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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03 September 2024

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Abstract

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

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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

3

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 volcaniclastic 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 biocalcarenite/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; Jerzmañska, 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 >>0; Skewness >>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 (*Delesserites* 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, anotophysans, 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

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 biostratinomic 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

17

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., Hellawell 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 invertebrativores, 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; Hellawell 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; Hellawell 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 (Hellawell 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

27

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

28

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.

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750 **Acknowledgements**

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762 **References**

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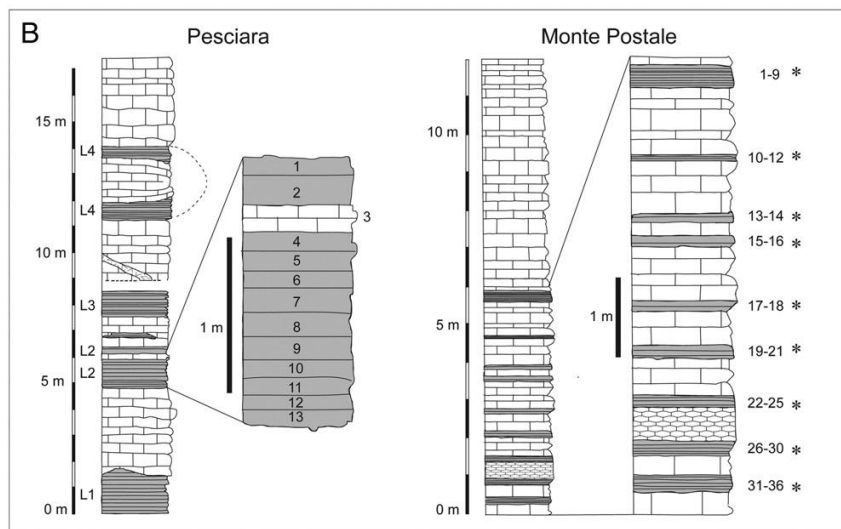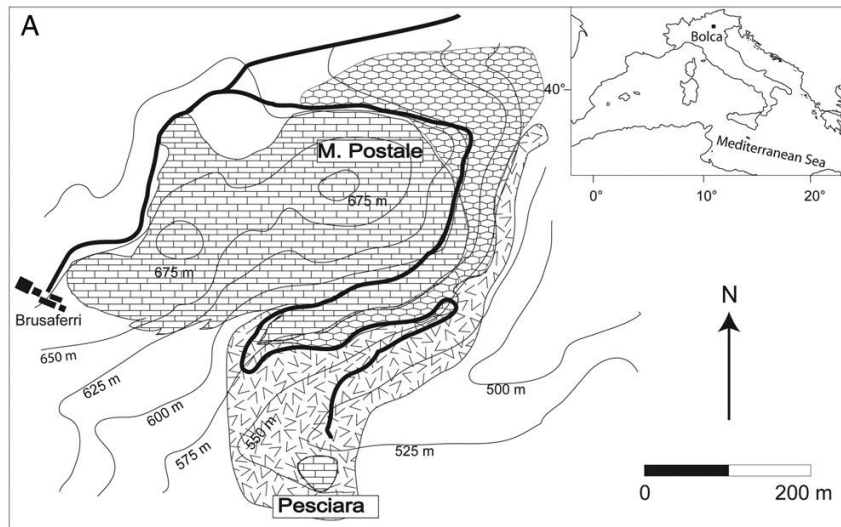
Fine-grained laminated micritic limestone with fish and plant remains
(Microfacies M of Papazzoni and Trevisani 2006; Lithofacies 3 of Trevisani 2015)

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

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

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

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

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

(2015).
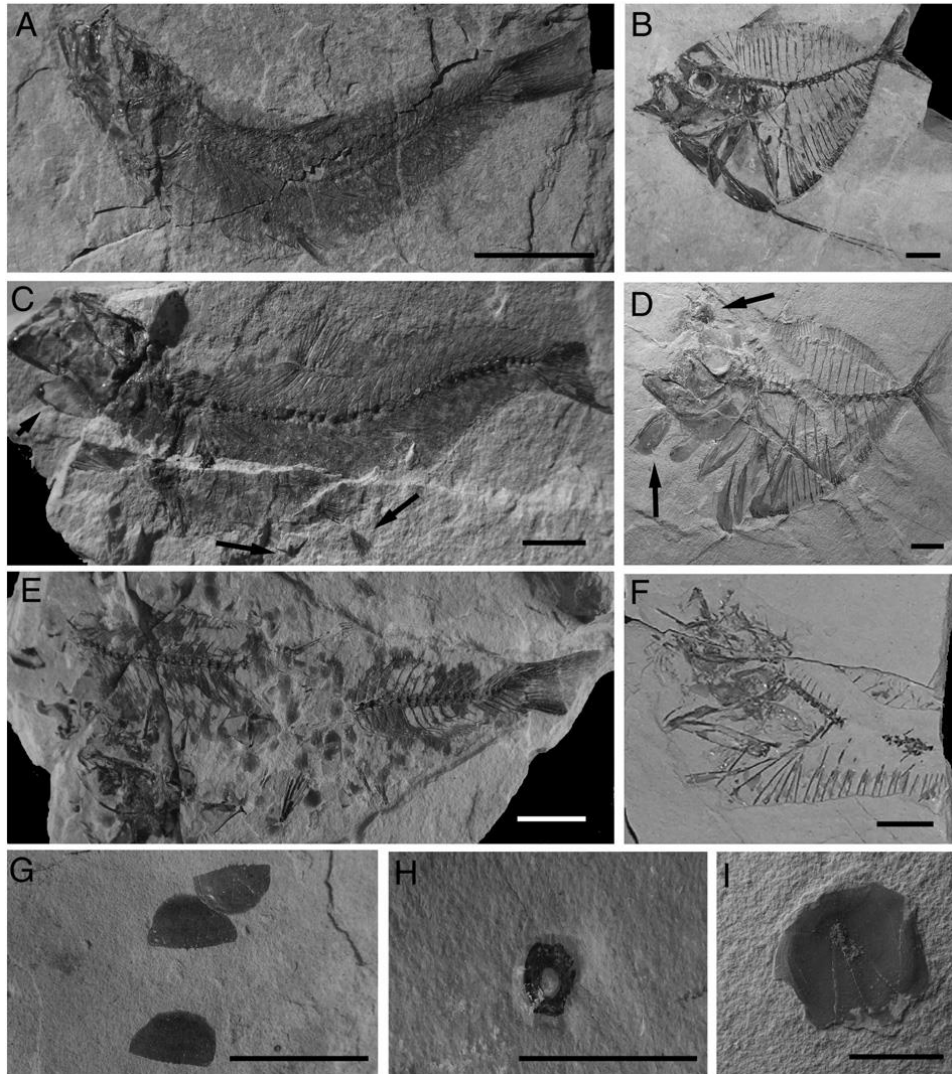
Fig. 2. Biostratinomic features showing the different preservation patterns in the sardine *Bolcaichthys catopygopterus* (left) and the moonfish *Mene rhombea* (right): A, B, complete and fully articulated specimens; C, D, partially articulated fishes (arrows indicate some dislodged elements); E, F, disarticulated skeletons, the body outline is not recognizable. G, H, I, isolated elements such as scales (G, I) and a vertebral centrum (H) of indeterminate fishes. (A) MCSNV IG.VR.69576; (B) MCNSV IG.VR.69600; (C) MCSNV IG.VR.69549; (D) MCSNV IG.VR.69374; (E) MCSNV IG.VR.71374; (F) MCSNV IG.VR.69275; (G) MCSNV IG.VR.82166; (H) MCSNV IG.VR.82177; (I) MCSNV IG.VR.69472. Scale bars represent 10 mm.
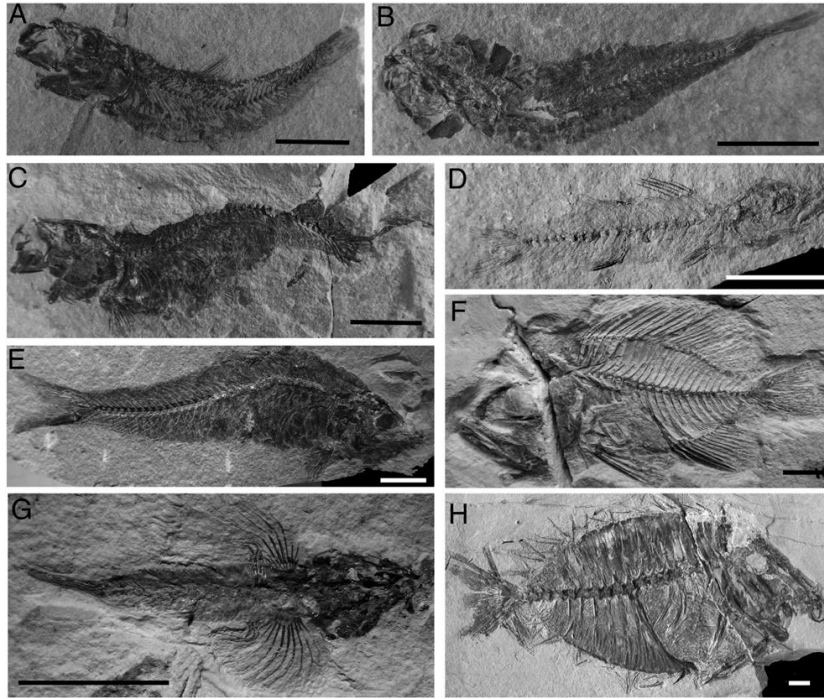
Fig. 3. Taphonomic features observed in Bolca fishes. A, the sardine *Bolcaichthys catopygopterus* (MCSNV IG.VR.71407) in "lateral" 3D orientation (with dorso-ventral axis of the body parallel with respect to the bedding plan), with concave backbone curvature and open mouth, Pesciara site. B, *B. catopygopterus* (MCSNV IG.VR. 71571) showing dorso-ventrally orientated body, Pesciara site. C, *B. catopygopterus* (MCSNV IG.VR.81852) with S-shaped vertebral column, Pesciara site. D, the percoid *Voltamulloides ceratorum* (MCSNV IG.VR.69585) showing "lateral" 3D orientation, no deformed backbone (straight) and closed mouth and fins, Pesciara site. E, *B. catopygopterus* (MCSNV IG.VR.71956) with convex curvature of the vertebral column and closed dorsal fin, Pesciara site. F, the percoid *Pavarottia lonardonii* (MCNSV IG.VR.71259) in "lateral" 3D orientation, with straight vertebral column and closed mouth, Monte Postale site. G, the dactylopteriform *Pterygocephalus paradoxus* (MCSNV IG.VR.70029) in "dorso-ventral" orientation with respect to the bedding plan, showing flabellate pectoral fins, Pesciara site. H, the acanthurid *Tylerichthys nuchalis* (MCSNV IG.VR.67382) in "lateral" 3D orientation, straight backbone and disordered disposition of the fins, Monte Postale site. Scale bars represent 10 mm.
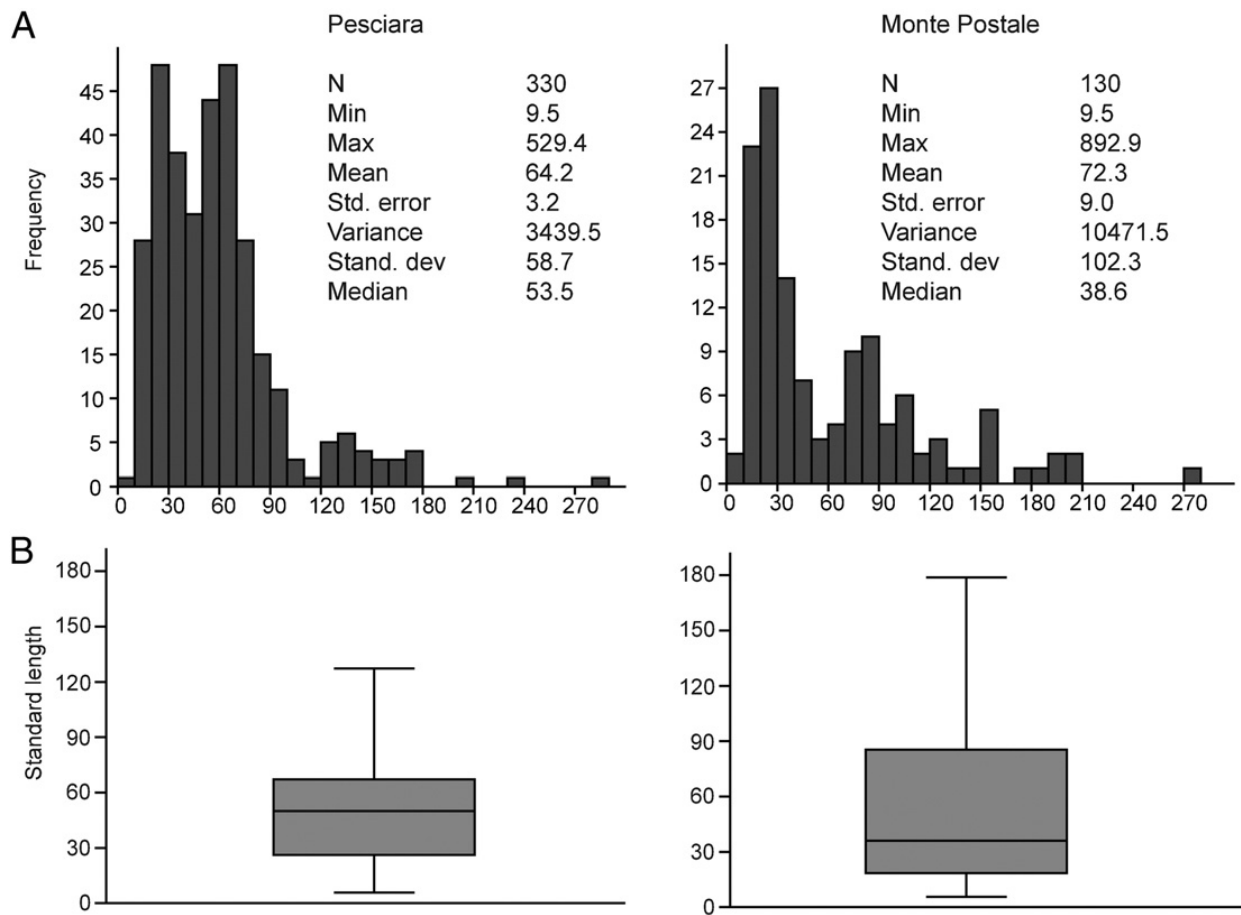
Fig. 4. Histograms with descriptive statistics (A) and box-plots (B) showing the size-frequency distribution of more than 95% of the specimens at the Pesciara and Monte Postale deposits. Measurements are in millimeter (mm). Outliers are not represented.
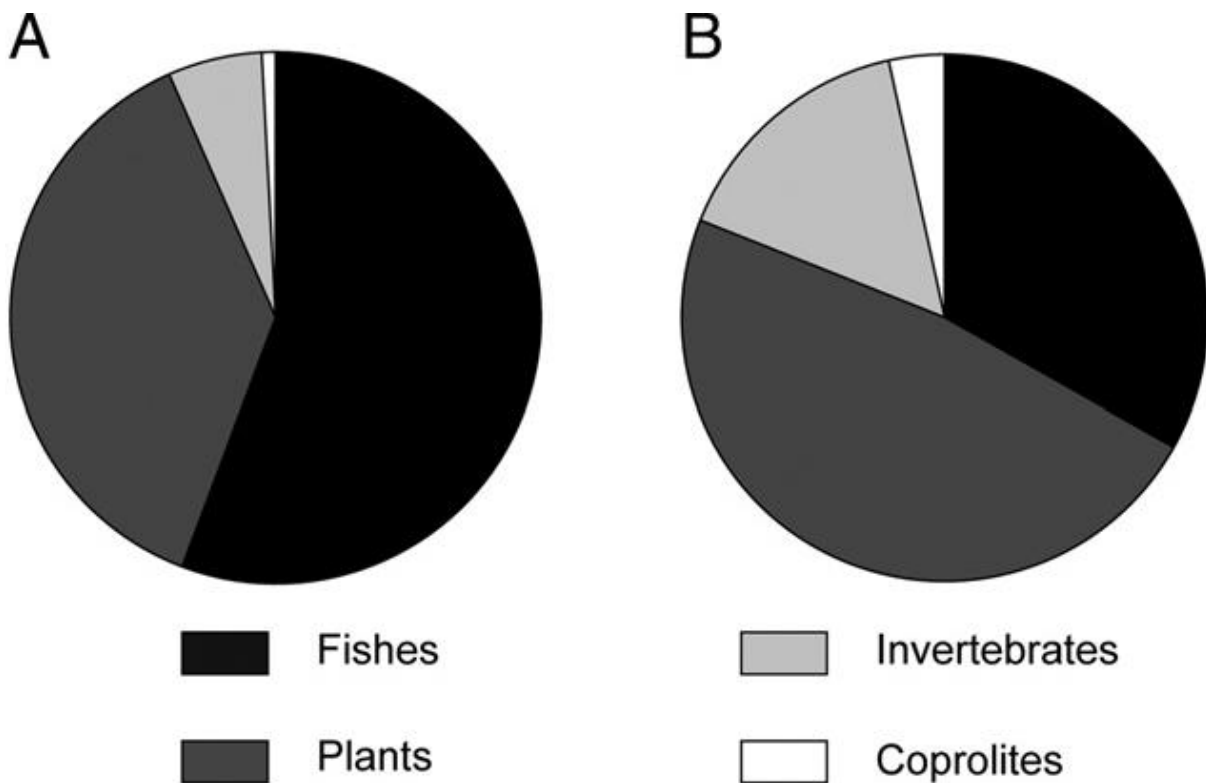
DIRECTIONALITY TESTS

Rayleigh's R: 0.28
p(random):   0.20

Chi^2:   1.29
p(random):   0.73

Rao's U: 145
p(random):   0.28
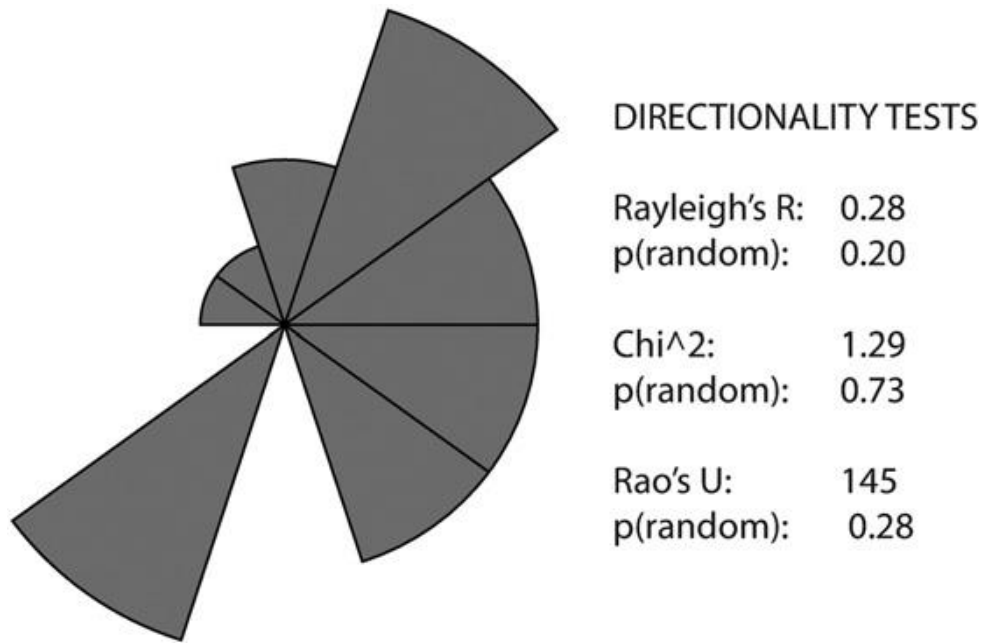
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1129   **Fig. 5.** Rose diagram and directionality tests showing no preferential orientation pattern at the

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

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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).
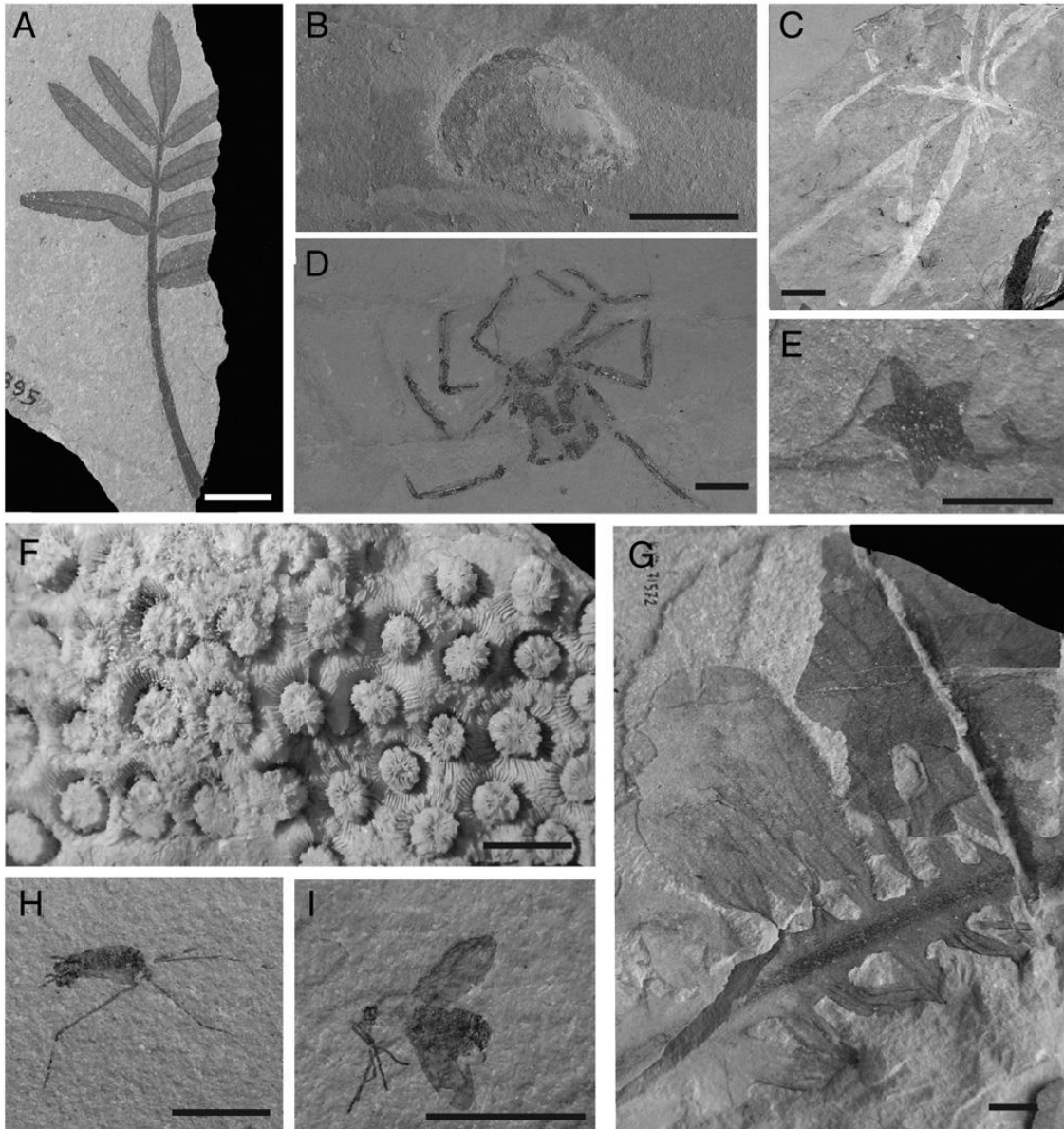
Fig. 7. Examples of the non-fish component of the Bolca assemblages. A, imparipinnate composite leaf (MCSNV IG.VR.81894), Pesciara site. B, inner prints of indeterminate bivalves (MCSNV IG.VR.71672), Pesciara site. C, seagrass remains, Monte Postale site (MCSNV IG.VR.66074). D, the spider *Archaeocypoda veronensis* (MCSNV IG.VR.67295), Monte Postale site. E, indeterminate starfish (MCSNV IG.VR.71546), Pesciara site. F, coral remains, Monte Postale site (MCSNV IG.VR.66706). G, red algae (MCSNV IG.VR.71943), Pesciara site. H, the water strider *Halobates ruffoi* (MCSNV IG.VR.91364), Pesciara site. I, indeterminate insect (MCSNV IG.VR.71652), Pesciara site. Scale bars 10 mm.
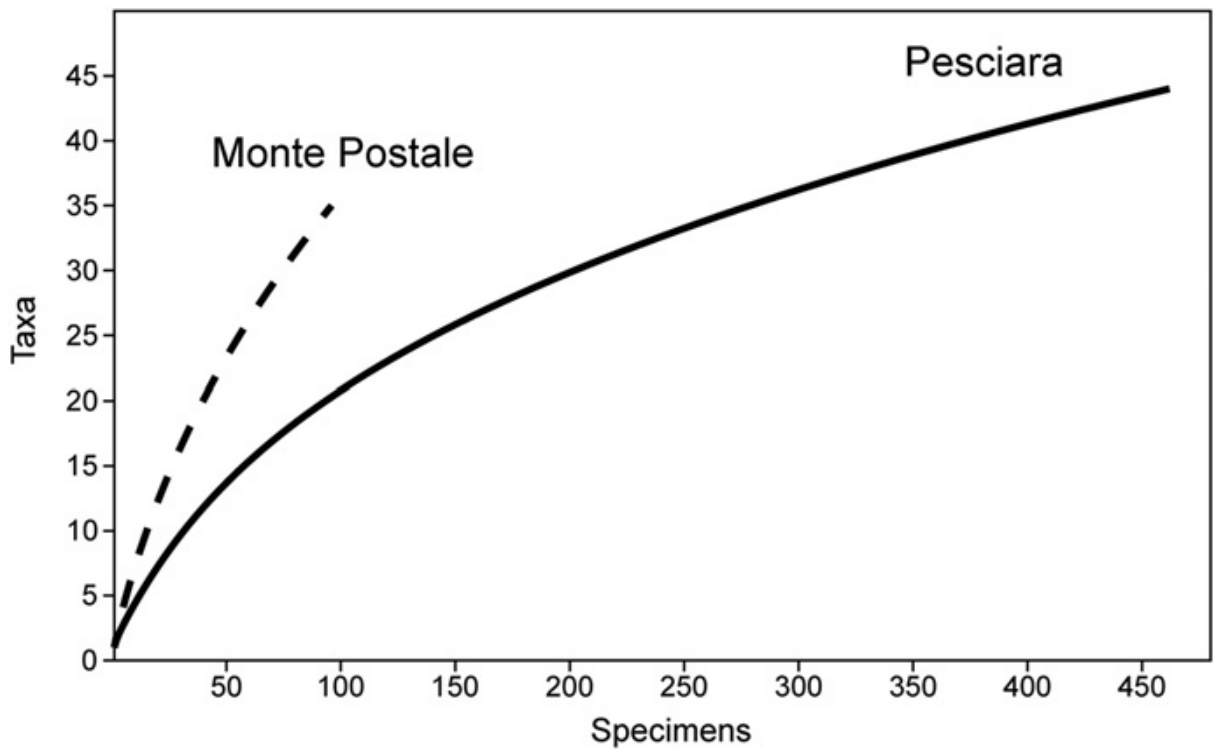
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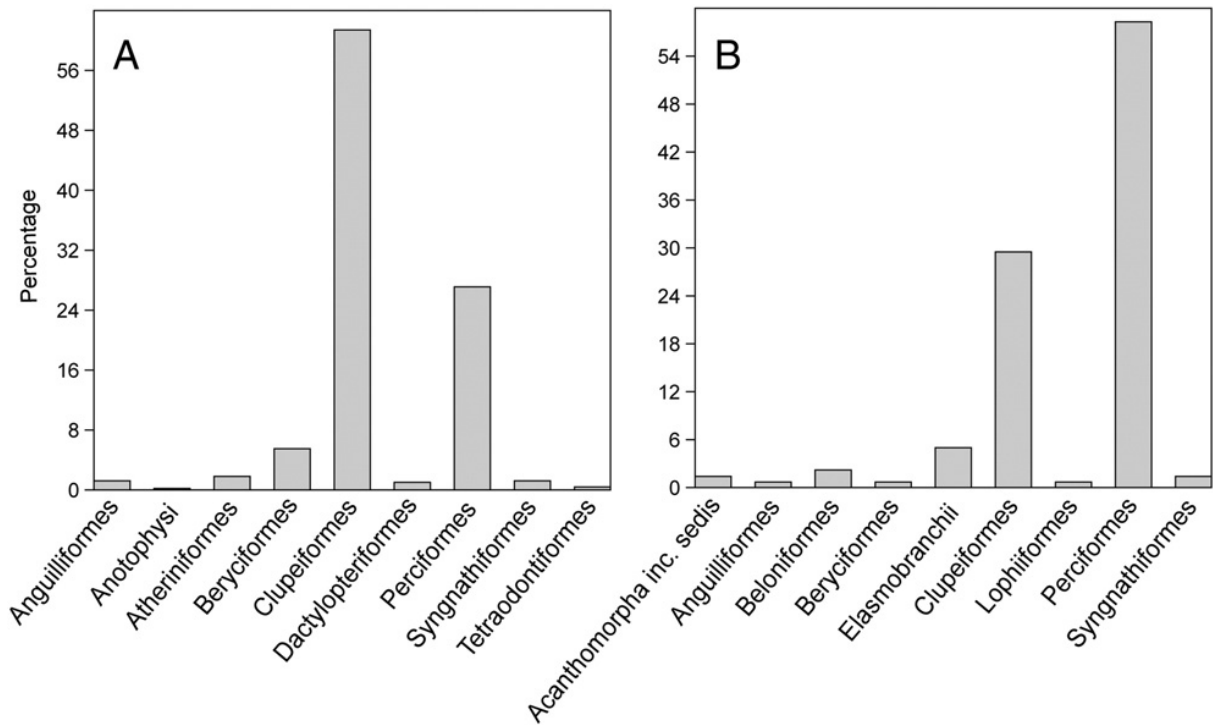
Fig. 8. Taxonomic composition of the identifiable fish remains of the Pesciara (A) and M.

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

specimens are not shown.

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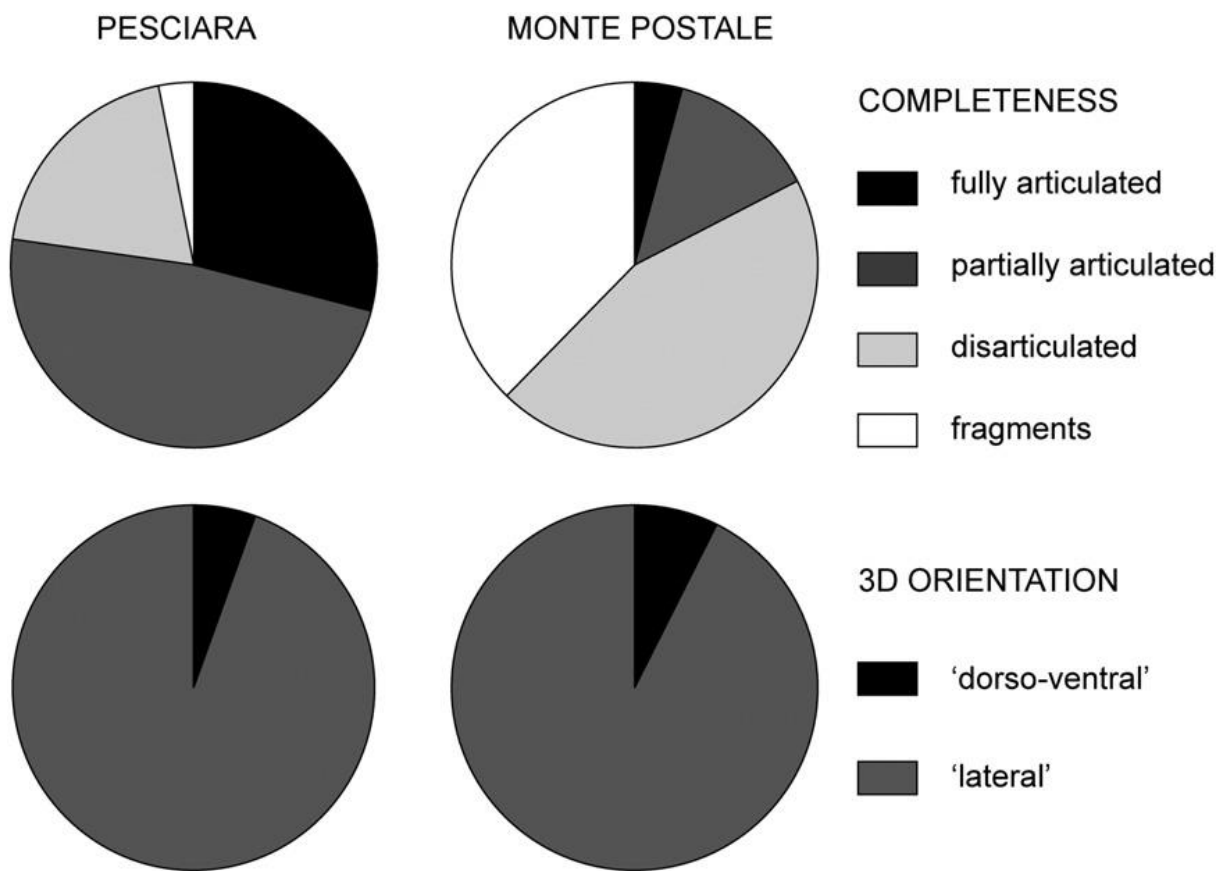
Fig. 9. Individual-based taxon accumulation curves for the Pesciara and Monte Postale fish
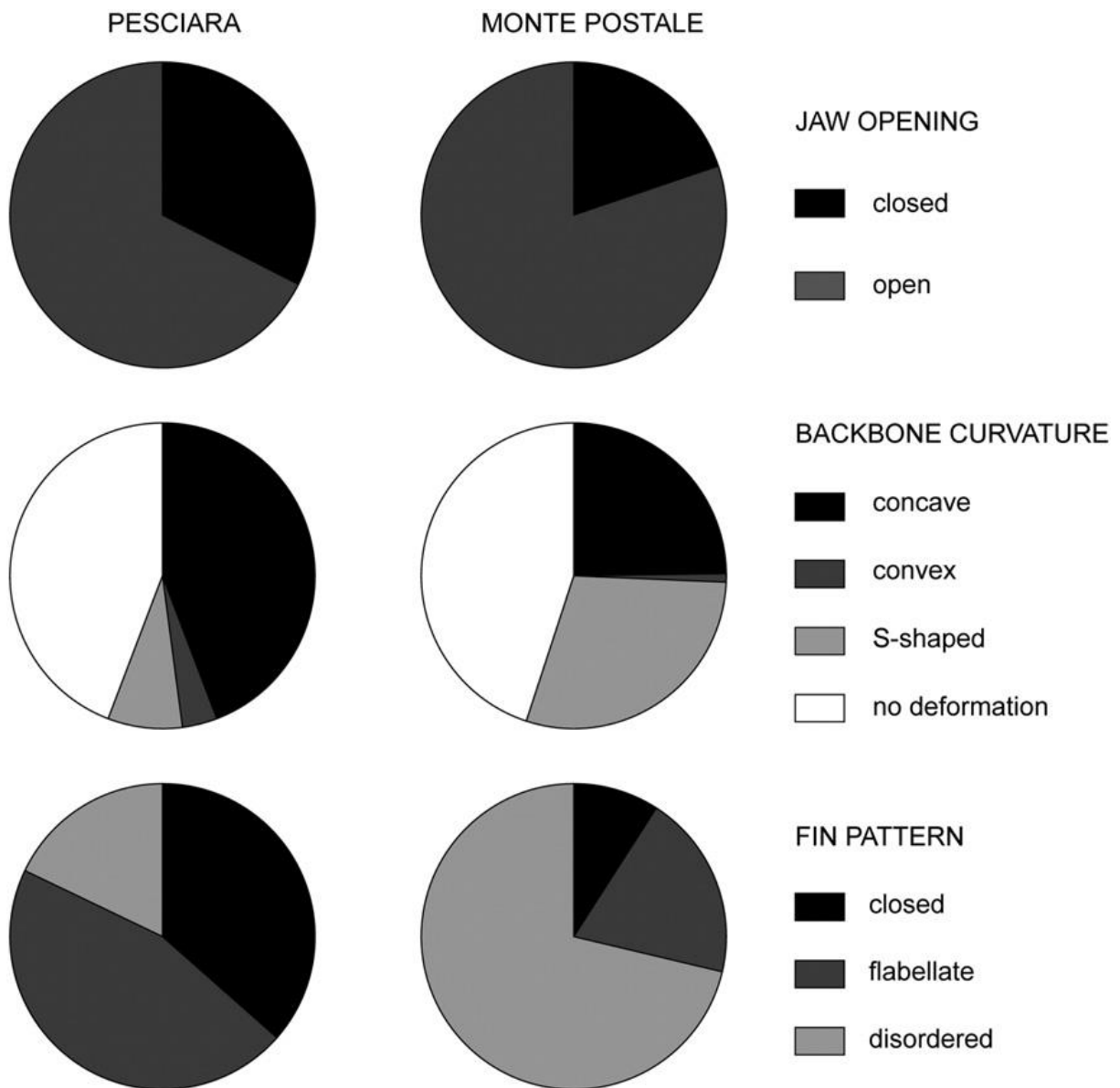
assemblages.

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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.

PESCIARA   MONTE POSTALE

JAW OPENING

■ closed

■ open

BACKBONE CURVATURE

■ concave

■ convex

■ S-shaped

□ no deformation

FIN PATTERN

■ closed

■ flabellate

■ disordered

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1157   **Fig. 11.** Tetany features in the Pesciara and Monte Postale fish assemblages. N. specimens:
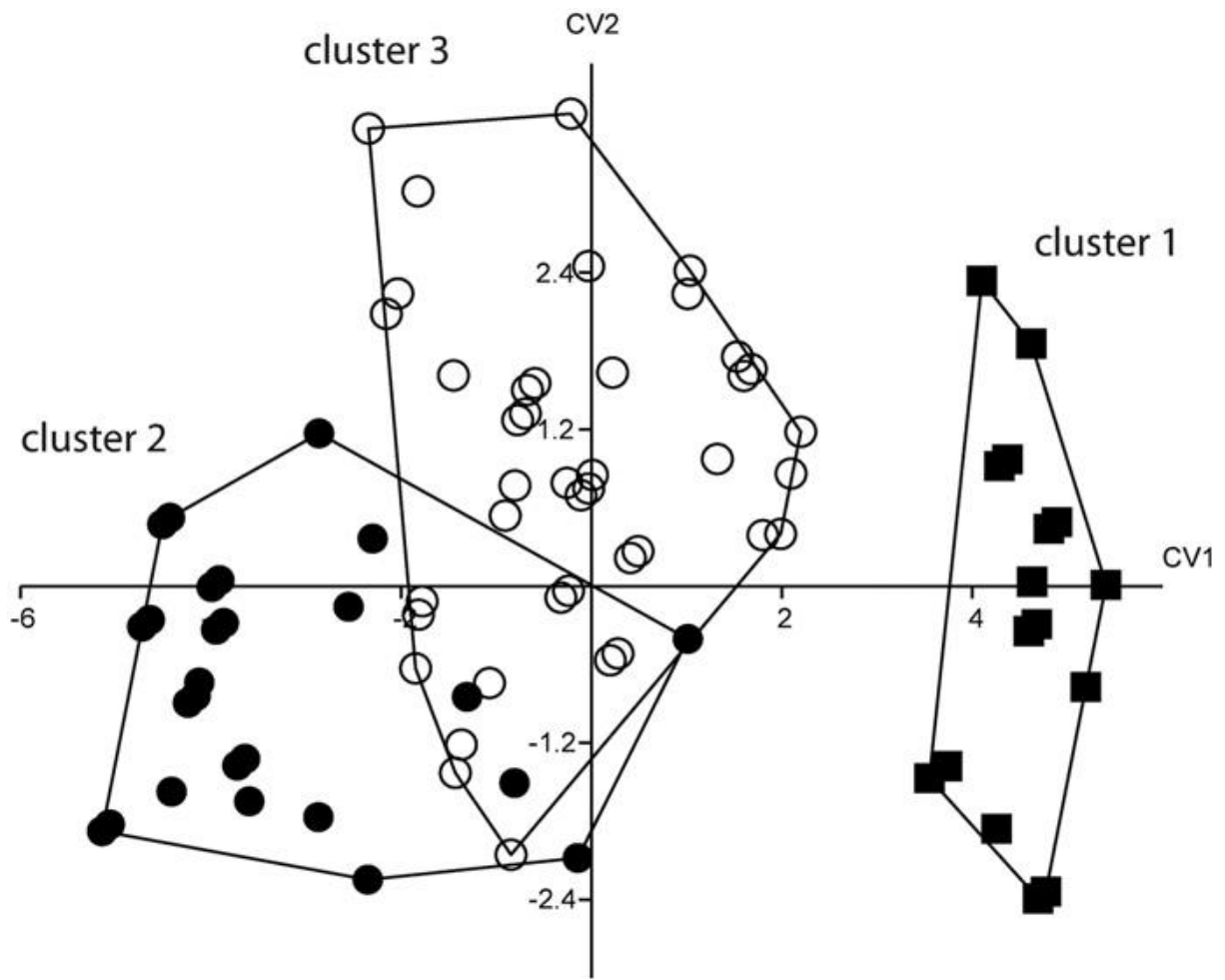
1158   Pesciara = 477; Monte Postale = 129.
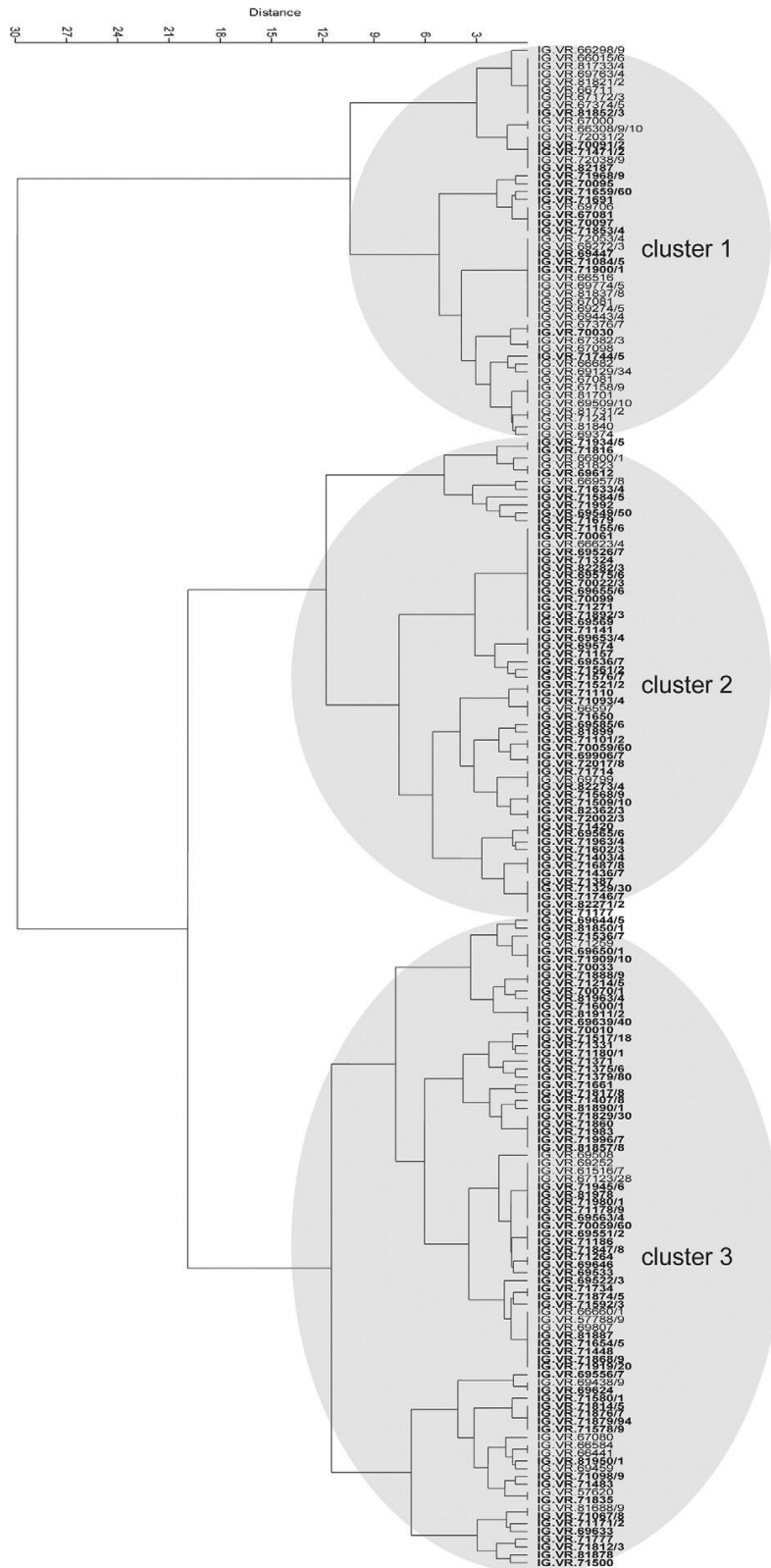
Fig. 12. Euclidean cluster analysis using the Ward's method showing the three main groups. Specimens from the Pesciara site are marked in bold (e.g., MCSNV IG.VR.69624).
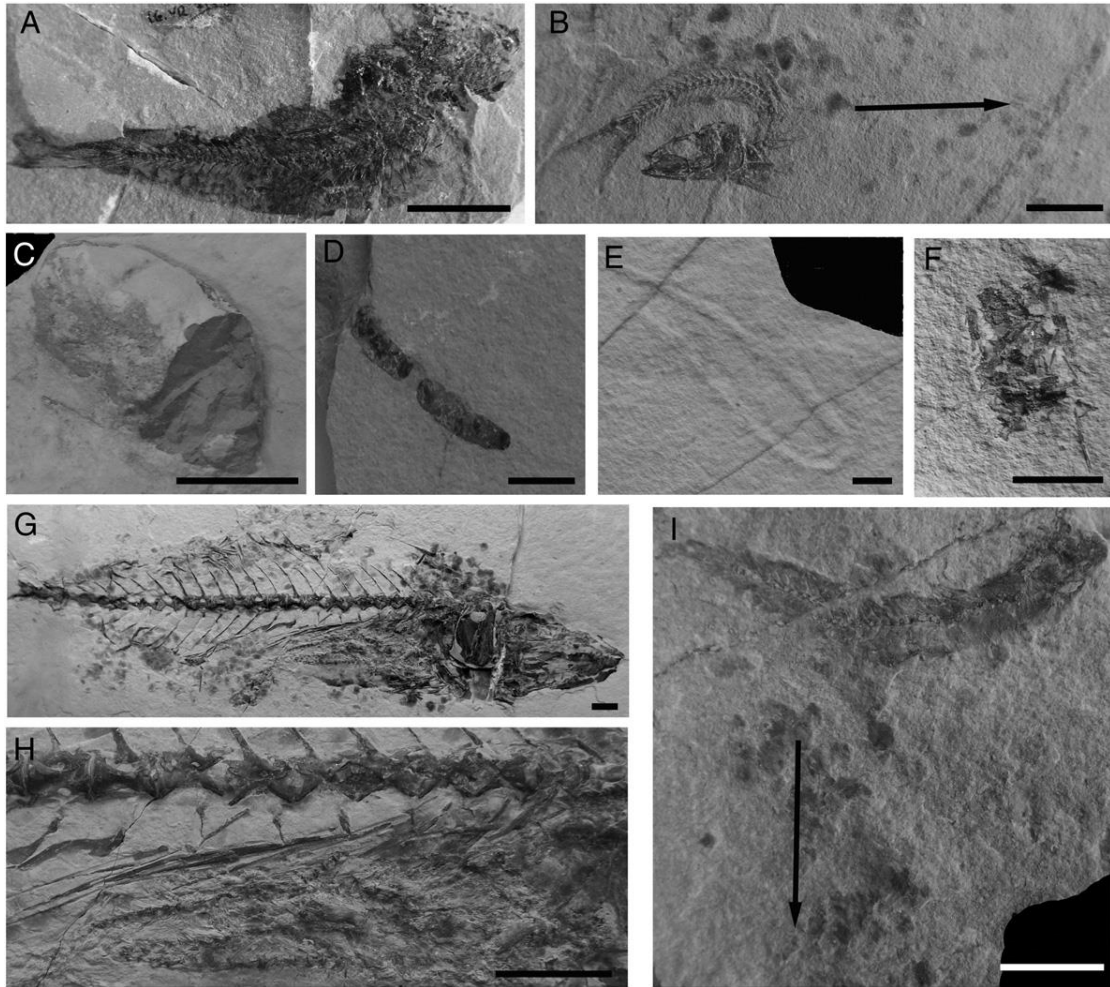
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1164 **Fig. 13.** Visual image of the clusters built on the first two canonical variate axes, resulting

1165 from the analysis of the nine standardized attributes, and representing the three main

1166 taphonomic states.

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

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

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

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

Table 2. Taxonomic composition and relative abundance of species in the Monte Postale fish

assemblage.

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	–

Table 3. The nine biostratinomic attributes used to perform the cluster analysis, the principal

component analysis (PCA) and the canonical variate analysis (CVA) in order to recognize the

different taphonomic states of the Pesciara and Monte Postale site.

	Pesciara	Monte Postale	p(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

Table 4. Diversity indices of the two fish assemblages of Bolca. The two fish assemblages have significant differences in terms of taxonomic diversity (Shannon diversity t-test: $p<0.001$).

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

Table 5. Values of the variance explained by the PC axes of the Principal Component analysis performed on the nine standardized attributes of 194 specimens from the two sites of Bolca.