

GEOLOGICAL FIELD TRIPS AND MAPS

2026
Vol. 18 (1.6)

The Bolca *Lagerstätten*: a one-day palaeontological field trip into the Eocene tropical marine life of the western Tethys



Pre-congress field trip of the Paleo4Alps Congress,
Bolzano - July 19-23, 2026

<https://doi.org/10.3301/GFT.2026.06>



SOCIETÀ GEOLOGICA ITALIANA ETS
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Geological Field Trips and Maps



Periodico semestrale del Servizio Geologico d'Italia - ISPRA e della Società Geologica Italiana ETS
Geol. F. Trips Maps, Vol. 18 No.1.6 (2026), 81 pp., 34 figs., 5 tabs. (<https://doi.org/10.3301/GFT.2026.06>)

The Bolca Lagerstätten: a one-day palaeontological field trip into the Eocene tropical marine life of the western Tethys

Pre-congress field trip of the Paleo4Alps Congress, Bolzano - July 19-23, 2026

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Cover page figure: Overview of the Bolca fossil sites and their excavation context. Top left: panoramic view of the Pesciara site. Top right: excavation activities showing the extraction of limestone slabs and the inspection of their fossil content. Bottom left: *Ceratoichthys pinnatiformis*, one of the iconic fossils of Bolca and symbol of the Società Paleontologica Italiana. Bottom right: view of the Monte Postale stratigraphic succession.

ISSN: 2038-4947 [online]

<http://gftm.socgeol.it/>

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ABSTRACT

The Eocene limestones exposed around the village of Bolca, northern Italy, have provided some of the most complete and well-preserved marine assemblages of the Cenozoic. The fossils of these deposits, especially the famous fossil fishes, are known for more than four centuries and document tropical marine shallow-water ecosystems of the western Tethys, representing a spectacular snapshot of Eocene marine life. The one-day palaeontological field trip presented herein constitutes a deep immersion into the early Cenozoic marine tropical biodiversity of the western end of the Tethys Ocean. The focus of this field trip is therefore to provide a general overview of the outstanding organism diversity of the two main sites of the Bolca *Lagerstätten*, Monte Postale and Pesciara, and to show their stratigraphic and palaeoenvironmental setting. The field trip starts with a visit to the Museo Civico di Storia Naturale, Verona, which includes the most important collection of Bolca fossils. Then, the second stop shows the Monte Postale stratigraphic succession, and the third stop illustrates the celebrated Pesciara site, exploited for the collection of spectacular fossils since the 16th century.

Keywords: Ypresian, Monte Postale and Pesciara sites, biostratigraphy, flora, invertebrates, fishes.

PROGRAM SUMMARY

The goal of this one-day field trip, proposed for the Paleo4Alps Congress (Bolzano, 18th of July 2026), is to provide an overview of the geology and palaeontological features of the Bolca *Lagerstätten*. This palaeontological field trip includes three stops (Fig. 1). The first stop consists of a visit at the Museo Civico di Storia Naturale in Verona (**Stop 1**) and is focused on introducing the extraordinary fossils of Bolca *Lagerstätten*. The itinerary then continues with the second and third stops at the Monte Postale (**Stop 2**) and Pesciara (**Stop 3**) sites.

Herein, the main geological and palaeontological features of the Bolca *Lagerstätten* are provided. For this purpose, we prepared a general description of the geology of the Bolca area, with a focus on the stratigraphic features of the Monte

Postale (**Stop 2**) and Pesciara (**Stop 3**) sites, followed by a synopsis of the outstanding palaeontological content of these two sites.

SAFETY AND LOGISTIC INFORMATION

The outcrops of the main fossiliferous sites of the Bolca *Lagerstätten* are easily accessible and located close to the areas where cars or buses can be parked. However, the use of hiking or trekking boots and comfortable clothing is recommended. The outcrops are close to the Bolca village where there are small shops, restaurants and bars.

EMERGENCY CONTACT NUMBERS

112 – Carabinieri
113 – State Police
115 – Fire Brigade
118 – Urgent and emergency medical attention

HOSPITALS

Ospedale Fracastoro San Bonifacio, Via Circonvallazione, 1 San Bonifacio (VR). Tel. +39 045 6138111.

ACCOMMODATIONS

This is a one-day-long palaeontological field trip. We suggest to start in Verona in the morning (10:00 a.m.) from the Museo Civico di Storia Naturale and return to the city in the afternoon. Verona offers a variety of accommodation solutions. Information can be found on the website <https://visitverona.it>.

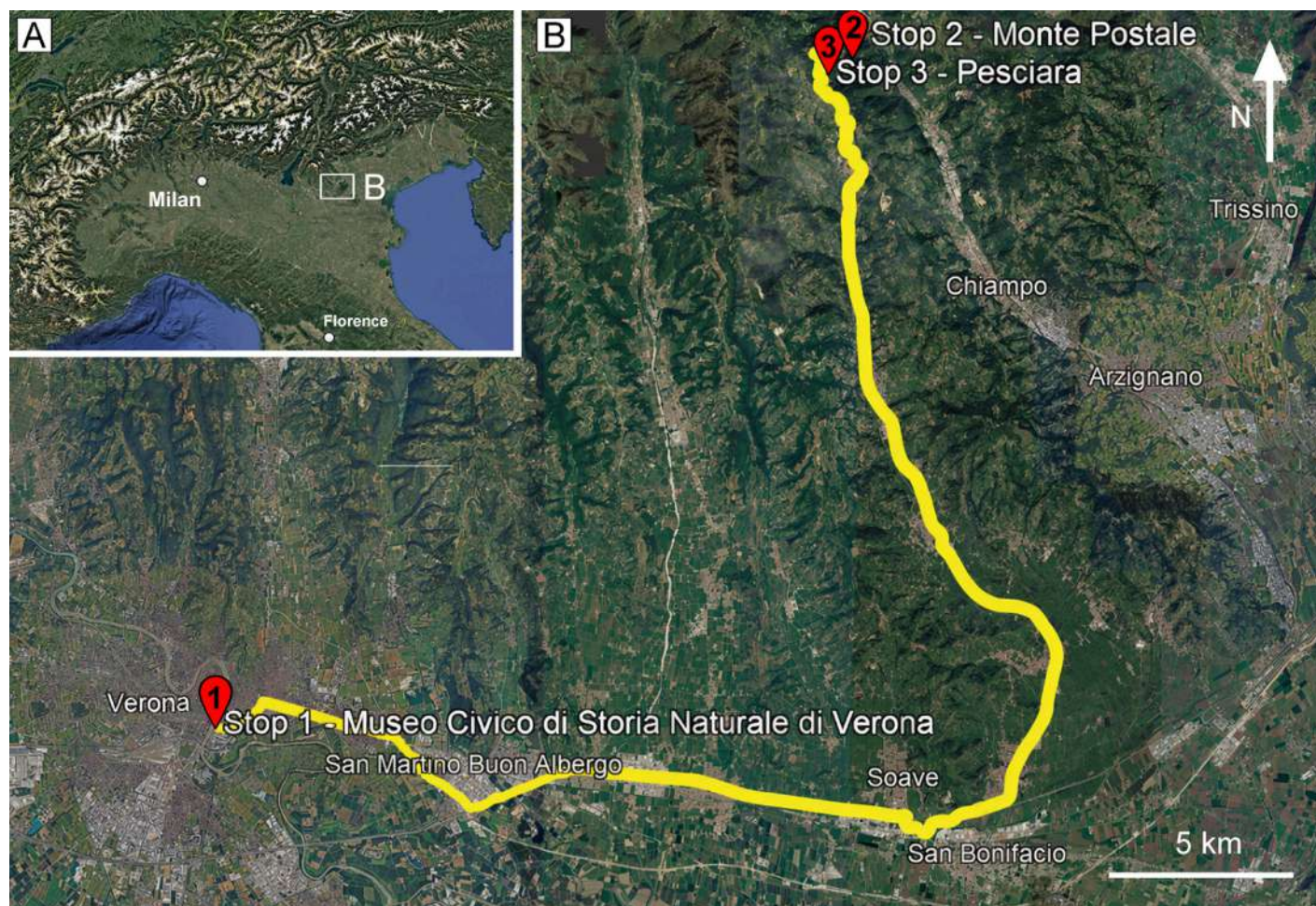


Fig. 1 - A) Location of field trip area in northern Italy; B) Itinerary map of the field trip. Stop 1 = Museo Civico di Storia Naturale di Verona; Stop 2 = Monte Postale; Stop 3 = Pesciara di Bolca. Satellite images taken from Google Earth.



INTRODUCTION

Known for more than four centuries, the Eocene fossils from the two main sites of the Bolca *Lagerstätten*, Monte Postale and Pesciara, have attracted the attention of scientists due to their astonishing beauty and exquisite preservation. Some of the Bolca fossils are certainly among the most representative remains of marine organisms from the entire Cenozoic Era and can be confidently considered the true icons of Italian palaeontology (Carnevale, 2020). These fossiliferous sites were placed near the western end of the Tethys Ocean within a tropical archipelago around 50 Ma, during the final part of the Early Eocene Climatic Optimum (EECO), the warmest interval of the last 65 million years (see Zachos et al., 2008). Centuries of extensive exploitation led to the discovery of more than 500 species of marine and terrestrial animals, plants, and protists. The most extensive collection of fossils from the Bolca *Lagerstätten* is currently housed in the Museo Civico di Storia Naturale in Verona (Stop 1).

In addition to their outstanding scientific relevance, the fossiliferous sites of the Bolca *Lagerstätten* are of considerable significance for the history of geology and palaeontology (Romano and Carnevale, 2023). The first documented report of a fossil from the Bolca *Lagerstätten* appeared in 1550 in the third edition of the “*Dioscorides De Materia Medicinale*” by the famous botanist and physician Pietro Andrea Mattioli. Mattioli (1550) was extremely impressed by the superb preservation of the anatomical details of some fossil fishes belonging to the collection of Diego Hurtado de Mendoza, the ambassador of Emperor Charles V to the Republic of Venice. In 1622, for the first time, a fish from Bolca belonging to the collection amassed by Francesco Calzolari, an apothecary from Verona, was figured in the catalogue “*Musaeum Francisci Calceolari Junioris Veronensis*” (Ceruti and Chiocco, 1622). The fossils from Bolca and their origins were extensively debated, particularly during the 18th century, by prominent naturalists, including Antonio Vallisneri, Ferdinando Marsili, Anton Lazzaro Moro, Giovanni Arduino, Alberto Fortis, and Déodat de Dolomieu. During the first half of the 18th century, several spectacular collections of Bolca fossils were assembled in the city of Verona by noblemen, including Vincenzo Bozza, Ottavio Canossa, and Giovanni Battista Gazola. Gazola purchased most of these prominent collections for his own museum, which, by the end of 1791, contained more than a thousand fish, plant, and invertebrate specimens. The large collection of fossil fishes of Vincenzo Bozza was thoroughly investigated by Abbot Giovanni Serafino Volta. Volta (1789) assigned most of the fossils to extant tropical species and prepared a beautifully illustrated catalogue, the “*Ittiolitologia Veronese del Museo*

Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti fossili Veronesi” (Volta, 1796–1809). Approximately 600 fossils from Bolca, part of the Gazola collection, were acquired by the armies of Napoleon that occupied Verona in 1797 and transported to Paris to the Muséum National d’Histoire Naturelle. This collection was used by Henri Ducrotay de Blainville (1818) and by Louis Agassiz, who described the fossils in great detail in his monumental “*Recherches sur les Poissons Fossiles*” (Agassiz, 1833–1844).

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The village of Bolca is located in the eastern part of the Lessini Mountains, approximately 30 km northeast of Verona, in northern Italy. The Lessini Mountains are part of the Southern Alps, located in the northernmost portion of the Adria Plate (Carminati et al., 2012), where they represented a relative structural high since the establishment of the shallow-water Trento Platform (Winterer and Bosellini, 1981) during the Early Jurassic. During the Middle Jurassic, the Monti Lessini domain drowned and was reduced to a basinal high (the Trento Plateau) until the early Palaeogene phases of the Alpine Orogeny that caused uplift and block-fault of this unit giving rise to the Cenozoic Lessini Shelf (Bosellini, 1989), connected to the north with an emerged area in the surroundings of Trento.

After the Adria-Europe collision, about 65 Ma (Stampfli et al., 1998; Brombin et al., 2019), extension developed (Ratschbacher et al., 1989) and subsequently the rigid block of the former Trento Platform block-faulted formed a horst-and-graben structure, called the Alpone–Agnò Graben (Zampieri, 1995) (Fig. 2). In the Lessini area, several pulses of volcanic activity are recorded between the Paleocene and the Oligocene (Barbieri et al., 1991; Barbieri and Zampieri, 1992; Zampieri, 1995; Brombin et al., 2019). The produced volcanic buildings acted as centres for the growth of shallow-water carbonate platforms since the early Eocene, eventually merging into the so-called “Lessini Shelf” between the latest Eocene and the Oligocene (Bosellini, 1989; Luciani, 1989).

The Alpone-Agnò Graben is bounded by the Castelveto fault (Barbieri, 1972) to the west, separating the western area, with limited basaltic rocks and abundant calcareous deposits (De Zanche and Conterno, 1972; Mietto, 1975; Beschin et al., 1998) from the eastern one, where volcanic deposits are widespread, and limestones are less frequent (Fabiani, 1915; Piccoli, 1966a, b; Antonelli et al., 1990). Bolca is located very close to the Castelveto fault, but within the Alpone-Agnò Graben. Within the graben, in the eastern area, subsidence was more active, and basaltic

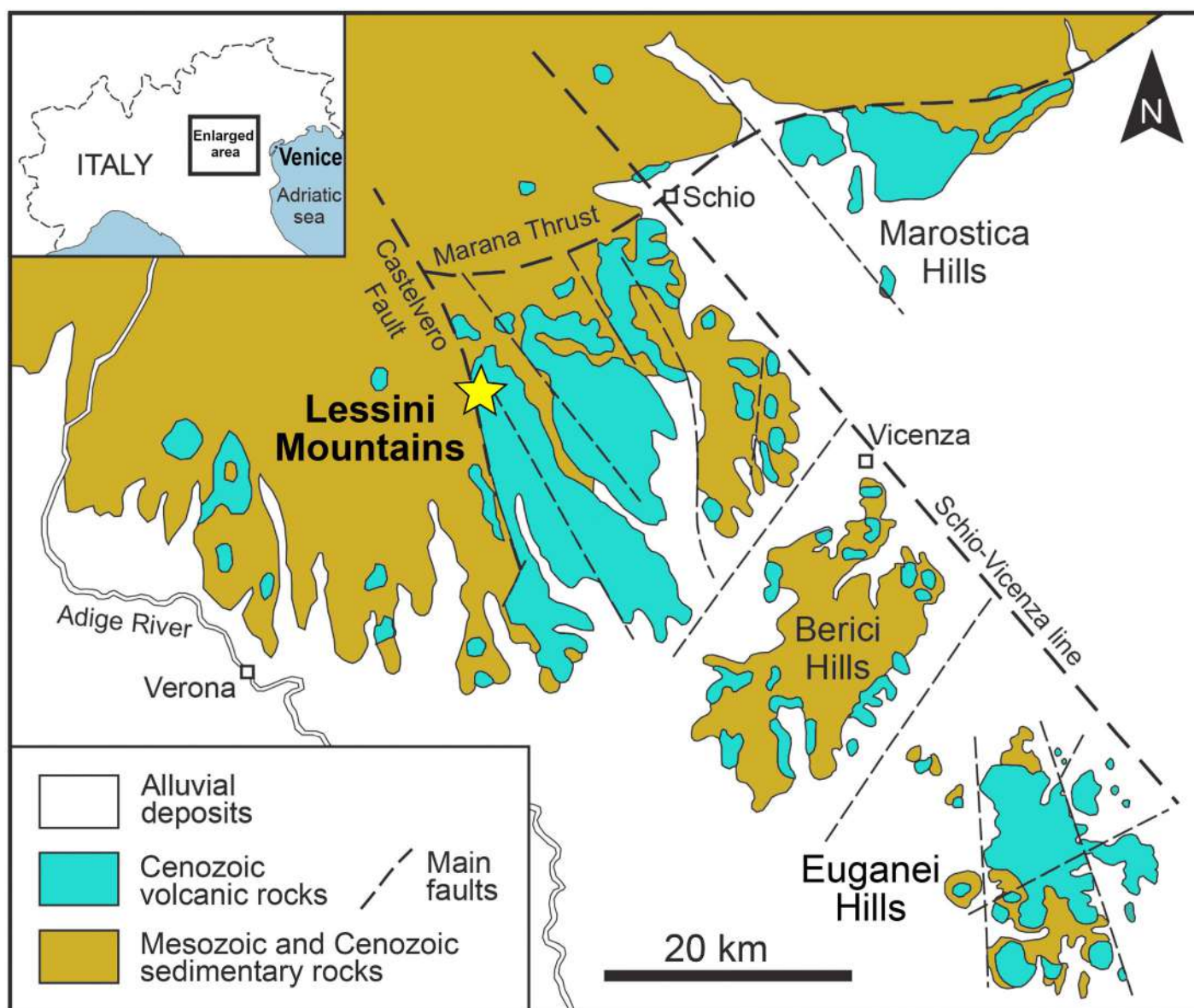


Fig. 2 - Simplified geological map of the Lessini Mountains, Berici Hills, and Euganei Hills (modified after Mattioli et al., 2016). The yellow star shows the position of Bolca.

rocks were sometimes intercalated with marine carbonates (Barbieri and Medizza, 1969; Barbieri, 1972; De Zanche and Conterno, 1972; Beccaro et al., 2001). Barbieri et al. (1991) recognised six volcanic pulses, one from the late Paleocene and the rest from the Ypresian to Bartonian; the thickness of volcanic deposits could reach 600 m for the Bartonian volcanic episode (Brombin et al., 2019). Recently, Brombin et al. (2019) obtained radiometric ages from a sample of volcanic rocks from the Purga di Bolca (38.73 ± 0.44 Ma, Bartonian) and another one coming from the road connecting Bolca to Zovo (45.21 ± 0.11 Ma, Lutetian); unfortunately, we have still no radiometric dating for the volcanic rocks from either the Monte Postale or the surroundings of the Pesciara (see below).

We have evidence of widespread emersion of the graben area during the Bartonian, with only local and temporary

marine episodes, witnessed by the deposition of the classic “Orizzonte di Roncà” (Fabiani, 1915). The volcanic activity stopped, and marine sediments came back during Priabonian, with the deposition of the relatively deep “*Marne di Priabona*” formation, starting with a transgressive conglomerate and rapidly becoming deeper (Barbieri et al., 1980; Mietto, 1992; Trevisani, 1997). During the early Oligocene, the Lessini area was covered by the shallow-water deposits of the “*Calcareni di Castelgomberto*” formation (Barbieri et al., 1980), which are interpreted as the result of deposition on a rimmed platform, with the reef margin located in the southeastern part of the Berici Hills and a wide, euphotic lagoon towards the northwest, punctuated by scattered patch reefs (Frost, 1981; Bosellini and Trevisani, 1992; Mietto, 1992; Bosellini et al., 2020a). In the western part of the Lessini Mountains



the Oligocene is lacking, probably due to an emersion (Luciani, 1989). Instead, in the eastern Lessini Mountains, the carbonate platform emerged most probably near the end of the Rupelian (Frost, 1981). The emersion is marked by widespread palaeokarst features, interpreted as a third-order sequence boundary (Mietto, 1988; Gianolla et al., 1992; Dal Molin et al., 2001).

After a late Oligocene hiatus, in the Lessini area marine sedimentation resumed with the deposition of the upper Chattian-Lower Miocene “*Arenarie e calcari di S. Urbano*” formation (Bosellini et al., 1967; Bassi et al., 2007, 2008; Bassi and Nebelsick, 2010). The marine sedimentation ends here with the Lower Miocene “*Marne argillose di M. Costi*” formation, only a few meters thick (Bosellini and Dal Cin, 1966; Bassi et al., 2007, 2008) (Fig. 3).

The stratigraphic setting of the Bolca area is quite complex and, in some ways, not completely understood. Herein, we restrict our analysis to the area of the Pesciara and Monte Postale sites (the Purga di Bolca-Vegroni and Spilecco sites are not discussed herein), where volcanic, volcanoclastic, and sedimentary rocks are present. Earlier studies on this area date back to the 19th century (e.g., Suess, 1868; Bayan, 1870a, Munier-Chalmas, 1891) but it is only with the detailed and accurate work by Fabiani (1914, 1915) that a comprehensive view of the Monte Postale section was described and illustrated, remaining almost unchanged for nearly a century (Papazzoni et al., 2014). The main contributions worthy of mention after Fabiani are Schweighauser (1953), who studied the larger foraminifera from Spilecco and the Monte Postale; Malaroda (1954), who revised the molluscs from the Monte Postale; Hottinger (1960), who studied the alveolinids from the Purga di Bolca, Brusaferrì, Monte Postale, and Valecco; Barbieri and Medizza (1969), who re-studied the geology and stratigraphy of the Bolca area, even if they did not include the Monte Postale and Pesciara sites.

There are still nomenclatural problems with the Palaeogene lithostratigraphy in the Bolca area. In the explanatory notes of the Geological Sheet 49 “Verona” published by the Servizio Geologico d’Italia (Bosellini et al., 1967), the Paleocene to lower Eocene limestones were assigned to the “*Calcarei di Spilecco*”, whereas the middle Eocene ones were referred to the informal unit called “*Calcarei Nummulitici*”. However, the Monte Postale limestones were traditionally attributed to the “*Calcarei Nummulitici*” (see e.g., Antonelli et al., 1990), even if these are Ypresian and not Lutetian in age (Papazzoni et al., 2014, 2017; Vescogni et al., 2016; Fornaciari et al., 2019; Bosellini et al., 2020b). Dal Degan and Barbieri (2005) published a detailed geological map (1:10.000) of Bolca and its surroundings, in which the ‘*Calcare di Spilecco*’ unit was separated from the ‘*Calcarei Nummulitici*’ due to a series of lithological features. In addition, the carbonate deposits exposed at the Pesciara

and Monte Postale sites have been attributed to the newly-introduced ‘*Formazione del Monte Postale-Pesciara*’ (also referred to as ‘*Formazione del Monte Postale*’ in the map; Dal Degan and Barbieri, 2005) (Fig. 4).

Recent biostratigraphic studies carried out at the Monte Postale and Pesciara sites (Vescogni et al., 2016; Papazzoni et al., 2017; Fornaciari et al., 2019; Tab. 1) defined the ages of both sites in great detail as well as their relative stratigraphic position.

The Monte Postale succession (**Stop 2**) was described in detail by Fabiani (1914, 1915), and is the most complete in the Bolca area, spanning from the Upper Cretaceous Scaglia Rossa up to the *Alveolina*-bearing Ypresian limestone, in its uppermost part containing also marine molluscs. These mollusc-rich levels were attributed to the Lutetian by Malaroda (1954). However, Hottinger (1960) listed a larger foraminiferal fauna characteristic of the Cuisian (= upper Ypresian). This age has been recently confirmed by studies on the *Alveolina* assemblages in the uppermost levels of the Monte Postale succession (Papazzoni et al., 2017; Fornaciari et al., 2019), which belong to the Shallow Benthic Zone (SBZ) 11 (Serra-Kiel et al., 1998). This part of the Monte Postale succession contains, in its lower-middle portion, different levels of laminated micritic wackestone similar to the fish-bearing layers of the Pesciara and also containing abundant fish and plant remains (Fig. 5). The analysis of the calcareous nannofossils indicates that the Monte Postale succession spans the entire NP13 and CNE 5 calcareous nannofossil zones of Martini (1971) and Agnini et al. (2014), in the time interval between 50.5 and 48.96 Ma (see Papazzoni et al., 2017).

The Pesciara di Bolca (**Stop 3**) is a large olistolith (a few hundred square meters, Zorzin et al., 2022) surrounded by volcanoclastic deposits (Roghi et al., 2015). It contains five levels of laminated micritic wackestone (Figs. 6, 7) that have provided, over more than four centuries, a remarkable amount of fossil fishes. The non-laminated limestone of the Pesciara contains abundant larger benthic foraminifera, first described by Hottinger (1960) and Schaub (1981), and recently restudied in detail (Trevisani et al., 2005; Papazzoni and Trevisani, 2006; Papazzoni et al., 2017), confirming its attribution to the SBZ 11 for all samples from this locality. The calcareous nannofossils of the Pesciara site, first examined by Medizza (1975) in the upper portion of the Pesciara succession, and referred to the NP 14 zone of Martini (1971), have also been recently reassigned to the CNE 6 calcareous nannofossil zone of Agnini et al. (2014) by Papazzoni et al. (2017). This implies that the laminated wackestone of the Pesciara are slightly younger than those of Monte Postale (Fig. 8), with an age possibly comprised between 48.96 and 48.5 Ma.

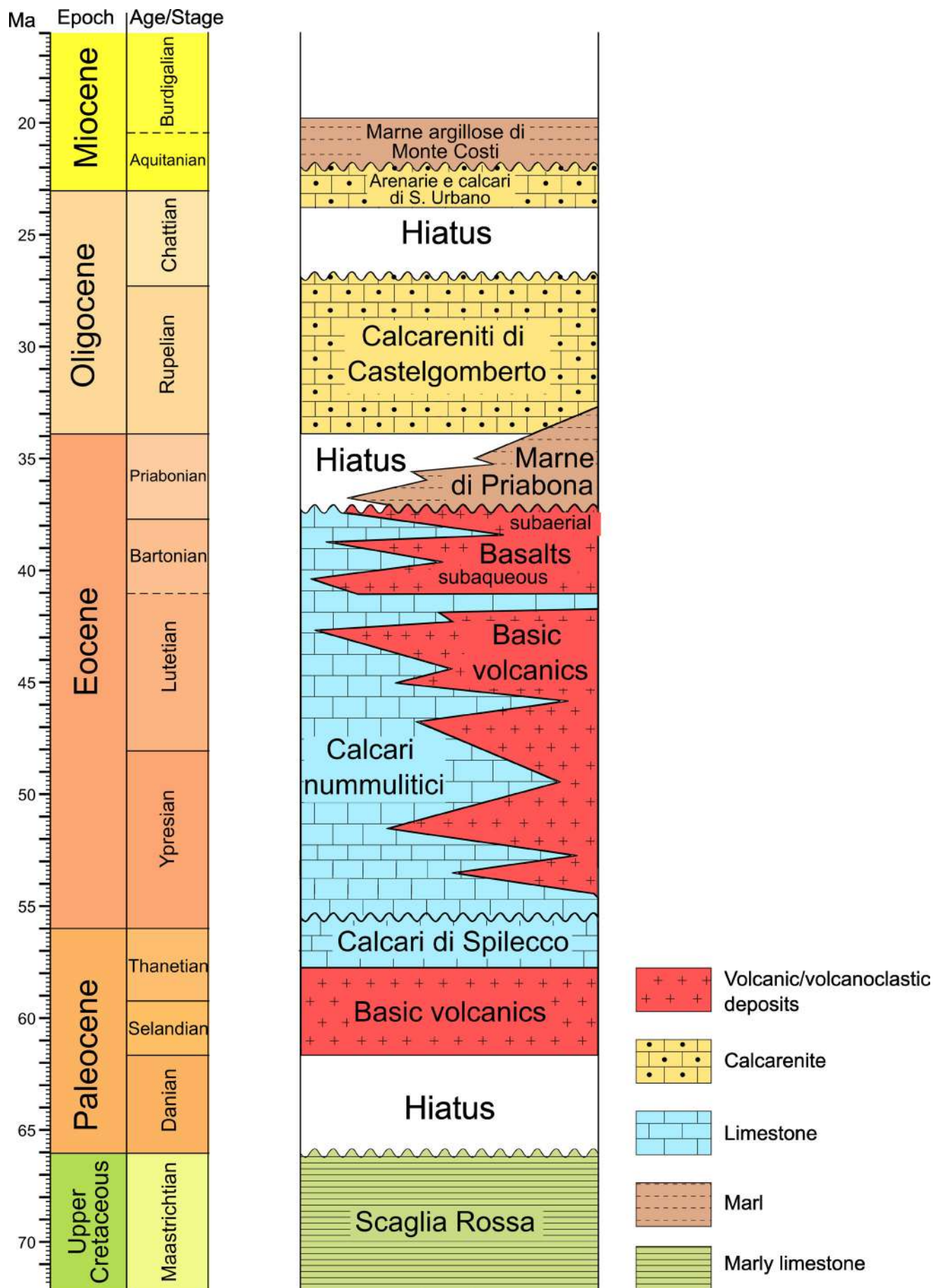


Fig. 3 - Generalised stratigraphy of the eastern Lessini Mountains. Modified after Brombin et al. (2019).

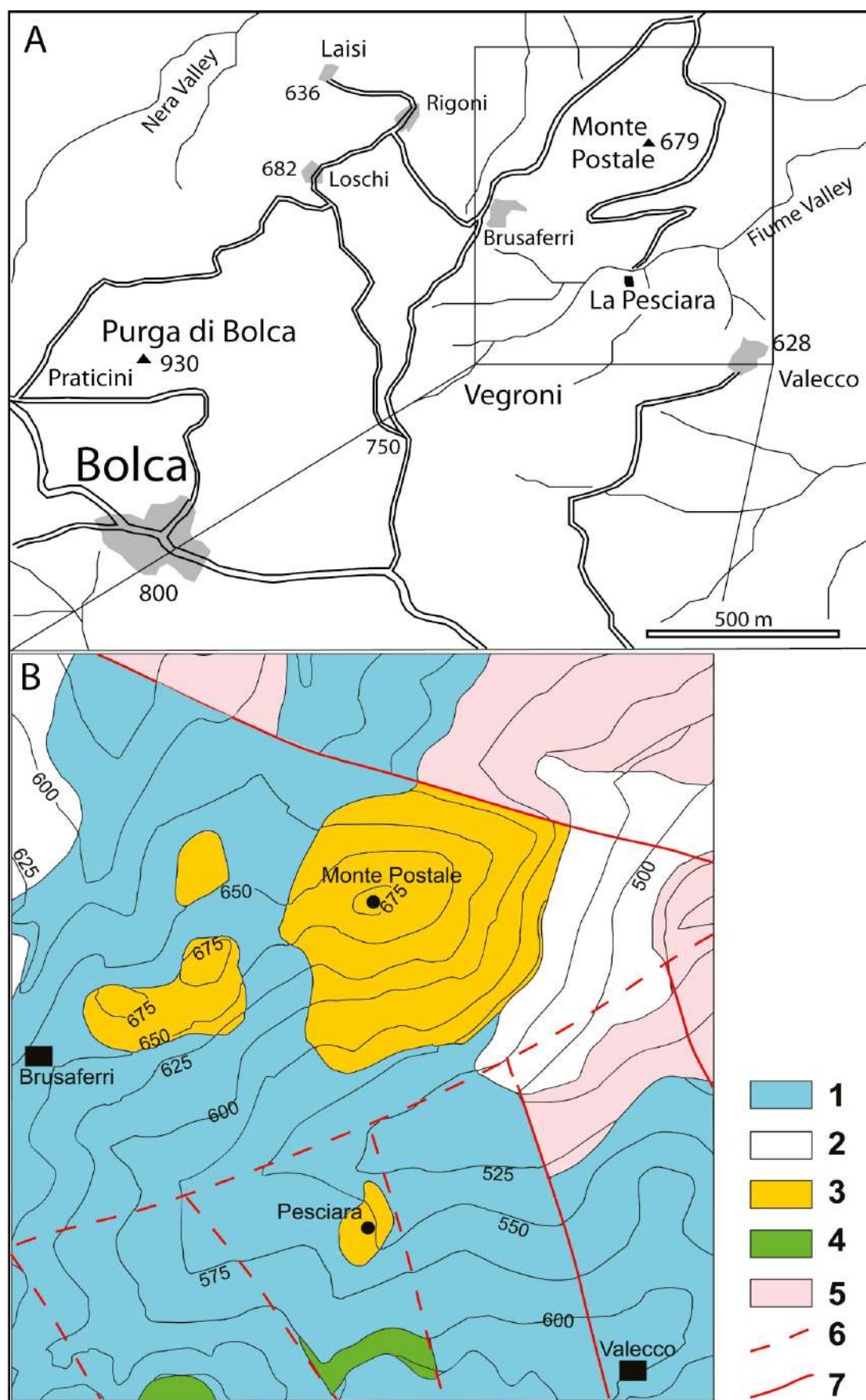
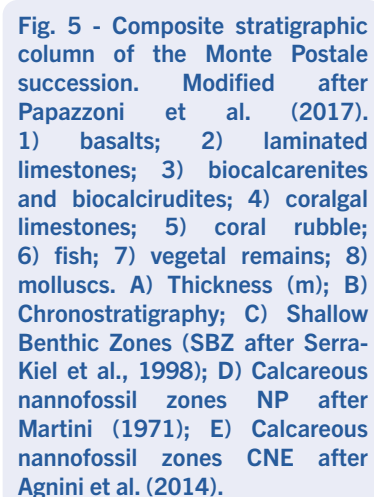


Fig. 4 - Simplified geological map of the Bolca area. Modified after Dal Degan and Barbieri (2005). 1) Volcanic and volcanoclastic deposits; 2) Quaternary alluvial and detrital deposit; 3) "Formazione del Monte Postale"; 4) "Calcarei Nummulitici"; 5) Mesozoic "Scaglia Rossa" and "Maiolica"; 6) Alleged fault; 7) Fault.



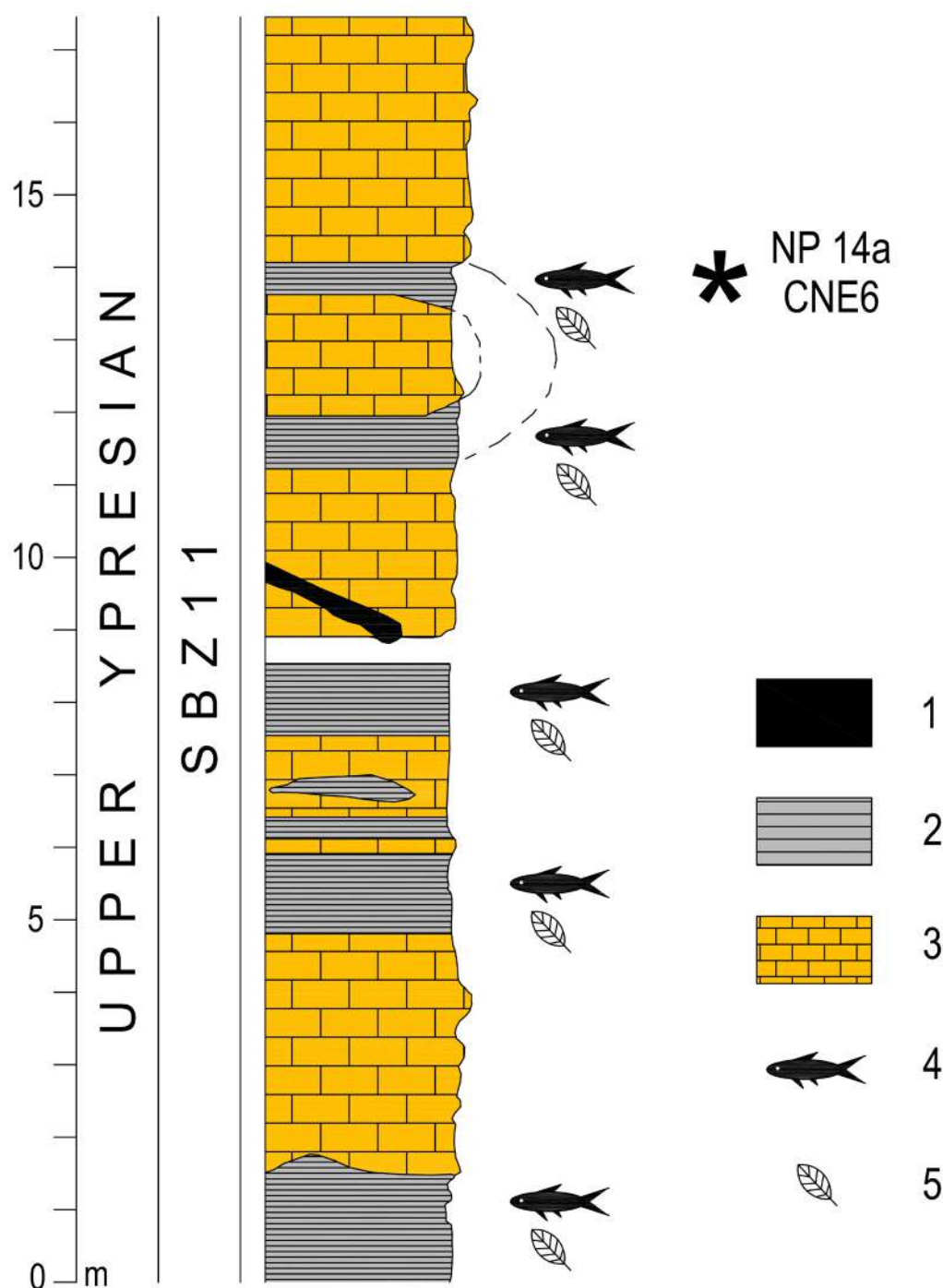


Fig. 6 - Stratigraphic column of the Pesciara site. Modified after Papazzoni and Trevisani (2006) and Mironenko et al. (2024). 1) basalts; 2) laminated limestones; 3) biocalcarenes and biocalcirudites; 4) fish; 5) vegetal remains.

INSTITUTIONAL ABBREVIATIONS

CM, Carnegie Natural History Museum, Pittsburgh; CMC, Collezione Cerato, Bolca; IGF, Museo di Geologia e Paleontologia dell'Università di Firenze, Firenze; MBR, Museum für Naturkunde, Berlin; MCBG, Museo Civico di Bassano del Grappa, Bassano del Grappa; MFB, Museo

dei Fossili di Bolca, Vestenanova; MGP-PD, Museo della Natura e dell'Uomo dell'Università di Padova, Sezione di Geologia e Paleontologia, Padova; MCSNV, Museo di Storia Naturale di Verona, Verona; MSNM, Museo di Storia Naturale di Milano, Milano; MSNVE, Museo di Storia Naturale di Venezia, Venezia; NHMUK, Natural History Museum, London; NHMW, Naturhistorisches Museum, Vienna.



Fig. 7 - Polished slab of the limestone of the Pesciara site showing the transition between the laminated limestone and the coarse-grained limestone. Scale bar 50 mm.

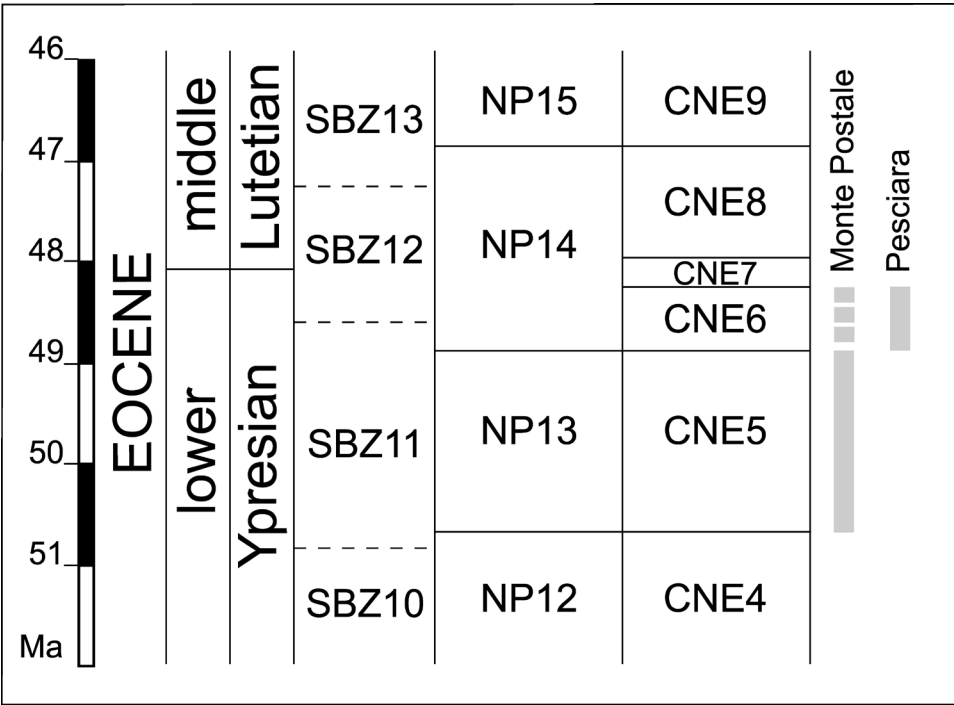


Fig. 8 - Biochronostratigraphic sketch showing the time spans covered by the Monte Postale and Pesciara limestone, incorporating the Shallow Benthic Zones (SBZ after Serra-Kiel et al., 1998) and calcareous nannofossil zones (NP after Martini, 1971 and CNE after Agnini et al., 2014). Time scale after Speijer et al. (2020). Modified after Fornaciari et al. (2019).



Table 1 - A synoptic list of Eocene larger benthic foraminifera of the Bolca Lagerstätten.

MP = Monte Postale, P = Pesciara.

Phylum Foraminifera	
Class Globothalamea	
Order Rotaliida	
Family Nummulitidae	
<i>Assilina laxispira</i> de la Harpe in Rozloznsnik, 1926	MP
<i>Nummulites aquitanicus</i> Benoist, 1889	MP
<i>Nummulites burdigalensis burdigalensis</i> de la Harpe in Rozloznsnik, 1926	MP
<i>Nummulites irregularis</i> Deshayes, 1838	MP
<i>Nummulites kaufmanni</i> Mayer-Eymar, 1876	MP
<i>Nummulites nitidus</i> de la Harpe, 1883	MP
<i>Nummulites partschi</i> de la Harpe, 1880	MP
<i>Nummulites planulatus</i> (Lamarck, 1804)	MP
<i>Nummulites pratti</i> d'Archiac and Haime, 1853	P, MP
<i>Nummulites preluasi</i> Douvillé, 1924	P
<i>Nummulites rotularius</i> Deshayes, 1838	P, MP
<i>Nummulites tauricus</i> de la Harpe in Rozloznsnik, 1926	MP
Class Tubothalamea	
Order Miliolida	
Family Alveolinidae	
<i>Alveolina cremae</i> Checchia-Rispoli, 1905	P, MP
<i>Alveolina dainellii</i> Hottinger, 1960	MP
<i>Alveolina decastroi</i> Scotto di Carlo, 1966	P, MP
<i>Alveolina distefanoi</i> Checchia-Rispoli, 1905	P, MP
<i>Alveolina fornasinii</i> Checchia-Rispoli, 1909	MP
<i>Alveolina frumentiformis</i> Schwager, 1883	MP
<i>Alveolina levantina</i> Hottinger, 1960	P, MP
<i>Alveolina minuta</i> Checchia-Rispoli, 1909	P, MP
<i>Alveolina postalensis</i> Fornaciari, Giusberti & Papazzoni, 2019	P, MP
<i>Alveolina ruetimeyeri</i> Hottinger, 1960	P, MP
<i>Alveolina rugosa</i> Hottinger, 1960	P, MP
<i>Alveolina</i> cf. <i>schwageri</i> Checchia-Rispoli, 1905	P, MP
<i>Alveolina triestina</i> Hottinger, 1960	MP
<i>Glomalveolina minutula</i> Reichel in Renz, 1936	MP



FLORA

The plant remains of the Bolca Lagerstätten (Figs. 9–11) constitute some of the most important Palaeogene macrofloras from Italy. The fossil plants of Bolca have been studied since the first half of the 19th century (Brongniart, 1828, 1828–1837, 1849), but it was in the second half of that century that, thanks to the work of Abramo Bartolomeo Massalongo (1824–1860), the macroflora was described in detail and compared with other well-known Italian and European deposits (Heer, 1855–1859, 1861; de La Harpe, 1856). Massalongo identified 105 genera and 277 species (Massalongo, 1850, 1851, 1853a, 1853b, 1855–1856, 1857, 1858, 1859a, 1859b), but unfortunately with a few descriptions and illustrations. Subsequent revisions of the Massalongo taxonomic interpretations were carried out by Meschinelli and Squinabol (1892) and Gola (1941). In addition, detailed taxonomic studies focused on a few taxa were carried out by De Visiani (1864), Beggiato (1865), Forti (1926), Fiore (1932, 1936a–d), Schmid and Schmid (1973, 1974), Caccin and Pallozzi (2001), and Kustatscher et al. (2022). Overall, the Bolca primary producer assemblage primarily consists of marine algae, especially red algae, and seagrasses.

Red algae are mainly represented by the genus *Delesseria* (*Delesseria* of Massalongo, 1859a; see also Fiore, 1936d, and Giusberti et al., 2016) (Fig. 9A) and, subordinately, by *Ceramites*, *Pterigophycos*, *Dictyotites*, *Laminarites*, *Pasinia*, *Arystophycos*, and *Zonarites*. The presence of red algae has also been suggested by analyses of organic matter (Schwark et al., 2009). A new, very well-preserved specimen, with a nearly complete and differently organised thallus belonging to *Pterigophycos* has been recently described (Kustatscher et al., 2022) (Fig. 9B). Brown algae are represented by the laminariacean *Postelsiopsis caputmedusae* (Forti, 1926), whereas green algae are represented by *Aristophycos agardhianus*, *Caulerpites araucaria*, *Halimeda*, *Sthenelaites dasiaeformis*, and newly discovered, still unpublished forms similar to the extant *Acetabularia* (Fig. 9C).

Among monocotyledonous angiosperms, seagrasses are represented by the presence of rhizomes, elongated leaves, and inflorescences pertaining to the Cymodaceae–Zosteraceae–Posidoniaceae groups (Wilde et al., 2014). The presence of Ruppiaceae and Najadaceae can also be observed in the form of leaves and shoots (Larkum et al., 2018), especially those of the genus *Halochloris* (Najadaceae), a genus apparently represented by several species (Massalongo, 1859a, b). These monocotyledons are very common in both the Pesciara and Monte Postale palaeobiotopes, where they probably provided shelter for organisms such as molluscs, crustaceans, annelids,

foraminifera, and fishes. An aquatic monocotyledon belonging to the genus *Eichornia* has also been reported by Fiore (1936e) from the Pesciara site.

Remains of terrestrial dicotyledonous angiosperms belonging to a variety of families have been discovered in the laminated micritic limestone of the Pesciara and Monte Postale sites (Massalongo, 1859a; Molon, 1867; Meschinelli and Squinabol, 1892; Fiore, 1936c, e; Gola, 1941). Double compound leguminous leaves and leaflets are the most common species (caesalpinoid leaf type) (Fig. 10A). Compound leaf bases with decurrent leaf bases are compared with those of *Zanthoxylum* (Rutaceae). Small imparipinnate leaves with leaflets with crenulate margins are compared to *Weinmannia* (Saxifragaceae) (Fig. 10B). A morphologically similar taxon has been referred to *Boswellia* (Burseraceae) by Kahlert and Rüffle (2007). Medium-sized, entire-margined leaves have been assigned to *Ficus* (Moraceae), *Laurophyllum* (Lauraceae), and *Salix* (Salicaceae). Typical rounded leaves have been traditionally referred to *Dombeyopsis* or *Grewia* (Fig. 10C), and a rounded outline with crenulate margin seems to be similar to *Cercidiphyllum* (Jähnichen et al., 1980). Infructescences are called *Bubulcia* (family ?Lythaceae in Wilde et al., 2014), and winged fruits have been traditionally assigned to *Getonia* (Fig. 10D).

Among the terrestrial angiosperms the following families have been identified, including the Araliaceae, Aurantiaceae, Bignoniaceae, Bromeliaceae, Burseraceae, Byttneriaceae, Cabombaceae, Caesalpiniaceae, Caryophyllaceae, Cyperaceae, Ericaceae, Gentianeaceae, Gramineae, Haloragidaceae, Liliaceae, Marsileaceae, Myricaceae, Myrtaceae, Najadaceae, Nymphaeaceae, Papilionaceae, Podostomaceae, Santalaceae, Sapindaceae, Sapotaceae, Saxifragaceae, Sterculiaceae, Urticaceae, Xanthoxylaceae and Zygophyllaceae (e.g., Massalongo, 1859a; Meschinelli and Squinabol, 1892; Gola, 1941; Fiore, 1936; Kahlert and Rüffle, 2007). Fruits are also present, pertaining to several species of *Fracastoria*, tentatively attributed to the Sterculiaceae by Massalongo (Massalongo, 1858) (Fig. 11A), as well as by the palms of the genus *Castellinia* and *Nypa*.

Conifers are rather rare, apparently represented by *Podocarpus* and *Taxodium* (Massalongo, 1859a; Fiore, 1936f).

Palynological analyses on Pesciara confirmed the abundant presence of angiosperms, rare gymnosperms, and ferns (Kedves and Zsivín, 1970).

The first record of amber from the Bolca Lagerstätten was probably that from the *Ittiolitologia Veronese* of Serafino Volta (1796–1809). Amber has been collected from both the Pesciara and Monte Postale sites, although the largest nodules (measuring several centimeters) have been found only in the Pesciara site. The Leguminosae have been



considered as the most plausible producers of the fossil resin of the Pesciara site (Trevisani et al., 2005) (Fig. 10B). The depositional environment of a shallow sea bordered by a nearby landmass is confirmed by the algal and marine phanerogam assemblages, which reinforce the palaeoenvironmental framework determined by the fish and arthropod fauna assemblages. The landmass was

characterised by a more or less distant forest, and the arrival of leaves of indehiscent herbaceous plants, such as ferns and monocotyledons, was in large part prevented. The forests were certainly characterised by the rich presence of leguminous and palm plants, including plants similar to the extant mangrove palm *Nypa*, directly floating and sinking to the sea lagoon and marginal marine bottom.

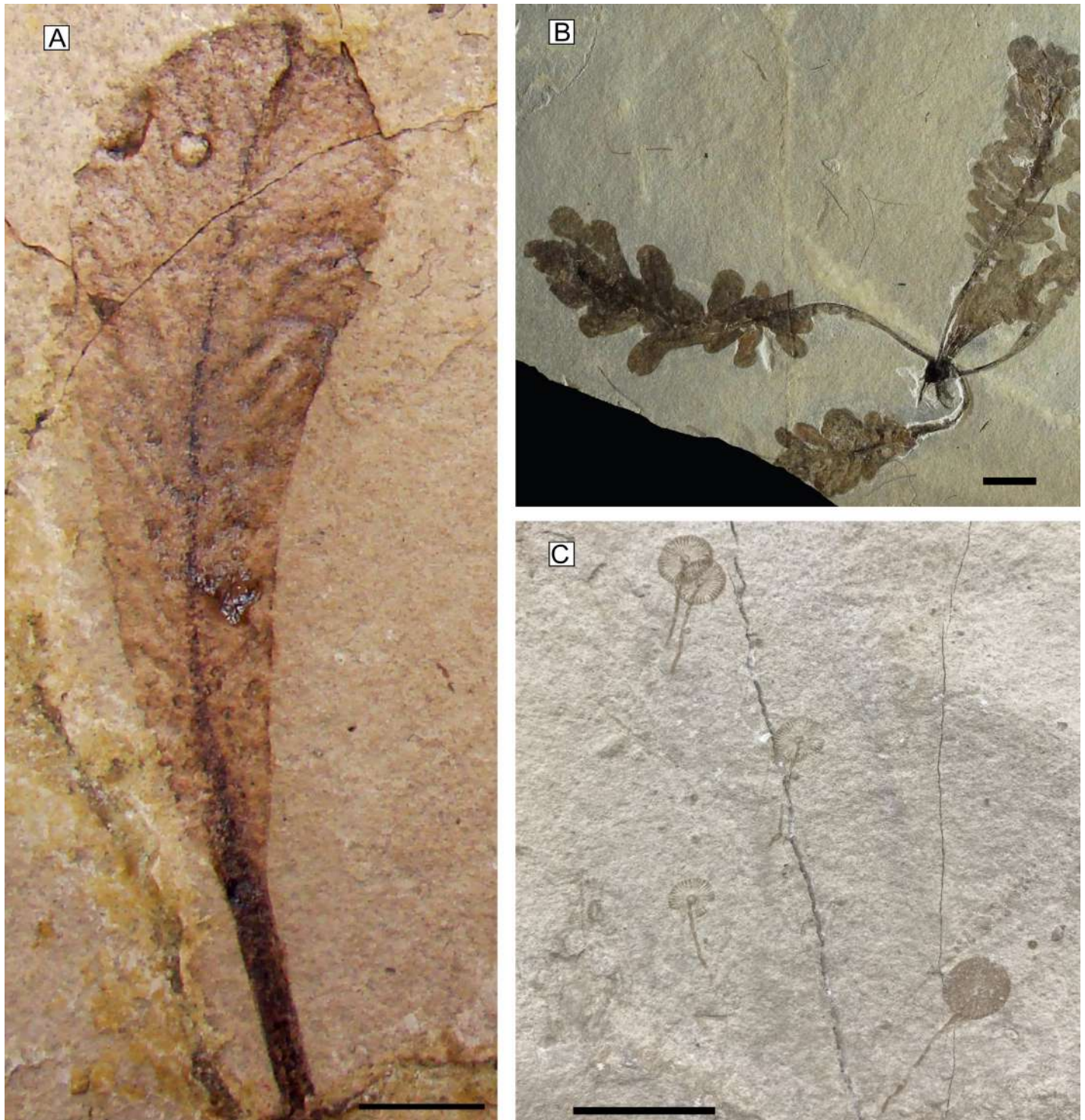


Fig. 9 - Selected plant remains from the Bolca Lagerstätten. A) Flat blades with rounded apices of the red alga *Delessertes*, MCSNV fg.142; B) *Pterigophycos* sp., a nearly complete thallus of a red alga specimen, MFB 22.116; C) the umbrella-shaped cap green alga *Acetabularia*, MCSNV 20.4.593. Scale bars 10 mm.

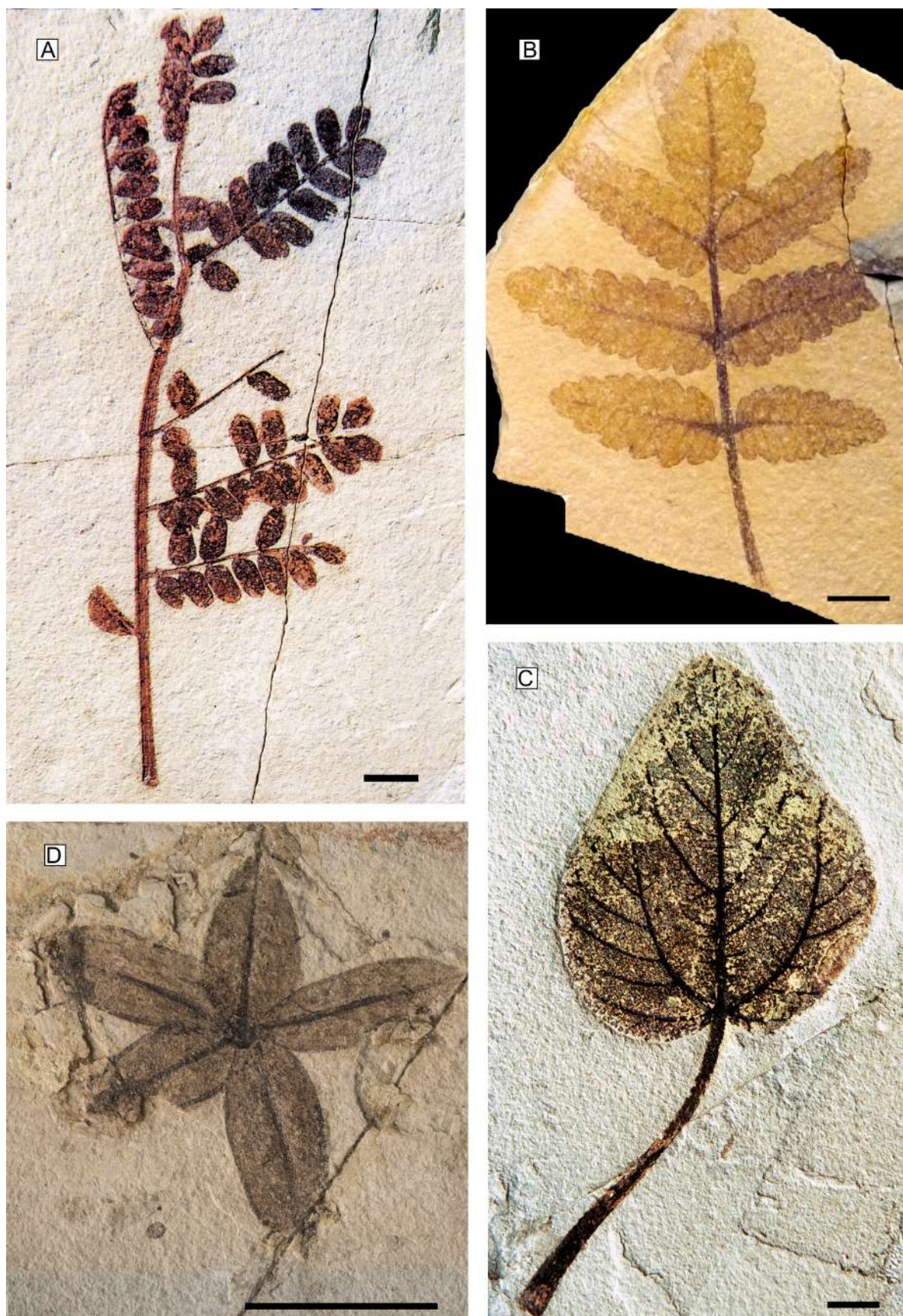


Fig. 10 - Selected plant remains from the Bolca Lagerstätten. A) Caesalpinoid leaf type of leguminous species belong to *Caesalpinia eocenica*, MCSNV fM.739; B) Imparipinnate leaves with leaflets with crenulate margin, *Weinmannia* (Sassifragaceae), MCSNV IG.VR. 71943; C) *Dombeyopsis*, a typical plant with rounded leaves attributed to Buttneriaceae family, MCSNV fB 143; D) Winged fruit of the “*Getonia*”-type, MCSNV fG 398. Scale bars 10 mm.

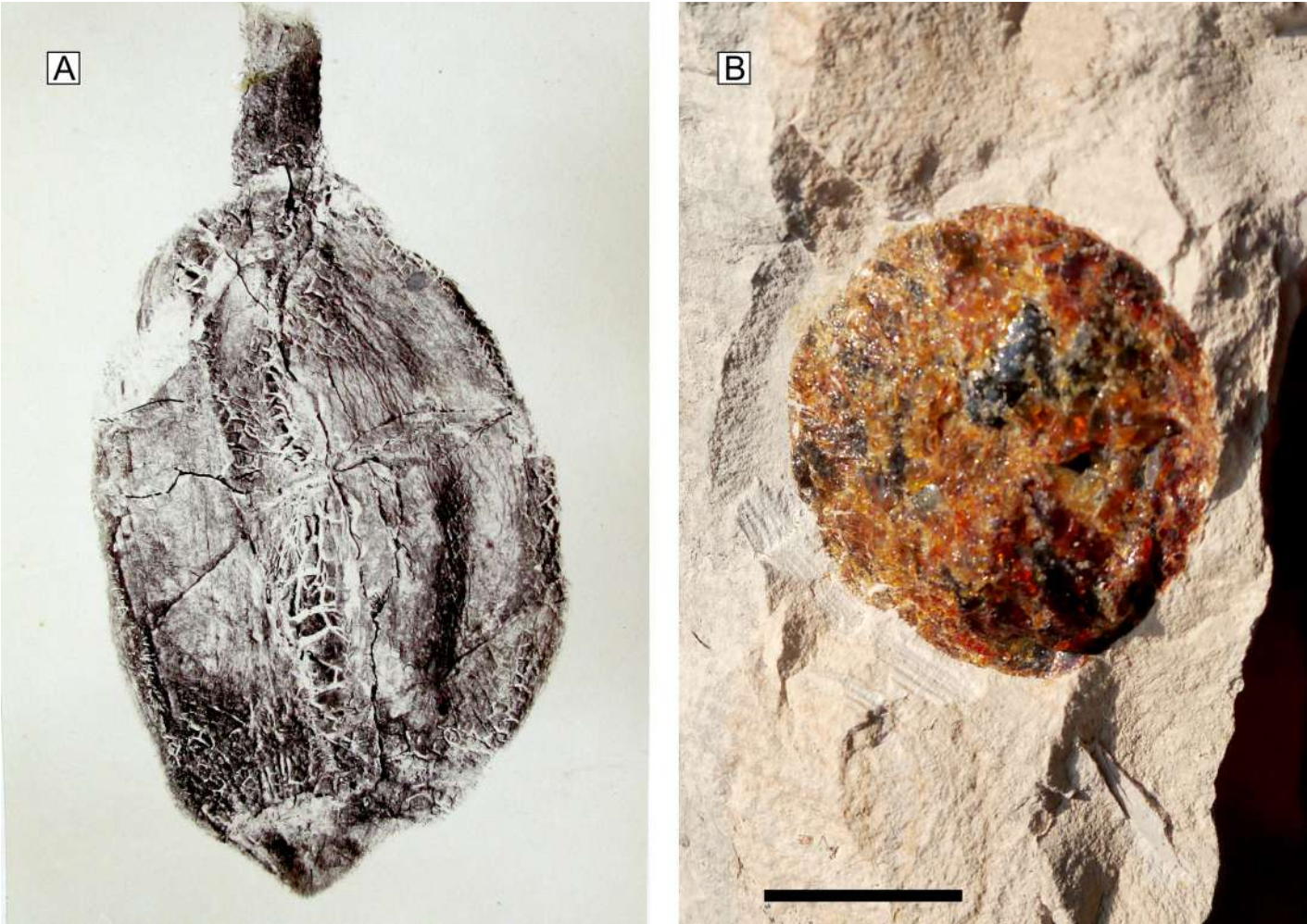


Fig. 11 - Selected plant remains from the Bolca Lagerstätten. A) Large fruit belonging to *Fracastoria*. This is one of the earliest published photographs of fossil plants (Massalongo, 1859b); B) Amber nodule (diameter 35 mm) from the fish-bearing laminated limestone of the Pesciara di Bolca, CMC 132. Scale bar 10 mm.

Table 2 - A synoptic list of Eocene algae and plants of the Bolca Lagerstätten.
B = Bolca, MP = Monte Postale, P = Pesciara.

Green Algae	<i>Aristophycos agardhianus</i> (Brogniart) Massalongo, 1858	B
	<i>Caulerpites araucaria</i> Massalongo, 1858	B
	Halimedeae	B
	Family Dasycladaceae	
	<i>Sthenelaites dasiaeformis</i> (Massalongo, 1855)	B
Red Algae	Family Confervaceae	
	<i>Nemalionites cristatus</i> Massalongo, 1858	B
	<i>Nemalionites limacoides</i> Massalongo, 1851	B
Class Floridae		
	<i>Amansites prionomorphus</i> Massalongo	B
	<i>Ceramites codioides</i> Massalongo, 1851a	B
	<i>Ceramites floccosa</i> Massalongo, 1851	B
	<i>Ceramites parasitica</i> Massalongo, 1851a	B
	<i>Ceramites pectinata</i> Massalongo, 1851a	B
	<i>Ceramites sphacelarioides</i> Massalongo, 1851a	B
	<i>Ceramites sciuroides</i> Massalongo	B
	<i>Delesseria bolcensis</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>bertrandi</i> (Massalongo) Meschinelli & Squinabol	B
		B



	<i>Delesseria bolcensis</i> v. <i>bicostatus</i> Massalongo, 1851	B
	<i>Delesseria bolcensis</i> v. <i>calophylla</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>catulli</i> Massalongo, 1851a	B
	<i>Delesseria bolcensis</i> v. <i>ceanothiphyllus</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>crassus</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>crenulatus</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>deltoideus</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>dimidiatus</i> Massalongo, 1851a	B
	<i>Delesseria bolcensis</i> v. <i>emarginatus</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>incurvus</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>latus</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>medius</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>macropus</i> Massalongo, 1851	B
	<i>Delesseria bolcensis</i> v. <i>manganotti</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>obovatus</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>panduriformis</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>pedunculata</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>prolifera</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>pusillus</i> (Massalongo, 1851a)	B
	<i>Delesseria bolcensis</i> v. <i>rhombaeus</i> Massalongo	B
	<i>Delesseria bolcensis</i> v. <i>rotundata</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>scyphophora</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>spathulata</i> (Massalongo) Meschinelli & Squinabol	B
	<i>Delesseria bolcensis</i> v. <i>strictus</i> Massalongo	B
	<i>Delesseria heckeliana</i> Massalongo, 1851	B
	<i>Delesseria ovatus</i> Sternberg	B
	<i>Delesseria sessilis</i> Massalongo	B
	<i>Pterigophycos podocarpiphyllus</i> Massalongo	B
	<i>Pterigophycos spectabilis</i> Massalongo, 1858	B
	<i>Pterigophycos gazolanus</i> Massalongo, 1858	B
	<i>Pterigophycos pinnatifidus</i> Massalongo, 1858	B
	<i>Pterigophycos canossae</i> Massalongo, 1858	B
	<i>Melobesites membranacea</i> Massalongo, 1858	B
	Family Solenoporaceae	
	<i>Parachaetetes</i> sp.	MP
	Family Fucaceae	
	<i>Zonarites (Dictyotites) aspergillum</i> Massalongo, 1851	B
	<i>Zonarites (Dictyotites) menegazzianus</i> Massalongo, 1851	B
	<i>Zonarites (Dictyotites) radiatus</i> Massalongo 1851	B
	<i>Zonarites (Dictyotites) rigidus</i> Massalongo, 1851a	B
	<i>Zonarites (Dictyotites) stipitatus</i> Massalongo, 1851a	B
	<i>Zonarites chloroplegma</i> Massalongo	B
	<i>Zonarites flabellaris</i> Massalongo, 1851	B
	<i>Zonarites fuliginosus</i> Massalongo, 1851	B
	<i>Laminarites irideaephyllus</i> Massalongo, 1858	B
	<i>Laminarites lamourexii</i> Massalongo, 1858	B
	<i>Laminarites macrophyllus</i> Massalongo, 1851	B
	<i>Laminarites scolopendra</i> Massalongo, 1851	B
	<i>Laminarites vestenae</i> Massalongo, 1851	B
	<i>Pasinia ?ambigua</i> Massalongo, 1851	B
	<i>Pasinia elliptica</i> Massalongo, 1851	B
	<i>Pasinia incurva</i> Massalongo, 1851	B
	<i>Pasinia ovalis</i> Massalongo, 1851	B
	<i>Pasinia pyriformis</i> Massalongo, 1851	B
	<i>Pasinia rotundata</i> Massalongo, 1851	B
Brown Algae		
	Family Laminariaceae	
	<i>Postelsiopsis caputmedusae</i> (Massalongo, 1850) Forti, 1926	B
Pteridophytes		
	Family Marsileaceae	
	<i>Cystorrhiza pillularioides</i> Massalongo	B
ANGIOSPERMS		
MONOCOTYLEDONS		



	Family Ceratophyllaceae (Ceratophylleae in Massalongo, 1859)	
	<i>Ceratophyllum cuspidatum</i> Massalongo, 1851	B
	Family Podostemaceae (Podostemeae in Massalongo, 1859)	
	<i>Glossophium proliferum</i> Massalongo, 1858	B
	<i>Glossophium eocenum</i> Massalongo, 1858	B
	<i>Maffeja ceratophylloides</i> Massalongo, 1858	B
	<i>Tympanophora discophora</i> Pomel, 1849	B
	<i>Tympanophora turbinata</i> Pomel, 1849	B
	Family Bromeliaceae	
	<i>Bromelianthus heuflerianus</i> Massalongo	B
	Family Liliaceae	
	<i>Albucastrium perinanthioideum</i> Massalongo, 1859	B
	<i>Crinanthus fenziianus</i> Massalongo, 1859	B
	Family Najadaceae (Najadeae in Mass. 1859)	
	<i>Caulinites equisetomorphus</i> Massalongo	B
	<i>Halochloris castelliniana</i> Massalongo, 1851	B
	<i>Halochloris cymodoceoides</i> Unger	B
	<i>Halochloris fluitans</i> Massalongo	B
	<i>Halochloris meneghinii</i> Massalongo, 1851	B
	<i>Halochloris stolonifera</i> Massalongo, 1851	B
	<i>Halochloris striata</i> Massalongo, 1851	B
	<i>Halochloris subsecunda</i> Massalongo, 1851a	B
	<i>Halochloris ungeri</i> Massalongo, 1851	B
	<i>Halochloris veronensis</i> Massalongo, 1851	B
	<i>Ruppia aristata</i> Massalongo, 1851	B
	<i>Zanichelliopsis repens</i> Massalongo, 1851	B
	Family Protorchidaceae (Protorchidae in Mass. 1859)	
	<i>Protorchis monorchis</i> Massalongo, 1859	B
	<i>Palaeorchis rhizoma</i> Massalongo, 1858	B
	Class Spadiciflorae	
	Family Palmae	
	<i>Hemiphoenices ??</i>	B
	<i>Latanites parvula</i> Massalongo, 1858	B
FRUITS		
	<i>Castellinia ambigua</i> Massalongo, 1858	B
	<i>Castellinia compressa</i> Massalongo, 1858	B
	<i>Castellinia elliptica</i> Massalongo, 1858	B
	<i>Castellinia ?incurva</i> Massalongo, 1852a	B
	<i>Castellinia macrocarpa</i> Massalongo, 1852a	B
	<i>Castellinia ?subrotunda</i> Massalongo, 1852a	B
	<i>Palaeospathe elliptica</i> Massalongo	B
	<i>Palaeospathe lata</i> Massalongo	B
	<i>Thecophyllum flabellatum</i> Massalongo	B
	Family Typhaceae	
	<i>Typhaeloipum spadae</i> Massalongo, 1858	B
Gymnosperms		
Class Coniferae		
	Family Cupressinae	
	<i>Podocarpus affinis</i> Massalongo, 1851a	B
	<i>Podocarpus bolcensis</i> Massalongo, 1851	B
	<i>Podocarpus incisa</i> Massalongo, 1851a	B
	<i>Podocarpus scolecophylla</i> Massalongo, 1851a	B
	<i>Podocarpus surianoides</i> Massalongo	B
	<i>Taxodium jacarandaefolium</i> Massalongo	B
Monocots Angiosperms		
	Family Smilacaceae	
	<i>Smilacites ?lanceae</i> Massalongo	B
	Family Ceratophylleae	
	<i>Ceratophyllum cuspidatum</i> Massalongo, 1851	B
	Family Nymphaeaceae	
	<i>Nymphaea arethusae</i> Brongniart	B
	<i>Nymphaea cherpica</i> Massalongo	B
	<i>Nymphaea</i> sp. ind. Brongniart	B



	<i>Peltophyllum nelumbioides</i> Massalongo, 1858	B
Class Frangulaceae		
	Family Celastrineae	
	<i>Celastrophyllum gaudinianum</i> Massalongo	B
	<i>Celastrophyllum oleaefolium</i> Massalongo	B
	<i>Celastrus bubulcae</i> Massalongo	B
	<i>Celastrus nitrariaefolius</i> Massalongo	B
	Family Rhamnaceae	
	<i>Ceanothus cornifolius</i> Massalongo	B
Class Glumaceae		
	Family Cyperaceae	
	<i>Cyperacites bolcensis</i> (Massalongo) Schimper	B
	<i>Cyperites eocenus</i> Massalongo	B
	Family Gramineae (Gramineae in Massalongo, 1858)	
	<i>Apludophyton cucubalooides</i> Massalongo	B
	<i>Apludophyton scleroides</i> Massalongo	B
	<i>Arundinites dracenophylla</i> Massalongo	B
	<i>Poacites juncooides</i> Massalongo	B
Class Iuliflorae		
	Family Ampelidae	
	<i>Ampelophyllum bolcense</i> Massalongo, 1851	B
	<i>Ampelophyllum noeticum</i> Massalongo, 1857	B
	<i>Ampelophyllum voltianum</i> Massalongo, 1851	B
	Family Apocynaceae	
	<i>Apocynophyllum bozzianum</i> Massalongo	B
	<i>Apocynophyllum oligocaenum</i> Massalongo, 1858b	B
	<i>Apocynophyllum terminaliaefolium</i> Massalongo	B
	Family Araliaceae	
	<i>Aralianthea brongniartii</i> Massalongo, 1858	B
	<i>Aralianthea laurina</i> Massalongo, 1858	B
	<i>Aralianthea zizioides</i> Massalongo, 1858	B
	<i>Aralia primaeca</i> Massalongo, 1851	B
	Family Aurantiaceae	
	<i>Hesperidophyllum citroides</i> Massalongo, 1858	B
	<i>Hesperidophyllum ettingshauseni</i> Massalongo, 1858	B
	<i>Hesperidophyllum scalpellum</i> Massalongo, 1858	B
	Family Berberidae	
	<i>Berberis ?prisca</i> Massalongo 1851a	B
	<i>Nandina ?consolatii</i> Massalongo 1851a	B
	Family Bignoniaceae	
	<i>Bigonia boroniaefolia</i> Massalongo	B
	<i>Bigonia limoniaefolia</i> Massalongo, 1851a	B
	<i>Bigonia moringaefolia</i> Massalongo, 1851a	B
	<i>Jacaranda italica</i> Massalongo	B
	<i>Jacaranda speciosa</i> Massalongo	B
	Family Buttneriaceae	
	<i>Dombeyopsis affinis</i> Massalongo, 1854	B
	<i>Dombeyopsis auriculata</i> Massalongo, 1854	B
	<i>Dombeyopsis bixaefolia</i> Massalongo, 1854	B
	<i>Dombeyopsis ceanothifolia</i> Massalongo, 1854	B
	<i>Dombeyopsis decipiens</i> Massalongo	B
	<i>Dombeyopsis deformis</i> Massalongo, 1854	B
	<i>Dombeyopsis glandulifera</i> Massalongo	B
	<i>Dombeyopsis granadilla</i> Massalongo, 1854	B
	<i>Dombeyopsis heufleriana</i> Massalongo, 1854	R
	<i>Dombeyopsis hibiscifolia</i> Massalongo, 1854	B
	<i>Dombeyopsis kleinhoviaefolia</i> Massalongo, 1854	B
	<i>Dombeyopsis incerta</i> Massalongo, 1854	B
	<i>Dombeyopsis populina</i> Massalongo	B
	<i>Dombeyopsis sublobata</i> Massalongo, 1854	B
	<i>Dombeyopsis tilioides</i> Massalongo, 1854	B
	<i>Pterospermum palpighiaceum</i> Massalongo	B
	Family Caryophylleae	



<i>Cucubalites ?flagellum</i> Massalongo	B
<i>Cucubalites postalensis</i> Massalongo, 1858	B
Family Cupuliferae	
<i>Quercus vegronia</i> Massalongo, 1858b	B
Family Ericaceae	
<i>Andromeda biloba</i> Massalongo, 1851a	B
<i>Andromeda cincinnati</i> Massalongo	B
<i>Andromeda latina</i> Massalongo	B
<i>Andromeda palaeogaea</i> Massalongo	B
<i>Andromeda santalina</i> Massalongo	B
<i>Andromeda stillingioides</i> Massalongo	B
<i>Andromeda tromodophylla</i> Massalongo	B
<i>Andromeda visianii</i> Massalongo, 1851a	B
<i>Gautiera trichoides</i> Massalongo	B
<i>Vaccinium convolvulinum</i> Massalongo	B
Family Gentianeae	
<i>Villarsites ungeri</i> Münster	B
Family Laurineae	
<i>Cinnamomum antiquum</i> Massalongo	B
<i>Cinnamomum veronense</i> Massalongo	B
Family Malpighiaceae	
<i>Malpighiastrum ambiguum</i> Massalongo	B
<i>Malpighiastrum dehaasioides</i> Massalongo	B
<i>Malpighiastrum hyraeaeoides</i> Massalongo	B
Family Moreae	
<i>Ficus bolcensis</i> Massalongo, 1858	B
<i>Ficus bolcensis</i> v. <i>lanceolata</i> Massalongo	B
<i>Ficus bolcensis</i> v. <i>ovalifolia</i> , Massalongo	B
<i>Ficus coelestis</i> Massalongo, 1858	B
<i>Ficus poniana</i> Massalongo, 1858	B
<i>Ficus psychotrioides</i> Massalongo	B
<i>Ficus veronensis</i> Massalongo, 1858	B
Family Myricaceae	
<i>Myrica zig-zag</i> Massalongo, 1858a	B
Family Polygonaceae (Poligonaceae, in Massalongo, 1959)	
<i>Coccolobites morindioides</i> Massalongo, 1858b	B
<i>Calligonopsis pallasioides</i> Massalongo	B
<i>Calligonopsis strumphsioides</i> Massalongo, 1858	B
Family Proteaceae	
<i>Anadenia italica</i> Massalongo	B
<i>Banksia longifolia</i> Ettinghausen	B
<i>Dryandra meneghinii</i> Ettinghausen	B
<i>Dryandra veronensis</i> Massalongo	B
<i>Manglesia synaphaeaeifolia</i> Massalongo	B
<i>Protea glossa</i> Massalongo	B
Family Santalaceae	
<i>Leptomera distans</i> Ettinghausen, 1853	B
<i>Leptomera elongata</i> Massalongo, 1851a	B
<i>Leptomera gracilis</i> Ettinghausen, 1853	B
<i>Leptomeria (Oxymeria) psilotina</i> Massalongo	B
<i>Santalum memecyloides</i> Massalongo	B
Family Sapindiaceae	
<i>Koelreuteria corcorifolia</i> Massalongo	B
<i>Koelreuteria maffejana</i> Massalongo, 1852b	B
<i>Sapindus göppertianus</i> Massalongo	B
<i>Sapindus pristinus</i> Massalongo, 1858	B
<i>Sapindus scynophyllus</i> Massalongo	B
Family Sapotaceae	
<i>Bumelia buxioides</i> Massalongo, 1851a	B
<i>Bumelia calceolarii</i> Massalongo	B
<i>Bumelia clusiaefolia</i> Massalongo	B
<i>Bumelia cuneifolia</i> Massalongo	B
<i>Sapotacites oleaeifolius</i> Massalongo	B



Family Sassifragaceae		
<i>Weinmannia ausoniae</i> Massalongo, 1858		B
<i>Weinmannia elaphriifolia</i> Massalongo, 1858		B
<i>Weinmannia fagaraefolia</i> Massalongo, 1858		B
<i>Weinmannia incerta</i> Massalongo, 1858		B
Family Sterculiaceae		
<i>Fracastoria anguria</i> Massalongo, 1858		B
<i>Fracastoria citrifolia</i> Massalongo, 1858		B
<i>Fracastoria citrullus</i> Massalongo, 1858		B
<i>Fracastoria clavaeformis</i> Massalongo, 1858		B
<i>Fracastoria cucurbitina</i> Massalongo, 1858		B
<i>Fracastoria gastrioides</i> Massalongo, 1858		B
<i>Fracastoria gigantea</i> Massalongo, 1858		B
<i>Fracastoria lagenaria</i> Massalongo, 1858		B
<i>Fracastoria megapepo</i> Massalongo, 1858		B
<i>Fracastoria melo</i> Massalongo, 1858		B
<i>Fracastoria pomiformis</i> Massalongo, 1858		B
<i>Fracastoria pyramidalis</i> Massalongo, 1858		B
<i>Fracastoria pyriformis</i> Massalongo, 1858		B
<i>Fracastoria rotunda</i> Massalongo, 1858		B
<i>Fracastoria signoana</i> Massalongo, 1858		B
<i>Sterculia labrusca</i> Unger		B
<i>Sterculia labrusca</i> v. <i>labrusca</i> Massalongo, 1859		B
<i>Sterculia labrusca</i> v. <i>squarrosa</i> Unger		B
<i>Sterculia labrusca</i> v. <i>tetrafida</i> Unger		B
<i>Sterculia labrusca</i> v. <i>syrii</i> Unger		B
Family Tiliaceae		
<i>Grewia coccolobaefolia</i> Massalongo & Lotze, 1959		B
Class Leguminosae		
<i>Caesalpinia eocenica</i> Unger Botan zeit, 1849		B
<i>Cassia enervis</i> Massalongo		B
<i>Drepanocarpus dacampii</i> Massalongo, 1858		B
<i>Drepanocarpus nummus</i> Massalongo, 1858		B
<i>Palaeolobium alnifolium</i> Massalongo		B
<i>Palaeolobium brennonicum</i> Massalongo		B
<i>Palaeolobium buteaefolium</i> Massalongo		B
<i>Palaeolobium cedrelaefolium</i> Massalongo		B
<i>Palaeolobium morindaefolium</i> Massalongo		B
<i>Palaeolobium nervosum</i> Massalongo		B
<i>Pterocarpus lestrigonum</i> Massalongo, 1858		B
<i>Pterocarpus targionii</i> Massalongo, 1858		B
<i>Pongamia protogeae</i> Massalongo, 1858		B
<i>Sophora capparifolia</i> Massalongo		B
Family Mimoseae		
<i>Acacia buellana</i> Massalongo		B
<i>Acacia eugenioides</i> Massalongo		B
<i>Acacia primordialis</i> Massalongo		B
<i>Leguminosites phaseolus</i> Massalongo		B
Class Terebinthineae		
Family Combretaceae		
<i>Getonia bolcensis</i> Unger		B
<i>Porana (Getonia) potentilloides</i> (Massalongo) Schimper		B
<i>Terminalia perseaeefolia</i> Massalongo, 1858a		B
Family Juglandaceae		
<i>Juglans ossilii</i> Massalongo		B
<i>Juglans sapindaceae</i> Massalongo		B
Family Meliantheae		
<i>Melianthus craccorum</i> Massalongo		B
Family Myrtaceae		
<i>Eucalyptus acanonicophylla</i> Massalongo		B
<i>Eucalyptus italica</i> Massalongo		B
<i>Eucalyptus italica</i> v. <i>lancheophylla</i> Massalongo		B
<i>Eucalyptus italica</i> v. <i>leptophylla</i> Massalongo		B



	<i>Eucalyptus italica</i> v. <i>oxyphylla</i> Massalongo	B
	<i>Eucalyptus italica</i> v. <i>pachyphylla</i> Massalongo	B
	<i>Eucalyptus italica</i> v. <i>platyphylla</i> Massalongo	B
	<i>Eucalyptus italica</i> v. <i>stenophylla</i> Massalongo	B
	<i>Eucalyptus rhododendrifolia</i> Massalongo	B
	<i>Eucalyptus targae</i> Massalongo	B
	<i>Eugenia andiraefolia</i> Massalongo	B
	<i>Eugenia dactylostemoides</i> Massalongo	B
	<i>Eugenia laurifolia</i> Massalongo	B
	<i>Eugenia laurifolia</i> v. <i>alata</i> Massalongo	B
	<i>Eugenia laurifolia</i> v. <i>apathulata</i> Massalongo	B
	<i>Eugenia laurifolia</i> v. <i>lanceolata</i> Massalongo	B
	<i>Eugenia laurifolia</i> v. <i>salicoides</i> Massalongo	B
	<i>Myrtomiophyton stephanophorus</i> Massalongo, 1858	B
	Family Pomaceae	
	<i>Crataegus moscardianus</i> Massalongo	B
	Family Trapeae	
	<i>Trapophyllum europaeum</i> Massalongo, 1858	B
	Family Zanthoxyleae	
	<i>Zanthoxylon ambiguum</i> Massalongo, 1858	B
	<i>Zanthoxylon ambiguum</i> v. <i>pasinii</i> Massalongo, 1851a	B
	<i>Zanthoxylon ambiguum</i> v. <i>platyphyllum</i> Massalongo, 1858	B
	<i>Zanthoxylon ambiguum</i> v. <i>stenophyllum</i> Massalongo, 1858	B
	<i>Zanthoxylon ambiguum</i> v. <i>toninianum</i> Massalongo	B
	<i>Zanthoxylon ambiguum</i> v. <i>ungeri</i> Massalongo, 1851a	B
	<i>Zanthoxylon cherpicum</i> Massalongo, 1858	B
	Family Zygothylae	
	<i>Bubulcia alismantha</i> Massalongo	B
	<i>Bubulcia globifera</i> Massalongo, 1858	B
	<i>Guajacites berengeri</i> Massalongo, 1858	B
	<i>Guajacites enervis</i> Massalongo, 1858	B
	<i>Guajacites heerii</i> Massalongo, 1858	B
Class Trioccae		
	Family Euphorbiaceae	
	<i>Omalanthus hekastophylloides</i> Massalongo	B
	<i>Phyllanthus ceanothoides</i> Massalongo	B
	<i>Phyllanthus populinum</i> Massalongo	B
	<i>Sarothrostachys eocenica</i> Massalongo	B
	Family Proteaceae	
	<i>Anadenia pighiana</i> Massalongo	B
	<i>Banksia dillenoides</i> Fiore, 1936	B
	<i>Castanea integra</i> Fiore, 1936	B
	<i>Delesserites pinnatus</i> Fiore, 1935a	B
	<i>Podogonium knorri</i> Fiore, 1936	B
	<i>Populus</i> sp. Fiore, 1936	B
	<i>Salix viviani</i> Fiore, 1936	B
Plantae incertae sedis		
	<i>Agnophyton aristatum</i> Massalongo, 1851a	B
	<i>Antholithes liliacea</i> Brongniart	B
	<i>Antholithes nymphoides</i> Brongniart	B
	<i>Carpolithes binocularis</i> Massalongo, 1851a	B
	<i>Carpolithes carandioides</i> Massalongo, 1851a	B
	<i>Carpolithes lacunosus</i> Massalongo, 1851a	B
	<i>Carpolithes longipes</i> Massalongo, 1851a	B
	<i>Carpolithes micropepo</i> Massalongo, 1851a	B
	<i>Carpolithes orbis</i> Massalongo	B
	<i>Carpolithes sapindaceous</i> Massalongo	B
	<i>Carpolithes subtriangularis</i> Massalongo, 1851a	B
Pollen morphospecies		
Clade Tracheophytes		
Division Pteridophyta		
	<i>Polypodiaceoisporites</i> sp.	P
	<i>Pteris</i> sp.	P



Species without precise affinity Normapolles

<i>Basopollis</i> sp.1	P
<i>Basopollis</i> sp.2	P
cf. <i>Basopollis</i> sp.	P
<i>Interpollis microsupplingensis</i>	P
<i>Interpollis supplingensis</i>	P
<i>Plicapollis pseudoexcelsus</i>	P
cf. <i>Pompeckjoidaepollenites</i> sp.	P
<i>Pseudoplicapollis</i> sp.	P
Family Icacinaceae	
<i>Compositoipollenites rhizophorus</i>	P
Family Juglandaceae	
<i>Boehlensipollis</i> sp.	P
<i>Gallopollis minimus</i> subsp. <i>concaformis</i>	P
cf. <i>Platycaryapollenites</i> sp.	P
<i>Plicatopollis</i> sp.	P
<i>Subtriporopollenites anulatus</i>	P
<i>Subtriporopollenites constans</i>	P
<i>Subtriporopollenites facilis</i>	P
<i>Subtriporopollenites magnoporatus</i>	P
<i>Subtriporopollenite</i> spp.	P
<i>Tricolporopollenites parmularius</i>	P
Family Restionaceae	
<i>Pentapollenites regulatus</i>	P
<i>Restionidites hungaricus</i>	P
Family Sapotaceae	
<i>Tetracolporopollenites ellipsus</i>	P
<i>Tetracolporopollenites halimbaense</i>	P
<i>Tetracolporopollenites hungaricus</i>	P
Order Arecales	
Family Palmae	
<i>Sabalpollenites areolatus</i>	P
<i>Sabalpollenites</i> sp.	P
Order Cornales	
Family Nyssaceae	
<i>Tricolporopollenites krutzschii</i>	P
Family Aquifoliaceae	
<i>Tricolporopollenites iliacus</i>	P
<i>Tricolporopollenites margaritatus</i>	P
Order Ericales	
Family Cyrillaceae	
<i>Tricolporopollenites megaexactus</i>	P
Order Fagales	
Family Fagaceae	
<i>Tricolporopollenites cingulum</i>	P
Family Betulaceae	
<i>Triporopollenites</i> sp.	P
Order Polypodiales	
Family Pteridaceae	
<i>Polypodiaceoisporites</i> sp.	P
Order Rosales	
Family Rosaceae	
<i>Tricolporopollenites aceroides</i>	P
Order Sapindales	
Family Simarubaceae	
<i>Tricolporopollenites</i> spp.	P



THE INVERTEBRATES OF THE FISH-BEARING LAMINITES

“Minor fauna” is the term commonly applied to non-fish animals (mostly invertebrates) recovered from the laminites of the Pesciara and Monte Postale sites (e.g., [Sorbini, 1980, 1999](#); [Giusberti et al., 2014](#)). This expression reflects how the remarkable abundance and exceptional preservation of the fossil fishes have overshadowed other components of this extraordinary fossil assemblage throughout more than four centuries of research. This section focuses exclusively on the invertebrate component of the Bolca palaeobiotic assemblage, encompassing both marine and terrestrial forms such as arthropods, annelids, jellyfish, molluscs, brachiopods, and bryozoans (Figs. 12–21; Tab. 3).

The first report on the presence of invertebrates in the Pesciara of Bolca likely dates back to the second half of the 17th century, when [Boccone \(1697\)](#) cited the presence of crabs associated with the fishes ([Guerra, 2014](#); [Pasini et al., 2019](#)). The palaeobotanist [Abramo Massalongo](#) was the first scholar to attempt a systematic investigation of the invertebrate assemblage of Bolca, but his planned monography (the *Compendium Faunae et Florae fossilis Bolcensis*) never came to light, likely due to his untimely death ([Giusberti et al., 2015](#)). After some partial studies in the 19th century (e.g., [Münster, 1842](#); [Massalongo, 1850, 1855, 1856](#); [Milne-Edwards, 1860](#); [Omboni, 1886](#)), the invertebrates of the Bolca Lagerstätten were mostly neglected up to the second half of the 20th century, when new discoveries probably encouraged some researchers to restart investigations ([Giusberti et al., 2014](#)).

Jellyfish—Jellyfish, exclusively recovered in the Pesciara site, were described for the first time by [Broglia Loriga and Sala Manservigi \(1973\)](#), who referred all six available specimens to “Scyphomedusae”. Four specimens were assigned to the rhizostome *Simplicibrachia bolcensis* ([Broglia Loriga and Sala Manservigi, 1973](#); Fig. 12A). The other two specimens were interpreted as young individuals possibly belonging to the orders Rhizostomeae and Semaestomeae. [Sala Manservigi \(1979\)](#) subsequently reported six additional jellyfish specimens, three of which were ascribed to adults of *Simplicibrachia*, and three were referred to ephyrae (larvae) of “Scyphomedusae”, possibly belonging to the genera *Simplicibrachia* and *Chrysaora*. The jellyfish from the Pesciara are preserved as mixed carbonaceous films, exhibiting features such as oral arms, gonads, and muscles ([Young and Hagadorn, 2020](#)). Recent works confirmed the validity of the taxon *Simplicibrachia bolcensis* (Fig. 12A), represented at least by nine specimens, whereas the other specimens were referred to a probable semaeostome similar to extant *Aurelia* (Fig. 12B), and other possible medusae (Fig. 12C) ([Young and Hagadorn, 2020](#); [Fernández-Alías et](#)

[al., 2023](#)). Among the Cenozoic Lagerstätten, the Pesciara of Bolca is one of the very few known Palaeogene sites with properly documented fossil jellyfish ([Žalohar et al., 2025](#)).

Lophophorata—The only bryozoan so far known from the laminites of the Pesciara site is a single specimen of Schizoporellidae (order Cheilostomata; Figs. 13A, B), preserved as an impression only and lacking the younger stage of the zoarium ([Broglia Loriga and Sala Manservigi, 1973](#)). Terebratulid brachiopods belonging to “*Terebratula*” *fumanensis* from the Pesciara site were reported by [Mellini and Quaggiotto \(1999\)](#).

Molluscs—[Catullo \(1842\)](#) and [Massalongo \(1850\)](#) were the first who took interest in the molluscs from the laminites and listed a few taxa, including *Cerithium bolcanum* (*nomen nudum*), *Ostrea* sp., *Mytilus* sp. indet., *Tellina* ?*bicingularis*, and *Unio* sp. According to [Massalongo \(1850\)](#), specimens of *Unio* from Bolca were sometimes misinterpreted as some kind of plant pod. Other taxa reported by [Oppenheim \(1896\)](#) and [Vinassa de Regny \(1897\)](#) cannot be confidently attributed to the Pesciara or to the Monte Postale laminites. [Malaroda \(1954\)](#) recognised the presence of *Modiolus* sp., *Cardita postalensis*, and *Teredo tournali subparisiensis*. [Mellini and Quaggiotto \(1999\)](#) described a small malacofauna from the Pesciara site, comprising the bivalves *Anomia* cf. *primaeva*, *Ctenoides papillifera* (Fig. 13C), *Meroena polita* and *Monitilora elegans*, and the gastropods *Pseudamaura circumfossa* and *Dialopsis semistriata*. [Giusberti et al. \(2014\)](#) also reported undescribed bivalves, including a Mytilidae (Fig. 13D). [Petit et al. \(2014\)](#) described two specimens of the gastropod ?*Aclis aenigmaticus* (Eulimidae) apparently fixed to the integument of the fish *Eoplatax papilio* from the Pesciara site. The association between the gastropods and fish has been interpreted as a case of mutualism or, more likely, of ectoparasitism, documented to date for similar gastropods in cnidarians and echinoids ([Petit et al., 2014](#)).

Cephalopods are exceedingly rare in the laminites and are primarily represented by coleoids, except for a single specimen of the nautiloid *Aturia ziczac* from Monte Postale cited by [Malaroda \(1954\)](#). [Broglia Loriga and Sala Manservigi \(1973\)](#) were the first to describe a well-preserved coleoid from the Pesciara showing the characteristic habitus of a decapodiform teuthoid, only hypothetically related to “metateuthoids”. After this first report, two other specimens were recovered on the site. [Mironenko et al. \(2024\)](#) investigated in detail the anatomical features of all the material available and reinterpreted these fossils as belonging to an octopodid, *Bolcaoctopus pesciaraensis* (Fig. 14), representing the only imprints of fossil octopodid bodies known to date from the Cenozoic ([Mironenko et al., 2024](#)). A unique specimen of coleoid from the Pesciara with preserved shelly parts is a small apical portion of a phragmocone possibly belonging to *Spirulirostra georgii*



(see Mellini and Quaggiotto, 1999b), a species previously reported in Lutetian and Priabonian beds of the Veneto region (Fornasiero, 1997; Fornasiero and Vicariotto, 1997). **Annelids** – The annelids from the Bolca Lagerstätten (Fig. 15) likely represent the first fully preserved fossil polychaetes to be formally described and recognised as such (Alessandrello, 1990). However, their fossils were initially attributed to vegetal remains (e.g., Brongniart, 1828; Massalongo, 1850; Catullo, 1862b). This interpretation was later revised by Massalongo (1855), who reassigned them to seven species of “worms”, all referred to the genus *Nereites*. Ehlers (1868) subsequently transferred these taxa to the genus *Eunicites*, whereas Rovereto (1904) referred the species described by Massalongo to three genera, *Eunicites*, *Sthenelaites*, and *Siphonostomites*. An extensive revision of the annelids of Bolca, also based on the original material of Massalongo, was provided by Alessandrello (1990), who assigned most of the specimens available to the polychaetes *Eunicites gazolae* (Figs. 15A, D, E), *E. affinis*, *E. pinnai*, and *Siphonostomites hesionoides* (Figs. 15B, C). A single specimen was recognised as representing an indeterminate leech. New annelid specimens recovered during recent excavations are still undescribed.

Crustaceans – Crustaceans are an important component of the invertebrate fauna of the Pesciara and Monte Postale sites and are represented by several specimens belonging to the orders Isopoda, Stomatopoda, and Decapoda (Sorbini, 1999; Giusberti et al., 2014; Figs. 16–19). Decapods make up most of the assemblage and include, among others, penaeids (Figs. 17A–D), palinurids (Figs. 17E, F, 18A, B), anomurids, and brachiurids (Figs. 18F–19). The investigation of the crustaceans of Bolca, in general, is problematic because in many groups the preservation of carbonate exoskeletons is suboptimal; the specimens are almost flattened and have lost any reliefs, with their outlines “confused” and part of the cuticle removed and dislocated (Busulini et al., 2020). In addition, several specimens are disarticulated, likely because they are represented by ecdyses (Pasini et al., 2019).

Giovanni Serafino Volta documented the presence of “three distinct and remarkable (*“singolari”*) species of crabs” (*“il Longimano, il Setifero e la Locusta”*, the latter most probably representing a mantis shrimp) within the collections of Vincenzo Bozza and Count Giovanni Battista Gazola (Volta, 1796–1809). In the same work, he also recorded under the name “*Oniscus*” what was likely a specimen of a marine isopod. Apart from the earliest reports, the first illustration and description of a crustacean from the fish-bearing beds of the Pesciara site was provided by the French geologist Faujas de Saint-Fond (1804), who illustrated and described a decapod, possibly a penaeid shrimp, subsequently assigned by Massalongo (1855) to “*Udora? faujassii*”. In the 19th century, palaeontologists such as Desmarest (1822),

Münster (1842), Catullo (1862a), Milne-Edwards (1860), and De Zigno (*vide* Garassino and Novati, 2001) took interest in the crustaceans of Bolca, but only two taxa were properly investigated. Münster (1842) described the mantis shrimp *Squilla antiqua* (now *Lysiosquilla antiqua*; Fig. 16D), whose holotype is probably lost (*vide* Secrétan, 1975a; De Angeli and Beschin, 2006), whereas Milne-Edwards (1860) reported the portunid *Eoplnotus armatus*, the first decapod species from Bolca to be formally named (Pasini et al., 2019). Abramo Massalongo was the first researcher to plan a detailed study of the crustaceans from the Pesciara and Monte Postale sites, but ultimately, he published only a list of 19 taxa, including eight new, undescribed species presented as *nomina nuda*, as an appendix to his monograph on the polychaete annelids from Bolca (Massalongo, 1855). The first comprehensive study of the crustaceans from Bolca was published more than a century later, when Secrétan (1975a) examined all the material available at that time, creating eleven new taxa. She recognised the presence of a small number of isopod specimens (*Palaega acuticauda*, *Heterosphaeroma veronensis*, and *Sphaeroma* sp.; Figs. 16A–C) and hypothesised that these taxa may have been parasitic on fishes. Förster (1984) later reported the occurrence at Bolca of a single specimen of scyllarid decapod (slipper lobster), referred to the new species *Parribacus cristatus* (Figs. 18D, E).

The past 25 years have witnessed a resurgence of scientific interest in Bolca crustaceans; previously established taxa were re-examined, new taxa were identified, also thanks to new excavations, and finally, the most substantial group, the decapods, was entirely revised.

Garassino and Novati (2001), investigated the most iconic crustacean from the Pesciara, the spiny lobster *Palinurus desmaresti* (Figs. 17E, 18A), and transferred this species to the extant genus *Justitia*. The complex nomenclatural history of this taxon was later disentangled by Giusberti et al. (2015).

De Angeli and Beschin (2006) described a specimen of *Lysiosquilla antiqua* from Bolca, whereas De Angeli and Garassino (2008) reported two new taxa recovered from the laminites of Monte Postale, *Pseudosquilla lessinea* (another mantis shrimp; Fig. 16E) and the slipper lobster *Scyllarides bolcensis* (Fig. 18C).

Garassino et al. (2014) revised the systematic position of *Parribacus cristatus* (Figs. 18D, E), transferring the species to the genus *Parsacus*, whereas Haug and Rudolf (2015), using macro-fluorescence imaging, reinvestigated its holotype and identified new characters indicating that the specimen clearly represents a postlarval stage of a neoscyllarid.

The isopod taxa originally established by Secrétan (1975a) were reassessed by Vonk et al. (2015), who studied the original scarce material of the type series and additional



new specimens coming from the Pesciara and Monte Postale sites. Vonk et al. (2015) noted that the two species (reassigned to the genera *Cirolana* and *Dynamenella*: *C. acuticauda* and *D. veronensis*; Figs. 16A, B) may have inhabited either supratidal and fluvial–terrestrial environments or true marine, shallow reef-like settings. A few years later, Robin et al. (2019) reported twenty-three isopods from the Monte Postale (*Cirolana titanophila* n. sp. and *Dynamenella* sp.) closely associated with two specimens of the electric ray *Titanonarke*. This rare case of isopods fossilised with large marine organisms might be explained either by a syn-vivo interaction (e.g., micropredation) or by a post-mortem scavenging behaviour on the ray carcasses (Robin et al., 2019). Beschin et al. (2016) reported a natural cast of a single carapace of the dromiacean crab *Eotrachynotocarcinus airaghii* from the Pesciara site. Pasini et al. (2019) reviewed the entire decapod record from Bolca, including previously unknown historical specimens together with new material recovered during excavations at Pesciara and Monte Postale conducted between 1999 and 2011. Seven species previously reported in the literature (that include penaeid shrimps, palinurids, portunoids, panopeid crabs, dorippids, and a dromiacean; Figs. 17, 18A, B, F, 19) were considered valid, one form (another portunoid) was left in open nomenclature, and other taxa were considered problematic due to their poor preservation. The re-evaluation of the type series of *Protaxius eocenicus* led to reassigning this species to the new callianassid (ghost shrimps) genus *Bolcacalliax* (Secrétan, 1975a). The new records of decapods reported in Pasini et al. (2019) are represented by a single specimen of a spider crab (Majidae) and two specimens of the frog crab *Lophoranina maxima* (Raninidae). Finally, Pasini et al. (2022) conducted an extensive re-examination of all available specimens (~30) of the Bolca spiny lobsters. This study resulted in the reassignment of most specimens previously attributed to *Justitia desmaresti* (Secrétan, 1975a) to the new genus *Eolinurus* (as *Eolinurus desmaresti* n. comb.; Figs. 17E, 18A), and in the recognition of a new species, *Justitia confusa* (Fig. 17F). A second new species, *Lessinoachela scaligera*, was also identified, but was assigned to an indeterminate family within the Achelata. In addition, two spiny lobster specimens were reported for the first time from the laminites of Monte Postale: a partially preserved *Justitia* sp. and a larval stage of a palinurid (Fig. 18B). The crustacean assemblage of the Pesciara site provides a unique Eocene record in Europe, documenting the co-occurrence of three spiny lobster genera within the same palaeobiotope (Pasini et al., 2022).

Arachnids – The Pesciara has yielded the only scorpion so far recovered from the Bolca Lagerstätten. Owing to its partial embedding within the matrix, the fossil was recognised as a scorpion only after careful preparation

(Giusberti et al., 2014). Kuhl and Lourenço (2017), providing a detailed description of this specimen, assigned it to *Eoeuscorpius ceratoi* (Fig. 20A). This taxon possibly represents the first fossil record of the family Euscorpiidae, which to date comprises only four extant genera. The alleged pseudoscorpion reported in Giusberti et al. (2014) was recently examined and unfortunately proved to be a pseudofossil vaguely resembling an arthropod (R.Z., pers. obs.).

Insects – Insects have been discovered exclusively in the Pesciara. They include, among others, mole crickets, beetles, water bugs, mosquitoes, and dragonflies (Tang, 2002; Giusberti et al., 2014; Figs. 20, 21). Most of them are housed in the Museo Civico di Storia Naturale, Verona whose collection consists of about 70 specimens. Regrettably, this fauna remains inadequately investigated and assessed in its entirety.

Insects from Bolca are known at least since the early 18th century, when Scheuchzer (1709) illustrated an alleged two-winged (!) dragonfly, reinterpreted by Krzeminski and Krzeminska (1990) as a possible female of Tipulidae (crane flies). Volta (1796–1809) also mentioned, among the invertebrates from Bolca, some other insects (probably a single hemipteran and two asilids; Malfatti, 1882) housed in the collection of Vincenzo Bozza. Massalongo (1856) was the first to undertake a systematic study of the Bolca insect fauna, recognising seven species, including two dipterans (*Dipterites angelinii* and *Bibio sereri*), the earwig *Forficula bolcensis*, the dragonfly ?*Cordulia scheuchzeri*, two jewel beetles (Coleoptera), *Ancylocheira deleta* (Fig. 20B) and *Perotis laevigata* (Figs. 20C, D), and the termite *Termes peccanae* (see also Malfatti, 1882 and Omboni, 1886). Fabiani (1915) subsequently questioned the provenance of most of these specimens, suggesting that some of them were collected in the Jurassic site of Solnhofen, southern Germany; the only taxon he considered as coming from Bolca was *Bibio sereri* (a march-fly) and, doubtfully, “*Dipterites*” *angelinii*. The buprestid coleopteran *Perotis laevigata* (Figs. 20C, D), originally illustrated by Massalongo (1856) and also reported by Omboni (1886), was recently traced back by one of us (LG) in the Parolini Collection at the Museo Civico di Bassano del Grappa (Vicenza) and bears an historical label reporting “Monte Bolca” (=Pesciara). The preservation of the insect and the lithology of the matrix may be consistent with those of the Pesciara site (Fig. 20C). After many years since the last publication on the insects of Bolca, Secrétan (1975b) and Capra (1977) reported a complete specimen of mole cricket (*Gryllotalpa tridactylina*), which was recently tentatively assigned to the genus *Pterotriamescaptor* (Gorochoy and Labandeira, 2012; Fig. 21B).

Krzeminski and Krzeminska (1990) studied the Tipulomorpha (four Tipulidae and three Limoniidae) from



the Pesciara and created a new species of Limoniidae, *Gnophomyia gentilini*. These authors also examined the entire insect collection of Bolca housed in the Museo Civico di Storia Naturale, Verona and subdivided the material into eight orders (?Thysanura, Odonata, Diptera, Trichoptera, Coleoptera, Orthoptera, Heteroptera, and Hymenoptera; Figs. 20, 21), revealing a sharp dominance of Diptera (Fig. 20E) in the assemblage. To date, the paper of [Krzeminski and Krzeminska \(1990\)](#) represents the only modern study that attempted a comprehensive assessment of the composition of the Bolca entomofauna.

[Andersen et al. \(1994\)](#) described one of the most remarkable insects recovered to date from the Pesciara site, a wingless female of the gerrid *Halobates ruffoi* (sea skater; Fig. 21C), representing the oldest known fossil record of the genus. Extant species of *Halobates* are among the most highly specialised water striders and inhabit tropical and subtropical oceans worldwide, where they are well adapted to fully oceanic conditions ([Cheng et al.,](#)

[2012](#)). The presence of *Halobates* in the Ypresian deposits of the Pesciara site suggests that sea-surface temperatures in this sector of the Tethys were not lower than 20°C, corresponding to the lower thermal tolerance limit of extant *Halobates* species ([Andersen et al., 1994](#); [Cheng et al., 2012](#)).

The order Odonata is well represented in the entomofauna of the Pesciara site (Figs. 20G, 21A, D) and consists of both immature stages (larvae) and adults, mostly discovered since the second half of 20th century. [Gentilini \(2002\)](#) described new genera and species of dragonflies (*Bolcathemis nervosa* and *Bolcacordulia paradoxa*; Fig. 20G) and damselflies (*Bolcathore colorata*; Figs. 21A, D). Some of them exhibit traces of their original colour pattern on the wings. The only dragonfly taxon from Bolca that had been described before [Gentilini \(2002\)](#), the problematic ?*Cordulia scheuchzeri* [Massalongo \(1856\)](#), is a poorly preserved imprint and could therefore be considered as nomen dubium (L.G., pers. obs.).

Table 3 - A synoptic list of Eocene invertebrates of the fish-bearing laminites of the Bolca Lagerstätten.

MP = Monte Postale, P = Pesciara.

Phylum Cnidaria		
Class Scyphozoa		
	Undetermined medusae	P
Order Rhizostomeae		
Family Rhizostomatidae		
	<i>Simplicibrachia bolcensis</i> Broglio Loriga & Sala Manservigi, 1973	P
Order Semaestomeae		
	Semaestome aff. <i>Aurelia</i> Lamarck, 1816	P
Phylum Brachiopoda		
Class Rhynchonellata		
Order Terebratulida		
Family Terebratulidae		
	" <i>Terebratula</i> " <i>fumanensis</i> Davidson, 1870	P
Phylum Mollusca		
Class Bivalvia		
Order Mytilida		
Family Mytilidae		
	Mytilidae indet.	P
	<i>Modiolus postalensis</i> Oppenheim, 1896	P
Order Limida		
Family Limidae		
	<i>Ctenoides papillifera</i> (Bayan, 1870)	P
Order Pectinida		
Family Anomiidae		
	<i>Anomia</i> cf. <i>primaeva</i> Deshayes, 1858	P
Order Ostreida		
Family Ostreidae		
	<i>Ostrea</i> sp.	P



Order Carditida	
Family Carditidae	
<i>Paraglans postalensis</i> (Vinassa de Regny, 1896)	MP
Order Lucinida	
Family Lucinidae	
<i>Monitilora elegans</i> (Defrance, 1823)	P
Order Venerida	
Family Veneridae	
<i>Meroena polita</i> (Lamarck, 1806)	P
Class Gastropoda	
Subclass Caenogastropoda	
Caenogastropoda incertae sedis	
Superfamily Campaniloidea	
Family Ampullinidae	
<i>Pseudamaura cf. circumfossa</i> (Rauff, 1884)	P
Superfamily Cerithioidea	
Family Diastomatidae	
<i>Dialopsis semistriata</i> (Deshayes, 1832)	P
Order Littorinimorpha	
Superfamily Vanikoroidea	
Family Eulimidae	
<i>Aclis? aenigmaticus</i> Merle, 2014	P
Class Cephalopoda	
Subclass Nautiloidea	
Order Nautilida	
Family Aturiidae	
<i>Aturia ziczac</i> (Sowerby, 1812)	MP
Subclass Coleoidea	
Order Octopoda	
Family Octopodidae	
<i>Bolcaoctopus pesciaraensis</i> Mironenko et al., 2024	P
Order Spirulida	
Family Spirulirostridae	
<i>Spirulirostra georgii</i> Fornasiero & Vicariotto, 1997	P
Phylum Annelida	
Class Polychaeta	
Order Eunicida	
Family Eunicidae	
<i>Eunicites gazolae</i> (Massalongo, 1855)	B
<i>Eunicites affinis</i> (Massalongo, 1855)	B
<i>Eunicites pinnae</i> Alessandrello, 1990	B
<i>Eunicites</i> sp. indet.	B
Class Hirudinea	
Hirudinea indet.	B
Order Phyllodocida	
Family Hesionidae	
<i>Siphonostomites hesionoides</i> (Massalongo, 1855)	B
Phylum Arthropoda	
Subphylum Crustacea	
Class Malacostraca	



Order Isopoda	
Family Cirolanidae	
<i>Cirolana acuticauda</i> (Secrétan, 1975)	P
<i>Cirolana titanophila</i> Robin et al., 2018	MP
Family Sphaeromatidae	
<i>Dynamenella veronensis</i> (Secrétan, 1975)	P, MP
<i>Sphaeroma</i> sp.	B
Order Stomatopoda	
Family Lysiosquillidae	
<i>Lysiosquilla antiqua</i> (Munster, 1842)	P, MP
Family Pseudosquillidae	
<i>Pseudosquilla lessinea</i> De Angeli & Garassino, 2008	MP
Order Decapoda	
Family Callianassidae	
<i>Bolcacalliax eocenica</i> (Secrétan, 1975)	P
Family Penaeidae	
<i>Penaeus bolcensis</i> Secrétan, 1975	P
Family Palinuridae	
<i>Eolinurus desmaresti</i> (Secrétan 1975)	P
<i>Justitia confusa</i> Pasini et al., 2022	P
<i>Justitia</i> sp.	MP
Family indet. within Achelata	
<i>Lessinoachela scaligera</i> Pasini et al., 2022	P
“Family” Scyllaridae	
? <i>Parsacus cristatus</i> (Forster, 1984)	MP
<i>Scyllarides bolcensis</i> De Angeli & Garassino, 2008	MP
Infraorder Brachyura	
Family Dorippidae	
<i>Archaeocypoda veronensis</i> Secrétan, 1975	P
Dromiacea incertae sedis	
<i>Eotrachynotocarcinus airaghii</i> Beschin et al., 2007	P
Family Portunidae	
<i>Enoplonotus armatus</i> Milne-Edwards, 1860	P
<i>Portunus</i> sp.	P
Family Panopeidae	
<i>Lophopanopeus bolcensis</i> (Secrétan, 1975)	P
Family Raninidae	
<i>Lophoranina maxima</i> Beschin et al., 2004	P, MP
Family Majidae	
Majidae indet.	MP
Brachyura incertae sedis	
? <i>Eriphia</i> sp.	P
? <i>Macropipus ovalipes</i> Secrétan, 1975a	P
Subphylum Chelicerata	
Class Arachnida	
Order Scorpiones	
?Family Euscorpiidae	
<i>Eeuscorpius ceratoi</i> Kühl & Lourenço, 2017	P
Subphylum Hexapoda	
Class Insecta	



Order Coleoptera	
Coleoptera indet.	P
Family Buprestidae	
<i>Buprestis (Ancylochira) deleta</i> Heer, 1847	P
<i>Perotis laevigata</i> Massalongo, 1856	P
Undetermined Buprestidae	P
Order Diptera	
Family Tipulidae	
Tipulidae indet.	P
Family Limoniidae	
Limoniidae indet.	P
<i>Gonomyia</i> sp.	P
<i>Gnophomyia gentilini</i> Krzeminski & Krzeminska, 1990	P
Family Rhagionidae	
<i>Dipterites angelinii</i> Massalongo, 1856	P
Order Heteroptera	
Heteroptera indet.	P
Order Hymenoptera	
Hymenoptera indet.	P
Order Odonata	
Suborder Zygoptera	
Family Bolcathoridae	
<i>Bolcathore colorata</i> Gentilini, 2002	P
Suborder Anisoptera	
Family Bolcathemidae	
<i>Bolcathemis nervosa</i> Gentilini, 2002	P
Family Bolcacorduliidae	
<i>Bolcacordulia paradoxa</i> Gentilini, 2002	P
Order Orthoptera	
Orthoptera indet.	P
Family Gryllotalpidae	
<i>Pterotriamescaptor tridactylina</i> (Secrétan, 1975)	P
Order Rhynchota	
Family Gerridae	
<i>Halobates ruffoi</i> Andersen et al., 1994	P
Order Thysanura	
?Thysanura indet.	P
Order Trichoptera	
Trichoptera indet.	P
Phylum Ectoprocta	
Class Gymnolaemata	
Order Cheilostomata	
Family Schizoporellidae	
Schizoporellidae indet.	P



Fig. 12 - Jellyfish from the Bolca Lagerstätten. A) *Simplicibrachia bolcensis*, holotype MCSNV m.B.2, scale bar 50 mm; B) Probable semaeostome similar to *Aurelia*, MCSNV m.B.11-12, scale bar 50 mm; C) Possible ephyra (larval stage) of Scyphozoa, MCSNV m.B.6, scale bar 20 mm.

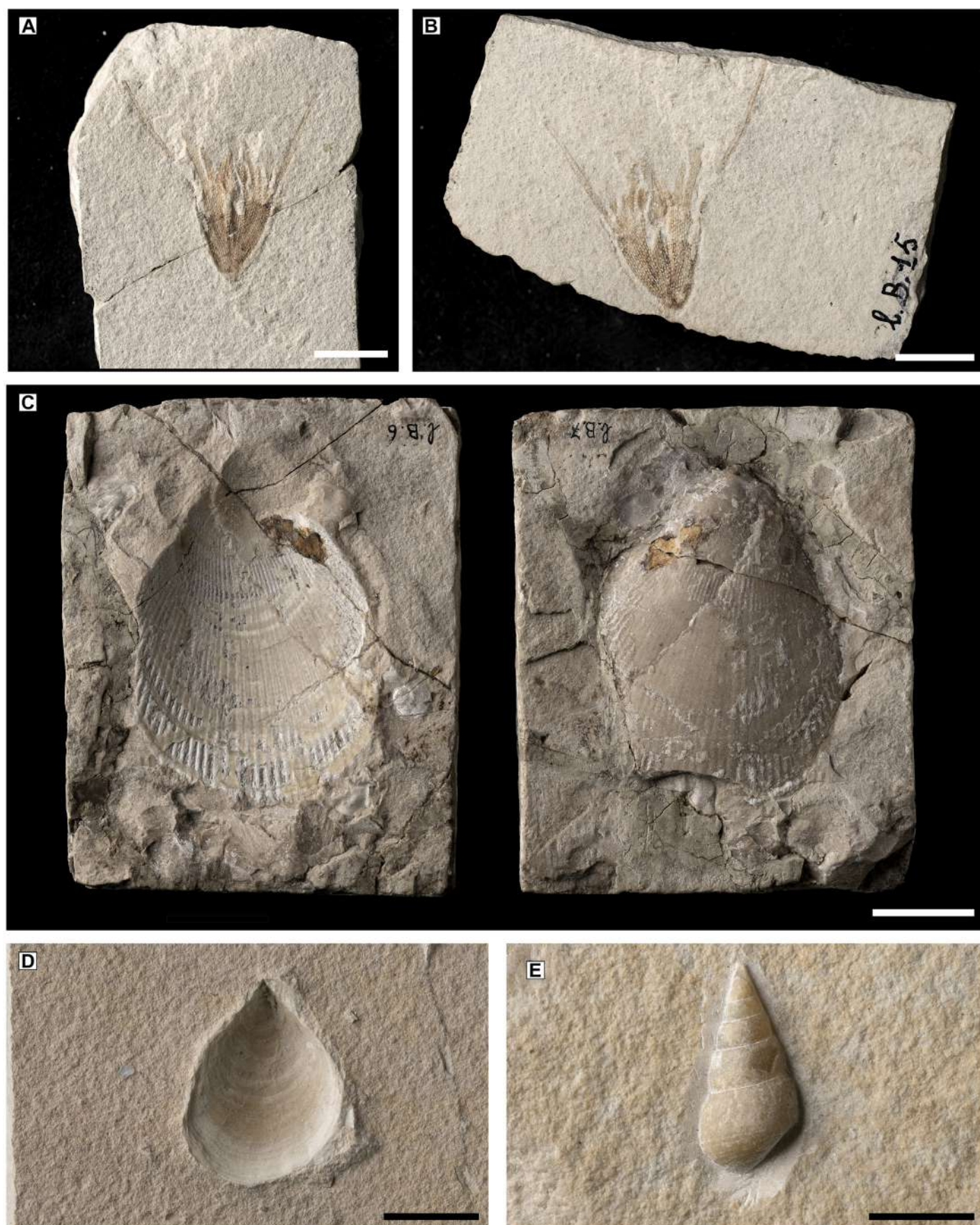


Fig. 13 - Lophophorates from the Bolca Lagerstätten. A) Schizoporellidae bryozoan, MCSNV IB14, scale bar 10 mm; B) Schizoporellidae bryozoan, MCSNV IB15, counterpart of MCSNV IB14, scale bar 10 mm. Mollusca: C) *Ctenoides papillifera* Bayan 1870, external and internal mould with traces of the original shell, MCSNV I.B.6 and I.B.7, scale bar 20 mm; D) Mytilidae indet., MCSNV IG 145139, scale bar 5 mm; E) *Dialopsis semistriata*, MCSNV I.B.9, scale bar 5 mm.

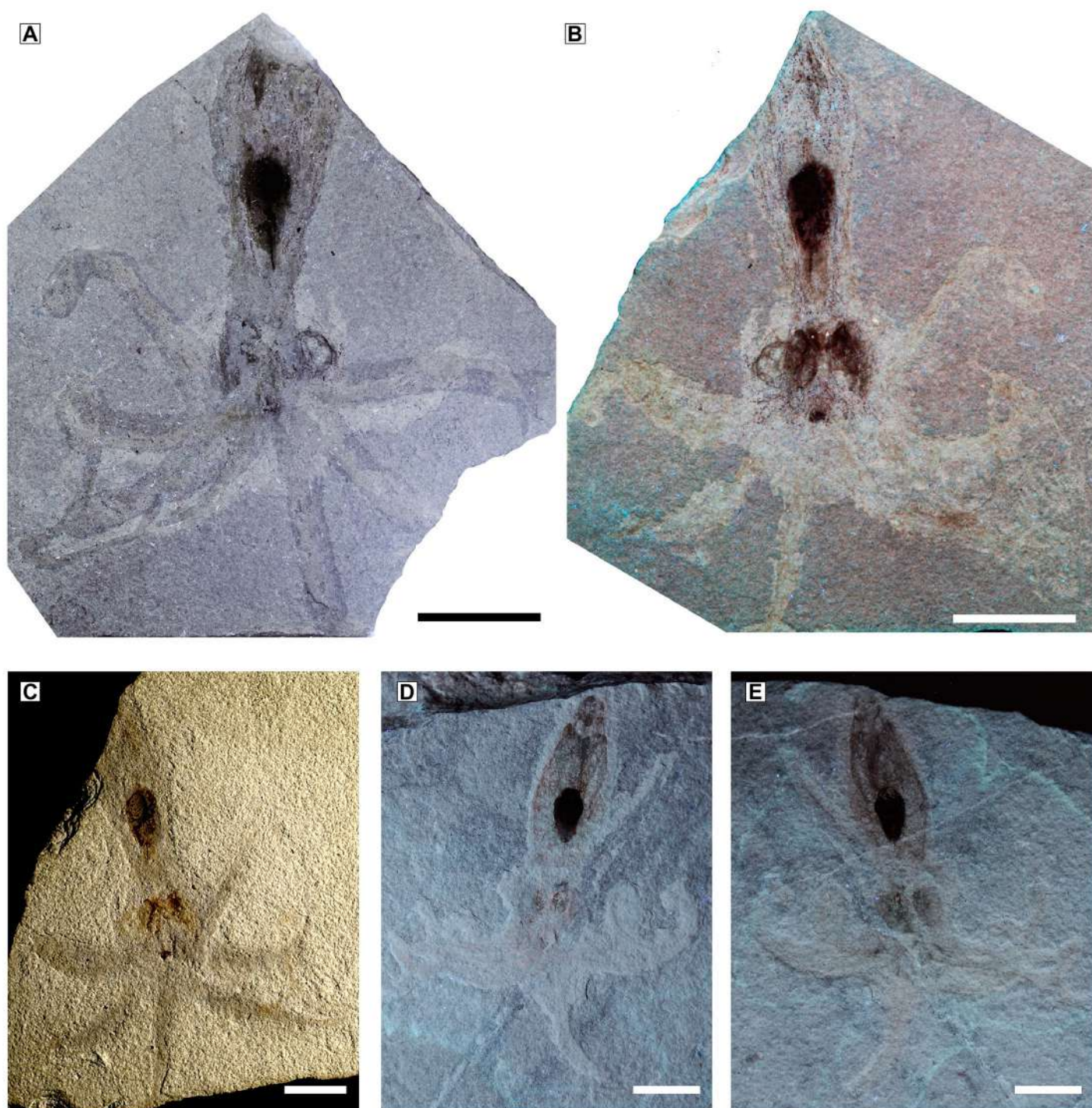


Fig. 14 - Cephalopods from the Bolca Lagerstätten. *Bolcaoctopus pesciaraensis*: A) holotype. MFB IG23682, under UV light; B) counterpart of MFB IG23682, MGP-PD 31434, under UV light; C) MGP-PD 31434 under natural light; D) and E) the paratype MCSNV IB13 under UV light and its counterpart, MCSNV IB12, under UV light. Scale bars of A, B and C 20 mm, scale bars of D and E 10 mm.

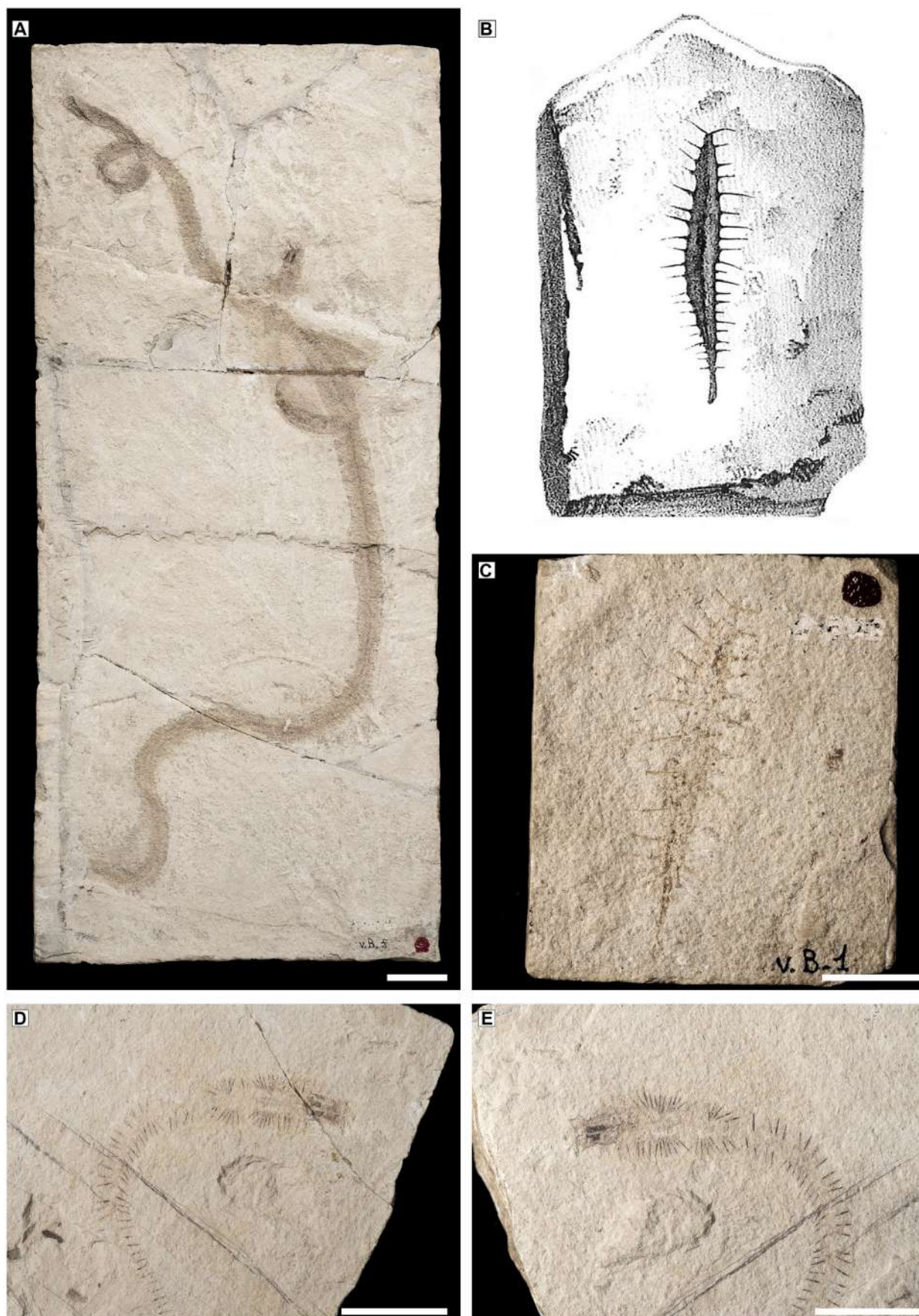


Fig. 15 - Polychaete worms from the Bolca Lagerstätten. A) *Eunicites gazolae*, holotype MCSNV v.B.5, scale bar equals 50 mm; B) the holotype of *Siphonostomites hesionoides* [excerpt from Massalongo (1855, Plate II)]; C) *Siphonostomites hesionoides*, holotype MCSNV v.B.1, scale bar 10 mm; D) *Eunicites gazolae*, MCSNV V.B.19, scale bar equals 20 mm; E) *Eunicites gazolae*, MCSNV V.B.19 (counterpart of MCSNV V.B.19), scale bar 20 mm.



Fig. 16 - Isopod crustaceans from the Bolca Lagerstätten. A) *Cirolana acuticauda*, MCSNV n. 13, holotype, scale bar 10 mm; B) *Dynamenella veronensis*, holotype MCSNV Cr.14, scale bar 2 mm; C) Undetermined isopod from Monte Postale MGP-PD 31433, scale bar 4 mm. Stomatopoda: D) *Lysiosquilla antiqua*, MCSNV B50, scale bar 20 mm; E) *Pseudosquilla lessinea*, holotype MFB IGVR 67497, scale bar 10 mm.

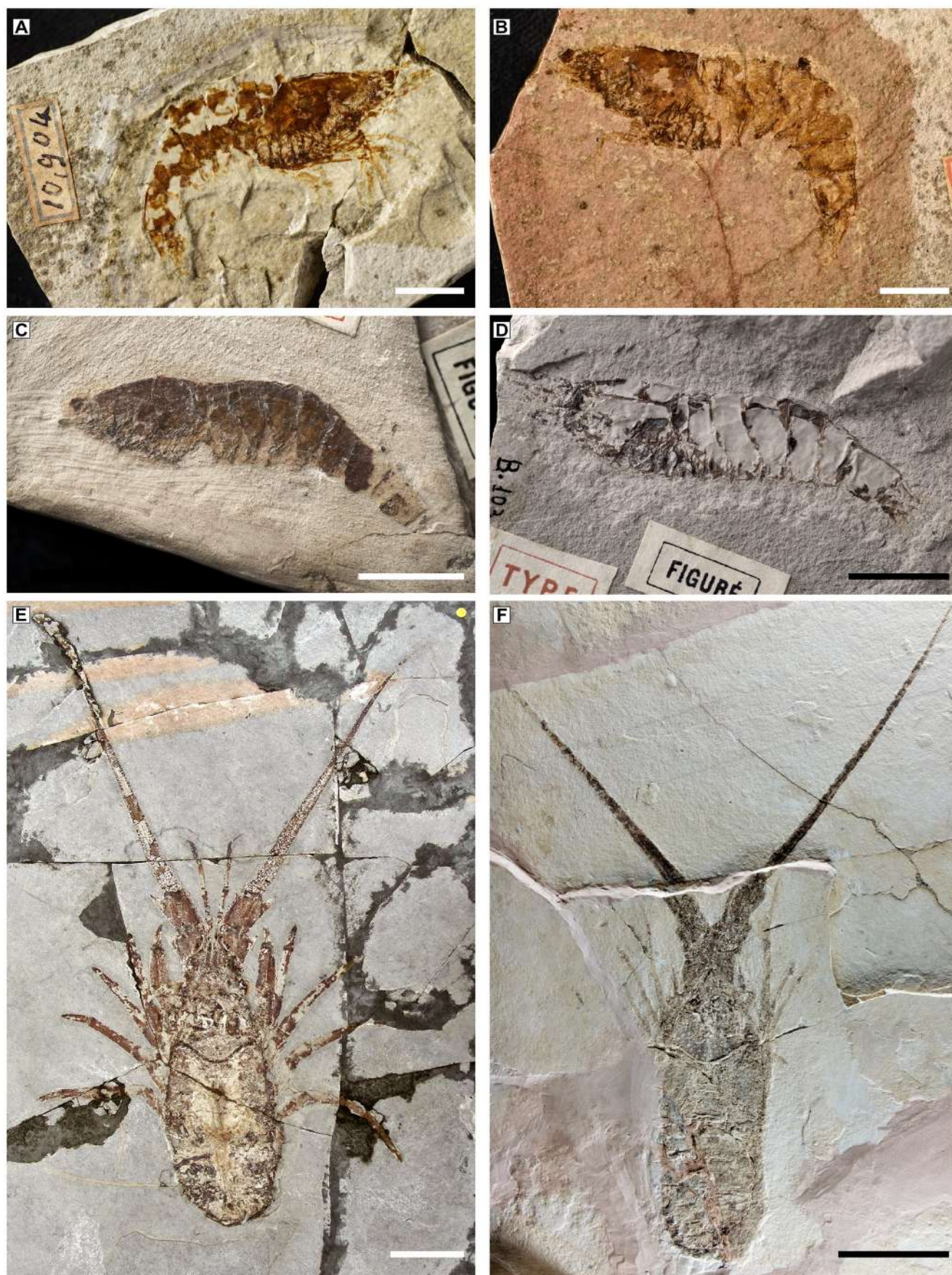


Fig. 17 - Penaeid crustaceans and spiny lobsters from the Bolca Lagerstätten. A) *Penaeus bolcensis*, MGP-PD 10904; B) *Penaeus bolcensis*, MGP-PD 6797Z; C) the problematic penaeid “*Penaeus obtusus*”, holotype MCSNV 106; D) holotype of the problematic “*Pseudobumbur nummuliticus*”, MCSNV 103; E) lectotype of the spiny lobster *Eolinurus desmaresti*, MCSNV 23; F) holotype of the spiny lobster *Justitia confusa*, MSNVE 6298. Scale bars of A-D 10 mm, scale bars of E and F 50 mm.



Fig. 18 - Spiny lobsters from the Bolca Lagerstätten. A) *Eolinurus desmaresti*, MGP-PD 7448 and 7449 (part and counterpart) preserved in lateral view. Scale bar 50 mm; B) “puerulus” larval stage of palinurid, MCSNV 43.2020 (alcohol-impregnated). Slipper lobsters: C) *Scyllarides bolcensis*, holotype MCSNV 69353; D) *Parsacus cristatus*, holotype, M.BA 88; E) *Parsacus cristatus*, MGP-PDZ 10033. Brachyura: F) *Archaeocypoda veronensis*, holotype, MSNM i4563. Scale bars of B-E 10 mm, scale bar of F 20 mm.

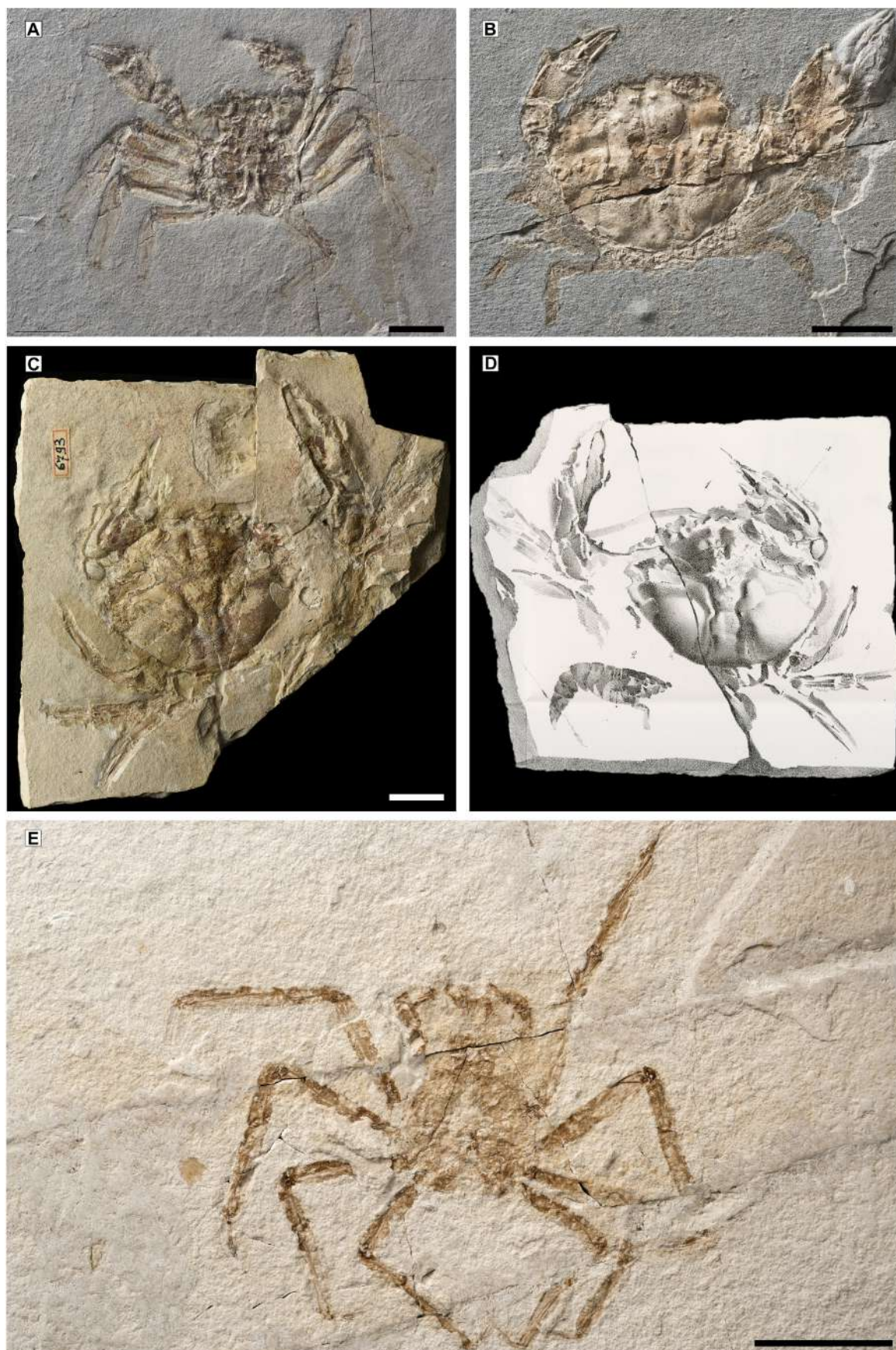


Fig. 19 - Brachyuran crustaceans from the Bolca Lagerstätten. A) *Archaeocypoda veronensis*, MCSNV 97; B) *Lophopanopeus bolcensis* CMC 4; C) *Lophopanopeus bolcensis*, lectotype, MGP-PD 6793Z; D) Unpublished plate of “Compendium faunae et florae fossilis bolcensis” of Abramo Massalongo illustrating the specimen MGP-PD 6793Z of *Lophopanopeus bolcensis*; E) Majidae indet. MFB IGVR 67295. Scale bars 20 mm.

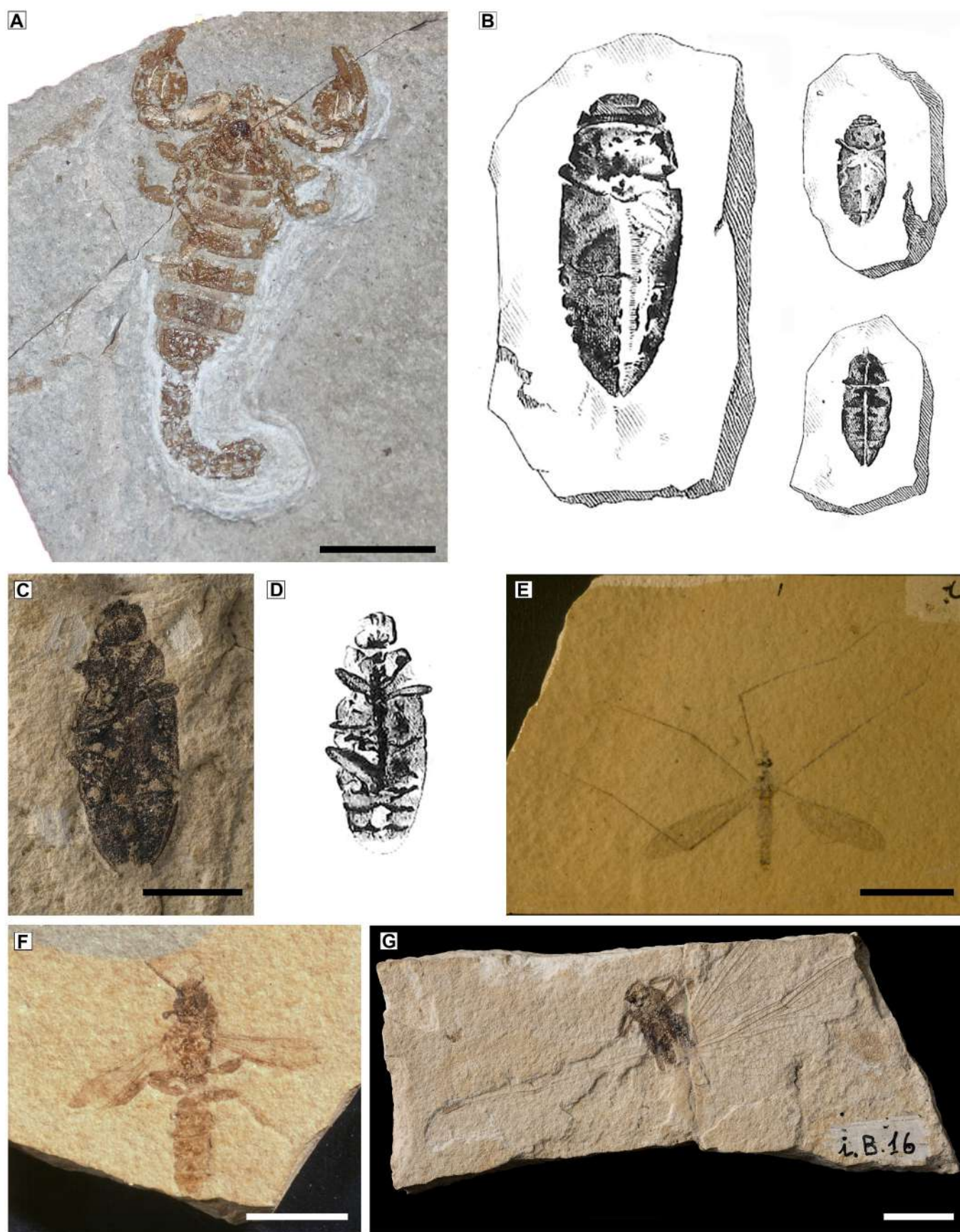


Fig. 20 - Arachnids from the Bolca Lagerstätten. A) *Eoescorpius ceratoi*, holotype, CMC 1. Insecta, Coleoptera: B) specimens of the coleopter *Buprestis* (*Ancylocheira*) *deleta* figured by Massalongo (1856, t. 1, Fig. 1-3); C) *Perotis laevigata*, MCBG 4222 (Parolini Collection); D) specimen MCBG 4222 originally figured by Massalongo (1856, t. 1, Fig. 4). Diptera: E) Undetermined dipteran, MCSNV i.B.8. Hymenoptera: F) Hymenopteran MCSNV i.c.2NS. Odonata: G) Holotype MCSNV i.B. 16 of the dragonfly *Bolcathemis nervosa*. Scale bars of A, C and E-G 10 mm.

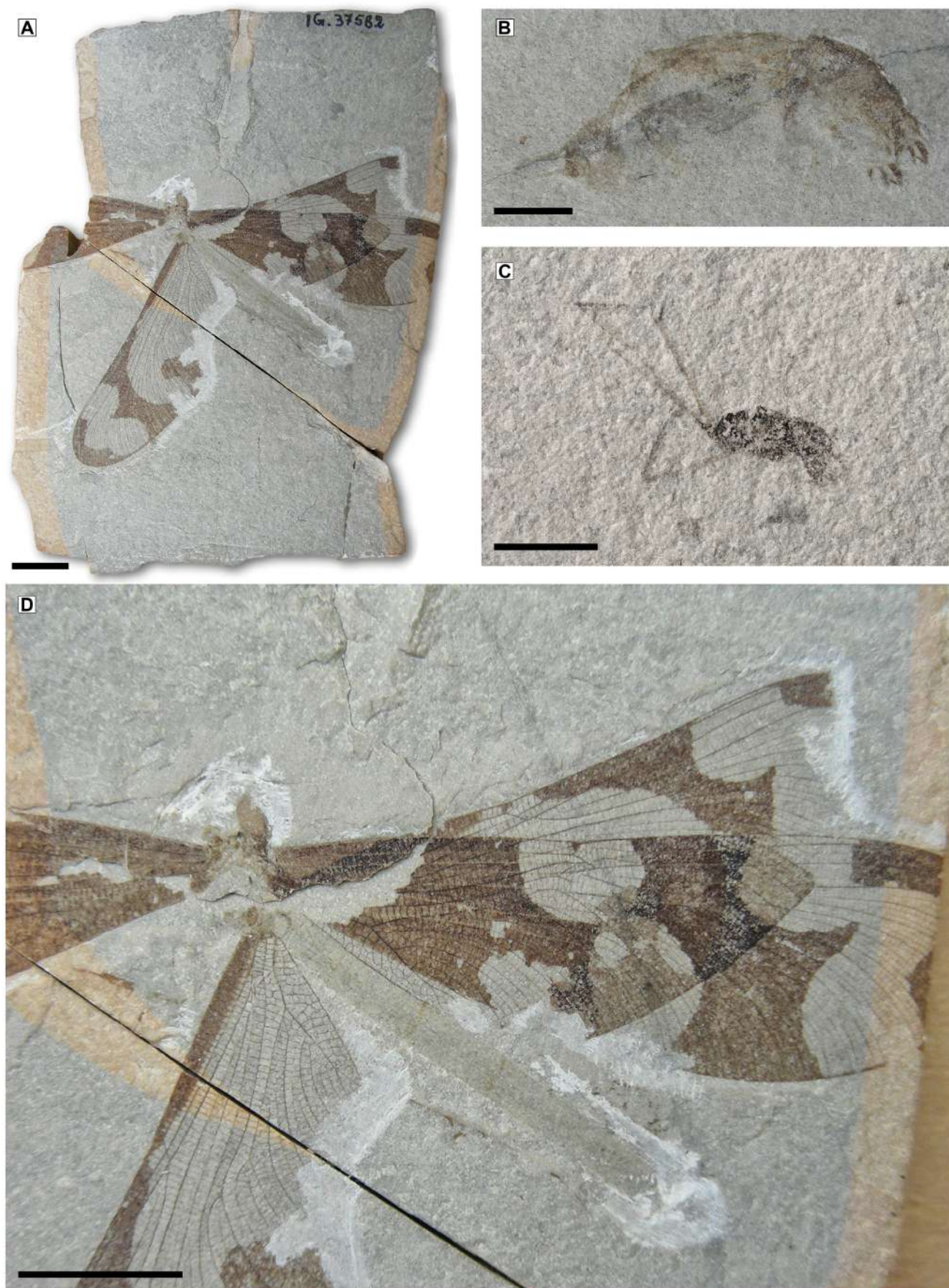


Fig. 21 - Insects from the Bolca Lagerstätten. A) Odonata: the damselfly *Bolcathore colorata*, holotype, MCSNV IG. 37582, scale bar 10 mm; B) Orthoptera: the mole cricket *Pterotriamescaptor tridactylina*, holotype, MCSNV 24517, scale bar 2 cm; C) Gerridae: the sea skater *Halobates ruffoi*, female, holotype, MCSNV I.G. 24527, scale bar 5 mm; D) Odonata: detail of the holotype of the damselfly *Bolcathore colorata*, scale bar 10 mm.



THE INVERTEBRATES OF THE MONTE POSTALE ALVEOLINA BEDS AND BIOCONSTRUCTIONS

Molluscs and associated fauna of the Alveolina beds – The invertebrates of the Monte Postale site (MP) form a coherent group of fossils, distinct from other assemblages of the Bolca area on both taphonomic and paleoecologic grounds. Since available evidence concurs to show that it can no longer be studied on outcrop, this can be defined as a historical fossil assemblage that can be approached only through museum collections.

As far back as 1740, fossil invertebrate remains were described and figured by Jean-François Séguier, a renowned scholar from Nîmes (Gaudant, 2004), in the unpublished manuscript *Les Pétrifications du Véronois*: “A mile from the hillside of the [Bolca] fishes, there is a high mountain, more than 120 fathoms above the level of the stream that flows in the small valley of Cherpa. It is called Postaglie [...]. Almost at its summit, on the side facing the Vicentine, there is a large, detached block of rock in which I found a great number of beautiful petrifications embedded in this very hard stone, and from which they can only be extracted with great care and effort.” From the same source we learn that by that time the site had been already overexploited (“the volume of this rock was almost three times what it is today, but by dint of extracting shells from it and breaking it into pieces, it has been reduced to a third, and the mine of these petrifications appears almost exhausted”; Séguier 1740, in Gaudant, 2005, p. 188-189; see also Pacaud, 2005). Extractions continued to the early days of stratigraphical geology, when the demand for fossil molluscs as a means to correlate Eocene formations across Europe brought public institutions to acquire from the local fossil collector Giovanni Meneguzzo systematic collections representative of the Monte Postale fauna (Bayan, 1870a, 1870b; Mayer, 1870; De Gregorio, 1894; Vinassa de Regny, 1896, 1897; Oppenheim, 1896). No significant acquisitions are recorded during most of the 20th century.

The Monte Postale macrofauna is associated with a hard, massive limestone, milky in colour and at places rich in alveolinids (Fig. 22). The assemblage and the associated matrix are distinctive, and the collections are easily recognised among Eocene analogues from the Veneto region. Among the bivalves (species richness, $S = 20$), the assemblage is dominated in number of species and individuals by the large lucinids *Pseudomiltha gigantea*, *P. escheri* (Fig. 23), *Fimbria major* and *F. lamellosa*, followed in abundance by the cardiid *Granocardium gratum*. Among the gastropods ($S = 50$), the assemblage is characterised by large and high-spined forms like *Campanile gomphoceras*, *Campanile vicetinum*, *Rhinoclavis chaperi* and *Bellatara janus*, the ampullinid *Pachycrommium circumfossa*, the

stromboidean *Semiterebellum postalensis* and *Seraphs sopitus*, and the naticid *Cepatia cepacea* (Figs. 23, Tab. 4). 18th century specimens of *Campanile giganteum*, *Pycnodonte gigantea* and a very large cardiid bivalve catalogued from “Monte Bolca”, can be reasonably attributed to the Monte Postale assemblage (Fig. 24). Cephalopods are represented by at least three genera (*Cimonia*, *Hercoglossa*, and *Aturia*), the corals are well-diversified ($S = 26$), with both colonial and solitary forms, and the echinoderms are relevant too ($S = 5$). Crustaceans are represented only by three taxa (Malaroda, 1954).

The trophic nucleus of the molluscan component, by far dominating the Monte Postale assemblage, is formed by the herbivores, whether measured in abundance (75%) or species richness (47). This is followed by carnivore gastropods (9%; 16% of the species), chemosymbiotic bivalves (6%; 9% of the species), and sponge-eating gastropods (4%; 9% of the species). If we consider that also the chemosymbiotic bivalves probably derived their food from the anaerobic decomposition of vegetal matter, then we can conclude that the Monte Postale assemblage reflected a vegetated bottom in the euphotic zone, not particularly favourable to the filter feeders, thence probably oligotrophic. Epifaunal forms dominate in both abundance (89%) and species richness (76%), consistent with a bioclastic seafloor with variable textures and under low sedimentation rates. The non-molluscan component in MP museum collections — characterised by a complex assemblage of photosymbiotic organisms (corals, alveolinids) — indicates a subtropical to tropical, shallow water environment (inner carbonate ramp).

The stratigraphic position on top (“almost at its summit”: Séguier, 1740, in Gaudant, 2005) of the succession places the Monte Postale assemblage either in coincidence with, or adjacent to, the coralgal rim facies documented in Vescogni et al. (2016). The Monte Postale invertebrates dwelled in a low-energy, open-marine environments, sustaining a flourishing mobile and structured epifaunal community. Neither the coralgal boundstone and polygenic bindstone facies, nor the adjacent *Alveolina*-limestone of the coralgal-rim facies, recurring at different points along the succession (Vescogni et al., 2016), are presently associated in the outcrop with large invertebrates. The Monte Postale assemblage, with its high-density bioclastic fabric and the presence of nektonic shells of pelagic organisms, suggests an important transgressive episode occurring on top of the Monte Postale succession, and before the deposition of the Pesciara laminites (see whole succession in Papazzoni et al. 2017).

The fauna of the bioconstructions – In their contribution to the knowledge of the geology of the territory of Bolca, Barbieri and Medizza (1969) documented the frequent occurrence of small Ypresian coralgal domes, noting that



these structures “are characteristic, occurring within a framework formed by calcareous algae, and include recognisable nummulites, corals, gastropods, and brachyurans”. These bioconstructions, detected in various localities around Bolca (Monte Postale, Zovo, Rama di Bolca, etc.), harbor an exceptional crustacean diversity; [Beschinn et al. \(2016\)](#) examined 777 specimens—most probably ecdyses—recording 119 taxa, many of which previously undescribed, across 46 families of Isopoda, Anomura, and Brachyura. A portion of this remarkable assemblage comes from Monte Postale whose crustacean fauna comprises 14 species, including Anomura (Galatheididae and Porcellanidae) and Brachyura (Dromiidae, Dynomenidae, Dromiacea *incertae sedis*, Parthenopidae, Carpiliidae, Pilumnidae, Domeciidae, Panopeidae, Xanthidae, and Xanthoidea *incertae sedis*; Fig. 25). [Beschinn et al. \(2016\)](#) reported also corals, gastropods, and bivalves associated

with this fauna. [Vescogni et al. \(2016\)](#) carried out the first detailed investigation of the reef-building bioconstructions of the Monte Postale, evidencing that their composition reveals the typical features of the Paleocene assemblages, including a moderate diversity of corals (up to 16 genera) with the dominance of massive colonies of *Actinacis*, a strong contribution of the solenoporacean alga *Parachaetetes* and the occurrence of ramose and phaceloid growth forms. Such assemblage, also composed of peyssonneliaceans and corallinean red algae and encrusting foraminifera, formed small reef structures characterising a coral rim within shallow-water and high hydrodynamic conditions that delimited a lagoon and influenced the exchange with the open sea. The coral assemblage of the Monte Postale includes a new genus of the family Euphyllidae, *Nancygyra*, a scleractinian that formed exceptional coenosteum-dominated colonies ([Bosellini et al., 2020](#)).

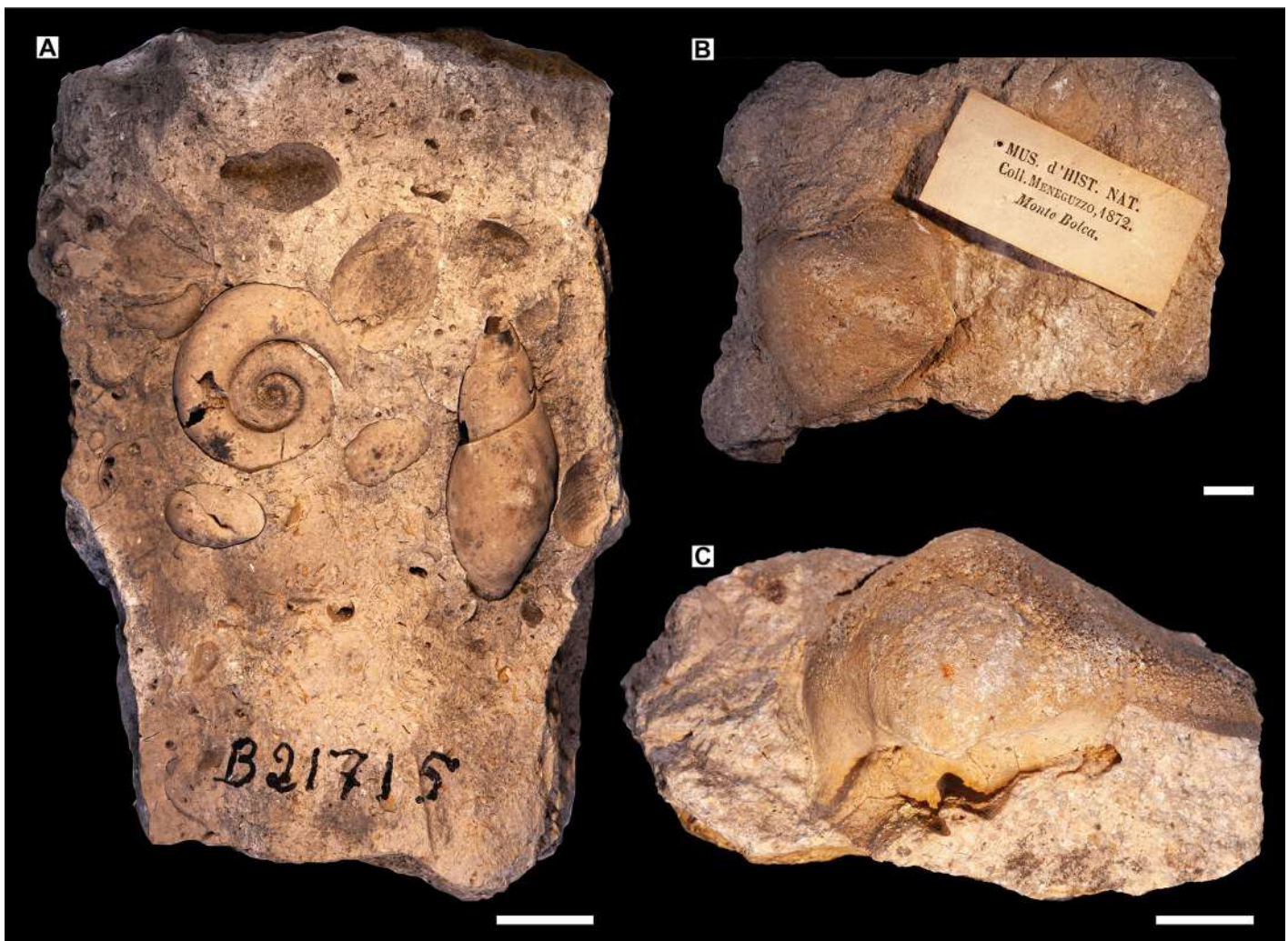


Fig. 22 - A) Loosely packed, poorly-sorted bioclastic fabric of the Monte Postale fossil assemblage (MNHN.F.B21715a); B) Label attesting the acquisition of the Monte Postale (referred to as “Monte Bolca”) collection now at the Muséum national d’Histoire naturelle (MNHN) in Paris from Giovanni Meneguzzo in 1872; C) disarticulated bivalve from the Monte Postale site dispersed in an *Alveolina* limestone (MNHN). Scale bars 10 mm.

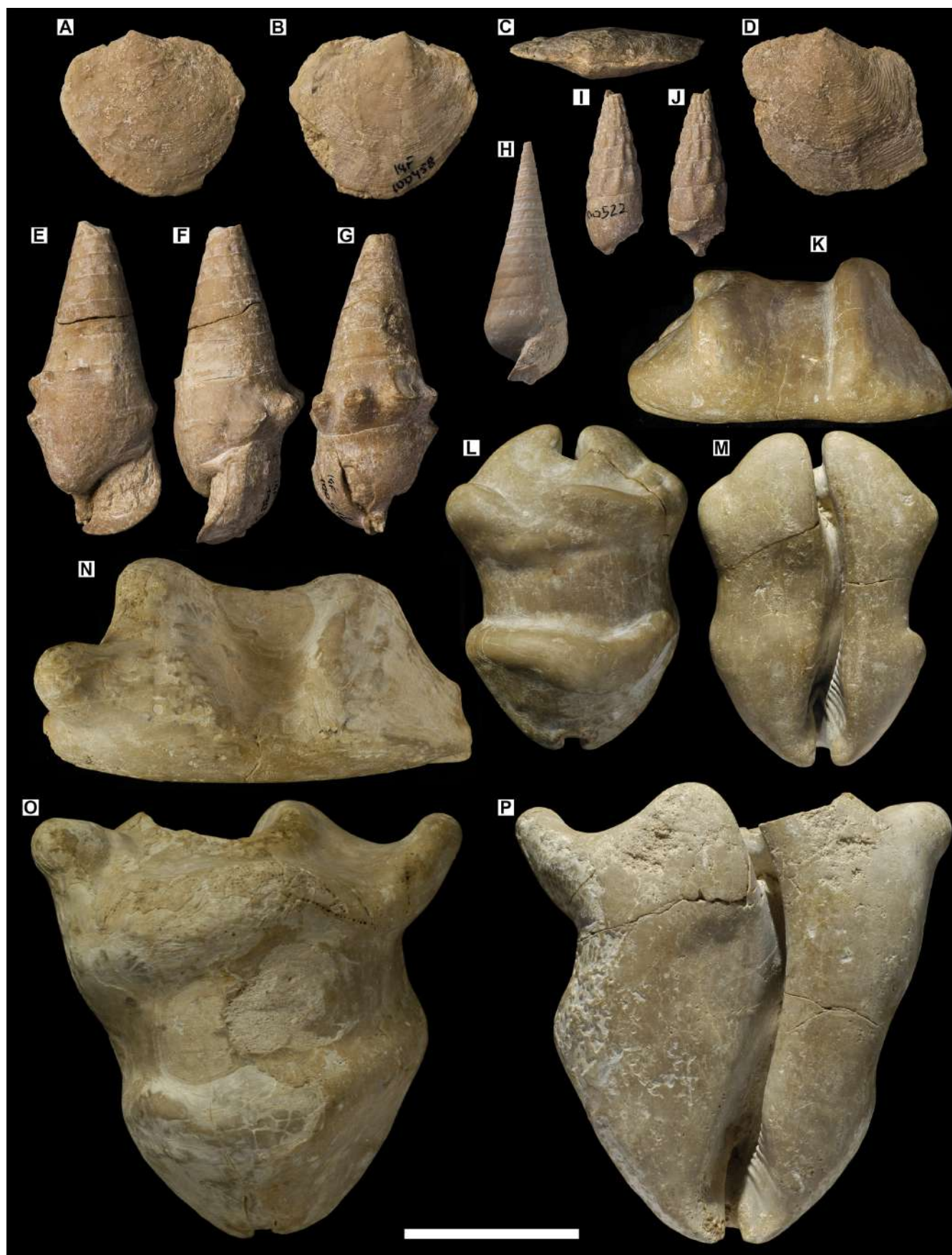


Fig. 23 - Molluscs from the Monte Postale Alveolina beds. A-D) *Pseudomiltha escheri*, A-C: IGF 100458A, left, right and dorsal view; D: IGF 100458B, left view; E-G) *Bellatara janus*, IGF 100516A, oral, lateral and dorsal view; H) *Campanile gomphoceras*, MNHN.F.A94698, lateral view; I-J) *Rhinoclavis chaperi*, IGF 100522A, oral and dorsal view; K-P) *Vicetia hantkeni*, K-M: MGP-PD 22083, lateral, dorsal and oral view; N-P: MGP-PD 32403, lateral, dorsal and oral view. Scale bar 100 mm.

**Table 4 - A synoptic list of Eocene invertebrates of the Monte Postale *Alveolina* beds and bioconstructions.**

List of invertebrate taxa from <i>Alveolina</i> beds of Monte Postale	
Phylum Cnidaria	
Class Anthozoa	
Subclass Zoantharia	
Order Scleractinia	
Family Acroporidae	
	<i>Astraeopora panicea</i> Blainville, 1854
	<i>Dendracis gervillei</i> (Defrance, 1823)
	<i>Dendracis seriata</i> Reuss, 1867
	<i>Dendracis subnodosa</i> De Gregorio, 1894
Family Agathiphyllidae	
	<i>Pattalophyllia cyclolitoides</i> (Michelin, 1846)
	<i>Pattalophyllia subinflata</i> (Catullo, 1857)
Family Caryophyllidae	
	<i>Trochocyathus taramellii</i> d'Achiardi, 1875
Family Meandrinidae	
	<i>Pachygyra savii</i> d'Achiardi, 1866
Family Montastraeidae	
	<i>Montastraea meneghinii</i> (Reuss, 1869)
Family Montlivaltiidae	
	<i>Trochosmilia acutimargo</i> Reuss, 1874
	<i>Trochosmilia cocchii</i> d'Achiardi, 1894
	<i>Trochosmilia incurva</i> d'Achiardi, 1866
Family Placosmiliidae	
	<i>Placosmilia multisinuosa</i> (Michelin, 1846)
	<i>Placosmilia</i> cf. <i>strangulata</i> d'Achiardi, 1875
Family Pocilloporidae	
	<i>Stylophora conferta</i> Reuss, 1868
Family Poritidae	
	<i>Goniopora elegans</i> (Leymerie, 1846)
	<i>Goniopora nummulitica</i> (Reuss, 1864)
Subclass Octocorallia	
Order Coenothecalia	
Family Helioporidae	
	<i>Parapolytremacis bellardii</i> (Haime, 1852)
Class Hydrozoa	
Order Anthoathecata	
Family Milleporidae	
	<i>Millepora cylindrica</i> Reuss, 1868
*The list of corals presented here is derived from Malaroda (1954). This assemblage of invertebrates from the mollusc-bearing <i>Alveolina</i> beds of Monte Postale has not been revised since that study. In the present work, the nomenclature has been updated where possible. Some uncertain or problematic taxa originally reported by Malaroda (1954) but not included herein are: <i>Isastraea</i> sp., <i>Rhabdophyllia solenastropsis</i> De Gregorio, 1894, <i>Turbinolia postalicola</i> De Gregorio, 1894, and <i>Stylocoenia zitteli</i> Pratz, 1883.	
Phylum Brachiopoda	
Class Rhynchonellata	
Order Terebratulida	
Family Terebratulidae	
	<i>Gryphus kickxii</i> (Galeotti, 1837)
Phylum Arthropoda	
Subphylum Crustacea	
Class Malacostraca	
Order Decapoda	
Infraorder Brachyura	
Family Dynomenidae	
	? <i>Cyamocarcinus angustifrons</i> Bittner, 1883
Family Raninidae	
	<i>Lophoranina marestiana</i> (König, 1825)
Family Panopeidae	
	<i>Glyphithyreus ellipticus</i> (Bittner, 1875)



Phylum Mollusca

Class Bivalvia

Order Mytilida

Family Mytilidae

Modiolus postalensis Oppenheim, 1896

Order Pectinida

Family Spondylidae

Spondylus radula Lamarck, 1806

Order Ostreida

Family Gryphaeidae

Pycnodonte rarilamella (Meleville, 1843)

Family Ostreidae

Crassostrea sparnacensis (Deshayes, 1821)

Order Carditida

Family Carditidae

Paraglans postalensis (Vinassa de Regny, 1896)

Order Lucinida

Family Lucinidae

Divalinga sp.

Fimbria lamellosa (Lamarck, 1806)

Fimbria major (Bayan, 1870)

Pseudomiltha escheri (Mayer, 1870)

Pseudomiltha gigantea (Deshayes, 1825)

Order Cardiida

Family Cardiidae

Granocardium gratum (Deshayes, 1829)

Granocardium sp.

Cardiidae gen. et sp. indet.

Family Tellinidae

Tellinella biangularis (Deshayes, 1825)

Tellina (Macaliopsis) scalaroides Lamarck, 1806

Tellina (Macaliopsis) sp.

Arcopagia erycinoides (Deshayes, 1824)

Order Venerida

Family Glossidae

Miocardiopsis carinata (Deshayes, 1829)

Family Veneridae

Katelsia texta (Lamarck, 1806)

Venerella secunda (Deshayes, 1857)

Pitar lunularia (Deshayes, 1825)

Pitar parisiensis (Deshayes, 1857)

Family Teredinae

Teredo sp.

Class Gastropoda

Subclass Patellogastropoda

Order Patellida

Superfamily Patelloidea

Family Patellidae?

"Patella" boreani Bayan, 1870

Subclass Vetigastropoda

Order Trochida

Superfamily Trochoidea

Family Trochidae

Calliostoma mayeri Fabiani, 1915

Calliostoma raffaelei (Mayer-Eymar, 1888)

Astele abavus (Mayer, 1870)

Homalopoma minimum (Malaroda, 1956)

Homalopoma zignoi (Bayan, 1870)

Leucodiscus helicinoides (Cossmann, 1888)

Subclass Neritimorpha



- Order Cycloneritida
 - Superfamily Neritoidea
 - Family Neritidae
 - Velates perversus* (Gmelin, 1791)
 - Neritopsis agassizi* Bayan, 1870
- Subclass Caenogastropoda
 - Caenogastropoda incertae sedis
 - Superfamily Campaniloidea
 - Family Ampullinidae
 - Pseudamaura* cf. *circumfossa* (Rauff, 1884)
 - Pachycrommium hybridum* (Lamarck, 1804)
 - Family Campanilidae
 - Campanile vicetinum* (Bayan, 1870)
 - Campanile giganteum* (Lamarck, 1804)
 - "*Campanile*" *gomphoceras* (Bayan 1870)
 - Superfamily Cerithioidea
 - Family Cerithiidae
 - Bezançonia cossmanni* (Oppenheim, 1896)
 - Cerithium fabianii* Malaroda, 1956
 - Ptychocerithium lamellosum* (Bruguière, 1792)
 - Rhinoclavis chaperi* (Bayan, 1870)
 - Rhinoclavis striatus* (Bruguière, 1792)
 - Family Pachychilidae
 - Bellatara palaeochroma* (Bayan, 1870)
 - Pseudobellardia auriculata* (Schlotheim, 1820)
 - Family Potamididae
 - "*Potamides*" *tristriatus* (Lamarck, 1804)
 - Pyrazopsis pentagonatus* (Schlotheim, 1820)
 - Family Siliquariidae
 - Tenagodus laevigatus* Malatesta, 1954
 - Tenagodus* sp.
 - Family Turritellidae
 - Vermicularia biangulatus* (Deshayes, 1832)
- Order Littorinimorpha
 - Superfamily Hipponicoidea
 - Family Hipponicidae
 - Vermicularia biangulatus* (Deshayes, 1832)
 - Superfamily Stromboidea
 - Family Rostellariidae
 - Digitolabrum princeps* (Vasseur, 1881)
 - Family Semiterebellum
 - Semiterebellum postalensis* (Bayan, 1870)
 - Family Seraphsidae
 - Seraphs sopitus* (Solander, 1766)
 - Superfamily Naticoidea
 - Family Naticidae
 - Cepatia cepacea* (Lamarck, 1804)
 - Superfamily Cypraeoidea
 - Family Cypraeidae
 - Gisortia hantkeni* (Lefèvre, 1878)
 - Archicypraea lioyi* (Bayan, 1870)
 - Luponovula praegnans* (De Gregorio, 1880)
 - Cypraedia elegans* (Sowerby, 1823)
 - Protocypraeda interposita* (Deshayes, 1865)
 - Superfamily Littorinoidea
 - Family Littorinidae
 - Littorina* (*Littorinopsis*) *postalensis* (De Gregorio, 1894)
 - Lacuna* sp.
 - Superfamily Tonnoidea
 - Family Cassidae



	<i>Cassis postalensis</i> Oppenheim, 1896
Order Neogastropoda	
Superfamily Buccinoidea	
Family Clavilithidae	
<i>Clavilithes rugosus</i> (Lamarck, 1803)	
Family undetermined	
<i>"Melongena" robusta</i> Dainelli, 1915	
Superfamily Muricoidea	
Family undetermined	
<i>"Drupa" crossei</i> (Mayer-Eymar, 1870)	
Family Volutidae	
<i>Voluta musicalis</i> (Lamarck, 1802)	
Superfamily Conoidea	
Family Conidae	
<i>Conus deperditus</i> (Bruguière, 1972)	
<i>Hemiconus incomptus</i> (Deshayes, 1865)	
Family Cryptoconidae	
<i>Cryptoconus priscus</i> (Solander, 1766)	
Subclass Heterobranchia	
Superfamily Acteonoidea	
Family Acteonidae	
<i>Hemiauricula hilarionis</i> (Bayan, 1870)	
<i>Acteon subinflatus</i> D'Orbigny, 1850	
Superfamily Architectonicoidea	
Family Architectonicidae	
<i>Architectonica bistriata</i> (Deshayes, 1832)	
Class Cephalopoda	
Subclass Nautiloidea	
Order Nautilida	
Superfamily Aturioidea	
Family Aturiidae	
<i>Aturia ziczac</i> (Sowerby, 1812)	
<i>Aturia postalensis</i> Malaroda, 1956	
Superfamily Nautiloidea	
Family Hercoglossidae	
<i>Hercoglossa</i> aff. <i>H. harrisi</i> Miller & Thompson, 1937	
Phylum Echinodermata	
Class Echinoidea	
Order Cassiduloida	
Family Echinolampadidae	
<i>Echinolampas suessi</i> Laube, 1868	
Order Spatangoida	
Family Micrasteridae	
<i>Cyclaster subquadratus</i> (Desor, 1858)	
<i>Cyclaster tuber</i> Laube, 1868	
Family Schizasteridae	
<i>Linthia biarritzensis</i> (Cotteau, 1863)	
<i>Schizaster postalensis</i> Bittner, 1891	
<i>Schizaster</i> sp.	
Class Asteroidea	
<i>"Astropecten"</i> sp.	
List of main invertebrate taxa from the bioconstructions of Monte Postale	
Phylum Cnidaria	
Class Anthozoa	
Subclass Exacorallia	
Order Scleractinia	
Family Acroporidae	
<i>Acropora</i> sp.	
<i>Astreopora</i> sp.	



	<i>Dendracis</i> sp.
Family Actinacididae	
	<i>Actinacis cognata</i> Oppenheim, 1901
Family Astrocoeniidae	
	<i>Astrocoenia</i> sp.
Family Cladocoridae	
	<i>Cladocora</i> sp.
Family Euphylliidae	
	<i>Euphyllia</i> sp.
	<i>Nancygyra dissepimentata</i> Bosellini & Stolarski, 2020
Family Faviidae	
	<i>Favia</i> sp.
Family Meandrinidae	
	<i>Pachygyra</i> sp.
Family Merulinidae	
	<i>Caulastraea</i> sp.
	<i>Paraleptoria</i> sp.
Family Montastraeidae	
	<i>Montastraea</i> sp.
Family Pocilloporidae	
	<i>Stylophora</i> sp.
Family Poritidae	
	<i>Goniopora</i> sp.
Family Rhizangiidae	
	<i>Siderofungia</i> sp.
	<i>Siderastraea</i> sp.
Phylum Arthropoda	
Subphylum Crustacea	
Class Malacostraca	
Order Decapoda	
Infraorder Anomura	
Family Galatheidae	
	<i>Acanthogalathea devecchii</i> Beschin et al., 2016
	<i>Petrolisthes lineatus</i> Beschin et al., 2016
Family Diogenidae Ortmann, 1892	
	<i>Dardanus bayani</i> Beschin et al., 2016
Infraorder Brachyura	
Family Dromiidae	
	<i>Dromiopsis ceratoi</i> Beschin et al., 2016
Family Dynomenidae	
	<i>Kromtitis subovatus</i> Beschin et al., 2016
	<i>Cyamocarcinus angustifrons</i> Bittner, 1883
Dromiacea incertae sedis	
	<i>Eotrachynotocarcinus airaghii</i> Beschin et al., 2007
Family Parthenopidae	
	<i>Mesolambrus declinatus</i> Müller & Collins, 1991
	<i>Mesolambrus ypresianus</i> Beschin et al., 2015
Family Carpiliidae	
	<i>Carpilius petreus</i> Beschin et al., 2007
Family Pilumnidae Samouelle, 1819	
	<i>Lobogalenopsis quadrilobata</i> (Lörenthey, 1898)
Family Domeciidae	
	<i>Palmyria levigata</i> sp. Beschin et al., 2016
Family Panopeidae	
	<i>Panopeus postalensis</i> Beschin et al., 2016
Family Xanthidae	
	<i>Etisus arduinoi</i> Beschin et al., 2007
	<i>Phlyctenodes multituberculatus</i> Beschin et al., 2007
Xanthoidea incertae sedis	
	<i>Prochlorodius ellipticus</i> Müller & Collins, 1991



Fig. 24 - Molluscs from the Monte Postale *Alveolina* beds. A-E) *Cardiidae* gen- et sp. indet., IGF 14604, ventral, dorsal, antero-dorsal, postero-dorsal and left view; F) *Pycnodonte gigantea*, IGF 100467, internal view of right valve; G-H) *Campanile giganteum*, IGF 100618, oral and dorsal view. Scale bar 100 mm.

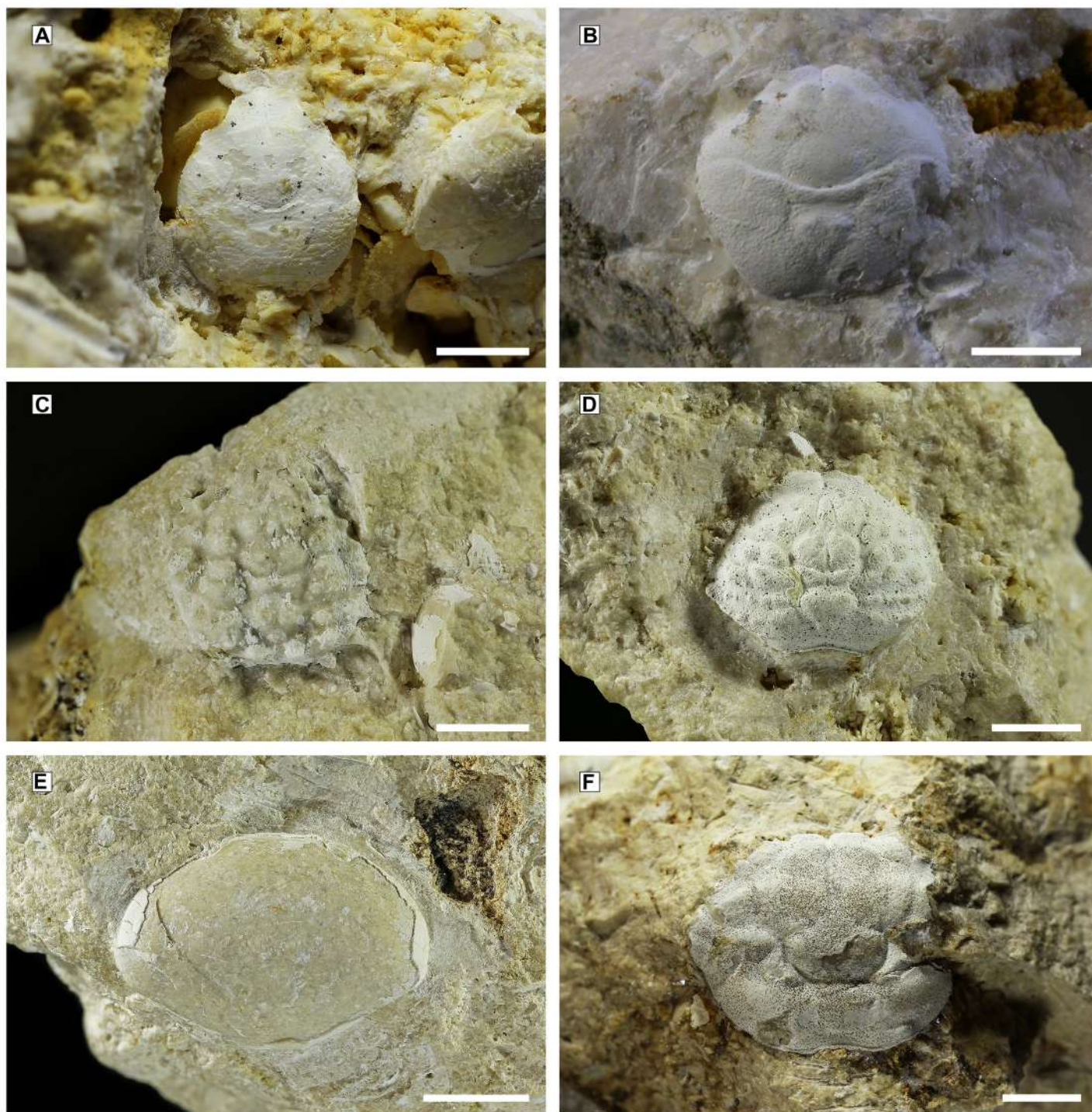


Fig. 25 - Crustaceans from the bioconstructions of the Monte Postale and other sites around Bolca. A) *Petrolisthes lineatus*, MCSNV 93914, scale bar 2 mm; B) *Dromiopsis ceratoi*, MCSNV 93954, holotype, scale bar 3 mm; C) *Kromtitis subovatus*, MCSNV 94033, scale bar 3 mm; D) *Eothrachinotocarcinus airaghii*, MCSNV 94086, scale bar 3 mm; E) *Carpilius petreus*, MCSNV 94168, scale bar 5 mm; F) *Panopeus postalensis*, MCSNV 94525, holotype, scale bar 5 mm.



FISHES AND OTHER VERTEBRATES

Taxonomic diversity - Fishes unquestionably represent the most celebrated and well-studied fossils of the Bolca Lagerstätten (e.g., Carnevale et al., 2014). Overall, the Eocene fish fauna of the Bolca Lagerstätten is one of the most important and best known ichthyofaunistic fossil assemblages, primarily due to the exceptional preservation quality and specimen richness. In addition, the remarkable taxonomic diversity of the Bolca fish assemblage makes it the most diverse of all the known Cenozoic ichthyofaunas and, more generally, one of the most diverse vertebrate assemblages in the fossil record.

As discussed above, the first written account documenting the fossil fishes from Bolca dates back to 1550 when the botanist and physician Pietro Andrea Mattioli described some nicely preserved “petrified” fishes from the Verona region belonging to Diego Hurtado de Mendoza, the ambassador of Emperor Charles V in Venice. Like many others after him, Mattioli (1550) was amazed by the superb preservation of these fossils that showed their anatomical details transformed into stone. For more than four centuries the fossil fishes of Bolca have been coveted for their attractive appearance and scientific interest. It is no exaggeration to state that the Bolca fishes have played a prominent role in the history of palaeoichthyology. In 1789, the Abbot Giovanni Serafino Volta published a short catalogue of the Bolca fishes, which he largely referred to extant fishes, primarily distributed in tropical seas. Just after the publication of this preliminary catalogue (Volta, 1789), he started preparing a superbly illustrated comprehensive catalogue of the fishes from Bolca comprising more than 120 species, namely the celebrated “*Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti fossili veronesi*”, which was produced by the printing house of Count Bartolomeo Giuliani in Verona between 1796 and 1809. The “*Ittiolitologia Veronese*” represents the earliest treatise on palaeoichthyology. The Bolca fishes also occupied a considerable part of the milestone of modern palaeoichthyology, the monumental “*Recherches sur les Poissons Fossiles*”, written by the Swiss naturalist Louis Agassiz (Agassiz, 1833-1844).

The exquisite preservation of the articulated fish skeletons typical of the Bolca fossils has traditionally favoured anatomical comparisons with extant fish taxa since these earlier studies. For this reason, the fossil fishes from Bolca have provided a remarkable contribution to the development of fish systematics, as well as to the interpretation of the diversification patterns of modern fish lineages, especially those of teleosts.

More than four centuries of extensive prospection in the laminated limestone of the Bolca Lagerstätten resulted in the extraction of about 100,000 fish specimens (Blot,

1969), primarily from the Pesciara site. Considering the reduced volume of exposed fossiliferous sediments, it is clear that these sites, especially the Pesciara, are very rich. Given the remarkable amount of potentially available specimens, currently disseminated in many museums and research institutions around the world, a comprehensive definition of the taxonomic diversity represents a challenging task. The taxonomic diversity of the fishes of the Bolca Lagerstätten is under constant revision, and new taxa are frequently discovered, including representatives of new families (e.g., Marramà et al., 2023). The list presented herein in Tab. 5 comprises 260 species-level taxa belonging to about 120 family-level taxa and at least 36 orders. The taxonomic composition of the assemblages of the two sites is remarkably different, with the Pesciara assemblage being considerably more diverse than that of the Monte Postale site, comprising 240 and 49 species-level taxa, respectively. About 211 species-level taxa are exclusive of the Pesciara assemblages, whereas only 20 species-level taxa are exclusive of the Monte Postale assemblage and 29 taxa are shared by the two assemblages. However, these data are susceptible to substantial variations in the near future, and the overall diversity is likely to increase with the description of new taxa.

The fish assemblage includes elasmobranchs (sharks and batoids), some of the last representatives of the neopterygian order Pycnodontiformes, and a considerable number of teleosts. More precisely, there are 14 elasmobranch species, four pycnodontiform species and at least 241 teleost species-level taxa. The vast majority of the teleosts pertain to the acanthomorph clade Percomorpha, which sharply dominates the assemblage, showing a diversity foreshadowing that of today (see Patterson, 1993; Friedman and Carnevale, 2018).

Cartilaginous fishes are relatively rare compared to bony fishes, represented by 14 species belonging to 12 families and five orders (Fig. 26). The Bolca fauna represents the most diverse Cenozoic assemblage of cartilaginous fishes based on articulated skeletal remains (e.g., Marramà et al., 2018a). Sharks include the tope shark *Galeorhinus cuvieri* and carcharhinid *Eogaleus bolcensis* (Marramà et al., 2018b). The occurrence of the small-sized sand tiger shark *Barchycarcharias lerichei* is documented solely based on isolated teeth (Marramà et al., 2019e). Batoids comprise 11 species pertaining to nine families of the orders Torpediniformes, Rhinopristiformes and Myliobatiformes (Marramà et al., 2018c, 2019b, c, d, 2020a, b, 2021, 2023). The cartilaginous fishes from Bolca have recently been re-examined in great detail, and new taxa with remarkable evolutionary implications have been discovered, including the putative potamotrygonid *Lessiniabatis aenigmatica*, which provides evidence of a unique body plan in stingrays (Marramà et al., 2019b), and



the spectacular *Dasyomyliobatis thomyorkei*, exhibiting a body intermediate between rajobenthic and the aquilopelagic stingrays (Marramà et al., 2023). Fossils of the electric ray *Titanonarke* from Monte Postale revealed amazing aspects of its palaeobiology, including reproductive features, feeding mode and possible micropredation by isopod crustaceans (Marramà et al., 2018b; Robin et al., 2019).

Of the 245 ray-finned fish species described to date from the Bolca Lagerstätten, only 33 do not belong to the Acanthomorpha (Fig. 27). Four species represent the late-surviving pycnodontiforms, deep-bodied neopterygians that were abundant during the Mesozoic (e.g., Cawley et al., 2018, 2021). The putative pachyrhizodontid *Platinx macropterus* possibly represents the youngest record of the Jurassic-Cretaceous basal teleost order Crossognathiformes (Taverne, 1980; Cavin, 2001; Arratia, 2008). Osteoglossiforms are represented by three species, documenting the last part of the Palaeogene marine history of this group, which is today restricted to freshwaters (e.g., Taverne, 1998; Capobianco et al., 2025). Elopomorphs are represented by 16 anguilliform species (see Blot, 1978, 1980, 1984), assigned to both extinct (Anguillioideae, Milananguillidae, Paranguillidae, Patavichthyidae, Proteomyridae) and extant (Anguillidae, Chlopsidae, Congridae, Ophichthyidae) families; the affinities of two of the eel species (*Bolcanguilla brachycephala*, *Gazolapodus homopterus*) are of problematic phylogenetic interpretation. Clupeomorphs are by far the most common fishes of the Bolca Lagerstätten, represented by the youngest marine record of the double-armoured herrings, *Eoellimmichthys superstes* (see Marramà et al., 2019a), and by four clupeiform species, including the extremely abundant gizzard shad *Bolcaichthys catopygopterus* and the oldest anchovy *Eoengraulis fasoloi* (Marramà and Carnevale, 2015a, b, 2016, 2018). The ostariophysans, a highly diverse group of primarily freshwater fishes, are represented by the anatomically primitive otophysan *Chanoides macropoma* (see Patterson, 1984) and by rare gonorhynchiforms. There is no record of 'protacanthopterygians', stomiiforms and myctophiforms in the Bolca fish assemblage, whereas aulopiforms are represented by the peculiar shallow water barracudina *Holosteus esocinus*, which shows a morphotype typical of ambush predators (Marramà and Carnevale, 2017).

Acanthomorphs, the spiny-rayed teleosts, largely dominate the ichthyofauna with 212 species-level taxa, representing at least 23 orders (Figs. 28–31). Spiny-rayed teleosts include about one-third of the living vertebrates. This group shows a considerable disparity, exemplified by a plethora of body plans such as those of flatfishes, pufferfishes and their allies, anglerfishes, seahorses and their allies, flyingfishes, mudskippers, etc. The majority

of the acanthomorphs pertains to the Percomorpha, a highly diverse radiation whose earliest representatives date back to the Late Cretaceous (Carnevale and Johnson, 2015). As suggested by Carnevale et al. (2014), in terms of taxonomic diversity, the number of acanthomorph species of the Bolca assemblage is more than six times that of non-acanthomorphs, although such an asymmetry is balanced in terms of individuals (and probably biomass) by the considerably high number of individuals of the gizzard shad *Bolcaichthys catopygopterus*. As demonstrated by Marramà et al. (2016), about half of the collected fishes resulted from the controlled excavations carried out by the Museo Civico di Storia Naturale, Verona in the past 25 years pertain to this clupeomorph species. Non-percomorph acanthomorphs comprise six species belonging to the lampridiform family Veliferidae (Carnevale and Bannikov, 2018), the relatively common beryciform squirrelfishes of the family Holocentridae and the peculiar long-bodied zeiform *Bajaichthys elegans* (see Davesne et al., 2017) (Fig. 28). Therefore, the number of percomorphs in the Bolca fish assemblage is very high, currently corresponding to more than 200 species-level taxa, representing 20 orders and 73 families (Figs. 29–31). About 33 species-level taxa cannot be confidently placed in any of the known percomorph families and are presented herein (Tab. 5) as *incertae sedis*. Percomorphs are represented by numerous benthic taxa, together with taxa clearly associated with open-water habitats, including mackerels and tuna (Scombridae; Fig. 28C), billfishes (Blochiidae, Palaeorhynchidae), and halfbeaks (Hemiramphidae) and flyingfishes (Exocoetidae; Fig. 29G) (e.g., Bannikov et al., 1985; Fierstine and Monsch, 2002; Monsch, 2006). Numerous percomorph groups recognised in the Bolca fish fauna are today associated with reefs and seagrass beds, including surgeonfishes (Acanthuridae), moorish idols (Zanclidae; Fig. 31A), wrasses (Labridae), cardinalfishes (Apogonidae; Fig. 29B), spadefishes (Ephippidae; Fig. 30C), damselfishes (Pomacentridae), porgies (Sparidae; Fig. 30D), snappers (Lutjanidae), barracudas (Sphyraenidae; Fig. 29I), jacks (Carangidae; Figs. 29H, J), scatties (Scatophagidae), bigeyes (Priacanthidae), goosfishes (Lophiidae; Fig. 30E), frogfishes (Antennariidae), batfishes (Ogcocephalidae), rabbitfishes (Siganidae; Fig. 31B), moonfishes (Menidae; Fig. 30A), and numerous syngnathiforms (Figs. 29D–F) and tetraodontiforms (Fig. 30F) (e.g., Blot 1969; Tyler and Bannikov, 1997; Tyler and Santini, 2002; Day, 2003; Carnevale and Pietsch, 2009, 2010, 2011, 2012, 2020; Bannikov and Carnevale, 2010, 2016, 2017; Pietsch and Carnevale, 2011; Carnevale et al., 2017; Carnevale and Tyler, 2024). Surgeonfishes are by far the most diverse percomorph family with 20 species belonging to 14 genera; the number of genera in the Bolca assemblage is more than two times greater than those (six) living today (e.g., Blot



and Tyler, 1990). One of the two species of the moonfish genus *Mene*, *M. rhombea*, is very abundant and represents a true icon of the Bolca Lagerstätte (e.g., Rossi et al., 2022). Despite the modern structure of the percomorph fauna, largely characterised by familiar phenotypes, there are also numerous extinct body plans, including the enigmatic *Dibango volans* (Davesne and Carnevale, 2025), the stem-flatfish family Amphistiidae that provides anatomical evidence of the gradual (not saltational) evolution of cranial asymmetry (Friedman, 2008), as well as representatives of many extinct families, in many cases solely recognised in the Bolca Lagerstätten, including the Acanthonemidae, Aulorhamphidae, Bolcabalistidae, Callipterygidae, Carangodidae, Ductoridae, Eocottidae, Eoplectidae, Exelliidae, Massalongiidae, Mesogasteridae, Pavarottiidae, Pietschellidae, Protobalistidae, Pterygocephalidae, Quasimullidae, Rhamphognathidae, Rhamphosidae, Robertanniidae, Sorbinipercidae, Tortonesiidae, Urosphenidae, Zignoichthyidae, and Zorzinichthyidae (e.g., Bannikov and Tyler, 1999; Tyler, 1999, 2004; Bannikov, 2004, 2008; Bannikov and Carnevale, 2011; Carnevale and Bannikov, 2015; Calzoni et al., 2023; Ridolfi et al., 2025). Terrestrial vertebrates have been rarely found in the Pesciara site, represented by a single carapace of a turtle (Sorbini, 1999), snakes (*Anomalophis bolcensis*, *Archaeophis proavus*, and *Serpentes indet.*; Seghetti et al., 2022) (Fig. 32A, B), and impressions of bird feathers (see Carnevale et al., 2014) (Fig. 32C).

Taphonomy and palaeoecological implications – As discussed above, exquisitely preserved fossil fishes characterised by a very attractive appearance have been extracted from the Pesciara and Monte Postale sites for more than four centuries. Because of the laminated fabric of the fossiliferous sediments, the fossils, especially the fishes, are usually known as part and counterpart with complete squamation, traces of the original pigmentation pattern and phosphatised soft tissues (e.g., Wilby and Briggs, 1997; Rossi et al., 2022). Marramà et al. (2016) analysed the results of controlled excavations carried out in both the Pesciara and Monte Postale between 1999 and 2011 and revealed that the quality of preservation and abundance of fossils are remarkably different in the two sites, due to different environmental features of the original depositional contexts (Marramà et al., 2016).

Exceptionally preserved fossils are abundant in the finely laminated micritic limestone of the Pesciara site, where they constitute the majority of the collected specimens. The taphonomic features (degree of completeness, 3D orientation patterns, tetany) observed in the fish skeletal remains and their excellent preservation concur to suggest that the carcasses rapidly accumulated on the anoxic bottom where a well-developed microbial biofilm delayed their decomposition, protected them from scavengers or

bottom currents and promoted their rapid mineralisation. The tetany features characteristic of many fish specimens indicate that toxic algal blooms possibly represented one of the main causes of death of marine organisms in the Pesciara palaeobiotope (Marramà et al., 2016).

A prominent part of the fossils from Monte Postale is incomplete or strongly disarticulated (about 90% of fish remains), and, in many cases, this inadequate preservation prevented their identification at genus or species level. The incompleteness and disarticulation of most of the fish skeletal remains, as well as the disordered disposition of their fins, the common S-shaped pattern of the vertebral column and the unidirectional dispersion of the scales around the body are indicative of hydrodynamic disturbance of the bottom with temporary mixing of the waters. These episodic disturbance events resulted in the development of normal aerobic conditions on the bottom that eventually allowed the settling of a moderately diverse benthic fauna, as revealed by the bioturbation tracks and remains of crustaceans and molluscs (Marramà et al., 2016).

During the early Eocene, the Bolca area was part of the northern margin of the western Tethys region, a region representing a biodiversity hotspot, with abundant coral reefs and mangrove systems. This biodiversity hotspot represents an Eocene analogue and a precursor of the modern Indo-Australian Archipelago hotspot, the centre of current maximum marine diversity (e.g., Renema et al., 2008).

The Bolca fish assemblage has been traditionally interpreted as closely linked to a coral reef system (e.g., Blot, 1969, 1980; Sorbini, 1972, 1999). Bellwood (1996) discussed the role of the fishes of the Bolca Lagerstätten in the evolution of modern reef fish communities and interpreted these fossils as the earliest evidence of a coral reef fish assemblage of modern type. The Bolca fish assemblage marks the earliest documented record of many fish families today associated with coral reefs (Bellwood and Wainwright, 2002), thereby suggesting that the morphological characteristics of tropical shallow-marine fish faunas have remained generally stable throughout the Cenozoic. The morphology of the Bolca fishes belonging to families today associated with coral reefs is very similar to that of their extant relatives. Most anatomical, functional and ecological characters of these Eocene taxa are comparable to those of modern reef fishes. The Bolca fish assemblage, however, also includes numerous taxa belonging to extinct lineages of uncertain ecological interpretation possibly representing the ecological vicariants of those fish groups commonly associated with Recent coral reefs (blenniids, gobioids, chaetodontids, mullids, serranids, etc.) that have not yet been discovered in the Pesciara and Monte Postale sites. In addition, the relative abundance of representatives of reef fish families in the Bolca assemblage significantly differs



from that observed in the coral reefs today (Bellwood, 1996; Carnevale, 2006). In any case, the existence of a sort of reefal signature in the Bolca fish assemblage is undeniable. The Bolca assemblage documents the origin of new feeding modes in fishes, including herbivory, nocturnal feeding, and high-precision benthic feeding (Bellwood, 2003; Goatley et al., 2010). Herbivores are represented by surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae), and nocturnal feeders are represented by squirrelfishes (Holocentridae) and cardinalfishes (Apogonidae). The surgeonfishes from Bolca are characterised by remarkable functional and ecological similarities to their extant counterparts, including browsers, grazers, and long-snouted crevice-feeding forms (Bellwood et al., 2014).

Substantial geological and palaeontological data indicate that the fossiliferous deposits of Bolca originated in a tropical coastal region close to coral reefs and emerged lands (e.g., Massari and Sorbini, 1975). Landini and Sorbini (1996) recognised three main ecological assemblages based on

the Pesciara fossils, the sand/seagrass bed assemblage characterised by *taxa* closely associated with the substrate (e.g., batoids, anguilliforms, lophiids, syngnathiforms, ehippids, eocottids, callipterygids, labrids, siganids, flatfishes, some tetraodontiforms), the coral assemblage (anguilliforms, lophiiforms, holocentrids, syngnathiforms, apogonids, sparids, carangids, monodactylids, ehippids, pomacentrids, labrids, acanthurids, siganids, and tetraodontiforms), and the perireefal and pelagic assemblage (sharks, clupeiforms, beloniforms, atheriniforms, veliferids, latids, ductorids, carangids, menids, exelliids, sphyraenids, euzaphlegids, scombrids, blochiids, and palaeorhynchids). Landini and Sorbini (1996) recognised that the trophic structure of the Pesciara fish assemblage exhibits an asymmetrical herbivore/predator relationship in terms of biomass and overall diversity and suggested that the original palaeobiotopes of the Pesciara should be regarded as perireefal trophic systems influenced by both the open sea and the coastal environments.

Table 5 - A synoptic list of Eocene fishes of the Bolca Lagerstätten. MP = Monte Postale, P = Pesciara.

Phylum Chordata	
Class Chondrichthyes	
Division Selachii	
Order Carcharhiniformes	
Family Triakidae	
<i>Galeorhinus cuvieri</i> (Agassiz, 1835)	P
Family Carcharhinidae	
<i>Eogaleus bolcensis</i> Cappetta, 1975	P, MP
Order Lamniformes	
Family Odontaspidae	
<i>Brachycarcharias lerichei</i> (Casier, 1946)	P, MP
Division Batomorphii	
Order Torpediniformes	
Family Narcinidae	
<i>Titanonarke molini</i> (Jaekel, 1894)	MP
<i>Titanonarke megapterygia</i> Marramà et al., 2018	MP
Family Platyrhinidae	
<i>Eoplatyrhina bolcensis</i> (Heckel, 1851)	MP
Order Rhinopristiformes	
Family Rhinobatidae	
<i>Eorhinobatos primaevus</i> (De Zigno, 1874)	P
<i>Pseudorhinobatos deznii</i> (Heckel, 1853)	MP
Order Myliobatiformes	
Family Zanobatidae	
<i>Plesiozanobatus egertoni</i> (De Zigno, 1876)	P
Family Urolophidae	
<i>Arechia crassicaudata</i> (Blainville, 1818)	MP
Family Dasyatidae	
<i>Tethytrygon muricatus</i> (Volta, 1796)	P
Family Dasyomyliobatidae	
<i>Dasyomyliobatis thomyorkei</i> Marramà et al., 2023	P
Family Myliobatidae	
<i>Promyliobatis gazolai</i> De Zigno, 1882	P



Family Potamotrygonidae (?)	
<i>Lessiniabatis aenigmatica</i> Marramà et al., 2019	P
Class Osteichthyes	
Subclass Actinopterygii	
Order Pycnodontiformes	
Family Pycnodontidae	
<i>Abdopalistum thyrsus</i> Poyato-Ariza & Wenz, 2002	P
<i>Nursallia veronae</i> Blot, 1987	P
<i>Palaeobalistum orbiculatum</i> Blainville, 1818	P
<i>Pycnodus apodus</i> (Volta, 1796)	P
Subdivision Teleostei	
Order Crossognathiformes	
Family Pachyrhizodontiformes	
<i>Platinx macropterus</i> (Blainville, 1818)	MP
Order Osteoglossiformes	
Family Foreyichthyidae	
<i>Foreyichthys bolcensis</i> Taverne, 1979	P
Family Osteoglossidae	
<i>Thrissopterus catullii</i> Heckel, 1856	MP
Family incertae sedis	
<i>Monopterus gigas</i> Volta, 1796	P
Order Anguilliformes	
Family Anguillidae	
<i>Eoanguilla leptoptera</i> (Agassiz, 1835)	P
Family Anguilloididae	
<i>Anguilloides branchiostegalis</i> (Eastman, 1905)	P
<i>Veronanguilla ruffoi</i> Blot, 1978	P
Family Chlopsidae	
<i>Whitapodus breviculus</i> (Agassiz, 1835)	P
Family Congridae	
<i>Bolcyrus bajai</i> Blot, 1978	P
<i>Bolcyrus formosissimus</i> (Eastman, 1905)	P
<i>Paracongroides heckeli</i> Blot, 1978	P
<i>Voltaconger latispinus</i> (Agassiz, 1839)	P
Family Milananguillidae	
<i>Milananguilla lehmani</i> Blot, 1978	P
Family Ophichthyidae	
<i>Goslinophis acuticaudus</i> (Agassiz, 1835)	P
Family Paranguillidae	
<i>Dalpiaziella brevicauda</i> Cadrobbi, 1962	P
<i>Paranguilla tigrina</i> (Agassiz, 1839)	P
Family Patavichthyidae	
<i>Patavichthys bolcensis</i> (Bassani, 1897)	P
Family Proteomyridae	
<i>Proteomyrus ventralis</i> (Agassiz, 1839)	P
Family incertae sedis	
<i>Bolcanguilla brachycephala</i> Blot, 1980	P
<i>Gazolapodus homopterus</i> Blot, 1980	P
Order Ellimmichthyiformes	
Family Paraclupeidae	
<i>Eoellimmichthys superstes</i> Marramà et al., 2018	P
Order Clupeiformes	
Family Spratelloididae	
<i>Trollichthys bolcensis</i> Marramà & Carnevale, 2015	P, MP
Family Engraulidae	
<i>Eoengraulis fasoloi</i> Marramà & Carnevale, 2016	P



Family Alosidae	
<i>Eoalosa janvieri</i> Marramà & Carnevale, 2018	P
Family Dorosomatidae	
<i>Bolcaichthys catopygopterus</i> (Woodward, 1901)	P, MP
Order Gonorynchiformes	
Family incertae sedis	
<i>"Chanos" forcipatus</i> (Eastman, 1905)	P
<i>Coelogaster leptostea</i> (Eastman, 1905)	P
Subcohort Otophysi	
Family incertae sedis	
<i>Chanoides macropoma</i> (Agassiz, 1844)	P
Order Aulopiformes	
Family Paralepididae	
<i>Holosteus esocinus</i> Agassiz, 1839	P
Acanthomorpha	
Order Lampridiformes	
Family Veliferidae	
<i>Veronavelifer sorbinii</i> Bannikov, 1990	P
<i>Wettonius angeloi</i> Carnevale & Bannikov, 2018	P
Order Zeiformes	
Family Bajaichthyidae	
<i>Bajaichthys elegans</i> Sorbini, 1983	P
Order Beryciformes	
Family Holocentridae	
<i>Berybolcensis leptacanthus</i> (Agassiz, 1838)	P, MP
<i>Eoholocentrum macrocephalum</i> (Blainville, 1818)	P
<i>Tenuicentrum lanceolatum</i> (Bassani, 1876)	P
Percomorpha	
Order Ophidiiformes	
Family incertae sedis	
<i>"Ophidium" voltianum</i> Massalongo, 1859	P
Order Gobiiformes	
Family incertae sedis	
<i>Carlomonnus quasigobius</i> Bannikov & Carnevale, 2016	P
<i>Carlomonnus carnevalei</i> Reichenbacher et al., 2025	P
Family Apogonidae	
<i>Apogoniscus pauciradiatus</i> Bannikov, 2005	P, MP
<i>Bolcapogon johnsoni</i> Bannikov, 2005	P
<i>Eoapogon fraseri</i> Bannikov, 2005	P
<i>Eosphaeramia pygopterus</i> (Agassiz, 1836)	P
<i>Leptolumamia vetula</i> Bannikov & Fraser, 2016	P
Order Scombriformes	
Family Centrolophidae	
<i>Zorzinia postalensis</i> Bannikov, 2000	MP
Family Pomatomidae	
<i>Carangopsis brevis</i> (Blainville, 1848)	P
<i>Carangopsis dorsalis</i> Agassiz, 1844	P
Family Euzaphlegidae	
<i>Veronaphleges brunae</i> Bannikov, 2008	P
Family Scombridae	
<i>Auxides propterygius</i> (Agassiz, 1835)	P
<i>Godsilia lanceolata</i> (Agassiz, 1835)	P
<i>Pseudauxides speciosus</i> (Agassiz, 1835)	P, MP
<i>Thunnuscoberoides bolcensis</i> (Agassiz, 1835)	P
Order Syngnathiformes	
<i>Gilmourella minuta</i> Carnevale & Bannikov, 2019	P
Family Rhamphosidae	



<i>Rhamphosus rastrum</i> (Volta, 1796)	P
<i>Rhamphosus biserratus</i> Bassani, 1876	P
<i>Rhamphosus bloti</i> Calzoni et al., 2023	P
<i>Rhamphosus brevirostris</i> Calzoni et al., 2023	P
<i>Rhamphosus longispinatus</i> Calzoni et al., 2023	P
<i>Rhamphosus tubulirostris</i> Calzoni et al., 2023	P
Family Aulostomidae	
<i>Eoaulostomus bolcensis</i> (Blainville, 1818)	P
<i>Eoaulostomus gracilis</i> Blot, 1980	P
<i>Jungersenichthys elongatus</i> Blot, 1980	P
<i>Macraulostomus veronensis</i> Blot, 1980	P
<i>Synhypuralis banisteri</i> Blot, 1980	P
<i>Synhypuralis jungerseni</i> Blot, 1980	P
<i>Tyleria necopinnata</i> Parin, 1993	P
Family Fistularioididae	
<i>Fistularioides phyllolepis</i> Blot, 1980	P
<i>Fistularioides veronensis</i> Blot, 1980	P
<i>Pseudosyngnathus opisthopterus</i> (Agassiz, 1833)	P
Family Parasynarcualidae	
<i>Parasynarcualis longirostris</i> (Blainville, 1818)	P
Family Aulorhamphidae	
<i>Aulorhamphus bolcensis</i> (Steindachner, 1863)	P
<i>Aulorhamphus capellinii</i> De Zigno, 1887	P
<i>Aulorhamphus chiasorbiniae</i> Bannikov & Tyler, 2011	MP
<i>Pesciaramphus carnevalei</i> Bannikov & Tyler, 2011	P
<i>Veronarhamphus canossae</i> (Heckel, 1856)	P
Family Centriscidae	
<i>Aeoliscoides longirostris</i> (Blainville, 1818)	P
<i>Paramphisile weileri</i> Blot, 1980	P
Family Paraeoliscidae	
<i>Paraeoliscus robinetae</i> Blot, 1980	P
Family Solenostomidae	
<i>Calamostoma lesiniiforme</i> (Volta, 1796)	P
<i>Solenorhynchus elegans</i> Heckel, 1854	MP
Family Syngnathidae	
<i>Prosolenostomus lessinii</i> Blot, 1980	P
" <i>Syngnathus</i> " <i>bolcensis</i> De Zigno, 1887	P
" <i>Syngnathus</i> " <i>heckeli</i> De Zigno, 1874	P
Family incertae sedis	
<i>Aulostomoides tyleri</i> Blot, 1980	P
Order Atheriniformes	
Family Atherinidae	
<i>Atherina</i> (?) <i>macrocephala</i> Woodward, 1901	P
Family Mesogasteridae	
<i>Latellagnathus teruzzii</i> Bannikov, 2008	P
<i>Mesogaster sphyraenoides</i> Agassiz, 1844	P
Family Rhamphognathidae	
<i>Rhamphognathus paralepoides</i> Agassiz, 1844	P
Family Exocoetidae	
<i>Rhamphexocoetus volans</i> Bannikov et al., 1985	P
" <i>Engraulis</i> " <i>evolans</i> (Blainville, 1818)	P
Family Hemiramphidae	
<i>Hemiramphus edwardsi</i> Bassani, 1876	P, MP
Order Blenniiformes	
Family Pomacentridae	
<i>Chiarachromis salazzarii</i> Bellwood et al., 2025	P
<i>Lorenzichthys olihan</i> Bellwood, 1999	P



	<i>Palaeopomacentrus orphae</i> Bellwood & Sorbini, 1996	P
	<i>Sorbinichromis francescoi</i> Bannikov & Bellwood, 2014	P
Order Carangiformes		
Family Sphyraenidae		
	<i>Sphyraena bolcensis</i> Agassiz, 1844	P, MP
Family Latidae		
	<i>Eolates gracilis</i> (Agassiz, 1833)	P
Family Carangidae		
	<i>Ceratoichthys pinnatiformes</i> (Blainville, 1818)	P
	<i>Eastmanalepes primaevus</i> (Eastman, 1904)	P
	<i>Lichia veronensis</i> Bannikov & Sorbini in Bannikov, 1990	P, MP
	<i>Paratrachinotus tenuiceps</i> (Agassiz, 1834)	
	<i>Seriola prisca</i> (Agassiz, 1834)	P, MP
	<i>Trachicarax pleuronectiformis</i> (Blot, 1969)	P
	<i>Vomeropsis triurus</i> (Volta, 1796)	P
Family Ductoridae		
	<i>Ductor vestenae</i> (Volta, 1796)	P, MP
Family Menidae		
	<i>Mene rhombea</i> (Volta, 1796)	P, MP
	<i>Mene oblonga</i> (Agassiz, 1833)	P, MP
Family Palaeorhynchidae		
	<i>Palaeorhynchus zorzini</i> Fierstine et al., 2009	MP
Family Blochiidae		
	<i>Blochius longirostris</i> Volta, 1796	P, MP
	<i>Blochius macropterus</i> De Zigno, 1887	P
Family Amphistiidae		
	<i>Amphistium paradoxum</i> Agassiz, 1844	P
	<i>Heteronectes chaneti</i> Friedman, 2008	P
Pleuronectoidei family incertae sedis		
	<i>Quasinectes durello</i> Bannikov & Zorzin, 2019	MP
	<i>Anorevus lorenzonii</i> Bannikov, 2020	P
	<i>Eobothus minimus</i> (Agassiz, 1839)	P
Series Eupercaria		
Order Perciformes		
Family incertae sedis		
	Scorpaenoidei gen. et sp. indet.	MP
Order Centrarchiformes		
Family Percichthyidae		
	<i>Cyclopoma gigas</i> Agassiz, 1833	P, MP
Order Pempheriformes		
Family Acropomatidae		
	<i>Acropoma</i> (?) <i>lepidotus</i> (Agassiz, 1836)	P, MP
Order Labriformes		
Family Labridae		
	<i>Bellwoodilabrus landinii</i> Bannikov & Carnevale, 2010	P
	<i>Eocoris bloti</i> Bannikov & Sorbini, 1990	P
	<i>Labrobolcus giorgioi</i> Bannikov & Carnevale, 2015	P
	<i>Paralabrus rossiae</i> Bannikov & Zorzin, 2019	P
	<i>Phyllopharyngodon longipinnis</i> Bellwood, 1990	P
	<i>Zorzinilabrus furcatus</i> Bannikov & Bellwood, 2017	P
Order Ehippiformes		
Family Ehippidae		
	<i>Archaehippus asper</i> (Volta, 1796)	P
	<i>Eoplatax papilio</i> (Volta, 1796)	P, MP
Order Spariformes		
Family Sparidae		
	<i>Abromasta microdon</i> (Agassiz, 1839)	P, MP



	<i>"Dentex" microdon</i> Agassiz, 1839	P
	<i>Ellaserrata monksi</i> Day, 2003	P
	<i>Pseudosparnodus microstomus</i> (Agassiz, 1839)	P
	<i>Sparnodus elongatus</i> Agassiz, 1839	P
	<i>Sparnodus vulgaris</i> (Blainville, 1818)	P, MP
	Nomen dubium <i>"Dentex" ventralis</i> Agassiz, 1839	P
Order Lophiiformes		
Family Lophiidae		
	<i>Sharfia mirabilis</i> Pietsch & Carnevale, 2011	P
	<i>Caruso brachysomus</i> (Agassiz, 1839)	P
Family Antennariidae		
	<i>Eophryne barbutii</i> Carnevale & Pietsch, 2009	P
	<i>Neilpeartia ceratoi</i> Carnevale et al., 2020	P
Family Brachionichthyidae		
	<i>Histionotophorus bassanii</i> (De Zigno, 1887)	P, MP
	<i>Orrichthys longimanus</i> Carnevale & Pietsch, 2010	P
Family Ogcocephalidae		
	<i>Tarkus squirei</i> Carnevale & Pietsch, 2011	P
Order Tetraodontiformes		
Family Triacanthidae		
	<i>Protacanthodes nimesensis</i> Tyler & Sorbini, 2001	P
	<i>Protacanthodes ombonii</i> (De Zigno, 1887)	P
Family Aracanidae		
	<i>Proaracana dubia</i> (Blainville, 1818)	P
Family Ostraciidae		
	<i>Eolactoria sorbinii</i> Tyler, 1975	P
Family Protobalistidae		
	<i>Protobalistum imperiale</i> (Massalongo, 1857)	MP
	<i>Spinacanthus cuneiformis</i> (Blainville, 1818)	P
Family Bolcabalistidae		
	<i>Bolcabalistes varii</i> Tyler & Sorbini, 1998	P
Family Eoplectidae		
	<i>Eoplectus bloti</i> Tyler, 1975	P
Family Zignoichthyidae		
	<i>Zignoichthys oblongus</i> (De Zigno, 1874)	P
Family Tetraodontidae		
	<i>Eotetraodon pygmaeus</i> (De Zigno, 1887)	P
	<i>Eotetraodon tavernei</i> Tyler & Bannikov, 2013	P
Family Diodontidae		
	<i>Heptadiodon echinus</i> (Heckel, 1854)	P
	<i>Prodiodon erinaceus</i> (Agassiz, 1844)	P
	<i>Prodiodon tenuispinus</i> (Agassiz, 1844)	P
	<i>Zignodon fornasieroae</i> Tyler & Sorbini, 2002	P
Order Caproiformes		
Family Caproidae		
	<i>Eoantigonia veronensis</i> (Sorbini, 1983)	P, MP
Family Acanthonemidae		
	<i>Acanthonemus subaureus</i> (Blainville, 1818)	P
Family Sorbinipercidae		
	<i>Sorbinicapros sorbiniorum</i> Bannikov & Tyler, 1999	P
	<i>Sorbiniperca scheuchzeri</i> Tyler, 1999	P
Family Zorzinichthyidae		
	<i>Zorzinichthys annae</i> Tyler & Bannikov, 2002	P
	<i>Zorzinichthys annei</i> Bannikov & Zorzin, 2025	P
Order Gerreiformes		
Family Gerreidae (?)		
	<i>Aspesiperca ruffoi</i> Bannikov, 2008	P



Order Priacanthiformes	
Family Priacanthidae	
<i>Pristigenys substriatus</i> (Blainville, 1818)	P
Family Scatophagidae	
<i>Eoscatophagus frontalis</i> (Agassiz, 1839)	P
Order Chaetodontiformes	
Family Leiognathidae	
<i>Eoleiognathus dorsalis</i> (Agassiz, 1838)	P
Order Acanthuriformes	
Family Massalungiidae	
<i>Massalongius gazolai</i> (Massalongo, 1859)	P
Family Zanclyidae	
<i>Angiolinia mirabilis</i> Carnevale & Tyler, 2024	P
<i>Eozanclus brevirostris</i> (Agassiz, 1835)	P
Family Acanthuridae	
<i>Acanthuroides massalongoi</i> Blot & Tyler, 1990	P
<i>Eorandallius elegans</i> Blot & Tyler, 1990	P
<i>Eorandallius rectifrons</i> (Agassiz, 1838)	P, MP
<i>Frigosorbinia baldwinae</i> (Sorbini & Tyler, 1998)	P
<i>Gazolaichthys vestenianovae</i> Blot & Tyler, 1990	P
<i>Lehmanichthys lessiniensis</i> Blot & Tyler, 1990	P
<i>Metacanthurus veronensis</i> Blot & Tyler, 1990	P
<i>Metaspisurus emmanueli</i> Blot & Tyler, 1990	P
<i>Padovathurus gaudryi</i> (De Zigno, 1887)	P
<i>Pesciarichthys punctatus</i> Blot & Tyler, 1990	P, MP
<i>Proacanthurus bonatoi</i> Blot & Tyler, 1990	P
<i>Proacanthurus elongatus</i> Blot & Tyler, 1990	P
<i>Proacanthurus ovalis</i> (Agassiz, 1838)	P
<i>Proacanthurus tenuis</i> (Agassiz, 1838)	P
<i>Protozebrasoma bloti</i> Sorbini & Tyler, 1998	P
<i>Sorbinithurus sorbinii</i> Tyler, 1999	P
<i>Tauichthys aspesae</i> Tyler & Bannikov, 2000	P
<i>Tauichthys padremenini</i> Tyler, 1999	P
<i>Tylerichthys milani</i> Blot & Tyler, 1990	P
<i>Tylerichthys nuchalis</i> (Agassiz, 1838)	P, MP
Eupercaria order incertae sedis	
Family Lutjanidae	
<i>Goujetia crassispina</i> (Agassiz, 1839)	P
<i>Lessinia horrenda</i> Bannikov & Zorzin, 2014	P
<i>Lessinia</i> sp.	P
<i>Ottaviana leptacanthus</i> (Agassiz, 1839)	P
<i>Ottaviana mariae</i> Sorbini, 1983	P
<i>Veranichthys ventralis</i> (Agassiz, 1839)	P
Family Monodactylidae	
<i>Psettopsis subarquatus</i> (Blainville, 1818)	P
<i>Zaiaichthys postalensis</i> Bannikov & Zorzin, 2023	MP
<i>Zaiaichthys watersi</i> Bannikov & Zorzin, 2023	P
Family Siganidae	
<i>Acanthopygaeus agassizi</i> (Eastman, 1904)	P
<i>Aspesiganus margaritae</i> Bannikov & Tyler, 2002	P, MP
<i>Ruffoichthys bannikovi</i> Tyler & Sorbini, 1990	P
<i>Ruffocinthus spinosus</i> Sorbini, 1983	P
Family Pavarottiidae	
<i>Pavarottia astescalpone</i> Bannikov & Zorzin, 2022	P
<i>Pavarottia lonardonii</i> Bannikov & Zorzin, 2011	MP
<i>Pavarottia maiseyi</i> Bannikov, 2016	P
Family incertae sedis	



<i>Acrorunoides eocaenicus</i> Bannikov et al., 2019	P
<i>Frigoichthys margaritae</i> Bannikov, 2004	P
<i>Squamibolcoides minciotti</i> Bannikov & Zorzin, 2013	P
Percomorpha order incertae sedis	
Family Callipterygidae	
<i>Callipteryx preciosus</i> Agassiz, 1838	P
Family Carangodidae	
<i>Carangodes bicornis</i> (Volta, 1796)	P, MP
Family Eocottidae	
<i>Bassanichthys pesciarenensis</i> (Volta, 1796)	P
<i>Eocottus veronensis</i> (Volta, 1796)	P
Family Exelliidae	
<i>Exellia velifer</i> (Volta, 1796)	P
Family Pietschellidae	
<i>Nickcaves pterygocephalus</i> Carnevale & Bannikov, 2015	MP
<i>Pietschellus aenigmaticus</i> Bannikov & Carnevale, 2011	MP
Family Pterygocephalidae	
<i>Pterygocephalus paradoxus</i> Agassiz, 1839	P
Family Quasimullidae	
<i>Quasimullus sorbinii</i> Bannikov, 1999	P, MP
Family Robertannidae	
<i>Hendrixella grandei</i> Bannikov & Carnevale, 2009	P
<i>Robertannia sorbiniorum</i> Bannikov, 2011	P
Family Tortonesidae	
<i>Guus macrocephalus</i> (Agassiz, 1839)	P
<i>Tortonesia esilis</i> Sorbini, 1983	P
Family incertae sedis	
<i>Blotichthys coleanus</i> (Agassiz, 1838)	P, MP
<i>Bolcaperca craccorum</i> Bannikov & Zorzin, 2023	P
<i>Bradyurus alessandroi</i> Bannikov & Zorzin, 2022	P
<i>Bradyurus szajnochae</i> (De Zigno, 1887)	P
<i>Dibango volans</i> Davesne & Carnevale, 2025	P
<i>Frippia labroiformis</i> Bannikov & Carnevale, 2012	P
<i>Gillidia antiqua</i> (Agassiz, 1835)	P
<i>Jimtylerius temnopterus</i> (Agassiz, 1836)	P
" <i>Labrus</i> " <i>valenciennesi</i> Agassiz, 1839	MP
<i>Latellopsis latellai</i> (Bannikov, 2009)	P
<i>Malacopygaeus oblongus</i> (Agassiz, 1838)	P
<i>Mattarellaperca brevis</i> Bannikov & Zorzin, 2026	P
<i>Montepostalia annamariae</i> Bannikov & Zorzin, 2004	MP
<i>Oncolepis isseli</i> Bassani, 1897	P
<i>Parapelates quindecimalis</i> (Agassiz, 1836)	P
<i>Parapygaeus polyacanthus</i> Pellégrin, 1907	P
<i>Pygaeus bolcanus</i> (Volta, 1796)	P
<i>Pygaeus nobilis</i> Agassiz, 1838	P
<i>Pygaeus nuchalis</i> Agassiz, 1838	P
<i>Quasicichla mucistonaver</i> Bannikov, 2004	P
<i>Sorbinia caudopunctata</i> Bellwood, 1995	P
<i>Stefanichthys mariannae</i> Bannikov & Zorzin, 2020	P
<i>Veronabrax schizurus</i> (Agassiz, 1836)	P
<i>Voltamulloidides ceratorum</i> Bannikov, 2008	P
<i>Xiphopterus falcatus</i> (Volta, 1796)	P

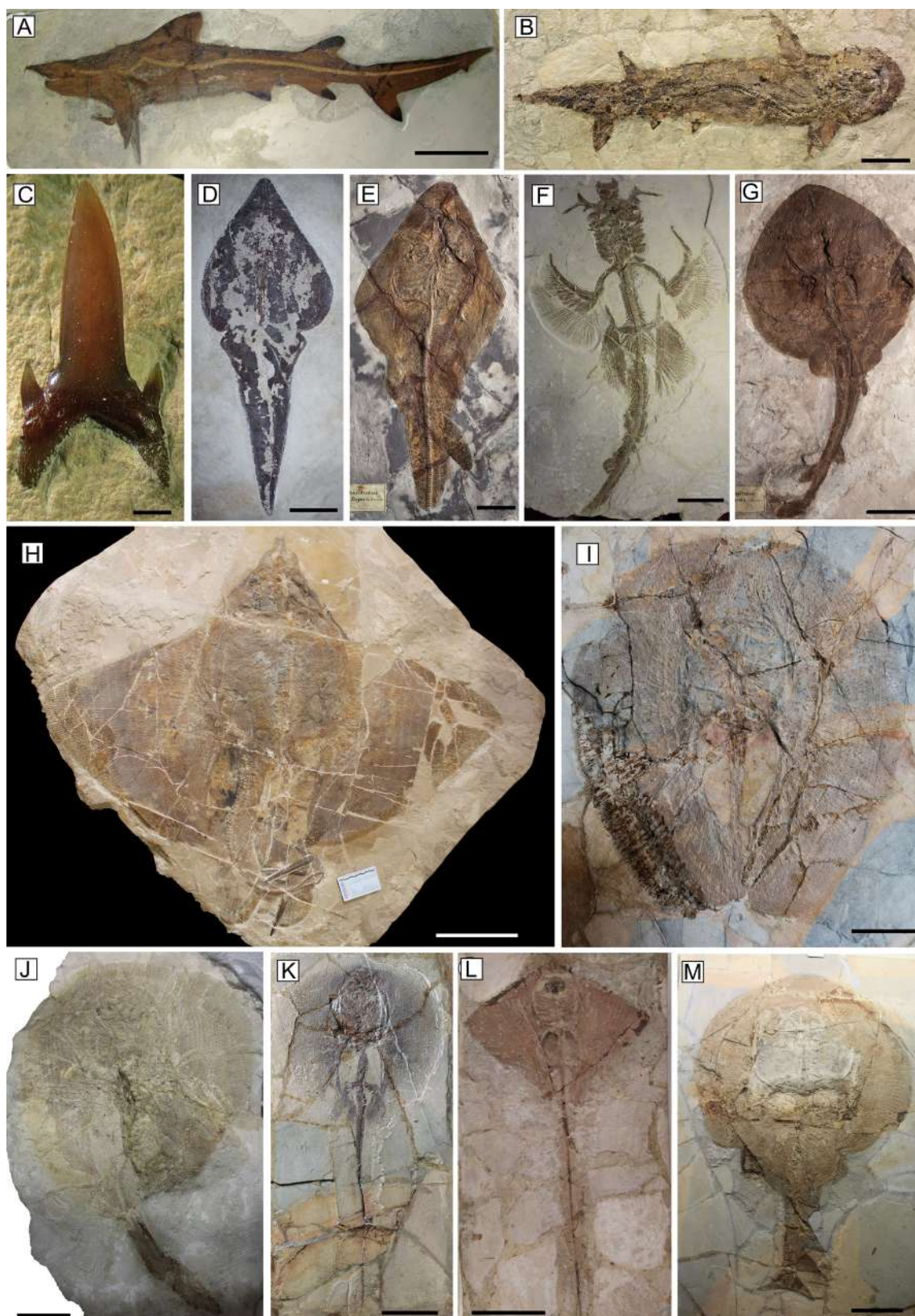


Fig. 26 - Sharks and rays (Elasmobranchii) from the Bolca Lagerstätten. A) *Galerorhinus cuvieri*, MCSNV T.1124; B) *Eogaleus bolcensis*, MCSNV T.311, holotype; C) *Brachycarcharias lerichei*, MCSNV IG.VR.69800; D) *Pseudorhinobatos dezigni*, NHMW 1853.XXVII.4, holotype; E) *Eorhinobatos primaevus*, MGP-PD 26278, holotype; F) *Titanonarke molini*, MCSNV IG.VR.67290; G) *Eoplatyrhina bolcensis*, MGP-PD 26279C; H) *Dasyomyliobatis thomyorkei*, MCSNV VR.21.107, holotype; I) *Lessiniabatis aenigmatica* MNHN F.Bol566, holotype; J) *Arechia crassicaudata*, MCSNV IG.VR.27607, neotype; K) *Tethytrygon muricatus*, MNHN F.Bol564, holotype; L) *Promyliobatis gazolai*, MCSNV VII.B.90, holotype; M) *Plesiozanobatus egertoni*, MCSNV VII.B.81. Scale bars of A-B, D-M 100 mm; scale bar of C 2 mm.

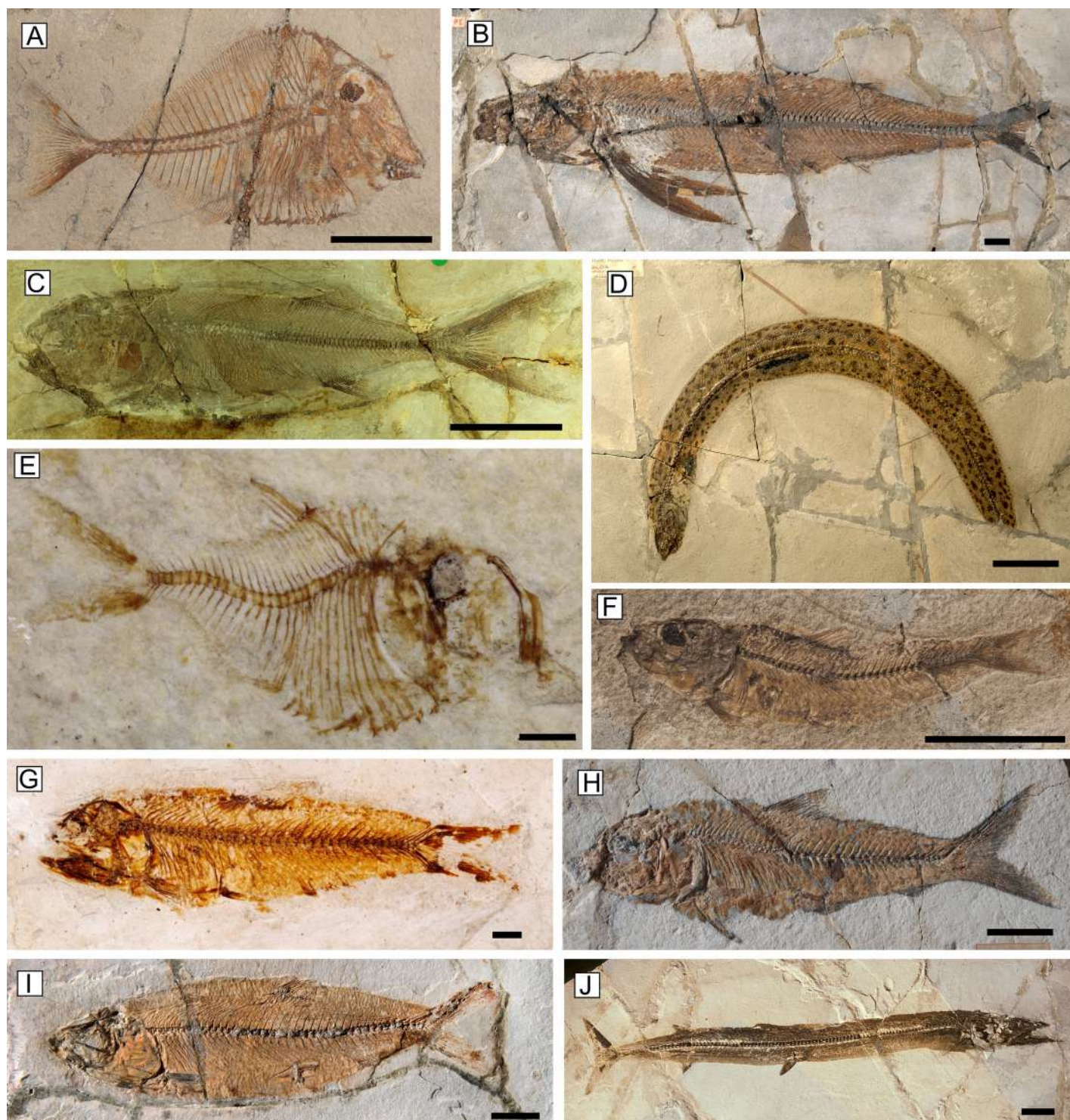


Fig. 27 - Non-acanthomorph teleosts from the Bolca Lagerstätten. A) *Pycnodus apodus*, CM 4480; B) *Platinx macropterus*, MNHN F.Bol289, holotype; C) *Foreyichthys bolcensis*, NHMUK P.16821, holotype; D) *Paranguilla tigrina*, MGP-PD 26288; E) *Eoellimmichthys superstes*, MCSNV IG.23695, holotype; F) *Bolcaichthys catopygopterus*, NHMUK P.3829a, holotype; G) *Eoengraulis fasoloi*, MCSNV T.54; H) *Chanoides macropoma* MNHN F.Bol77, holotype; I) *Coelogaster leptostea*, MNHN F.Bol85, holotype; J) *Holosteus esocinus*, MCSNV IG.23602. Scale bars of A-D, F, H-J 20 mm; scale bars of E, G 2 mm.

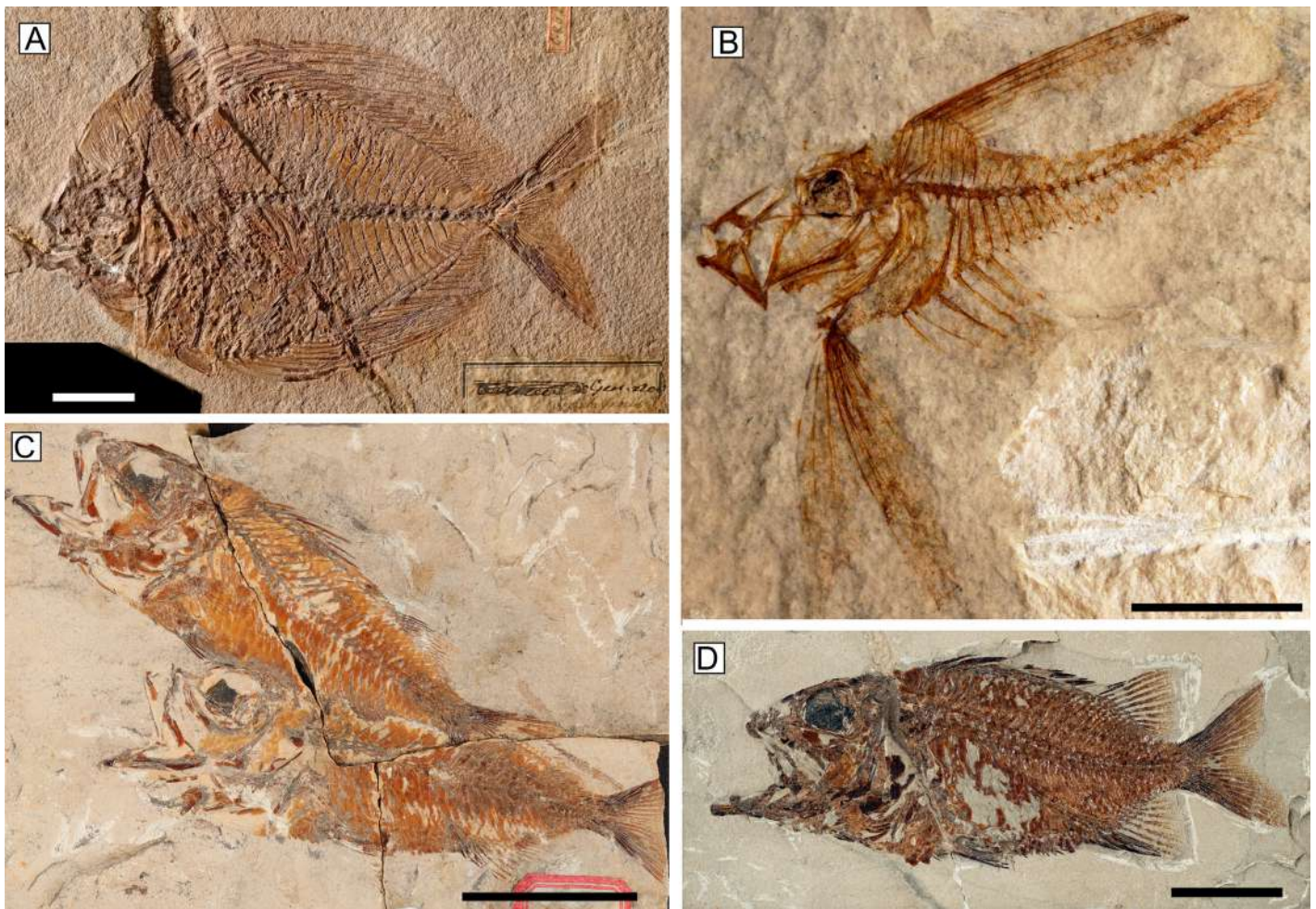


Fig. 28 - Non-percomorph acanthomorphs from the Bolca Lagerstätten. A) *Wettonius angeloi*, MGP-PD 6852, holotype; B) *Bajaichthys elegans*, MCSNV T.922, holotype; C) *Berybolcensis leptacanthus*, CM 4216; D) *Eoholocentrum macrocephalum*, CM 4455. Scale bars of A, C-D 20 mm; scale bar B 10 mm.

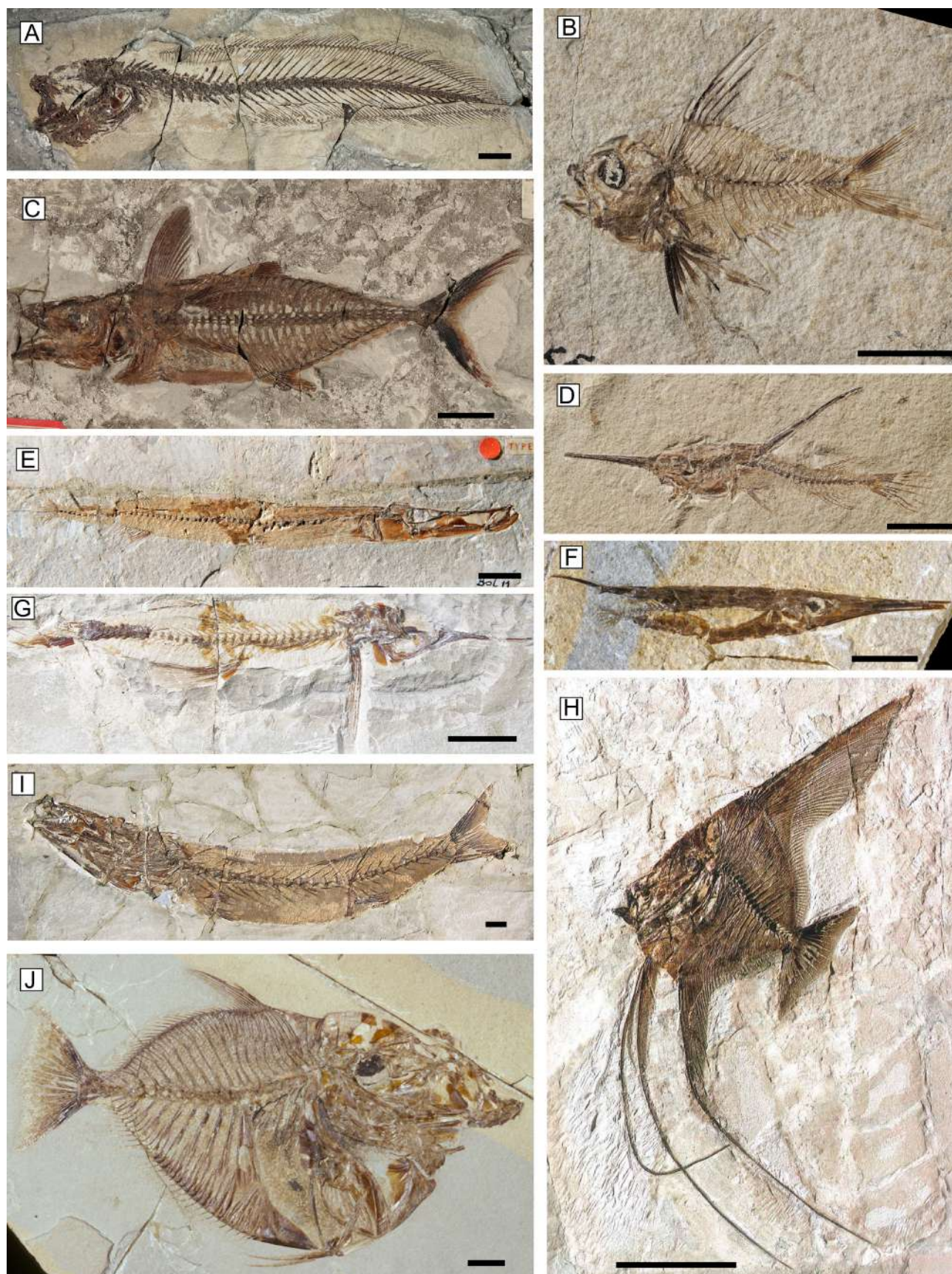


Fig. 29 - Percomorphs from the Bolca Lagerstätten. A) *“Ophidium” voltianum*, MCSNV T.156; B) *Eosphaeramia pygopterus*, MCSNV IG.129655; C) *Godsilia lanceolata*, CM 4533; D) *Rhamphosus rastrum*, MCSNV T.286, neotype; E) *Eoaulostomus bolcensis*, MNHN F.Bol11; F) *Paramphisile weileri*, MCSNV T 989; G) *Rhamphoexocoetus volans*, MCSNV V.294; H) *Ceratoichthys pinnatiformis*, MCSNV T.950; I) *Sphyræna bolcensis*, MCSNV VIII.A.13; J) *Vomeropsis triurus*, MCSNV T.1022. Scale bars of A-G, I, J 10 mm; scale bar of H 100 mm.

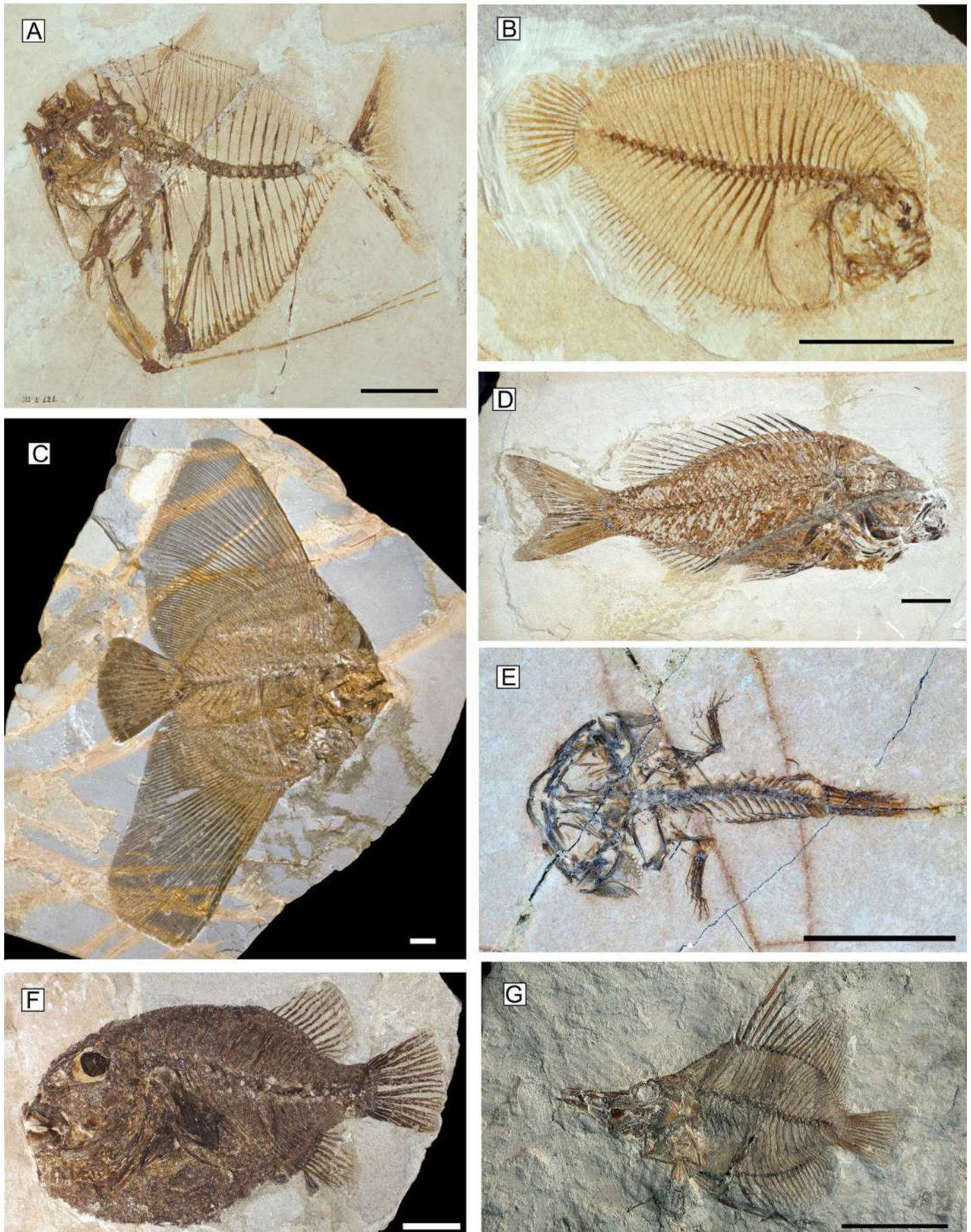


Fig. 30 - Percomorphs from the Bolca Lagerstätten. A) *Mene rhombea*, MCSNV VII.E.122; B) *Eobothus minimus*, MCSNV T.968; C) *Eoplatax papilio*, MCSNV IG.24573; D) *Sparnodus vulgaris*, MCSNV IG.24546; E) *Sharfia mirabilis*, MNHN F.Bol38-39, holotype; F) *Zignoichthys oblongus*, CMC 40; G) *Massalongius gazolai*, MCSNV VIII.D.200, holotype. Scale bars 20 mm.

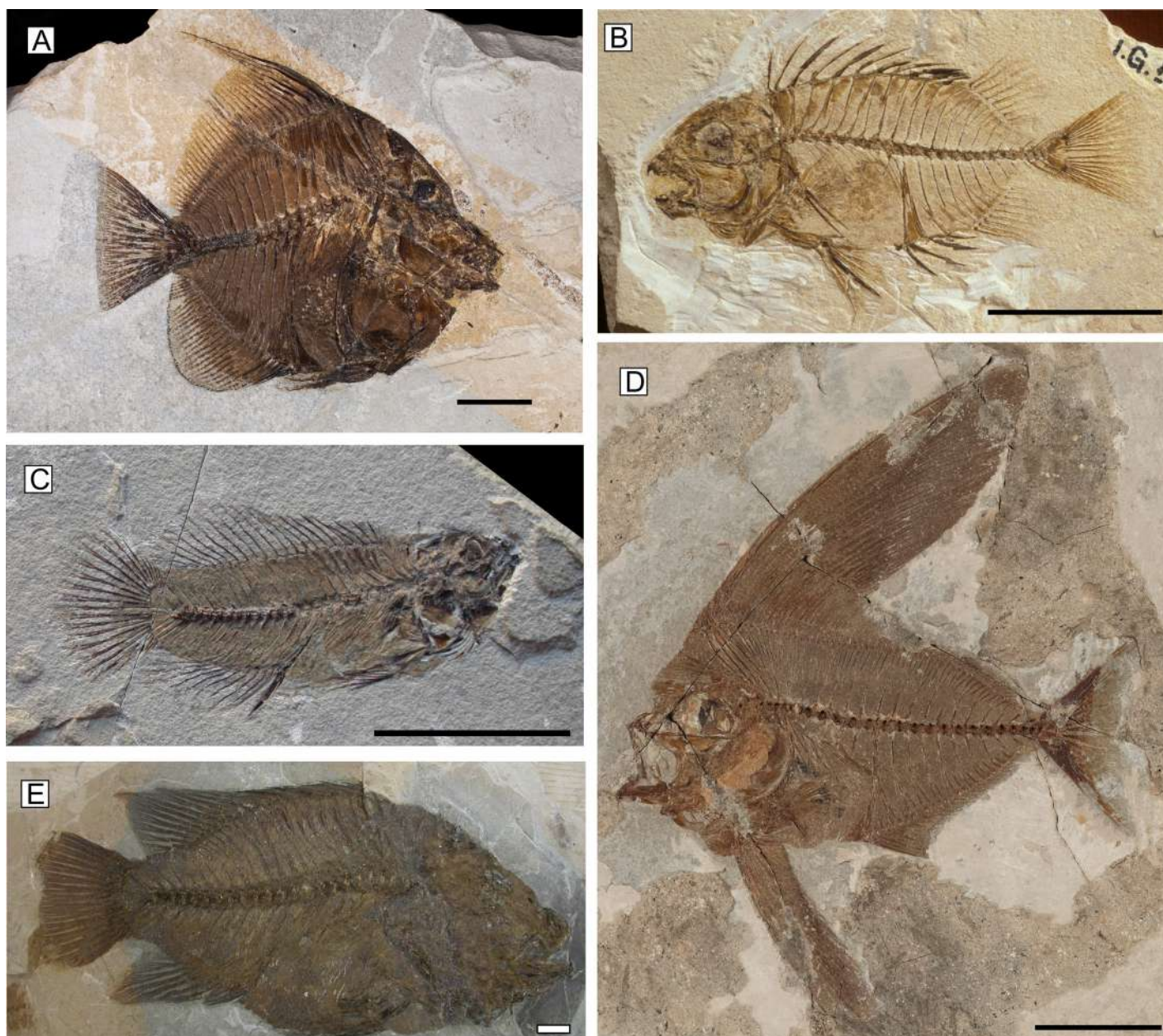


Fig. 31 - Percomorphs from the Bolca Lagerstätten. A) *Angiolinia mirabilis*, CMC 39, holotype; B) *Ruffoichthys bannikovi*, MCSNV IG.132596, holotype; C) *Frippia labroiformis*, MCSNV T.187; D) *Exellia velifer*, CM 4467; E) *Pygaeus bolcanus*, MCSNV IG.VR.81911. Scale bars 20 mm.

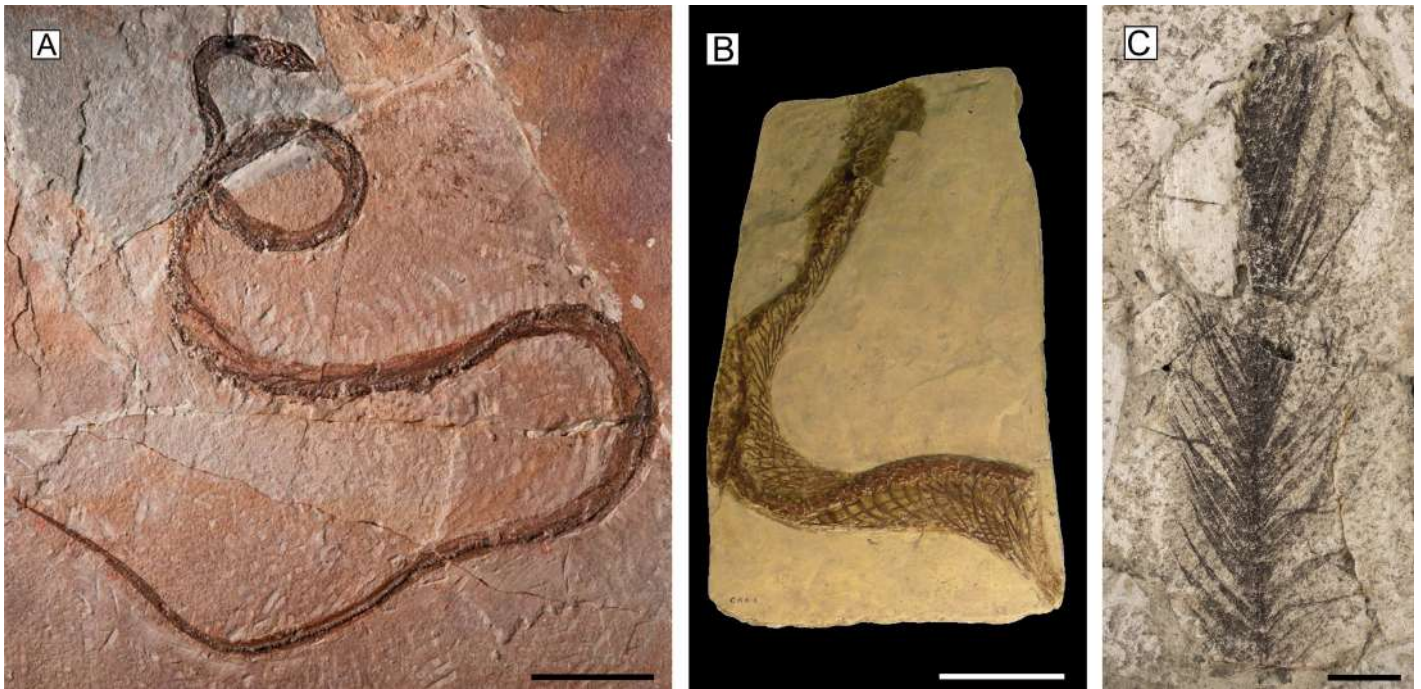


Fig. 32 - Terrestrial vertebrates from the Bolca Lagerstätten. A) the snake *Archaeophis proavus*, MBR 3554, holotype; B) the snake *Anomalophis bolcensis* MCSNV C.A.R1; C) *Ornitholites* sp., MCSNV a.B.2. Scale bars of A and B 50 mm; scale bar of C 10 mm.



PALAEOENVIRONMENTAL INTERPRETATION

The palaeoenvironmental setting of the laminated micritic limestone of the Bolca Lagerstätten, particularly that of the Pesciara, has been discussed in a number of studies, resulting in a complex scenario of palaeophysiographic and palaeoecological reconstructions. The remarkable taxonomic diversity of the fish assemblages of the Bolca sites, their clear shallow water nature, and the relative abundance of terrestrial invertebrates and plants have been traditionally used to interpret the origin of the fossiliferous laminated deposits in a tropical coastal lagoon in close proximity to coral reefs and seagrass beds (e.g., Sorbini, 1968; Blot, 1969). The different composition of the fish assemblages and preservation of the fossil material, however, suggest that the two main sites of the Bolca area record different environmental settings characterised by different palaeogeographic and palaeoecological features. Based on the composition of the Pesciara fish assemblage, Landini and Sorbini (1996) hypothesised that the deposition of the laminated micritic limestone occurred in a silled depression with restricted circulation on the bottom, many dozens of meters in depth, at a short distance from the coast. According to these authors, coral reefs, open expanses of *Halochloris* sand, and seagrass beds were present in close proximity to the depositional environment. An integrated approach based on facies analysis and foraminiferal paleoecology was used by Papazzoni and Trevisani (2006) to hypothesise the configuration of the Pesciara palaeobiotope as a subtropical lagoon close to an emerged area and characterised by seasonal changes of water circulation, which modulated oxygen content on the sea floor. Although some aspects of the physiography of the Pesciara palaeobiotope remains not conclusively defined, all the recent studies concluded that it was part of a peri-reefal system subject to the ecological influence of both the coastal environment and the open sea, and that the deposition of the fossiliferous micritic limestone took place in a depressed basin characterised by permanent bottom dysoxia or anoxia and very low hydrodynamic energy (Marramà et al., 2016). In this context, the primary production was at times conspicuous and dominated by diatoms (Schwark et al., 2009), which constituted the base of the trophic chain of the Pesciara assemblage, sustaining large shoals of the sardine *Bolcaichthys catopygopterus*, the most common element of the Pesciara fish assemblage (Marramà and Carnevale, 2015b).

Moreover, Schwark et al. (2009) found that the organic matter in the Pesciara laminated limestones contain a minor admixture of terrigenous material. The biomarkers indicate that this terrigenous fraction is predominantly made up by land plant waxes transported by aeolian

processes. Only in the lowermost fish-bearing level of the Pesciara (Fig. 6), the terrigenous-derived organic matter indicates significant terrestrial freshwater runoff (Schwark et al., 2019).

About 50% of the fossil content of the fossiliferous laminated limestone of the Monte Postale succession consists of remains of algae and plants, which are followed by fish skeletal remains (about 30%) showing different degrees of completeness and abundant invertebrates (corals, molluscs and crustaceans). Fishes primarily consist of small-sized epibenthic taxa that are associated with a few large-sized individuals (Marramà et al., 2016). A detailed stratigraphic and paleontological analysis of the Monte Postale succession (Vescogni et al., 2016) concluded that the laminated limestone originated in a lagoon surrounded by small-sized corallgal buildups made of corals, calcareous algae, and encrusting foraminifera, alternated with loose accumulations of sands made up by *Alveolina*, giving rise to a narrow, elevated margin (Fig. 33) with paleodepth typically of a few meters. This margin, acting as a threshold, faced on the distal side the open sea, most probably with a steep ramp going rapidly to significant depth, whereas on the proximal side delimited a more or less restricted basin (lagoon) which was periodically subjected to dysoxic-anoxic conditions (Fig. 34). The accumulations of loose bioclastic sediments on the threshold probably acted as substrate for the colonisation of seagrass patches and dasycladacean green algae. The corallgal rim structure was not continuous, presumably crossed by shallow channels allowing at least intermittent connection of the open seawater with the protected lagoon; the observed high degree of abrasion of the *Alveolina* tests is reasonably related to the action of waves and tides, and probably also to the relatively frequent storms hitting this palaeoenvironment. The rim, whose extension is estimated to be no more than 20–30 m across, was maintained close to the sea-level over time by a robust, skeletal framework built by heavily calcified organisms, limiting the water exchange between the lagoon and the open sea both during phases of highstand and lowstand (Fig. 34). However, sea-level fluctuations periodically allowed a less-effective barrier during sea-level rise periods (transgressions; see Fig. 34), and the anoxic conditions disappeared, allowing the deposition of non-laminated wackestones that are quite common in the Monte Postale succession.

ACKNOWLEDGEMENTS

We are particularly obliged to Mariagabriella Fornasiero (MGP-PD), Sarah Davis (CM), Emma Bernard (NHMUK), Gaël Clement, Alan Pradel, Monette Veran and Jean-Michel Pacaud (MNHN), Ursula Göhlich, Mathias Harzhauser and Thomas Nichterl (NHMW), Carola



Radke (MBR), Barbara Favaretto (MSNVE), Giorgio Teruzzi (MSNM), the late Magda Biasiolo (MCBG), and Massimo Cerato (CMC, MFB) for access to fossil material in their care and logistic support. We are grateful to Stefano Castelli (Dipartimento di Geoscienze, Università degli Studi di Padova) for his valuable help with photographs. Francesca Bosellini (Dipartimento di Scienze Chimiche e Geologiche, Università di Modena e Reggio Emilia, Modena) is thanked for her support with the taxonomy of corals from Monte Postale. Alessandra Busulini (Società Veneziana di Scienze Naturali, Venezia) provided the pictures of the

crustaceans of the bioconstructions. For reviewing the manuscript and providing many constructive suggestions for its improvement, we are particularly grateful to Giulia Bosio (Dipartimento di Scienze della Terra, Università di Pisa), Manuel Amadori (Department of Palaeontology, University of Vienna) and Simone Fabbi (Dipartimento di Scienze della Terra, Sapienza Università di Roma). The Italian Ministry of Culture - Superintendence of Archaeology, Fine Arts and Landscape for the provinces of Verona, Rovigo and Vicenza made available the photographs of the fossils housed in the MCSNV.

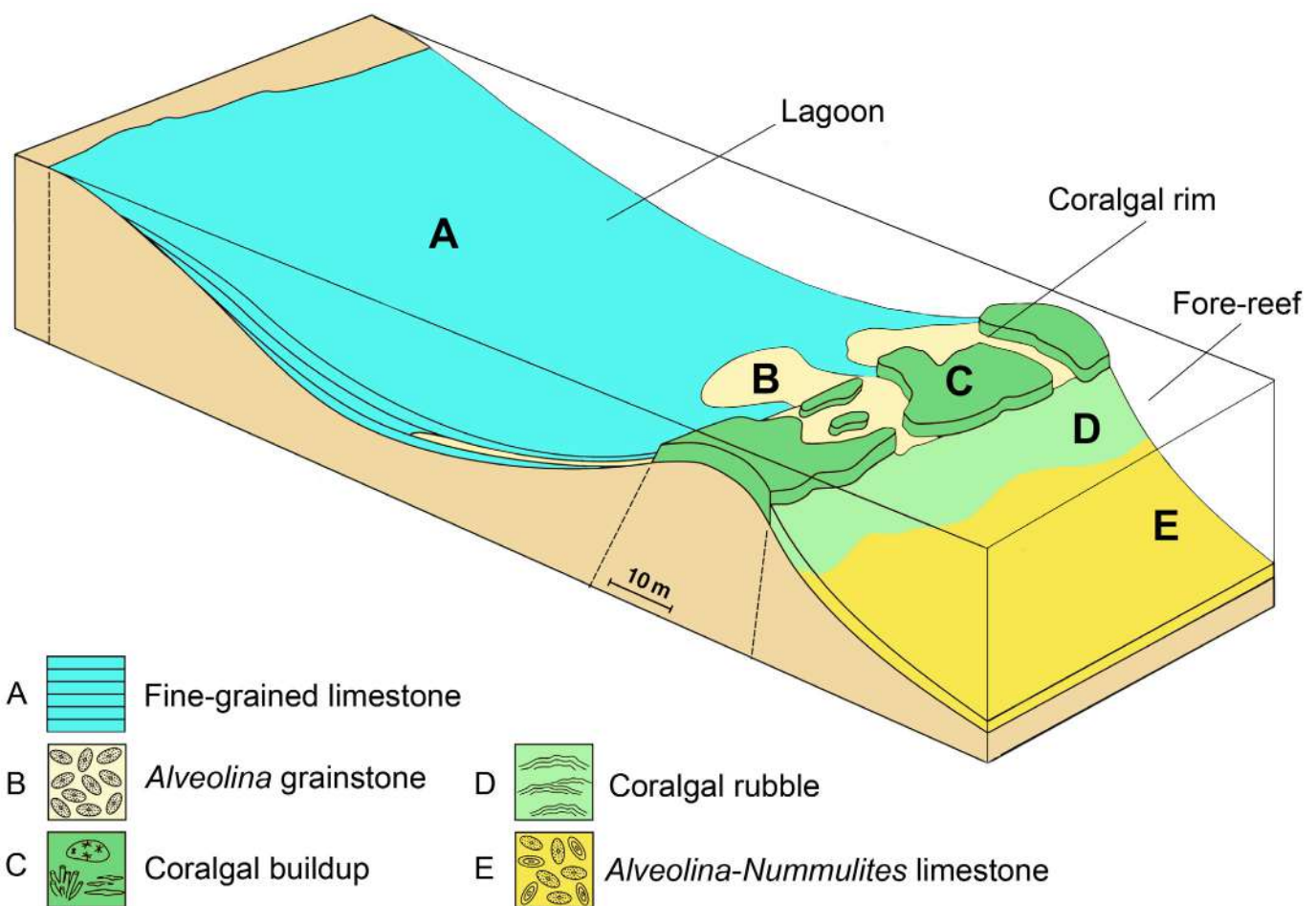


Fig. 33 - Idealised reconstruction of the depositional system of the sites of the from the Bolca *Lagerstätten*. The width and depth of the lagoon are not to scale. Modified after Vescogni et al. (2016).

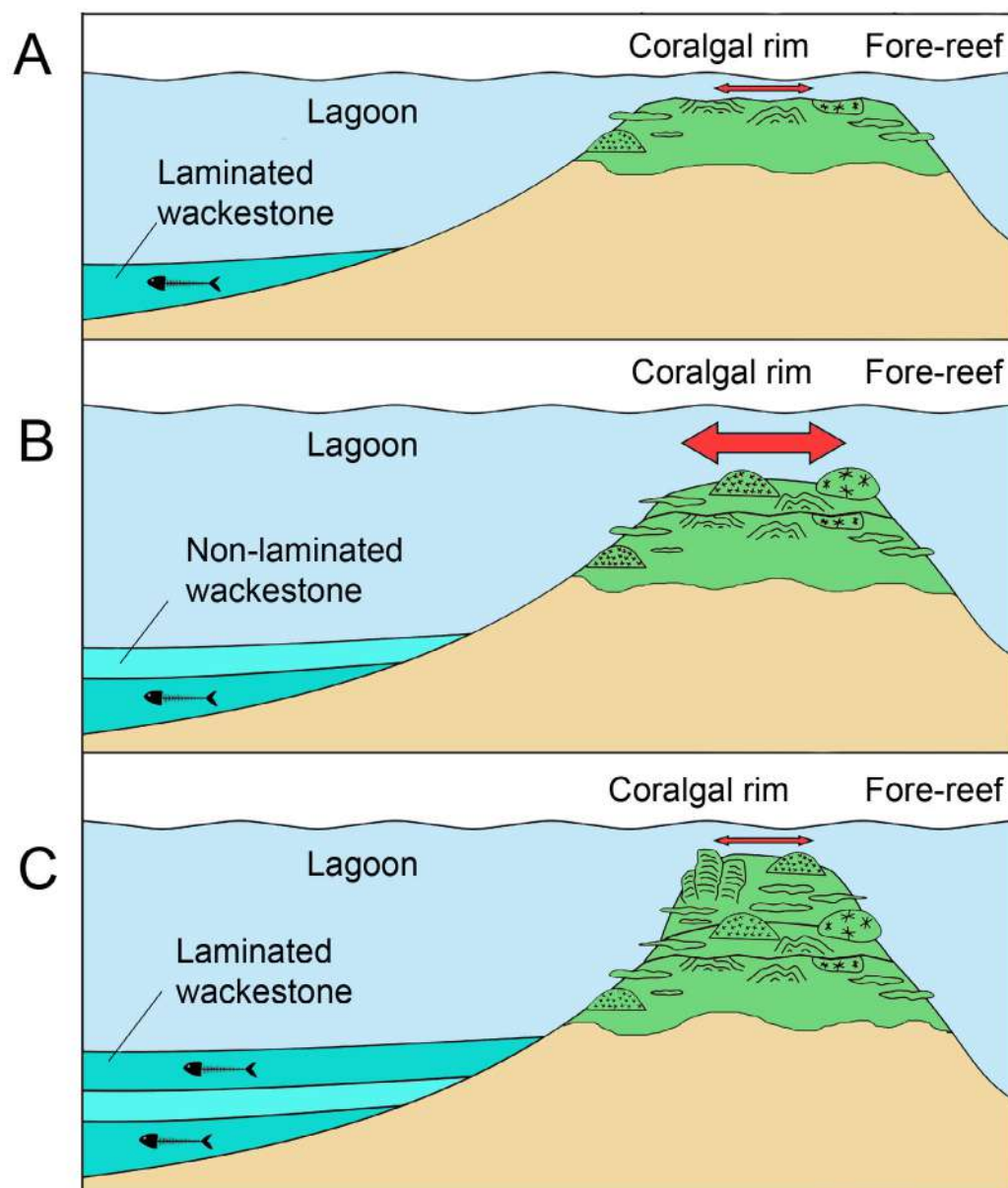


Fig. 34 - Palaeoenvironmental model showing changes in the relative influence of the threshold on the deposition of fine-grained or laminated limestones of the Monte Postale site. Modified after Vescogni et al. (2016).

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Manuscript received 20 March 2026; accepted 05 May 2026; published online 26 May 2026;
editorial responsibility and handling by S. Fabbi.