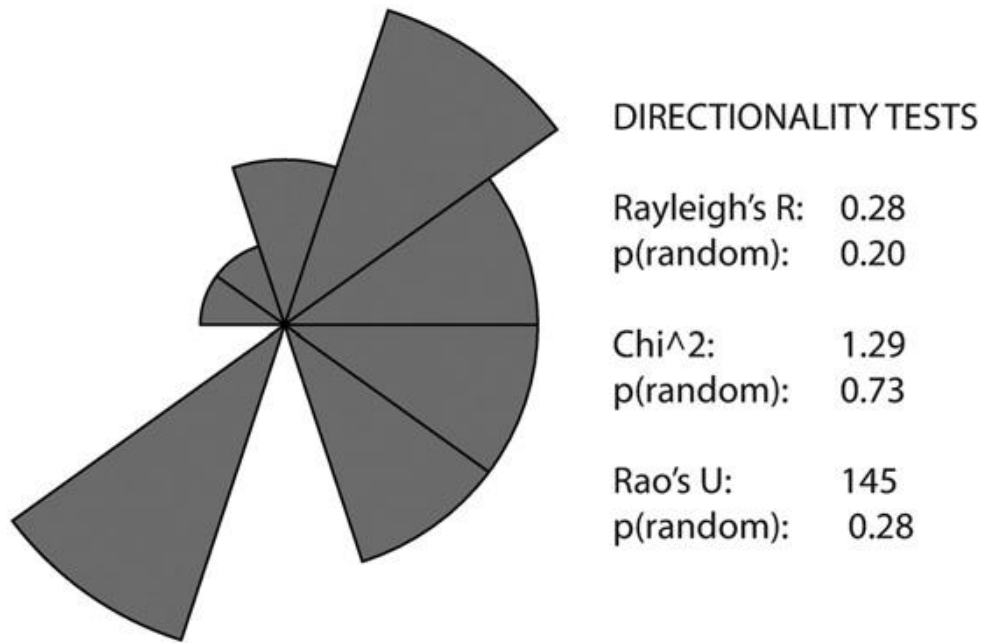




1122

1123 **Fig. 4.** Histograms with descriptive statistics (A) and box-plots (B) showing the size-  
 1124 frequency distribution of more than 95% of the specimens at the Pesciara and Monte Postale  
 1125 deposits. Measurements are in millimeter (mm). Outliers are not represented.

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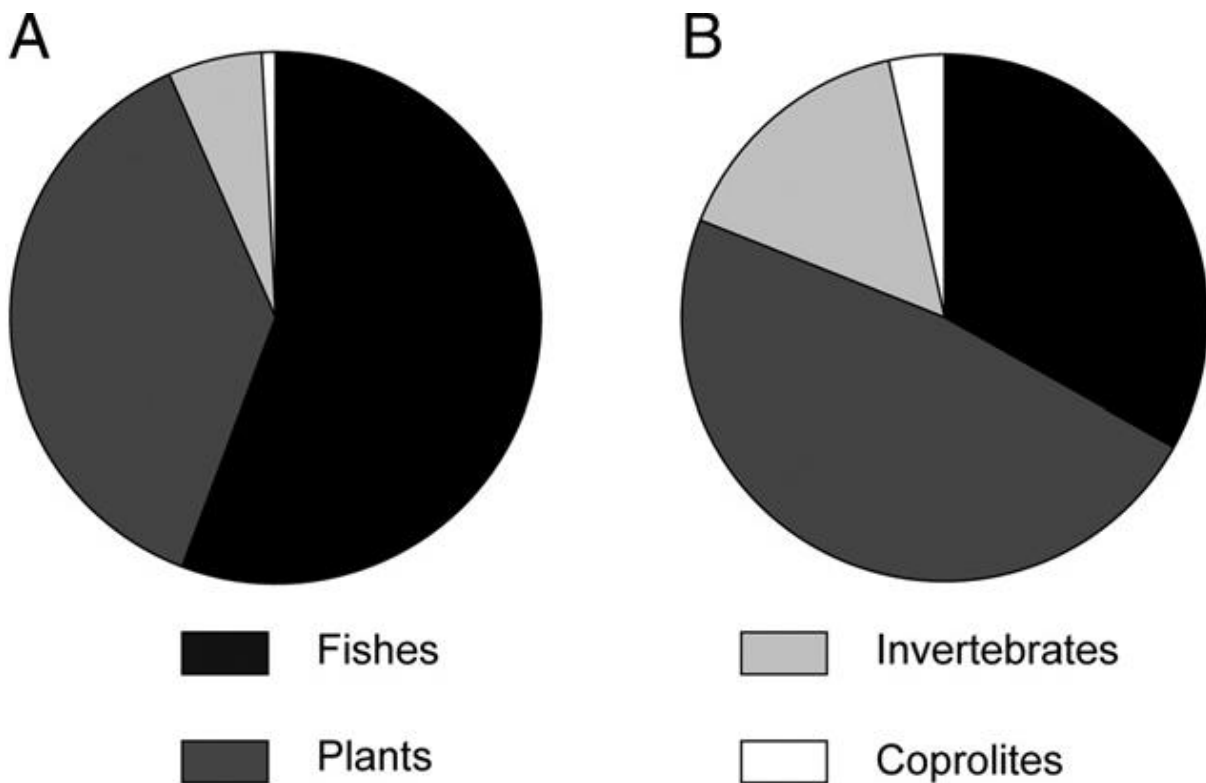


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1129 **Fig. 5.** Rose diagram and directionality tests showing no preferential orientation pattern at the

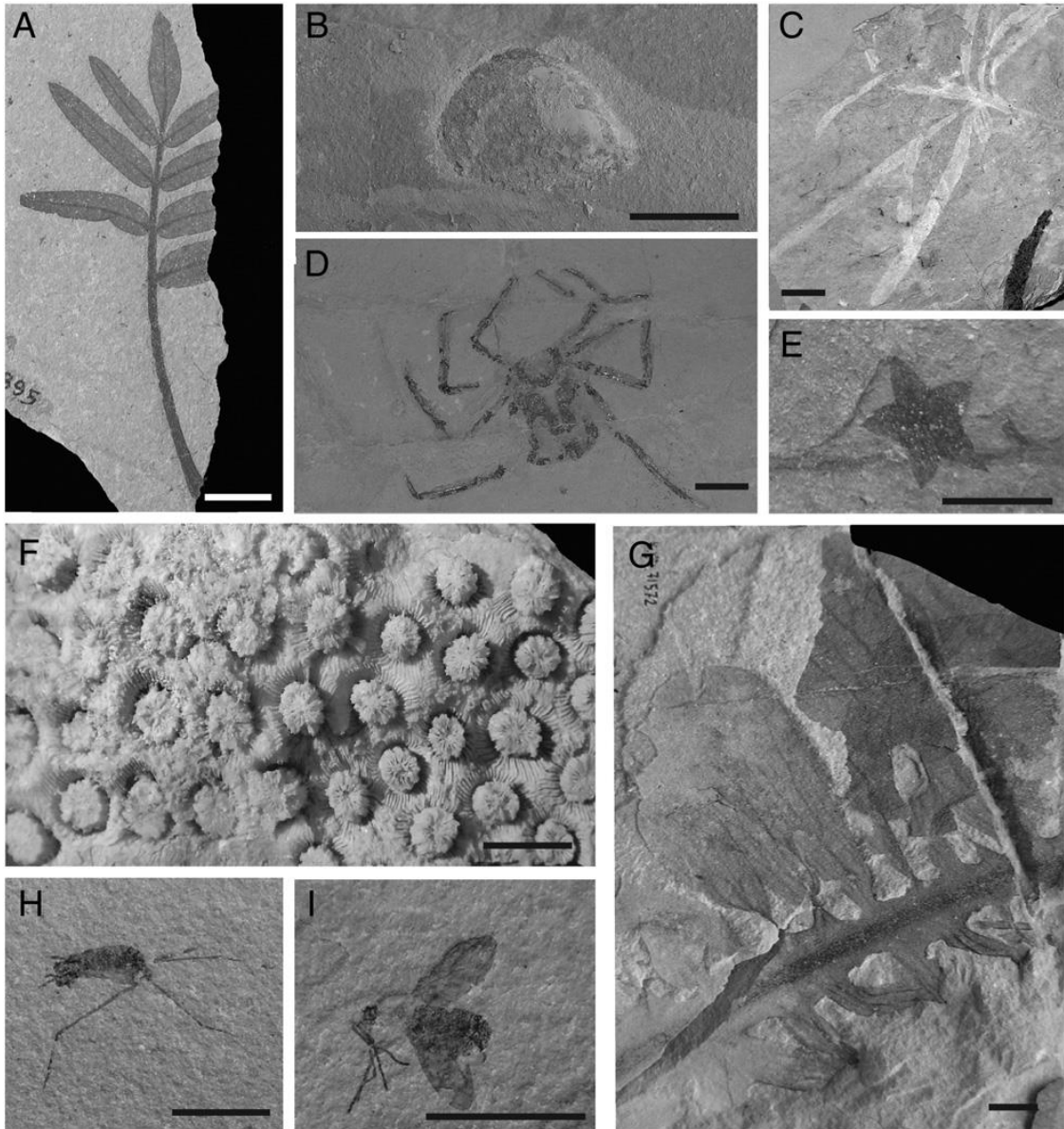
1130 Pesciara site (all  $p > 0.05$ ); N. specimens = 21.



1131

1132 **Fig. 6.** Overall content of the 1070 fossil remains from the Pesciara site (A), and of the 1803

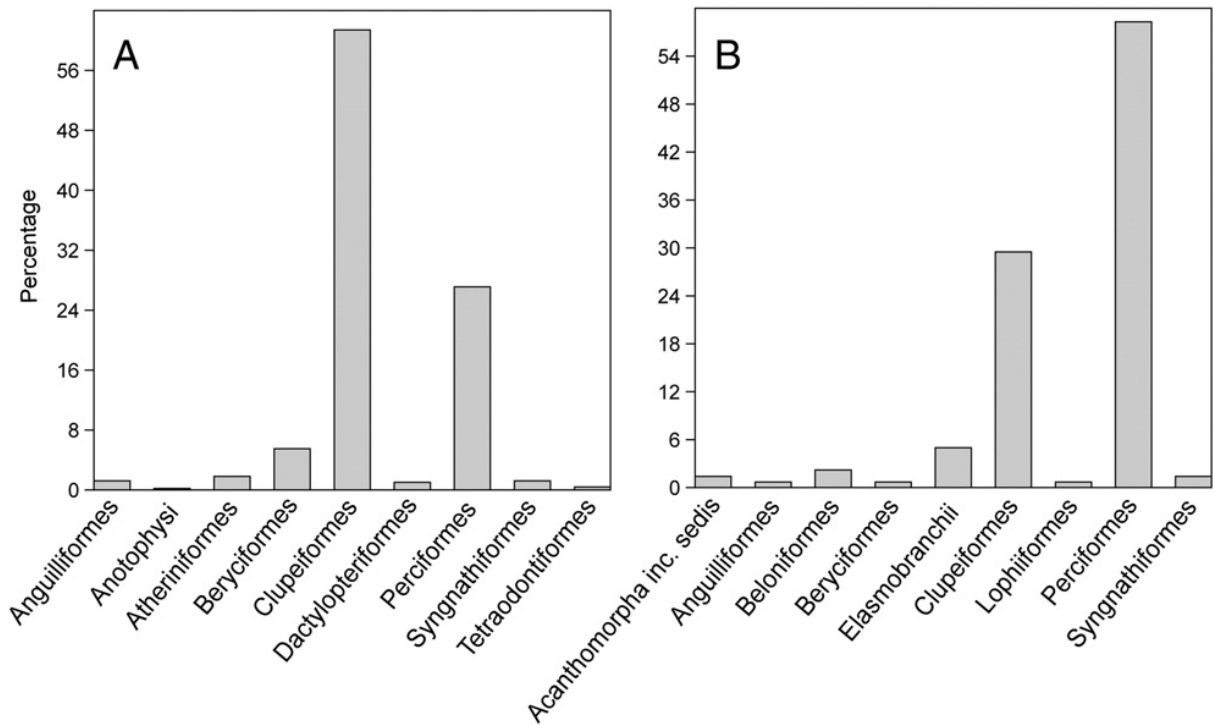
1133 specimens from the Monte Postale site (B).



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1135 **Fig. 7.** Examples of the non-fish component of the Bolca assemblages. A, imparipinnate  
 1136 composite leaf (MCSNV IG.VR.81894), Pesciara site. B, inner prints of indeterminate  
 1137 bivalves (MCSNV IG.VR.71672), Pesciara site. C, seagrass remains, Monte Postale site  
 1138 (MCSNV IG.VR.66074). D, the spider *Archaeocypoda veronensis* (MCSNV IG.VR.67295),  
 1139 Monte Postale site. E, indeterminate starfish (MCSNV IG.VR.71546), Pesciara site. F, coral  
 1140 remains, Monte Postale site (MCSNV IG.VR.66706). G, red algae (MCSNV IG.VR.71943),  
 1141 Pesciara site. H, the water strider *Halobates ruffoi* (MCSNV IG.VR.91364), Pesciara site. I,  
 1142 indeterminate insect (MCSNV IG.VR.71652), Pesciara site. Scale bars 10 mm.

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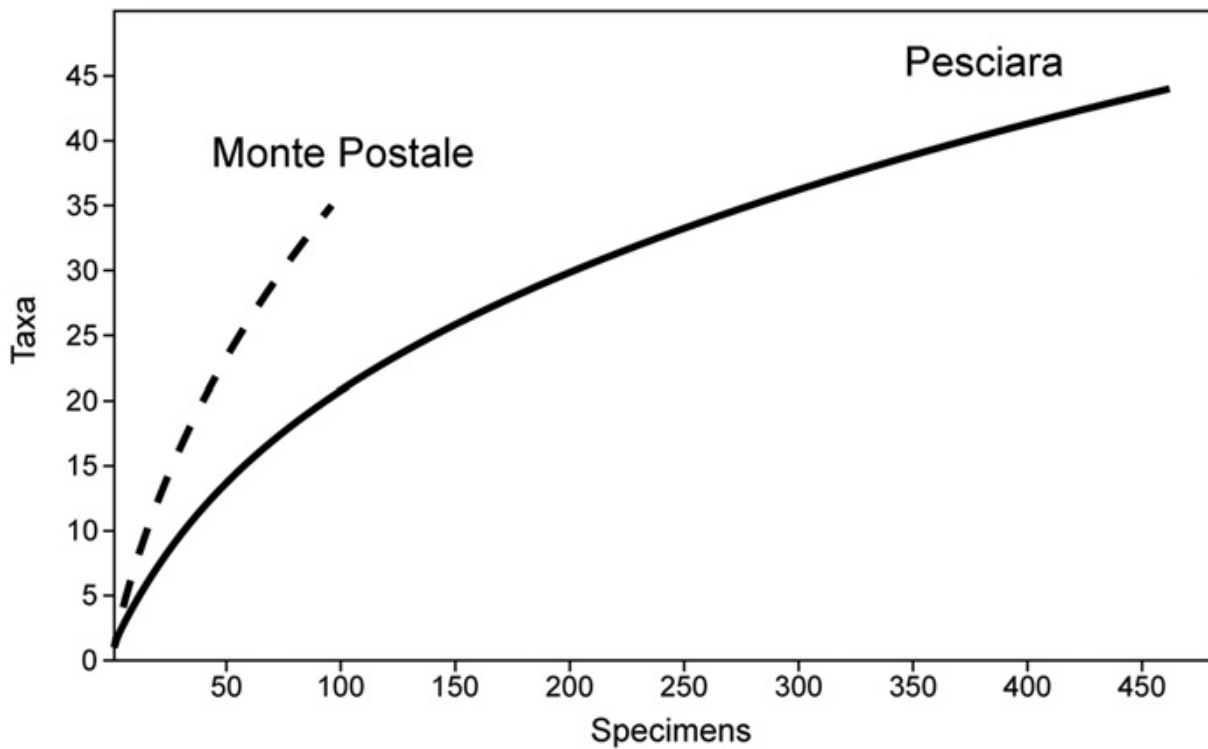


1144

1145 **Fig. 8.** Taxonomic composition of the identifiable fish remains of the Pesciara (A) and M.

1146 Postale (B) assemblages. N. specimens: Pesciara = 491; Monte Postale = 139. Indeterminate

1147 specimens are not shown.



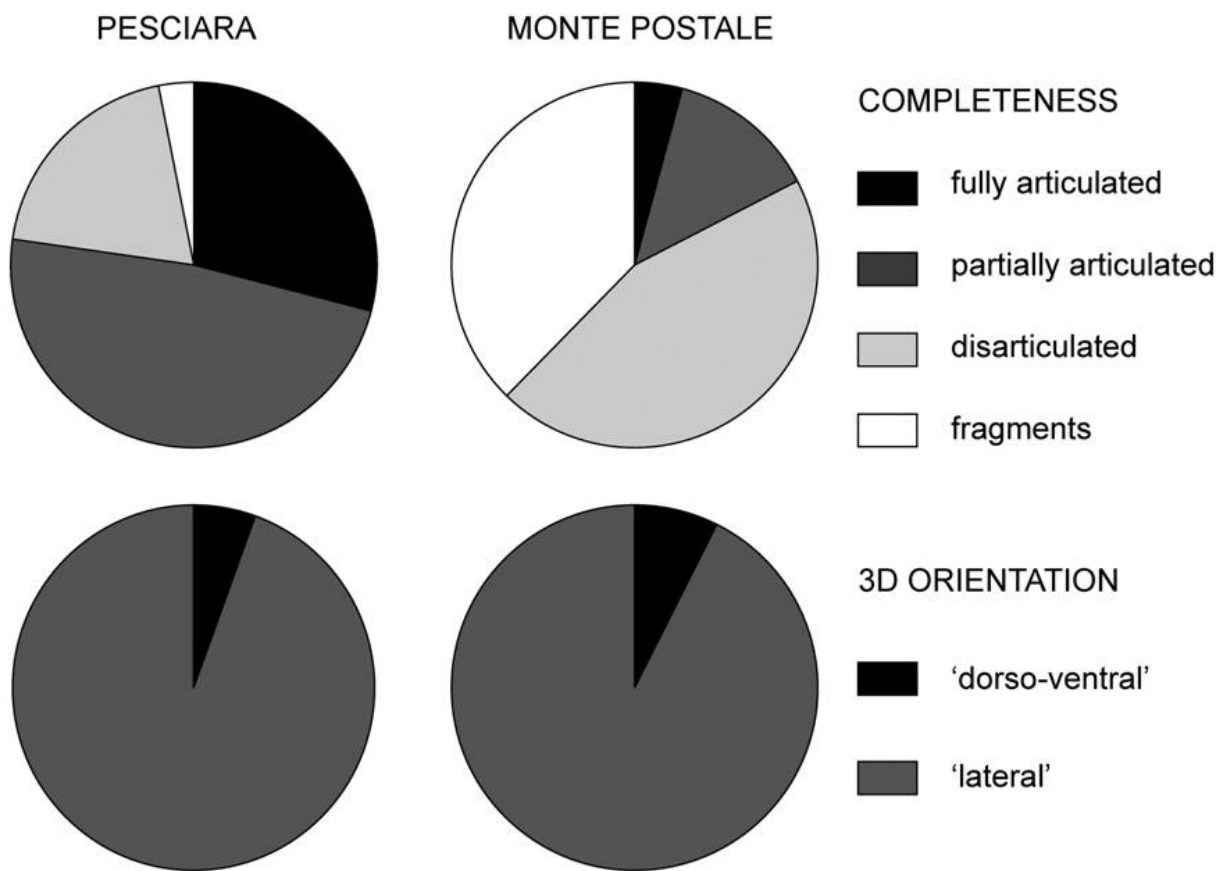
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1149 **Fig. 9.** Individual-based taxon accumulation curves for the Pesciara and Monte Postale fish

1150 assemblages.

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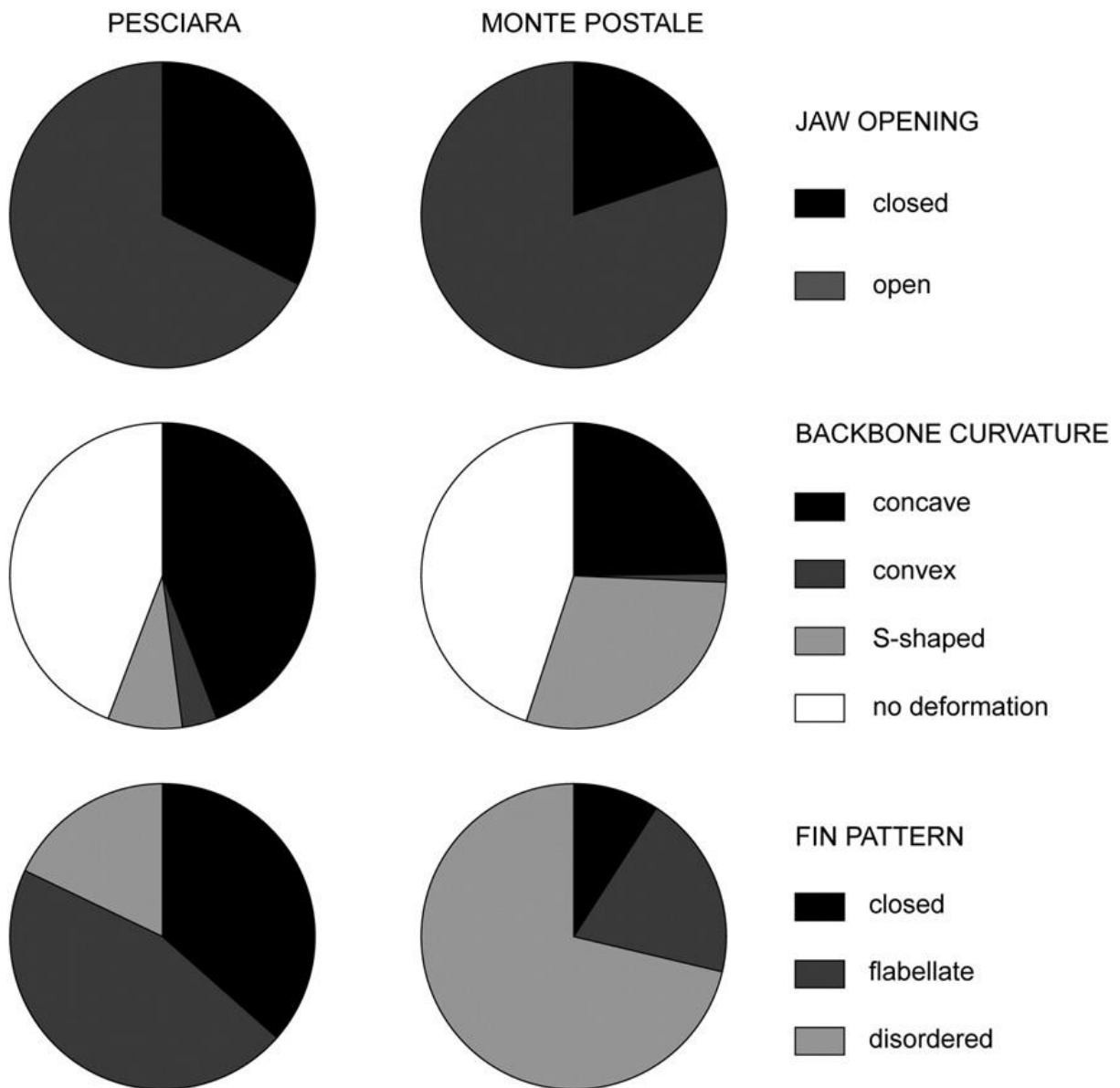
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1154 **Fig. 10.** Degree of completeness and 3D orientation patterns of the specimens in the Pesciara

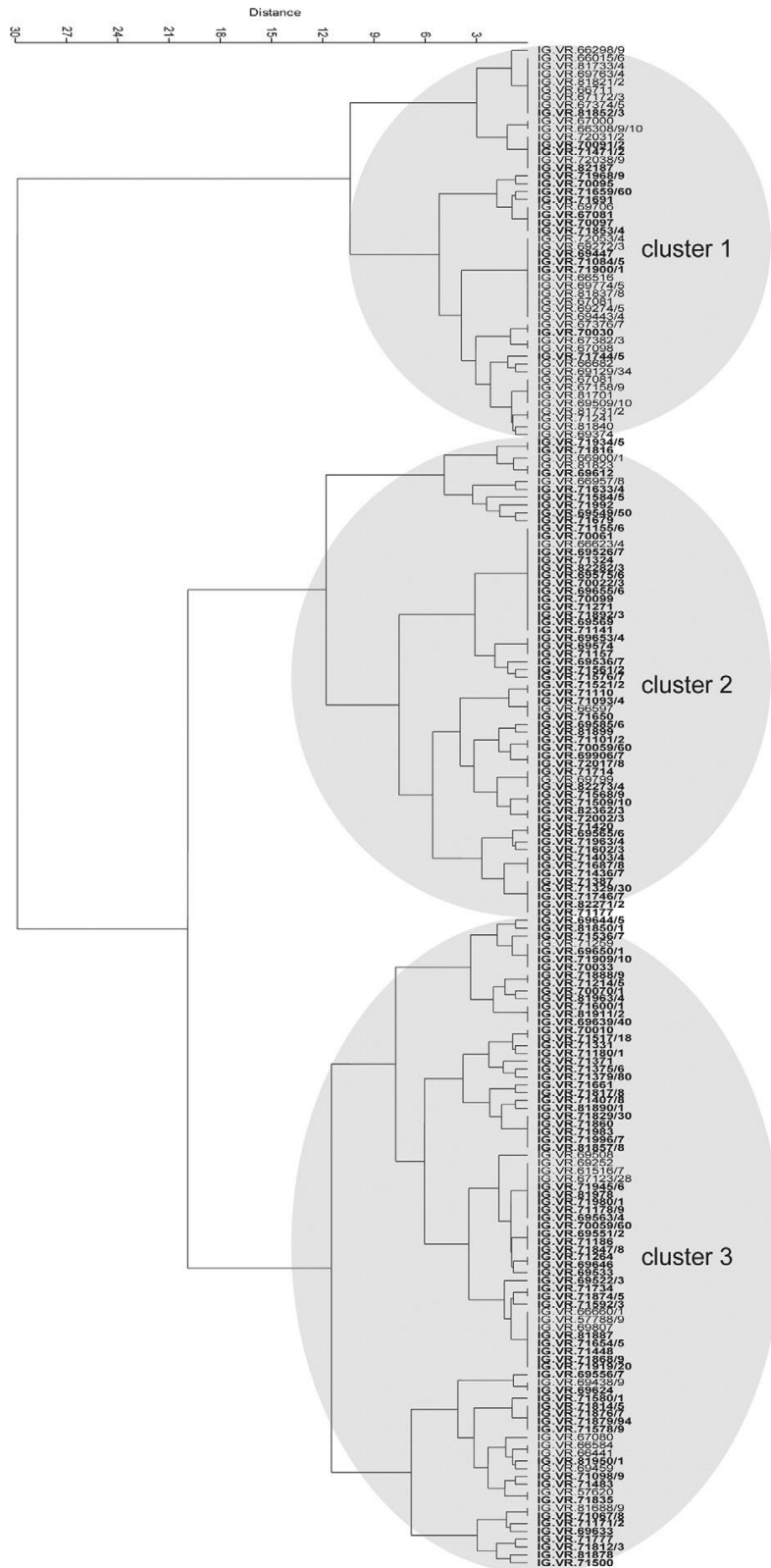
1155 and Monte Postale deposits. N. specimens: Pesciara = 524; Monte Postale = 577.



1156

1157 **Fig. 11.** Tetany features in the Pesciara and Monte Postale fish assemblages. N. specimens:

1158 Pesciara = 477; Monte Postale = 129.

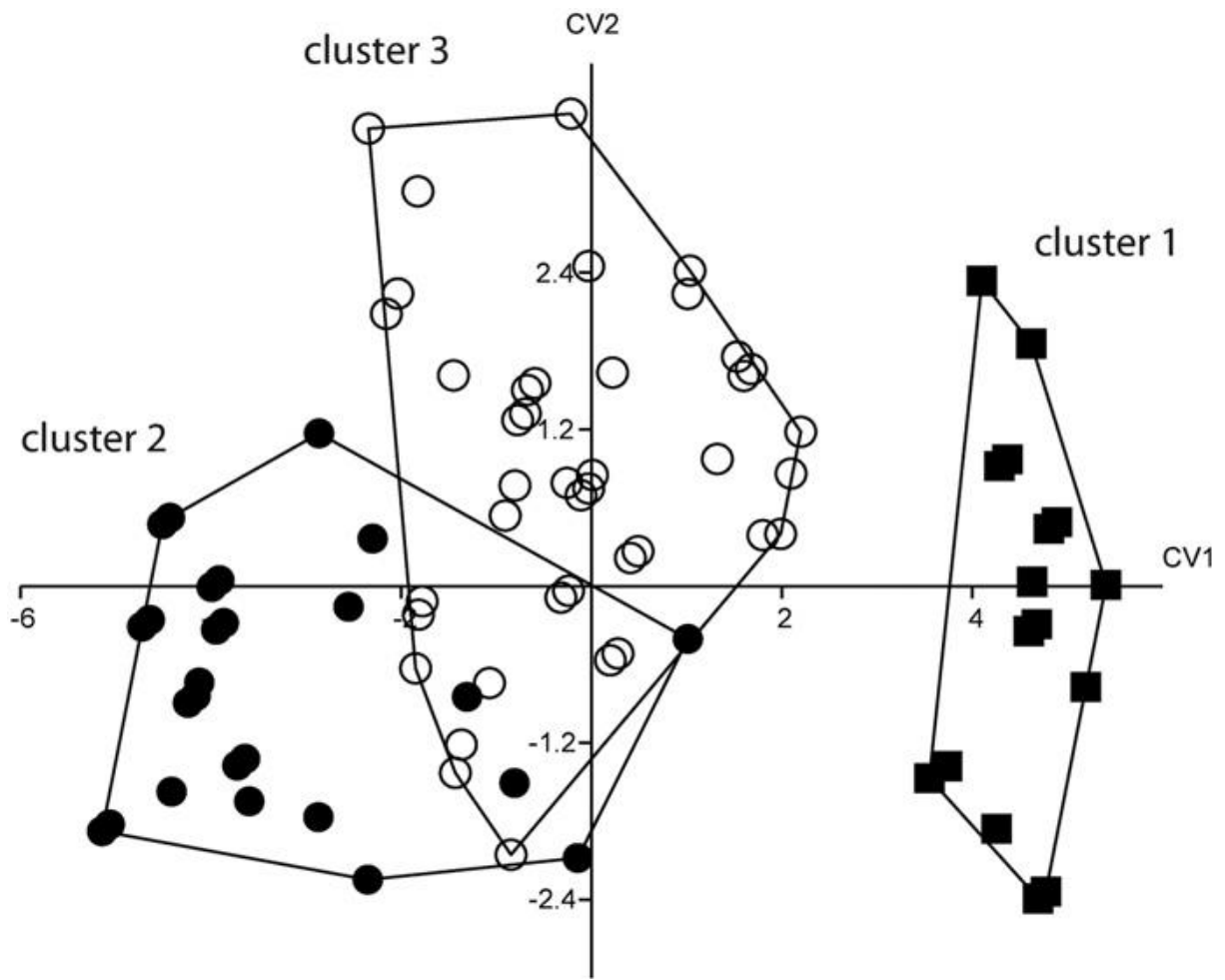


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1160 **Fig. 12.** Euclidean cluster analysis using the Ward's method showing the three main groups.

1161 Specimens from the Pesciara site are marked in bold (e.g., MCSNV IG.VR.69624).

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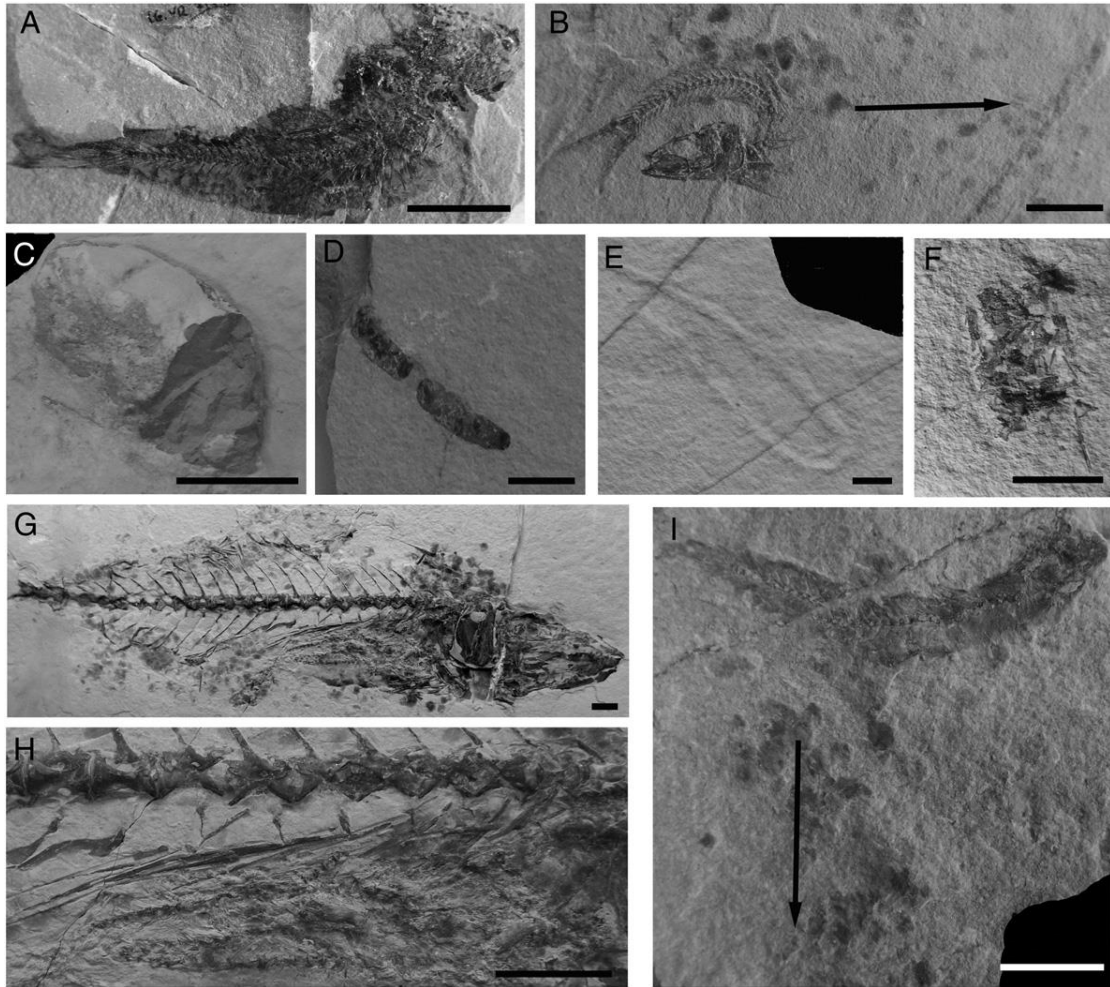


1163

1164 **Fig. 13.** Visual image of the clusters built on the first two canonical variate axes, resulting  
 1165 from the analysis of the nine standardized attributes, and representing the three main  
 1166 taphonomic states.

1167





1168

1169 **Fig. 14.** Examples of further taphonomic features. A, the sardine *Bolcaichthys catopygopterus*  
 1170 from the Pesciara site (MCSNV IG.VR.71786) showing the so called “half-and-half”  
 1171 preservation pattern. B, the round herring *Trollichthys bolcensis* from the Monte Postale site  
 1172 (MCSNV IG.VR.72041) showing unimodal dispersion of scales. C, D, coprolites  
 1173 (respectively MCSNV IG.VR.81998 and MCSNV IG.VR.91386), Monte Postale site. E,  
 1174 bioturbation from the Monte Postale site (MCSNV IG.VR.82212). F, regurgitate of an  
 1175 indeterminate fish from the Monte Postale site (MCSNV IG.VR.81758). G, H, the large  
 1176 scombrid *Pseudauxides speciosus* from the Monte Postale site (MCSNV IG.VR.71261)  
 1177 showing at least two articulated *Trollichthys bolcensis* as stomach content (in H). I, the round  
 1178 herring *T. bolcensis* from the Monte Postale site (MCSNV IG.VR.72054) showing unimodal  
 1179 arrangement of scales across a preferential direction. Scale bars 10 mm.

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Order	Family	Taxon	N. of specimens	Relative abundance
Anguilliformes	Anguilliformes indet.	Anguilliformes indet.	7	
Anotophysii	Anotophysii incertae sedis	Anotophysii incertae sedis	1	
Atheriniformes	Atherinidae	<i>Atherina macrocephala</i>	5	Occasional
	Mesogasteridae	<i>Mesogaster sphyraenoides</i>	4	Rare
Beryciformes	Holocentridae	<i>Berybolcensis leptacanthus</i>	11	Occasional
	Holocentridae indet.		16	
Clupeiformes	Clupeidae	<i>Bolcaichthys catopygopterus</i>	293	Abundant
		<i>Trollichthys bolcensis</i>	2	Rare
		Clupeidae indet.	4	
Dactylopteriformes	Pterygocephalidae	<i>Pterygocephalus paradoxus</i>	5	Occasional
Perciformes	Acanthuridae	<i>Pesciarichthys punctatus</i>	1	Rare
		<i>Proacanthurus</i> sp.	1	Rare
	Acropomatidae	<i>Acropoma lepidotum</i>	6	Occasional
		<i>Apogoniscus pauciradiatus</i>	10	Occasional
	Apogonidae	<i>Eopogon fraseri</i>	3	Rare
		Apogonidae indet.	5	
	Blochiidae	<i>Blochius</i> sp.	2	Rare
		<i>Seriola prisca</i>	2	Rare
	Carangidae	<i>Trachicarax pleuronectiformis</i>	1	Rare
	Ductoridae	<i>Ductor vestenae</i>	1	Rare
	Gobioidei indet.	Gobioidei indet.	1	
	Labridae	<i>Bellwoodilabrus landinii</i>	1	Rare
	Labroidei	Labroidei indet.	2	
	Lutjanidae	<i>Lessinia horrenda</i>	1	Rare
		<i>Veranichthys ventralis</i>	3	Rare
	Menidae	<i>Mene rhombea</i>	17	Occasional
	Percichthyidae	<i>Cyclopoma gigas</i>	20	Occasional
	Percoidei	<i>Pygaeus bolcanus</i>	2	Rare
		<i>Squamibolcoides minciottii</i>	1	Rare
		<i>Voltamulloidis ceratorum</i>	7	Occasional
		Percoidei indet.	24	
	Pomatomidae	<i>Carangopsis</i> sp.	1	Rare
	Quasimulidae	<i>Quasimullus sorbinii</i>	1	Rare
	Robertanniidae	<i>Robertannia sorbiniorum</i>	1	Rare
	Siganidae	<i>Ruffoichthys</i> sp.	1	Rare
	Sparidae	<i>Abromasta microdon</i>	1	Rare
		<i>Pseudospamosus microstomus</i>	4	Rare
		<i>Sparnodus elongatus</i>	2	Rare
		<i>Sparnodus vulgaris</i>	10	Occasional
	Sphyraenidae	<i>Sphyraena bolcensis</i>	1	Rare
Syngnathiformes	Aulorhamphidae	<i>Pesciarhamphus camevalei</i>	1	Rare
		<i>Veronarhamphus canossae</i>	1	Rare
	Fistularioididae	<i>Fistularioides</i> sp.	2	Rare
	Syngnathidae	Syngnathide indet.	2	
Tetraodontiformes	Diodontidae	<i>Prodiodon</i> sp.	1	Rare
	Triacanthidae	<i>Protacanthodes nimesensis</i>	1	Rare
Actinopterygii indet.		Actinopterygii indet.	106	

1183

1184 **Table 1.** Taxonomic composition and relative abundance of species in the Pesciara fish

1185 assemblage.

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Order	Family	Taxon	N. of specimens	Relative abundance
Torpediniformes	Narcinidae	<i>Titanonarke molini</i>	1	Occasional
Elasmobranchii indet.	Elasmobranchii indet.		6	
Percomorpha inc. sedis	Percomorpha inc. sedis	<i>Pletschellus aenigmaticus</i>	2	Occasional
Anguilliformes	Anguilliformes indet.		1	
Beloniformes	Hemiramphidae	<i>Hemiramphus edwardsi</i>	3	Occasional
Beryciformes	Holocentridae	<i>Beryolcensis leptacanthus</i>	1	Occasional
Clupeiformes	Clupeidae	<i>Bolcaichthys catopygopterus</i>	9	Frequent
		<i>Trollichthys bolcensis</i>	29	Common
		Clupeidae indet.	2	
Lophiiformes	Brachionichthyidae	<i>Histionotophorus bassani</i>	1	Occasional
Perciformes	Acanthuridae	<i>Tylerichthys nuchalis</i>	1	Occasional
	Acropomatidae	<i>Acropoma lepidotum</i>	5	Frequent
	Apogonidae	<i>Apogoniscus pauciradiatus</i>	1	Occasional
		Apogonidae indet.	1	
	Caproidae	<i>Eoantigonia veronensis</i>	1	Occasional
	Carangidae	<i>Lichia veronensis</i>	1	Occasional
		<i>Seriola prisca</i>	1	Occasional
	Carangodidae	<i>Carangodes bicornis</i>	1	Occasional
	Ductoridae	<i>Ductor vestenae</i>	1	Occasional
	Ephippidae	<i>Eoplatax papilio</i>	1	Occasional
	Labroidei indet.	Labroidei indet.	4	
	Menidae	<i>Mene oblonga</i>	2	Occasional
		<i>Mene rhombea</i>	3	Occasional
	Palaeorhynchidae	<i>Palaeorhynchus zorzini</i>	1	Occasional
	Percoidei	<i>Blotichthys coleanus</i>	3	Occasional
		<i>Pavarottia lonardonii</i>	1	Occasional
		Percoidei indet.	24	
	Quasimullidae	<i>Quasimullus sorbinii</i>	1	Occasional
	Scombridae	<i>Pseudauxides speciosus</i>	3	Occasional
	Scorpaenoidei	Scorpaenoidei indet.	1	
	Siganidae	<i>Aspesiganus margaritae</i>	1	Occasional
	Sparidae	<i>Abromasta microdon</i>	1	Occasional
		Sparidae indet.	2	
	Perciformes indet.	Perciformes indet.	20	
	Aulorhamphidae	<i>Aulorhamphus chiarasorbiniae</i>	1	Occasional
Syngnathiformes	Centriscidae	Centriscidae indet.	1	
Actinopterygii indet.			455	

1195

1196 **Table 2.** Taxonomic composition and relative abundance of species in the Monte Postale fish  
1197 assemblage.

1198

Taphonomic features	0	1	2	3
1) Completeness	Fully articulated	Partially articulated	Disgregated	-
2) 3D orientation	Lateral	Dorso-ventral	-	-
3) Jaw opening	Closed	Open	-	-
4) Backbone deformation	Straight	Concave	Convex	S-shaped
5) Pectoral fin condition	Closed	Flabellate	Disordered	-
6) Pelvic fin condition	Closed	Flabellate	Disordered	-
7) Dorsal fin condition	Closed	Flabellate	Disordered	-
8) Anal fin condition	Closed	Flabellate	Disordered	-
9) Caudal fin condition	Closed	Flabellate	Disordered	-

1199

1200 **Table 3.** The nine biostratigraphic attributes used to perform the cluster analysis, the principal  
1201 component analysis (PCA) and the canonical variate analysis (CVA) in order to recognize the  
1202 different taphonomic states of the Pesciara and Monte Postale site.

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	Pesciara	Monte Postale	<i>p</i> ( same)
n. taxa	40	34	
Dominance	0.4027	0.0804	<0.001
Berger–Parker	0.6288	0.2021	<0.001
Simpson	0.5973	0.9196	<0.001
Shannon	1.88	3.01	<0.001

1206

1207 **Table 4.** Diversity indices of the two fish assemblages of Bolca. The two fish assemblages

1208 have significant differences in terms of taxonomic diversity (Shannon diversity *t*-test:

1209 *p*<0.001).

1210

PC axes	Eigenvalue	% variance
1	2.8	60.1
2	1.0	20.6
3	0.3	6.2
4	0.2	4.7
5	0.2	3.7
6	0.1	2.0
7	0.1	1.7
8	0.0	1.0
9	0.0	0.1

1211

1212 **Table 5.** Values of the variance explained by the PC axes of the Principal Component

1213 analysis performed on the nine standardized attributes of 194 specimens from the two sites of

1214 Bolca.