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

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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.

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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.

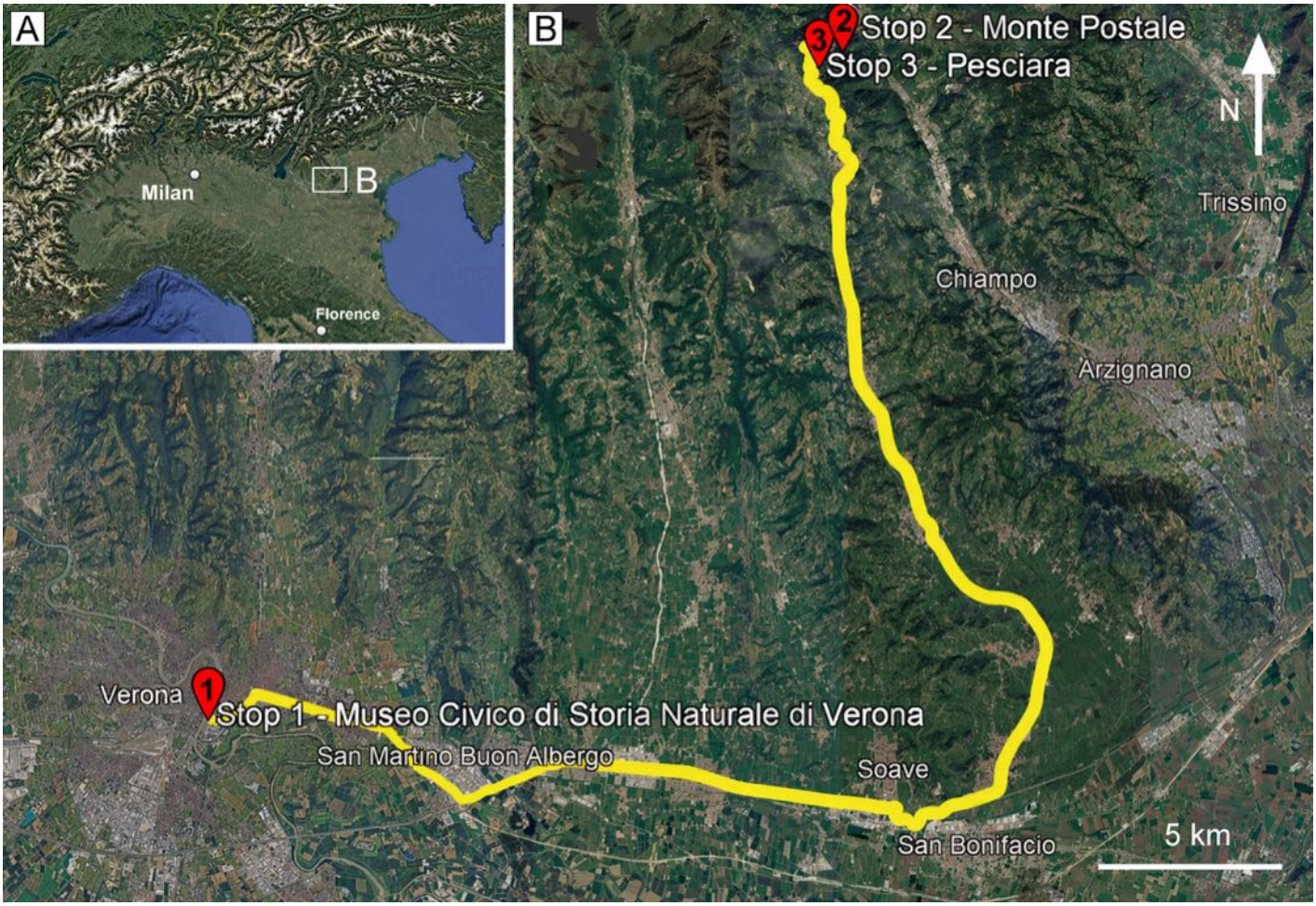

Fig. 1 - A) Location of field trip are in northern Italy; B) Itinerary map of the field trip. Stop 1 = Museo Civico di Storia Naturale di Verona; Stop 2 = Monte Postale; Stop 3 = Pesciara di Bolca. Satellite images taken from Google Earth.

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 Francesci Calceolari Iunioris 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–Agno 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-Agno Graben is bounded by the Castelvero 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 Castelvero fault, but within the Alpone-Agno Graben. Within the graben, in the eastern area, subsidence was more active, and basaltic

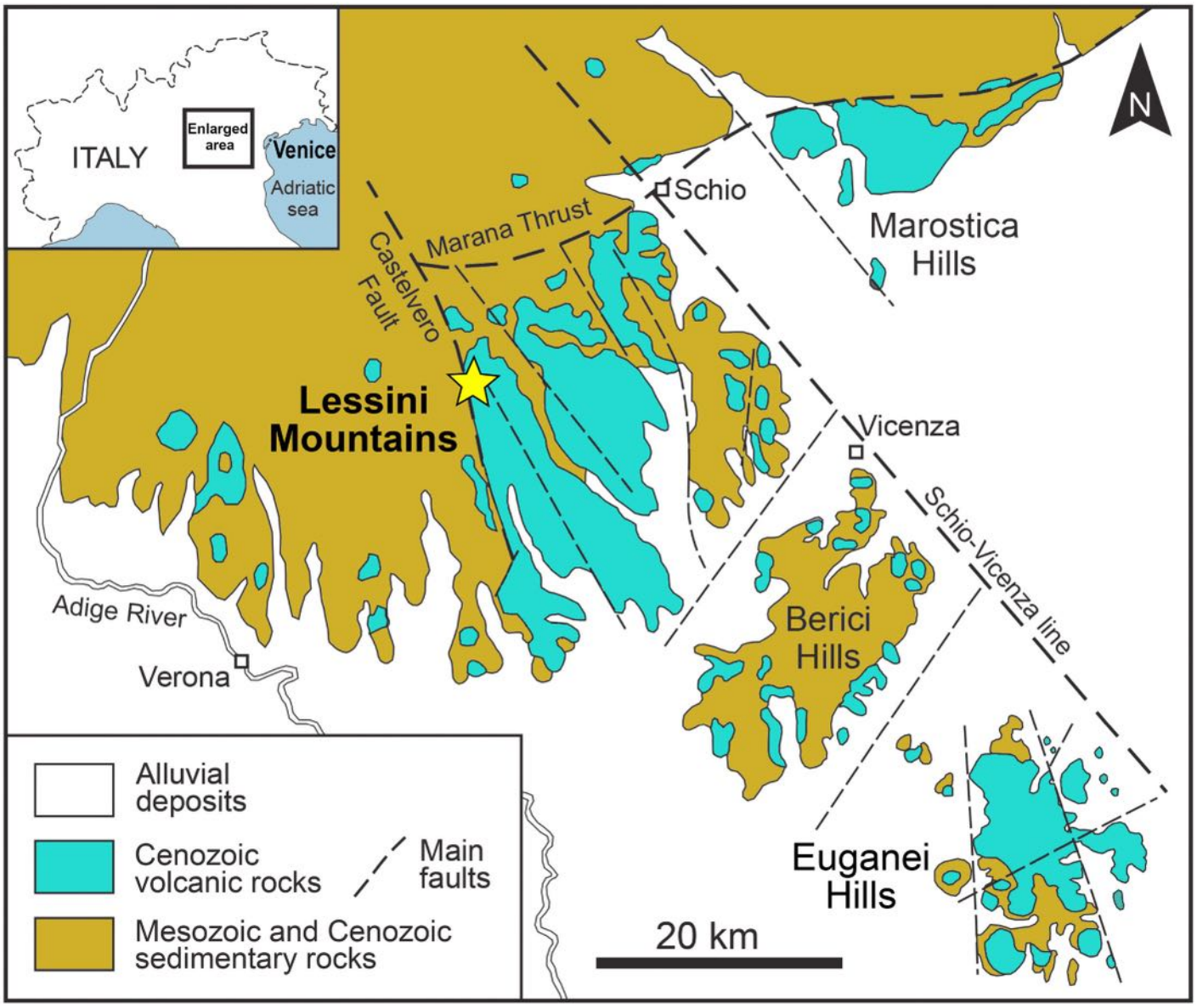

Fig. 2 - Simplified geological map of the Lessini Mountains. Berici Hills, and Euganei Hills (modified after Mattioli et al., 2016). The yellow star shows the position of Bolca.

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 "*Calcareniti 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, volcaniclastic, 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, Brusaferri, 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 "*Calcari di Spilecco*", whereas the middle Eocene ones were referred to the informal unit called "*Calcari Nummulitici*". However, the Monte Postale limestones were traditionally attributed to the "*Calcari 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 '*Calcari 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 volcaniclastic 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.

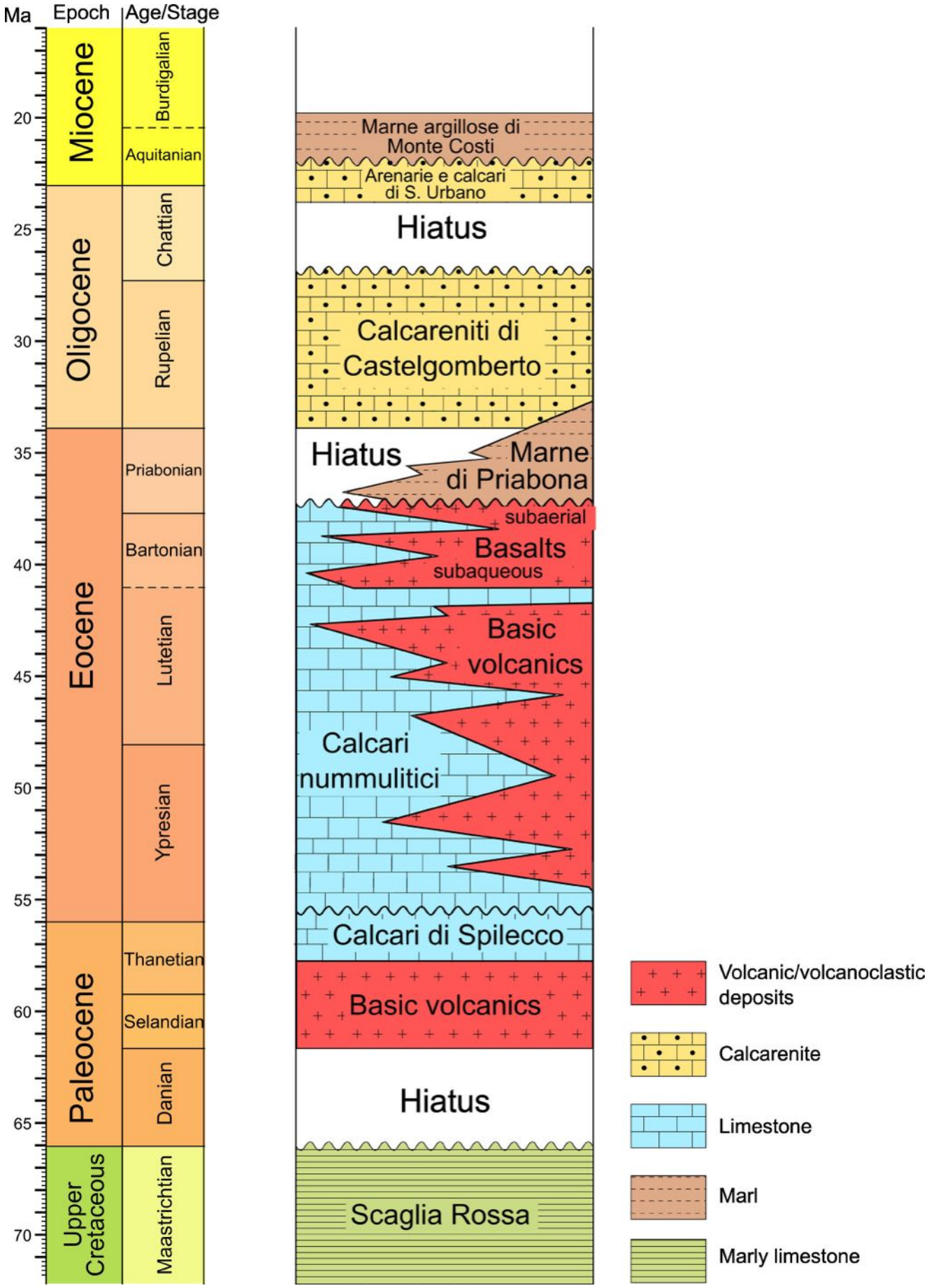

Fig. 3 - Generalised stratigraphy of the eastern Lessini Mountains. Modified after Brombin et al. (2019).

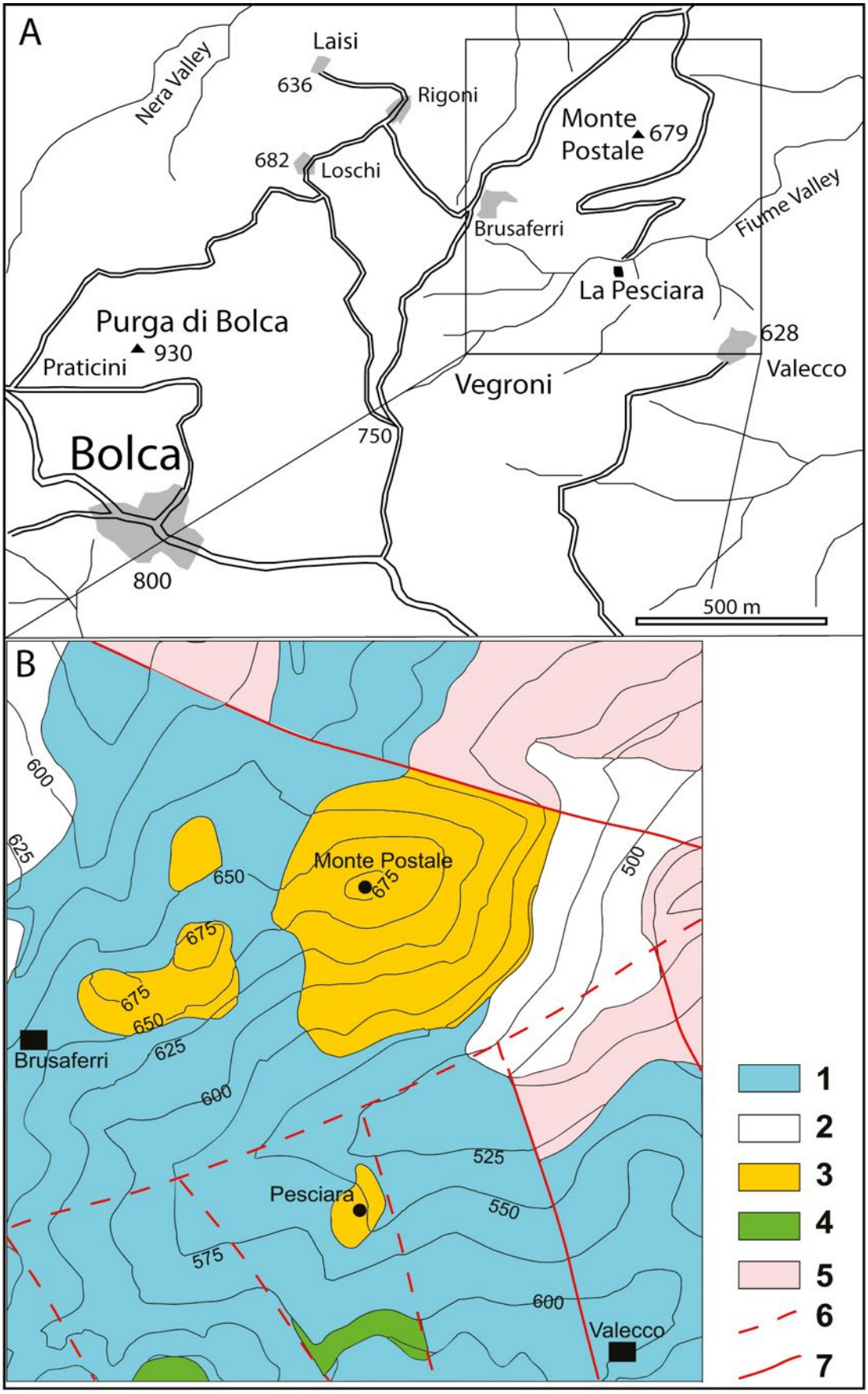

Fig. 4 - Simplified geological map of the Bolca area. Modified after Dal Degan and Barbieri (2005). 1) Volcanic and volcanoclastic deposits; 2) Quaternary alluvial and detrital deposit; 3) "Formazione del Monte Postale"; 4) "Calcari Nummulitici"; 5) Mesozoic "Scaglia Rossa" and "Maiolica"; 6) Alleged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

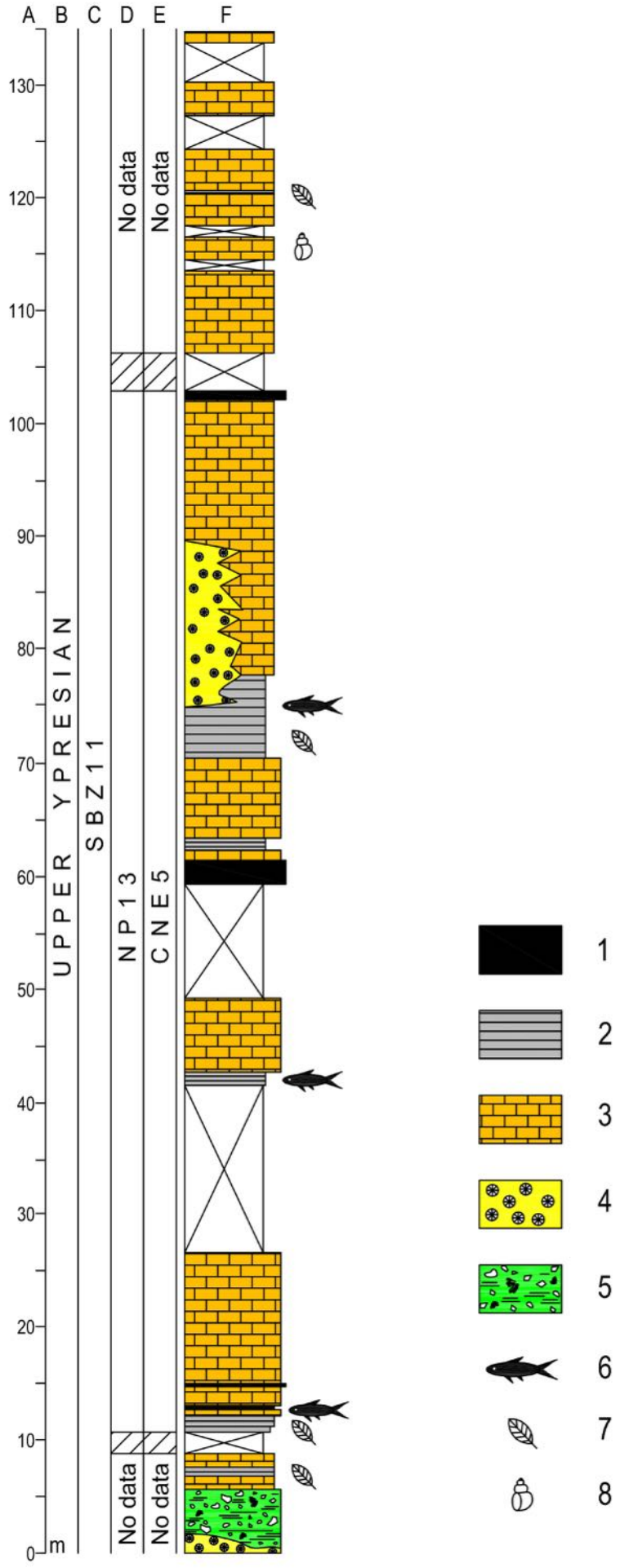

Fig. 5 - Composite stratigraphic column of the Monte Postale succession. Modified after Papazzoni et al. (2017). 1) basalts; 2) laminated limestones; 3) biocalcarenites and biocalcirudites; 4) coralgal limestones; 5) coral rubble; 6) fish; 7) vegetal remains; 8) molluscs. A) Thickness (m); B) Chronostratigraphy; C) Shallow Benthic Zones (SBZ after Serra-Kiel et al., 1998); D) Calcareous nannofossil zones NP after Martini (1971); E) Calcareous nannofossil zones CNE after Agnini et al. (2014).

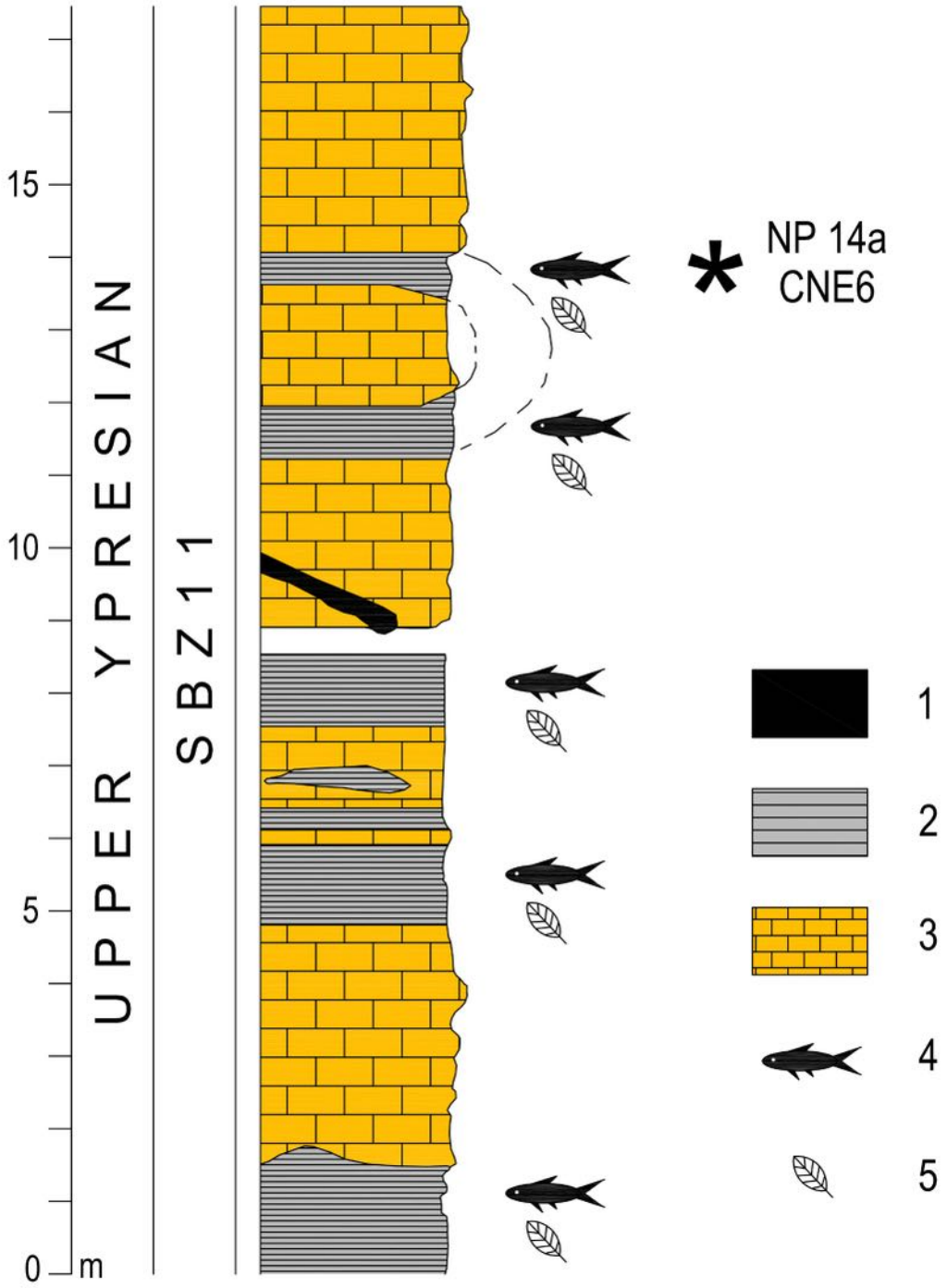

Fig. 6 - Stratigraphic column of the Pesciara site. Modified after Papazzoni and Trevisani (2006) and Mironenko et al. (2024). 1) basalts; 2) laminated limestones; 3) biocalcarenites and biocalcirudites; 4) fish; 5) vegetal remains.

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.

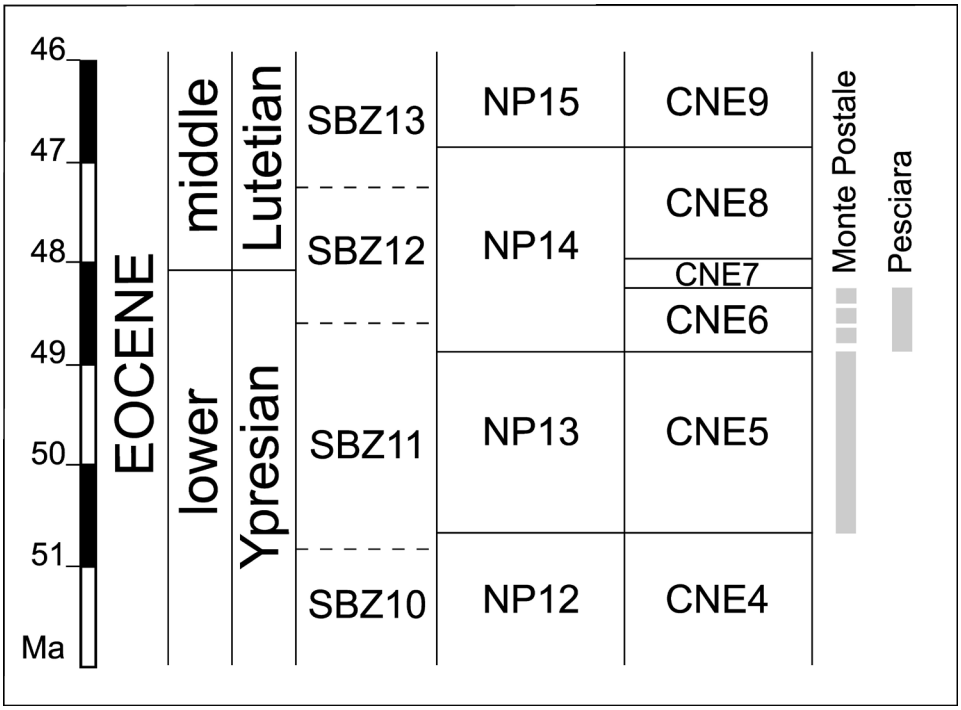

Fig. 8 - Biochronostratigraphic sketch showing the time spans covered by the Monte Postale and Pesciara limestone, incorporating the Shallow Benthic Zones (SBZ after Serra-Kiel et al., 1998) and calcareous nannofossil zones (NP after Martini, 1971 and CNE after Agnini et al., 2014). Time scale after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

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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	
Assilina laxispira de la Harpe in Rozlozsnik, 1926	MP
Nummulites aquitanicus Benoist, 1889	MP
Nummulites burdigalensis burdigalensis de la Harpe in Rozlozsnik, 1926	MP
Nummulites irregularis Deshayes, 1838	MP
Nummulites kaufmanni Mayer-Eymar, 1876	MP
Nummulites nitidus de la Harpe, 1883	MP
Nummulites partschi de la Harpe, 1880	MP
Nummulites planulatus (Lamarck, 1804)	MP
Nummulites pratti d'Archiac and Haime, 1853	P, MP
Nummulites prelucasi Douvillé, 1924	P
Nummulites rotularius Deshayes, 1838	P, MP
Nummulites tauricus de la Harpe in Rozlozsnik, 1926	MP
Class Tubothalamea	
Order Miliolida	
Family Alveolinidae	
Alveolina cremae Checchia-Rispoli, 1905	P, MP
Alveolina dainellii Hottinger, 1960	MP
Alveolina decastroi Scotto di Carlo, 1966	P, MP
Alveolina distefanoi Checchia-Rispoli, 1905	P, MP
Alveolina fornasinii Checchia-Rispoli, 1909	MP
Alveolina frumentiformis Schwager, 1883	MP
Alveolina levantina Hottinger, 1960	P, MP
Alveolina minuta Checchia-Rispoli, 1909	P, MP
Alveolina postalensis Fornaciari, Giusberti & Papazzoni, 2019	P, MP
Alveolina ruetimeyeri Hottinger, 1960	P, MP
Alveolina rugosa Hottinger, 1960	P, MP
Alveolina cf. *schwageri* Checchia-Rispoli, 1905	P, MP
Alveolina triestina Hottinger, 1960	MP
Glomalveolina minutula 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 *Delesserites* (*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*, *Halimedae*, *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 *Eichorniopsis* 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 (caesalpinioid 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, Gentianeceae, Graminaceae, Haloragidaceae, Liliaceae, Marsileaceae, Myricaceae, Myrtaceae, Najadaceae, Nymphaeaceae, Papilionaceae, Podostomaceae, Santalaceae, Sapindaceae, Sapotaceae, Saxifragaceae, Sterculariaceae, 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 Sterculariaceae 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 Zsivin, 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.

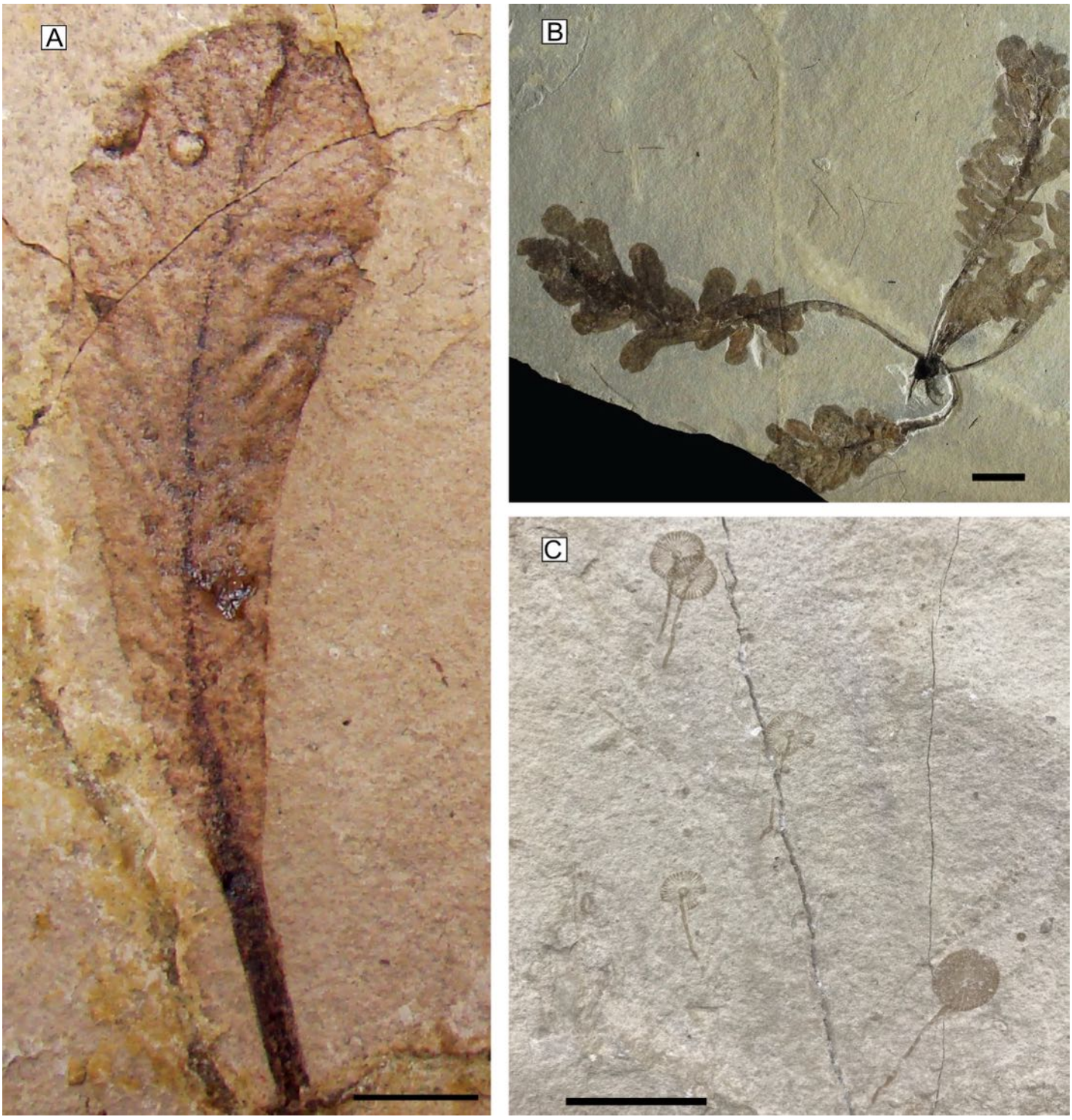

Fig. 9 - Selected plant remains from the Bolca *Lagerstätten*. A) Flat blades with rounded apices of the red algae *Delesserites*, MCSNV fG.142; B) *Pterigophycos* sp., a nearly complete thallus of a red alga specimen, MFB 22.116; C) the umbrella-shaped cap green algae *Acetabularia*, MCSNV 20.4.593.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

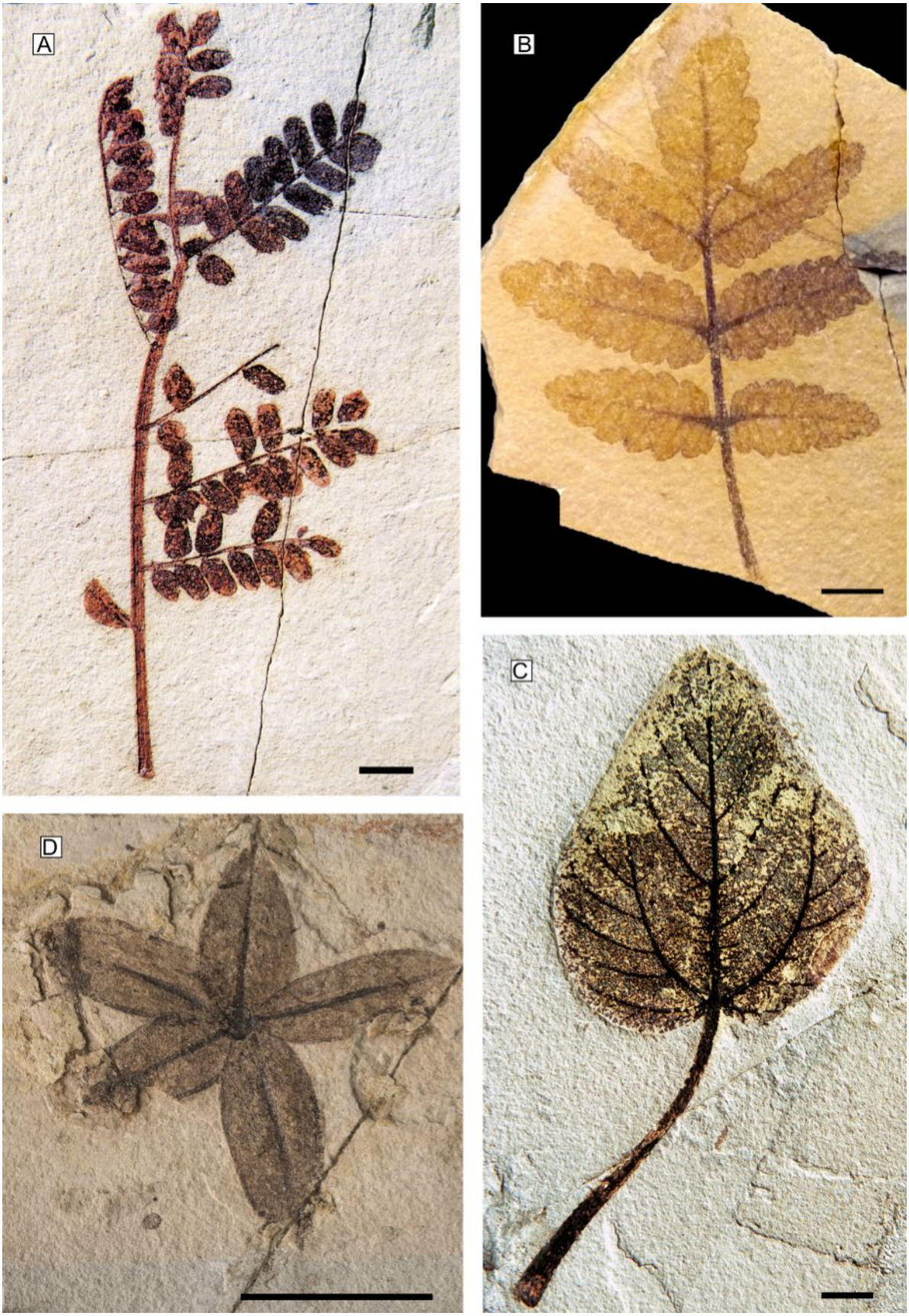

Fig. 10 - Selected plant remains from the Bolca *Lagerstätten*. A) Caesalpinioid leaf type of leguminous species belong to *Caesalpinia eocenica*, MCSNV fM.739; B) Imparipinnate leaves with leaflets with crenulate margin, *Weinmannia* (Sassifragaceae), MCSNV IG.VR. 71943; C) *Dombeyopsis*, a typical 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.

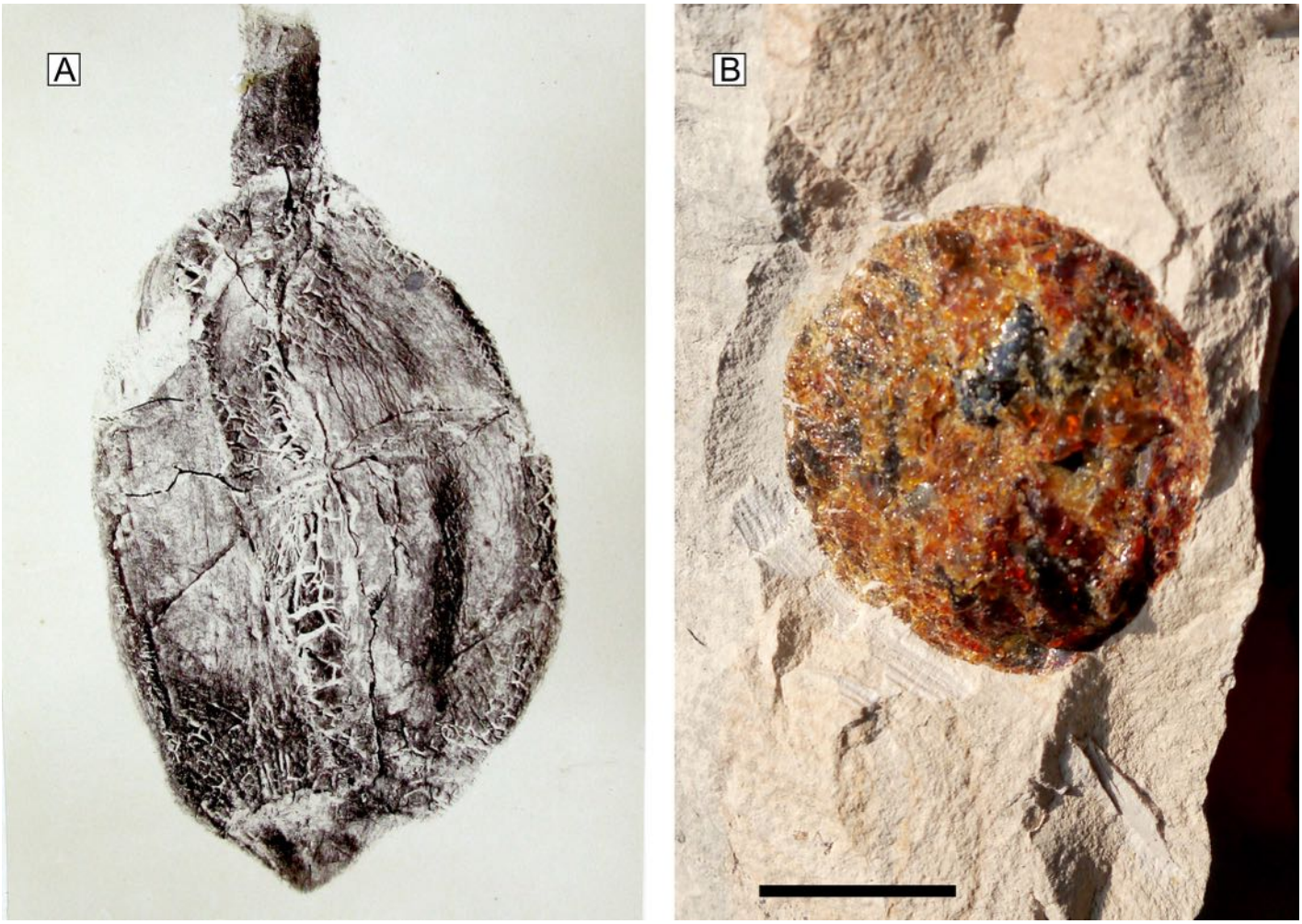

Fig. 11 - Selected plant remains from the Bolca *Lagerstätten*. A) Large fruit belonging to *Fracastoria*. This is one of the earliest published photographs of fossil plants (Massalongo, 1859b); B) Amber nodule (diameter 35 mm) from the fish-bearing laminated limestone of the Pesciara di Bolca, CMC 132. 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		
	Aristophycos agardhianus (Brogniart) Massalongo, 1858	B
	Caulerpites araucaria Massalongo, 1858	B
	Halimedeae	B
	Family Dasycladaceae	
	Sthenelaites dasiaeformis (Massalongo, 1855)	B
Red Algae		
	Family Confervaceae	
	Nemalionites cristatus Massalongo, 1858	B
	Nemalionites limacoides Massalongo, 1851	B
Class Floridae		
	Amansites prionomorphus Massalongo	B
	Ceramites codioides Massalongo, 1851a	B
	Ceramites floccosa Massalongo, 1851	B
	Ceramites parasitica Massalongo, 1851a	B
	Ceramites pectinata Massalongo, 1851a	B
	Ceramites sphacelarioides Massalongo, 1851a	B
	Ceramites sciuroides Massalongo	B
	Delesseria bolcensis (Massalongo) Meschinelli & Squinabol	B
	Delesseria bolcensis v. *bertrandi* (Massalongo) Meschinelli & Squinabol	B

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

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

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

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

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

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

Species without precise affinity Normapolles		
	Basopollis sp.1	P
	Basopollis sp.2	P
	cf. *Basopollis* sp.	P
	Interpollis microsupplingensis	P
	Interpollis supplingensis	P
	Plicapollis pseudoexcelsus	P
	cf. *Pompeckjoidaepollenites* sp.	P
	Pseudoplicapollis sp.	P
Family Icacinaceae		
	Compositoipollenites rhizophorus	P
Family Juglandaceae		
	Boehlensipollis sp.	P
	Gallopollisminimus subsp. concaviformis	P
	cf. *Platycaryapollenites* sp.	P
	Plicatopollis sp.	P
	Subtriporopollenites anulatus	P
	Subtriporopollenites constans	P
	Subtriporopollenites facilis	P
	Subtriporopollenites magnoporatus	P
	Subtriporopollenite spp.	P
	Tricolporopollenites parmularius	P
Family Restionaceae		
	Pentapollenites regulatius	P
	Restioniidites hungaricus	P
Family Sapotaceae		
	Tetracolporopollenites ellipsus	P
	Tetracolporopollenites halimbaense	P
	Tetracolporopollenites hungaricus	P
Order Arecales		
Family Palmae		
	Sabalpollenites areolatus	P
	Sabalpollenites sp.	P
Order Cornales		
Family Nyssaceae		
	Tricolporopollenites krutzschi	P
Family Aquifoliaceae		
	Tricolporopollenites iliacus	P
	Tricolporopollenites margaritatus	P
Order Ericales		
Family Cyrillaceae		
	Tricolporopollenites megaexactus	P
Order Fagales		
Family Fagaceae		
	Tricolporopollenites cingulum	P
Family Betulaceae		
	Triporopollenites sp.	P
Order Polypodiales		
Family Pteridaceae		
	Polypodiaceoisporites sp.	P
Order Rosales		
Family Rosaceae		
	Tricolporopollenites aceroides	P
Order Sapindales		
Family Simarubaceae		
	Tricolporopollenites 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 Broglio Loriga and Sala Manservigi (1973), who referred all six available specimens to "Scyphomedusae". Four specimens were assigned to the rhizostome *Simplicibrachia bolcensis* (Broglio Loriga and Sala Manservigi, 1973; Fig. 12A). The other two specimens were interpreted as young individuals possibly belonging to the orders Rhizostomeae and Semaeostomeae. 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 (Broglio 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). Broglio 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 (*fide* 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 (*fide* Secrétan, 1975a; De Angeli and Beschin, 2006), whereas Milne-Edwards (1860) reported the portunid *Eoplonotus 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* (Gorochov 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 gentilinii*. 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	
Simplicibrachia bolcensis Broglio Loriga & Sala Manservigi, 1973	P
Order Semaeostomeae	
Semaeostome aff. *Aurelia* Lamarck, 1816	P
Phylum Brachiopoda	
Class Rhynconellata	
Order Terebratulida	
Family Terebratulidae	
"*Terebratula*" *fumanensis* Davidson, 1870	P
Phylum Mollusca	
Class Bivalvia	
Order Mytilida	
Family Mytilidae	
Mytilidae indet.	P
Modiolus postalensis Oppenheim, 1896	P
Order Limida	
Family Limidae	
Ctenoides papillifera (Bayan, 1870)	P
Order Pectinida	
Family Anomiidae	
Anomia cf. *primaeva* Deshayes, 1858	P
Order Ostreida	
Family Ostreidae	
Ostrea sp.	P

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

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

Order Coleoptera		
	Coleoptera indet.	P
Family Buprestidae		
	Buprestis (*Ancylochira*) *deleta* Heer, 1847	P
	Perotis laevigata Massalongo, 1856	P
	Undetermined Buprestidae	P
Order Diptera		
Family Tipulidae		
	Tipulidae indet.	P
Family Limoniidae		
	Limoniidae indet.	P
	Gonomyia sp.	P
	Gnophomyia gentilinii Krzeminski & Krzeminska, 1990	P
Family Rhagionidae		
	Dipterites angelinii Massalongo, 1856	P
Order Heteroptera		
	Heteroptera indet.	P
Order Hymenoptera		
	Hymenoptera indet.	P
Order Odonata		
Suborder Zygoptera		
Family Bolcathoridae		
	Bolcathore colorata Gentilini, 2002	P
Suborder Anisoptera		
Family Bolcathemidae		
	Bolcathemis nervosa Gentilini, 2002	P
Family Bolcacorduliidae		
	Bolcacordulia paradoxa Gentilini, 2002	P
Order Orthoptera		
	Orthoptera indet.	P
Family Gryllotalpidae		
	Pterotriamescaptor tridactylina (Secrétan, 1975)	P
Order Rhynchota		
Family Gerridae		
	Halobates ruffoi 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

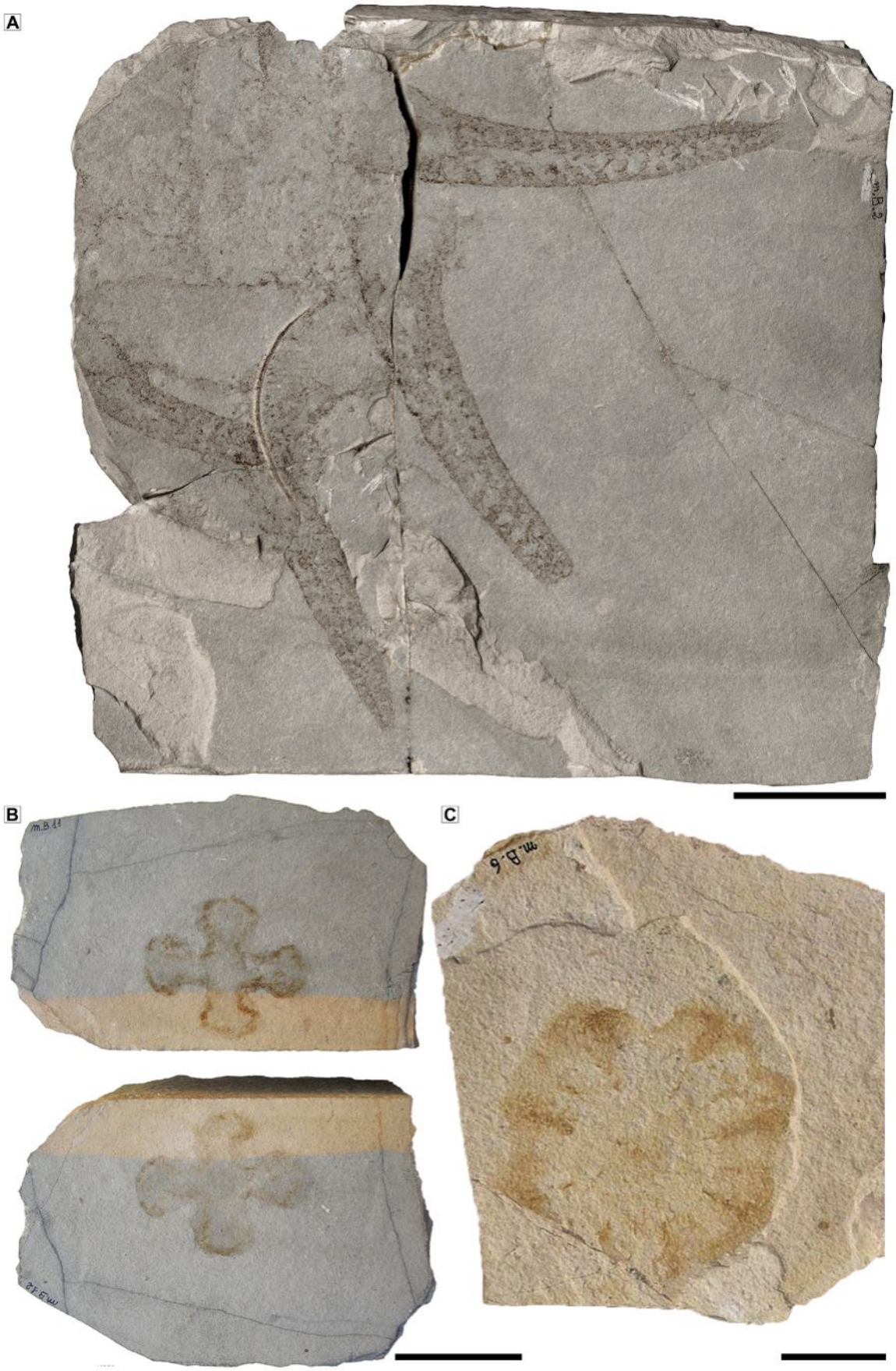

Fig. 12 - Jellyfish from the Bolca *Lagerstätten*. A) *Simplicibrachia bolcensis*, holotype MCSNV m.B.2, scale bar 50 mm; B) Probable semaeostome similar to *Aurelia*, MCSNV m.B.11-12, scale bar 50 mm; C) Possible ephyra (larval stage) of Scyphozoa, MCSNV m.B.6, scale bar 20 mm.

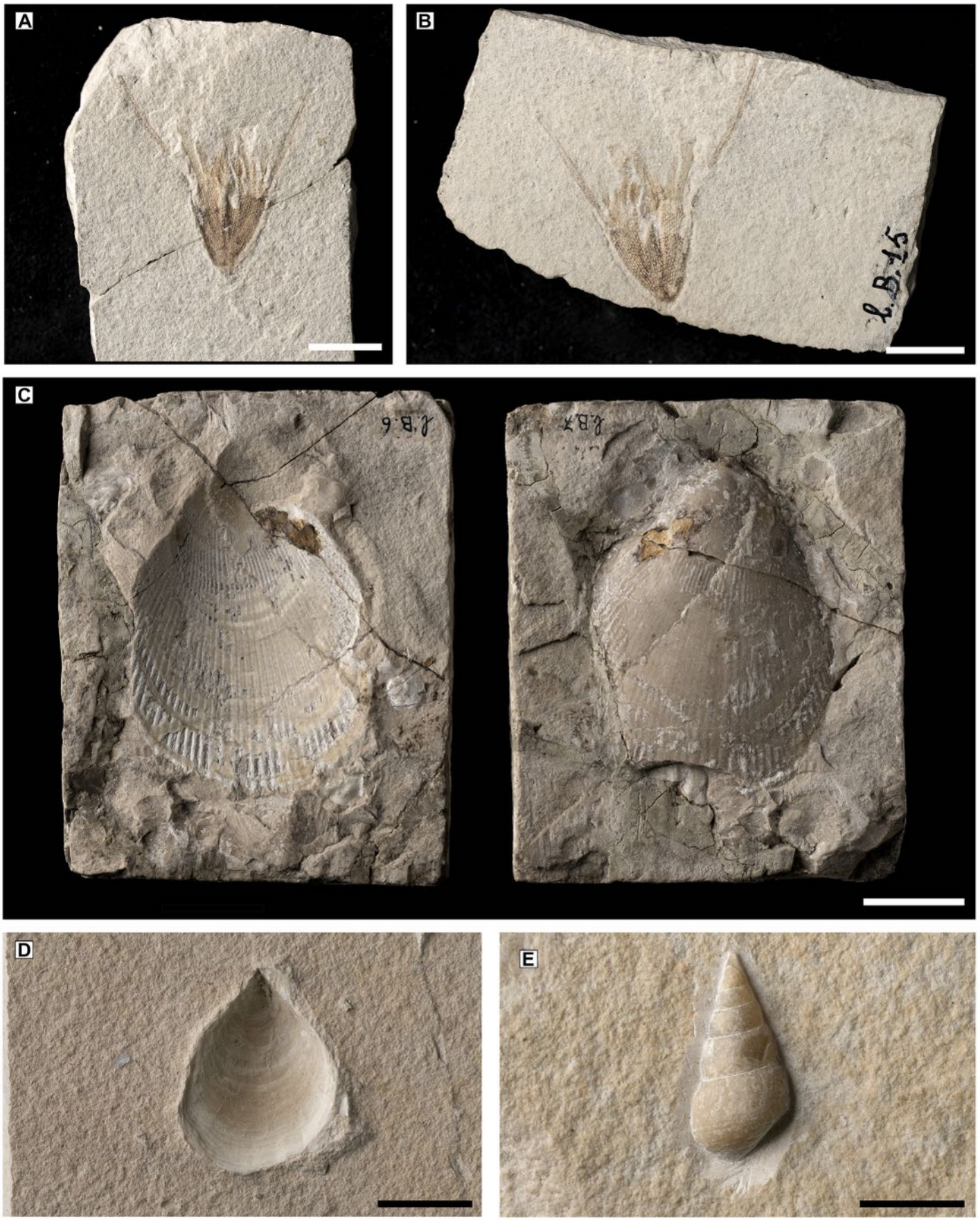

Fig. 13 - Lophophorates from the Bolca *Lagerstätten*. A) Schizoporellidae bryozoan, MCSNV IB14, scale bar 10 mm; B) Schizoporellidae bryozoan, MCSNV IB15, counterpart of MCSNV IB14, scale bar 10 mm. Mollusca: C) *Ctenoides papillifera* Bayan 1870, external and internal mould with traces of the original 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.

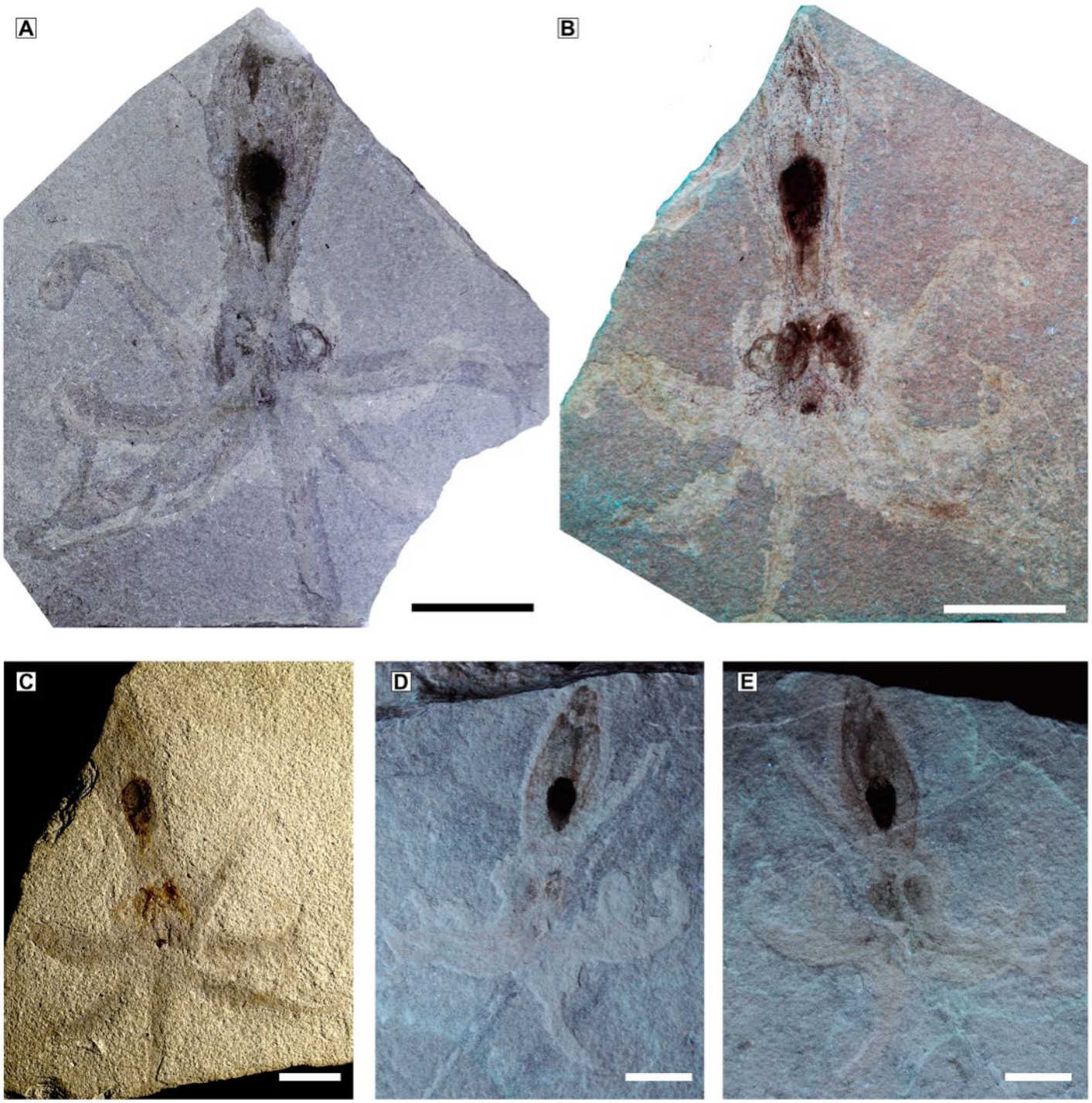

Fig. 14 - Cephalopods from the Bolca *Lagerstätten*. *Bolcaoctopus pesciaraensis*: A) holotype. MFB IG23682, under UV light; B) counterpart of MFB IG23682, MGP-PD 31434, under UV light; C) MGP-PD 31434 under natural light; D) and E) the paratype MCSNV IB13 under UV light and its counterpart, MCSNV IB12,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

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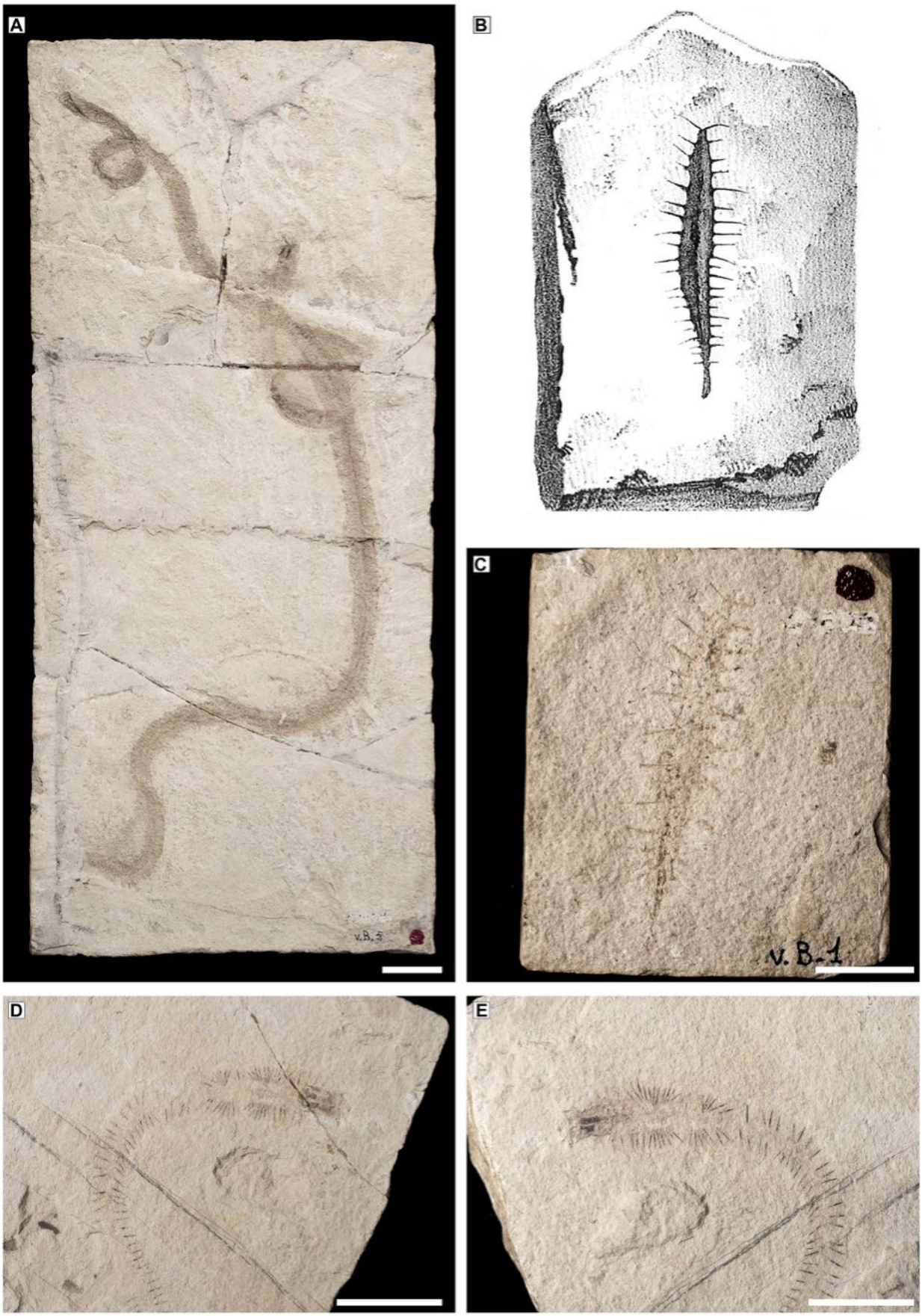

Fig. 15 - Polychaete worms from the Bolca *Lagerstätten*. A) *Eunicites gazolae*, holotype MCSNV v.B.5, scale bar equals 50 mm; B) the holotype of *Siphonostomites hesionoides* [excerpt from Massalongo (1855, Plate II)]; C) *Siphonostomites hesionoides*, holotype MCSNV v.B.1, scale bar 10 mm; D) *Eunicites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

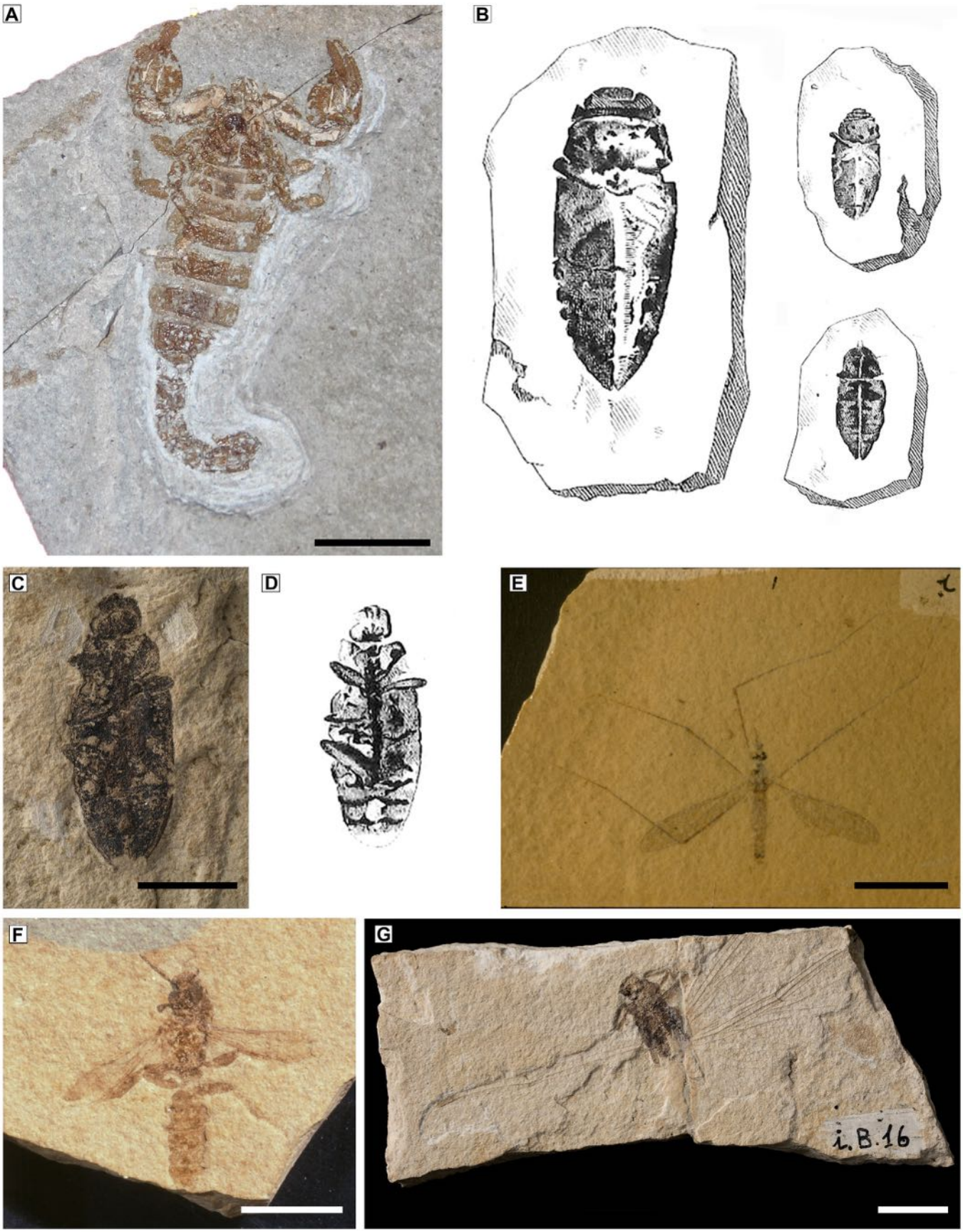

Fig. 20 - Arachnids from the Bolca *Lagerstätten*. A) *Eoeuscorpius ceratoi*, holotype, CMC 1. Insecta, Coleoptera: B) specimens of the coleopter Buprestis (Ancylocheira) deleta figured by Massalongo (1856, t. 1, Fig. 1-3); C) *Perotis laevigata*, MCBG 4222 (Parolini Collection); D) specimen MCBG 4222 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.

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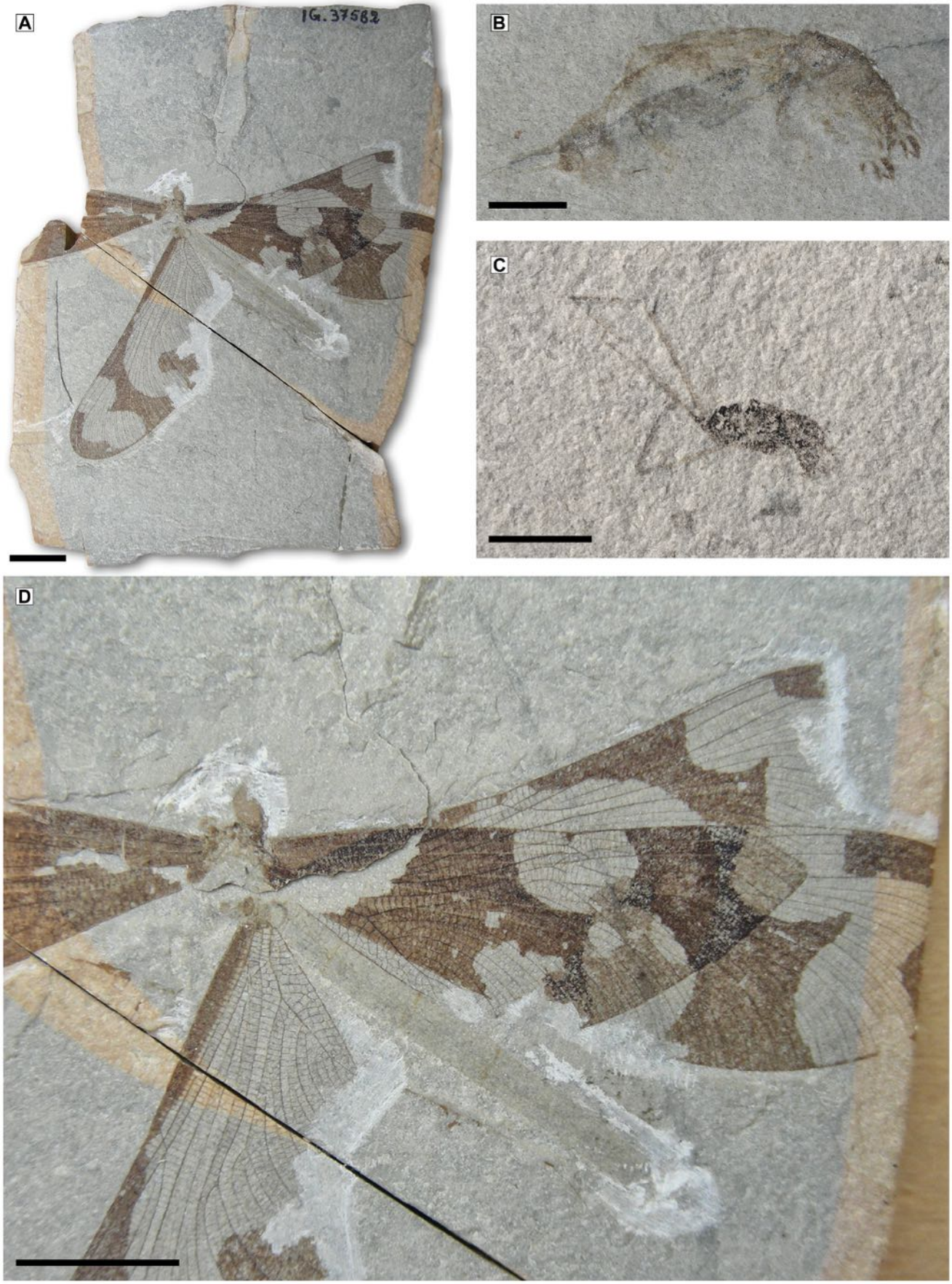

Fig. 21 - Insects from the Bolca *Lagerstätten*. A) Odonata: the damselfly *Bolcathore colorata*, holotype, MCSNV IG. 37582, scale bar 10 mm; B) Orthoptera: the mole cricket *Pterotriamescaptor tridactylina*, holotype, MCSNV 24517, scale bar 2 cm; C) Gerridae: the sea skater *Halobates ruffoi*, female, 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 Nimes (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-spired 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 gigantica* 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; Beschin 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 (Galatheidae and Porcellanidae) and Brachyura (Dromiidae, Dynomenidae, Dromiacea *incertae sedis*, Parthenopidae, Carpiliidae, Pilumnidae, Domeciidae, Panopeidae, Xanthidae, and Xanthoidea *incertae sedis*; Fig. 25). Beschin 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 corallinacean 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).

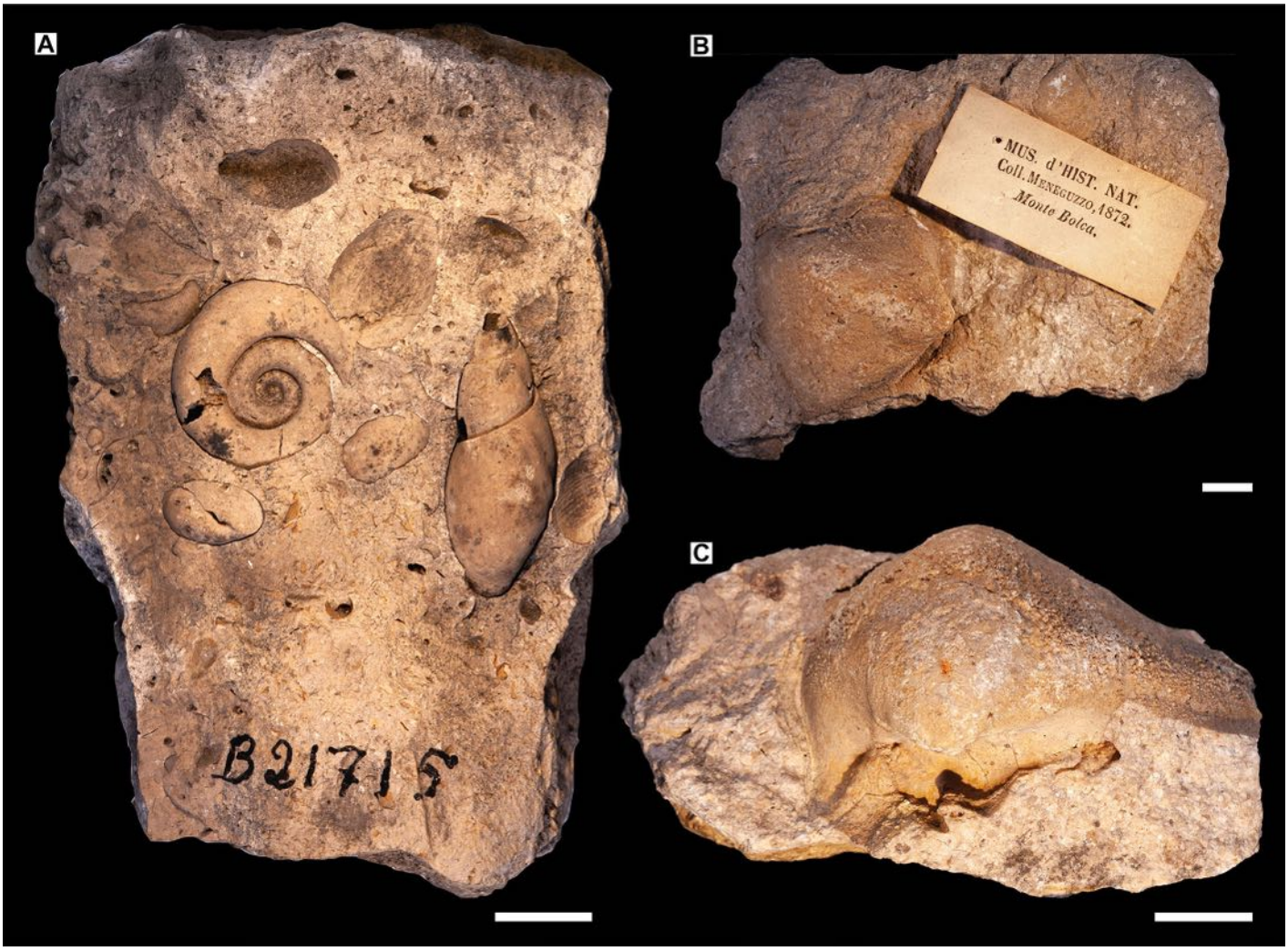

Fig. 22 - A) Loosely packed, poorly-sorted bioclastic fabric of the Monte Postale fossil assemblage (MNHN.F.B21715a); B) Label attesting the acquisition of the Monte Postale (referred to as "Monte Bolca") collection now at the Muséum national d'Histoire naturelle (MNHN) in Paris from Giovanni Meneguzzo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

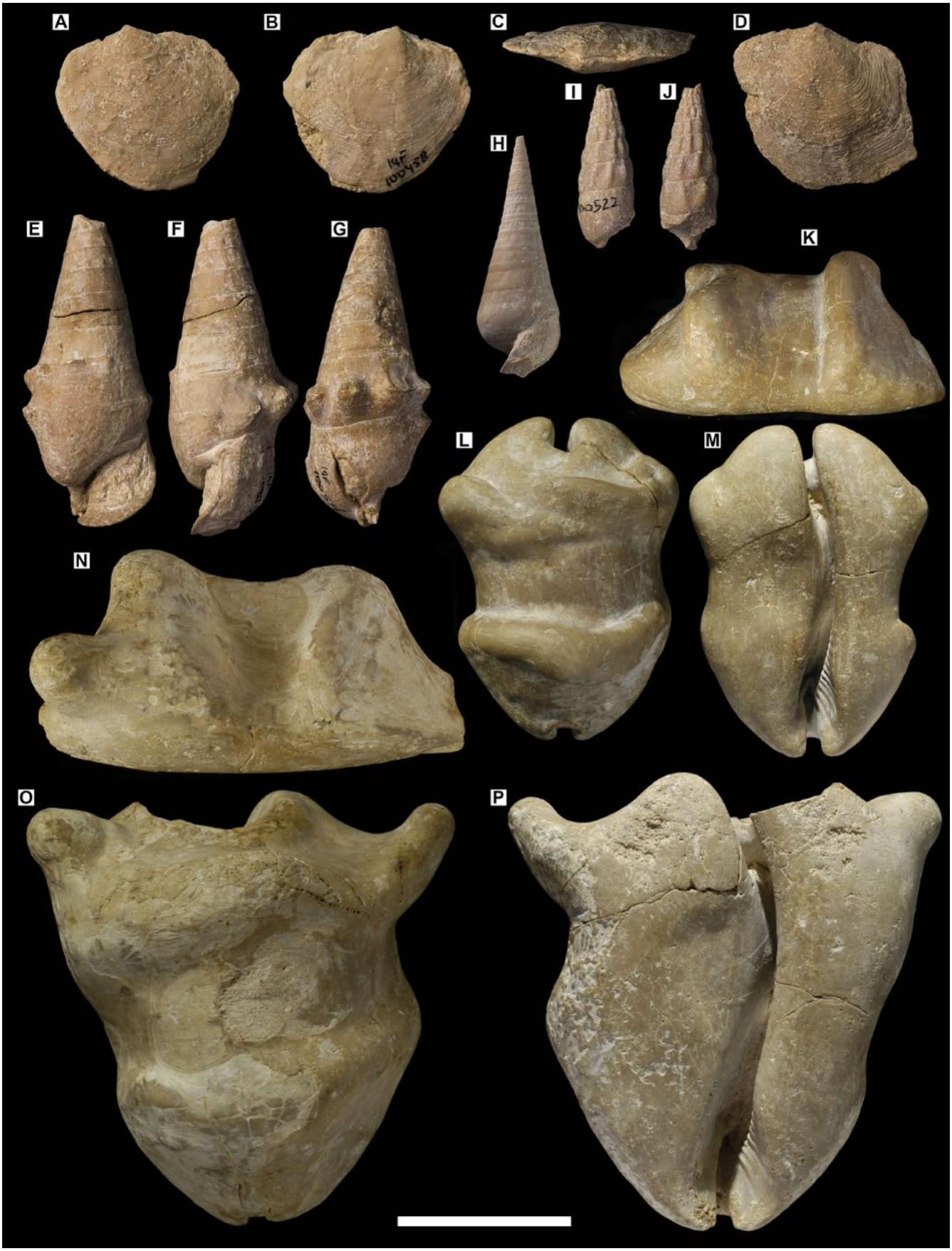

Fig. 23 - Molluscs from the Monte Postale *Alveolina* beds. A-D) *Pseudomiltha escheri*, A-C: IGF 100458A, left, right and dorsal view; D: IGF 100458B, left view; E-G) *Bellatara janus*, IGF 100516A, oral, lateral and dorsal view; H) *Campanile gomphoceras*, MNHN.F.A94698, lateral view; I-J) *Rhinoclavis 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 *Alveolina* beds of Monte Postale

Phylum Cnidaria
- Class Anthozoa
  - Subclass Zoantharia
    - Order Scleractinia
      - Family Acroporidae
        - *Astraeopora panicea* Blainville, 1854
        - *Dendracis gervillei* (Defrance, 1823)
        - *Dendracis seriata* Reuss, 1867
        - *Dendracis subnodosa* De Gregorio, 1894
      - Family Agathiphyllidae
        - *Pattalophyllia cyclolitoides* (Michelin, 1846)
        - *Pattalophyllia subinflata* (Catullo, 1857)
      - Family Caryophyllidae
        - *Trochocyathus taramellii* d'Achiardi, 1875
      - Family Meandrinidae
        - *Pachygyra savii* d'Achiardi, 1866
      - Family Montastraeidae
        - *Montastraea meneghinii* (Reuss, 1869)
      - Family Montlivaltiidae
        - *Trochosmilia acutimargo* Reuss, 1874
        - *Trochosmilia cocchii* d'Achiardi, 1894
        - *Trochosmilia incurva* d'Achiardi, 1866
      - Family Placosmiliidae
        - *Placosmilia multisinuosa* (Michelin, 1846)
        - *Placosmilia* cf. *strangulata* d'Achiardi, 1875
      - Family Pocilloporidae
        - *Stylophora conferta* Reuss, 1868
      - Family Poritidae
        - *Goniopora elegans* (Leymerie, 1846)
        - *Goniopora nummulitica* (Reuss, 1864)
  - Subclass Octocorallia
    - Order Coenothecalia
      - Family Helioporidae
        - *Parapolytremacis bellardii* (Haime, 1852)
  - Class Hydrozoa
    - Order Anthoathecata
      - Family Milleporidae
        - *Millepora cylindrica* Reuss, 1868

*The list of corals presented here is derived from Malaroda (1954). This assemblage of invertebrates from the mollusc-bearing *Alveolina* 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: Isastraea sp., *Rhabdophyllia solenastropsis* De Gregorio, 1894, *Turbinolia postalincola* De Gregorio, 1894, and *Stylocoenia zitteli* Pratz, 1883.

Phylum Brachiopoda
- Class Rhynconellata
  - Order Terebratulida
    - Family Terebratulidae
      - *Gryphus kickxii* (Galeotti, 1837)

Phylum Arthropoda
- Subphylum Crustacea
- Class Malacostraca
  - Order Decapoda
  - Infraorder Brachyura
    - Family Dynomenidae
      - ?*Cyamocarcinus angustifrons* Bittner, 1883
    - Family Raninidae
      - *Lophoranina marestiana* (König, 1825)
    - Family Panopeidae
      - *Glyphithyreus ellipticus* (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
      - *Katelysia 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 (Bruguiére, 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)
Protocypraedia interposita (Deshayes, 1865)
Superfamily Littorinoidea
Family Littorinidae
Littorina (*Littorinopsis*) *postalensis* (De Gregorio, 1894)
Lacuna sp.
Superfamily Tonnoidea
Family Cassidae

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

List of main invertebrate taxa from the bioconstructions of Monte Postale
Phylum Cnidaria
Class Anthozoa
Subclass Exacorallia
Order Scleractinia
Family Acroporidae
Acropora sp.
Astreopora sp.

Dendracis sp.
Family Actinacididae
Actinacis cognata Oppenheim, 1901
Family Astrocoeniidae
Astrocoenia sp.
Family Cladocoridae
Cladocora sp.
Family Euphylliidae
Euphyllia sp.
Nancygyra dissepimentata Bosellini & Stolarski, 2020
Family Faviidae
Favia sp.
Family Meandrinidae
Pachygyra sp.
Family Merulinidae
Caulastraea sp.
Paraleptoria sp.
Family Montastraeidae
Montastraea sp.
Family Pocilloporidae
Stylophora sp.
Family Poritidae
Goniopora sp.
Family Rhizangiidae
Siderofungia sp.
Siderastraea sp.

Phylum Arthropoda
Subphylum Crustacea
Class Malacostraca
Order Decapoda
Infraorder Anomura
Family Galatheidae
Acanthogalathea devecchii Beschin et al., 2016
Petrolisthes lineatus Beschin et al., 2016
Family Diogenidae Ortmann, 1892
Dardanus bayani Beschin et al., 2016
Infraorder Brachyura
Family Dromiidae
Dromiopsis ceratoi Beschin et al., 2016
Family Dynomenidae
Kromtitis subovatus Beschin et al., 2016
Cyamocarcinus angustifrons Bittner, 1883
Dromiacea incertae sedis
Eotrachynotocarcinus airaghii Beschin et al., 2007
Family Parthenopidae
Mesolambrus declinatus Müller & Collins, 1991
Mesolambrus ypresianus Beschin et al., 2015
Family Carpiliidae
Carpilius petreus Beschin et al., 2007
Family Pilumnidae Samouelle, 1819
Lobogalenopsis quadrilobata (Lörenthey, 1898)
Family Domeciidae
Palmyria levigata sp. Beschin et al., 2016
Family Panopeidae
Panopeus postalensis Beschin et al., 2016
Family Xanthidae
Etisus arduinoi Beschin et al., 2007
Phlyctenodes multituberculatus Beschin et al., 2007
Xanthoidea incertae sedis
Prochlorodius ellipticus Müller & Collins, 1991

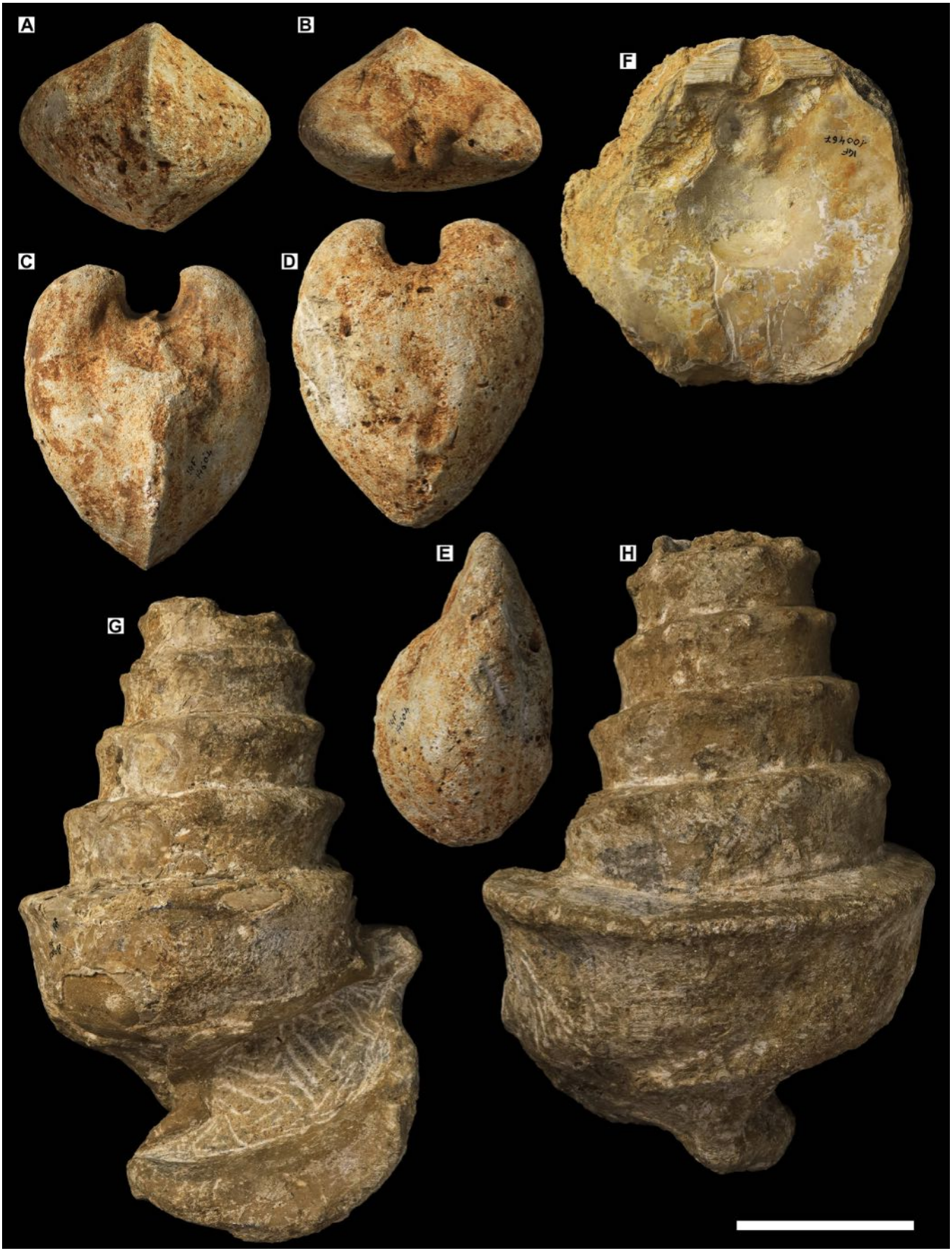

Fig. 24 - Molluscs from the Monte Postale *Alveolina* beds. A-E) Cardiidae gen- et sp. indet., IGF 14604, ventral, dorsal, antero-dorsal, postero-dorsal and left view; F) *Pycnodonte gigantica*, IGF 100467, internal view of right valve; G-H) *Campanile giganteum*, IGF 100618, oral and dorsal view. Scale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

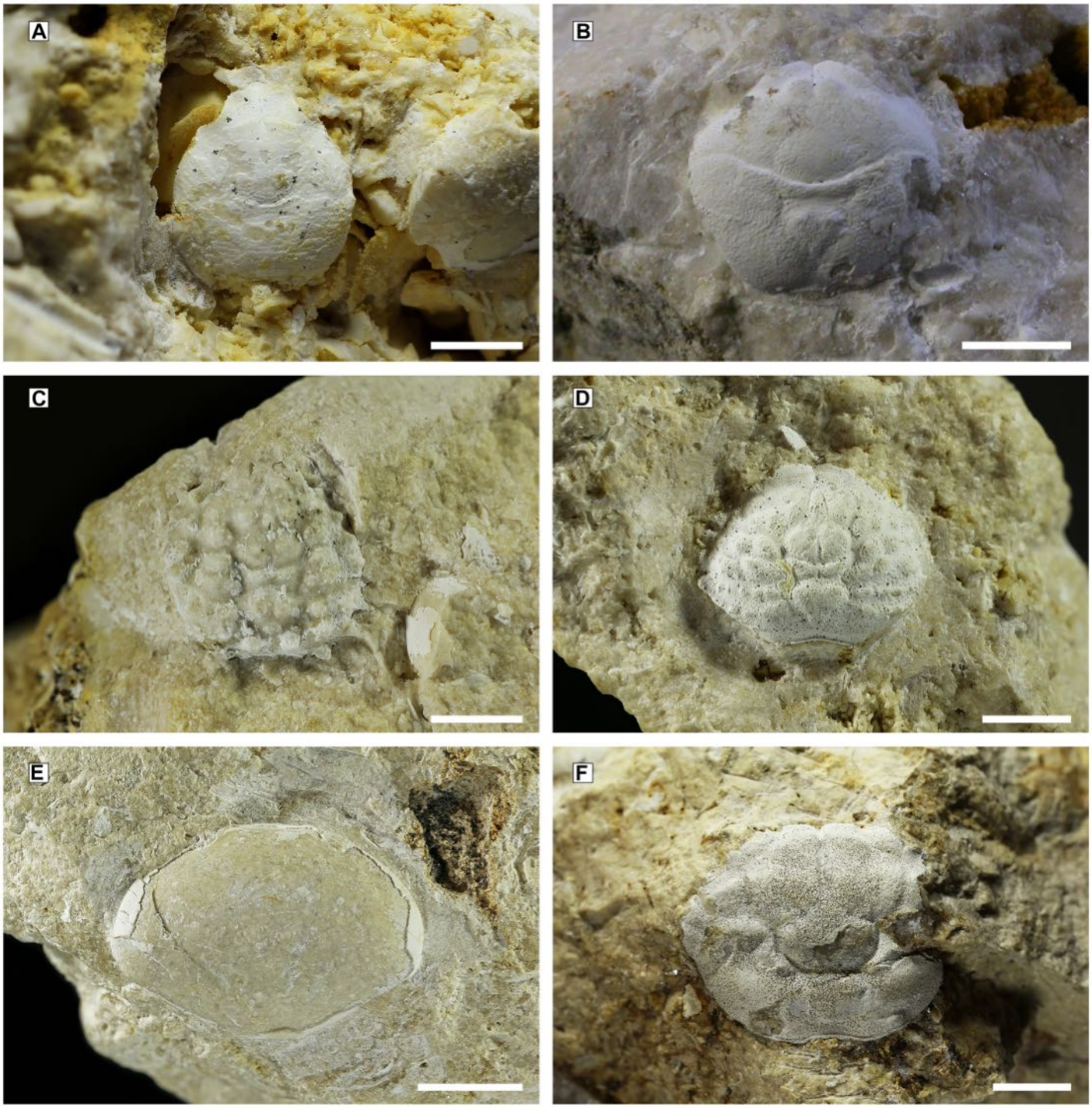

Fig. 25 - Crustaceans from the bioconstructions of the Monte Postale and other sites around Bolca. A) *Petrolisthes lineatus*, MCSNV 93914, scale bar 2 mm; B) *Dromiopsis ceratoi*, MCSNV 93954, holotype, scale bar 3 mm; C) *Kromtitis subovatus*, MCSNV 94033, scale bar 3 mm; D) *Eothrachinotocarcinus 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 Giuliari 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 (Anguilloididae, 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), goosefishes (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, ephippids, eocottids, callipterygids, labrids, siganids, flatfishes, some tetraodontiforms), the coral assemblage (anguilliforms, lophiiforms, holocentrids, syngnathiforms, apogonids, sparids, carangids, monodactylids, ephippids, 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	
Galeorhinus cuvieri (Agassiz, 1835)	P
Family Carcharhinidae	
Eogaleus bolcensis Cappetta, 1975	P, MP
Order Lamniformes	
Family Odontaspididae	
Brachycarcharias lerichei (Casier, 1946)	P, MP
Division Batomorphii	
Order Torpediniformes	
Family Narcinidae	
Titanonarke molini (Jaekel, 1894)	MP
Titanonarke megapterygia Marramà et al., 2018	MP
Family Platyrhinidae	
Eoplatyrhina bolcensis (Heckel, 1851)	MP
Order Rhinopristiformes	
Family Rhinobatidae	
Eorhinobatos primaevus (De Zigno, 1874)	P
Pseudorhinobatos dezignii (Heckel, 1853)	MP
Order Myliobatiformes	
Family Zanobatidae	
Plesiozanobatus egertoni (De Zigno, 1876)	P
Family Urolophidae	
Arechia crassicaudata (Blainville, 1818)	MP
Family Dasyatidae	
Tethytrygon muricatus (Volta, 1796)	P
Family Dasyomyliobatidae	
Dasyomyliobatis thomyorkei Marramà et al., 2023	P
Family Myliobatidae	
Promyliobatis gazolai De Zigno, 1882	P

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

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

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

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

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

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

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

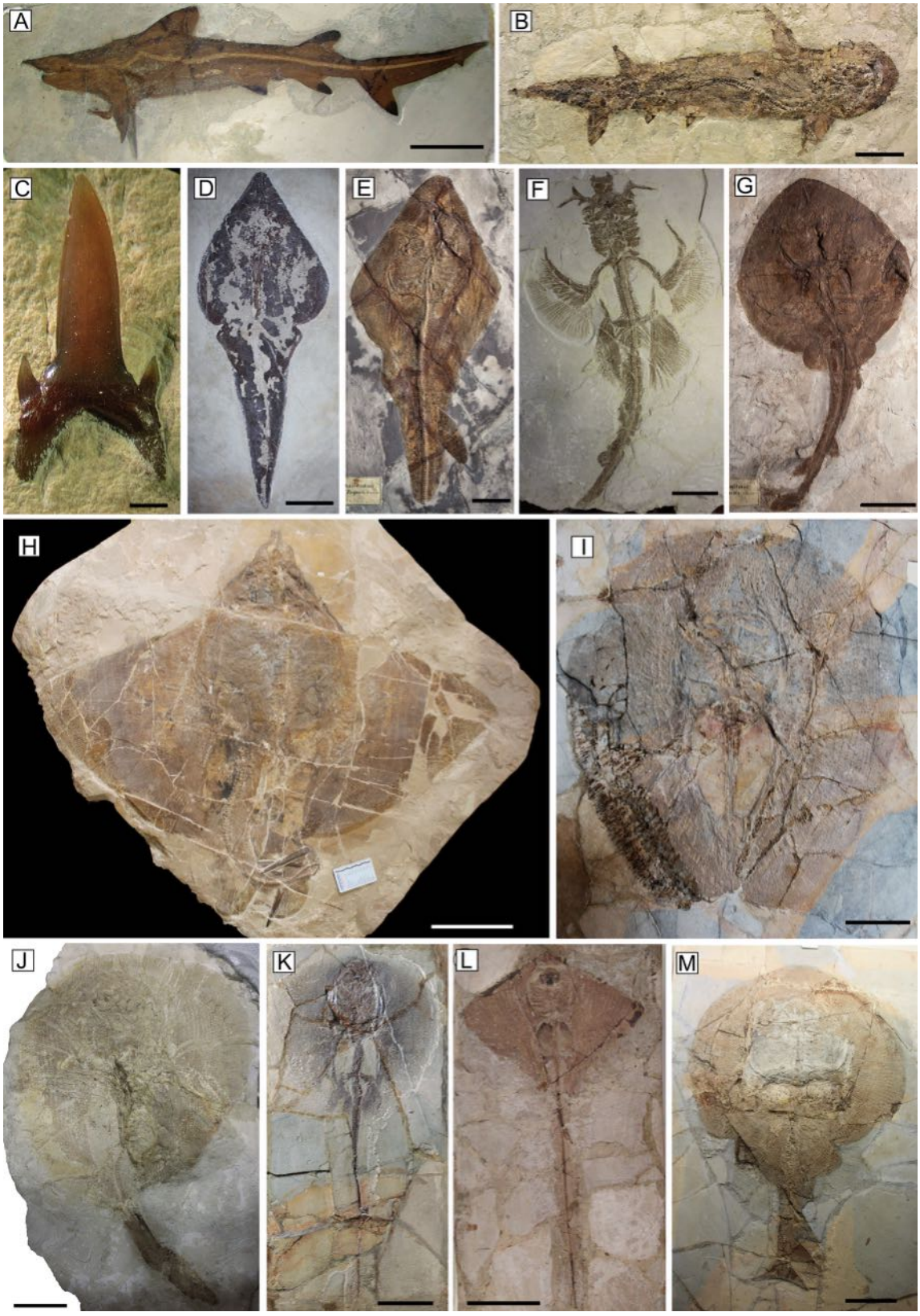

Fig. 26 - Sharks and rays (Elasmobranchii) from the Bolca *Lagerstätten*. A) *Galerorhinus cuvieri*, MCSNV T.1124; B) *Eogaleus bolcensis*, MCSNV T.311, holotype; C) *Brachycarcharias lerichei*, MCSNV IG.VR.69800; D) *Pseudorhinobatos dezigni*, NHMW 1853.XXVII.4, holotype; E) *Eorhinobatos primaevus*, 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.

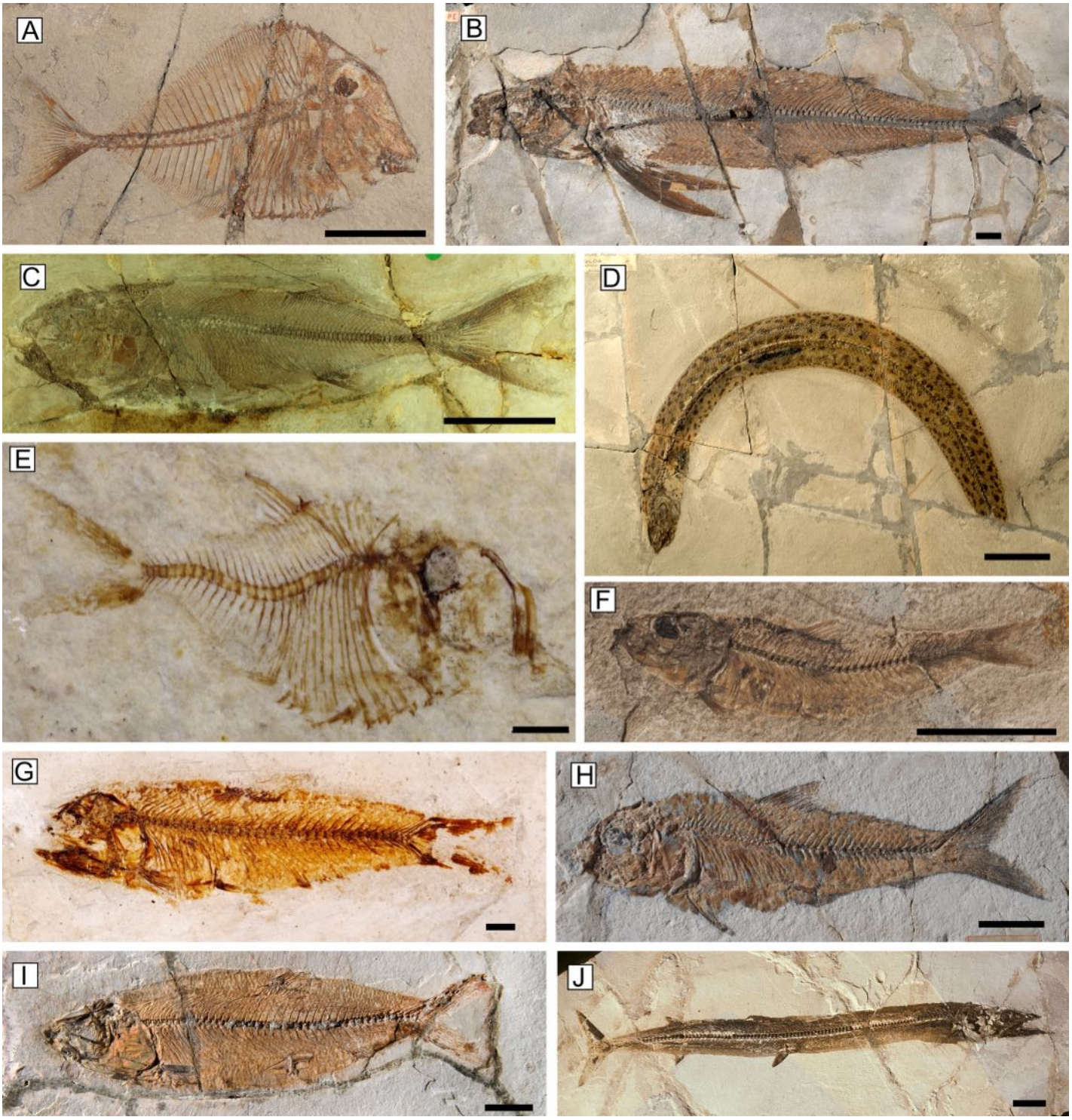

Fig. 27 - Non-acanthomorph teleosts from the Bolca *Lagerstätten*. A) *Pycnodus apodus*, CM 4480; B) *Platinx macropterus*, MNHN F.Bol289, holotype; C) *Foreyichthys bolcensis*, NHMUK P.16821, holotype; D) Paranguilla tigrina, MGP-PD 26288; E) *Eoellimmichthys superstes*, MCSNV IG.23695, holotype; F) *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.

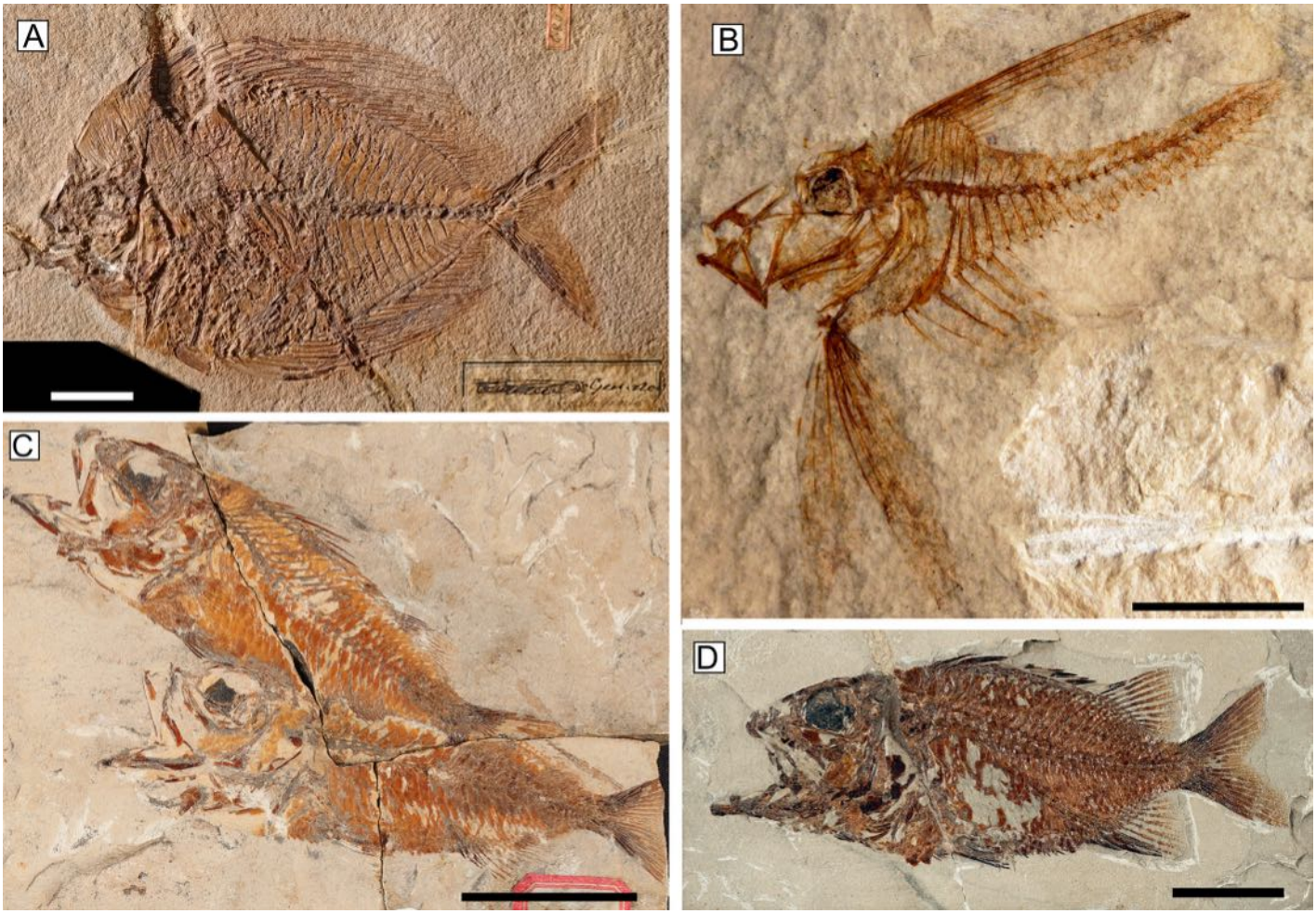

Fig. 28 - Non-percomorph acanthomorphs from the Bolca *Lagerstätten*. A) *Wettonius angeloi*, MGP-PD 6852, holotype; B) *Bajaichthys elegans*, MCSNV T.922, holotype; C) *Berybolcensis leptacanthus*, CM 4216; D) *Eoholocentrum macrocephalum*, CM 4455. Scale bars of A, C-D 20 mm; scale bar B 10 mm.

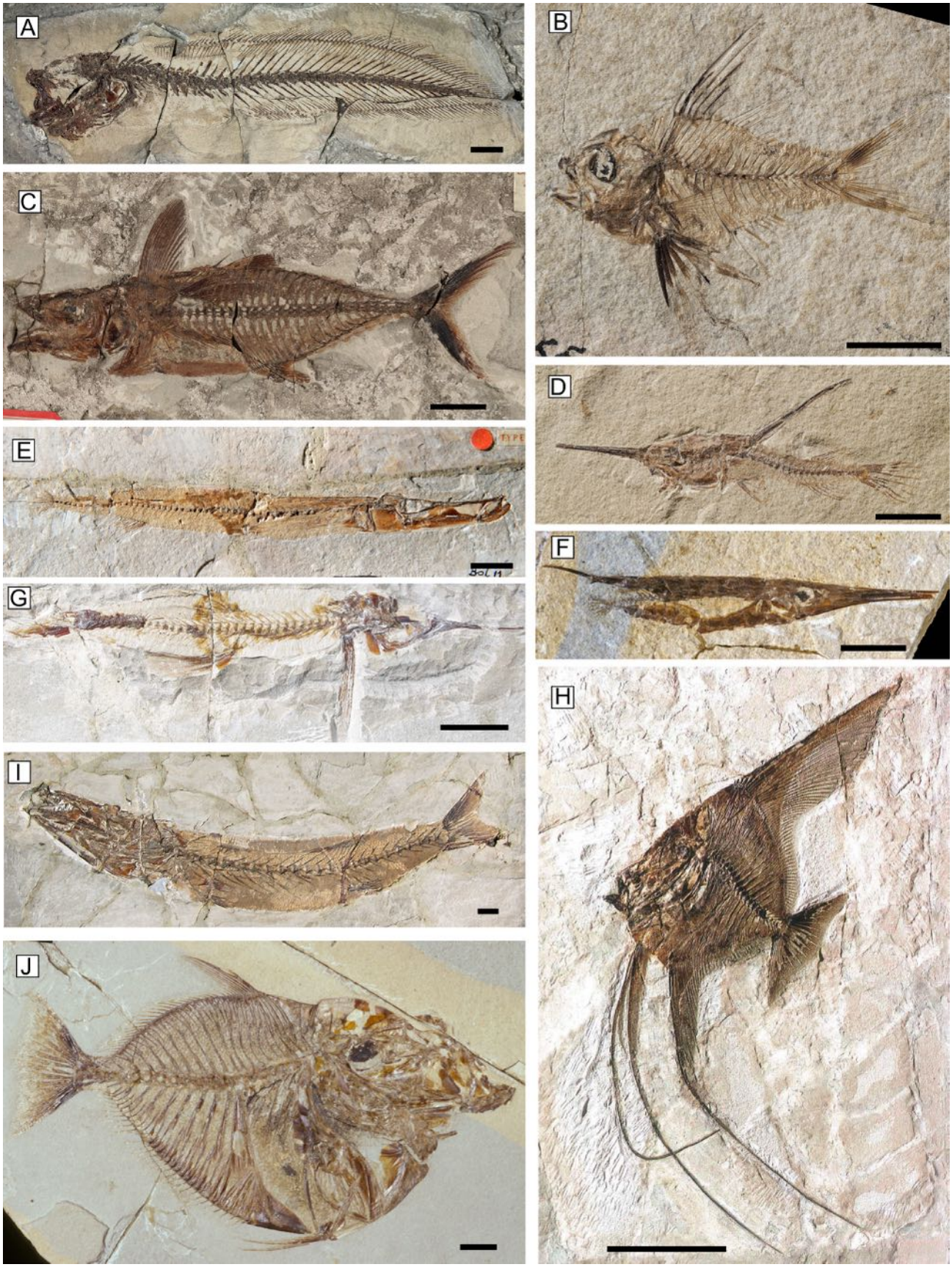

Fig. 29 - Percomorphs from the Bolca *Lagerstätten*. A) *"Ophidium" voltianum*, MCSNV T.156; B) *Eosphaeramia pygopterus*, MCSNV IG.129655; C) *Godsilia lanceolata*, CM 4533; D) *Rhamphosus rastrum*, MCSNV T.286, neotype; E) *Eoaulostomus bolcensis*, MNHN F.Bol11; F) *Paramphisile weileri*, MCSNV T 989; G) *Rhamphoexocoetus volans*, MCSNV V.294; H) *Ceratoichthys pinnatiformis*, MCSNV T.950; I) *Sphyraena 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.

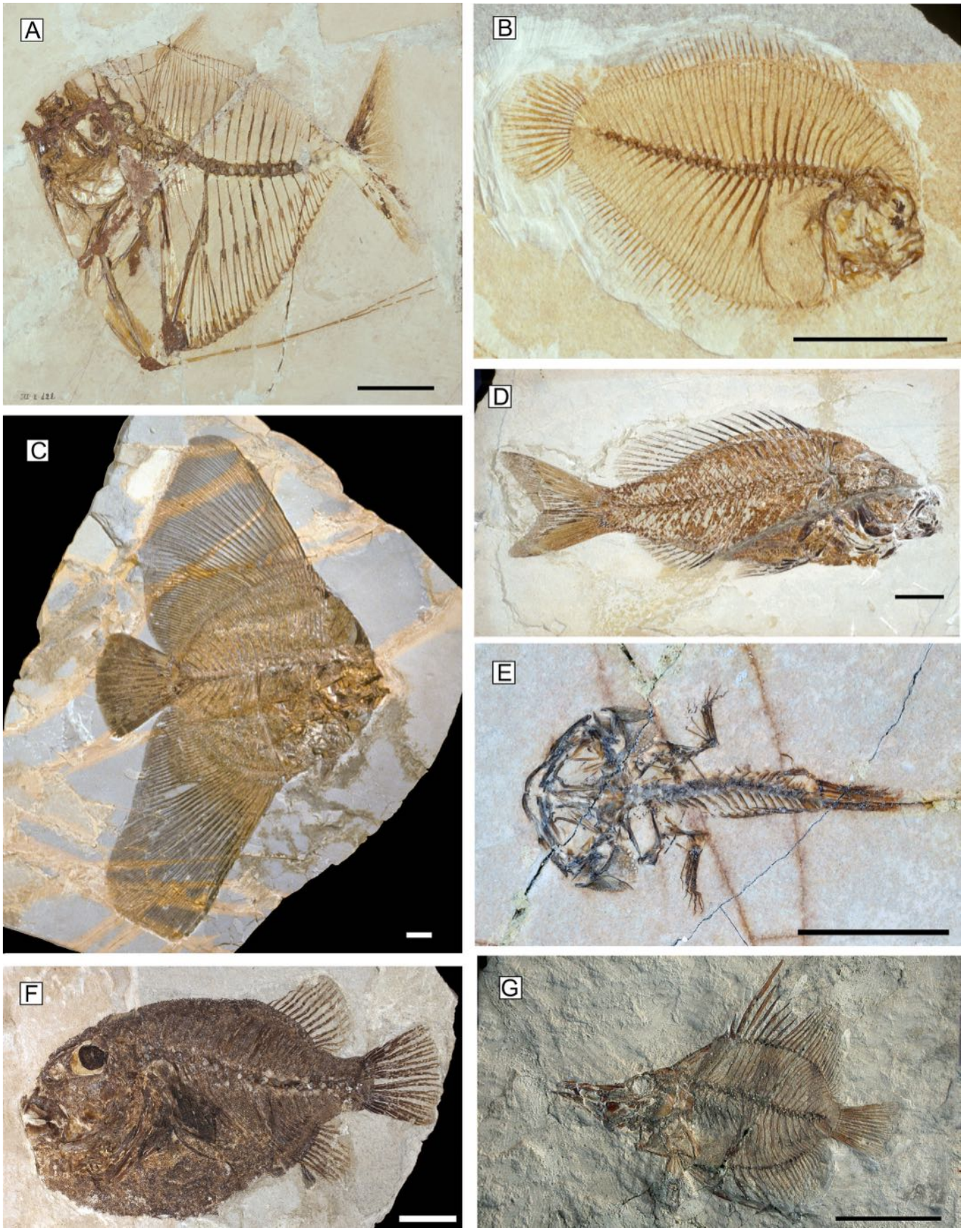

Fig. 30 - Percomorphs from the Bolca *Lagerstätten*. A) *Mene rhombea*, MCSNV VII.E.122; B) *Eobothus minimus*, MCSNV T.968; C) *Eoplatax papilio*, MCSNV IG.24573; D) *Sparnodus vulgaris*, MCSNV IG.24546; E) *Sharfia mirabilis*, MNHN F.Bol38-39, holotype; F) *Zignoichthys oblongus*, CMC 40; G) *Massalongius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

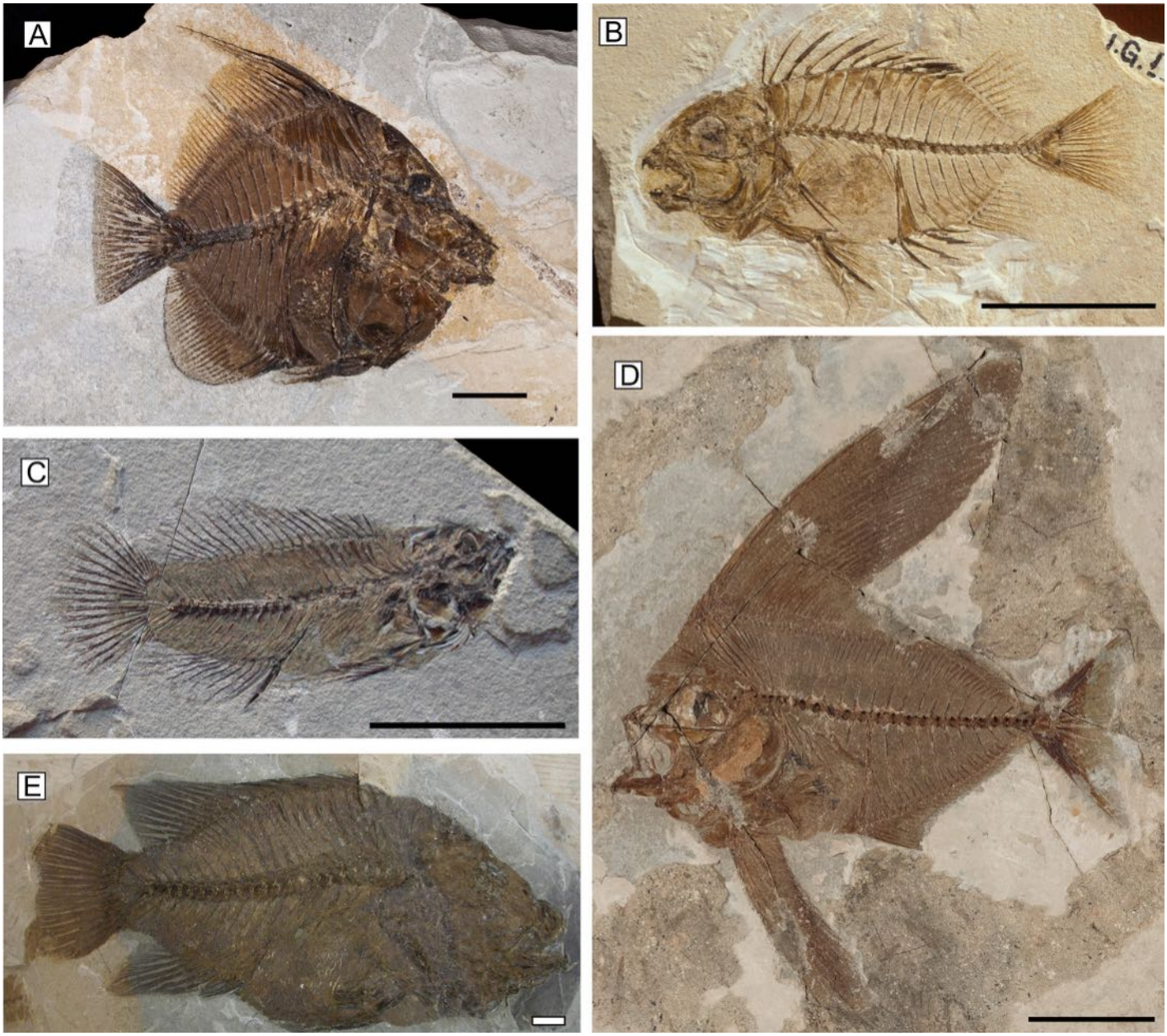

Fig. 31 - Percomorphs from the Bolca *Lagerstätten*. A) *Angiolinia mirabilis*, CMC 39, holotype; B) *Ruffoichthys bannikovi*, MCSNV IG.132596, holotype; C) *Frippia labroiformis*, MCSNV T.187; D) *Exellia velifer*, CM 4467; E) *Pygaeus bolcanus*, MCSNV IG.VR.81911. Scale bars 20 mm.

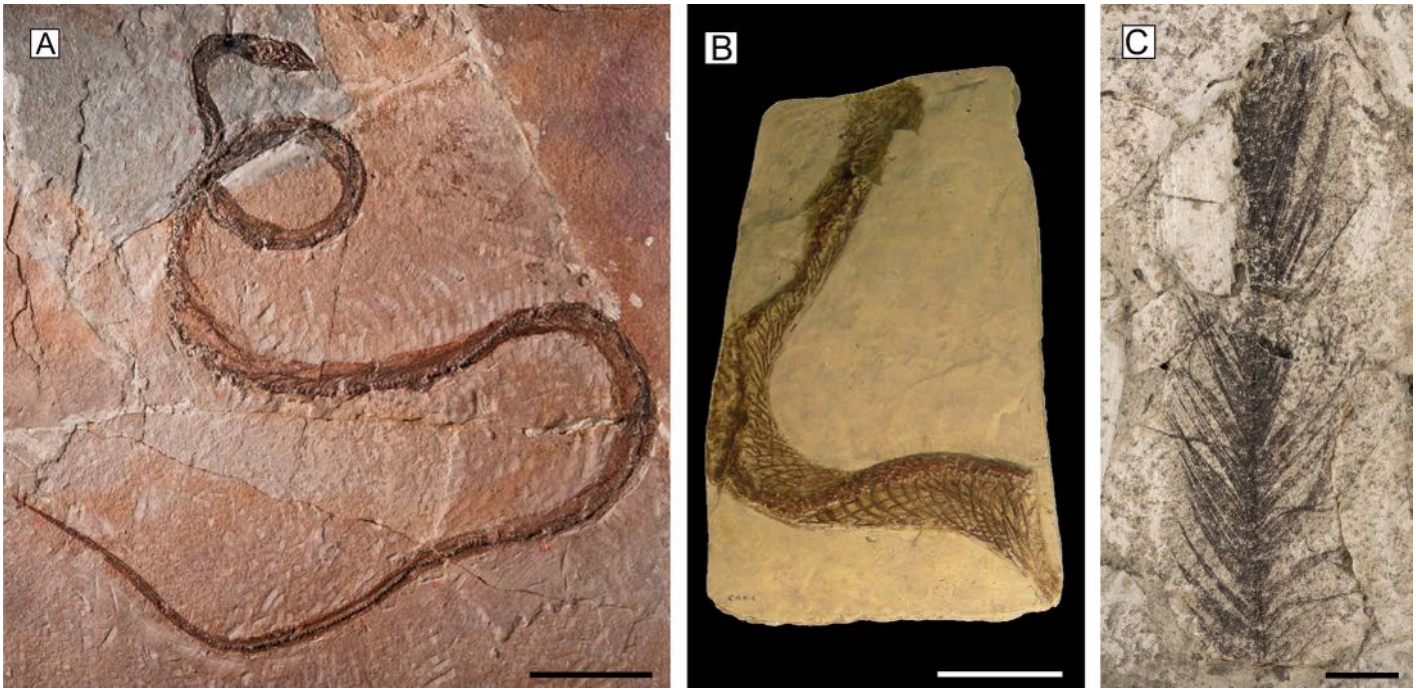

Fig. 32 - Terrestrial vertebrates from the Bolca *Lagerstätten*. A) the snake *Archaeophis proavus*, MBR 3554, holotype; B) the snake *Anomalophis bolcensis* MCSNV C.A.R1; C) *Ornitholites* sp., MCSNV a.B.2. Scale bars of A and B 50 mm; scale bar of C 10 mm.

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 coralgal 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 coralgal 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 paleoenvironment. 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.

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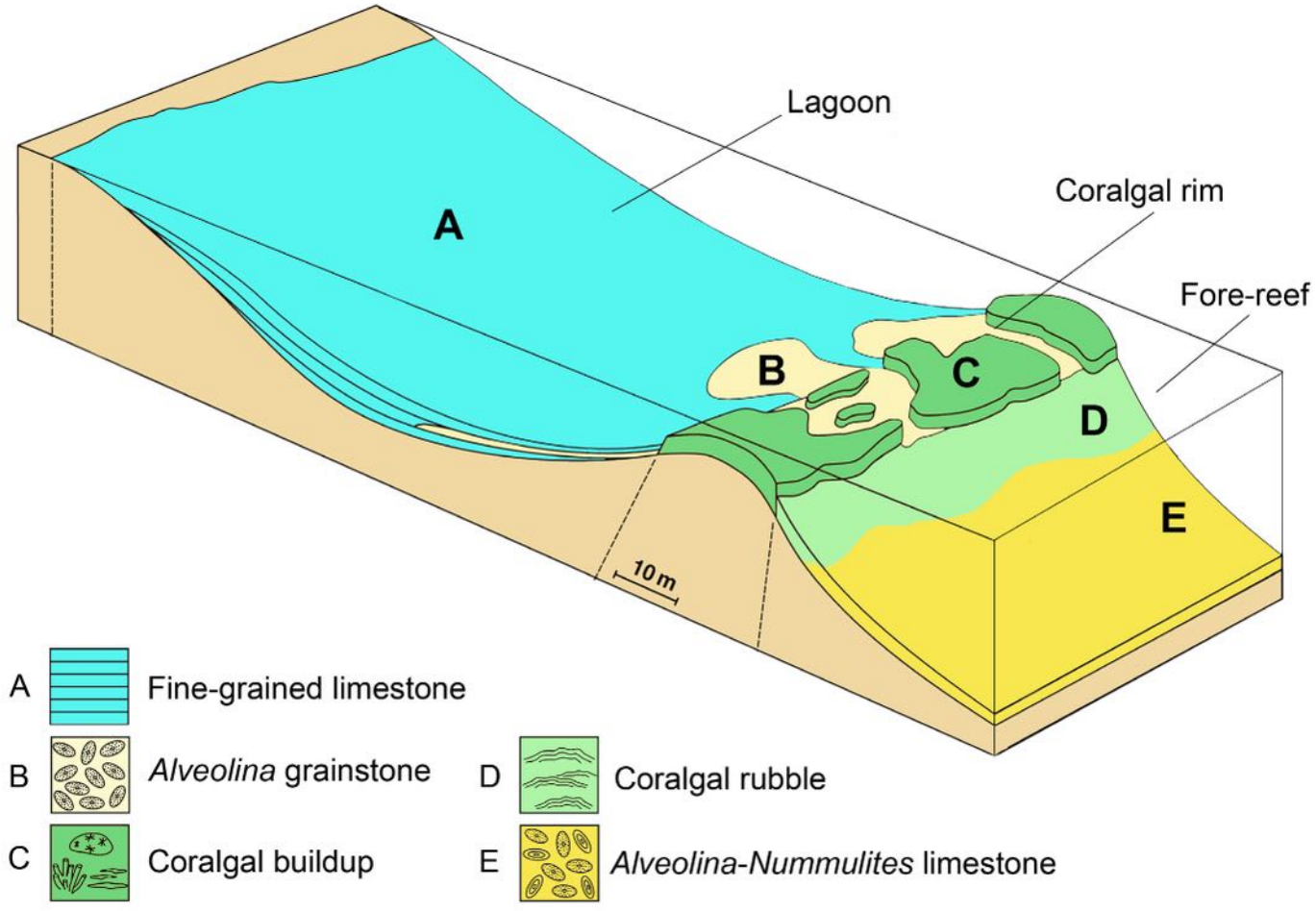

Fig. 33 - Idealised reconstruction of the depositional system of the sites of the from the Bolca *Lagerstätten*. The width and depth of the lagoon are not to scale. Modified after Vescogni et al. (2016).

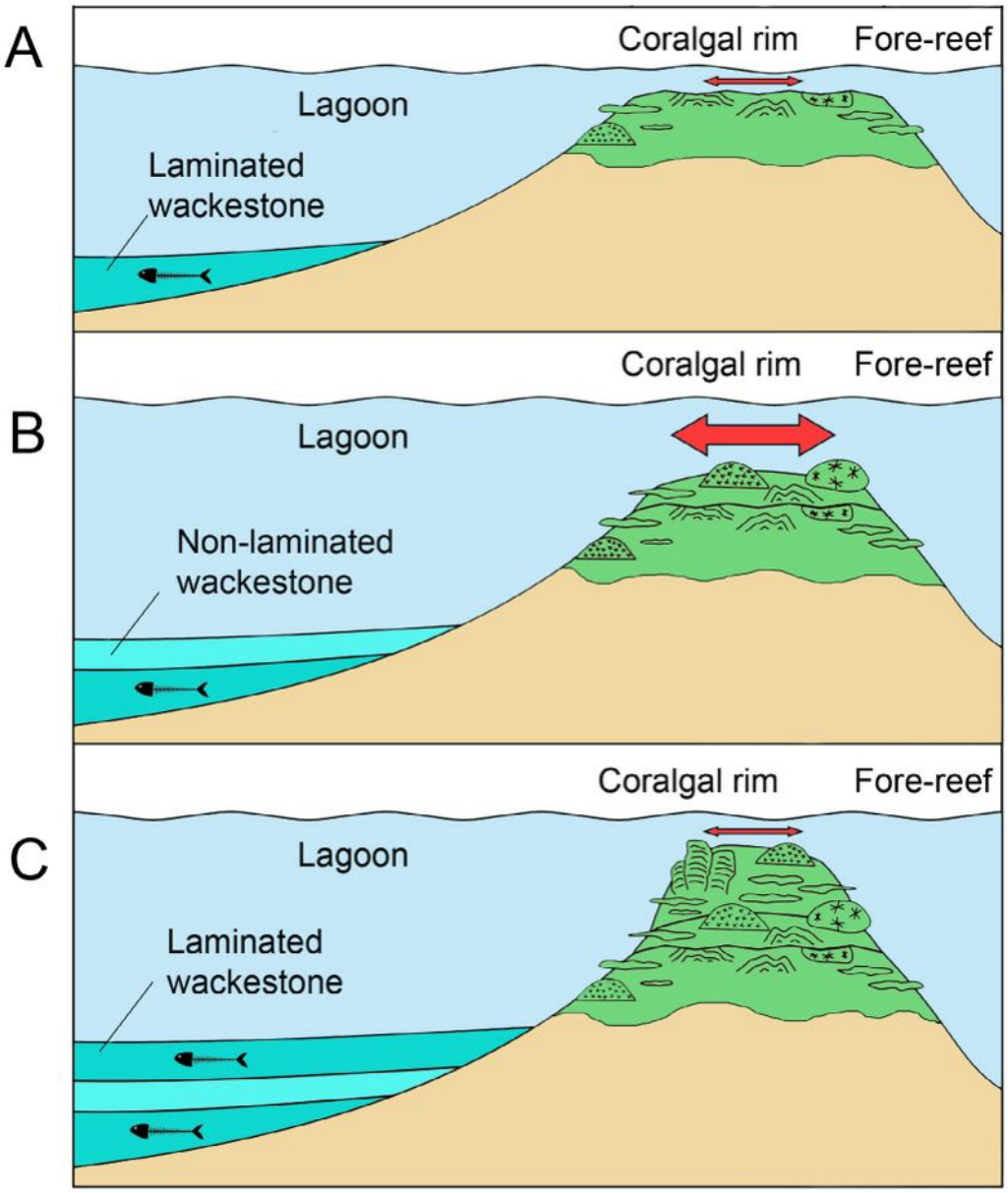

Fig. 34 - Palaeoenvironmental model showing changes in the relative influence of the threshold on the deposition of fine-grained or laminated limestones of the Monte Postale site. Modified after Vescogni et al. (2016).

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