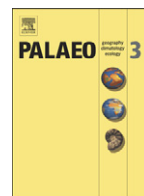




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Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy

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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 biostratigraphic 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 an 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 disaggregation of fish skeletons, coupled with the unimodal dispersion of the elements and bioturbations, clearly indicate a high degree of disturbance in the Monte Postale palaeoenvironment, suggesting at least periodic aerobic conditions at the bottom.

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1. Introduction

The Eocene locality of Bolca, northern Italy, has one of the most important and well-known ichthyofaunistic fossil assemblages. The study of these fossils started in 1950 when the Italian botanist and physician Pietro Andrea Mattioli reported the existence of exquisitely preserved petrified fishes in the limestone of Bolca in the third edition of the translation of his “Dioscorides De Materia Medicinale” (see Sorbini, 1972; Carnevale et al., 2014).

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

Although more than 100,000 fish specimens have been collected from the two main sites of Bolca, the Pesciara and Monte Postale, during the last four centuries (Blot, 1969) and more than 230 species

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

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

Despite the fish diversity of the Bolca ichthyofauna having been extensively explored in the last several decades, a complete quantitative palaeoecological analysis and a taphonomic study are still lacking. Such studies could clarify several aspects of the community structure and palaeoenvironment of this famous Konservat-Lagerstätte. From 1999 to 2011 the Museo Civico di Storia Naturale di Verona, Italy, conducted controlled excavations at the Pesciara and Monte Postale sites. About 3000 fossils were extracted, including fishes, plants, invertebrates and coprolites. In this paper we present the first quantitative palaeoecological study and a taphonomic analysis of the fish assemblages of the two main sites of Bolca. The aim of this work is to contribute to the reconstruction of the structure of the fish assemblages of the Pesciara and Monte Postale sites based on their taxonomic composition and diversity. We also provide a comprehensive analysis of the preservation patterns (e.g., disarticulation and displacement of the skeletal elements, tetany features) in order to interpret the biostratigraphic processes that led to the remarkable accumulation of fish skeletons at Bolca.

2. Geological setting

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

During the 1999–2011 excavations, specimens from the Pesciara site were quarried from a less than 2 m thick sequence with 13 fish-bearing strata corresponding to the L2 fine-grained laminated micritic level of Papazzoni and Trevisani (2006) (Fig. 1B). The stratigraphic sequence of the Pesciara site has been investigated by several authors who referred the fossiliferous layers to the “Calcarei Nummulitici”, an informal

unit of Eocene age widely distributed in northeastern Italy (e.g., Fabiani, 1914; Sorbini, 1968; Barbieri and Medizza, 1969; Dal Degan and Barbieri, 2005; Papazzoni and Trevisani, 2006). The entire succession of the Pesciara site consists of a less than 20 m thick cyclic alternation of finely laminated micritic limestone, rich in exquisitely well-preserved fishes, plants and invertebrates, and coarse-grained biocalcarene/biocalcirudite with a benthic fauna (Fig. 1B). Based on their larger benthic foraminiferan content, the fish-bearing limestone of the Pesciara site has been referred to the *Alveolina dainelli* Zone (Papazzoni and Trevisani, 2006), or to the SBZ 11 Biozone (Serra-Kiel et al., 1998), corresponding to the late Cuisian (late Ypresian, slightly less than 50 Ma).

The entire Monte Postale succession includes the Cretaceous Scaglia Rossa Formation up to the Ypresian–?Lutetian limestone. The first detailed stratigraphic study of the Monte Postale site was carried out by Fabiani (1914, 1915), who assigned the entire succession to the Lutetian. More recently, a preliminary report by Papazzoni and Trevisani (2009) considered the lower-middle strata of the Monte Postale site to be Ypresian. At present, there are no detailed biozonal assignments for the uppermost sequence of the Monte Postale section, where the specimens of the 1999–2011 excavations were extracted. The fossils of the Monte Postale site, discussed herein, were collected from 36 fine-grained laminated micritic layers pertaining to the uppermost part of the succession (Fig. 1B); based on their benthic fauna, these strata were interpreted to be Lutetian in age by Fabiani (1914, 1915) and Malaroda (1954), or Ypresian by Hottinger (1960). Recently, Trevisani (2015) referred the fish-bearing layers of the uppermost part of the Monte Postale succession to the microfacies M of Papazzoni and Trevisani (2006), consisting of pale to dark finely laminated mudstone containing abundant plants, small foraminiferans, invertebrates and fish remains. Although coral bioconstructions were reported only for the Monte Postale succession (Papazzoni et al., 2014), and the overall preservational features of the skeletal remains differ from those of the Pesciara site, Trevisani (2015) proposed a unique model for the Pesciara–Monte Postale system, in which the two successions are considered coeval, being part of a tropical coastal lagoon bordered by a volcanic archipelago and a carbonate buildup. According to Trevisani (2015), the different preservational quality of the fossil remains between these two sites is related to differences in proximity to the offshore environment, which is considered less favorable to high-quality preservation.

3. Material and methods

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

For quantitative palaeoecology, the standard length (SL) of fishes is used throughout. Orientation data were also assessed. In order to detect sampling quality, individual-based taxon accumulation curves were obtained for each site (Gotelli and Colwell, 2001). The curve rises quickly as more taxa are recorded, whereas it arises slowly if few taxa are recognized in a large sample. Therefore, the taxon accumulation curve can also be indicative of species richness. The taxonomic diversity of the two fish assemblages was computed by selecting different diversity indices: we used the Dominance, Berger–Parker, Simpson and Shannon indices that are insensitive to sample size and describe different patterns of taxonomic diversity such as the abundance of taxa, species richness and evenness (Magurran, 2004). The Shannon *t*-test was used in order to detect if the two fish assemblages exhibit different species diversity. The relative abundance of each species in its own assemblage was evaluated using the semi-quantitative ACFOR approach, ranking

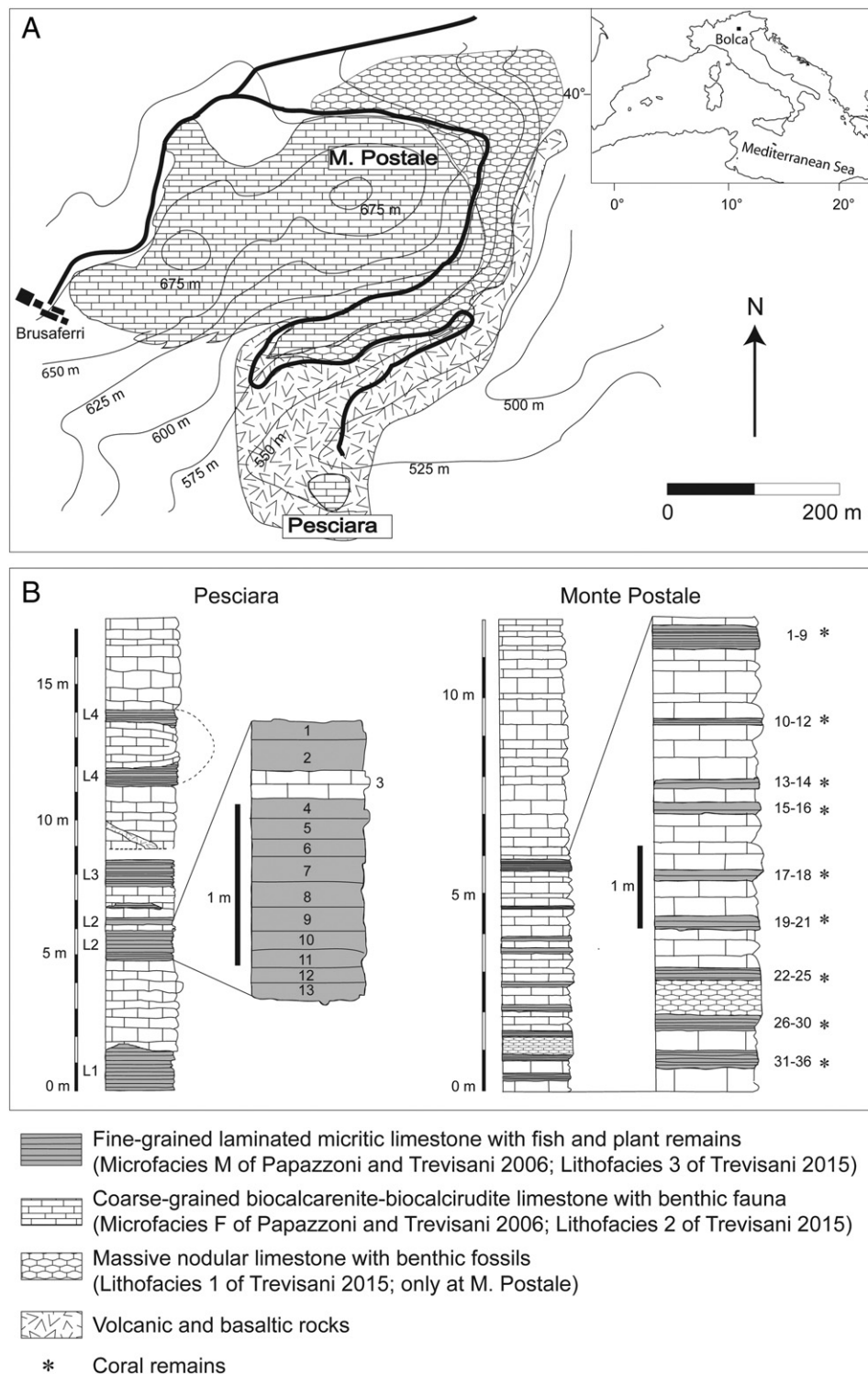


Fig. 1. A, Location and geological map of the Bolca area. B, Stratigraphic sections of the Pesciara and uppermost part of the Monte Postale sequences; the 13 productive levels of Pesciara and the 36 productive levels of Monte Postale from which all specimens were extracted are also indicated. Modified from Papazzoni and Trevisani (2006) and Trevisani (2015).

the species as abundant (>50%), common (50–26%), frequent (25–6%), occasional (5–1%) and rare (<1%). Detailed content of the two samplings with the relative abundance of species is provided in Tables 1 and 2. Since the preservation of most of the specimens from Monte Postale did not allow for the identification of many taxa of fishes at the species level, the overall composition of the Pesciara and Monte Postale fish assemblages was computed in terms of percentage at high taxonomic level, following, e.g., Bieñkowska-Wasiluk (2010) and Iserbyt and De Schutter (2012).

The taphonomy of the Pesciara and Monte Postale sites was measured in terms of the completeness of specimens, 3D orientation of the body with respect to the bedding plane, and analysis of tetany features. Completeness was based on the degree of articulation of the skeletons (Fig. 2). Four degrees of completeness were distinguished, as follows. “Fully articulated” for specimens in which the skeletal elements are completely articulated and in anatomical connection without remarkable signs of disgregation; and the scales are all firmly attached and the body outline is well-defined (Fig. 2A–B). “Partially articulated”

Table 1

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

Order	Family	Taxon	N. of specimens	Relative abundance
Anguilliformes	Anguilliformes indet.	Anguilliformes indet.	7	
Anotoptysi	Anotoptysi incertae sedis	Anotoptysi 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
	Carangidae	<i>Seriola prisca</i>	2	Rare
		<i>Trachicaranx pleuronectiformis</i>	1	Rare
	Ductoridae	<i>Ductor vestenae</i>	1	Rare
	Gobioidae indet.	Gobioidae indet.	1	
	Labridae	<i>Bellwoodilabrus landinii</i>	1	Rare
	Labroidae	Labroidae indet.	2	
		<i>Lessinia horrenda</i>	1	Rare
	Lutjanidae	<i>Veranichthys ventralis</i>	3	Rare
		<i>Mene rhombea</i>	17	Occasional
	Menidae	<i>Cyclopoma gigas</i>	20	Occasional
	Percichthyidae	<i>Pygaeus bolcanus</i>	2	Rare
	Percoidei	<i>Squamibolcoides minciottii</i>	1	Rare
		<i>Voltamulloid ceratorum</i>	7	Occasional
		Percoidei indet.	24	
	Pomatomidae	<i>Carangopsis</i> sp.	1	Rare
	Quasimullidae	<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>Pseudosparnosus 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 carnevalei</i>	1	Rare
		<i>Veronarhamphus canossae</i>	1	Rare
		<i>Fistularioides</i> sp.	2	Rare
	Fistularioididae	<i>Singnathide</i> indet.	2	
	Singnathidae	<i>Prodiodon</i> sp.	1	Rare
Tetraodontiformes	Diodontidae	<i>Protacanthodes nimesensis</i>	1	Rare
	Triacanthidae	Actinopterygii indet.	106	
Actinopterygii indet.				

for specimens with recognizable body outline (Fig. 2C–D) and articulated vertebral centra, even if some skeletal elements are unjoined or disarticulated (e.g., ribs, jaws, fins); and most of the scales are still attached but some of them may be scattered and lie around the skeleton. “Disarticulated” for specimens with unclear body outline (Fig. 2E–F) and dislodged or unjoined vertebral centra; and most of the skeletal elements are fully disarticulated, spread out and sometimes lost. Fragmentary or isolated elements (scales, vertebral centra, teeth, isolated bones) represent a separate degree of completeness (Fig. 2G–I).

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

Tetany is a postmortem contraction of the muscles of the fish caused by traumatic environmental conditions (e.g., Schaeffer and Mangus, 1976; Ferber and Wells, 1995). In order to define the degree of tetany, three features were recorded: jaw aperture with closed (Fig. 3D, F) or open mouth (Figs. 2A–B, 3A, C); backbone curvature showing concave (Figs. 2A, 3A), convex (Fig. 3E), S-shaped (Fig. 3C) or straight vertebral

column (Fig. 3D, F, H); fin disposition pattern including flabellate (Figs. 2C, 3F, G), closed (Figs. 2A, 3D) or disordered fin elements (Fig. 3H). Of these features, gaping jaw, dorsally concave backbone (i.e., opisthotonic posture) and flabellate fins can be referred to as tetany features (Faux and Padian, 2007; Anderson and Woods, 2013; Pan et al., 2015), whereas an S-shaped vertebral column and disordered fin elements may be indicative of weak currents acting when the fish was already partially decomposed (Hecker and Merklin, 1946; Jerzmańska, 1960; Bieñkowska, 2004; Pan et al., 2015). Incomplete specimens were taken into account when the features used in the taphonomy were recognizable (see Bieñkowska-Wasiluk, 2010).

In order to identify the overall taphonomic state of each fish assemblage, a cluster analysis was performed using the Ward's method on the nine standardized attributes described above and summarized in Table 3. Then, a combination of principal component analysis (PCA) and canonical variate analysis (CVA) was performed in order to have a visual image of the degree of separation between taphonomic states. Obviously, the analysis was performed only for those specimens having all nine of the standardized attributes; incomplete specimens, fragments and isolated elements cannot be included because of the lack of most of the features.

Table 2

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

Order	Family	Taxon	N. of specimens	Relative abundance
Torpediniformes	Narcinidae	<i>Titanonarke molini</i>	1	Occasional
Elasmobranchii indet.	Elasmobranchii indet.	Elasmobranchii indet.	6	
Percomorpha inc. sedis	Percomorpha inc. sedis	<i>Pietschellus aenigmaticus</i>	2	Occasional
Anguilliformes	Anguilliformes indet.	Anguilliformes indet.	1	
Beloniformes	Hemiramphidae	<i>Hemiramphus edwardsi</i>	3	Occasional
Beryciformes	Holocentridae	<i>Berybolcensis 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
	Labroidae indet.	Labroidae indet.	4	
	Menidae	<i>Mene oblonga</i>	2	Occasional
		<i>Mene rhombea</i>	3	Occasional
	Palaeorhynchidae	<i>Palaeorhynchus zorzi</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>Pseudaxoides 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	
Syngnathiformes	Aulorhamphidae	<i>Aulorhamphus chiasorbiniae</i>	1	Occasional
	Centriscidae	Centriscidae indet.	1	
Actinopterygii indet.			455	

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

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

4. Results

4.1. Quantitative palaeoecology

4.1.1. Size-frequency analysis and rose diagram

Fishes from the Pesciara site range from 10 to 530 mm SL; 95% of the specimens are less than 130 mm (Fig. 4). The plot has a bimodal pattern, with a first peak at about 20–30 mm reflecting the abundance of small-sized fishes, mostly apogonids and holocentrids; the second distinct peak is around 50–70 mm and reflects the abundance of the epipelagic sardine *Bolcaichthys catopygopterus*, whose individuals reached their

maturity at about this size (Marramà and Carnevale, 2015b). There is no apparent relationship between the SL of the fishes and their stratigraphic position as shown in the box plots whose medians range from 30 to 60 mm in all levels of the Pesciara section (Fig. S1A). The ANOSIM suggests the same trend, indicating no significant difference in size-frequency between layers ($R = -0.02$, $p = 0.56$).

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

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

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

4.1.2. Taxonomic composition

The overall composition of the two assemblages is very different in terms of category percentages (Fig. 6). Although fishes are the most studied component of the Bolca Konservat-Lagerstätte, plant remains, invertebrates and coprolites are well-represented in both deposits

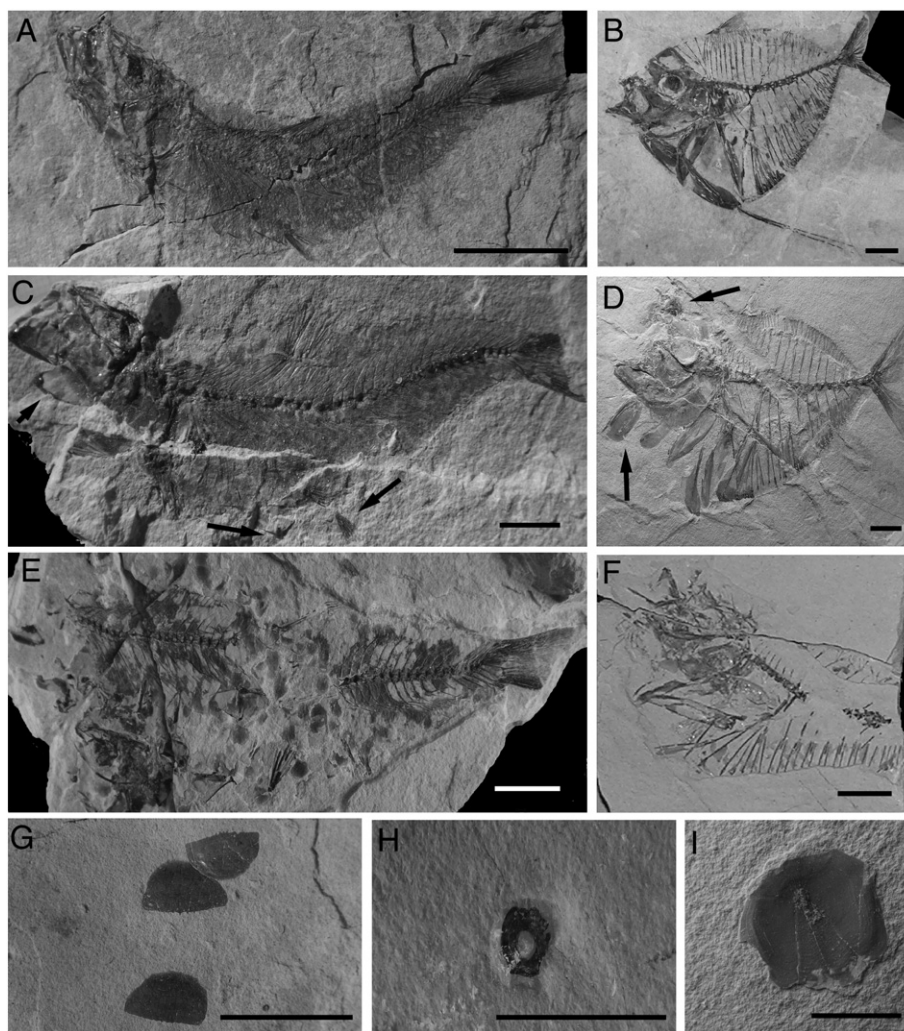


Fig. 2. Biostratigraphic features showing the different preservation patterns in the sardine *Bolcaichthys catopygopterus* (left) and the moonfish *Mene rhombea* (right): A, B, complete and fully articulated specimens; C, D, partially articulated fishes (arrows indicate some dislodged elements); E, F, 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) MCSNV 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. 7). Terrestrial vertebrates were not found during the controlled excavations.

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

The Pesciara and Monte Postale sites are characterized by notably diverse fish assemblages containing several species each. Although in terms of presence/absence, Pesciara and Monte Postale share most of the main fish groups, but their relative abundances are very different (Fig. 8A–B). A total of 595 specimens collected from the 13 fossiliferous layers at the Pesciara site yielded at least 40 species belonging to 27 families and nine orders (Table 1). The most striking feature of the taxonomic composition of the Pesciara fish assemblage is the overwhelming abundance of clupeids, with the sardine *B. catopygopterus* being the

dominant species in all layers (about 60% of the specimens, Fig. 8A). The size-frequency distribution for this taxon and the survivorship curve approximating a Type I convex-up curve (Fig. S2A–B) clearly indicate increasing mortality with age, suggesting that juvenile *B. catopygopterus* are not well-represented. Perciforms are the second most abundant lineage, with apogonids, menids, percichthyids and sparids together representing about 27% of the sample. Squirrelfishes (Holocentridae) represent the third most abundant lineage, and the second most abundant family after clupeids (about 6% of the specimens). Representatives of anguilliforms, atheriniforms, anotoptysans, syngnathiforms, tetraodontiforms and dactylopteriform-like fishes together account for the remaining 7% of the sample. There are no significant differences in relative abundance of the fish lineages in any of the sampled fossiliferous layers (Fig. S3; ANOSIM: $R = 0.16$, $p = 0.30$); this suggests that the structure of the fish assemblage was very similar throughout the stratigraphic sequence of the Pesciara site.

A total of 593 specimens from the 36 fossiliferous levels at Monte Postale yielded 34 identifiable species belonging to 25 families and 8 orders (Table 2). Perciforms are dominant, with scombrids, acropomatids, menids, putative labroids and sparids together accounting for about 60% of the sample (Fig. 8B). Clupeids constitute about 30% of the specimens, with the round herring *Trollichthys bolcensis* being the most common species. The size-frequency distribution and the survivorship curve of

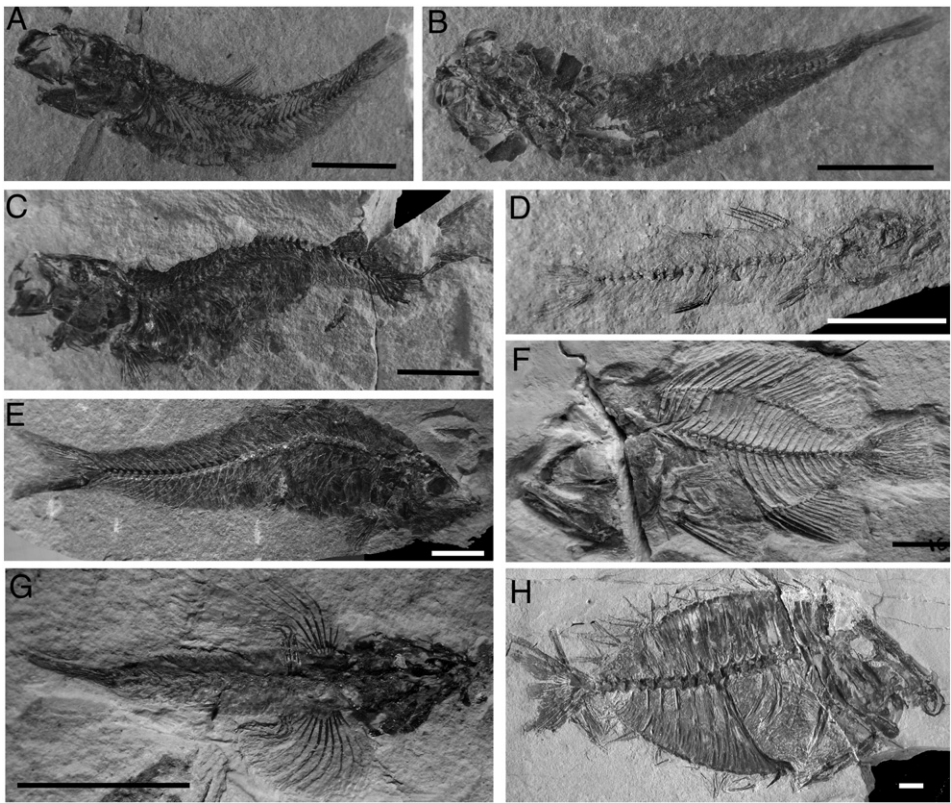


Fig. 3. Taphonomic features observed in Bolca fishes. A, the sardine *Bolcaichthys catopygopterus* (MCSNV IG.VR.71407) in “lateral” 3D orientation (with dorso-ventral axis of the body parallel with respect to the bedding plan), with concave backbone curvature and open mouth, Pesciara site. B, *B. catopygopterus* (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 *Voltamuloides 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* (MCSNV 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.

this taxon approximate a sigmoid-shape curve (Fig. S2C–D), suggesting an increasing mortality in young individuals. Another interesting feature of the Monte Postale assemblage is the relative abundance of isolated shark teeth that, together with the large numbfish, *Titanonarke molini*, represent 5% of the specimens, making elasmobranchs the third most common lineage. Anguilliforms, beloniforms, beryciforms, lophiiforms and syngnathiforms account for about 7% of the sample. The ANOSIM did not indicate significant difference in relative abundance of the lineages in the 36 fossiliferous layers sampled (Fig. S3; $R = 0.11$, $p = 0.12$), suggesting that the abundance of taxa was similar in the Monte Postale sequence.

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

4.1.3. Sampling and taxonomic diversity

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

Diversity indices clearly suggest different taxonomic diversity for the two assemblages (Table 4). The overwhelming abundance of the sardine *B. catopygopterus* results in the highest values of Dominance and Berger–Parker indices and the lowest scores for the Simpson and Shannon indices in the Pesciara fish assemblage. On the other hand,

Table 3
The nine biostratigraphic 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 Pesciara and Monte Postale site.

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	–

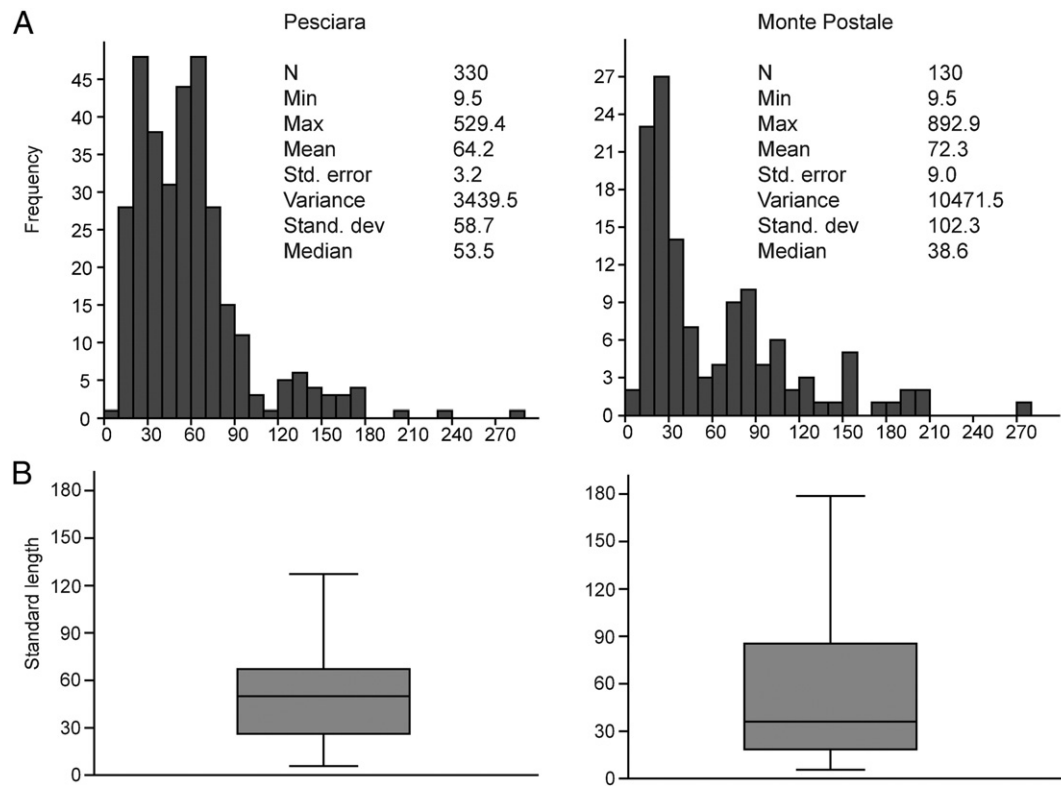


Fig. 4. Histograms with descriptive statistics (A) and box-plots (B) showing the size-frequency distribution of more than 95% of the specimens at the Pesciara and Monte Postale deposits. Measurements are in millimeter (mm). Outliers are not represented.

the absence of dominant species in the Monte Postale assemblage produces low values of Dominance and Berger–Parker, as well as the highest scores of the Simpson and Shannon indices. The different taxonomic diversity of the two assemblages is corroborated by the Shannon *t*-test ($p < 0.001$).

4.2. Taphonomy

4.2.1. Completeness and 3D orientation patterns

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

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

By contrast, more than 85% of the specimens of the Monte Postale assemblage have a low degree of completeness of the skeletal remains

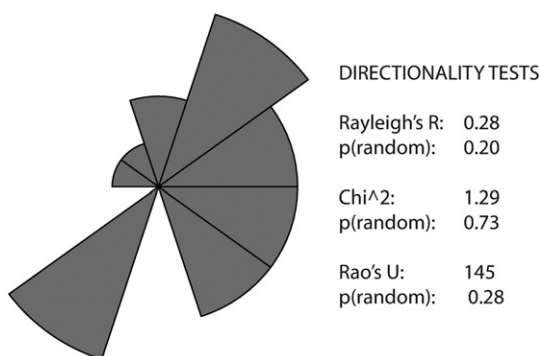


Fig. 5. Rose diagram and directionality tests showing no preferential orientation pattern at the Pesciara site (all $p > 0.05$; N. specimens = 21).

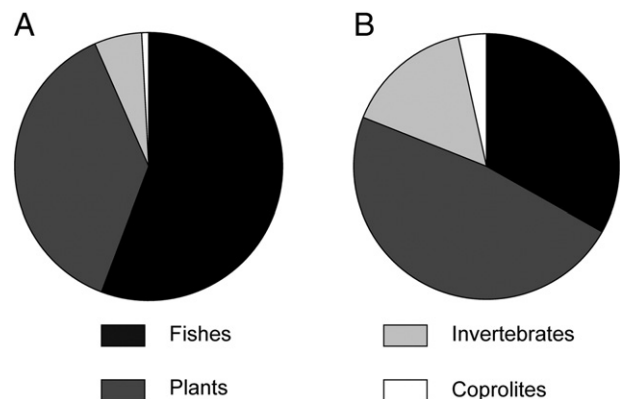


Fig. 6. Overall content of the 1070 fossil remains from the Pesciara site (A), and of the 1803 specimens from the Monte Postale site (B).

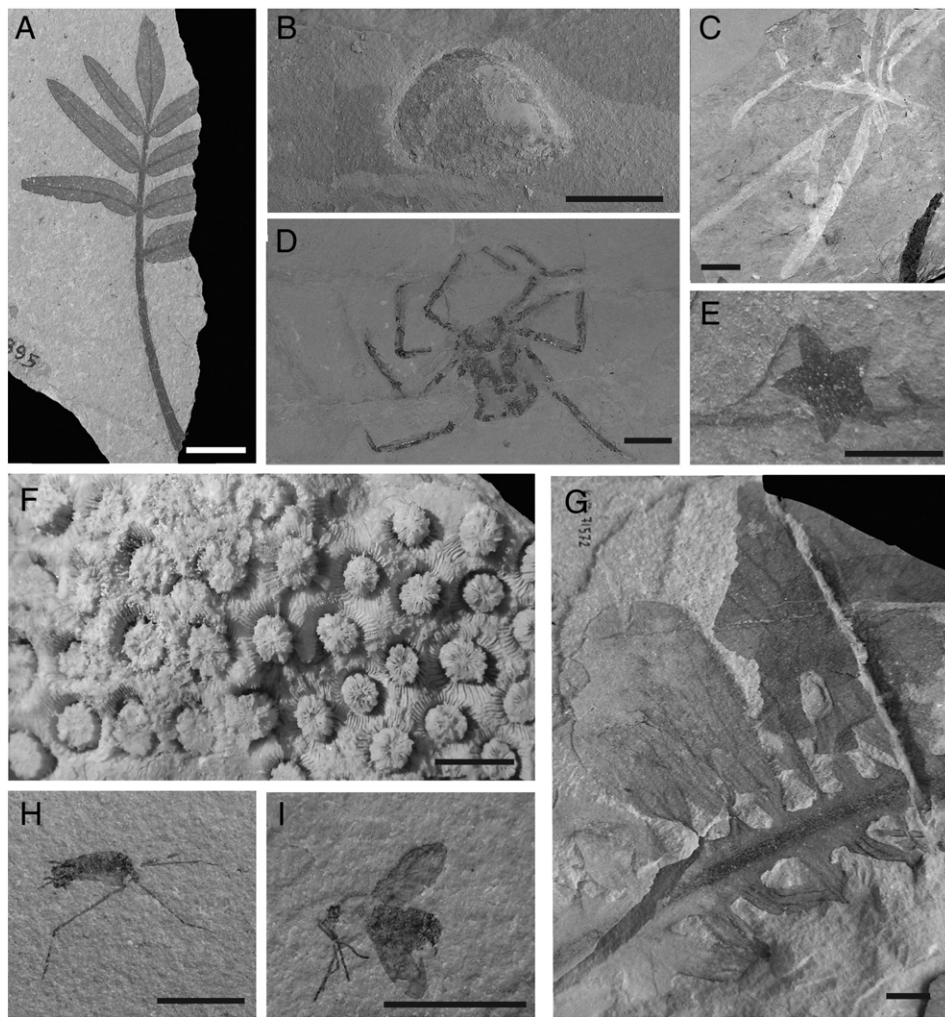


Fig. 7. Examples of the non-fish component of the Bolca assemblages. A, imparipinnate composite leaf (MCSNV IG.VR.81894), Pesciara site. B, inner prints of indeterminate bivalves (MCSNV IG.VR.71672), Pesciara site. C, seagrass remains, Monte Postale site (MCSNV IG.VR.66074). D, the spider *Archaeocypoda 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.

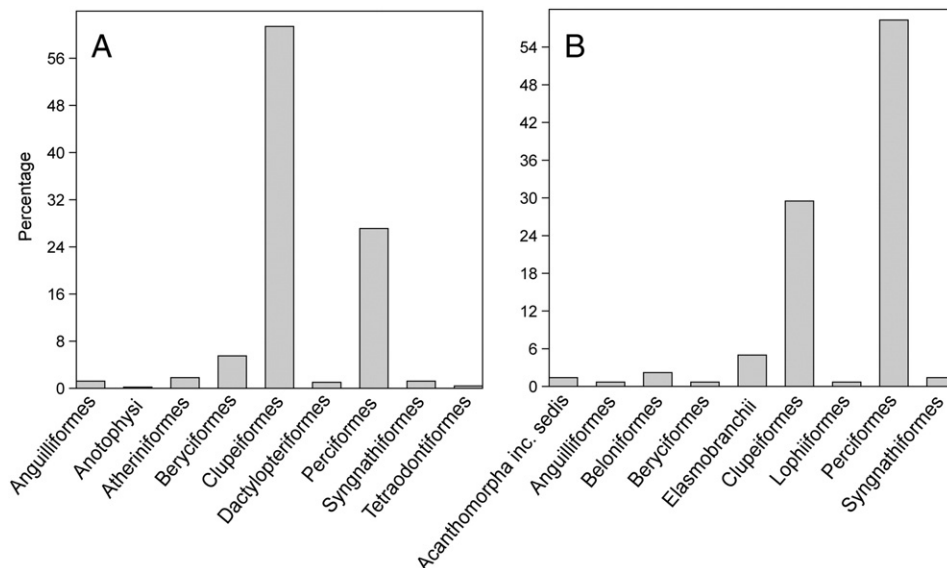


Fig. 8. Taxonomic composition of the identifiable fish remains of the Pesciara (A) and M. Postale (B) assemblages. N. specimens: Pesciara = 491; Monte Postale = 139. Indeterminate specimens are not shown.

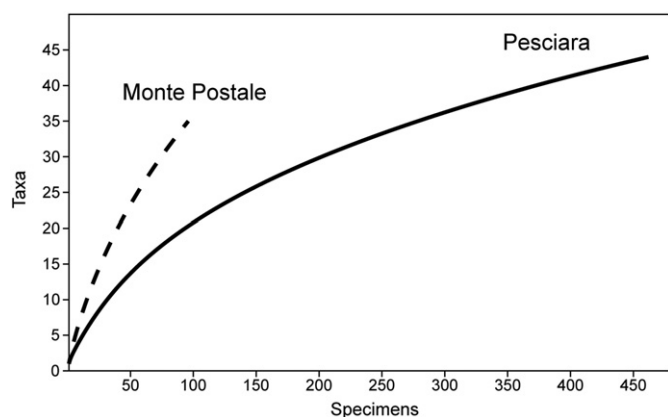


Fig. 9. Individual-based taxon accumulation curves for the Pesciara and Monte Postale fish assemblages.

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

4.2.2. Tetany features

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

20% of the specimens from the Monte Postale site. On the other hand, more than 70% of the specimens from Monte Postale have disordered fins; this feature was found in only about 18% of the specimens from the Pesciara site.

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

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

4.2.3. Cluster analysis

A cluster analysis based on the nine standardized taphonomic features discussed above and reported in Table 3 was performed on 194 specimens from the two assemblages. The analysis divides the specimens into three well-separated groups representing the combinations of different identifiable taphonomic states (Fig. 12). Cluster 1 contains almost exclusively poorly-preserved specimens from the Monte Postale assemblage having mainly disarticulated bones and disordered disposition of the fin elements. Cluster 2 contains mainly taxa from the Pesciara site that are fully or partially articulated, with a concave bending of the vertebral column, open mouth and flabellate fins; this particular combination of features typically characterizes tetany, involving mainly the sardine *B. catopygopterus*, which is the dominant species in the Pesciara fish assemblage. Cluster 3 includes specimens with a more variable combination of taphonomic features that are common in both the Pesciara and Monte Postale assemblages. The specimens of cluster 3 are fully or partially articulated, primarily with straight backbone, and flabellate, closed or disordered fins. This latter combination of features is typical of perciforms, which only rarely have the backbone bent, unlike clupeids which tend to undergo a concave curvature of the vertebral column (Bieñkowska, 2004).

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

4.2.4. Additional biostratigraphic features

Other taphonomic characters observed in the examined fossils include the so-called “half-and-half” fishes, current marks, evidence of predator–prey relationships, and bioturbation. Some specimens from the Pesciara site have a particular pattern of preservation in which the posterior part of the body is well-preserved and articulated whereas its anterior part is totally or partially disintegrated (Fig. 14A). This particular pattern is typical of the so-called “half-and-half” fishes and is regarded as possible evidence of the presence of a microbial mat (e.g., Hellawell and Orr, 2012; see Section 5). Several fishes from the

Table 4

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

	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

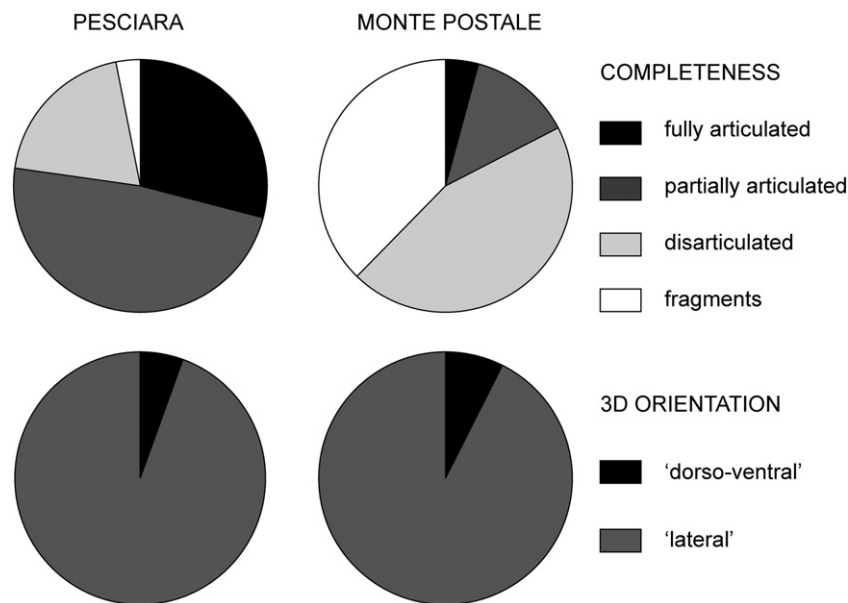


Fig. 10. Degree of completeness and 3D orientation patterns of the specimens in the Pesciara and Monte Postale deposits. N. specimens: Pesciara = 524; Monte Postale = 577.

Monte Postale site have a unimodal distribution of scales, orientated along a preferential direction (Fig. 14B, I), that has been interpreted as clear evidence of biological or hydrodynamic disturbance (e.g., Tintori, 1992; Chellouche et al., 2012). Specimens from the Pesciara site never exhibit this kind of taphonomic feature.

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

abdominal region of *B. catopygopterus* specimens. The cololites are not coiled and are relatively short in relation to the zooplanktivorous diet of these fishes (see Marramà and Carnevale, 2015b). Further evidence of predation is exclusive to the Monte Postale site and is represented by regurgitates entirely composed of fish bones (Fig. 14F). An exquisite direct evidence of predator–prey relationships from the Monte Postale site is represented by a single specimen of *Pseudaxides speciosus* (Scombridae) having at least two articulated small prey fishes as stomach content, likely representing the round herring *T. bolcensis*

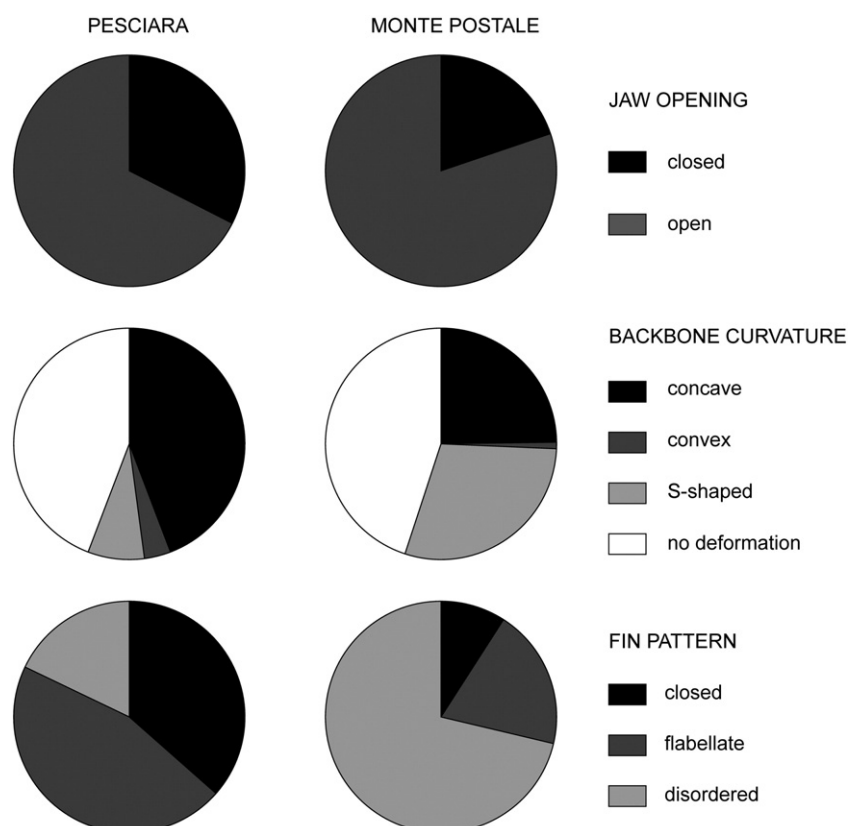


Fig. 11. Tetany features in the Pesciara and Monte Postale fish assemblages. N. specimens: Pesciara = 477; Monte Postale = 129.



(Fig. 14G–H). Evidence of bioturbation appears to be not present in the slabs extracted from the Pesciara site, whereas these are common in the material from the Monte Postale site (Fig. 14E).

5. Discussion

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

5.1. The Pesciara fish assemblage

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

From a trophodynamic point of view, the taxonomic composition concurs to suggest that the Pesciara assemblage was dominated by zooplanktivorous fishes. The overwhelming abundance of the sardine *B. catopygopterus* results in the lower diversity of the Pesciara fish assemblage with respect to that of Monte Postale. The analyses of the size frequency and the survivorship curve of this taxon (Fig. S2A–B) indicate that juveniles were not well-represented, contrary to what would be expected in a population in which young individuals should be the most abundant (see Newbrey and Bozek, 2003). Modern juvenile clupeids primarily inhabit very shallow bays and inlets (e.g., Blaxter and Hunter, 1982; Munroe, 2000); consequently, the presence of a large number of adult *B. catopygopterus* in the Pesciara assemblage seems to exclude these kinds of biotopes as possible modern analogues of the Pesciara palaeoenvironment (see Marramà and Carnevale, 2015b). Genner et al. (2004) demonstrated that in inshore marine fish assemblages, environmental fluctuations may have a negative effect on the abundance of the dominant species. Since commonness and rarity of taxa can be related to their permanence in the assemblage (Magurran and Henderson, 2003), it is possible to hypothesize that the dominance of *B. catopygopterus* in the Pesciara assemblage can be related to the permanent presence of this taxon in a stable environment, remarkably influenced by the open sea. In particular, the very large number of sardine specimens could be related to the abundance of zooplankton in a nutrient-rich environment. According to Schwark et al. (2009), molecular biomarkers measured in the fossiliferous limestone of the Pesciara site suggest that the primary production was dominated by diatoms. Therefore, diatoms possibly constituted a large part of the base of the trophic chain of the Pesciara assemblage, sustaining zooplankton, which in turn represented the main food resource of sardines. Extant clupeids represent a fundamental prey for higher trophic level fishes, playing a central role in the ecology of modern tropical coastal marine environments (e.g., Longhurst and Pauly, 1987). These fishes possibly represented the trophic nucleus in the Pesciara palaeobiotope,

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.

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

being extensively exploited by the diverse assemblage of piscivorous fishes. Nocturnal invertebratavores, represented by squirrelfishes (Holocentridae) and cardinalfishes (Apogonidae), are also relatively common in the Pesciara palaeobiotope, where they probably occupied the role of commuters of energy from adjacent habitats feeding on invertebrates living around seagrass beds and mangroves (see Parrish, 1989). The abundance of clupeids and nocturnal feeders is therefore consistent with the hypothesis that the Pesciara palaeobiotope was not directly associated with a coral reef system, but, rather, most likely represented a peri-reefal system, strongly subject to the ecological influence of both the coastal environment and the open sea (Landini and Sorbini, 1996).

The most striking taphonomic feature of the Pesciara site is the remarkable large number of well-preserved complete and partially complete fish specimens that constitute about 80% of the collected fishes. The good preservation of the fishes and, in particular, the complete squamation, clearly indicates an early interruption of the decay processes (e.g., Weiler, 1929; Bieńkowska-Wasiluk, 2010). Taphonomic studies conducted on fossil fish assemblages (e.g., Elder, 1985; Elder and Smith, 1988; Wilson and Barton, 1996; Barton and Wilson, 2005; Pan et al., 2015) suggested that high-quality preservation in Konservat-Lagerstätten is the result of a combination of several factors. The overall completeness of the specimens indicates that carcasses were not subject to prolonged floating after death, likely being rapidly accumulated on the bottom. The presence over an extended period of time of fishes in the water column after their death may also be excluded because all the skeletal elements (lower jaw, fins, ribs) of the disarticulated or partially disarticulated specimens are concentrated around the carcasses, thereby suggesting that decay processes took place on the bottom (see Chellouche et al., 2012). The possibility of a prolonged floatation of the carcasses may also be excluded because of the presence of only a few “dorso-ventrally” oriented specimens. Although the dorso-ventral orientation of the specimens could be also related to the anatomy of fish, or, alternatively, the result of sinking of the carcasses into a soft substrate (Schäfer, 1972), these fishes are usually indicative of prolonged floating due to the considerable amount of gases that expand the abdominal cavity and lead to the fish floating with its belly up, and subsequently to be deposited with its dorso-ventral axis perpendicular to the bedding plane (see, e.g., Pan et al., 2015).

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

Several studies have demonstrated that high temperatures over 20 °C contribute to accelerate decomposition (e.g., Swift et al., 1979), whereas low temperatures may promote good preservation of fossil fishes (e.g., Pan et al., 2015). The possibility of cold temperature as a

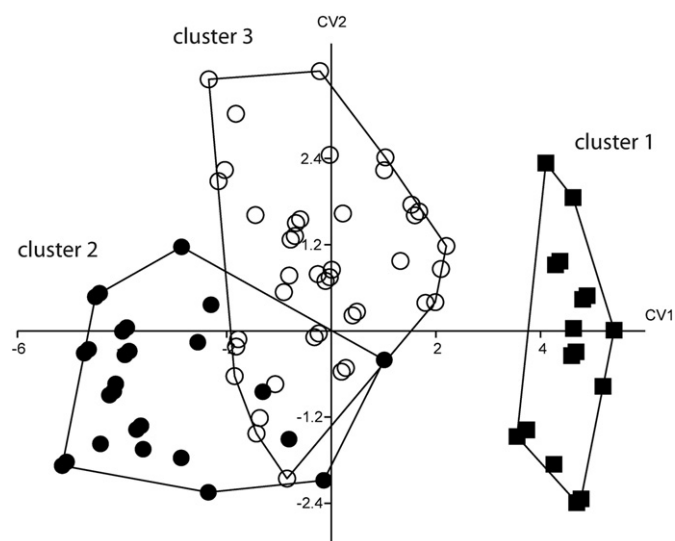


Fig. 13. Visual image of the clusters built on the first two canonical variate axes, resulting from the analysis of the nine standardized attributes, and representing the three main taphonomic states.

major cause for the good preservation of specimens in the Pesciara deposit can be excluded because of the very high mean annual palaeotemperature estimated for this region of the northwestern Tethys (see Giusberti et al., 2014). Moreover, the occurrence of the specialized marine water strider *Halobates* (Fig. 7H) suggests sea surface palaeotemperatures exceeding 20 °C, the latter representing the lower value tolerated by the extant species of this genus (Andersen et al., 1994; Cheng et al., 2012).

Papazzoni and Trevisani (2006) demonstrated that the main feature of the Pesciara fish-bearing microfacies is the regular or slightly wavy, varve-like lamination with a nearly complete absence of bioturbation. These kinds of structures are also typical of other Konservat-Lagerstätten, including the Jurassic Solnhofen (Viohl, 1990) and the Eocene Green River Formation (Fischer and Roberts, 1991). The alternation of light and dark laminae has been traditionally interpreted as the product of seasonal changes (e.g., Bradley, 1929, 1948; McGrew, 1975; Crowley et al., 1986). More recently, the origin of the varved deposits has been reinterpreted and considered to be the result of the development of conspicuous microbial mats at the sediment–water interface (Fischer and Roberts, 1991; Schieber, 1999, 2007; Papazzoni and Trevisani, 2006; Hellawell and Orr, 2012). Several studies concur to demonstrate that microbial mats are implicated in the high quality preservation of fossils by delaying their decomposition, inhibiting floating and disarticulation, protecting the carcasses from scavengers and bottom currents, preventing contact with the oxygenated water column, and promoting the formation of a calcium-rich film that protects the remains from the oxygen produced by cyanobacteria (e.g., Briggs, 2003; Hellawell and Orr, 2012; Iniesto et al., 2013, 2015). The substrate of the Pesciara site was probably further stabilized by the accumulation of diatoms that were probably directly implicated in the high-quality preservation of the fossils (Schwark et al., 2009); diatoms with their gelatinous extracellular exudates also represent a substrate for development of microbial mats (see Westall and Rincé, 1994; Carnevale, 2004). Additional indirect evidence of the presence of a microbial biofilm in the fossiliferous laminated micritic limestone of the Pesciara site appears to be the presence of the so-called “half-and-half” fishes (Fig. 14A). This particular type of preservation is also commonly observed in the Eocene fishes of the Green River Formation and has been experimentally replicated in the laboratory (Hellawell and Orr, 2012). Subsequent to an early envelopment of the body within the microbial mat, muscle contraction in certain cases caused a lateral bending of the anterior part of the body of the fish. Consequently, the anterior

portion of the body partially protruded from the mat and underwent a progressive decay of the soft and skeletal parts. The biofilm is also likely responsible for the preferential splitting surfaces (Hagadorn and Bottjer, 1999) of the Pesciara fish-bearing slabs that can be easily separated along individual laminations. By preventing the action of currents, the presence of a microbial biofilm can also explain the absence of unimodal dispersion of skeletal elements around disarticulated carcasses (Briggs, 2003). The rose diagram and directionality tests indicate a random orientation of fish bodies (Fig. 5), therefore suggesting the absence of significant unidirectional palaeocurrents.

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

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

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

Bieñkowska-Wasiluk (2010) suggested that if one group has a predominant preservational pattern, it is possible to assume stable conditions at the bottom. The Pesciara clupeids share a similar type of preservation, in most cases exhibiting tetany features, thereby supporting the hypothesis of permanent dysoxic or anoxic conditions at the bottom, as also proposed by Papazzoni and Trevisani (2006).

5.2. The Monte Postale fish assemblage

The inadequate preservation of most of the specimens from Monte Postale greatly reduced the percentage of fishes identifiable at the species level (about 20%), with negative implications on the interpretation of the original palaeoecological spectrum. The quantitative analysis presented herein clearly demonstrates the high taxonomic diversity of this assemblage, as well as the presence of a large number of small-sized

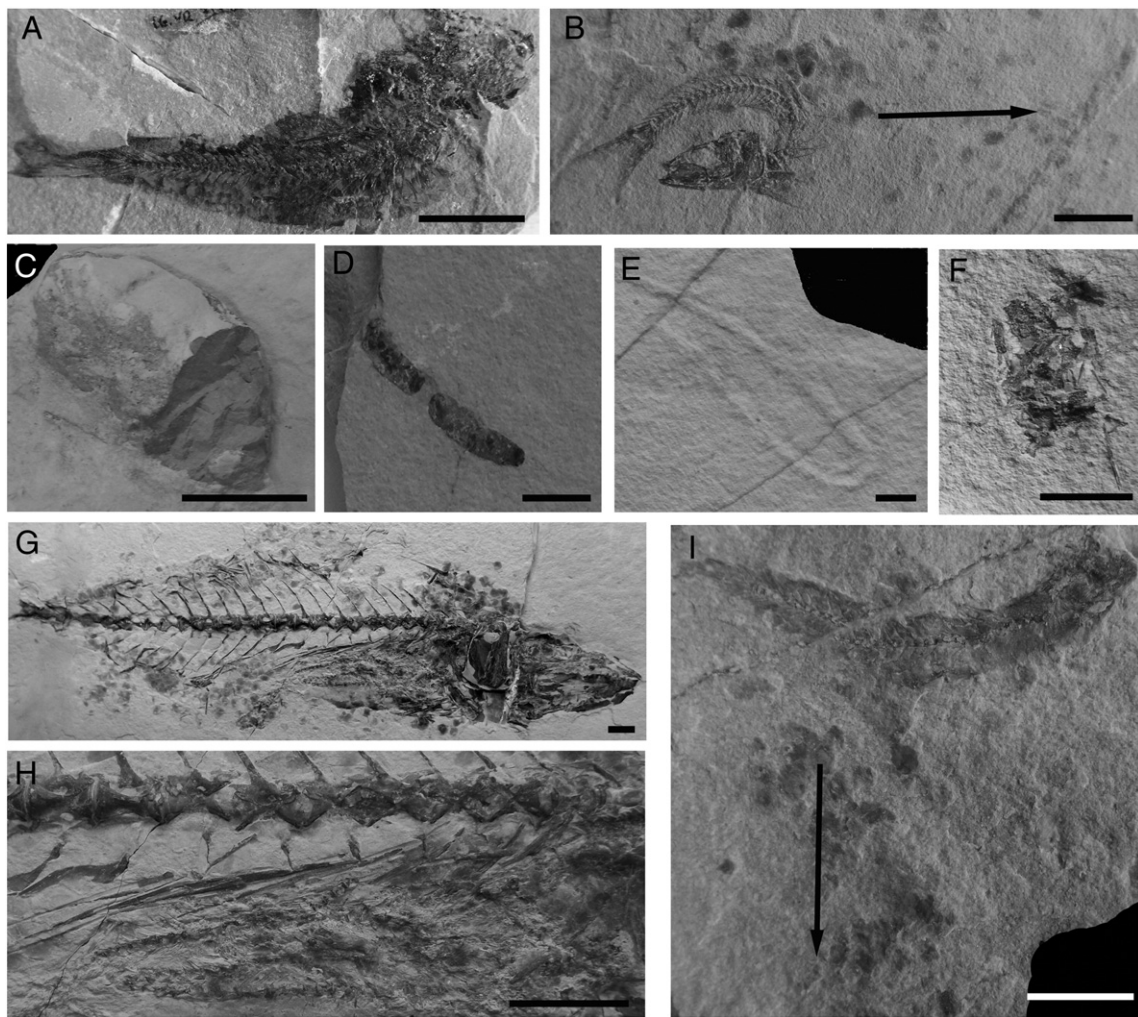


Fig. 14. Examples of further taphonomic features. A, the sardine *Bolcaichthys catopygopterus* from the Pesciara site (MCSNV IG.VR.71786) showing the so-called “half-and-half” preservation pattern. B, the round herring *Trollichthys bolcensis* from the Monte Postale site (MCSNV IG.VR.72041) showing unimodal 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.

individuals (more than 50% of the specimens are less than 40 mm SL). In general, it seems evident that there is a correlation between body size and preservation quality of the fishes from Monte Postale, in which the well-preserved fishes are primarily of small-size. Although the large number of small individuals might reflect their effective original abundance in the Monte Postale palaeobiotope, it is likely that taphonomic biases selectively prevented the preservation of large-sized individuals. For example, large fishes are able to more easily escape environmentally stressed conditions, and small-sized individuals are more likely to become quickly buried or covered by biofilm than are large fishes, preventing decomposition and the action of scavengers or predators (e.g., Grogan and Lund, 2002).

The abundance and high taxonomic diversity of small-sized fishes possibly reflects the original structure of the ichthyofauna. Most of these small-sized taxa were certainly benthic, more particularly epibenthic and cryptobenthic (see Miller, 1979). Small-sized epibenthic and cryptobenthic fishes play a relevant ecological role in the trophodynamics of tropical shallow water biotopes, particularly in coral reef systems (e.g., Ackerman and Bellwood, 2002). Therefore, the abundance of small-sized fishes appears to be consistent with the presence of coral bioherms in the Monte Postale palaeobiotope; this is also revealed by the presence of coral remains in all of its fossiliferous strata

(Fig. 7F), as well as by the presence of a bioconstructed coral threshold (already indicated by Papazzoni et al. (2014)). The analysis herein of the overall fossil content demonstrates the overwhelming abundance of plant remains, mainly macroalgae, seagrasses and terrestrial angiosperms. Seagrass beds and mangroves form part of the modern coral reef ecosystems and have high fish diversity, particularly of small-sized and juveniles individuals (e.g., Parrish, 1989; Laegdsgaard and Johnson, 1995; Beck et al., 2001; Sichum and Tantichodok, 2013), whereas the density of adults and large-sized fishes is generally low (Blaber, 1980, 1986). Several studies focused on the role of shallow-water habitats in modern tropical seas demonstrated that seagrass beds and mangroves provide protective cover for many species of fishes and invertebrates, acting as nurseries and safe havens for many families living on coral reefs (Parrish, 1989; Laegdsgaard and Johnson, 1995; Nagelkerken et al., 2002; Verweij et al., 2006). The abundance of fossil macroalgae and seagrasses, and the ecological affinities of the fish taxa of the Monte Postale assemblage, might indicate that seagrass beds and mangroves (primarily constituted by the mangrove palm *Nypa*; see Wilde et al., 2014) surrounding a coral reef system characterized the Monte Postale palaeobiotope. Anguilliforms, lophiiforms, holocentrids, syngnathiforms, ehippids, labroids, apogonids, sparids, carangids, acanthurids and siganids possibly inhabited both the densely

vegetated peri-reefal areas and the reefs (see Landini and Sorbini, 1996). Round herrings are abundant in modern mangrove fish assemblages of tropical regions associated with coral reefs (e.g., Castellanos-Galindo et al., 2013). Large-size pelagic fishes such as scombrids, carangids, and sharks possibly occupied the role of top predators in the Monte Postale palaeobiotope.

The most striking taphonomic feature exhibited by the fish specimens from Monte Postale is the remarkably large number of disarticulated and fragmented specimens (about 88% of the sample). The inadequate preservation of most of the fish remains is clearly indicative of a rapid decay of the soft tissues (e.g., Weiler, 1929; Tintori, 1992; Bieñkowska-Wasiluk, 2010). The extended floatation of dead fishes over a long period of time might be plausible because of the abundance of disarticulated specimens, and fragmentary and isolated bones, suggesting that the decomposition of the carcasses began in the water column (Fürsich et al., 2007; Chellouche et al., 2012). About 70% of the fishes have disordered disposition of the fins, whereas about 60% of specimens with deformed backbones have a S-shaped disposition of the vertebral column. These characters likely represent the result of the action of weak bottom currents acting on the skeleton when the tissues were partially decomposed (Hecker and Merklin, 1946; Jerzmańska, 1960; Bieñkowska, 2004). The presence of palaeocurrents at the bottom may also be supported by the unidirectional dispersion of the scales around the bodies of fishes (Fig. 13B, I). Several studies (Elder and Smith, 1988; Tintori, 1992; Chellouche et al., 2012) have suggested that the arrangement of the skeletal elements along a preferential direction may be indicative of the presence of bottom currents. Therefore, the high degree of fragmentation and disarticulation of carcasses, S-shaped backbones, disordered fin elements, and unimodal dispersion of skeletal elements clearly indicate episodic hydrodynamic disturbance at the sediment–water interface. Bottom currents in shallow-water basins produce a temporary mixing of water, bringing oxygen to the bottom (Tintori, 1992; Barton and Wilson, 2005; Mancuso, 2012). The clear evidence of bioturbation tracks (Fig. 14E) suggests that normal aerobic conditions that allowed for a moderately abundant invertebrate fauna (mainly worms, crustaceans and mollusks) often characterized the Monte Postale palaeoenvironment. Periodic changes of environmental conditions can also be inferred by the different degrees of preservation of specimens belonging to a single fish taxon. Unlike at the Pesciara site, in which specimens belonging to a specific lineage (i.e., clupeids) have a unique degree of preservation pattern (i.e., mostly articulated), the fishes belonging to a specific lineage have different degrees of preservation at the Monte Postale site. Bieñkowska-Wasiluk (2010) suggested that the presence of several fishes of a single specific lineage in at least three different stages of disarticulation may be indicative of highly variable bottom conditions. Therefore, we can hypothesize that stable environmental conditions were interrupted by periodic disturbance events. In any case, traumatic conditions at the bottom can be inferred by the moderate degree of tetany in well-preserved specimens. Moodie (1918) suggested that the abundance of specimens with a straight backbone may be indicative of the absence or remarkable reduction of the factors that can produce the opisthotonic posture in death throes. However, the reduced number of specimens characterized by a deformed vertebral column in the Monte Postale fish assemblage (with respect to that of the Pesciara) is probably due to the relative scarcity of fish taxa (i.e., clupeids) that are potentially more prone to have this kind of deformation. Moreover, the specimens that do not have backbone distortion (e.g., perciforms) in some cases exhibit gaping mouths and flabellate fins, two signs of tetany (Anderson and Woods, 2013; Pan et al., 2015).

6. Conclusions

Although the controlled excavations of 1999–2011 did not include the full diversity of the Bolca ichthyofauna, the analysis of the extracted material helps us to confirm and better define some palaeoecological and palaeoenvironmental aspects of the two most important productive

sites of the Bolca Konservat-Lagerstätte. The quantitative and taphonomic analyses of the Pesciara and Monte Postale fish assemblages clearly defined two distinctive palaeocommunities and two different depositional settings.

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

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

Unfortunately, the detailed reconstruction of the actual trophic and ecological relationships of the Bolca fish fauna cannot be hypothesized solely using museum collections because these fossils usually do not have precise stratigraphic data and their abundance was surely biased by artificial selection of well-preserved specimens. For example, very common taxa like clupeids are not proportionally well represented in collections, whereas rare species are far more likely to become part of a museum collection. Further systematic excavations in these two deposits are therefore necessary to expand our knowledge about this extraordinary Eocene Konservat-Lagerstätte.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.04.021>.

References

- Ackerman, J.L., Bellwood, D.R., 2002. Comparative efficiency of clove oil vs rotenone for sampling tropical reef fish assemblages. *J. Fish Biol.* 60, 893–901.

- Andersen, N.M., Farma, A., Minelli, A., Piccoli, G., 1994. A fossil *Halobates* from the Mediterranean and the origin of sea skaters (Hemiptera, Gerridae). *Zool. J. Linn. Soc. Lond.* 112, 479–489.
- Anderson, K., Woods, A.D., 2013. Taphonomy of Early Triassic fish fossils of the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation near Wapiti Lake, British Columbia, Canada. *J. Palaeogeogr.* 2, 321–343.
- Bannikov, A.F., 2004a. Eocottidae, a new family of perciform fishes (Teleostei) from the Eocene of northern Italy (Bolca). *St. Ric. Giac. Terz. Bolca* 10, 17–35.
- Bannikov, A.F., 2004b. Fishes from the Eocene of Bolca, northern Italy, previously classified with the Chaetodontidae (Perciformes). *St. Ric. Giac. Terz. Bolca* 10, 55–74.
- Bannikov, A.F., 2006. Fishes from the Eocene of Bolca, northern Italy, previously classified in the Sparidae, Serranidae and Haemulidae (Perciformes). *Geodiversitas* 28, 249–275.
- Bannikov, A.F., 2008. Revision of the atheriniform fish genera *Rhamphognathus* Agassiz and *Mesogaster* Agassiz (Teleostei) from the Eocene of Bolca, northern Italy. *St. Ric. Giac. Terz. Bolca* 12, 77–97.
- Bannikov, A.F., 2014. The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *St. Ric. Giac. Terz. Bolca* 15, 23–34.
- Bannikov, A.F., Carnevale, G., 2010. *Bellwoodilabrus landinii*, a new genus and species of labrid fish (Teleostei: Perciformes) from the Eocene of Bolca. *Geodiversitas* 32, 201–220.
- Bannikov, A.F., Tyler, J.C., 1999. *Sorbinicapros*, a new second taxon of the caproid-related fish family Sorbinipercidae, from the Eocene of Bolca, Italy. *St. Ric. Giac. Terz. Bolca* 8, 129–142.
- Bannikov, A.F., Zorzin, R., 2004. A new genus and species of percoid fish (Perciformes) from the Eocene of Bolca, northern Italy. *St. Ric. Giac. Terz. Bolca* 7, 7–16.
- Barbieri, G., Medizza, F., 1969. Contributo alla conoscenza geologica della regione di Bolca (Monti Lessini). *Mem. Ist. Geol. Min. Univ. Padova* 27, 1–36.
- Barthel, K.W., Swinburne, N.H.M., Conway Morris, S., 1990. Solnhofen: A Study in Mesozoic Palaeontology. Cambridge University Press, Cambridge (246 pp.).
- Barton, D.G., Wilson, M.V.H., 2005. Taphonomic variations in Eocene fish-bearing varves at Horsefly, British Columbia, reveal 10,000 years of environmental change. *Can. J. Earth Sci.* 42, 137–149.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Weinstein, M.P., 2001. The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51, 633–641.
- Bellwood, D.R., 1996. The Eocene fishes of Bolca: the earliest coral reef fish assemblage. *Coral Reefs* 15, 11–19.
- Biełkowska, M., 2004. Taphonomy of ichthyofauna from an Oligocene sequence (Tylawa Limestones horizon) of the Outer Carpathians, Poland. *Geol. Q.* 48, 181–192.
- Biełkowska-Wasiluk, M., 2010. Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland. *Acta Geol. Pol.* 60, 479–533.
- Blaber, S.J.M., 1980. Fish of the Trinity Inlet system of North Queensland with notes on the ecology of fish fauna of tropical Indo-Pacific estuaries. *Aust. J. Mar. Freshwat. Res.* 31, 137–146.
- Blaber, S.J.M., 1986. Feeding selectivity of a guild of piscivorous fish in mangrove areas of north-west Australia. *Aust. J. Mar. Freshwat. Res.* 37, 329–336.
- Blaxter, J.H.S., Hunter, J.R., 1982. The biology of the clupeoid fishes. *Adv. Mar. Biol.* 20, 1–223.
- Blot, J., 1969. Les poissons fossiles du Bolca classés jusqu'ici dans les familles des Carangidae, Menidae, Ehippididae, Scatophagidae. *St. Ric. Giac. Terz. Bolca* 1, 1–525.
- Blot, J., 1978. Les apodes fossiles du Monte Bolca. *St. Ric. Giac. Terz. Bolca* 3, 1–260.
- Blot, J., 1980. La faune ichthyologique des gisements du Bolca (Province de Verone, Italie). Catalogue systématique présentant l'état actuel des recherches concernant cette faune. *Bull. Mus. Natl. Hist. Nat. Paris* 2, 339–396.
- Blot, J., Tyler, J.C., 1990. New genera and species of fossil surgeonfishes and their relatives (Acanthuridae, Teleostei) from the Eocene of Monte Bolca, Italy, with application of the Blot formula to both fossil and Recent forms. *St. Ric. Giac. Terz. Bolca* 6, 13–92.
- Bradley, W.H., 1929. Varves and climate of the Green River Epoch. *Geol. Surv. Prof. Pap.* 158, 87–110.
- Bradley, W.H., 1948. Limnology and the Eocene lakes of the Rocky Mountain region. *Geol. Soc. Am. Bull.* 59, 635–648.
- Bray, J.R., Curtis, J.Y., 1957. An ordination of upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Briggs, D.E.G., 2003. The Role of Biofilms in the Fossilization of Non-biomineralized Tissues. In: Krumbein, W.E., Paterson, D.M., Zavarzin, G.A. (Eds.), *Fossil and Recent Biofilms: A Natural History of Life on Earth*. Kluwer Academic, Dordrecht, pp. 281–290.
- Carnevale, G., 2004. *Tafonomia, paleoecologia e paleobiogeografia delle ittiofaune mioceniche dell'Italia centrale*. Unpublished Ph.D. Dissertation, Università di Pisa, Pisa.
- Carnevale, G., Pietsch, T.W., 2009. An Eocene frogfish from Monte Bolca, Italy: the earliest skeletal record for the family. *Palaeontology* 52, 745–752.
- Carnevale, G., Pietsch, T.W., 2010. Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family Brachionichthyidae (Teleostei: Lophiiformes). *Zool. J. Linnean Soc.* 160, 621–647.
- Carnevale, G., Pietsch, T.W., 2011. Batfishes from the Eocene of Bolca. *Geol. Mag.* 148, 461–472.
- Carnevale, G., Pietsch, T.W., 2012. †*Caruso*, a new genus of anglerfishes from the Eocene of Bolca, Italy, with a comparative osteology and phylogeny of the teleost family Lophiidae. *J. Syst. Palaeontol.* 10, 47–72.
- Carnevale, G., Bannikov, A.F., Marramà, G., Tyler, J.C., Zorzin, R., 2014. The Pesciara-Monte Postale Fossil-Lagerstätte: 2. Fishes and other vertebrates. In: Papazzoni, C.A., Giusberti, L., Carnevale, G., Roghi, G., Bassi, D., Zorzin, R. (Eds.), *The Bolca Fossil-Lagerstätte: A Window into the Eocene World*. *Rend. Soc. Paleont. Ital.* 4, pp. 37–63.
- Castellanos-Galindo, G.A., Krumme, U., Rubio, E.A., Saint-Paul, U., 2013. Spatial variability of mangrove fish assemblage composition in the tropical eastern Pacific Ocean. *Rev. Fish Biol. Fish.* 23, 69–86.
- Chellouche, P., Fürsich, F.T., Mäuser, M., 2012. Taphonomy of neopterygian fishes from the Upper Kimmeridgian Wattendorf Plattenkalk of Southern Germany. *Palaeobiodivers. Palaeoenviron.* 92, 99–117.
- Cheng, L., Dang Aard, J., Garrouste, R., 2012. The sea-skater *Halobates* (Heteroptera: Gerridae) – probable cause for extinction in the Mediterranean and potential for re-colonization following climate change. *Aquat. Insects* 2012, 1–11.
- Choat, J.H., Bellwood, D.R., 1991. In: Sale, P.F. (Ed.), *Reef Fishes: Their History and Evolution The Ecology of Fishes on Coral Reefs*. Academic Press, p. 754 (Chapter 3).
- Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Crowley, K.D., Cuchon, C.E., Rhi, J., 1986. Climate record in varved sediments of the Eocene Green River Formation. *J. Geophys. Res.* 91 (D8), 8637–8647.
- Dal Degan, D., Barbieri, S., 2005. Rilievo geologico dell'area di Bolca (Monti Lessini orientali). *Boll. Mus. Civ. St. Nat. Verona* 27, 3–10.
- Elder, R.L., 1985. Principles of Aquatic Taphonomy with Examples from the Fossil Record (Ph.D. Thesis) University of Michigan.
- Elder, R.L., Smith, G.R., 1988. Environmental Interpretation of Burial and Preservation of Clarkia Fishes. In: Smiley, C.J. (Ed.), *Late Cenozoic History of the Pacific Northwest: San Francisco, CA. American Association for the Advancement of Science, Pacific Division*, pp. 85–94.
- Etter, W., 1999. Community Analysis. In: Harper, D.A.T. (Ed.), *Numerical Palaeobiology*. John Wiley and Sons, New York, pp. 285–360.
- Fabiani, R., 1914. La serie stratigrafica di Bolca e dei suoi dintorni. *Mem. Ist. Geol. R. Univ. Padova* 2, 223–235.
- Fabiani, R., 1915. Il Paleogene del Veneto. *Mem. Ist. Geol. R. Univ. Padova* 3, 1–336.
- Fara, E., Saraiva, A.A.F., Campos, D.A., Moreira, J.K.R., Siebra, D.C., Kellner, A.W.A., 2005. Controlled excavations in the Romualdo Member of the Santana Formation (Early Cretaceous, Araripe Basin, northeastern Brazil): stratigraphic, palaeoenvironmental and palaeoecological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 218, 145–160.
- Faux, C.M., Padian, K., 2007. The opisthotonic posture of vertebrate skeletons: postmortem contraction or death throes? *Paleobiology* 33, 201–226.
- Ferber, C.T., Wells, N.A., 1995. Paleolimnology and taphonomy of some fish deposits in 'Fossil' and 'Uinta' lakes of the Eocene Green River Formation, Utah and Wyoming. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 117, 185–210.
- Fischer, A.G., Roberts, L.T., 1991. Cyclicity in the Green River Formation (lacustrine Eocene) of Wyoming. *J. Sediment. Petrol.* 6, 1146–1154.
- Friedman, M., 2008. The evolutionary origin of flatfish asymmetry. *Nature* 454, 209–212.
- Fürsich, F.T., Werner, W., Schneider, S., Mäuser, M., 2007. Sedimentology, taphonomy and palaeoecology of a laminated plattenkalk from the Kimmeridgian of the northern Franconian Alb (southern Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 243, 92–117.
- Genner, M.J., Sims, D.W., Wearmouth, V.J., Southall, E.J., Southward, A.J., Henderson, P.A., Hawkins, S.J., 2004. Regional climate warming drives long-term community changes of British marine fish. *Proc. R. Soc. Lond. [Biol.]* 271, 655–661.
- Giusberti, L., Bannikov, A.F., Boscolo Galazzo, F., Fornaciari, E., Frieling, J., Luciani, V., Papazzoni, C.A., Roghi, G., Schouten, S., Sluijs, A., Bosellini, F.R., Zorzin, R., 2014. A new Fossil-Lagerstätte from the Lower Eocene of Lessini Mountains (northern Italy): a multidisciplinary approach. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 403, 1–15.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Grande, L., 1984. Paleontology of the Green River Formation, with a review of the fish fauna. *Geol. Surv. Wyoming Bull.* 63, 1–333.
- Granéli, E., Carlsson, P., Olsson, P., Sundström, B., Granéli, W., Lindahl, O., 1989. From anoxia to fish poisoning: the last ten years of phytoplankton blooms in Swedish marine waters. *Coast. Estuar. Stud.* 35, 407–427.
- Grogan, E.D., Lund, R., 2002. The geological and biological environment of the Bear Gulch Limestone (Mississippian of Montana, USA) and a model for its deposition. *Geodiversitas* 24, 295–315.
- Hagadorn, J.W., Bottjer, D.J., 1999. Restriction of a Late Neoproterozoic biotope: suspect-microbial structures and trace fossils at the Vendian–Cambrian transition. *Palaio* 14, 73–85.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 1–9.
- Hecker, R.F., Merklin, R.L., 1946. Ob osobennostakh zahoronyenya ryb v maikopskikh glinastykh slancakh sewernoy Osieti. *Izvest. Akad. Nauk SSSR Otdeleniya Biologitsnykh Nauk* 6, 647–674.
- Hellawell, J., Orr, P.J., 2012. Deciphering taphonomic processes in the Eocene Green River Formation of Wyoming. *Palaeobiodivers. Palaeoenviron.* 92, 353–365.
- Hottinger, L., 1960. Recherches sur les Alvéolines du Paléocène et de l'Eocène. *Schweiz. Pfl. Abh.* 75–76, 1–243.
- Iniesto, M., López-Archilla, A.I., Fregenal-Martínez, M., Buscalioni, A.D., Guerrero, M.C., 2013. Involvement of microbial mats in delayed decay: an experimental essay on fish preservation. *Palaio* 28, 56–66.
- Iniesto, M., Laguna, C., Florín, M., Guerrero, M.C., Chicote, A., Buscalioni, A.D., López-Archilla, A.I., 2015. The impact of microbial mats and their microenvironmental conditions in early decay of fish. *Palaio* 30, 792–801.
- Iserbyt, A., De Schutter, P.J., 2012. Quantitative analysis of elasmobranch assemblages from two successive Ypresian (early Eocene) facies at Marke, western Belgium. *Geol. Belg.* 15, 146–153.
- Jerzmańska, A., 1960. Ichthyofauna from the Jasło shales at Sobniów (in Polish with English summary). *Acta Palaeontol. Pol.* 5, 367–412.

- Laegdsgaard, P., Johnson, C.R., 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Mar. Ecol. Prog. Ser.* 126, 67–81.
- Landini, W., Sorbini, L., 1996. Ecological and Trophic Relationships of Eocene Bolca (Pesciara) Fish Fauna. In: Cherchi, A. (Ed.), *Autoecology of Selected Fossil Organisms: Achievements and Problems*. Boll. Soc. Paleontol. It. Spec. vol. 3, pp. 105–112.
- Longhurst, A., Pauly, D., 1987. *Ecology of Tropical Oceans*. Academic Press, San Diego (407 pp.).
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell, Oxford (260 pp.).
- Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature* 422, 714–716.
- Malaroda, R., 1954. Il Luteziano di Monte Postale (Lessini medi). *Mem. Ist. Geol. Min. Univ. Padova* 19, 3–107.
- Mancuso, A.C., 2012. Taphonomic analysis of fish in rift lacustrine system: environmental indicators and implications for fish speciation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 339–341, 121–131.
- Marramà, G., Carnevale, G., 2015a. Eocene round herring from Bolca, Italy. *Acta Palaeontol. Pol.* 60, 701–710.
- Marramà, G., Carnevale, G., 2015b. The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Bolca, Italy: osteology, taxonomy and paleobiology. *J. Vertebr. Paleontol.* <http://dx.doi.org/10.1080/02724634.2015.1014490>.
- Marramà, G., Carnevale, G., 2016. An Eocene anchovy from Bolca, Italy: the earliest known record for the family Engraulidae. *Geol. Mag.* 153, 84–94. <http://dx.doi.org/10.1017/S0016756815000278>.
- Martill, D.M., Brito, P.M., Washington-Evans, J., 2008. Mass mortality of fishes in the Santana Formation (Lower Cretaceous, ?Albian) of northeast Brazil. *Cretac. Res.* 29, 649–658.
- McGrew, P.O., 1975. Taphonomy of Eocene fish from Fossil Basin, Wyoming. *Fieldiana Geol.* 33, 257–270.
- Miller, P.J., 1979. Adaptiveness and implications of small size in teleosts. *Symp. Zool. Soc. Lond.* 44, 263–306.
- Monsch, K., 2006. A revision of scombrid fishes (Scombroidei, Perciformes) from the Middle Eocene of Monte Bolca, Italy. *Palaeontology* 49, 873–888.
- Moodie, R.L., 1918. Studies in paleopathology III: opisthotonus and allied phenomena among fossil vertebrates. *Am. Nat.* 52, 384–394.
- Munroe, T., 2000. An overview of the biology, ecology, and fisheries of the clupeoid fishes occurring in the Gulf of Maine. *Northeast Fish. Sci. Cent. Ref. Doc.* 00–02, 1–226.
- Nagelkerken, C.M., van Der Velde, R.G., Dorenbosch, M., van Riel, M.C., De La Morinière, E.C., Nienhuis, P.H., 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale I. *Mar. Ecol. Prog. Ser.* 244, 299–305.
- Newbrey, M.G., Bozek, M.A., 2003. Age, growth, and mortality of *Joffrichthys triangulipetris* (Teleostei: Osteoglossidae) from the Paleocene Sentinel Butte Formation, North Dakota, U.S.A. *J. Vertebr. Paleontol.* 23, 494–500.
- Nixon, S.W., 1989. An extraordinary red tide and fish kill in Narragansett Bay. *Coast. Estuar. Stud.* 35, 429–447.
- Pan, Y., Fürsich, F.T., Zhang, J., Wang, Y., Zheng, X., 2015. Biostratigraphic analysis of *Lycopera* beds from the Early Cretaceous Yixian Formation, Western Liaoning, China. *Palaeontology* 58, 1–25.
- Papazzoni, C.A., Trevisani, E., 2006. Facies analysis, paleoenvironmental reconstruction, and biostratigraphy of the 'Pesciara di Bolca' (Verona, northern Italy): an Early Eocene Fossil-Lagerstätte. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 242, 21–35.
- Papazzoni, C.A., Trevisani, E., 2009. Relationships between the Pesciara di Bolca and the Monte Postale Fossil-Lagerstätten (Lessini Mts., Northern Italy). In: Billon-Bruyat, J.P., Marty, D., Costeur, L., Meyer, C.A., Thuring, B. (Eds.), *5th International Symposium on Lithographic Limestone and Plattenkalk*. Naturhistorisches Museum Basel, Switzerland. *Actes 2009 bis de la Société jurassienne d'Emulation*, Porrentruy, pp. 65–66.
- Papazzoni, C., Vescogni, A., Bosellini, F., Giusberti, L., Roghi, G., Dominici, S., 2014. First evidence of coral bioconstructions in the Monte Postale succession (Lower Eocene of Lessini Mts., Veneto, northern Italy). *Rend. Online Soc. Geol. Ital.* 31, 163–164.
- Parrish, J.D., 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Mar. Ecol. Prog. Ser.* 58, 143–160.
- Petit, G., 2010. Skin nodules in fossil fishes from Monte Bolca (Eocene, Northern Italy). *Geodiversitas* 32, 157–163.
- Schaeffer, B., Mangus, M., 1976. An Early Triassic fish assemblage from British Columbia. *Bull. Am. Mus. Nat. Hist.* 156, 517–563.
- Schäfer, W., 1972. *Ecology and Palaeoecology of Marine Environments*. The University of Chicago Press, Chicago, p. 520.
- Schieber, J., 1999. Microbial mats in terrigenous clastics: the challenge of identification in the rock record. *Palaios* 14, 3–12.
- Schieber, J., 2007. Benthic microbial mats as an oil shale component: Green River Formation (Eocene) of Wyoming and Utah. In: Schieber, J., Bose, P.K., Eriksson, P.G., Banerjee, S., Sarkar, A., Altermann, W., Catuneau, O. (Eds.), *Atlas of Microbial Mat Features Preserved within the Clastic Rock Record*. Elsevier, Amsterdam, pp. 225–232.
- Schwark, L., Ferretti, A., Papazzoni, C.A., Trevisani, E., 2009. Organic geochemistry and paleoenvironment of the Early Eocene 'Pesciara di Bolca' Konservat-Lagerstätte, Italy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 273, 272–285.
- Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Ferrández, C., Jauhari, A.K., Less, G., Pavlovic, R., Pignatti, J., Samsó, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, J., Zakrevskaya, E., 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bull. Soc. Geol. Fr.* 169, 281–299.
- Sichum, S., Tantichodok, P., 2013. Diversity and assemblage patterns of juvenile and small sized fishes in the nearshore habitats of the Gulf of Thailand. *Raffles B. Zool.* 61, 795–809.
- Sorbini, L., 1968. Contributo alla sedimentologia della 'Pesciara' di Bolca. *Mem. Mus. Civ. St. Nat. Verona* 15, 213–221.
- Sorbini, L., 1972. I Fossili di Bolca. I Edizione, Corev, Verona (133 pp.).
- Sorbini, L., 1984. Les Holocentridae du Monte Bolca. III: *Berybolcensis leptacanthus* (Agassiz). *St. Ric. Giac. Terz. Bolca* 4, 19–35.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. University of California Press, Berkeley (372 pp.).
- Tintori, A., 1992. Fish taphonomy and Triassic anoxic basins from the Alps: a case history. *Riv. Ital. Paleontol. Stratigr.* 97, 393–408.
- Trevisani, E., 2015. Upper Cretaceous–Lower Eocene succession of the Monte Postale and its relationship with the 'Pesciara di Bolca' (Lessini Mountains, northern Italy): deposition of a fossil-fish lagerstätte. *Facies* 61, 1–17.
- Tyler, J.C., Santini, F., 2002. Review and reconstructions of the tetraodontiform fishes from the Eocene of Bolca, Italy, with comments on related Tertiary taxa. *St. Ric. Giac. Terz. Bolca* 9, 47–119.
- Verweij, M.C., Nagelkerken, I., De Graaff, D., Peeters, M., Bakker, E.J., van Der Velde, G., 2006. Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. *Mar. Ecol. Prog. Ser.* 306, 257–268.
- Viohl, G., 1990. Taphonomy of Fossil-Lagerstätten. Solnhofen Lithographic Limestones. In: Briggs, D.E.G., Crowther, P.R. (Eds.), *Palaeobiology: A Synthesis*. Blackwell, Oxford, pp. 33–64.
- Weiler, W., 1929. Über das Vorkommen isolierter köpfe bei fossilen Clupeiden. *Senckenbergiana* 11, 40–43.
- Westall, F., Rincé, Y., 1994. Biofilms, microbial mats and microbe–particle interactions: electron microscope observations from diatomaceous sediments. *Sedimentology* 41, 147–162.
- Wilde, V., Roghi, G., Martinetto, E., 2014. The Pesciara–Monte Postale Fossil-Lagerstätte: 3. Flora. In: Papazzoni, C.A., Giusberti, L., Carnevale, G., Roghi, G., Bassi, D., Zorzin, R. (Eds.), *The Bolca Fossil-Lagerstätte: A Window into the Eocene World*. Rend. Soc. Paleont. Ital. 4, pp. 65–71.
- Wilson, M.V.H., Barton, D.G., 1996. Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. *Paleobiology* 22, 535–542.