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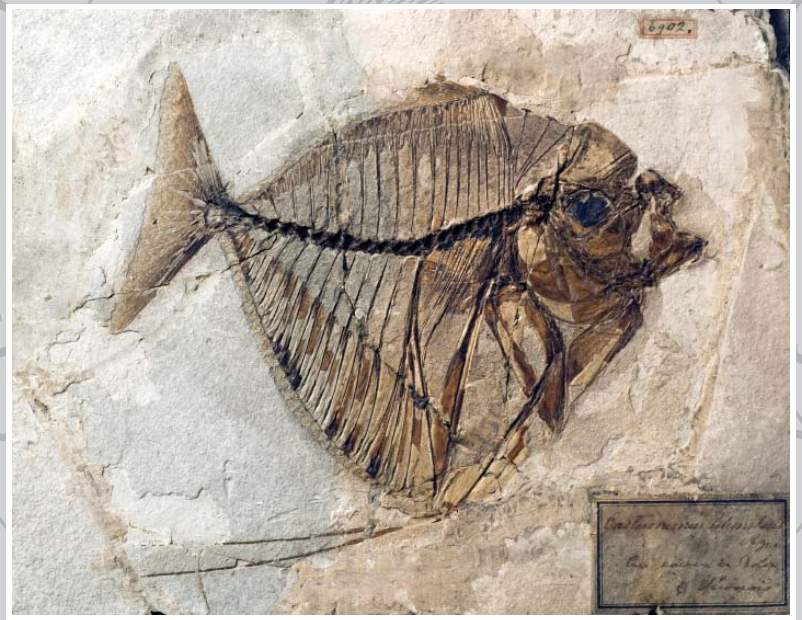
The Bolca *Fossil-Lagerstätten*: A window into the Eocene World



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The Bolca *Fossil-Lagerstätten*: A window into the Eocene World

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Ferrara (Italy), 1-6 July, 2014

9th European Palaeobotany and Palynology Conference (EPPC 2014)
Padova (Italy), 26-31 August, 2014

XII Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP 2014)
Torino (Italy), 24-28 June, 2014

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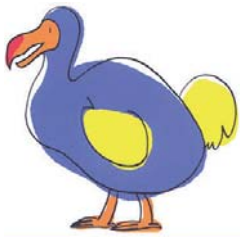

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Foreword

This volume of the Rendiconti della Società Paleontologica Italiana series represents a new step in the effort of our Society to widen its patronage of scientific activities in paleontology. For the first time it does not refer to a Conference directly organized by the SPI, but there are some reasons supporting my decision to provide the editors with the opportunity to contribute to the Rendiconti SPI.

Primarily, the subject of the volume is a field guide dedicated to the Bolca location, as this is the most famous Italian fossil site in the world. Bolca always has a special significance for Italian paleontologists, and the symbol of our Society is, not by chance, Ceratoichthys*, one of the amazing fishes extracted from the Bolca limestones. I think our Society has to support, wherever possible, all the scientific efforts aimed at increasing or spreading knowledge about the Bolca fossil sites.*

Secondly, this guide will be distributed to researchers coming from all continents to the Conferences for which this volume has been prepared. We, as Italian paleontologists, aim to welcome the participants of these meetings with a synthesis of the state-of-the-art in the paleontological knowledge of Bolca.

Finally, the number and quality of the participants to the four Conferences for which this guide has been prepared is a unique chance to have four international meetings in Italy in less than three months, all independently deciding to organize a fieldtrip to Bolca. The topics are only apparently loosely associated as they include Paleogene, paleobotany, vertebrate paleontology, and taphonomy. All of them can be easily related to Bolca, however, as all of them are aspects of the paleontology of this area. All paleontologists, regardless of their specialization, can find something of unique interest in Bolca.

The Società Paleontologica Italiana warmly welcomes all the readers of this volume.

Urbino, June 2014

Rodolfo Coccioni
President of the Società Paleontologica Italiana

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Excursion guidebook CBEP 2014-EPPC 2014-EAVP 2014-Taphos 2014 Conferences
The Bolca *Fossil-Lagerstätten*:
A window into the Eocene World
(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

1. Introduction to the Bolca *Fossil-Lagerstätten*

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This volume is aimed to be a synopsis of the present knowledge about the world-famous Eocene Bolca *Fossil-Lagerstätten* (Veneto Region, northern Italy). Even if the studies regarding the Bolca area never stopped, the most recent overview of this locality is a short book (in Italian) by Sorbini-Frigo & Sorbini (1999). It came about twenty years after the multi-language book by Stanghellini (1979) and more than twenty-five years after the fundamental book (also in Italian language) by Sorbini (1972). Some new data and ideas were presented by Dalla Vecchia et al. (2005) in an exhibition catalogue, whereas the papers of Tang (2002) and Viohl (2008) testify the international importance and fame of the site.

The contemporary presence in 2014 of four international congresses in Italy, each scheduling a fieldtrip to Bolca, underlined the necessity of an updated summary of the current knowledge about this celebrated locality. Since the meetings will consider different aspects of the Bolca *Fossil-Lagerstätten*, namely the fossil vertebrates, the paleobotany, the taphonomy, and the biostratigraphic/paleoecological features, we thought it would be a good idea to deal with all those topics in a single volume.

Moreover, the new data recently published as articles in scientific journals substantially changed and improved our vision of the Bolca *Fossil-Lagerstätten*. The modern research approaches to the issues solved some problems and raised new ones. The work is still in progress, and a lot of specialists (including many of us) are directly involved in new researches that hopefully will result in further knowledge. Therefore, the reader has to bear in mind that what is presented in this volume is the state-of-the-art, which could be overwhelmed in a near future by new data and new interpretations.

To introduce the contents of this book, we would like to start pointing out that in the Bolca area there is much more than a single *Fossil-Lagerstätte*. The most famous one, which yielded most of the amazingly-preserved fossil fishes (Fig. 1), is the so-called "Pesciara" site. The Monte Postale beds, also with fossil fishes and plants, are maybe slightly less famous, and in the past frequently confused with the Pesciara beds when the locality was reported as 'Monte Bolca'. Unfortunately, such a toponym in the Bolca area does not exist, even if its use is still widespread both in Italian and foreign scientific

Fig. 1 - Exquisitely preserved specimen of *Eoplatax papilio* (Volta, 1796), an extremely rare batfish from the Ypresian of Bolca (Cerato collection).

literature; we think it's better to avoid using it and to use more specific and valid names (i.e., Pesciara or Monte Postale) to identify clearly the provenance of the fossils.

Anyway, these two sites represent the 'core' of the Bolca area and the main source of what we could call the Bolca biota. For this reason they are the main subject of this guide and will be treated in several chapters. Nevertheless, there are some other historical fossil sites in the surroundings of the Bolca village, such as the Purga di Bolca, with freshwater and brackish sediments around a volcanic neck; Vegroni, which returned mainly palm trees; and Spilecco, maybe the oldest witness of Paleogene shallow carbonate development in the Veneto area. A brief exposition about these localities will be given as the concluding chapters.

This special volume, as testified by the high number of authors, is the result of a collective effort, a fruitful collaboration among researchers of universities, museums and research institutions. We hope it will be a useful guide for the participants to the international meetings, as well as a compendium for anybody interested to the Bolca fossils.

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(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

2. Historical outline

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Introduction

Since the sixteenth century Bolca and its fossils have yielded materials for philosophical and naturalistic discussions, yet such is still unfinished after four centuries. Long debates and rival theories to explain the presence of fish and plant fossils within sedimentary rocks at Bolca have preceded and were beneficial to the development of paleontology as a separate scientific discipline. In fact, the fossils of Bolca have a special and important place in the history of natural science. A vast number of publications have dealt with the fossils from Bolca, in many cases reporting on ongoing debates among members of the intellectual community, be it of philosophers, naturalists, or modern paleontologists (cf. Vallisneri, 1721; Volta, 1796; Brocchi, 1814; Blot, 1969; Sorbini, 1972; Gaudant, 1997, 1999, 2005, 2011).

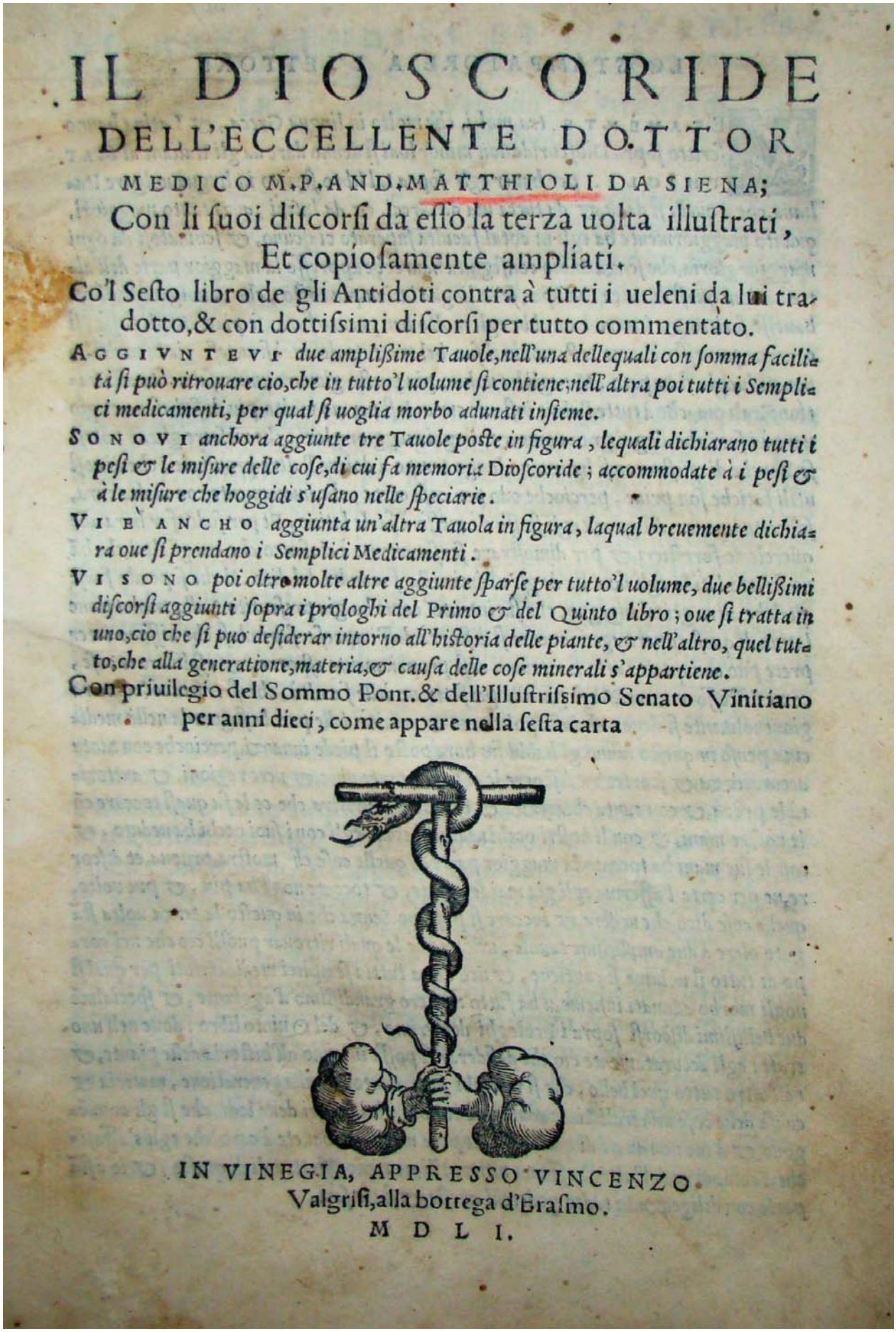
16th and 17th century

The first report of fossils from Bolca is documented in the third edition of the comments of Pietro Andrea Mattioli (1501-1578) to Dioscoride, published in Venezia in 1550 (fourth edition in 1551; Fig. 1).

"Le Chiocciole poi, le Gongole, et parimente alcuni piccioli topi, che si ritrovano alle volte dentro a i sassi, non possono essersi generati se non di calore, e di grassa materia, ne di questo però si meravigli alcuno, percioche gia mi ricordo essermi stato mostrato dal Signor Don Diego Urtado di Medozza Oratore Cesareo a quel tempo in Vinegia alcune lastre di pietra state portate del Veronese in cui (sfendendosi per mezo) si ritrovano scolpiti diverse specie di pesci con ogni lor particula conversa in sasso, e di cotali affermava sua S. ritrovarsene numero infinito la ove quelle erano state cavate, tanto grandi, et maravigliose sono le opere della natura…"

Mattioli did not mention the specific site, although Don Diego's fish slabs, of "infinite number", directly point to Bolca as the only plausible candidate.

Possible mentions of Bolca fossils are given by Simone Majoli, the bishop of Volterra who was remembered by Brocchi (1814) and Lyell (1833) for his theories on the origin



IL DIOSCORIDE
DELL'ECCELLENTE DOTTOR
MEDICO M.P.AND.MATTHIOLI DA SIENA;
Con li ſuoi diſcorſi da eſſo la terza uolta illuſtrati,
Et copioſamente ampliati.
Co'l Seſto libro de gli Antidoti contra à tutti i ueleni da lui tradotto,& con dottiſsimi diſcorſi per tutto commentato.
AGGIVNTEVI due ampliſsime Tauole,nell'una dellequali con ſomma facilità ſi può ritrouare cio,che in tutto'l uolume ſi contiene;nell'altra poi tutti i Semplici medicamenti, per qual ſi uoglia morbo adunati inſieme.
SONOVI anchora aggiunte tre Tauole poſte in figura, lequali dichiarano tutti i peſi & le miſure delle coſe,di cui fa memoria Dioſcoride; accommodate à i peſi & à le miſure che hoggidi s'uſano nelle ſpeciarie.
VI È ANCHO aggiunta un'altra Tauola in figura, laqual breuemente dichiara oue ſi prendano i Semplici Medicamenti.
VI SONO poi oltre molte altre aggiunte ſparſe per tutto'l uolume, due belliſsimi diſcorſi aggiunti ſopra i prologhi del Primo & del Quinto libro; oue ſi tratta in uno,cio che ſi puo deſiderar intorno all'hiſtoria delle piante, & nell'altro, quel tutto,che alla generatione,materia,& cauſa delle coſe minerali s'appartiene.
Con priuilegio del Sommo Pont.& dell'Illuſtriſsimo Senato Vinitiano per anni dieci, come appare nella ſeſta carta
IN VINEGIA, APPRESSO VINCENZO Valgriſi,alla bottega d'Eraſmo.
M D L I.

FIG. 1 - The fourth edition of the comments of Pietro Andrea Mattioli (1501-1578) to Dioscoride, published in Venezia in 1551 reporting on the Bolca fossils.

of the fossils by volcanic activity, and who reported in his "Dies Caniculares" (1597) on the presence of fossil fishes in the Verona area. Anselmus De Boodt (1550-1632), in "Gemmarum et Lapidum Historia" (1609), mentioned fossil fishes from the "Veronensi agro" (the territory around Verona).

During the first part of the 17th century, collecting natural curiosities became fashionable. In particular, the collection belonging to Ulisse Aldrovandi (1522-1605) in Bologna was highly prized and became a means to make hypotheses on the nature of petrifactions. Ulisse Aldrovandi ideas about Bolca fishes were published posthumously, in 1613, in "De piscibus libri V", containing the oldest engravings of these fossils. New illustrations of Aldrovandi specimens were published in 1648, in his "Museum Metallicum".

Another important collection was accumulated in Verona in the Calceolari's Museum, described by Benedetto Ceruti and Andrea Chiocco in 1622 in their "Musaeum Calceolarianum Veronense" (Fig. 2). Most of the specimens of the Calceolari collection went to enrich the Museo del Conte Ludovico Moscardo, also in Verona. Aware that they represented the remains of once-living beings, Moscardo illustrated his holdings in his "Note overo memorie del museo" in 1656, with descriptions and tentative names for some of the fossil fishes, such as "Orada" and "Anguilla" (Fig. 2).

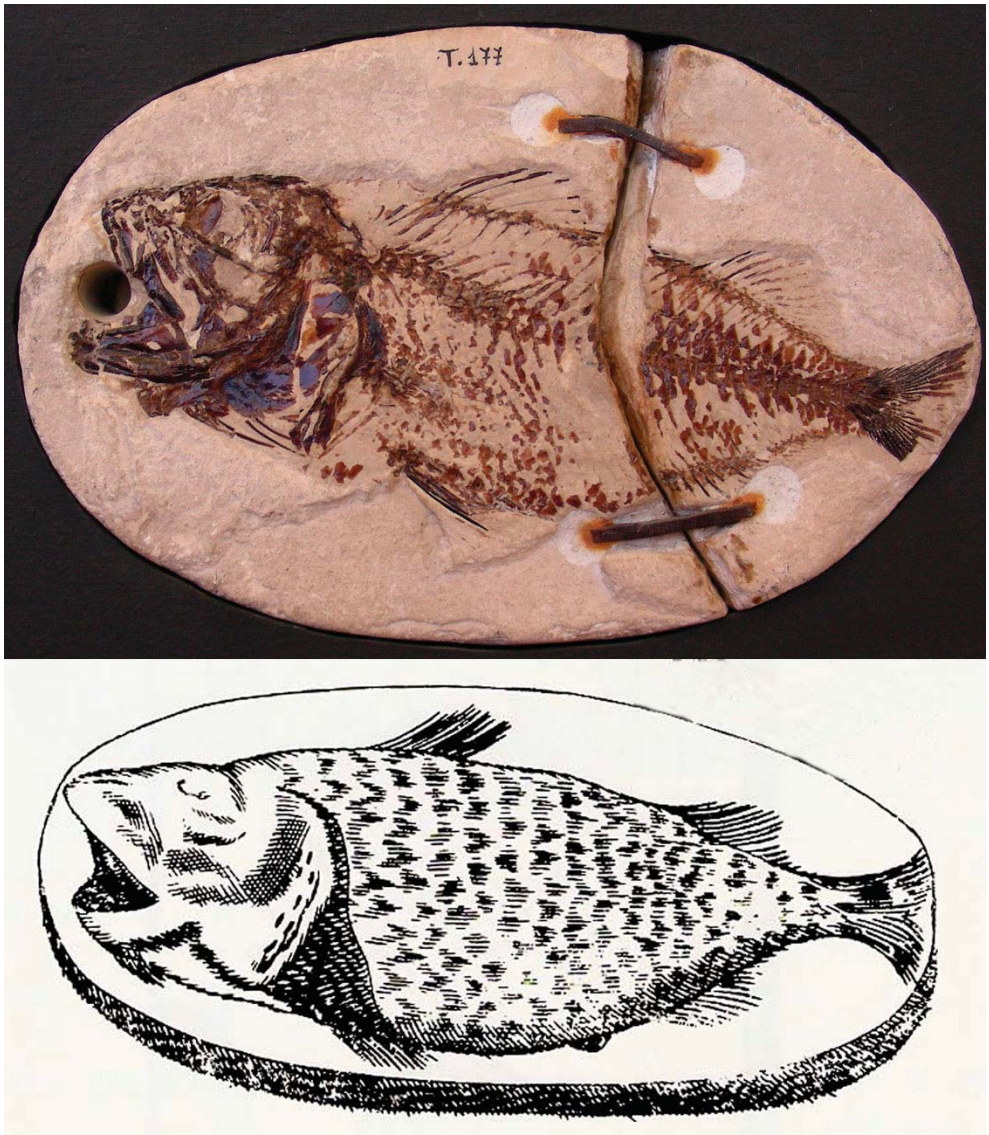


Fig. 2 - The original sample described in the Museo Calceolari (above) and the specimen illustrated by Benedetto Ceruti and Andrea Chiocco in 1622, in their "Musaeum Calceolarianum Veronense" (below).

18TH CENTURY

In 1703 the Italian astronomer Giacomo Filippo Maraldi (1669-1729) presented the Royal Academy of Science of Paris with some fossil fish and plants found by a certain "Mr. Bianchi" (Fontenelle, 1703; Vallisneri, 1721; Volta, 1769). These were interpreted as proof of the theory that fossils developed from seeds, or from eggs, transported by phreatic waters flowing within mountains. Johann Jacob Scheuchzer (1672-1733), a Switzerland physician and naturalist, in his monumental work "Herbarium diluvianum collectum" (1709) described and figured fossils of plants, insects and fishes from Bolca, recognizing among the latter the existence of Indian species (Volta, 1796). Scheuchzer defended the organic origin of fossils, linking their presence to the Universal Deluge described in the Bible (Fig. 3).

Carl Linnaeus studied Bolca fishes adding five new genera to those already described by Scheuchzer. Together with Nils Wallerius (1706-1764), Linnaeus concluded that the Veronese assemblage included the following genera: *Murena*, *Scarus*, *Pleuronectes*, *Scorpaena*, *Scomber,* and *Trigla* (cf. Volta, 1796-1808).

Antonio Vallisneri senior (1661-1730), in a letter to Luigi Ferdinando Marsili written in 1705, came to consider the fossils found in his journey through the Apennines as "sedimenta antediluviana", and not "diluviana" (Vallisneri, 1991). Sebastiano Rotari (1667-1742) visited the Pesciara of Bolca in the autumn of 1716, writing an enthusiastic letter to Vallisneri with a precise description of the locality, later used as the starting passage of "De' Corpi marini, che su' Monti si trovano" (Vallisneri, 1721). Responding to Rotari's questions, Vallisneri claimed to be against Maraldi's thesis (Fontenelle, 1703; see also Sorbini, 1972, Gaudant, 2005, Luzzini, 2009). Vallisneri developed his idea in ten "doubts", criticizing the French astronomer in proposing theories without knowing the geological context. Instead, Vallisneri believed only what he saw with his own

FIG. 3 - Header of the "Herbarium diluvianum" of Scheuchzer (1709) with the representation of the Universal Deluge described by the Bible (Archivio Antico della Biblioteca del Dipartimento di Geoscienze dell'Università di Padova).

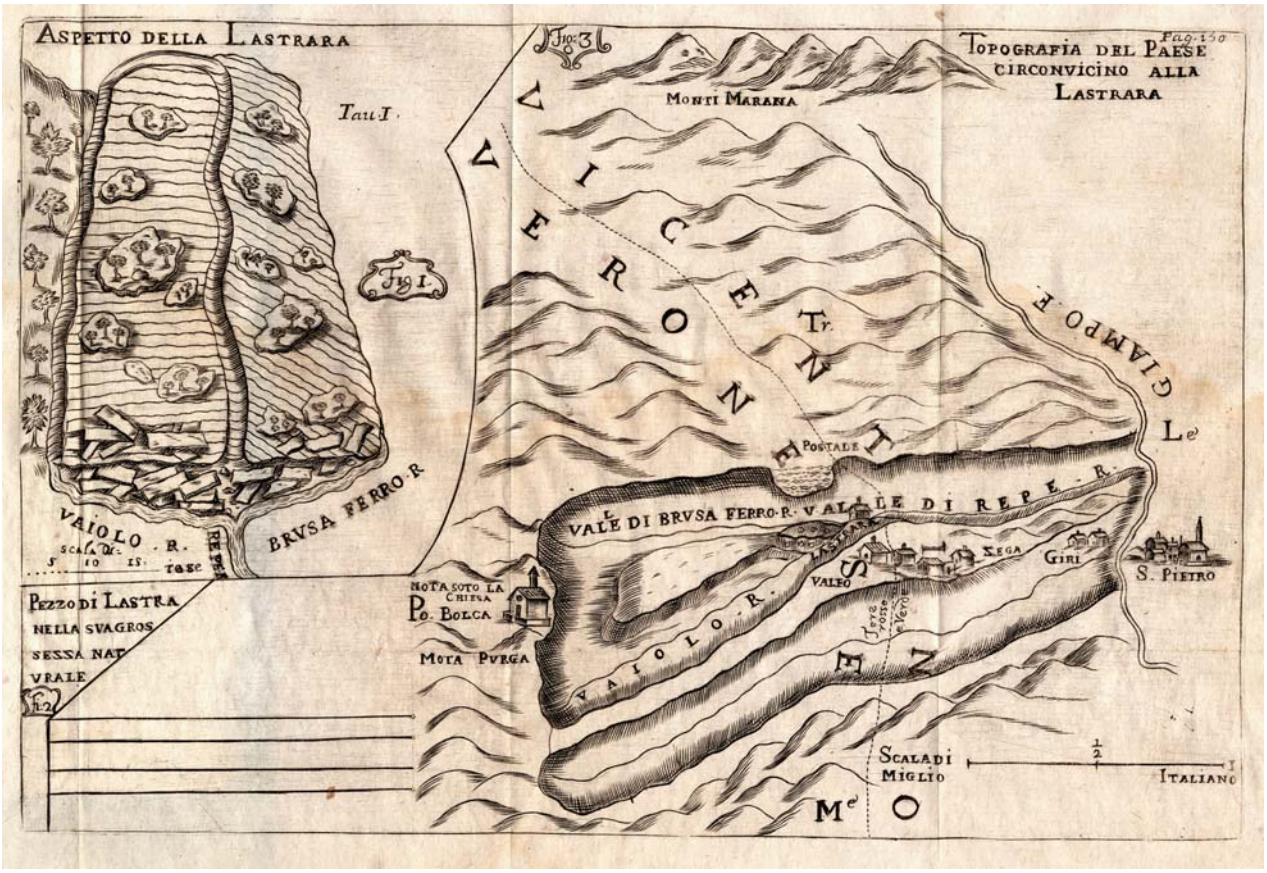


FIG. 4 - Map of Bolca locality by Ferdinando Marsili, in a letter wrote to Vallisneri in 1725 and published in "Opere Fisico-Mediche" of Vallisneri (1733) (Archivio Antico della Biblioteca del Dipartimento di Geoscienze dell'Università di Padova).

eyes, claiming that marine fishes and plants within mountains where not related to any universal deluge, and introducing the concept of upward movements of the rock strata, while excluding the influence of water flow (Vallisneri, 1715, 1721). He was following the ideas of Agostino Scilla (1670) and Bernardino Ramazzini (1691), deeply rooted in the empiricism of Galileo Galilei. The Vallisneri collection was largely built in 1707 with more than fifty samples of fishes, plants, and insects given by Scipione Maffei (1675-1755), an erudite naturalist and collector from Verona who informed Vallisneri on the existence of a complete pigeon skeleton, enclosed in the shaly stone ("pietra scissile") of "Monte Bolca". This is the only bird specimen so far mentioned from Bolca; unfortunately, it was not illustrated and it has never subsequently come to light. Maffei's work on Bolca fishes was published in "Verona illustrata" (1735, chapter III) and "Della formazione dei fulmini" (1747), in which it is suggested that fishes belonging to different habitats had been mingled together by the upsurge of water masses, triggered by volcanic activity, and their subsequent evaporation (Sorbini, 1972; Lazzari, 2002). After the death of his father, Antonio Vallisneri junior (1708-1777) gave the collection to the Padova University, in 1733.

Maps of Bolca were illustrated by Ferdinando Marsili (1658-1730) in a letter he wrote to Vallisneri in 1725 (see Vallisneri's "Opere Fisico-Mediche", 1733)(Fig. 4) and to Arduino, which was published by Giovanni Giacomo Spada (1679-1749) in 1744, who was a priest and an important collector of fossils (Filippi, 1999). Without depending to the Deluge, Spada hypothesized that Bolca fishes were inhabitants of an ancient small basin, their skeletons slowly covered by sediment coming from the nearby mountains (Sorbini, 1972). Girolamo Cesare Fantasti wrote a letter opposing Spada in

Fig. 5 - Drawings of Bolca plants by Jean-Francois Séguier (Plate LVIII from Gaudant, 2005).

1737, referring to the presence of marine animals in the mountains due to the Biblical Deluge, counting that 1656 years had elapsed since the world's creation (Sorbini, 1972). Giovanni Arduino (1714-1745) described Bolca as "a big stone" surrounded by volcanic rocks, the ancient sea floor having been elevated by volcanic eruptions (Arduino, 1769; see also Volta, 1796; Sorbini, 1972; Lazzari, 2002). In "De crostacei e degli altri corpi marini che si trovano sui monti" (1740) Anton Lazzaro Moro (1687-1764) suggested that volcanic eruptions were the main cause underlying the origin of the Pesciara of Bolca strata. In this influential work, Moro claimed that "underground fires push-up the sediment transformed in mountains (that it is not strange as I so explained the set up of the mountains) so nothing lacks to completely explain the rocks and its fishes content" "che da' fuochi sotterranei sia stata all'insù cacciata, e convertita in monte: (il che pare strano non debbe, dappoiché tale mostrato abbiamo essere stato il nascimento di tutti i monti) già nulla più manca per ispiegare compiutamente il Fenomeno degli strati, e de Pesci rinchiusi, del monte Bolca." (Moro, 1740, p. 369; see also Sorbini, 1972).

The unfinished work on fossils ("pétrifications") of the Verona province, written around 1750 by Jean-Francois Séguier (1703-1784), contains very fine engravings of Bolca fossils, such as plants and fishes (Gaudant, 1997, 2005) (Fig. 5). Séguier, who was the secretary and a good friend of Maffei, illustrated fossils coming from the surroundings of Verona, including some from the Maffei collection that, after the death of the latter, were moved to Nimes.

Previously unrecorded fossils of fishes and plants from Bolca housed in the Ginanni Museum in Ravenna were described, identified and illustrated by Camillo Zampieri (1762).

A significant change in the interpretation of Bolca fishes was caused in 1785 by the observations published by Abbot Alberto Fortis (1741-1803) (Fig. 6). He recognized the

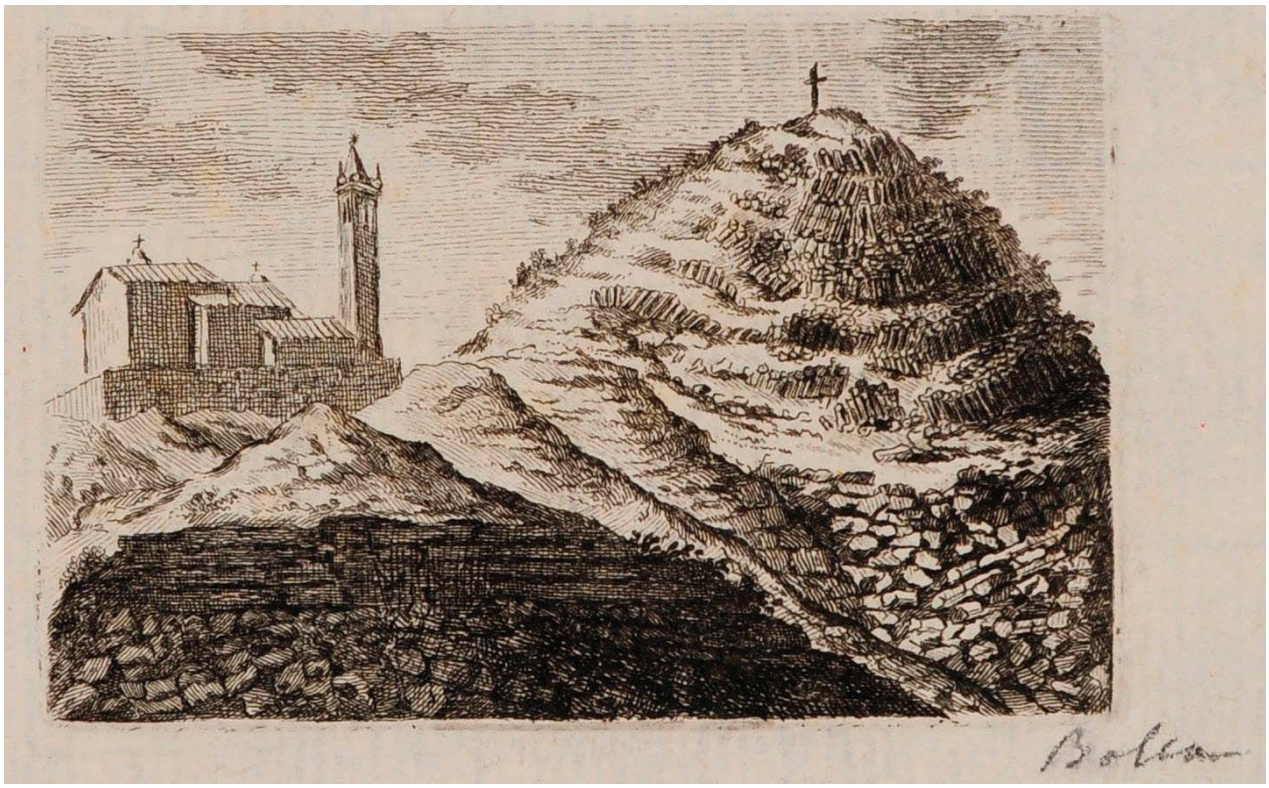


Fig. 6 - Header of Fortis (1778), "Della Valle vulcanico-marina di Roncà nel territorio veronese. Memoria orittografica." Ed. Carlo Palese, published in Venezia. This work, intended to the description of the geology and paleontology of the Roncà area, start with this image referred to Bolca (Archivio Antico della Biblioteca del Dipartimento di Geoscienze dell'Università di Padova).

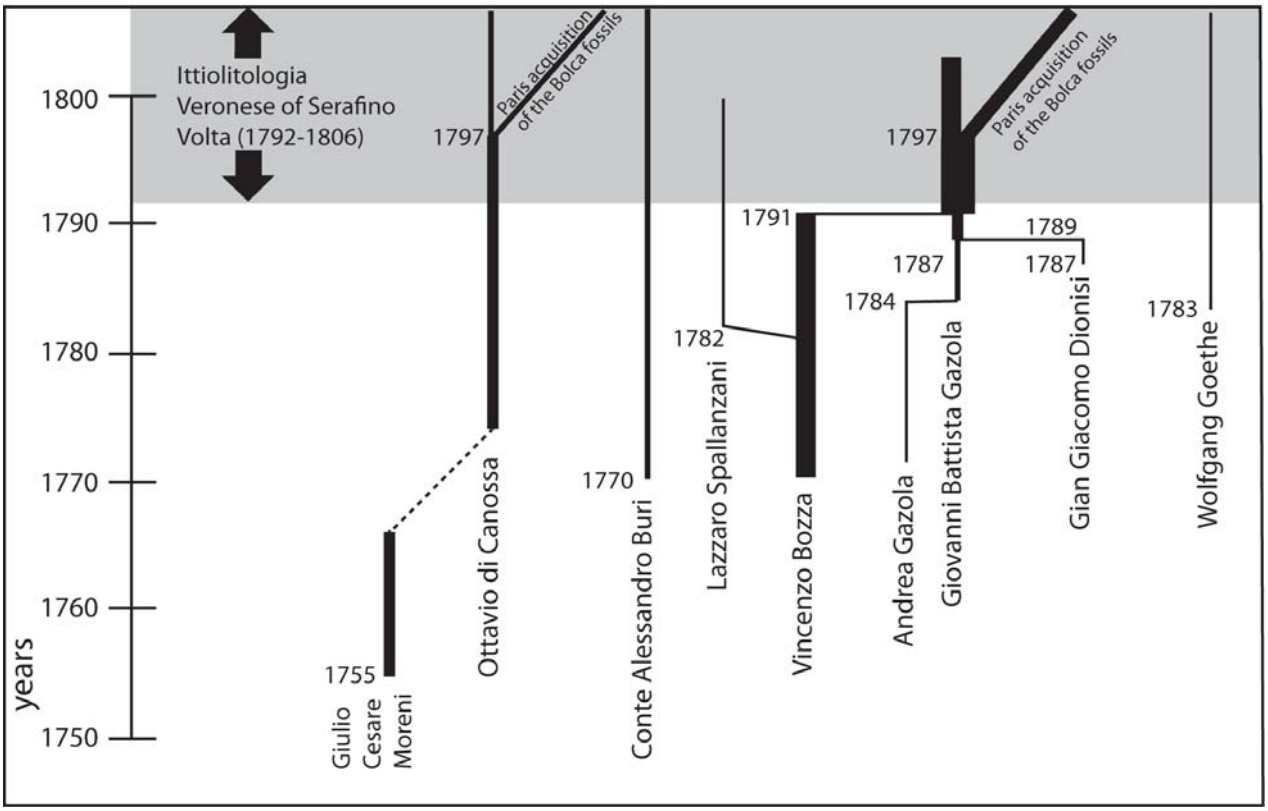


Fig. 7 - History of the acquisitions of the main Bolca fossil collections at the end of the 18th century. The thickness of the vertical black lines is proportional to the consistence of each collection.

presence of tropical fishes in the Bolca assemblage, based on comparison with modern fishes from Tahiti that had recently been described. Fortis addressed his letters to Abbot Testa, while Vincenzo Bozza in 1788 interpreted the Bolca fishes as exotic elements, and Serafino Volta recognized sixty different tropical forms in 1789. These were the years when first arose the idea that the Bolca fauna had an exotic character (Sorbini, 1972). Abbot Testa disapproved of some of Fortis's and Volta's ideas, proposing an alternative explanation by invoking volcanic exhalations that killed and distributed the fishes (Testa, 1793; see also Gaudant, 1999). During the second half of the 18th century, several naturalists were thus engaged in a great unrest by an intense exchange of letters, preparing the ground for more modern studies. Many other naturalists visited, or knew of, Bolca at the end of that century, like Déodat de Dolomieu (1750-1801) in 1784 and 1791, accompanied by Alberto Fortis (Rizzi, 2003). Johann Wolfgang von Goethe had a collection of Bolca fossils, as reported in "Tagebuch der italianischen Reise" (1786), and in the epistolar correspondence with Gian Giacomo Dionisi (1724-1808), an intellectual, naturalist, and collector (Marchi, 2004). The Pesciara fossils were described in some of the oldest instructions to voyagers, such as "Notizia delle cose più osservabili della città di Verona", edited by Moroni (Tommaselli in Moroni, 1795).

In 1797 Napoleone Bonaparte confiscated several hundred Bolca specimens for the Paris Museum (Fig. 7). Around the same time, Serafino Volta (1796-1808) published "Ittiolitologia Veronese", a great work that represented the final outcome of a discussion that had involved the "gabinetti naturalistici" of Verona at the end of the 18th century, first of all with the study of Count Gazola (Fig. 7) (Riva, 1966; Sorbini, 1972; 1998; Frigo & Sorbini, 1997; Gaudant, 2011). The "Ittiolitologia Veronese" included historical aspects and an update on the origin of the fossils and the ancient environment of Bolca. It was subdivided into three parts, the first attempting to explain the origin of the fishes ("Filosofia

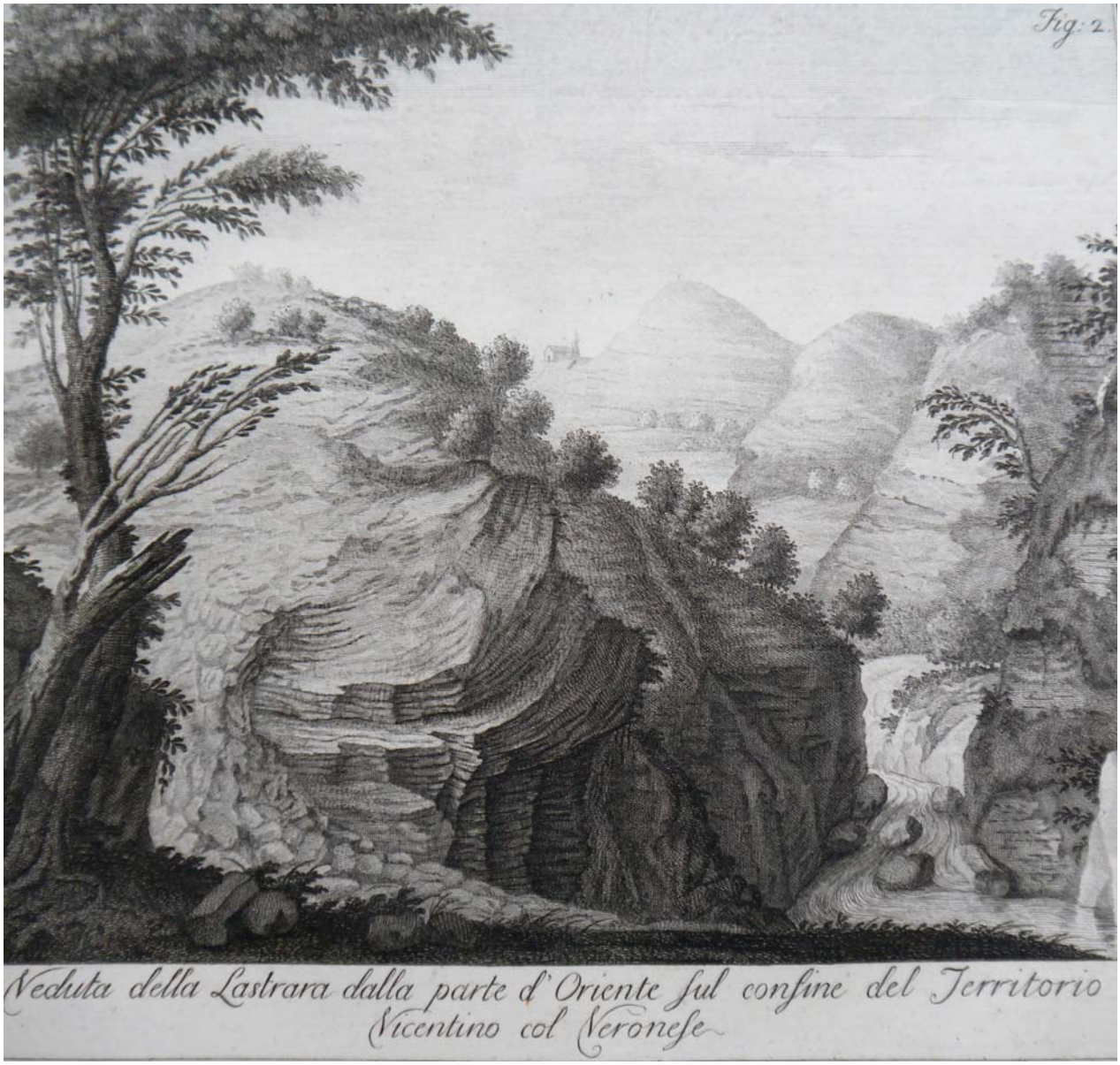


Fig. 8 - Outcrops around the valley of the Pesciara in the Bolca area, from the "Ittiolitologia Veronese" by Serafino Volta (Volta, 1796-1808). Archivio Antico della Biblioteca del Dipartimento di Geoscienze dell'Università di Padova.

Ittiologica") and the geology of the site, the second describing the collections subdivided by the collectors, the third part carrying out the systematic study subdividing the fishes in "cartilaginous, fish-snake and squamous", with an appendix on the deformed fishes. Volta attributed the origin of the site to volcanism, assigning to marine sedimentation a secondary role, and for the first time analyzing the outcrops around Bolca with a positivist attitude (Fig. 8). Since 1777, members of Cerato family have been active in coal mining at the Purga di Bolca, and soon thereafter became involved in the excavation of fossils at the sites of the Pesciara and Monte Postale (Cerato, 2011).

The first half of 19th century

The Bolca collection housed in Paris was studied by de Blainville (1818) and by Barthélemy Faujas de Saint-Fond (1819, 1820), for fishes and plants, respectively. The

first detailed and modern study was contained in the "Recherches sur les Possons Fossiles" published between 1833-1843 by Louis Agassiz. The great paleontologist from Neuchatel, reconsidering Volta's specimens among others, recognized 90 species and 69 genera and established that all the species, although of modern type, were extinct (Agassiz, 1835, 1833-43; Blot, 1969; Sorbini, 1972).

Catullo was the author of a brief historical compilation, describing the structure of the deposit, further revising the fishes of the Bozza and Gazola catalogues (Bozza, 1788; Gazola & Tommaselli, 1794), and listing the different hypotheses on the origin of the deposit (Catullo, 1818). In a later publication, Catullo considered Bolca plants and amber fragments (Catullo, 1826-1827), the latter also cited by Bevilacqua Lazise (1812).

After his journey in Italy, undertaken with Bertrand-Geslin in 1820, Adolphe Théodore Brongniart published on the Bolca flora through the years (Brongniart, 1822, 1823, 1828-1837, 1849), followed by Unger's descriptions and illustrations (Unger, 1845, 1850), and finally by the important paleobotanical studies of Abramo Massalongo, De Visiani and Beggiato (Massalongo, 1850, 1851, 1852, 1853a, b, 1855-1856, 1857, 1858, 1859, 1861; De Visiani, 1864; Beggiato, 1865). A numbered catalogue of fossil fishes, including several new species and the indications of the collectors, was published by Achille De Zigno (1874a, b, 1887).

More historical information on Bolca fossils is given in the other chapters of this volume, as part of the current scientific knowledge on this key locality of Eocene paleontology. Finally, modern paleontological collections housed in the Museo di Geologia e Paleontologia dell'Università di Padova, built through the centuries by subsequent additions to the original nucleus of the Vallisneri collection donated in 1733 (Dal Piaz, 1922; Piccoli & Stiran Rea, 1988), form one of the most important sources of additional information on these important fossils, along with the collections at the Museo Civico di Storia Naturale di Verona and Muséum National d'Histoire Naturelle in Paris.

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The Bolca *Fossil-Lagerstätten*:
A window into the Eocene World
(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

3. Geological and stratigraphical setting of the Bolca area

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Geological setting

Bolca is located in the eastern part of the Lessini Mountains, which are part of the Southern Alps, a structural element forming the northernmost part of the Adria (or Adriatic) Plate (e.g., Carminati et al., 2012).

During the early Paleogene, the Southern Alpine area was subdivided into two basins roughly separated by the present-day Brenta River. The Monte Baldo, the Monti Lessini, the Monti Berici, the Colli Euganei and the Vicenza Pre-Alps belonged to the western basin, whereas the eastern basin embraced the Belluno and Treviso areas (Bassi et al., 2008).

From Paleocene to Oligocene, the western basin was subjected to several pulses of volcanic activity (Barbieri et al., 1991; Barbieri & Zampieri, 1992; Zampieri, 1995) and large part of it allowed the shallowing of the seafloor, contributing to the growth of the carbonate platform called "Lessini Shelf" (Bosellini, 1989). This paleogeographic unit is characterized by widespread deposition of shallow-water carbonates starting from the Early Eocene (Luciani, 1989). The Lessini Shelf (Fig. 1), limited northwards by land and surrounded by deeper marine basins, partially covered the area that, in Jurassic times, was occupied by the shallow-water Trento Platform (Bosellini, 1989; Zampieri, 1995).

During the Paleogene, the central-eastern Lessini and western Berici formed a graben system known as "Alpone-Chiampo graben" (Barbieri et al., 1982), or "Alpone-Agno half-graben" (Barbieri et al., 1991), or "Alpone-Agno graben" (Zampieri, 1995). Since the late Paleocene this structure was bounded toward the west by the east-dipping Castelvero fault (Barbieri, 1972), which dammed the western accumulation of the basaltic volcanics and related subaqueous epiclastics (Fabiani, 1915; Piccoli, 1966a, b). The Bolca area is

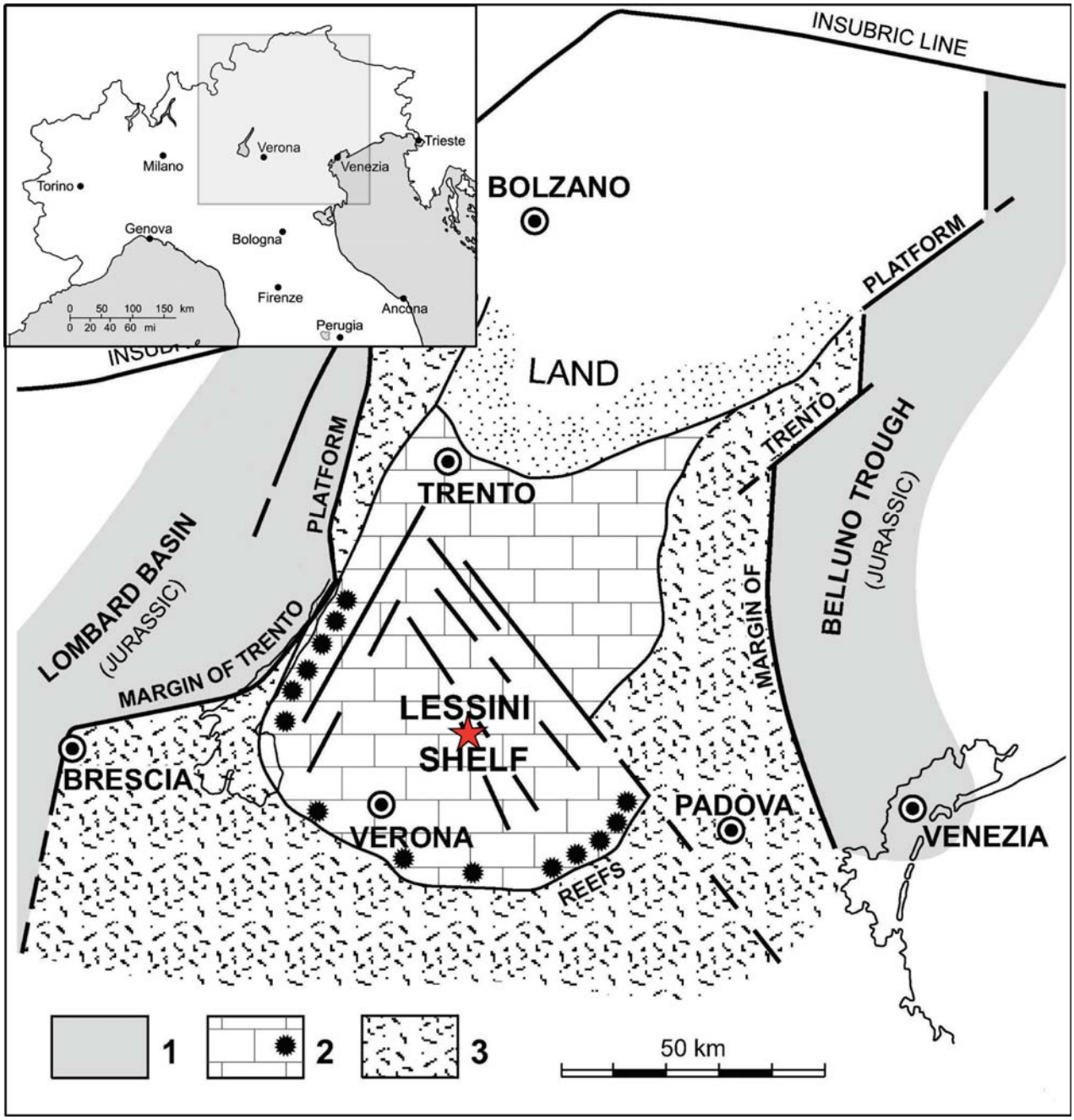

Fig. 1 - Paleogeographic reconstruction of the Lessini Shelf in the Southern Alps during the Paleogene (modified after Bosellini & Papazzoni, 2003). Bolca is indicated by the red star. Legend: 1) deep-water sediments in the Jurassic-Paleogene basins; 2) Paleogene shallow-water limestones with reefs (asterisks); 3) Paleogene deep-water sediments on the former Jurassic Trento Platform.

very close to the Castelvero fault whilst its western part is bounded by the Monte Postale fault (Barbieri & Medizza 1969; Dal Degan & Barbieri 2005; Schwark et al. 2009).

From the earliest Late Paleocene, this graben influenced the sedimentation on the Lessini Shelf, with two areas where different stratigraphic successions deposited (Antonelli et al., 1990): at first, on the eastern area (the graben), pelagic carbonates and resedimented calcarenites deposited, whilst on the western area (western Lessini) shallow-water marine carbonates dominated (De Zanche & Conterno, 1972; Mietto, 1975; Beschin et al., 1998) with the deposition of the 'Calcari Nummulitici' formation. East to the Castelvero fault, the subsidence was more active, and volcanic rocks (basaltic flows, hyaloclastites and volcaniclastics) intercalated with marine carbonate deposits

(Barbieri & Medizza, 1969; Barbieri, 1972; De Zanche & Conterno, 1972; Beccaro et al., 2001). Six volcanic stages were recognized by Barbieri et al. (1991), one from the Late Paleocene and the other five from the Early to the late Middle Eocene. The thickness of volcanics locally exceeds 400 m for the latter volcanic stage (Piccoli, 1966a, b; Barbieri et al., 1991; Zampieri, 1995).

During the Middle Eocene, close to the Lutetian-Bartonian boundary, the volcanic buildups lead to the emersion of the former graben. Therefore, in the Bartonian a volcanic ridge was substantially emerged, except for local and temporary marine episodes leading to the deposition of the so-called "Orizzonte di Roncà" (Fabiani, 1915).

During the Late Eocene the volcanic activity stopped within the graben and the Marne di Priabona Formation deposited in open marine, deep platform setting. This unit onlaps on the margins of the emerged volcanic ridge, with its base marked by a transgressive conglomerate (Barbieri et al., 1980; Mietto, 1992; Trevisani, 1997).

The still-emerging part of the Bartonian volcanic ridge and the whole eastern Lessini were then covered by the Lower Oligocene Calcareniti di Castelgomberto Formation, shallow-water carbonates probably deposited in the backreef of a rimmed platform, with the bioconstructed reef margin localized on the southeastern Berici Mts. (Frost, 1981; Bosellini & Trevisani, 1992; Mietto, 1992). Such peculiar depositional system lasted probably along the whole Rupelian (Geister & Ungaro, 1977).

In the western part of the Lessini Mountains the Oligocene is lacking, probably due to emersion (Luciani, 1989). In the eastern Lessini the carbonate shelf represented by the Calcareniti di Castelgomberto emerged only at the end of the Rupelian (Frost, 1981). The emersion surface of this platform, marked by evident paleokarst features, is interpreted as a 3rd order sequence boundary (Mietto, 1988; Gianolla et al., 1992; Dal Molin et al., 2001).

In the Lessini area, the Upper Oligocene-lowermost Miocene Arenarie e Calcari di S. Urbano Formation (Bosellini et al., 1967; Bassi et al., 2007, 2008; Bassi & Nebelsick, 2010) is overlain by the Lower Miocene Marne Argillose di Monte Costi Formation, only a few meters thick (Bosellini & Dal Cin, 1966; Bassi et al., 2007, 2008), which represents the last marine deposit of Cenozoic age in this area.

Stratigraphy

The Cenozoic stratigraphy of the Bolca area is not easy to reconstruct, because of the widespread occurrence of faults displacing the Eocene sedimentary succession into different blocks (the Castelvero Fault is close to this area), and also the presence of volcanic and volcaniclastic rocks intercalated or cutting the sedimentary succession (Fig. 2).

The first modern geological reports on the Bolca area date back to the 19th century (e.g., Suess, 1868; Bayan, 1870; Munier-Chalmas, 1891). Oppenheim (1894) studied the larger foraminiferal fauna, erecting among others the species *Nummulites bolcensis* and *N. spileccensis*, characteristic of this area.

Ramiro Fabiani (1912) defined the "Spileccian" stage after the name of the Spilecco hill, close to the Bolca village. He described in detail the geology of this area (Fabiani, 1914, 1915), drawing a stratigraphic sketch of the Monte Postale succession. The Fabiani's studies represent a cornerstone for the geological and stratigraphic interpretation of Bolca, being subsequently used and widely cited by all the researchers dealing with this locality. Among them, a mention is due to Schweighauser (1953), who studied the larger foraminifera from Spilecco and Monte Postale; to Malaroda (1954), who revised the mollusk fauna from the Monte Postale; to Hottinger (1960), who studied the alveolinids

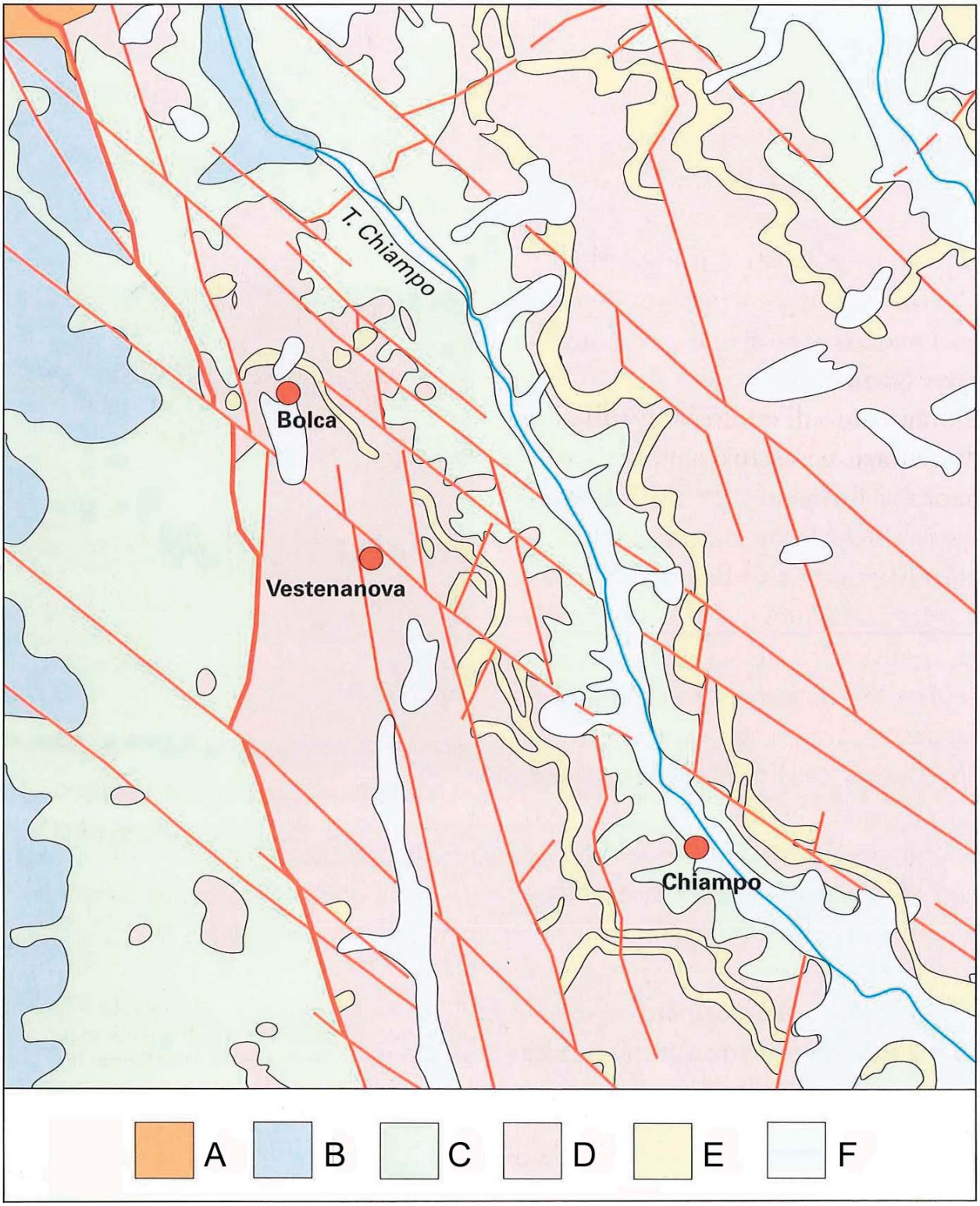

FIG. 2 - Simplified geological sketch map of the Bolca area (modified from Muscio & Tintori, 2005). A) Triassic dolostones; B) Jurassic limestones; C) Cretaceous limestones; D) Paleocene-Eocene volcanic rocks; E) Eocene limestones; F) Quaternary deposits.

from the Purga di Bolca, Brusaferri, Monte Postale, and Valecco; to Cita & Bolli (1961), who determined the biozonal assignment of the type-Spileccian by means of planktonic foraminifera; to Brönnimann et al. (1965), who studied planktonic foraminifera and calcareous nannoplankton from Spilecco and Purga di Bolca; to Barbieri & 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.

Fig. 3 - Panorama view of the Pesciara site.

The geological map by Bosellini et al. (1967) distinguished the Calcari di Spilecco formation, dated to the Paleocene-Early Eocene, from the Calcari Nummulitici formation (Middle Eocene). The former were restricted to the beds from Spilecco, whereas the Purga di Bolca and Monte Postale were included in the Calcari Nummulitici. Antonelli et al. (1990) retained the name 'Calcari Nummulitici' for both the biocalcarenites and organogenic limestones of the Monte Postale and the laminated calcilutites of Bolca (Pesciara; Fig. 3). Muscio & Tintori (2005) published a simplified geological sketch map of the surroundings of Bolca (Fig. 2). Dal Degan & Barbieri (2005) gave the most updated synopsis of the geology of the Bolca area, with a new detailed geological map (1:10,000) of Bolca and its surroundings. They distinguished the 'Calcare di Monte Spilecco' unit, dated at 56-58 Ma, the volcanic rocks (subdivided into several different units: lavas, basalt veins and breccias, hyaloclastics, epiclastics, caothic breccias, and volcaniclastics) and the Calcari Nummulitici. However, they used this term with restricted sense, apparently applying it only to the limestones which indeed contain nummulites. For the remaining limestones (mainly containing alveolinas or laminated beds with fishes and plants) they introduced the name "Formazione del Monte Postale-Pesciara".

All these lithostratigraphic units should be treated as informal ones, and the "Calcari Nummulitici" urgently need a revision, because it includes much different lithologies, paleoenvironments, and ages.

The biostratigraphy of the different localities (see Papazzoni et al., 2014, this volume) is currently under study.

The products of the volcanic activity are probably to be referred to the third phase recognized by Barbieri et al. (1991), but no radiometric ages are at present available for this material.

The fossiliferous sites of the Bolca area

Even if the most famous fossiliferous sites near the Bolca village are the Pesciara (Fig. 3) and the Monte Postale, several other localities with peculiar fossil contents and different stratigraphic settings are known (Fig. 4).

Among them, it is widely cited the Spilecco hill, or simply Spilecco. As mentioned above, it was the type locality of the local stage "Spilecciano", defined by Fabiani (1912) as equivalent to the whole Paleocene-Lower Eocene. The Spilecciano was retained in the literature until the end of 1960's (Bosellini et al., 1967; Barbieri & Medizza, 1969), but restricted to a short timespan within the latest part of the Paleocene (Schweighauser, 1953; Cita & Bolli, 1961) and then definitively abandoned. The characteristic gray-green limestones to reddish marly limestones of the Spilecco outcrops (poorly exposed at present) bear a rich fossil content made up mainly by planktonic foraminifera (in the gray-green limestones), larger foraminifera (nummulitids and orthophragminids) and macrofossils (in the reddish marly limestones); the glauconite is widespread in both lithologies. The larger foraminiferal fauna, containing among others *Nummulites*

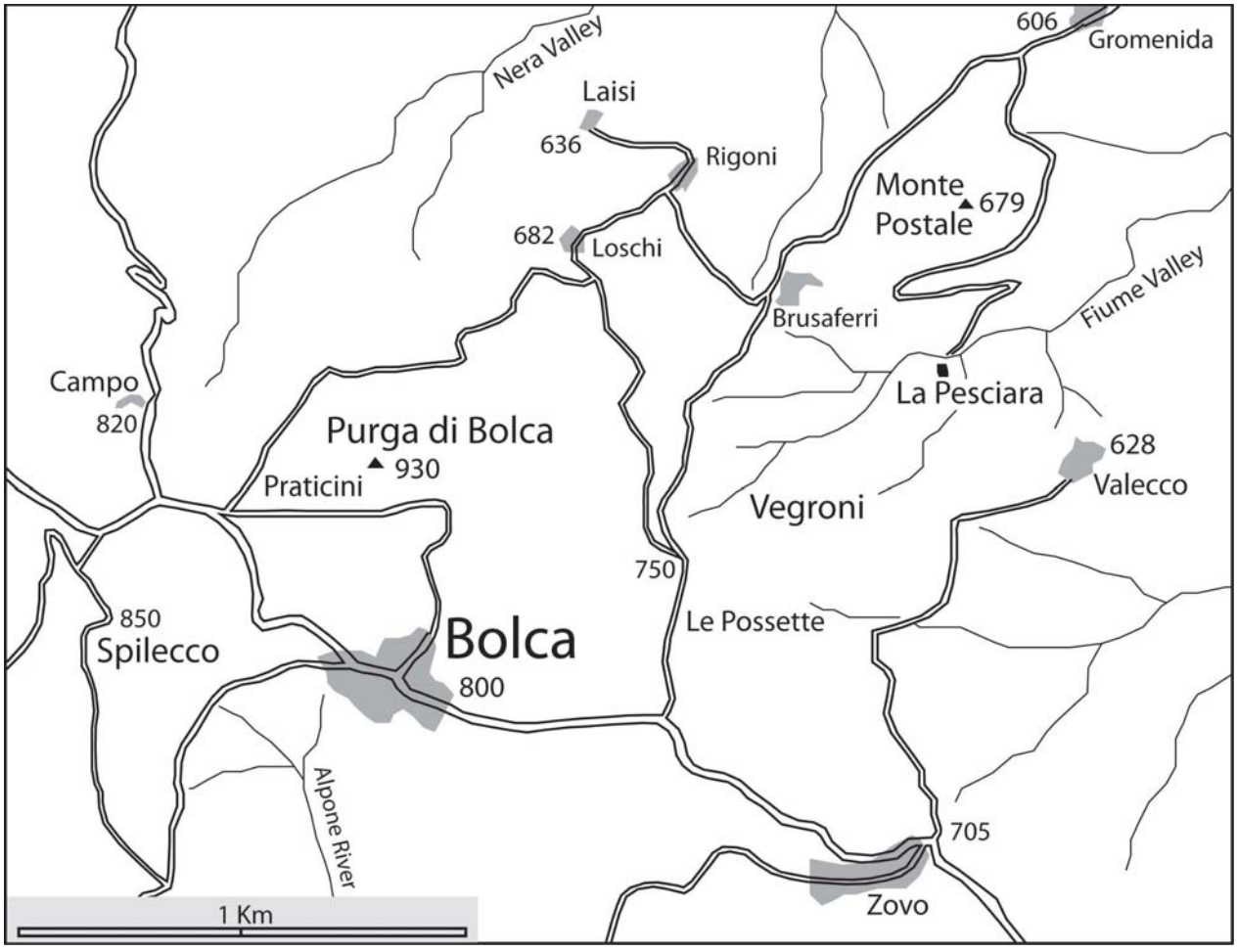

Fig. 4 - Location map of the main fossiliferous sites cropping out in the surroundings of Bolca (Verona).

bolcensis and *N. spileccensis*, allow to refer the Spilecco beds to the SBZ 7 (Trevisani & Papazzoni, 2003) of Serra-Kiel et al. (1998), or lower Ypresian, in good agreement with the nannoplankton zone NP 10 and the planktonic foraminifera zone P 5 (Barbieri & Medizza, 1969). The Spilecco beds represent the oldest Cenozoic evidence of shallow-water deposition in the Lessini Shelf (Trevisani & Papazzoni, 2003), even if they are indeed resedimented periplatform deposits. According to the chronology of volcanic phases (Barbieri et al., 1991), the Spilecco beds were deposited right after the first period of volcanic activity, so it is possible the volcano structures acted as areas of starting for small shallow-water platforms then coalesced into a larger one.

The Purga di Bolca is another important locality where a volcanic neck is preserved as a characteristic conical hill (Monte Purga). Barbieri & Medizza (1969) dated this neck to "post-Cuisian" times, giving a radiometric age of 36 Ma, or 'Early Oligocene'. No modern radiometric dating has been performed on this material, so this age needs confirmation. The neck cuts through 10-20 m of freshwater-brackish sediments (shales, siltites, lignites) containing ostracods, continental and brackish mollusks, crocodiles, and chelonians (Medizza, 1980). The sediments are in turn overlaid by volcaniclastic rocks with palm trees (*Latanites*). The sedimentary levels in the lowermost part of the succession bear calcareous nannofossils allowing their assignment to the NP 12 Zone (Barbieri & Medizza, 1969), in the middle Ypresian. The continental beds do not contain any marker, so their age is quite debated (see Giusberti et al., 2014, this volume), even if it could be still Ypresian (Sorbini, 1972; Medizza, 1980). The crocodile and turtle-bearing beds cropping out at Praticini mentioned by Blot (1969) probably correspond to the freshwater-brackish sediments of the Purga di Bolca. Other localities often cited as source of crocodiles and turtles include Loschi, Le Possette, and Valecco-Zovo (Blot, 1969), but no data about their geological setting and stratigraphy are at present available; maybe they represent the same levels present in the Monte Purga. Also the Vegroni locality, known for its beautiful palm trees, could probably be correlated with the Purga, but all these localities need further study to confirm or discard the correlation.

The Monte Postale succession, thoroughly described by Fabiani (1914, 1915), is the most complete in the Bolca area, spanning from the Cretaceous Scaglia Rossa Fm. up to the Ypresian-Lutetian(?) limestones with *Alveolina*, in their uppermost part containing also marine and continental-brackish mollusks, Lutetian according to Malaroda (1954), or more probably Cuisian according to the larger foraminiferal fauna (Hottinger, 1960). The lower-middle part of this section was recently re-studied by Papazzoni & Trevisani (2009), who attributed the *Alveolina* limestones to the SBZ 11 (middle Cuisian, or upper part of the Ypresian). At present, there are no updated biozonal assignments for the uppermost part of the Monte Postale section. In the lower-middle portion of this section there are laminated limestones very similar to the ones in the Pesciara, also bearing fish and plants.

Brusaferri is very close to the Monte Postale section. It gives its name to the so-called "horizon de Brusaferri" (Blot, 1969), or "calcari a *Numm. irregularis*" (Fabiani, 1915), rich in nummulites, assilinas, echinoids, and mollusks. According to Schaub (1981), this is the type locality of *Nummulites pratti* and it also indicates the middle Cuisian (SBZ 11 according to Serra-Kiel et al., 1998).

The Pesciara di Bolca is the most famous locality, and together with the laminated limestones of the Monte Postale, the major source of fossil fish and plants. In the old collections these two localities are often not separated and sometimes they are referred to as "Monte Bolca", even if this has no correspondence in any official toponym. The larger foraminifera from the Pesciara limestones, already mentioned by Hottinger (1960) and Schaub (1981), were recently re-studied (Trevisani et al., 2005; Papazzoni & Trevisani,

2006) and the section was entirely assigned to the SBZ 11 (Serra-Kiel et al., 1998). The nannofossils recognized in a single sample indicated the NP 14, also compatible with the uppermost part of the Ypresian (Medizza, 1975). The direct correlation between the Pesciara and Monte Postale sites is hampered because the Pesciara is an isolated block surrounded by volcanic and volcaniclastic deposits. Therefore, there is no continuity between the limestone of the Pesciara succession and the similar rocks of the Monte Postale, on the opposite side of the valley. A detailed stratigraphic and sedimentological study is needed to clarify the Pesciara-Postale relationships.

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The Bolca *Fossil-Lagerstätten*:
A window into the Eocene World
(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

4. The Pesciara-Monte Postale *Fossil-Lagerstätte*: 1. Biostratigraphy, sedimentology and depositional model

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Biostratigraphy

The age assignment of the Monte Postale and Pesciara *Fossil-Lagerstätten* has been longly debated. Fabiani (1914, 1915) assigned all the strata to the Lutetian (Middle Eocene) (Fig. 1). Also Malaroda (1954) considered the mollusks from the Monte Postale as Lutetian.

Medizza (1975) studied the calcareous nannofossils on a single sample from the Pesciara, attributing it to the *Discoaster sublodoensis* Zone (NP 14 or CP 12), whose

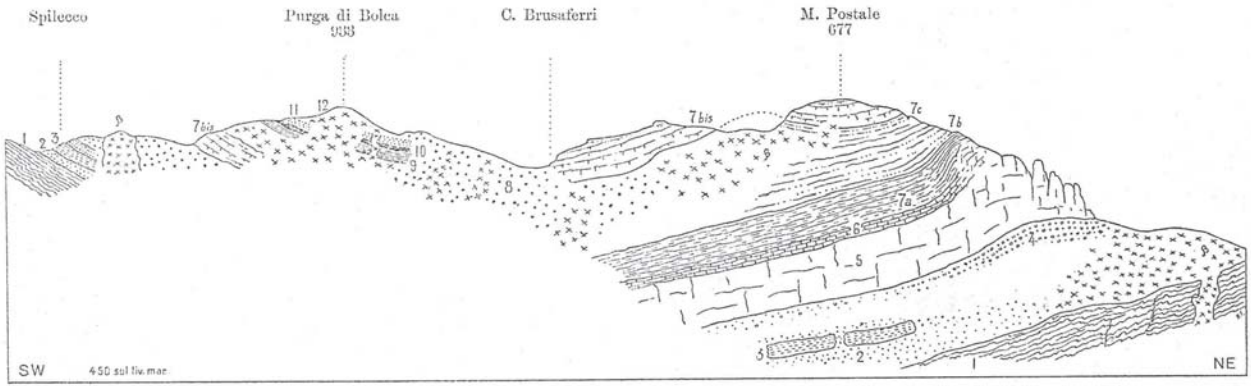

Fig. 1 - Monte Postale-Purga di Bolca-Spilecco profile and section according to Fabiani (1915). 1) "Senonian" (Upper Cretaceous) Scaglia Rossa; 2) "Early Eocene" (probably Upper Paleocene) tuffs; 3) "Early Eocene" (probably Upper Paleocene-lowermost Eocene) limestones; 4) basaltic breccias with red algae ("Nullipore"); 5) algal ("Nullipore") limestones; 6) laminated limestones with crustaceans; 7) *Alveolina* limestones: 7a) with plants and fishes; 7b) with marine mollusks; 7c) with marine, brackish, and terrestrial mollusks; 7bis) *Nummulites irregularis* limestones; 8) basaltic breccias; 9) Marls; 10) shales and lignite with *Crocodylus vicetinus*; 11) Tuffs with palm trees and freshwater-terrestrial mollusks; β) basalts.

range covers the uppermost Ypresian and lowermost Lutetian. This age contrasted with the larger foraminiferal *Alveolina dainellii* Zone determined by Hottinger (1960), which is well below the Lower/Middle Eocene boundary. Medizza (1975) stated that the larger foraminifera were reworked, as already declared by Sorbini (1967) and reaffirmed by Massari & Sorbini (1975).

Papazzoni & Trevisani (2006) found that the alveolinid tests are usually either quite well preserved or present a degree of abrasion consistent with a penecontemporaneous transport from a nearby area. Moreover, the taxonomic study of the whole fauna indicated a larger foraminiferal assemblage belonging to a single biozone, the SBZ 11 (middle Cuisian; Serra-Kiel et al., 1998), corresponding exactly to the *A. dainellii* Zone determined by Hottinger (1960). A single sample in the lowermost part of the Pesciara section bears surely reworked alveolinids from the *Alveolina oblonga* Zone (SBZ 10, early Cuisian; Papazzoni & Trevisani, 2006). The correlations among different biozonations allowed to better precise the age of the Pesciara limestones, restricting it to a narrow interval between the base of the NP 14 and the top of the SBZ11 (Fig. 2).

At present there are no published updated biostratigraphic data regarding the Monte Postale succession. A preliminary report assigning the lower-middle part of the Monte Postale to the SBZ 11 has been published by Papazzoni & Trevisani (2009).

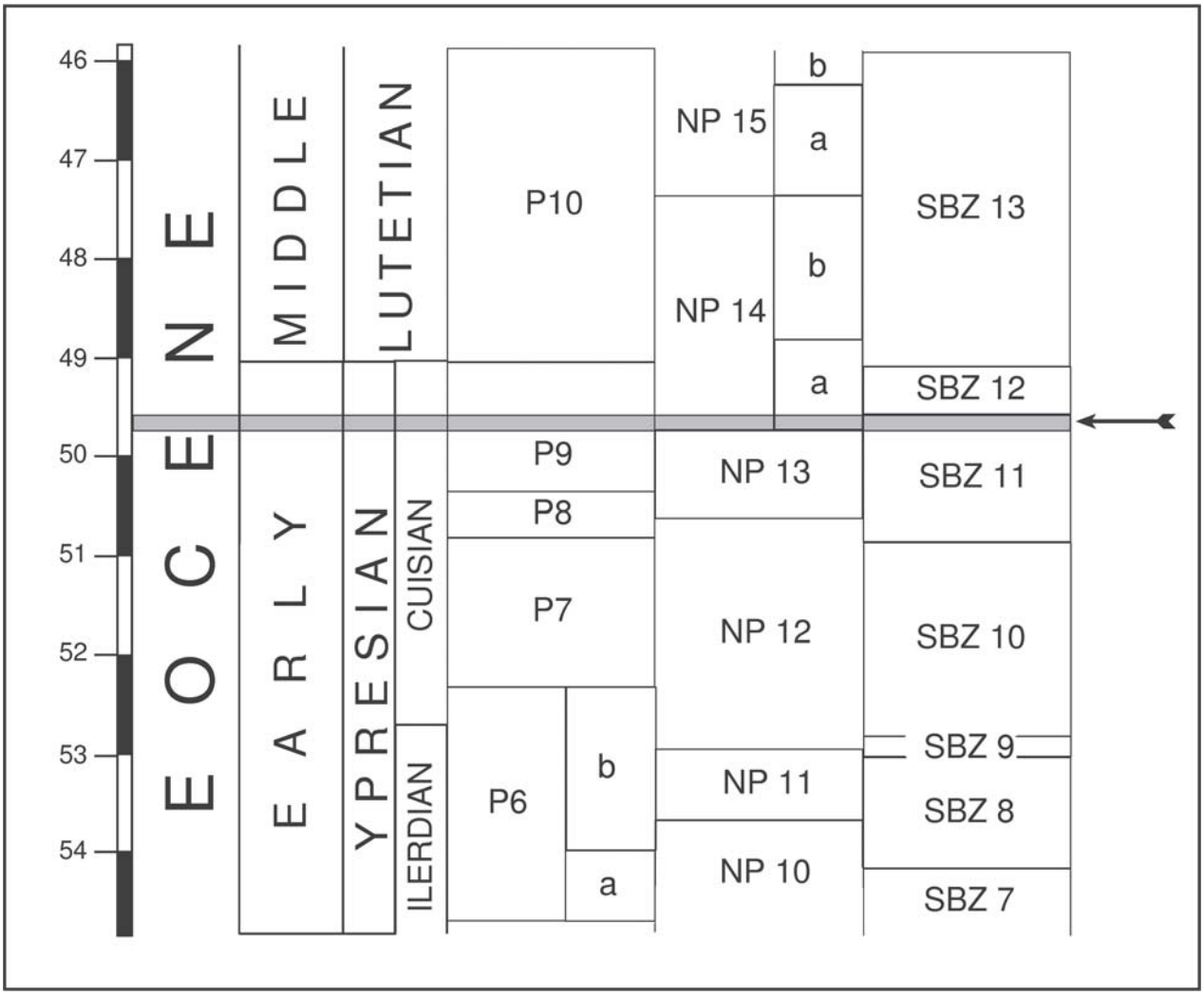

Fig. 2 - Correlation between the planktonic (P), calcareous nannofossils (NP) and the shallow benthic (SBZ) biozonations (modified after Serra-Kiel et al., 1998); the arrow indicates the estimated biostratigraphic assignment of the Pesciara section (after Papazzoni & Trevisani, 2006).

Sedimentology and depositional model

Bolca is worldwide famous mainly for its fossil fish fauna, which comes entirely from the two localities of the Pesciara di Bolca and Monte Postale. The two localities are very close each other and, even if their stratigraphic relationships are still not completely understood (see above), they share common features, such as the presence of finely laminated limestone containing the fish and plant fossils. These lithologies are common in other *Fossil-Lagerstätten* of different ages, such as for instance the Jurassic Solnhofen lithographic limestone, where intra-platform depressions or basins were protected from the wash and wave action of the open ocean by one or several thresholds (Barthel et al., 1990; Papazzoni & Trevisani, 2006). Usually these deposits are assumed to have been developed in shallow water environments (less than 200 m depth), characteristic for most *Fossil-Lagerstätten*, though upper bathyal depths were proposed by Giusberti et al. (2014) for the recently described Early Eocene *Fossil-Lagerstätte* of Solane (Verona province), very close to Bolca both in time and space.

In these restricted basins the reconstructed paleoenvironment is commonly anoxic and eventually euxinic due to the lack of bottom dwellers, except for washed in organisms or rare currents marks. The conditions of scarce to absent oxygenation enhance the preservation of organic matter primarily produced within the water column by autotrophic organisms and also the production of floating or benthic microbial mats. However, the organic matter content of the Pesciara di Bolca limestone is rather low with Total Organic Carbon (TOC) < 0.5% (Schwark et al., 2009). In accordance with these data, exceptional fossilization in anoxic conditions does not appear to guarantee high organic matter contents. The investigation of the organic matter from the Pesciara *Fossil-Lagerstätte* provided important information about the paleoenvironmental parameters allowing the exceptional preservation of fossils in the laminated limestone (Schwark et al., 2009).

The fossil content of the fish-bearing beds includes, together with the fish, plant remains, algae, worms, crustaceans, insects, very rare jellyfishes, cephalopods, reptiles, and birds (Sorbini, 1972). In addition, the occurrence of amber has also been reported (Trevisani et al., 2005). The rarity of autochthonous benthic invertebrates may suggest that the Pesciara is a stagnation deposit according to the classification of Seilacher et al. (1985). The fish fauna, however, includes several benthic taxa (batoids, pleuronectiforms, eocottids, callipterygids, and lophiiforms) and many others which certainly were closely associated with the substrate (see Carnevale et al., 2014, this volume, for a more detailed discussion).

The high taxonomic diversity of the fish assemblage and its tropical shallow-water character have been traditionally interpreted as the evidences of a close link to a coral reef system (e.g., Blot, 1969). Moreover, the Bolca fish assemblage includes the earliest representatives of several families today closely associated with coral reefs. The morphology of the Bolca taxa belonging to reef fish families is extremely similar, if not undistinguishable, from that of their extant counterparts. For this reason, Bellwood (1996) and, subsequently Bellwood & Wainwright (2002), considered the fossil fishes of Bolca as the earliest clearly defined evidence of coral reef fish assemblage, documenting the starting point of the association between certain fish families and coral reef systems.

At the same time, based on auto- and synecological considerations, Landini & Sorbini (1996) assigned the Pesciara fossil fish assemblage to a perireefal system influenced by both the heterogenous coastal environments and the open sea. According to Landini & Sorbini (1996), the sedimentation of the laminated limestone took place in a silled depression located parallel to the coast at many dozens of meters of depth. In this model,

the overall physiographic context consists of a coastal area influenced by the open sea and characterized by fluvial systems, coastal lagoons and open expanses of *Halochloris* sand and seagrass beds surrounding reef zones.

A more recent model proposed by Papazzoni & Trevisani (2006) suggests that the Pesciara-Monte Postale laminated limestone were deposited in a subtropical lagoon, close to an emerged area with rivers and coastal swamps. The transition to the open sea was partially interrupted by a rising threshold, passing seawards to an oceanic setting testified by the presence of pelagic fishes (e.g., clupeids, paralepidids, carangids, ductorids, scombrids, blochiids, palaeorhynchids, euzaphlegids, pomatomids, etc.; Landini & Sorbini, 1996). The nature of this threshold is still uncertain: even if some coral-bearing limestones have been described in the past (e.g., Barbieri & Medizza, 1969), there are at present no reports of reefal bioconstructed limestones.

The facies analysis of the Pesciara limestones distinguished the evenly laminated micrite with fish and plant remains, interpreted as deposited in a lagoon with very low hydrodynamic energy, and the miliolid-dominated or *Alveolina*-dominated limestones, interpreted as detrital deposits generated by storm events wiping out the threshold, destroying part of it, and transporting into the Pesciara lagoon the washover sands. The alternating abundance or scarcity of this detrital deposition was explained as controlled by periodical relative sea-level oscillations influencing the effectiveness of the threshold in sheltering the lagoon (Papazzoni & Trevisani, 2006).

The total thickness of the Pesciara limestones is not easy to be measured, because of the uneven distribution of the detrital levels, which have laterally variable thickness and erosive base. Moreover, some slumps are clearly visible on the outcrop and at least in one case a fish-bearing level has been involved in synsedimentary deformation (Fig. 3). However, the total thickness measured by Papazzoni & Trevisani (2006) do not exceed 17 m at present. Other than the present-day four evenly-laminated limestones (L1-L4 in Fig. 3), there was in the past one more fish-bearing level (L5 in Fig. 3) above, but it has been completely destroyed by the digging activity for collecting fossil fishes.

The presence of drylands close to the Pesciara is also witnessed by the fossil continental plants (trees, bushes, herbs, coconuts, etc.; Massalongo, 1856, 1859; amber; Trevisani et al., 2005) and animals, e.g., insects (hymenopterans, orthopterans, termites, etc.; Massalongo, 1856; Omboni, 1886; Secretan, 1975), arachnids (a scorpion; Cerato, 2011), snakes (Janensch, 1904, 1906; Auffenberg, 1959), and birds (Omboni, 1885; Cerato, 2011).

According to the organic geochemical data, the predominant origin of kerogenous organic matter in the Pesciara sediments can be attributed to marine organisms with a minor admixture of terrigenous material. Biomarkers reveal that the terrigenic fraction is predominantly made up by land plant waxes that were transported into the depositional environment by eolian processes. Only in the lowermost fish-bearing level in the Pesciara the terrigenous-derived organic matter indicates significant terrestrial freshwater run-off (Schwark et al., 2009).

Molecular biomarkers indicate that the marine organic production was dominated by diatoms, even if they were never reported in the fossil assemblages. Their absence is tentatively attributed to dissolution of diatom tests under alkaline pore water conditions; the dissolved biogenic silica could be in turn the source of the observed silicified levels in different parts of the Pesciara succession. A potential role of benthic diatom mats in the preservation process of fossils has been speculated by Schwark et al. (2009), because of the low abundance of cyanobacteria inferred from the moderate amounts of mid-chain branched alkanes and other cyanobacterial biomarkers.

The depositional environment in the Pesciara paleobiotope was most probably anoxic though not euxinic, with a water column stratification due to episodic freshening of the

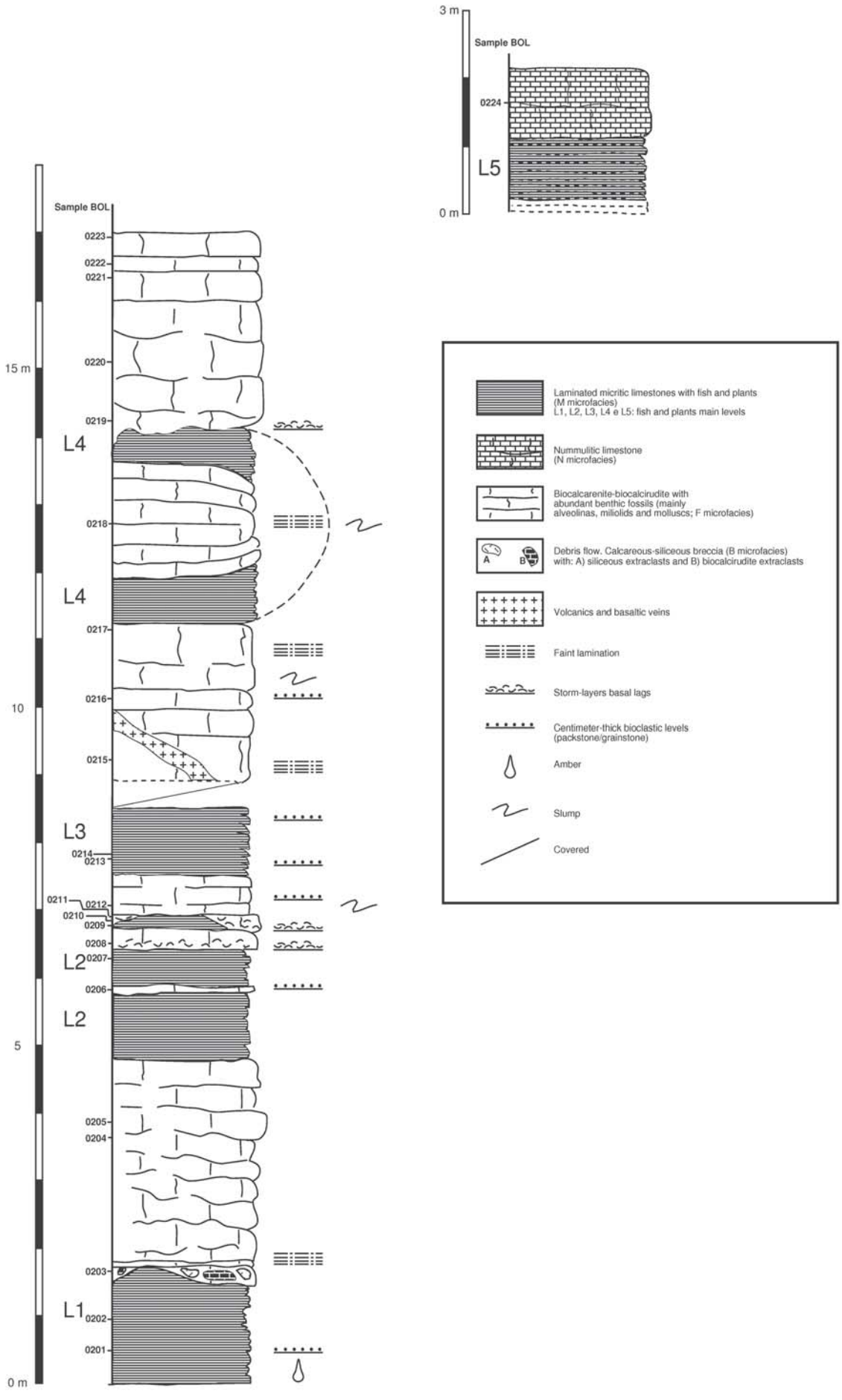

FIG. 3 - Stratigraphic column of the Pesciara section (after Papazzoni & Trevisani, 2006).

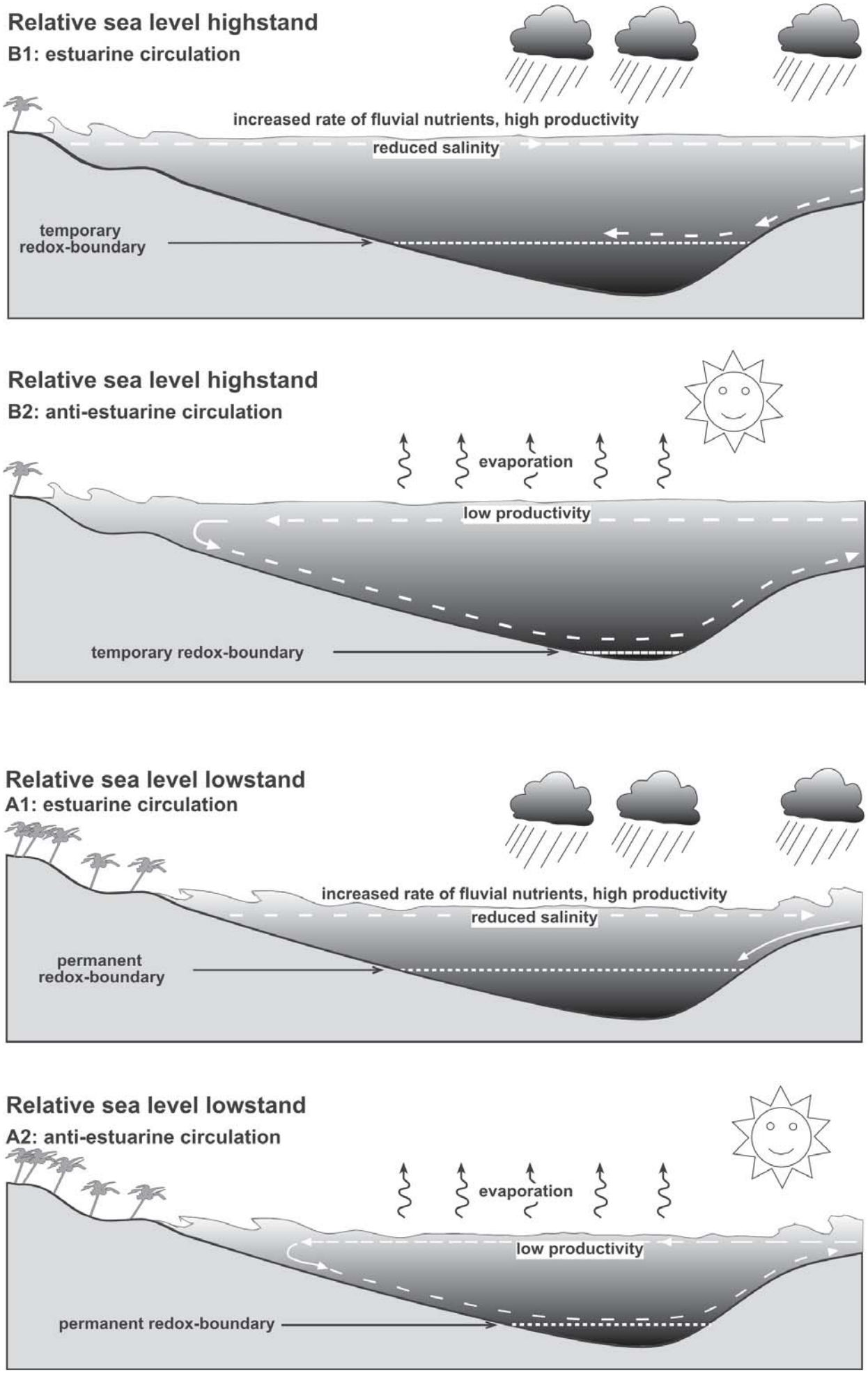
Relative sea level highstand
B1: estuarine circulation
increased rate of fluvial nutrients, high productivity
reduced salinity
temporary
redox-boundary
Relative sea level highstand
B2: anti-estuarine circulation
evaporation
low productivity
temporary redox-boundary
Relative sea level lowstand
A1: estuarine circulation
increased rate of fluvial nutrients, high productivity
reduced salinity
permanent
redox-boundary
Relative sea level lowstand
A2: anti-estuarine circulation
evaporation
low productivity
permanent redox-boundary

FIG. 4

upper water layers by monsoonal rain and terrestrial run-off, as shown by terrigenous biomarkers and fossils (Fig. 4). No organic markers of hypersaline bottom waters were found, though this condition is plausible as a consequence of high evaporation conditions in an equatorial carbonate platform. The very high (about 37°C) mean annual paleotemperature estimates for the nearby and nearly contemporaneous Solane *Lagerstätte* (Giusberti et al., 2014) suggest this hypothesis is not to be discarded.

The relative sea-level lowstands maximized the effectiveness of the threshold, inducing stagnation and very restricted circulation in the deeper parts of the basin (Fig. 4A). On the contrary, during relative sea-level highstand intervals the threshold was less effective, allowing to some extent admixing and slight oxygenation of the bottom waters with lower E_h values compared with the former (Fig. 4B).

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Fig. 4 - Interpretation of the Pesciara depositional environment, according to Schwark et al. (2009). A) Depositional setting during lowstand times, with effective threshold and permanent water stratification; these conditions are recorded in the lower part of the Pesciara section. B) Depositional setting during highstand times, with less effective threshold and temporary water stratification; these conditions are recorded in the upper part of the Pesciara section (after Schwark et al., 2009).

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A window into the Eocene World
(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

5. The Pesciara-Monte Postale *Fossil-Lagerstätte*: 2. Fishes and other vertebrates

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Introduction

Fossil fishes are by far the most celebrated and well studied component of the Bolca biota. The fish fauna of Bolca is certainly one of the most important and best known ichthyofaunistic fossil assemblages. The fish material is outstanding in terms of preservation quality and number of specimens, making this extraordinary assemblage the most diverse of all the Cenozoic marine ichthyofaunas. Because of the beauty and scientific relevance of these fossils, one of the most spectacular species from Bolca, *Ceratoichthys pinnatiformis*, has been used for many years as the symbol of the Società Paleontologica Italiana (Fig. 1).

Because of their exquisite preservation and attractive appearance, the fossil fishes from Bolca have been coveted for more than four centuries by aristocrats and noblemen to enrich and enhance their collections of natural history objects.

The existence of excellently preserved "petrified" fishes in the limestone of Bolca was reported for the first time in 1550 by the famous botanist and physician Pietro Andrea Mattioli in the third edition of the translation of his "Dioscorides De Materia Medicinale". Mattioli examined some fossil fishes from Bolca belonging to the collection of Diego Hurtado de Mendoza, the ambassador of Emperor Charles V to the Venezia Republic from 1539 to 1547, and was impressed by their superb preservation, with the complete transformation into stone of all of their anatomical details.

By 1571 Francesco Calceolari, a renowned apothecary from Verona, had amassed a vast collection of natural history objects, including several fishes from Bolca, in the so-called "Musaeum Calceolarium". In the 1584 catalogue of the contents of the Calceolari museum by the physician Giovan Battista Olivi, the fossils, including those from Bolca, were regarded as lusus naturae. In 1622 the physicians Benedetto Ceruti and Andrea Chiocco from Verona figured for the first time a fish from Bolca in the descriptive catalogue "Musaeum Francesci Calceolari Iunioris Veronensis", which was gracefully embellished with illustrations, representing a philosophical excursus occasioned by the objects of

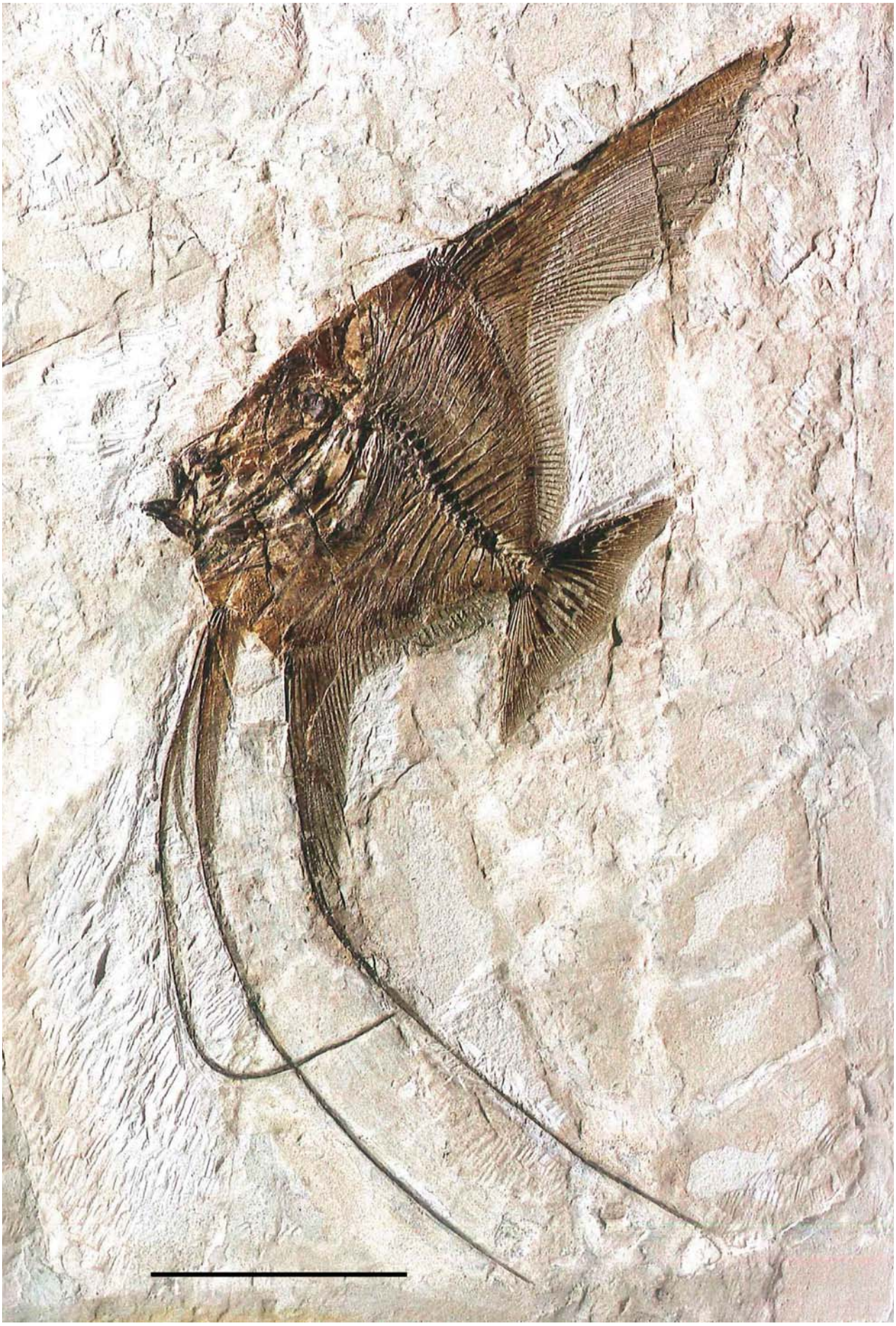

Fig. 1 - *Ceratoichthys pinnatiformis* (Blainville 1818), MCSNV T.950, left lateral view; scale bar 100 mm.

the museum in which the authors provided an elevated status to the museum and its owners (Findlen, 1994). Meanwhile, the bishop and canon lawyer Simone Majoli in his encyclopaedic "Dies Caniculares" (1597) considered the fishes from Bolca as remains of marine organisms which had been carried to the mountains through the activity of ancient volcanoes. On the other hand, the naturalist Ulisse Aldrovandi (1648) interpreted the fish skeletons from Bolca as Islebian fish-stones, following the theory elaborated one century earlier by Georgius Agricola. In 1656, the Count Lodovico Moscardo figured some fossil fishes from Bolca in his "Note, overo, Memorie del Museo di Lodovico Moscardo", including what he interpreted as a gilthead seabream (Orada) and an eel (Anguilla).

The fishes of Bolca and their origins were extensively discussed during the 18th century by several prominent naturalists, including Johann Jakob Scheuchzer, Antonio Vallisneri, Ferdinando Marsili, Anton Lazzaro Moro, Scipione Maffei, Déodat de Dolomieu, and Giovanni Arduino (Sorbini, 1972). Towards the end of the century (1793-1795), a cogent debate about the origin and significance of these fossils involved three abbots, Domenico Testa, Alberto Fortis, and Giovanni Serafino Volta (Gaudant, 1999). During the first half of the 18th century, several large collections of Bolca fishes were assembled in Verona by noblemen such as Vincenzo Bozza, Alessandro Buri, Ottavio Canossa, Giulio Moreni, Ignazio Ronconi, Sebastiano Rotari, and Giovanni Battista Gazola. Most of these collections were purchased by count Gazola and eventually flowed into his own museum, which, at the end of 1791, contained more than a thousand well-preserved fossil fishes from Bolca. One of the abbots involved in the controversy, Giovanni Serafino Volta, who was the brother of the well-known physicist Alessandro Volta, published a short first catalogue of Bolca fishes, based on the large collection of Vincenzo Bozza (Volta, 1789); Volta (1789) assigned most of the fossil fishes to extant species, many of which are distributed in tropical seas. However, in order to properly document the extent of these collections, in 1789 Volta started preparing a beautifully illustrated comprehensive catalogue of the fossil fishes from Bolca, this being the famous "Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del conte Giovambattista Gazola e di altri gabinetti fossili Veronesi", published between 1796 and 1809, and produced by the printing house of the count Bartolomeo Giuliari. The "Ittiolitologia Veronese" constitutes the earliest treatise on paleoichthyology and included the description of more than 120 species.

In May 1797, about 600 specimens of the Gazola collection of fossils from Bolca were confiscated by the revolutionary armies of Napoleon that occupied Verona, transported to Paris, and deposited in the Muséum National d'Histoire Naturelle (e.g., Eastman, 1904; Frigo & Sorbini 1997; Gaudant, 2011). Henry Ducrotay De Blainville (1818) used this collection for his account of fossil fishes which appeared in the "Nouveau dictionnaire d'histoire naturelle". However, the first critical analysis of the collection was that of the Swiss naturalist Louis Agassiz, a founder of comparative zoology, who reviewed (Agassiz, 1835) the identifications presented by Volta (1796-1809) in the "Ittiolitologia Veronese", and later (Agassiz, 1844) described the fossils in great detail in his monumental "Recherches sur les Poissons Fossiles" (1833-1844).

In the years following the confiscation of part of his collection, Giovanni Battista Gazola purchased the collection of Ignazio Ronconi and, together with the naturalist Tommaso Antonio Catullo, organized new excavations in the productive sites of Bolca in order to amass a new collection of fossil fishes, which is now part of the vast collection housed in the Museo Civico di Storia Naturale, Verona.

Modern paleoichthyology began with the publication of the "Recherches sur les Poissons Fossiles" (Agassiz, 1833-1844), of which Bolca fishes composed a considerable part. After the publication of this transformative work, numerous authors have contributed

to expand our knowledge about the diversity of the Bolca fish assemblage, including Johann Jakob Heckel, Rudolf Kner, Abramo Massalongo, Wladislaw Szajnocha, Paolo Lioy, Dragutin Gorjanović-Kramberger, Otto Jaekel, Achille de Zigno, Franz Steindachner, Arthur Smith Woodward, Francesco Bassani, Charles R. Eastman, Geremia D'Erasmo, and, more recently, Jacques Blot at the Paris museum and Lorenzo Sorbini at the Verona museum, as well as the authors of this chapter.

Overall, the excellent preservation of the fully articulated fish skeletal remains of Bolca has traditionally favoured detailed morphological comparisons with extant taxa. As a consequence, these fossils contributed significantly to the development of modern fish systematics, especially to that of teleosts. Therefore, the fossil fishes from Bolca have exerted a considerable influence in the fields of paleo- and neoichthyology.

The Bolca fish assemblage: taxonomic diversity

Blot (1969) estimated that about 100,000 fish specimens have been extracted from the Pesciara and Monte Postale sites at Bolca during approximately four centuries of extensive exploitation. Considering the reduced volume of available fossiliferous deposits, it is evident that these two productive sites are extremely rich in terms of numbers of specimens. Such a huge number of specimens available for study, now disseminated in many museums, research institutions, and private collections around the world, has allowed for the description of an impressive number of taxa, making Bolca the most diverse fossil marine fish assemblage known to date.

As mentioned above, the first list of Bolca fishes was provided by Volta (1789), who recognized slightly less than 100 species within the material of the collection of Vincenzo Bozza. A few years later, based on investigations on the large collection of the Count Giovanni Battista Gazola, he (Volta, 1796) recognized 123 species, most of which were illustrated in 76 magnificent plates. In his magnum opus "Recherches sur les Poissons Fossiles", Agassiz (1833-1844) recognized 127 species of fishes belonging to 55 genera. Subsequently, updated catalogues of Bolca fishes were provided by de Zigno (1874) and D'Erasmo (1922). A resurgence of studies of Bolca fishes started in the 1960s, mostly due to the efforts of Jacques Blot, and culminated with the publication of a new catalogue (Blot, 1980), in which he listed 208 nominal species belonging to 117 genera included in not less than 72 families. Since the publication of Blot's (1980) catalogue, many new taxa have been described and the taxonomic status of many others has been corrected. When Lorenzo Sorbini, a former doctoral student of Blot in Paris, became the director of the Verona museum, he encouraged and expedited the study of the Verona collection of Bolca fishes by a broad array of international scientists. Subsequent directors of the Verona museum, Alessandra Aspes and, presently, Giuseppe Minciotti, have wisely continued that fine tradition.

In order to properly define the full extent of the known ichthyofaunal diversity, Bannikov (in press) recently assembled a new catalogue of Bolca actinopterygians, listing 219 species in 191 genera. The list presented herein in Tab. 1 comprises 238 taxa and represents a modified version of that by Bannikov (in press), with the inclusion of cartilaginous fishes plus a few insertions and deletions within the teleostean fishes.

The compositional differences between the fish assemblages of the Pesciara and Monte Postale are difficult to define. However, the overall structure of the two assemblages appears to be rather similar (Sorbini, 1972) even if the Monte Postale site may have a somewhat larger component of off-shore and pelagic taxa (Bannikov & Tyler, 1999; Bannikov & Zorzin, 2004).

Order	Family	Taxon
Carcharhiniformes	Carcharhinidae	*Eogaleus bolcensis* Cappetta, 1975
		Physogaleus cuvieri (Agassiz, 1835)
		Alopiopsis plejodon Lioy, 1865
Orectolobiiformes	Hemiscylliidae	*Mesiteia emiliae* Kramberger, 1885
Rajiformes	Rhinobatidae	*Rhinobatus dezignoi* Heckel, 1853
		Rhinobatus primaevus de Zigno, 1874
Torpediniformes	Narcinidae	*Titanonarke molini* (Jaekel, 1894)
		n. gen. et n. sp.
Myliobatiformes	Dasyatidae	"*Dasyatis*" *muricata* (Volta, 1796)
		"*Dasyatis*" *dezignoi* Molin, 1861
	Myliobatidae	*Promyliobatis gazolae* de Zigno, 1885
	Urolophidae	"*Urolophus*" *crassicaudatus* (Blainville, 1818)
		"*Urolophus*" sp.
	Plathyrhinidae	*Platyrhina bolcensis* Heckel, 1851
		Platyrhina gigantea (Blainville, 1818)
		Platyrhina egertoni de Zigno, 1878
Pycnodontiformes	Pycnodontidae	*Pycnodus apodus* (Volta, 1796)
		Nursallia veronae Blot, 1987
		Abdobalistum thyrsus Poyato-Ariza & Wenz, 2002
		Palaeobalistum orbiculatum Blainville, 1818
Crossognathiformes	Pachyrhizodontidae	*Platinx macropterus* (Blainville, 1818)
Osteoglossiformes	Foreyichthyidae	*Foreyichthys bolcensis* Taverne, 1979
	Arapaimidae	*Thrissopterus catullii* Heckel, 1856
	Osteoglossiformes incertae sedis	*Monopteros gigas* Volta, 1796
Anguilliformes	Anguilloididae	*Anguilloides branchiostegalis* (Eastman, 1905)
		Veronanguilla ruffoi Blot, 1978
	Milananguillidae	*Milananguilla lehmani* Blot, 1978
	Anguillidae	*Eoanguilla leptoptera* (Agassiz, 1835)
	Paranguillidae	*Paranguilla tigrina* (Agassiz, 1839)
		Dalpiaziella brevicauda Cadrobbi, 1962
	Congridae	*Voltaconger latispinus* (Agassiz, 1839)
		Bolcyrus formosissimus (Eastman, 1905)
		Bolcyrus bajai Blot, 1978
		Paracongroides heckeli Blot, 1978
	Chlopsidae	*Whitapodus breviculus* (Agassiz, 1835)
	Proteomyridae	*Proteomyrus ventralis* (Agassiz, 1839)
	Ophichthyidae	*Goslinophis acuticaudus* (Agassiz, 1835)
	Patavichthyidae	*Patavichthys bolcensis (*Bassani, 1897)
	Anguilliformes incertae sedis	*Bolcanguilla brachycephala* Blot, 1980
		Gazolapodus homopterus Blot, 1980
Clupeiformes	Clupeidae	*Bolcaichthys catopygopterus* (Woodward, 1901)
		Trollichthys bolcensis Marramà & Carnevale, 2014
	Engraulidae	n. gen. et n. sp.
Anotophysi	Anotophysi incertae sedis	*Coelogaster leptostea* (Eastman, 1905)
		"*Chanos*" *forcipatus* (Heckel, 1854)
Otophysi	Chanoididae	*Chanoides macropoma* (Agassiz, 1844)
Aulopiformes	Paralepididae	*Holosteus esocinus* Agassiz, 1839
Lampridiformes	Veliferidae	*Velifer* n. sp.
		Veronavelifer sorbinii Bannikov, 1990

Tab. 1 - A synoptic list of the Eocene fishes of Bolca.

	Bajaichthyidae	*Bajaichthys elegans* Sorbini, 1983
	Lampridiformes incertae sedis	"*Pegasus*" *volans* Volta, 1796
Ophidiiformes	Ophidiidae	"*Ophidium*" *voltianum* Massalongo, 1859
Lophiiformes	Lophiidae	*Caruso brachysomus* (Agassiz, 1839)
		Sharfia mirabilis Pietsch & Carnevale, 2011
	Brachionichthyidae	*Histionotophorus bassanii* (de Zigno, 1887)
		Orrichthys longimanus Carnevale & Pietsch, 2010
	Antennariidae	*Eophryne barbutii* Carnevale & Pietsch, 2009
	Ogcocephalidae	*Tarkus squirei* Carnevale & Pietsch, 2011
Atheriniformes	Atherinidae	*Atherina* (?) *macrocephala* Woodward, 1901
	Rhamphognathidae	*Rhamphognathus paralepoides* Agassiz, 1844
	Mesogasteridae	*Latellagnathus teruzzii* Bannikov, 2008
		Mesogaster sphyraenoides Agassiz, 1844
Beloniformes	Exocoetidae	*Rhamphexocoetus volans* Bannikov, Parin & Pinna, 1985
		"*Engraulis*" *evolans* (Blainville, 1818)
	Hemiramphidae	*Hemiramphus edwardsi* Bassani, 1876
Beryciformes	Holocentridae	*Berybolcensis leptacanthus* (Agassiz, 1838)
		Eoholocentrum macrocephalum (Blainville, 1818)
		Tenuicentrum lanceolatum (Bassani, 1876)
Syngnathiformes	Rhamphosidae	*Ramphosus rastrum* (Volta, 1796)
		Ramphosus biserratus Bassani, 1876
	Urosphenidae	*Urosphen dubius* (Blainville, 1818)
	Aulostomidae	*Eoaulostomus bolcensis* (Blainville, 1818)
		Eoaulostomus gracilis Blot, 1980
		Synhypuralis jurgenseni Blot, 1980
		Synhypuralis banisteri Blot, 1980
		Jurgensenichthys elongatus Blot, 1980
		Macroaulostomus veronensis Blot, 1980
		Tyleria necopinnata N.N. Parin, 1993
	Parasynarcualidae	*Parasynarcualis longirostris* (Blainville, 1818)
	Fistularioididae	*Fistularioides veronensis* Blot, 1980
		Fistularioides phyllolepis Blot, 1980
		Pseudosyngnathus opisthopterus (Agassiz, 1833)
	Aulostomoidea incertae sedis	*Aulostomoides tyleri* Blot, 1980
	Aulorhamphidae	*Aulorhamphus bolcensis* (Steindachner, 1863)
		Aulorhamphus capellinii de Zigno, 1887
		Aulorhamphus chiarasorbiniae Bannikov & Tyler, 2011
		Veronarhamphus canossae (Heckel, 1856)
		Pesciarhamphus carnevalei Bannikov & Tyler, 2011
	Paraeoliscidae	*Paraeoliscus robinetae* Blot, 1980
	Centriscidae	*Aeoliscoides longirostris* (Blainville, 1818)
		Paramphisile weileri Blot, 1980
	Syngnathidae	"*Syngnathus*" *heckeli* de Zigno, 1874
		"*Syngnathus*" *bolcensis* de Zigno, 1887
		Prosolenostomus lessinii Blot, 1980
	Solenostomidae (?)	*Solenorhynchus elegans* Heckel, 1854
	Syngnathoidei incertae sedis	*Calamostoma breviculum* (Blainville, 1818)
Dactylopteriformes	Pterygocephalidae	*Pterygocephalus paradoxus* Agassiz, 1839
Perciformes	Latidae	*Eolates gracilis* (Agassiz, 1833)
	Percichthyidae	*Cyclopoma gigas* Agassiz, 1833
	Acropomatidae	*Acropoma lepidotum* (Agassiz, 1836)

Tab. 1 - Continuation.

Priacanthidae	*Pristigenys substriatus* (Blainville, 1818)
Apogonidae	*Eosphaeramia pygopterus* (Agassiz, 1836)
	Eoapogon fraseri Bannikov, 2005
	Bolcapogon johnsoni Bannikov, 2005
	Apogoniscus pauciradiatus Bannikov, 2005
	Apogonidae gen. et sp. indet.
Pomatomidae	*Carangopsis brevis (*Blainville, 1818)
	Carangopsis dorsalis Agassiz, 1844
Ductoridae	*Ductor vestenae* (Volta, 1796)
Carangidae	*Seriola prisca* (Agassiz, 1834)
	Vomeropsis triurus (Volta, 1796)
	Ceratoichthys pinnatiformis (Blainville, 1818)
	Eastmanalepes primaevus (Eastman, 1904)
	Lichia veronensis Bannikov & Sorbini in Bannikov, 1990
	Paratrachinotus tenuiceps (Agassiz, 1834)
	Trachicaranx pleuronectiformis (Blot, 1969)
Menidae	*Mene rhombea* (Volta, 1796)
	Mene oblonga (Agassiz, 1833)
Leiognathidae	*Eoleiognathus dorsalis* (Agassiz, 1838)
Exelliidae	*Exellia velifer* (Volta, 1796)
Lutjanidae	*Ottaviania mariae* Sorbini, 1983
	Ottaviania leptacanthus (Agassiz, 1839)
	Veranichthys ventralis (Agassiz, 1839)
	Goujetia crassispina (Agassiz, 1839)
	Lessinia horrenda Bannikov & Zorzin, 2014
	Lessinia sp.
Gerreidae (?)	*Aspesiperca ruffoi* Bannikov, 2008
Sparidae	*Sparnodus elongatus* Agassiz, 1839
	Sparnodus vulgaris (Blainville, 1818)
	Pseudosparnodus microstomus (Agassiz, 1839)
	Ellaserrata monksi Day, 2003
	Abromasta microdon (Agassiz, 1839)
	"*Dentex*" *microdon* Agassiz, 1839
	"*Dentex*" *ventralis* Agassiz, 1839
Quasimullidae	*Quasimullus sorbinii* Bannikov, 1999
Monodactylidae	*Psettopsis subarcuatus* (Blainville, 1818)
	Psettopsis latellai Bannikov, 2005
Ephippidae	*Archaephippus asper* (Volta, 1796)
	Eoplatax papilio (Volta, 1796)
Scatophagidae	*Eoscatophagus frontalis* (Agassiz, 1839)
Pomacentridae	*Palaeopomacentrus orphae* Bellwood & Sorbini, 1996
	Lorenzichthys olihan Bellwood, 1999
	Sorbinichromis francescoi Bannikov & Bellwood, 2014
Carangodidae	*Carangodes bicornis* (Volta, 1796)
Eocottidae	*Eocottus veronensis* (Volta, 1796)
	Bassanichthys pesciaraensis (Bannikov, 2004)
Robertanniidae	*Robertannia sorbiniorum* Bannikov, 2011
	Hendrixella grandei Bannikov & Carnevale, 2009
Percoidei incertae sedis	*Veronabrax schizurus* (Agassiz, 1836)
	Voltamulloides ceratorum Bannikov, 2008
	Parapelates quindecimalis (Agassiz, 1836)

Tab. 1 - Continuation.

	Jimtylerius temnopterus (Agassiz, 1836)
	Pavarottia lonardonii Bannikov & Zorzin, 2011
	Montepostalia annamariae Bannikov & Zorzin, 2004
	Blotichthys coleanus (Agassiz, 1838)
	Pygaeus bolcanus (Volta, 1796)
	Pygaeus nobilis Agassiz, 1838
	Pygaeus nuchalis Agassiz, 1838
	*Malacopygaeus oblongus (A*gassiz, 1838)
	Gillidia antiqua (Agassiz, 1835)
	Bradyurus szainochae (de Zigno, 1887)
	Frigoichthys margaritae Bannikov, 2004
	Frippia labroiformis Bannikov & Carnevale, 2012
	Squamibolcoides minciottii Bannikov & Zorzin, 2013
Sphyraenidae	*Sphyraena bolcensis* Agassiz, 1844
Tortonesidae	*Tortonesia esilis* Sorbini, 1983
Labridae	*Eocoris bloti* Bannikov & Sorbini, 1990
	Phyllopharyngodon longipinnis Bellwood, 1990
	Bellwoodilabrus landinii Bannikov & Carnevale, 2010
Labroidei incertae sedis	"*Labrus*" *valenciennesi* Agassiz, 1839
	Sorbinia caudopunctata Bellwood, 1995
Callipterygidae	*Callipteryx recticaudus* Agassiz, 1838
	Callipteryx speciosus Agassiz, 1838
Gobioidei incertae sedis	"*Gobius*" *microcephalus* Agassiz, 1839
Caproidae	*Eoantigonia veronensis* (Sorbini, 1983)
Sorbinipercidae	*Sorbiniperca scheuchzeri* Tyler, 1999
	Sorbinicapros sorbiniorum Bannikov & Tyler, 1999
Zorzinichthyidae	*Zorzinichthys annae* Tyler & Bannikov, 2002
Acanthonemidae	*Acanthonemus subaureus* (Blainville, 1818)
Siganidae	*Ruffoichthys spinosus* Sorbini, 1983
	Ruffoichthys bannikovi Tyler & Sorbini, 1990
	Aspesiganus margaritae Bannikov & Tyler, 2002
	Acanthopygaeus agassizi (Eastman, 1904)
Acanthuridae	*Proacanthurus tenuis* (Agassiz, 1838)
	Proacanthurus bonatoi Blot & Tyler, 1990
	Proacanthurus ovalis (Agassiz, 1838)
	Proacanthurus elongatus Blot & Tyler, 1990
	Metacanthurus veronensis Blot & Tyler, 1990
	Eorandallius rectifrons (Agassiz, 1838)
	Eorandallius elegans Blot & Tyler, 1990
	Acanthuroides massalongoi Blot & Tyler, 1990
	Lehmanichthys lessiniensis Blot & Tyler, 1990
	Metaspisurus emmanueli Blot & Tyler, 1990
	Pesciarichthys punctatus Blot & Tyler, 1990
	Frigosorbinia baldwinae (Sorbini & Tyler, 1998)
	Tylerichthys nuchalis (Agassiz, 1838)
	Tylerichthys milani Blot & Tyler, 1990
	Protozebrasoma bloti Sorbini & Tyler, 1998
	Sorbinithurus sorbinii Tyler, 1999
	Tauichthys padremenini Tyler, 1999
	Tauichthys aspesae Tyler & Bannikov, 2000
	Gazolaichthys vestenanovae Blot & Tyler, 1990

Tab. 1 - Continuation.

		Padovathurus gaudryi (de Zigno, 1887)
	Zanclidae	*Eozanclus brevirostris* (Agassiz, 1835)
	Massalongiidae	*Massalongius gazolai* (Massalongo, 1859)
	Euzaphlegidae	*Veronaphleges brunae* Bannikov, 2008
	Scombridae	*Auxides propterygius* (Agassiz, 1835)
		Pseudaxides speciosus (Agassiz, 1835)
		Thunnoscomberoides bolcensis (Agassiz, 1835)
		Godsilia lanceolata (Agassiz, 1835)
	Blochiidae	*Blochius longirostris* Volta, 1796
		Blochius macropterus de Zigno, 1887
	Palaeorhynchidae	*Palaeorhynchus zorzini* Fierstine, Bannikov & Monsch, 2008
	Centrolophidae	*Zorzinia postalensis* Bannikov, 2000
	Perciformes incertae sedis	*Quasicichla mucistonaver* Bannikov, 2004
		Parapygaeus polyacanthus Pellégrin, 1907
Pleuronectiformes	Amphistiidae	*Amphistium paradoxum* Agassiz, 1844
		Heteronectes chaneti Friedman, 2008
	Pleuronectiformes incertae sedis	*Eobothus minimus* (Agassiz, 1839)
Tetraodontiformes	Triacanthidae	*Protacanthodes ombonii* (de Zigno, 1887)
		Protacanthodes nimesensis Tyler & Santini, 2001
	Protobalistidae	*Spinacanthus cuneiformis* (Blainville, 1818)
		Protobalistum imperiale (Massalongo, 1857)
	Bolcabalistidae	*Bolcabalistes varii* Tyler & Sorbini, 1998
	Aracanidae	*Proaracana dubia* (Blainville, 1818)
	Ostraciidae	*Eolactoria sorbinii* Tyler, 1975
	Eoplectidae	*Eoplectus bloti* Tyler, 1975
	Zignoichthyidae	*Zignoichthys oblongus* (de Zigno, 1874)
	Tetraodontidae	*Eotetraodon pygmaeus* (de Zigno, 1887)
		Eotetraodon tavernei Tyler & Bannikov, 2013
	Diodontidae	*Prodiodon tenuispinus* (Agassiz, 1844)
		Prodiodon erinaceus (Agassiz, 1844)
		Heptadiodon echinus (Heckel, 1854)
		Zignodon fornasieroae Tyler & Santini, 2002
Acanthomorpha incertae sedis		*Pietschellus aenigmaticus* Bannikov & Carnevale, 2011
		Xiphopterus falcatus (Volta, 1796)
		Oncolepis isseli Bassani, 1897
		Protoaulopsis bolcensis Woodward, 1901

Tab. 1 - Continuation.

The fossil fishes of Bolca are usually represented by complete or partially complete articulated skeletons, in many cases in part and counterpart, often characterized by preservation of the complete scale covering and occasionally by the original pigmentation pattern (e.g., Fig. 2d). Incomplete or disarticulated skeletal remains and isolated scales are also present.

Overall, the fish assemblage consists of sharks, batoids, remnants of Mesozoic neopterygians (pycnodontiforms) and teleosts, representing the earliest record of an acanthomorph dominated fish assemblage with an overall diversity foreshadowing that of today (Patterson, 1993a). The size of specimens is extremely variable, ranging from a few millimeteres to more than one meter.

Cartilaginous fishes are relatively uncommon and scarcely diversified compared to bony fishes (16 vs 222 taxa; see Tab. 1). The only comprehensive account of the Bolca

cartilaginous fishes was provided by Jaekel (1894). According to Blot (1980), sharks are represented by members of the families Carcharhinidae (Fig. 2a) and Orectolobidae. The Carcharhinidae were partially reviewed by Cappetta (1975), who assigned some of the best preserved specimens formerly referred to *Galeus* (=*Alopiopsis*, *Protogaleus*, *Carcharias*, *Notidanus*) *cuvieri* to the triakid genus *Galeorhinus*; a recent close examination of the dentition, however, demonstrated that this material must be assigned to the extinct carcharhinid genus *Physogaleus* (see Adnet & Cappetta, 2008). Blot (1980) tentatively referred to the family Orectolobidae the material assigned to *Mesiteia emiliae,* even though the genus *Mesiteia* is currently regarded as a member of the family Hemiscylliidae; this material is badly in need of revision. Batoids are relatively diverse and include rhinobatids (Blot, 1980), narcinids (Carvalho, 2010), platyrhinids (Blot, 1980; Carvalho, 2004), dasyatids (Fig. 2b; Carvalho et al. 2004), myliobatids (de Zigno, 1885; Carvalho et al., 2004), and urolophids (Carvalho et al., 2004).

The Bolca bony fish assemblage includes the youngest occurrence of the extinct Mesozoic clade Pycnodontiformes (Fig. 2c), represented by four taxa (see Poyato-Ariza & Wenz, 2002), being the last members of a group that was very common in shallow-water marine habitats up to the end of the Cretaceous.

Non-acanthomorph teleosts are represented by only 27 taxa of anguilliforms, aulopiforms, clupeiforms, crossognathiforms, ostariophysans, and osteoglossiforms.

Another relict among the bony fishes of Bolca is the pachyrhizodontid *Platinx macropterus*, which possibly represents the youngest record of the order Crossognathiformes, a clade of Late Jurassic-Cretaceous primarily marine basal teleosts (Taverne, 1980; Arratia, 2008).

Members of the order Osteoglossiformes are relatively uncommon in the Bolca assemblage, represented by three taxa, the small *Foreyichthys bolcensis*, *Monopterus gigas,* and the arapaimid *Thrissopterus catullii* (see Taverne, 1998; Bonde, 2008). These fossils document the last part of the marine history of this heterogeneous group which today is restricted to freshwaters with a Gondwana distribution.

Eels of the order Anguilliformes are relatively common, with 16 taxa belonging to both extant (Anguillidae, Chlopsidae, Congridae, Ophichthyidae) and extinct [Anguilloididae, Milananguillidae, Paranguillidae (Fig. 2d), Patavichthyidae, Proteomyridae] families, plus several taxa (*Bolcanguilla brachycephala*, *Gazolapodus homopterus*) of difficult phylogenetic interpretation. The diversity of the anguilliforms of Bolca has been the subject of monographic studies by Cadrobbi (1962) and Blot (1978, 1980, 1984a).

Of the ostariophysans, only the otophysan *Chanoides macropoma* has been investigated in detail (Patterson, 1984). The relatively rare anotophysans *Coelogaster leptostea* and "*Chanos*" *forcipatus* need revisionary study.

Herrings of the order Clupeiformes are by far the most common elements of the Bolca fish assemblage. However, despite their abundance, these fossils have been scarcely investigated. A recent revision of the collections of the main Italian museums with Bolca materials led to the recognition of two taxa, the extremely abundant sardine *Bolcaichthys*

Fig. 2 - a) *Eogaleus bolcensis* Cappetta 1975, MGP-PD 8870C, left lateral view; scale bar 100 mm. b) "*Dasyatis*" *muricata* (Volta 1796), MCSNV 1021, dorsal view; scale bar 50 mm. c) *Pycnodus apodus* (Volta 1796), MCSNV T999, left lateral view; scale bar 10 mm. d) *Paranguilla tigrina* (Agassiz 1839), MGP-PD 26288, left lateral view; scale bar 20 mm. e) *Bolcaichthys catopygopterus* (Woodward 1901), NHMUK P.3829, holotype, left lateral view; scale bar 10 mm. f) *Veronavelifer sorbinii* Bannikov 1990, MCSNV I.G. 37576, holotype, left lateral view; scale bar 10 mm. g) *Bajaichthys elegans* Sorbini 1983, MCSNV T923, holotype, right lateral view; scale bar 10 mm.

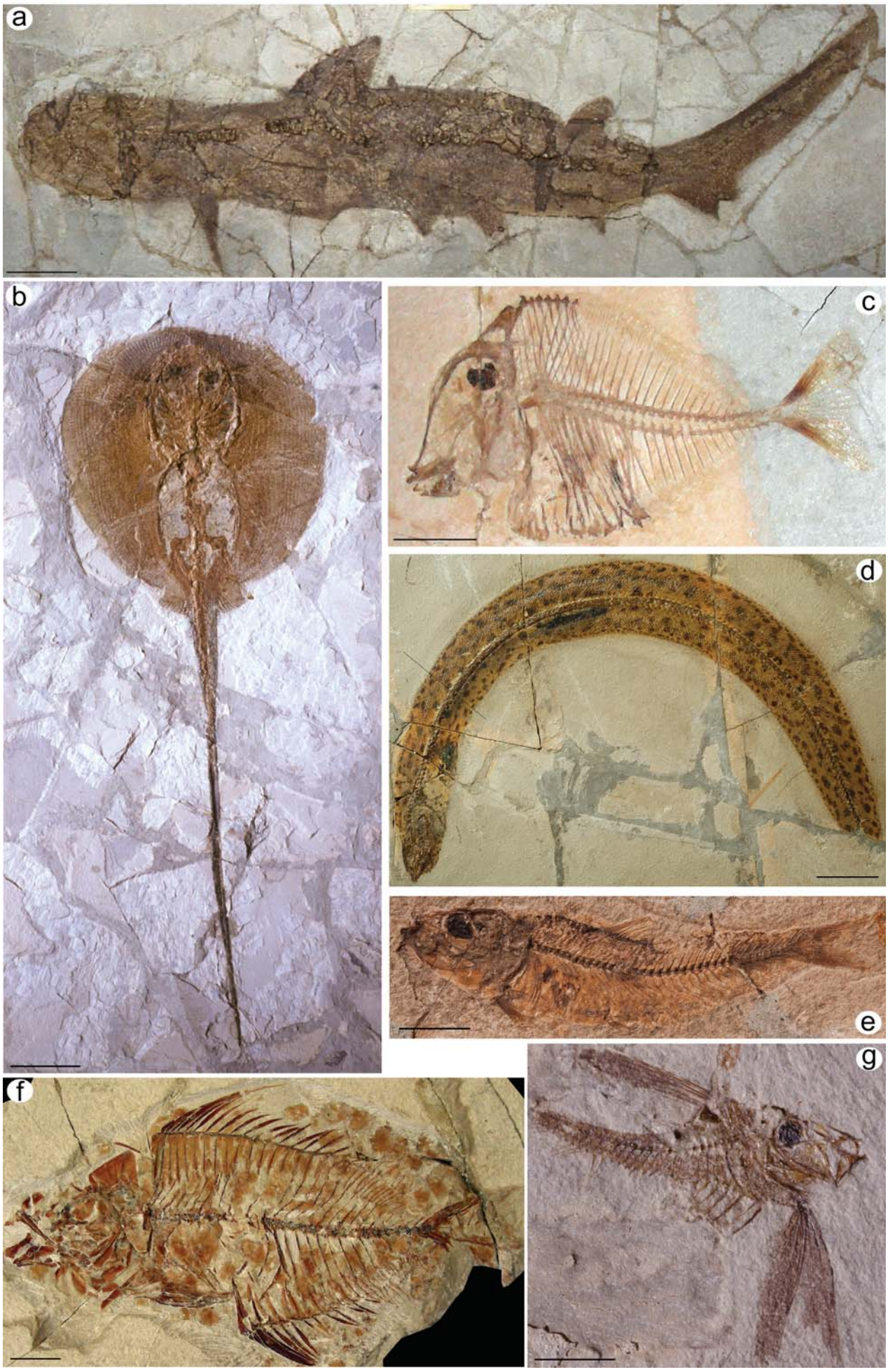

FIG. 2

catopygopterus (Fig. 2e) and the round herring *Trollichthys bolcensis* (Marramà & Carnevale, in press). A single specimen of a new anchovy genus and species has recently been found in the collection of the Museo Civico di Storia Naturale, Verona, representing the earliest evidence of the family Engraulidae in the fossil record.

The relatively large shallow water barracudina *Holosteus esocinus* is the only aulopiform taxon present in the Bolca fish assemblage.

The large majority of the Bolca fish assemblage consists of acanthomorph taxa, represented by almost 200 known taxa. In terms of taxonomic diversity, acanthomorphs are more than seven times more abundant than non-acanthomorphs. However, such an asymmetric ratio is balanced in terms of individuals/biomass by the extremely abundant sardine *Bolcaichthys catopygopterus* (Fig. 2e). Recent excavations carried out between 1999 and 2011 by the Museo Civico di Storia Naturale, Verona demonstrated that about half of the collected fossil fishes are sardines, followed by members of the extant perciform families Apogonidae, Latidae, Menidae, and Sparidae. The perciforms (sensu Johnson & Patterson, 1993) are conspicuously diverse, with about 120 taxa, followed by syngnathiforms and tetraodontiforms. Other acanthomorph groups (atheriniforms, beloniforms, beryciforms, dactylopteriforms, lampridiforms, lophiiforms, ophidiiforms, and pleuronectiforms) are represented by six or less taxa each; a few acanthomorph taxa of problematic phylogenetic interpretation are also present (e.g., Bannikov & Carnevale, 2011). Overall, this remarkable number of taxa exhibits a vast morphological diversity, providing a robust documentation of the early Cenozoic diversification of the perciforms, with the proliferation of new anatomical body plans and the exploitation of new ecological strategies (Friedman, 2010).

The basal acanthomorph order Lampridiformes is presently represented by six specimens representing four taxa. There are two taxa of the family Veliferidae (Fig. 2f; Bannikov, 1990), one of which is currently under study by two of us (G.C. and A.F.B.). The bizarre *Bajaichthys elegans* is currently regarded as a lampridiform of uncertain affinities (Fig. 2g; Sorbini & Bottura, 1988; Olney et al., 1993). Finally, the enigmatic "*Pegasus*" *volans* is tentatively interpreted herein as a taeniosomous lampridiform; this taxon is greatly in need of revision.

Cusk-eels (Ophidiiformes) are extremely rare in the Bolca fish assemblage and are unquestionably in need of revision.

Lophiiformes are represented by taxa of the families Antennariidae, Ogcocephalidae (Fig. 3c), Brachionichthyidae (Fig. 3b), and Lophiidae (Fig. 3a); the lophiiform material from Bolca constitutes the earliest known skeletal record for all four of these families. The Lophiidae includes two taxa (Pietsch & Carnevale, 2011; Carnevale & Pietsch, 2012), one of which, *Sharfia mirabilis*, is characterized by a peculiar set of characters and is currently regarded as a stem-lophiid, being the sister taxon of all the other genera of the family. A single frogfish (Antennariidae) taxon has been described to date (Carnevale & Pietsch, 2009) but additional undescribed specimens have been recognized in the collections of the Museo Civico di Storia Naturale, Verona and of the Museo dei Fossili di Bolca. Handfishes of the family Brachionichthyidae are represented by two taxa (Carnevale & Pietsch, 2010); this family is today restricted in distribution to the shallow temperate and subtropical waters of Tasmania and southern and eastern Australia. Finally, the Bolca assemblage includes six individuals of the batfish *Tarkus squirei* (family Ogcocephalidae) (Carnevale & Pietsch, 2011).

According to Bannikov (2008), the Bolca fish assemblage includes four atheriniform taxa, the small atherinid *Atherina* (?) *macrocephala* and the streamlined predatory species of the extinct families Mesogasteridae and Rhamphognathidae.

Flying fishes (Fig. 3d) and halfbeaks (Beloniformes) are a rare component of the Bolca fish assemblage (see Bannikov et al., 1985).

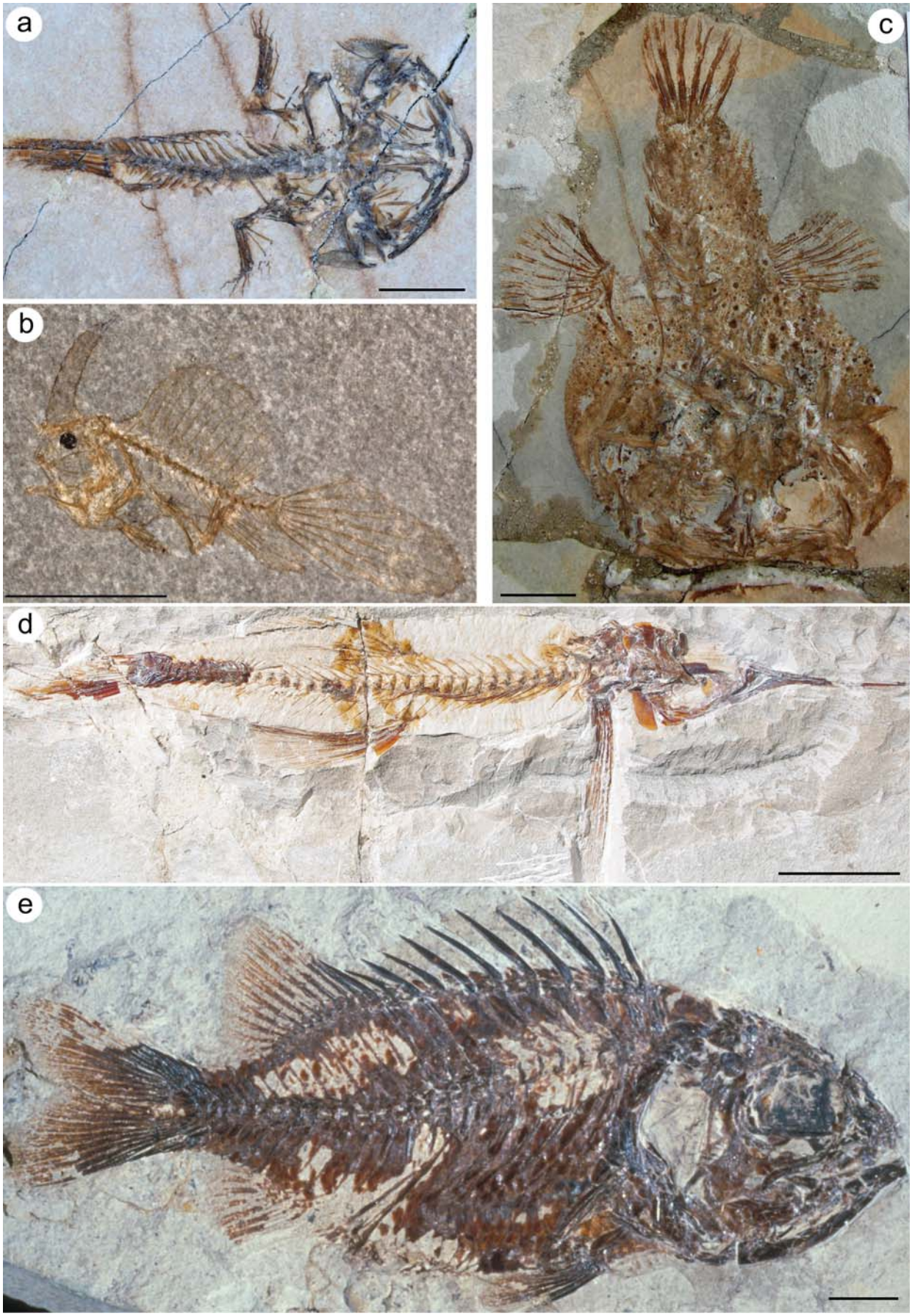

Fig. 3 - a) *Sharfia mirabilis* Pietsch & Carnevale 2011, MNHN Bol 38, holotype, dorsal view; scale bar 10 mm. b) *Histionotophorus bassani* (de Zigno 1887), NHMUK 19060, left lateral view; scale bar 10 mm. c) *Tarkus squirei* Carnevale & Pietsch 2011, MCSNV T159, holotype, dorsal view; scale bar 20 mm. d) *Rhamphoexocoetus volans* Bannikov, Parin & Pinna 1985, MCSNM V294, holotype, right lateral view; scale bar 20 mm. e) *Eoholocentrum macrocephalum* (Blainville 1818), MCSNV T969, right lateral view; scale bar 10 mm.

Squirrelfishes of the order Beryciformes are relatively common, represented by three taxa (Fig. 3e); the morphology and affinities of these taxa have been extensively discussed (Sorbini, 1975, 1984; Sorbini & Tirapelle, 1975).

Syngnathiforms are relatively common and highly diverse. At least ten families [Aulorhamphidae, Aulostomidae, Centriscidae (Fig. 4a), Fistularioididae, Paraeoliscidae, Parasynarcualidae, Rhamphosidae (Fig. 4b), Solenostomidae, Syngnathidae, Urosphenidae] plus two incertae sedis taxa (*Aulostomoides tyleri*, *Calamostoma breviculum*) are known. Except for the extinct family Aulorhamphidae, which has been recently investigated in great detail (e.g., Tyler, 2004), the other syngnathiforms were cursorily and inadequately described by Blot (1980) and are in need of a comprehensive revision.

The phylogenetic affinities of the enigmatic *Pterygocephalus paradoxus* have been discussed by several authors (e.g., Hubbs, 1952; Blot, 1980, 1984b; Springer, 1993); we follow the opinion of Blot (1984) and tentatively consider this fish as in some way related to the dactylopteriforms.

As discussed above, the perciforms (Figs 4c-j, 5-7c) are represented by a remarkably large number of species, representing at least 37 families, both extinct [Acanthonemidae, Blochiidae (Fig. 6a), Callipterygidae, Carangodidae, Ductoridae, Eocottidae (Fig. 7b), Euzaphlegidae, Exelliidae (Fig. 4g), Massalongiidae (Fig. 7c), Palaeorhynchidae, Quasimullidae, Robertanniidae, Sorbinipercidae, Tortonesidae, Zorzinichthyidae] and extant [Acanthuridae (Figs 6b, 7a), Acropomatidae, Apogonidae (Fig. 4c), Caproidae, Carangidae (Figs 1, 4d), Centrolophidae, Ephippidae (Figs 4f, 5), Gerreidae, Labridae, Leiognathidae, Latidae, Lutjanidae, Menidae (Fig. 6a), Monodactylidae, Percichthyidae, Pomacentridae, Pomatomidae, Priacanthidae, Scatophagidae (Fig. 4h), Scombridae, Siganidae (Fig. 4j), Sparidae (Fig. 4e), Sphyraenidae, Zanclidae]; a number of species are of difficult phylogenetic interpretation and are currently considered as *incertae sedis* within the Perciformes or within one of the perciform suborders (Gobioidei, Labroidei, Percoidei; see Tab. 1). The family Acanthuridae is by far the most diverse of the perciform families with 20 species (Figs 6b, 7a; e.g., Blot & Tyler, 1990; Tyler, 1999a).

Fig. 4 - a) *Paramphisile weileri* Blot 1980, MCSNV T22, right lateral view; scale bar 10 mm. b) *Rhamphosus rastrum* (Volta 1796), MCSNV I.G. 24560, left lateral view; scale bar 10 mm. c) *Eosphaeramia pygopterus* (Agassiz 1836), MCSNV I.G. 23172, right lateral view; scale bar 10 mm. d) *Vomeropsis triurus* (Volta 1796), MCSNV T1022, right lateral view; scale bar 20 mm. e) *Sparnodus vulgaris* (Blainville 1818), MCSNV I.G. 24546, right lateral view; scale bar 20 mm. f) *Archaephippus asper* (Volta 1796), MCSNV VIII D.98, left lateral view; scale bar 20 mm. g) *Exellia velifer* (Volta 1796), MCSNV VIII D.87, right lateral view; scale bar 10 mm. h) *Eoscatophagus frontalis* (Agassiz 1839), MCSNV VII C.68, left lateral view; scale bar 50 mm. j) *Ruffoichthys bannikovi* Tyler & Sorbini 1990, MCSNV I.G. 132596, holotype, left lateral view; scale bar 10 mm.

Fig. 5 - *Eoplatax papilio* (Volta 1796), MGP-PD 26285, right lateral view; scale bar 50 mm.

Fig. 6 - a) *Mene rhombea* (Volta 1796) and *Blochius longirostris* Volta 1796, MCSNV T1133; scale bar 100 mm. b) *Eorandallius rectifrons* (Agassiz 1838), MCSNV T986, right lateral view; scale bar 50 mm.

Fig. 7 - a) *Gazolaichthys vestenanovae* Blot & Tyler 1990, MCSNV B65.14, holotype, left lateral view; scale bar 10 mm. b) *Bassanichthys pesciaraensis* (Bannikov 2004), MCSNV T.111, holotype, right lateral view; scale bar 10 mm. c) *Massalongius gazolai* (Massalongo 1859), MCSNV VIII D.200, holotype, left lateral view; scale bar 10 mm. d) *Eobothus minimus* (Agassiz 1839), MCSNV T968, right lateral view; scale bar 10 mm. e) *Amphistium paradoxum* Agassiz 1844, MCSNV V D91, right lateral view, scale bar 20 mm. f) *Eolactoria sorbinii* Tyler 1975, MCSNV T6, holotype, right lateral view; scale bar 10 mm.

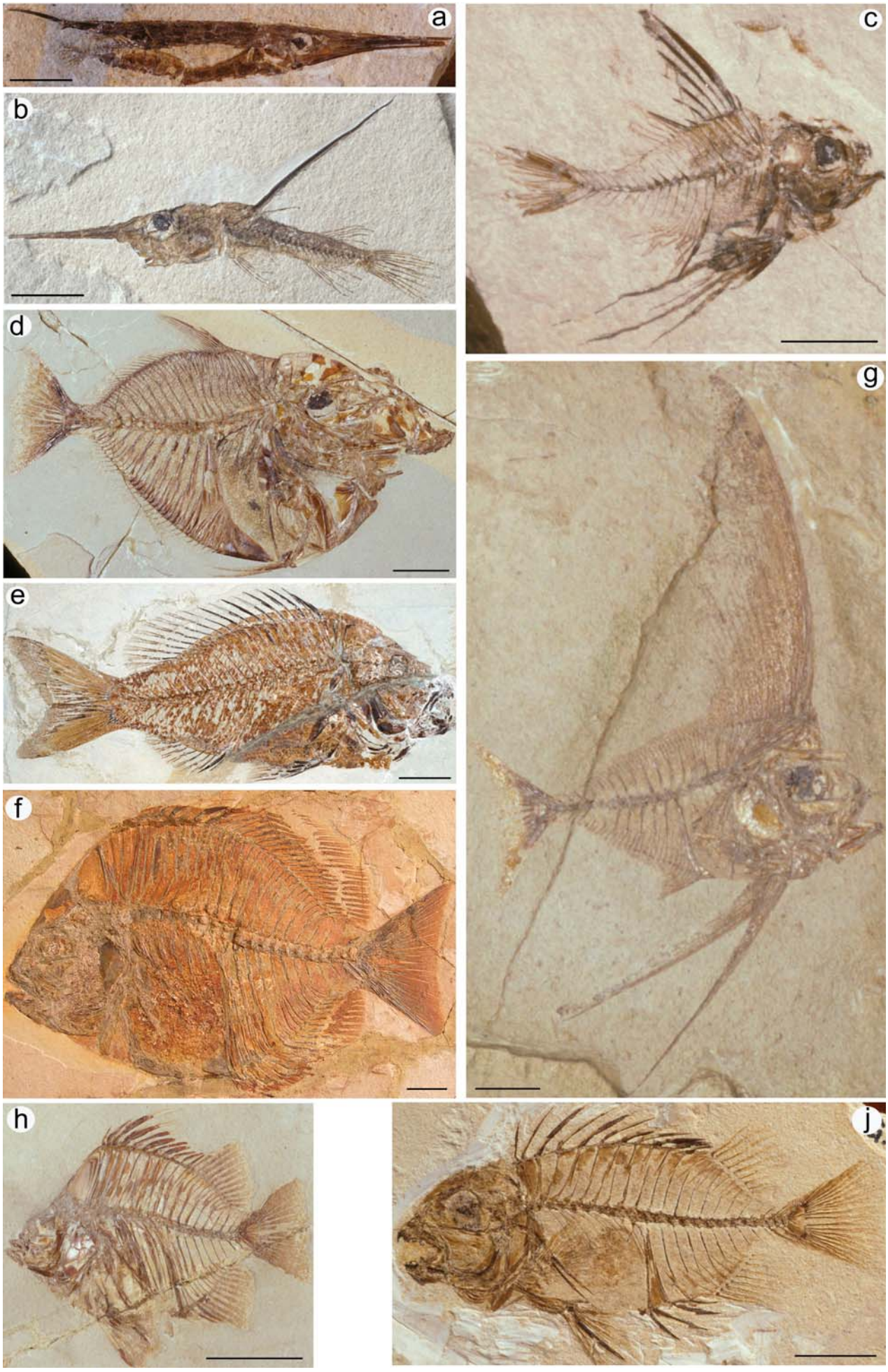

FIG. 4

Fig. 5

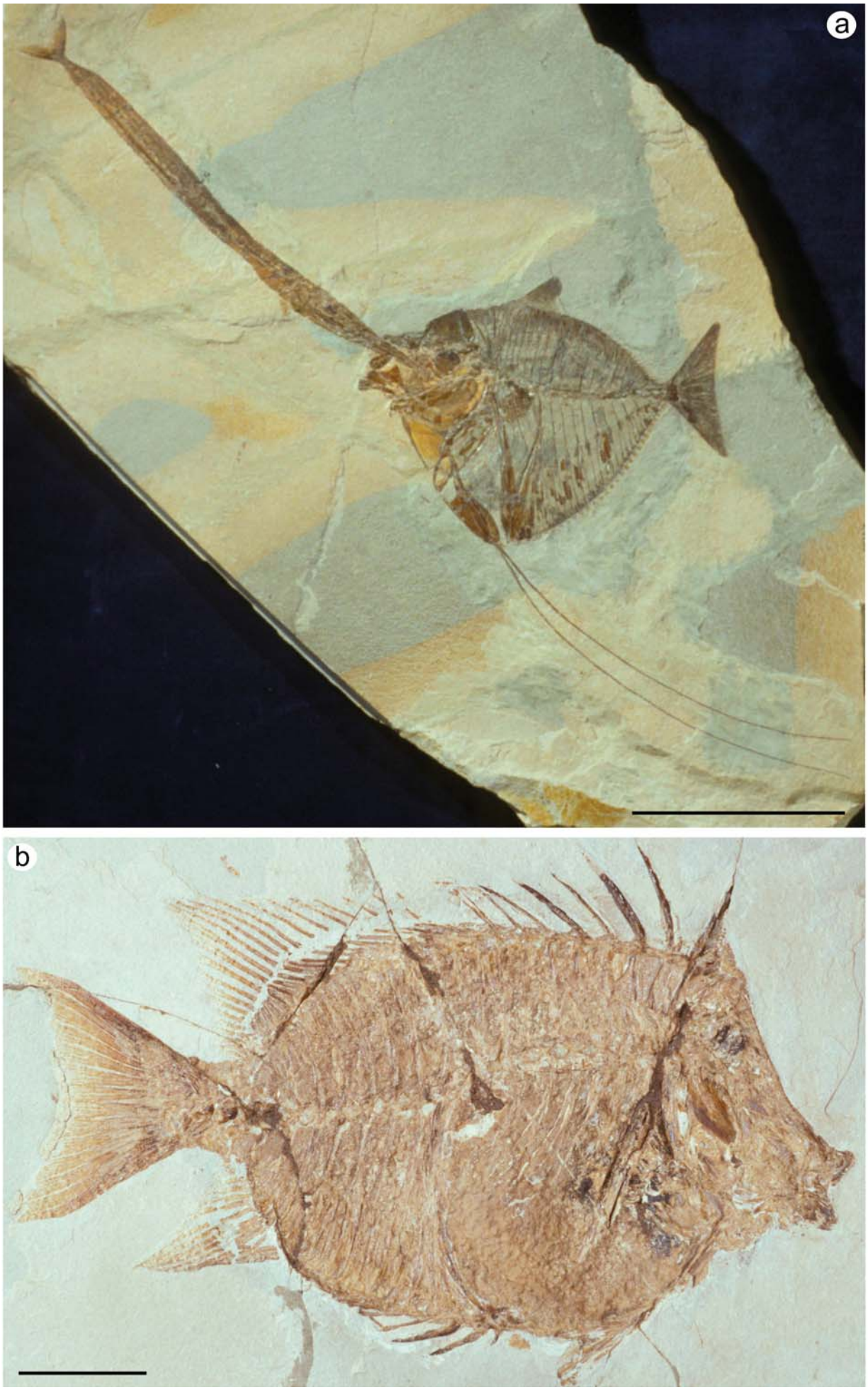

FIG. 6

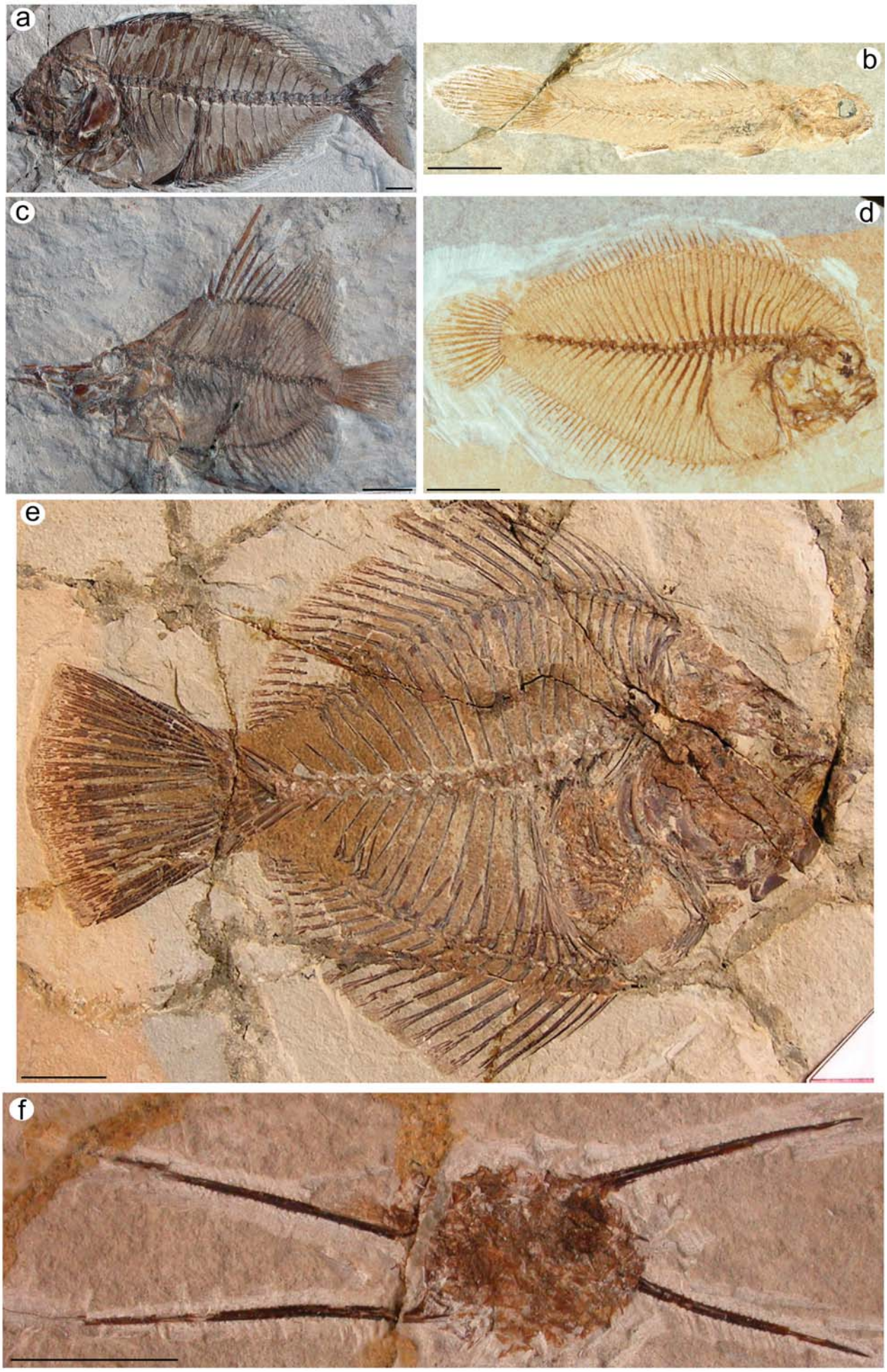

Fig. 7

The amazing diversity of this family is clearly exemplified by the 14 genera known from Bolca, several times the number of those (six) living today; see Tyler & Micklich (2011) for a classification of the fossil (mostly Bolca) and extant genera of acanthurids and their immediate outgroups. Other families exhibiting a considerable diversity are the Apogonidae, Carangidae, Lutjanidae, and Sparidae. Our knowledge of the morphology and taxonomic status of the perciform taxa of the Bolca fish assemblage is in general satisfactory, and many groups have been investigated in great detail (e.g., Blot, 1969; Tyler & Bannikov, 1997, 2005; Tyler, 1999b; Fierstine & Monsch, 2002; Day, 2003; Bannikov, 2004, 2005, 2006; Monsch, 2006; Bannikov & Carnevale, 2010). For many perciform families, Bolca constitutes their earliest evidence in the fossil record (Patterson, 1993b). It is interesting to note that despite the extraordinarily high diversification rates characteristic of perciform fishes (see Alfaro et al., 2009), a few taxa of the Bolca assemblage belong to morphologically conservative genera (*Acropoma*, *Lichia*, *Mene*, *Pristigenys*, *Seriola*, *Sphyraena*) that are still living today; therefore, the evolutionary history of these genera extends back at least to the Early Eocene, about 50 Mya.

Flatfishes are moderately abundant, being represented by the "bothoid" *Eobothus minimus* (Fig. 7d; see Chanet, 1999) and two stem-pleuronectiforms, *Amphistium paradoxum* and *Heteronectes chaneti* (Fig. 7e; see Friedman, 2008, 2012). Despite their low diversity, the Bolca flatfishes are of remarkable evolutionary significance. The two stem-pleuronectiforms can be considered as transitory forms providing anatomical evidence of the gradual evolution of the marked cranial asymmetry of flatfishes (Friedman, 2008), whereas *Eobothus minimus* appears to be the oldest known crown pleuronectiform (Chanet, 1999).

In the Bolca fish assemblage, the tetraodontiforms comprise 15 taxa belonging to nine families. Because of their broad taxonomic diversity, the tetraodontiform fishes of Bolca constitute an unparalleled source of information about the earliest stages in the evolutionary history of the extant lineages of this clade [Aracanidae, Diodontidae, Ostraciidae (Fig. 7f), Tetraodontidae, Triacanthidae]. The extinct groups comprise taxa characterized by a very peculiar morphology (*Eoplectus bloti*, *Proaracana dubia*, *Protobalistum imperiale*, *Spinacanthus cuneiformis, Bolcabalistes varii*; Tyler, 1975a, b; Tyler & Santini, 2002) that clearly indicate that the anatomical diversity of tetraodontiforms was remarkably high at least since the earliest part of the Eocene.

Paleoecological implications

Despite the considerable efforts devoted to the definition of the taxonomic composition and phylogenetic significance of the Bolca fish assemblage, its paleoecological and biogeographical features have received only limited attention.

During the Eocene, the Bolca area was part of the northern margin of the West Tethys region, a region characterized by remarkably high α-diversity, and very abundant coral reefs and mangrove systems. This biodiversity hotspot constitutes a precursor and a sort of Eocene analogue of the modern Indo-Australian Archipelago hotspot, the center of current maximum marine diversity (e.g., Renema et al., 2008).

Because of its high taxonomic diversity and evident tropical shallow-water nature, the Bolca fish assemblage has been traditionally interpreted as closely linked to a coral reef system (e.g., Blot, 1969, 1980; Sorbini, 1972, 1999). This hypothesis appears to be supported (at least in part) by the presence of remains of hermatypic corals in Lower Eocene sediments exposed in the surroundings of Bolca and possibly approximately coeval with the fish-bearing strata (Malaroda, 1954; Blot, 1969).

Bellwood (1996) emphasized the role of Bolca fishes in understanding the evolution of modern reef fish communities and considered these fossils as the earliest clearly defined evidence of a coral reef fish assemblage. The Bolca fish assemblage seems to mark the starting point of the documented evolution of many fish families associated with coral reefs (Bellwood & Wainwright, 2002), providing substantial evidence of a general stability of the morphological characteristics of tropical shallow marine fish faunas throughout the Cenozoic. In many cases, the morphology of the Bolca taxa belonging to reef fish families is very similar to that of extant representatives. Most structural characters and functional (and possibly ecological) features of these Eocene taxa are in some ways comparable to those of modern reef fishes. The Bolca fish assemblage, however, also includes numerous taxa belonging to extinct lineages of uncertain ecological interpretation and, at the same time, representatives of some of the fish groups commonly associated with Recent coral reefs (blenniids, chaetodontids, mullids, parrotfishes, serranids) have not been found at Bolca. Moreover, the relative abundance of representatives of reef fish families in the Bolca assemblage is significantly different than that observed on Recent coral reefs (Bellwood, 1996). Despite the compositional differences between the Bolca fish assemblage and those characteristic of modern reefs, a general affinity is evident and the presence of a reefal signature in the Bolca assemblage is undeniable. Indeed, recent investigations on the evolutionary dynamics of modern reef fishes have revealed that one of the main waves of invasion of reef habitats occurred in the Paleocene and that by approximately 50 Mya reef lineages saturated the ecomorphological niches available on reefs with the origination of many functional groups within reef-dwelling acanthomorphs (Price et al., 2014).

Overall, sedimentological and paleontological evidence concur to indicate that the fossiliferous deposits of Bolca originated in a tropical coastal region in close proximity to coral reefs and emerged areas (e.g., Massari & Sorbini, 1975). Based on the ecological requirements of the fish taxa, Landini & Sorbini (1996) proposed a paleoenvironmental scenario in which the general physiographic context is a heterogeneous coastal area characterized by fluvial systems, coastal lagoons and open expanses of *Halochloris* sand and seagrass beds surrounding reef zones and influenced by the open sea. In such context, Landini & Sorbini (1996) placed the fish taxa into three main ecological assemblages, the sand/seagrass bed assemblage characterized by taxa (e.g., batoids, anguilliforms, lophiids, syngnathiforms, ephippids, eocottids, callipterygids, labrids, siganids, pleuronectiforms, some tetraodontiforms) closely associated with the sediment, the true coral assemblage (anguilliforms, lophiiforms, holocentrids, syngnathiforms, apogonids, sparids, carangids, monodactylids, ephippids, pomacentrids, labrids, acanthurids, siganids, tetraodontiforms), and the perireefal and pelagic assemblage (sharks, clupeids, beloniforms, atheriniforms, veliferids and other lampridiforms, latids, ductorids, carangids, menids, exelliids, sphyraenids, euzaphlegids, scombrids, blochiids, palaeorhynchids).

The excellent preservation of fish skeletons and their remarkable similarity to extant tropical shallow water fishes allow for the interpretation of the trophic significance of the various taxa and to hypothesize the main trophic relationships that characterized the Bolca paleobiotopes (Landini & Sorbini, 1996). The highly diverse fish assemblage includes taxa of a variety of trophic guilds, such as planktivores (clupeiforms, holocentrids,

Fig. 8 - a) Detail of *Archaeophis proavus* Massalongo 1859 [excerpt from Massalongo (1859, Plate II)]. b) Detail of *Anomalophis bolcensis* (Massalongo 1859) [excerpt from Massalongo (1859, Plate III)]. c) Fossil feather from Bolca illustrated by Faujas de Saint-Fond (1804).

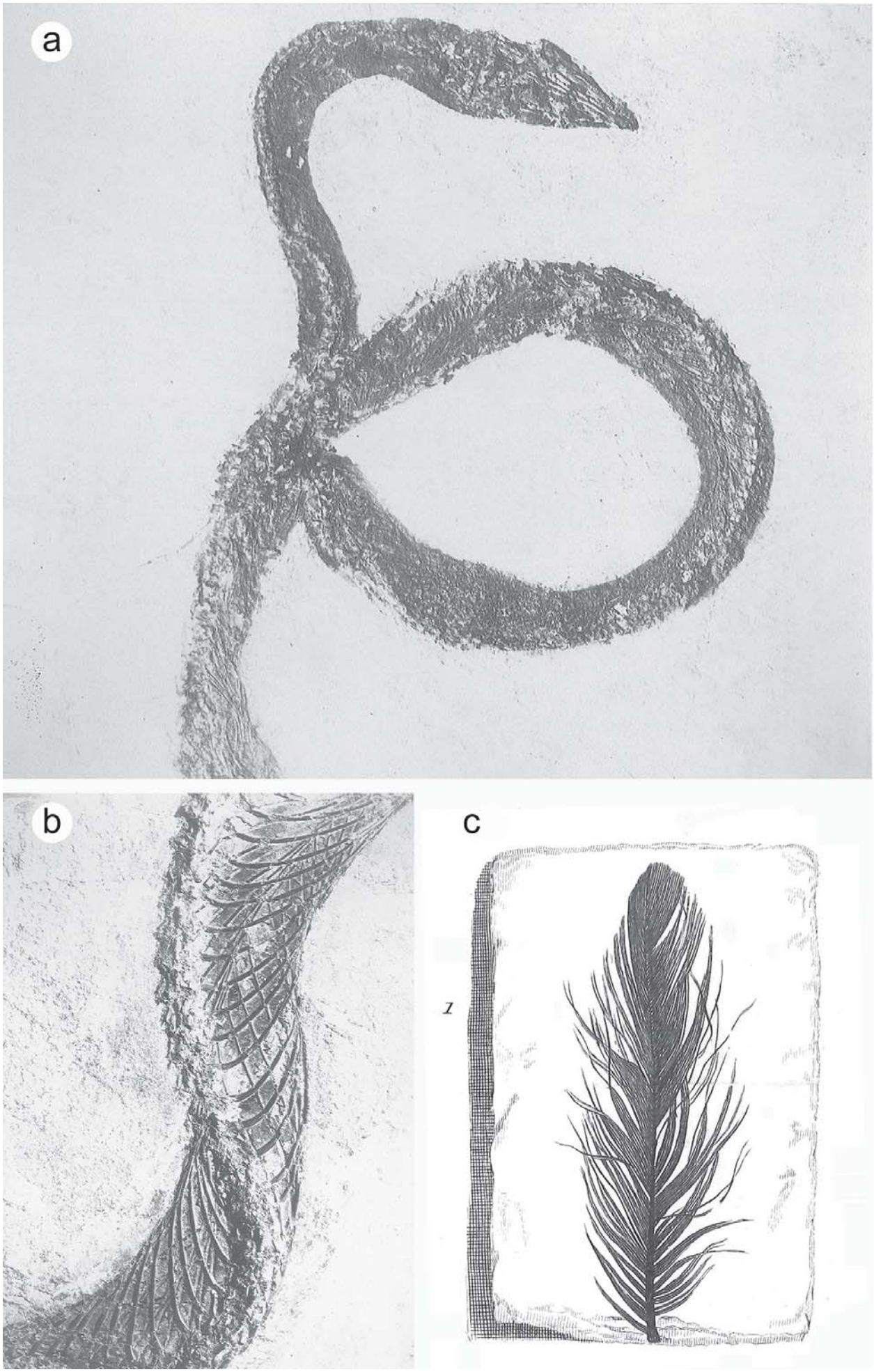

FIG. 8

menids, monodactylids, exelliids, pomacentrids), invertebrate feeders (batoids, veliferids, holocentrids, syngnathiforms, latids, percichthyids, caproids, priacanthids, carangids, menids, sparids, ephippids, pomacentrids, labrids, tetraodontiforms), piscivores (sharks, batoids, anguilliforms, lophiiforms, larger atheriniforms, latids, percichthyids, acropomatids, apogonids, carangids, sparids, sphyraenids, euzaphlegids, scombrids, blochiids, palaeorhynchids, pleuronectiforms), and herbivores (acanthurids, siganids, labrids, pomacentrids). The Bolca assemblage documents the origin of new feeding modes in fishes: herbivory, nocturnal feeding, and high-precision benthic feeding (Bellwood, 2003; Goatley et al., 2010). Nocturnal feeders are relatively abundant in the assemblage, represented by squirrelfishes (Holocentridae) and cardinalfishes (Apogonidae), whereas herbivores are primarily represented by surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae). The acanthurids from Bolca are characterized by remarkable functional and ecological similarities to their extant counterparts, with grazers, browsers, and long-snouted crevice-feeding forms that possibly have played a significant role as herbivores during the origin of modern coral reef systems (Bellwood et al., 2014). The analysis of the Bolca trophic system reveals a strongly asymmetric herbivore/predator relationship in terms of biomass and overall diversity; the dominance of predators and the abundance of nocturnal feeders and clupeids seem to indicate that the original paleobiotopes of Bolca were not characterized by typical coral reef trophic systems, but, rather, these can be confidently interpreted as perireefal trophic systems largely influenced by both the open sea and the coastal environments (Landini & Sorbini, 1996).

Other vertebrates

Remains of other vertebrates have been occasionally found at the Pesciara site. Reptiles are represented by two specimens of boid-like snakes assigned to *Anomalophis bolcensis* and *Archaeophis proavus* (see Massalongo, 1859; Janensch, 1904, 1906; Auffenberg, 1959; Figs 8a-b, 9) and by a single carapace of a terrestrial turtle (Sorbini, 1999). Impressions of bird feathers, known since 1777 (Faujas de Saint-Fond, 1804; Fig. 8c), are relatively common at Bolca and have been traditionally referred to the genus *Ornitholites* (e.g., Omboni, 1885). According to Massimo Cerato, his great-grandfather Massimiliano found also a fragment of a single wing and an isolated beak (Cerato, 2011; pp. 166-167).

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Fig. 9 - *Archaeophis proavus* Massalongo 1859, MBR 3554, holotype; scale bar 50 mm. Photo by Carola Radke (2012) © Museum für Naturkunde, Berlin.

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Excursion guidebook CBEP 2014-EPPC 2014-EAVP 2014-Taphos 2014 Conferences
The Bolca *Fossil-Lagerstätten*:
A window into the Eocene World
(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

6. The Pesciara-Monte Postale *Fossil-Lagerstätte:* 3. Flora

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One of the most important Ypresian plant localities in northern Italy is the worldwide famous Pesciara-Monte Postale *Lagerstätte*, located NE of the Bolca village (Verona and Vicenza Province). But, as seen in this guide (Carnevale et al., 2014, this volume), the fishes found in the respective sites are so beautifully preserved that they initially received all attention and plant fossils (Figs 1-3) have been almost neglected up to the second half of the 19th century (see also Roghi, 2014 and Giusberti et al., 2014).

Abramo Bartolomeo Massalongo was the first providing systematic descriptions of the Bolca macroflora. He recognized 105 genera and 277 species, but with sparse descriptions and illustrations (Massalongo, 1850, 1851, 1852, 1853a, b, 1855-1856, 1857, 1858, 1859). Massalongo's determinations were partly revised by Meschinelli & Squinabol (1892) and Gola (1941). Successively, partial studies were also published by De Visiani (1864), Beggiato (1865), Fiore (1932, 1936a-d), Schmid & Schmid (1973, 1974) and, more recently, Caccin & Pallozzi (2001). Maria Fiore recognized the presence of *Delesserites pinnatus* Unger in the Pesciara site (Fiore, 1936d) and re-determined the fern *Thecophyllum flabellatum* Massalongo as an aquatic monocotyledon (*Eichorniopsis*; Fiore, 1936a). From the same locality, Fiore (1936b) also reported *Podogonium knorii* Heer and *Banksia dillenioides* Ettinghausen. Forti (1926) emended *Zoophycos caputmedusae* (Massalongo, 1850) Massalongo 1851 (previously named *Zonarites*? *caputmedusae*), recognizing its affinity with brown algae of the family Laminariaceae. Based on its similarity with the living genus *Postelsia*, he erected the new genus *Postelsiopsis*. The name *Zoophycos* Massalongo also included four species of true trace fossils, among which Olivero (2007) designed the lectotype of this well-known ichnogenus (*Zoophycos brianteus* Massalongo, 1855).

Following the older literature, the main group of the Bolca macroflora is represented by dicotyledonous angiosperms which have been assigned to different genera of Gramineae, Cyperaceae, Najadaceae, Liliaceae, Bromeliaceae, Myricaceae, Urticaceae, Nymphaeaceae, Cabombaceae, Caryophyllaceae, Sterculiaceae (big fruits of *Fracastoria*), Byttneriaceae, Aurantiaceae, Xanthoxylaceae, Zygophyllaceae, Sapindaceae, Araliaceae, Saxifragaceae, Podostemaceae, Haloragidaceae, Myrtaceae, Papilionaceae, Caesalpiniaceae, Santalaceae, Ericaceae, Sapotaceae, Gentianaceae, and Bignoniaceae (Massalongo, 1859; Meschinelli & Squinabol, 1892; Fiore, 1936e; and Gola, 1941). Large

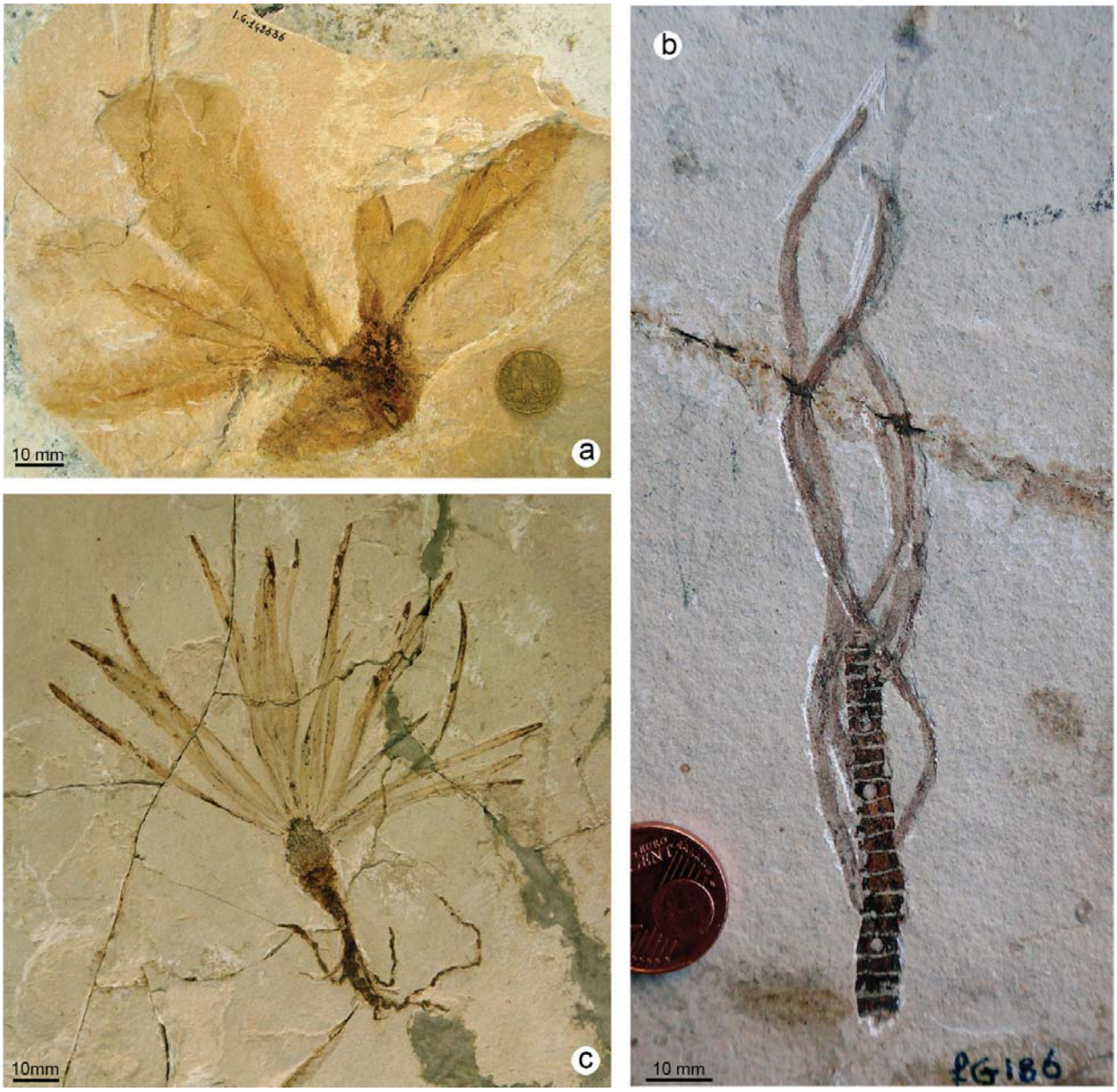

Fig. 1 - a) Leaf-like thalli of *Delesserites* (red algae) still attached to a common holdfast, MCSNV IG. 142536. b) Seagrass of potential affinity to extant *Thalassodendron*, MCSNV fG186. c) Seagrass of potential affinity to extant *Phyllospadix* or *Posidonia*, MCSNV fB47.

palm fruits such as *Castellinia* Massalongo, *Geonomites* De Visiani, and *Palaeospathe* Unger, have also been noted. The conifers are represented by *Podocarpus* and *Taxodium* (Massalongo, 1859; Fiore, 1936e).

Regrettably, Massalongo's determinations are hardly accompanied by appropriate descriptions and comparatively few illustrations. As seen above, his determinations have partly been revised and some new information has been added. However, the taphocoenosis is in urgent need of revision, which is hampered by the common mode of preservation as pure imprints without remaining organic material. As a first step, and for preparation of the fieldtrip guide, the authors have re-visited the material as preserved in the rich historical collections at Padova and Verona and the more recently collected material at Bolca and Verona. Independent of a planned systematic revision this resulted in some interesting observations helping for an interpretation of the plant taphocoenosis. This is only part of the so-called "Florenkomplex Montebolca" of Mai (1995) which is in fact a composite from several more or less coeval localities between Sardinia and Croatia.

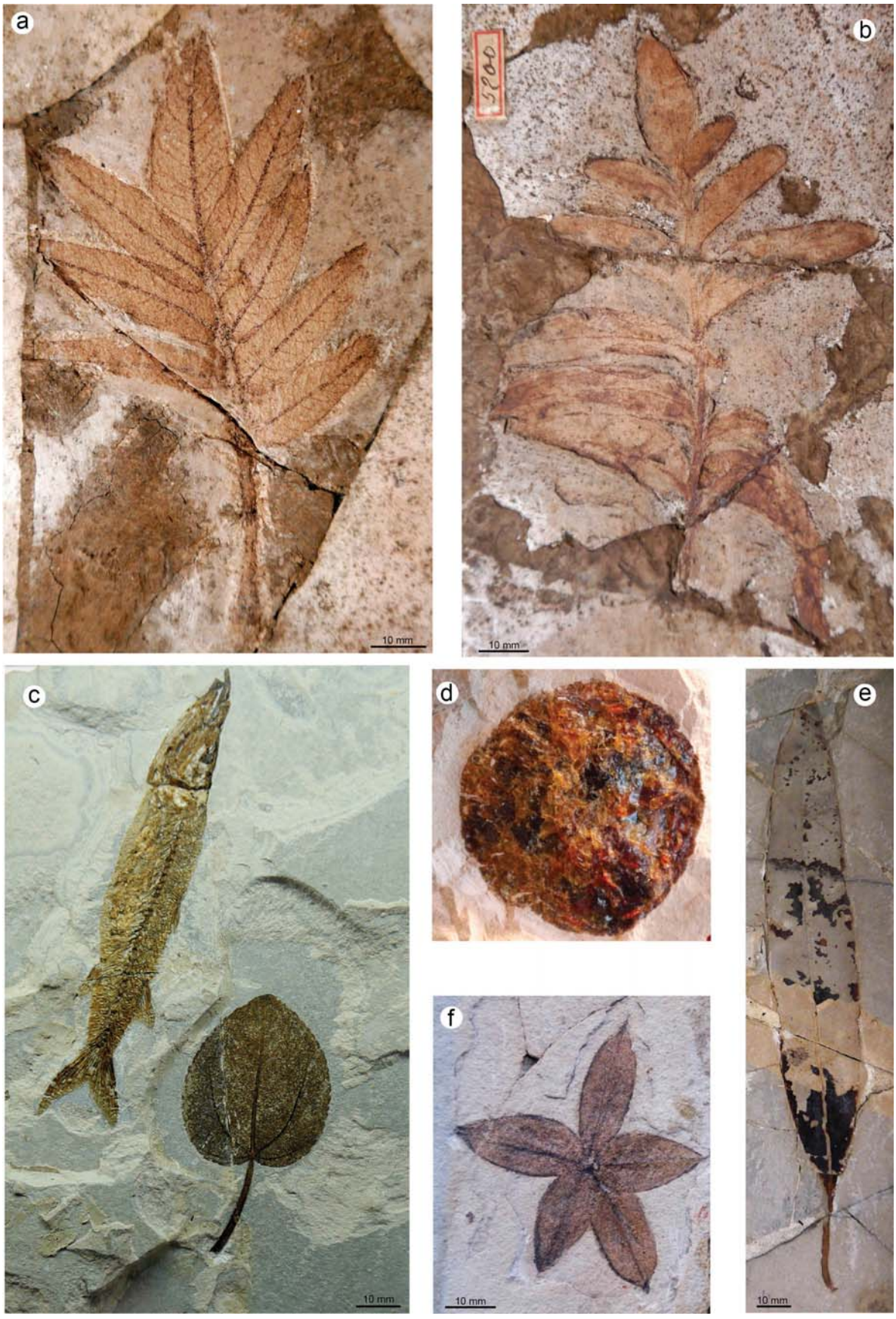

FIG. 2 - a) Imparipinnate legume leaf similar to "Leguminosae sp. 5" from Messel (Wilde 1989), MGPPD23. b) Imparipinnate composite leaf with decurrent leaf bases and potential affinities to *Zanthoxylon* (Rutaceae), MGPPD 5200. c) Leaf of "*Dombeyopsis*" with crenulate margin on a slab together with a ramphognathids fish (*Latellagnathus teruzzii* Bannikov, 2008). d) Large piece of resin, probably derived from legumes (diameter 3.5 cm). e) Entire-margined leaf of "*Laurophyllum*" with remnant organic material possibly suitable for cuticular analysis, MCSNV fM179. f) Winged fruit of the "*Getonia*"-type, MCSNV fG399.

From a systematic point of view, the Pesciara-Monte Postale macroflora is remarkably rich in remains of marine macroalgae, especially the leaf-like thalli of *Delesserites* (red algae; Fig. 1a). Interestingly, red algae have also been suggested by biomarker studies of the host rock (Schwark et al., 2009). Ferns have not been detected, and conifers are putatively represented only by long needle-like leaves showing transverse wrinkling possibly caused by sclereids, such as seen in *Amentotaxus* today. The most frequent angiosperms are floating salt-tolerant or even marine monocotyledons, such as seagrasses (Figs 1b-c), commonly preserved as large fragments or almost whole plants. Remains of other monocotyledons are rare and do not include palms, except for some of the large fruits.

Dicotyledonous angiosperms are mainly represented by leaves together with some fruits, fruiting twigs/infructescences and rare flowers. In addition, there are whole-plant specimens including roots and fruits ("*Maffeia*"), but at least some of them appear artificially (re)constructed (Fig. 3d). The leaves are dominated by compound leaves and their leaflets. About five legume taxa may probably be distinguished (Fig. 2b), including a double-compound caesalpinioid leaf type and leaves morphologically quite similar to those described as "Leguminosae sp. 5" from the Middle Eocene of Messel (Germany; Wilde, 1989; Figs 2a-b). There is another type of compound leaves characterized by decurrent leaf bases which were compared to leaves of extant *Zanthoxylum* (Rutaceae). *Weinmannia* (Cunoniaceae) has commonly been suggested for small imparipinnate leaves in the Italian collections, carrying leaflets with a crenulate margin (Figs 3a-b). But, a single specimen of the same distinct type in the Berlin collection has later been assigned to Burseraceae (*Boswellia*) by Kahlert & Rüffle (2007). There are surprisingly few types of mostly medium-sized entire-margined leaves in the collections which have been assigned to genera like, e.g., *Ficus* (Moraceae), *Laurophyllum* (Lauraceae) and *Salix* (Salicaceae), but their true affinities need to be checked by careful comparisons. Putative malvalean leaves are common and have been assigned to genera such as e.g. *Dombeyopsis* or *Grewia* (Fig. 2c). However, some of them show a crenate margin which is uncommon in the malvalean alliance, but makes them sometimes similar to leaves of *Cercidiphyllum* (Jähnichen et al., 1980).

Among the fertile material, branched infructescences (or fruiting twigs) should be mentioned which were called "*Bubulcia*". They are superficially similar to the infructescences of extant and fossil *Decodon* (Lythraceae) as described by Kvaček & Sakala (1999), but detailed comparisons are needed. Furthermore, there are few winged fruits which were traditionally assigned to *Getonia* (Fig. 2f), but also need detailed comparisons. Some of the quite large fruits were obviously fibrous and may have been derived from palms, possibly including *Nypa* (Fig. 3c).

Frequency and diversity of marine elements such as macroalgae and seagrasses among the plant macrofossils at Pesciara-Monte Postale is not surprising in a sheltered lagoonal basin as suggested for the time of deposition (Papazzoni & Trevisani, 2006; Schwark et al., 2009). Compared to the similarly well collected earliest Middle Eocene lacustrine oil shale of Messel, the rest of the association is only moderately diverse with a surprising dominance of legume leaves and leaflets. Except for lobed leaves (Fig. 3e), only entire-margined leaves have been noted otherwise (Fig. 2e). Fruits and seeds are comparatively rare, but even include specimens of considerable size, most of them probably palm fruits. Major deficiencies are ferns and legume pods, conifers and winged fruits are rare. The comparatively selective taphocoenosis can mostly be explained by taphonomic processes. Probably most of the plant material (including amber; Trevisani et al., 2005) was washed from nearby sources into the lagoon by rain or minor tributaries leaving no obvious record in the sediments except for dispersed fine grained material. This excluded leaves of indehiscent herbaceous plants, especially ferns and monocotyledons.

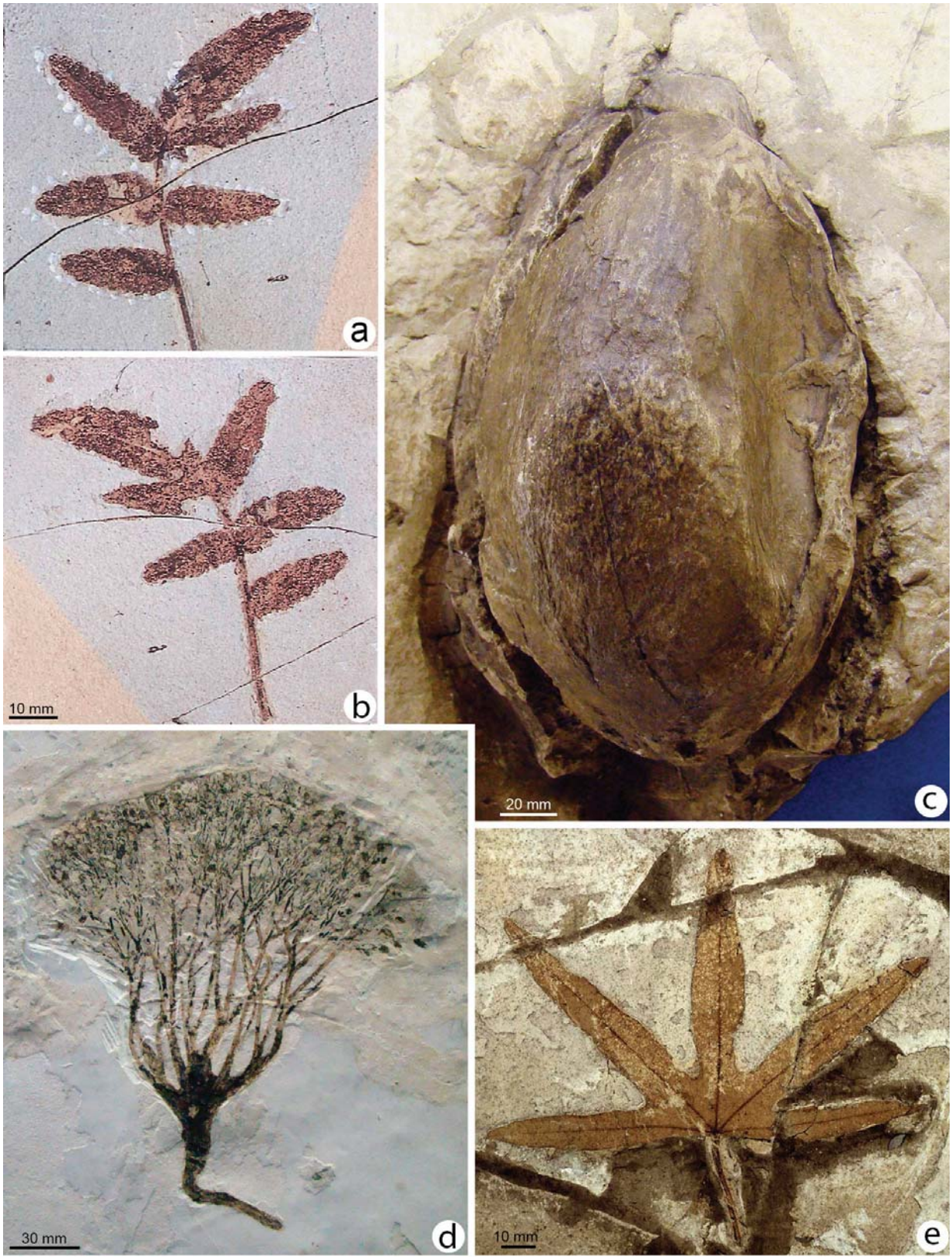

Fig. 3 - a) Small compound leaf showing leaflets with a crenulate margin which have been assigned either to *Weinmannia* (Cunoniaceae), or to *Boswellia* (Burseraceae), MCSNV fB221. b) Counterpart of a, MCSNV fB222. c) Large fibrous fruit similar to fruits of the mangrove palm *Nypa*, MCSNV fG416. d) Partly (re) constructed whole-plant specimen ("*Maffeia*"), MCSNV fB203. e) Leaf of a kind which has frequently been assigned to "*Sterculia*" (Sterculiaceae), MGPPD 20V.

Floating of the plant material at the surface before sinking to the bottom led to further selection. Still surprising is the frequency of legumes which are not only represented by

leaves but also by amber (Trevisani et al., 2005). They may have been blown directly into the lagoon from trees growing nearby on a well-drained (drier) substrate by occasional storms (Papazzoni & Trevisani, 2006), and large palm fruits may just have fallen down into the water. Storms may also be responsible for occasionally removing whole-plant specimens from the substrate. Similar to the macroflora, ferns and gymnosperms are rare in the microflora, however, there is considerably more diversity in pollen of angiosperms than in macroscopic remains (Kedves & Zsivin, 1970; Trevisani et al., 2005). Since pollen is more easily transported for some distance, they may have been derived from a diverse tropical forest in some distance to the lagoon. Summing up, we have to envisage a tropical lagoon for the Ypresian of Pesciara-Monte Postale which was probably surrounded especially by legumes and palms including the mangrove palm *Nypa*. A regular tropical forest followed with distance.

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7. The Pesciara-Monte Postale *Fossil-Lagerstätte*: 4. The "minor fauna" of the laminites

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The epithet "minor fauna" has been commonly used in the Italian literature to indicate non-fish animal fossils recovered within the laminites of the Pesciara-Monte Postale localities (e.g., Sorbini, 1980, 1999). Specimens of non-fish vertebrates (snakes, bird feathers, and a turtle), even if traditionally included in the minor fauna (e.g., Sorbini, 1972, 1980, 1999; Landini et al., 2005), are not the object of the present work. As used herein, the minor fauna of the "Bolca biota" includes both marine and terrestrial forms, and comprises arthropods (mostly insects and crustaceans), polychaete worms, jellyfishes, mollusks, brachiopods, and bryozoans. The preservation of the organic parts of delicate organisms such as jellyfishes and polychaete worms testifies to the exceptional sedimentological and diagenetic conditions that lead to the formation of one of the most internationally famous *Konservat-Lagerstätten*. Invertebrates from the Pesciara have been known since the early 18th century, when Scheuchzer (1709) figured an insect identified as a dragonfly. Abramo Massalongo was the first scholar to attempt a comprehensive investigation of the minor fauna of Bolca, but his planned "Compendium Faunae et Florae fossilis Bolcensis" never came to light. After some partial studies (e.g., Massalongo, 1850, 1855, 1856; Omboni, 1886), the invertebrates of the Bolca laminites were mostly neglected up to the late 20th century, when new discoveries encouraged researchers to restart investigations (e.g., Broglio Loriga & Sala Manservigi, 1973; Secretan, 1975a, b; Capra, 1977). The largest collections of minor fauna are presently housed at the Museo Civico di Storia Naturale di Verona (MCSNV), the Museo dei Fossili di Bolca (Verona) and the Museo di Geologia e Paleontologia dell'Università di Padova (MGP-PD).

Jellyfishes

Fossil Medusae from the Pesciara at Bolca (Figs 1a-d) were first described by Broglio Loriga & Sala Manservigi (1973). All six of the studied specimens were referred to Scyphomedusae and are fossilized as carbonaceous films reproducing either the complete morphology or parts of the organism. Four of these specimens were assigned to a new genus (Broglio Loriga & Sala Manservigi, 1973), the rhizostomid *Simplicibrachia* (type

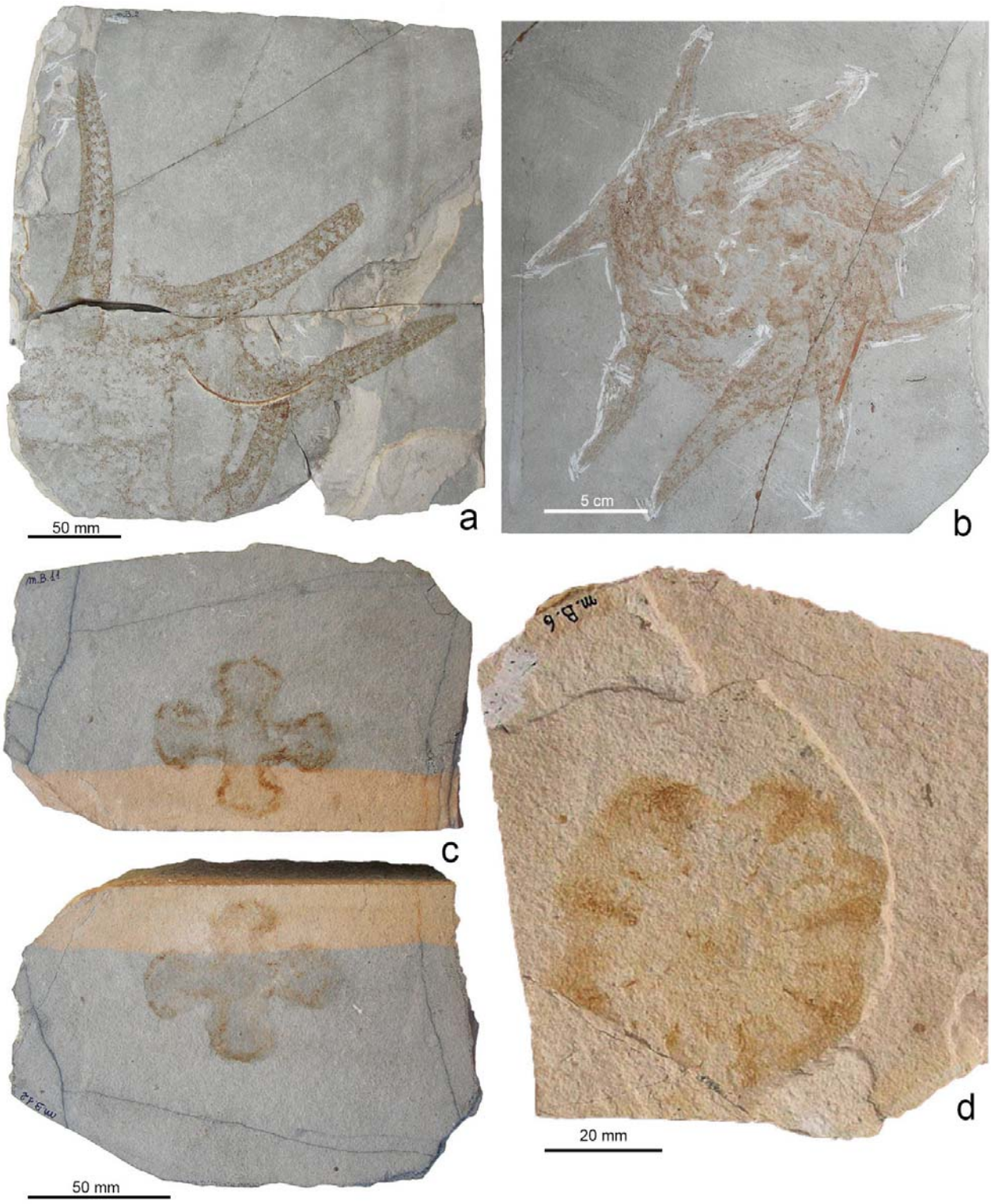

Fig. 1 - Medusae. a) *Simplicibrachia bolcensis* Broglio Loriga & Sala Manservigi 1973. Holotype. MCSNV m.B.2. b) *Simplicibrachia bolcensis* Broglio Loriga & Sala Manservigi 1973. Paratype. MCSNV m.B.1. c) Undetermined scyphomedusa. MCSNV m.B.11-12. d) Possible ephyra of scyphomedusa (aff. *Chrysaora* or *Rhizostoma*). MCSNV m.B.6.

species *S. bolcensis*) in which even the finest details, such as the frilled ostioles, are preserved (Figs 1a, b). The other two specimens are young individuals possibly belonging to the orders Rhizostomeae and Semaeostomeae. Both of these show traces of the ring muscle. In the rhizostomatid the oral disk is also preserved, whereas the semaeostomid

perhaps preserves the membranous oral arms. Sala Manservigi (1979) studied six other jellyfishes from Bolca: three were ascribed to adults of *Simplicibrachia* and three were referred to ephyras (larvae) of Scyphomedusae, possibly belonging to the genera *Simplicibrachia* and *Chrysaora* (Fig. 1d).

Arthropods

Insects

Various insects have been discovered at the Pesciara-Monte Postale localities, including mole crickets, termites, beetles, water bugs, mosquitoes, and dragonflies (Tang, 2002; Figs 2-3). Massalongo (1856) was the first to study in detail the insect fauna of Bolca, recognizing seven species, five of which were new: two dipterans (*Dipterites angelinii* and *Bibio sereri*), the earwig *Forficula bolcensis*, the dragonfly *Cordulia*? *scheuchzeri*, the coleopters *Ancylochira deleta* (a jewel beetle) and *Perotis laevigata,* and lastly the termite *Termes peccanae*. In an early overview of fossil insects of the Veneto region, Omboni (1886) included all the taxa previously studied by Massalongo. However, Fabiani (1915, p. 290), in his benchmark paper on the Paleogene of Veneto, contested the provenance of the insects described by Massalongo (1855), hypothesizing that most of them (apart from *Bibio sereri* and, perhaps, *Dipterites angelinii*) had been instead recovered at Solnhofen in Germany.

After several decades of inactivity in Bolca insect studies, Secretan (1975b) described a complete specimen of mole cricket from Bolca (Fig. 2a) and ascribed it to a new species, *Gryllotalpa tridactylina,* which later was described in more detail by Capra (1977). This finding has been considered the first unquestionable report of that genus from Eocene sediments (Secretan, 1975b; Capra, 1977), even though Gorochov & Labandeira (2012) recently proposed to transfer *G. tridactylina* to the genus *Pterotriamescaptor*. Krzeminski & Krzeminska (1990) studied the Tipulomorpha (four Tipulidae and three Limoniidae) from the Pesciara housed in the Verona Museum and erected a new species of Limoniidae, *Gnophomyia gentilinii*. These authors examined the entire insect collection housed in the Museo Civico di Storia Naturale di Verona (40 specimens) and subdivided these materials into eight orders (?Thysanura, Odonata, Diptera, Trichoptera, Coleoptera, Orthoptera, Heteroptera, and Hymenoptera), with a predominance of Diptera (Figs 2-3).

One of the most astonishing and better preserved insects recovered from the Pesciara is a wingless female of the sea skater *Halobates ruffoi* (Fig. 2e) that represents the oldest fossil record of this genus (Andersen et al., 1994). The taxa of *Halobates* include some of the most specialized water striders; these occur in tropical and subtropical seas around the world and are successful in the oceanic habitat (Cheng et al., 2012). The occurrence of *Halobates* in the Ypresian beds of Bolca indicates that sea surface temperatures in this portion of the Tethys were not lower than 20°C, which is the tolerance temperature of extant *Halobates* species (Andersen et al., 1994; Cheng et al., 2012).

The Order Odonata is well represented in the entomofauna of the Pesciara housed at the Museo Civico di Storia Naturale di Verona and consists of both immature stages (larvae) and adults, mostly discovered in recent years (1970-1980). Gentilini (2002) studied adult Odonata in detail, describing new genera and species ascribed to dragonflies (*Bolcathemis nervosa* and *Bolcacordulia paradoxa*) and damselflies (*Bolcathore colorata*); the latter is fairly well preserved and show its beautiful color pattern (Figs 3a, d). The only dragonfly from Bolca that had been described prior to Gentilini (2002) was *Cordulia*? *scheuchzeri* Massalongo (1856), but the attribution and provenance is uncertain and the type is in

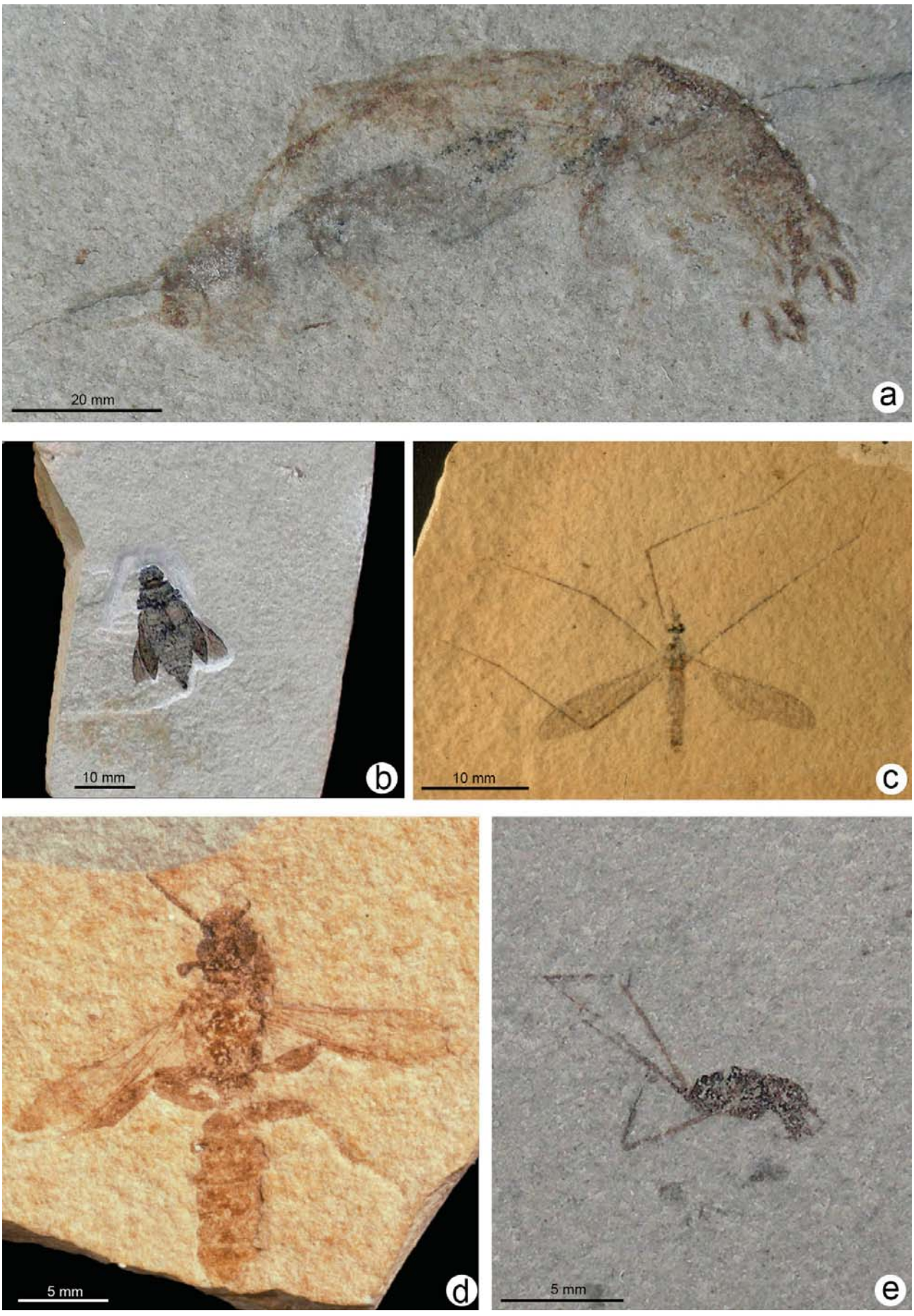

Fig. 2 - Insects. a) *Gryllotalpa tridactylina* Secretan 1975a. Holotype. MCSNV 24517. b) Coleopter MCSNV i.B.20. c) Mosquito (Diptera). MCSNV i.B.8. d) Hymenopteran MCSNV i.c.2NS. e) *Halobates ruffoi* Andersen et al. 1994. MCSNV I.G. 24527.

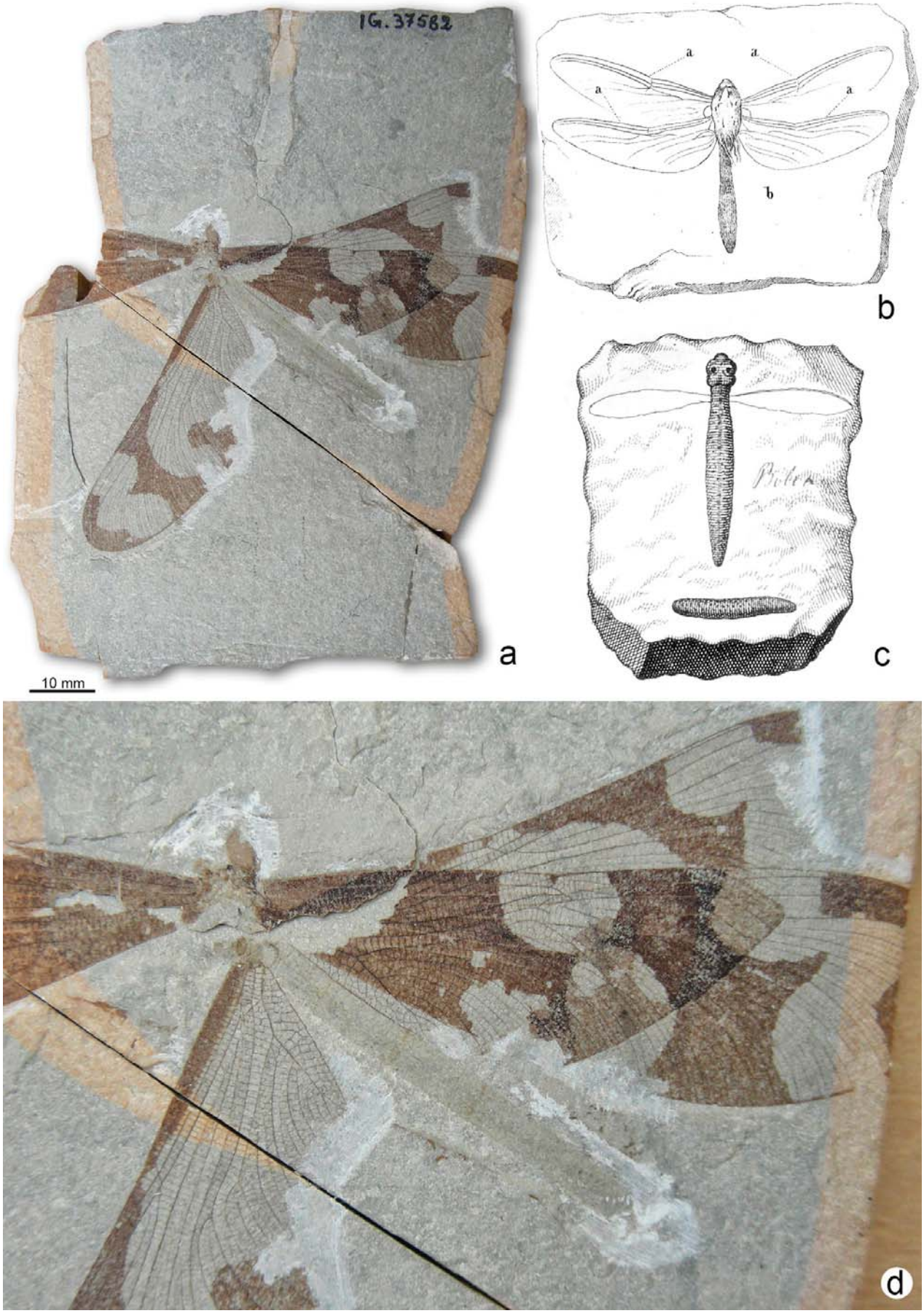

Fig. 3 - Insects. a) The damselfly *Bolcathore colorata* Gentilini 2002. Holotype. MCSNV I.G. 37582. b) *Cordulia*? *scheuchzeri* Massalongo 1856 [excerpt from Massalongo (1856, Plate II, Fig. 7)]. c)The dragonfly figured by Scheuchzer (1709), probably a Tipulomorpha. d) Detail of the holotype of *Bolcathore colorata* Gentilini 2002.

need of revision (Fig. 3b). According to Krzeminski & Krzeminska (1990), the insect with two wings figured by Scheuchzer (1709) was not an Odonata (dragonfly) but most probably was a female of Tipulidae (Fig. 3c).

Arachnids

The laminites of the Pesciara yielded a beautiful scorpion in excellent state of preservation (Cerato, 2011; Fig. 4a). Because of the partial inclusion within the matrix, the specimen, which was discovered by Massimiliano Cerato in the '70s, had previously been labeled as a "terrestrial arthropod" and only a careful cleaning permitted the specimen to be revealed in its full splendor (Massimo Cerato, pers. comm.). A possible pseudoscorpion from Bolca is also housed in the Museo Civico di Storia Naturale di Verona.

Crustaceans

Crustaceans are the most conspicuous component of the Bolca laminites minor fauna and are represented in the collections of the Verona and Padova museums by many specimens belonging to the orders Isopoda, Stomatopoda, and Decapoda (Sorbini, 1999). Decapods make up most of the collections and include penaeids, palinurids, anomurids, and brachiurids (Figs 4b-d, 5, 6). Crustaceans from Bolca have been reported at least since the beginning of the 19th century, when the French geologist Faujas de Saint-Fond (1804) figured a decapod (possibly a penaeid shrimp; Figs 4b-c), donated by Count Gazola of Verona to the National Museum of Natural History in Paris. Later, paleontologists such as Desmarest (1822), Münster (1842), Catullo (1854), and De Zigno (fide Garassino & Novati, 2001) took interest in the crustaceans discovered in the laminites of Pesciara-Monte Postale. Specifically, Münster (1842) described the species *Squilla antiqua* (now *Lysiosquilla antiqua*; Fig. 4d), a mantis shrimp, whose holotype is probably lost (fide Secretan, 1975a; De Angeli & Beschin, 2006). Massalongo was the first investigator who planned to study in detail the crustaceans of Pesciara-Monte Postale. As a matter of fact, he prepared seven plates (12-18) figuring about 20 crustaceans from Bolca for the never published "Compendium Faunae et Florae fossilis Bolcensis", whose 20 plates survive (De Visiani, 1861; Forti, 1924). Only a list of 19 taxa of crustaceans of Bolca, including seven new undescribed species, was published as an appendix to the "Monografia delle Nereidi fossili del M. Bolca" (Massalongo, 1855). In the same paper, the author ascribed to "*Udora*? *faujassii"* the decapod figured by Faujas de Saint-Fond (Massalongo, 1855; p. 33). More than one century later, Secretan (1975a) finally published an extensive study of crustaceans from Bolca, describing several species and erecting eight new taxa. That author also recognized for the first time in the crustacean assemblage the occurrence of isopods (*Palaega acuticauda* and *Heterosphaeroma veronensis*), hypothesizing that they were parasites on fishes (Figs 6a-b). According to Secretan (1975a), the crustacean fauna of Bolca populated a subtropical shallow sea. Förster (1984) reported for the first time the occurrence at Bolca of a scyllarid decapod (slipper lobster), ascribed to the new species *Parribacus cristatus*. Garassino & Novati (2001) later revised the most iconic crustacean from the Pesciara, the spiny lobster *Palinurus desmaresti* (Fig. 5), and transferred the species to the living genus *Justitia*, completing and integrating the previous description given by Secretan (1975a). More recently, De Angeli & Beschin (2006) described a specimen of *L. antiqua* from Bolca, housed in the Museo Civico "G. Zannato" of Montecchio Maggiore (Vicenza). Finally, De Angeli & Garassino (2008) studied two new taxa recovered from the laminites of Monte Postale: the mantis shrimp *Pseudosquilla lessinea* (Fig. 6c) and the slipper lobster *Scyllarides bolcensis*.

Summarizing, the species of crustaceans figured and described to date from Pesciara-Monte Postale are the following:

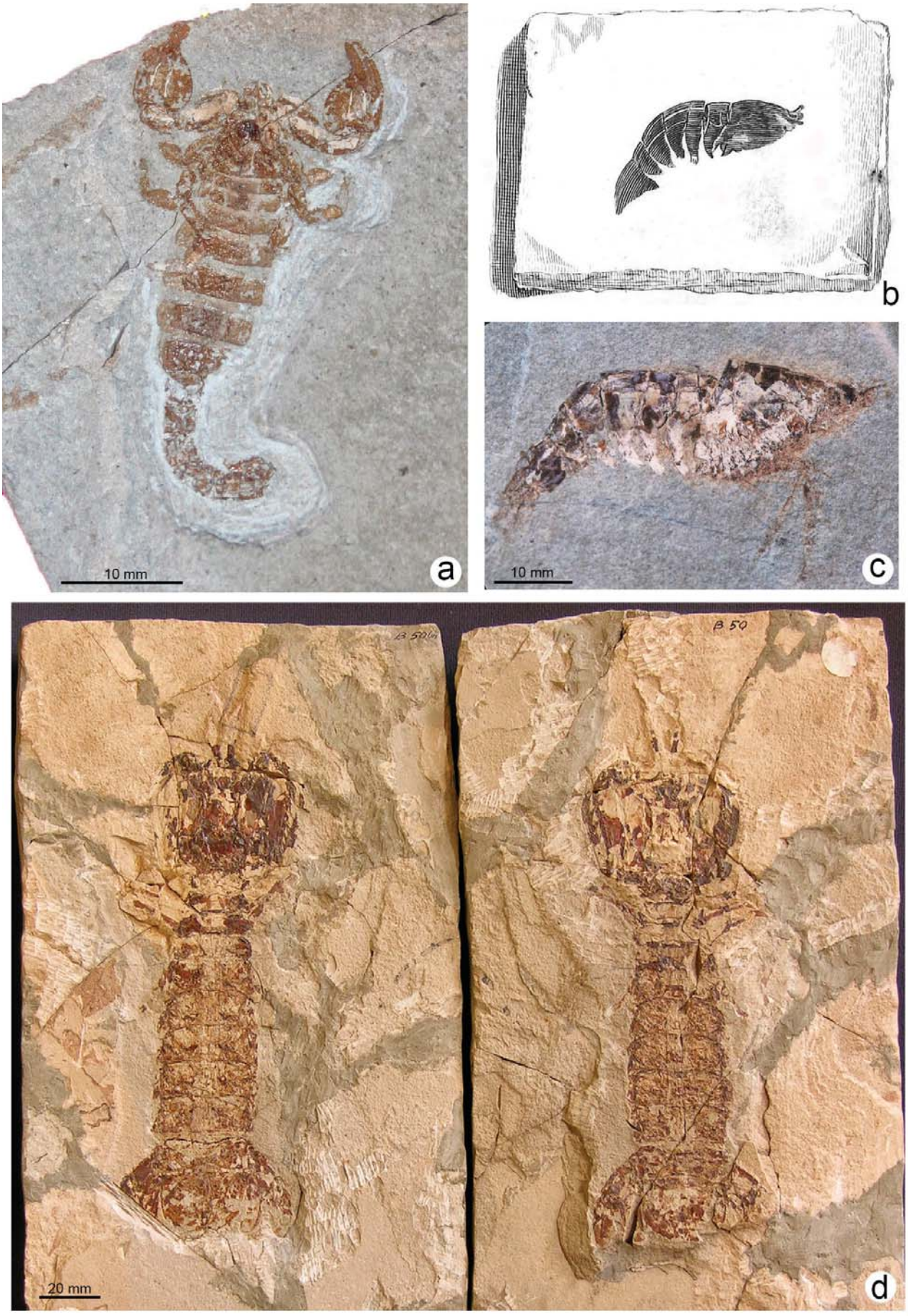

Fig. 4 - Arachnids and crustaceans. a) Scorpion. Cerato collection. b) The first illustration of a crustacean from Bolca, possibly a penaeid [excerpt from Faujas de Saint-Fond (1804, Plate I, Fig. 5)]. c) *Penaeus* sp. Cerato collection. d) *Lysiosquilla antiqua* (Münster 1842). MCSNV B50 and 50bis.

Fig. 5 - The spiny lobster *Justitia desmaresti* (Massalongo, 1854). MCSNV 23.

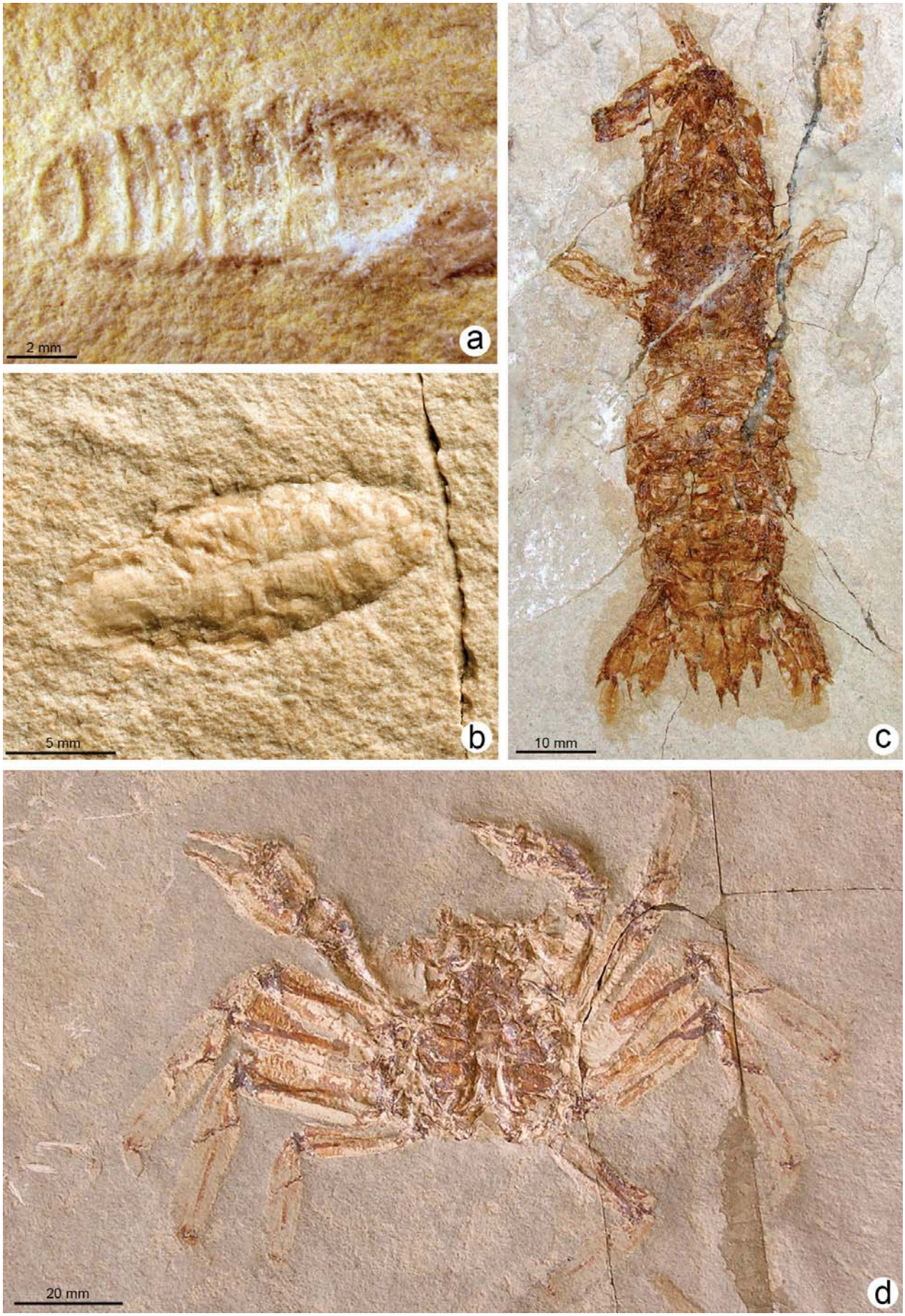

Fig. 6 - Crustaceans. a) *Heterosphaeroma veronensis* Secretan 1975a. Holotype. MCSNV Cr.14. b) *Palaega* sp. MGP-PD 31433. c) *Pseudosquilla lessinea* De Angeli & Garassino 2008. Holotype. MCSNV I.G. VR 67497. d) *Archaeocypoda veronensis* Secretan 1975a. MCSNV n. 97.

Order Isopoda: *Palaega acuticauda* Secretan 1975a; *Heterosphaeroma veronensis* Secretan 1975a (Fig. 6a); *Sphaeroma* sp. in Secretan 1975a.

Order Stomatopoda: *Lysiosquilla antiqua* (Münster, 1842; Fig. 4d); *Pseudosquilla lessinea* De Angeli & Garassino, 2008 (Fig. 6c). The subspecies *Lysiosquilla antiqua minor* has been recently synonymized with *L. antiqua* by Schram & Müller (2004).

Order Decapoda: *Penaeus bolcensis* Secretan, 1975a; *Penaeus obtusus* Secretan, 1975a; *Pseudobombur nummuliticus* Secretan, 1975a; *Protaxius eocenicus* Secretan, 1975a; *Protaxius* sp. in Secretan, 1975a; *Justitia desmaresti* (Massalongo, 1854) *fide* Garassino & Novati, 2001 (Fig. 5); *Parribacus cristatus* Förster, 1984; *Scyllarides bolcensis* De Angeli & Garassino, 2008; *Enoplonotus armatus* A. Milne Edwards, 1860; *Macropipus ovalipes* Secretan, 1975a; *Portunus* sp. in Secretan, 1975a; *Panopeus bolcensis* Secretan, 1975a; *Eriphia* ? sp. in Secretan, 1975a; *Archaeocypoda veronensis* Secretan, 1975a (Fig. 6d).

Mollusks

In the Pesciara-Monte Postale sites, mollusk shells, associated with corals, commonly occur in the form of transported debris in the coarse-grained limestones intercalated within the fossiliferous laminites (e.g., Tang, 2002; Papazzoni & Trevisani, 2006). In the following paragraph, however, we refer exclusively to the remains of mollusks discovered within the laminites (Figs 7a-c).

Bivalves and gastropods

Catullo (1842) and Massalongo (1850) were the first who took interest in the mollusks from the laminites and listed the following taxa: *Cerithium bolcanum* (*nomen nudum*), *Ostrea* sp., *Mytilus* sp. indet., *Tellina* ?*bicingularis*, and *Unio* sp. According to Massalongo (1850), specimens of *Unio* from Bolca had been sometimes misinterpreted as some kind of plant pod. Other taxa reported by Oppenheim (1896) and Vinassa de Regny (1897) cannot be confidently attributed neither to the Pesciara nor Monte Postale laminites. Malaroda (1954) recognized the presence of the following taxa: *Modiolus* sp., *Cardita postalensis,* and *Teredo tournali subparisiensis*. Mellini & Quaggiotto (1999a, b) more recently described a small malacofauna: the bivalves *Anomia* sp. ind., *Lima* (*Ctenoides*) cf. *papillifera*, and *Monitilora elegans,* and the gastropods *Pseudamaura circunfossa* and *Dialopsis incompleta* (Figs 7a-b). Still undescribed bivalves from Pesciara are housed in the collections of Museum of Natural History of Verona (Fig. 7c).

Cephalopods

Cephalopods are exceedingly rare in the laminites and are mostly represented by Coleoidea, apart from one specimen of nautiloid (*Aturia ziczac*) studied by Malaroda (1954, p. 73). Broglio Loriga & Sala Manservigi (1973) described for the first time a well-preserved coleoid from the Pesciara with a characteristic teuthoid habitus. It consists of an impression and compression in which is visible a tapering body with large eyes in the cephalic part and carbonaceous residues of the ink sac. The internal shell is missing; therefore, the specimen has been only hypothetically related to "metateuthoids". After this first report, other squids in various degrees of preservation have been discovered, but they are still undescribed (Fig. 7d). The first coleoid from the Pesciara with preserved shelly parts is a small apical portion of a phragmocone belonging to *Spirulirostra georgii* (see Mellini & Quaggiotto, 1999b). Such sepiid have also been reported in the Lutetian and Priabonian of the Veneto region (Fornasiero, 1997, 1999).

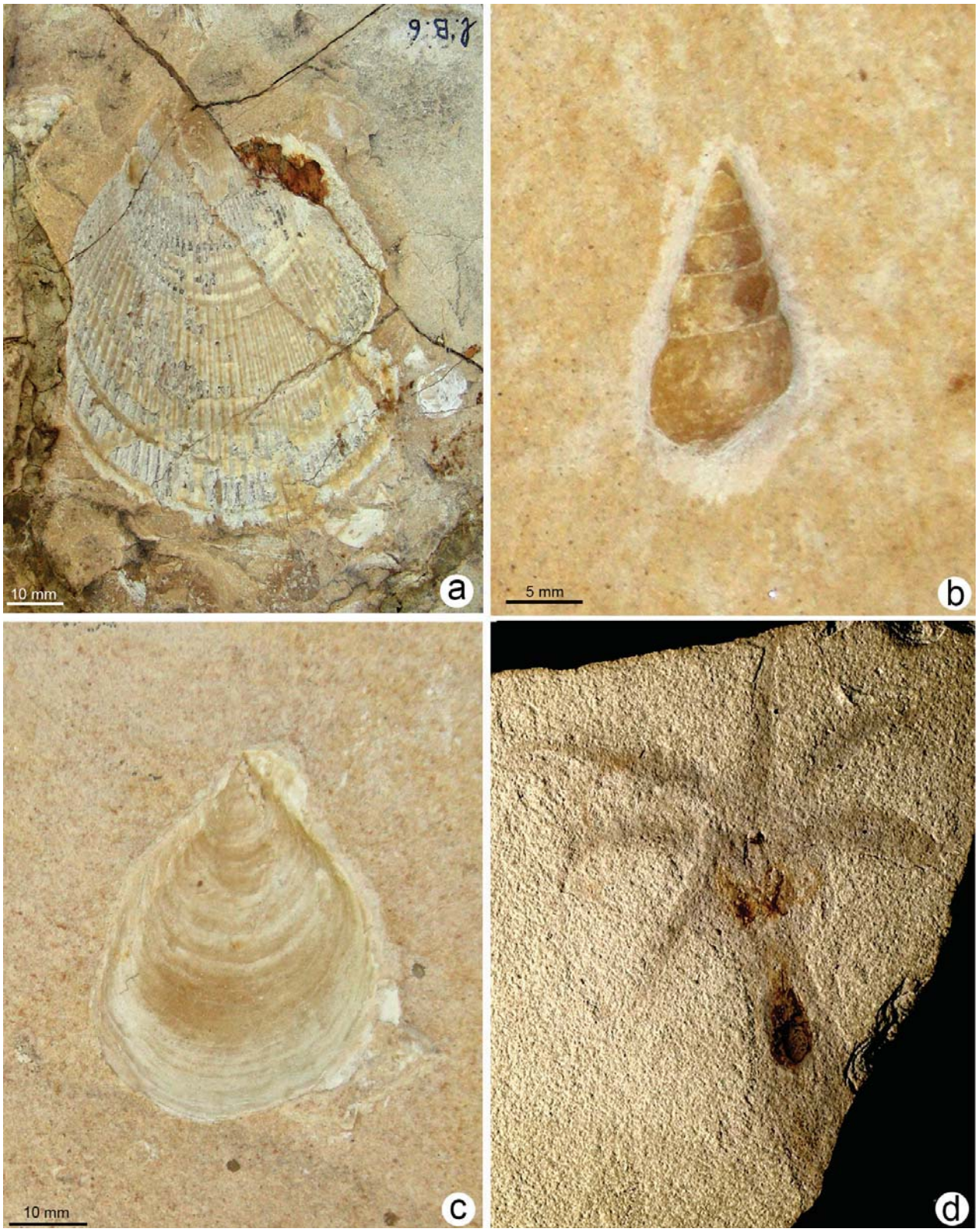

Fig. 7 - Mollusks. a) *Lima* (*Ctenoides*) cf. *papillifera* Bayan 1870. Imprint. MCSNV l.B.6. b) *Dialopsis incompleta* (Deshayes 1861). MCSNV l.B.9. c) Mytilidae. MCSNV 145139. d) Teuthoid. MGP-PD 31434. Maximum length of the specimen about 10 cm.

Lophophorata

Bryozoans

The only bryozoan so far recovered from laminites is a unique specimen preserved as compression and impression and lacking the younger stage of the zoarium. It has been

ascribed to the order Cheilostomata, family Schizoporellidae Jullien, 1903 (Broglio Loriga & Sala Manservigi, 1973).

Brachiopods

Brachiopods from the Pesciara were reported for the first time by Mellini & Quaggiotto (1999a, b), who described six terebratulids: five of these belong to "*Terebratula" fumanensis*, and the sixth is an undetermined specimen.

Annelids

The annelids from Pesciara-Monte Postale probably represent the first fully preserved fossil Polychaeta to be recognized and described as such (Alessandrello, 1990). These fossils, however, were initially misinterpreted as vegetal remains (e.g., Brongniart, 1828; Massalongo, 1850; Catullo, 1858). Abramo Massalongo corrected his initial mistake in 1855, when he published the "Monografia delle Nereidi fossili del Monte Bolca" in which he described in detail and figured seven new species of "worms", all ascribed to the genus "*Nereites*" (Fig. 8). Ehlers (1868) later assigned all these taxa to the genus *Eunicites*, without giving any descriptions or illustrations of the specimens. At the beginning of the 20th century, a new taxonomic reassessment of the annelids from Bolca was proposed by Rovereto (1904), who assigned the original species of Massalongo to three different genera: *Eunicites, Sthenelaites*, and *Siphonostomites*, but without figuring the material. Alessandrello (1990) finally published an extensive and detailed revision of these fossils based on 20 specimens, four of which were originally studied by Massalongo and the remaining having been found in Pesciara-Monte Postale after the publication of Massalongo's monograph. Most of the specimens have been assigned to the class Polychaeta (*Eunicites gazolae*, *Eunicites affinis*, *Eunicites pinnai,* and *Siphonostomites hesionoides*; Figs 8a-e), one has been referred to the class Hirudinea, and the others remain uncertain or undetermined. Moreover, four specimens ascribed to *Sthenelaites dasiaeformis* (Massalongo; Fig. 8f) have been reinterpreted as vegetal remains with a morphological configuration typical of seaweeds of the family Dasycladaceae (Alessandrello, 1990). It should be emphasized that Massalongo himself (1855) recognized the strong analogy between his *Nereites dasiaeformis* (Fig. 8f) and some vegetal forms, choosing the specific name *dasiaeformis* based upon the rhodophycean seaweed *Dasya*.

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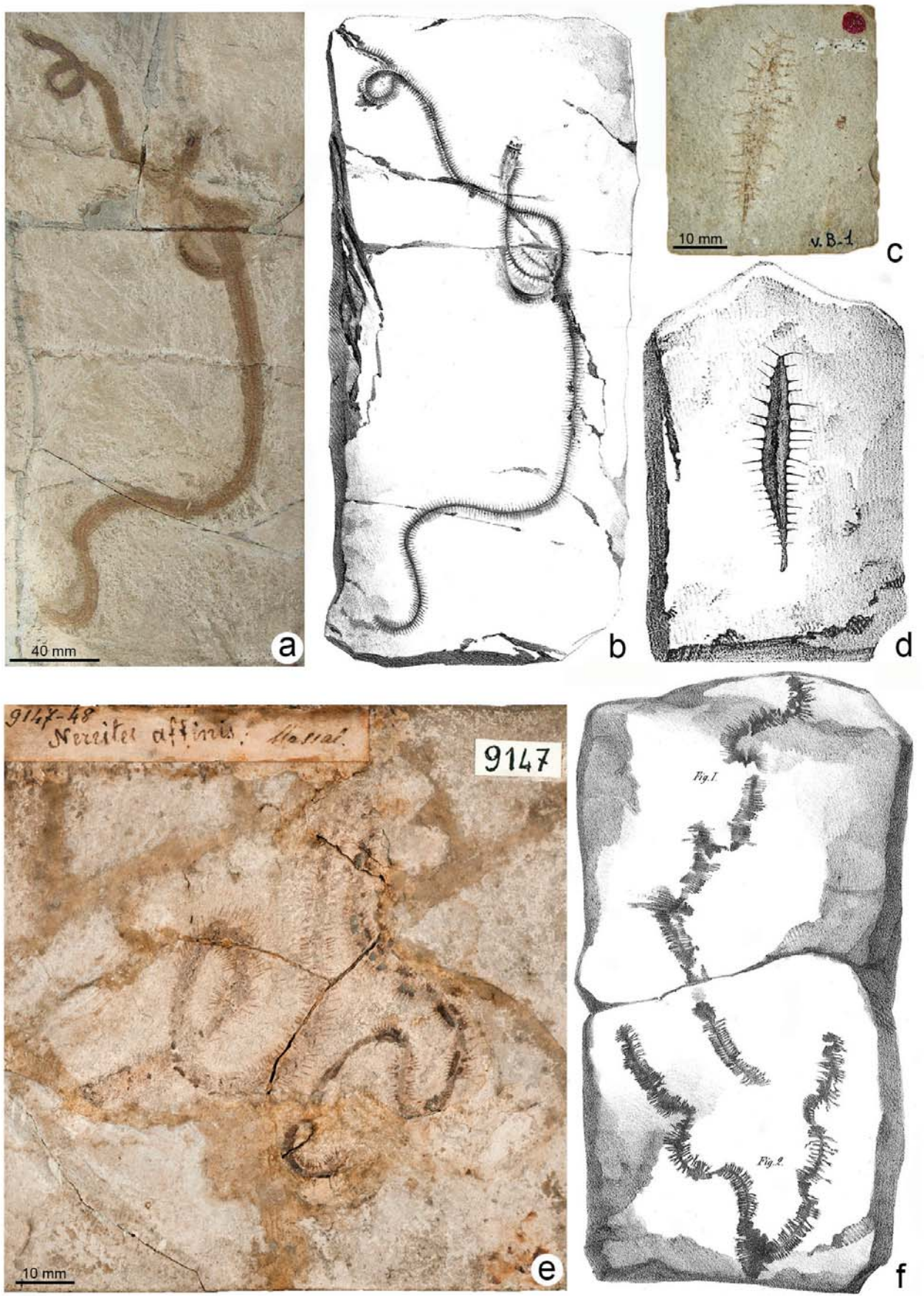

Fig. 8 - Polychaete worms. a) *Eunicites gazolae* (Massalongo 1855). Holotype. MCSNV v.B.5. b) The holotype of *Eunicites gazolae* [excerpt from Massalongo (1855, Plate I)]. c) *Siphonostomites hesionoides* (Massalongo 1855) Holotype. MCSNV v.B.1. d) The holotype of *Siphonostomites hesionoides* [excerpt from Massalongo (1855, Plate II)]. e) *Eunicites affinis* (Massalongo 1855). Holotype. MGP-PD 9147C. f) *Sthenelaites dasiaeformis* (Massalongo 1855; Plate IV), reinterpreted by Alessandrello (1990) as a seaweed of the family Dasycladaceae.

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The Bolca *Fossil-Lagerstätten*:
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(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

8. The mollusk fauna of the Monte Postale

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Fossil marine mollusks from Monte Postale, about one mile NE of Bolca (Verona and Vicenza Provinces) and 300 m N of the "Pesciara" (see the map in Papazzoni & Trevisani, 2006), were collected and catalogued at least since the 18th century. Shells were first seen, in the second decade of the 19th century, as means to date the rocks, and the already famous "Monte Bolca" fauna was one of the first tackled by a new generation of modern geologists. In 1823, on the footsteps of Alberto Fortis (1778), Alexandre Brongniart drew stratigraphic sections and collected fossils in the Vicenza province, assigning the Bolca and Roncà invertebrates to one and the same geological interval. In the newly introduced bipartition of the Tertiary, the Bolca fossils showed close affinities with mollusks of the Paris Basin. This meant to Brongniart that they belonged to the older Tertiary, and were distinct from the fossil shells described by Giambattista Brocchi in 1814, typifying the younger Tertiary (Rudwick, 2005). "I can relate the calcareous-trappic terrains of Northern Italy to the lower formation, the most ancient of the upper sediment [i.e., the Tertiary]. I'm struck by the analogy between these two terrains, their utter similarity under almost any aspect. Nothing of the lower terrains of the Parisian limestone is missing in Bolca, Roncà, etc. Many shells are absolutely of the same species: Strombus, Melania, Turritella, Caryophillia are present in both" (Brongniart, 1823).

Tommaso Antonio Catullo, successor of Stefano Andrea Renier at the Natural History chair of the University of Padova, reported that the Monte Postale fossil shells belonged to the uppermost part of the local succession, above the famous ichthyolithic strata. "The grey shelly limestone covers the basalt, forming the top of the mountain. (…) The shells collected so far belong to the upper sedimentary formation" (Catullo, 1826).

The first modern account of these fossil shells was published by Ferdinand Bayan in 1870, after a tour guided by Giovanni Meneguzzo in 1869. The shelly limestone, close to the top of Monte Postale, was dubbed "Limestone with *Cerithium gomphoceras*, *Alveolina longa*, etc.". Bayan listed 16 characteristic species of gastropods, and one lucinid bivalve, assigning the unit to his Eocene "interval B", immediately preceding the strata with the Roncà and San Giovanni Ilarione faunas (Bayan, 1870a). Bayan dedicated a short monograph to many new species he had encountered, including *Cerithium gomphoceras* and other characteristic gastropods, such as *Cerithium vicetinum* and *Cerithium chaperi* (Bayan, 1870b; the monograph faced heavy, unjustified criticism: Anonymous, 1871) (Figs 1-2).

In the same year, Karl Mayer introduced *Lucina escheri* and other new taxa from the "strata with *Cerithium giganteum* of Monte Postale" (Mayer, 1870), together with new names for species already described by Bayan. "*Cerithium giganteum*" of Mayer

Fig. 1- Plate I of Bayan (1870b) showing, among the others, the adult shells of *Bellatara palaeochroma* (1), *Pseudobellardia gomphoceras* (2, 3), *Cerithium chaperi* (4, 5), and juveniles of *Velates schmidelianus* (6).

(1870), in fact distinct from the Paris Basin congeneric form, was *Cerithium vicetinum* Bayan (1870b), so that their descriptions coincide. A short species list, very similar to Bayan's, was given in 1877 by Edmond Hébert & Ernest Munier-Chalmas, with additional information of the stratigraphy of the "Monte Postale limestone with *Cerithium gomphoceras*": "Immediately above [the ichthyolithic limestone], and deeply connected with it, we find the limestone exploited at the Monte Postale. Here the rock is filled with alveolinae, but a new fauna appears, together with some rare *Nummulites* and *Nerita schimdeliana*". These strata were referred to the "middle Eocene" by analogy with the Paris Basin fauna (Hébert & Munier-Chalmas, 1877).

The first dedicated paleontological monograph was published in 1895 by Antonio De Gregorio. This was introduced by a summary of previous studies, comprising a mention of the Bayan-Mayer priority issue, and with some information on the provenance of the fossils. Although De Gregorio partly collected the shells himself ("some specimens"), the bulk of his collection was purchased from Meneguzzo, who regularly provided other collectors and museums of the time. "Many species I have myself extracted from the blocks I was sent -I'm sure of the provenance of all my fossils, because I recommended to rigorously avoid all promiscuities, but also because the color of the fossils and the nature of the matrix are characteristic and impossible to misinterpret" (De Gregorio, 1895). De Gregorio lists some 21 species-level bivalves, 62 gastropods, and one cephalopod. He also reported that, compared to the Monte Postale species, "the S. Giovanni Ilarione and Roncà are much more numerous". The following year Paul Oppenheim, with a brief stratigraphic introduction based on Hébert & Munier (1877), raised the species count to 32 bivalves, 82 gastropods, and two cephalopods (Oppenheim, 1896). Meanwhile, two rather large collections were acquired by the Universities of Pisa and Firenze, thanks respectively to Giuseppe Meneghini and Igino Cocchi, and studied at the end of the century by Paolo Vinassa de Regny. In 1896 Vinassa listed 15 bivalve and 50 gastropod species, recognizing the paleoenvironmental meaning of the association, interpreting all cerithiiform gastropods as indicative of restricted coastal conditions. "Probably Monte Postale formed a bay of the Eocene sea, then becoming separated from it, towards subaerial conditions; the overall shallow marine aspect of the fauna, the abundance of new forms, decidedly of little marine affinity, prove this opinion, together with the brackish and terrestrial overlying faunas" (Vinassa de Regny, 1896).

The Monte Postale stratigraphy was revised and published by Ramiro Fabiani in his study of the Veneto Paleogene (Fabiani, 1915), confirming that the shells came from a single and very limited stratigraphic interval, his "unit 7b", or "*Alveolina* limestones with marine mollusks". Building on the Fabiani stratigraphy, and after revising all the existing literature and available species lists, Roberto Malaroda studied and published in 1954 a thorough study of all the specimens then hosted in the Padova, Verona, Pisa and Firenze museums. The Padova collection includes a small lot of specimens originally belonging to the De Gregori collection, once hosted in Palermo, and saved from destruction during World War II. According to this ultimate revision, the Monte Postale species-level list of Mollusca amount to 47 Bivalvia, 120 Gastropoda, and four Cephalopoda. However, the list includes many species cited by previous authors that Malaroda did not find in the collections he examined. Given the updated comparison with species lists from other European faunas, the study assigned the Monte Postale mollusks to the Lutetian (lower part of the middle Eocene) (Malaroda, 1954). In 2005 Cesare Papazzoni and Enrico Trevisani dated to the late Ypresian (Early Eocene) the portion of the Monte Postale succession below the mollusk levels. Since there are no updated biostratigraphic studies regarding the mollusk levels, they could be either of Ypresian age, as the underlying limestones, or

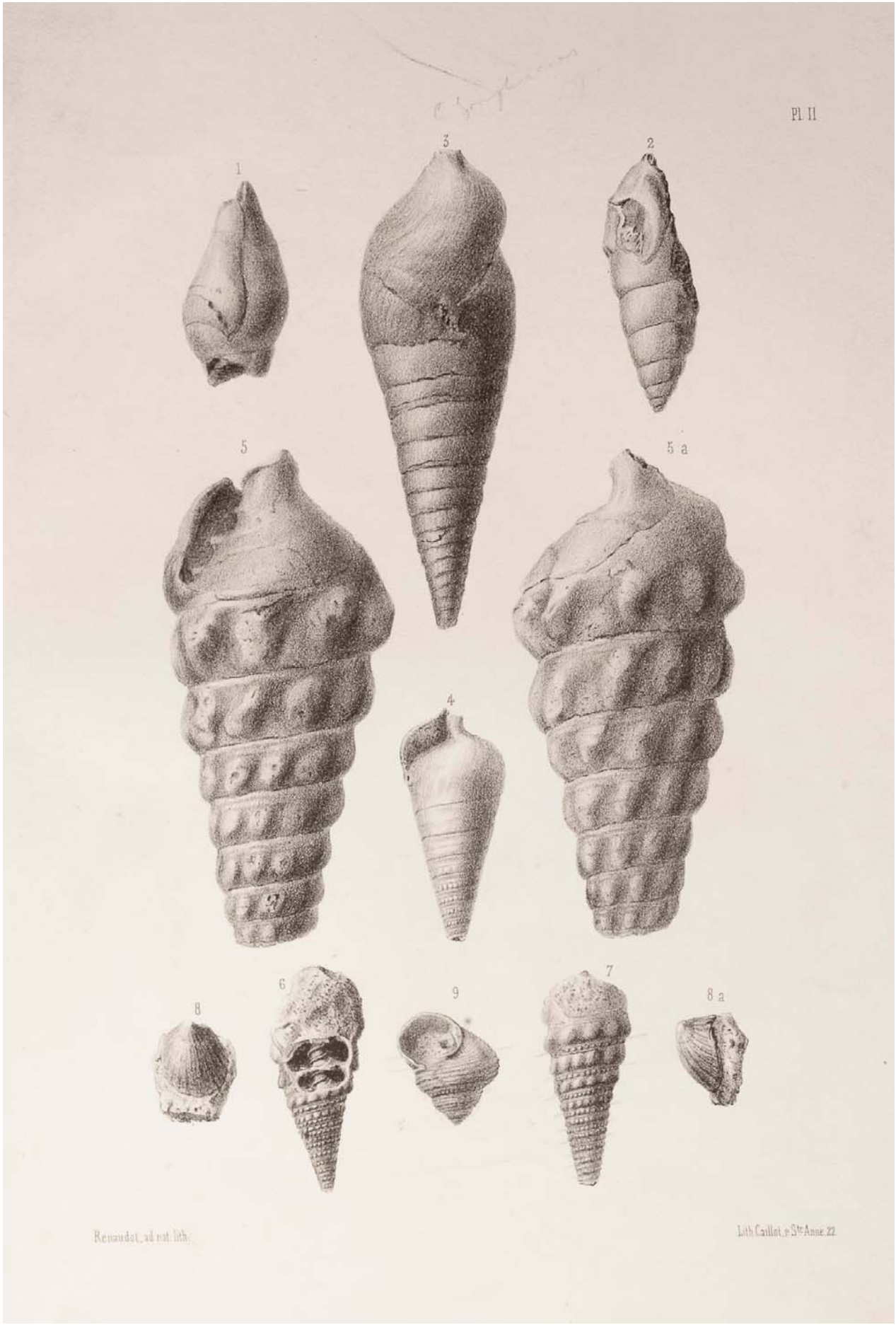

FIG. 2 - Plate II of Bayan (1870b), with *Pseudobellardia gomphoceras* (3, 4), and *Campanile vicetinum* (5, 5a, 6, 7).

	Superfamily	Family	Species	This paper (2014) (Firenze)	Malaroda (1954) (Firenze)	Malaroda (1954) (Padova)	Malaroda (1954) (Pisa)	Malaroda (1954) (Verona)	Malaroda (1954) (TOTAL)
1	Mytiloidea	Mytilidae	*Modiola postalensis* Oppenheim, 1896	0	0	0	0	2	2
2	Ostreoidea	Ostreidae	*Crassostrea sparnacensis* (Defrance, in Deshayes, 1821)	1	1	0	0	0	1
3	Pectinoidea	Spondylidae	*Spondylus radula* Lamarck, 1806	0	0	1	0	0	1
4	Lucinoidea	Lucinidae	*Pseudomiltha escheri* (Deshayes, 1824)	4	4	6	2	3	15
5	Lucinoidea	Lucinidae	*Pseudomiltha gigantea* (Deshayes, 1825)	2	0	16	3	9	28
6	Lucinoidea	Lucinidae	*Divalinga* sp.	0	0	2	0	0	2
7	Lucinoidea	Lucinidae	*Fimbria lamellosa* (Lamarck, 1806)	0	0	2	1	0	3
8	Lucinoidea	Lucinidae	*Fimbria major* (Bayan, 1870)	0	0	8	2	3	13
9	Tellinoidea	Tellinidae	*Tellina (Tellinella) biangularis* Deshayes, 1825	0	0	2	2	0	4
10	Tellinoidea	Tellinidae	*Tellina (Macaliopsis) scalaroides* Lamarck, 1806	0	0	1	0	0	1
11	Tellinoidea	Tellinidae	*Tellina (Macaliopsis)* sp.	0	0	0	0	1	1
12	Tellinoidea	Tellinidae	*Arcopagia (Bertinella) erycinoides* (Deshayes, 1824)	0	0	7	1	3	11
13	Cardioidea	Cardiidae	*Criocardium gratum* (Defrance, in Deshayes, 1829)	1	1	16	1	1	19
14	Cardioidea	Cardiidae	*Granocardium* sp.	1	1	1	1	3	6
15	Glossoidea	Glossidae	*Meiocardia carinata* (Deshayes, 1824)	0	0	1	0	0	1
16	Veneroidea	Veneridae	*Katelysia (Textivenus) texta* (Lamarck, 1806)	0	0	0	0	1	1
17	Veneroidea	Veneridae	*Venerella secunda* (Deshayes, 1857)	0	0	0	0	1	1
18	Veneroidea	Veneridae	*Pitar (Chionella) lunularia* (Deshayes, 1825)	0	0	1	0	0	1
19	Veneroidea	Veneridae	*Pitar (Calpitaria) parisiensis* (Deshayes, 1857)	0	0	1	0	0	1
20	Patelloidea	Patellidae	*"Patella" boreani* Bayan, 1870	0	0	1	0	0	1
21	Phasianelloidea	Colloniidae	*Homalopoma minimum* (Malaroda, 1954)	0	0	1	0	0	1
22	Trochoidea	Trochidae	*Clanculus zignoi* (Bayan, 1870)	6	6	24	8	6	44
23	Trochoidea	Calliostomatidae	*Calliostoma raffaelei* (Mayer-Eymar, 1888)	2	2	2	0	2	6
24	Trochoidea	Calliostomatidae	*Calliostoma mayeri* Fabiani, 1915	0	0	1	0	0	1
25	Trochoidea	Skeneidae	*Leucodiscus helicinoides* (Cossmann, 1888)	0	0	0	0	1	1
26	Neritoidea	Neritidae	*Velates schmidelianus* Chemnitz, 1786	0	0	44	2	17	63
27	Neritoidea	Neritidae	*Neritopsis agassizi* Bayan, 1870	0	0	1	0	0	1
28	Cerithioidea	Cerithiidae	*Cerithium chaperi* (Bayan, 1870)	15	16	14	5	20	55
29	Cerithioidea	Cerithiidae	*Cerithium fabianii* Malaroda, 1954	0	0	5	0	1	6
30	Cerithioidea	Cerithiidae	*Pseudovertagus striatus* (Bruguiére, 1792)	4	4	6	0	0	10
31	Cerithioidea	Cerithiidae	*Besançonia pyrenaica* (Cossmann, 1898)	0	0	3	1	3	7
32	Cerithioidea	Cerithiidae	*Ptychocerithium lamellosum* Bruguiére, 1792	0	0	0	0	1	1
33	Cerithioidea	Cerithiidae	*Bellatara palaeochroma* (Bayan, 1870)	7	6	34	2	11	53
34	Cerithioidea	Thiaridae	*Pseudobellardia auriculata* (Schlotheim, 1820)	0	0	1	0	1	2
35	Cerithioidea	Thiaridae	*Pseudobellardia gomphoceras* Bayan, 1870	24	21	52	21	33	127
36	Cerithioidea	Potamididae	*Tympanotonos tristriatus* (Lamarck, 1804)	0	0	1	0	0	1
37	Cerithioidea	Batillariidae	*Pyrazopsis pentagonatus* (Schlotheim, 1820)	0	0	1	0	0	1
38	Cerithioidea	Siliquariidae	*Tenagodus* sp.	0	0	1	0	3	4
39	Cerithioidea	Turritellidae	*Vermicularia biangulatus* (Deshayes, 1832)	0	0	0	0	13	13
40	Campaniloidea	Campanilidae	*Campanile vicetinum* (Bayan, 1870)	7	9	53	11	19	92
41	Campaniloidea	Ampullinidae	*Ampullina vulcani* Brongniart, 1823	1	1	6	0	5	12
42	Campaniloidea	Ampullinidae	*Ampullina hybrida* (Lamarck, 1804)	1	1	39	5	5	50
43	Campaniloidea	Ampullinidae	*Pachycrommium circumfossa* (Rauff, 1884)	2	2	10	1	3	16
44	Littorinoidea	Littorinidae	*Littoraria (Littorinopsis) postalensis* (De Gregorio, 1870)	1	1	0	0	1	2
45	Vanikoroidea	Hipponicidae	*Hipponix cornucopiae* (Röding, 1798)	7	7	34	6	9	56
46	Naticoidea	Naticidae	*Cepatia cepacea* (Lamarck, 1804)	13	13	40	0	19	72
47	Stromboidea	Aporrhaidae	*Digitolabrum princeps* (Vasseur, 1881)	1	1	0	0	0	1
48	Stromboidea	Rostellariidae	*Semiterebellum postalensis* (Bayan, 1870)	10	11	42	8	9	70
49	Stromboidea	Seraphsidae	*Seraphs convolutum* (Lamarck, 1802)	8	8	23	9	5	45
50	Cypraeoidea	Cypraeidae	*Archicypraea lioyi* (Bayan, 1870)	3	3	19	3	4	29
51	Cypraeoidea	Cypraeidae	*Vicetia hantkeni* (Lefèvre, 1878)	0	0	3	0	1	4
52	Cypraeoidea	Cypraeidae	*Cypraedia elegans* (Sowerby, 1823)	0	0	1	1	0	2
53	Cypraeoidea	Cypraeidae	*Cypraedia (Protocypraedia) interposita* (Deshayes, 1855)	0	0	2	1	0	3
54	Cypraeoidea	Cypraeidae	*Cypraeglobina praegnans* (De Gregorio, 1880)	0	0	0	0	1	1
55	Tonnoidea	Cassidae	*Cassis postalensis* Oppenheim, 1896	0	0	1	0	0	1
56	Muricoidea	Muricidae	*"Drupa" crossei* (Mayer-Eymar, 1870)	0	0	0	1	0	1
57	Muricoidea	Volutidae	*Voluta musicalis* (Lamarck, 1802)	0	0	6	1	2	9
58	Buccinoidea	Fasciolariidae	*Clavilithes (Rhopalites) rugosus* (Lamarck, 1803)	0	0	2	1	0	3
59	Buccinoidea	Melongenidae	*"Melongena" robusta* Dainelli, 1915	0	0	1	0	0	1
60	Conoidea	Conidae	*Leptoconus deperditus* (Bruguiére, 1972)	0	0	1	0	0	1
61	Conoidea	Conidae	*Hemiconus incomptus* (Deshayes, 1865)	0	0	1	0	2	3
62	Conoidea	Conidae	*Cryptoconus priscus* (Solander, in Brander, 1766)	0	0	1	0	0	1
63	Actenoidea	Acteonidae	*Liocarenus hilarionis* (Bayan, 1870)	1	1	0	0	0	1
64	Actenoidea	Acteonidae	*Acteon subinflatus* D'Orbigny, 1850	1	1	0	0	0	1
65	Architectonicoidea	Architectonicidae	*Architectonica bistriata* (Deshayes, 1832)	1	1	0	0	0	1
				124	122	542	100	224	988

Tab. 1- Species list of the Monte Postale molluscan fauna, with updated taxonomy and number of specimens. The latter refers to the collections of Firenze (checked by the author and according to Malaroda, 1954), Padova, Pisa, and Verona (all according to Malaroda, 1954).

younger (Lutetian) as pointed out by Malaroda (1954). A summary of the Monte Postale collection hosted at the Museo di Storia Naturale of the Università di Firenze is here reported with updated taxonomy (Tab. 1).

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(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

9. The Purga di Bolca-Vegroni sites

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In the localities of Purga di Bolca, Praticini, and Vegroni (Fig. 1), historically famous for reptiles and fossil palms, crop out freshwater and brackish sediments traditionally considered more recent than Pesciara and Monte Postale beds (e.g., Massalongo, 1861; Nicolis, 1884; Fabiani, 1912, 1915; Barbieri & Medizza, 1969; Sorbini, 1972; Medizza, 1980). The stratigraphy of these important sites was firstly outlined by Nicolis (1884).

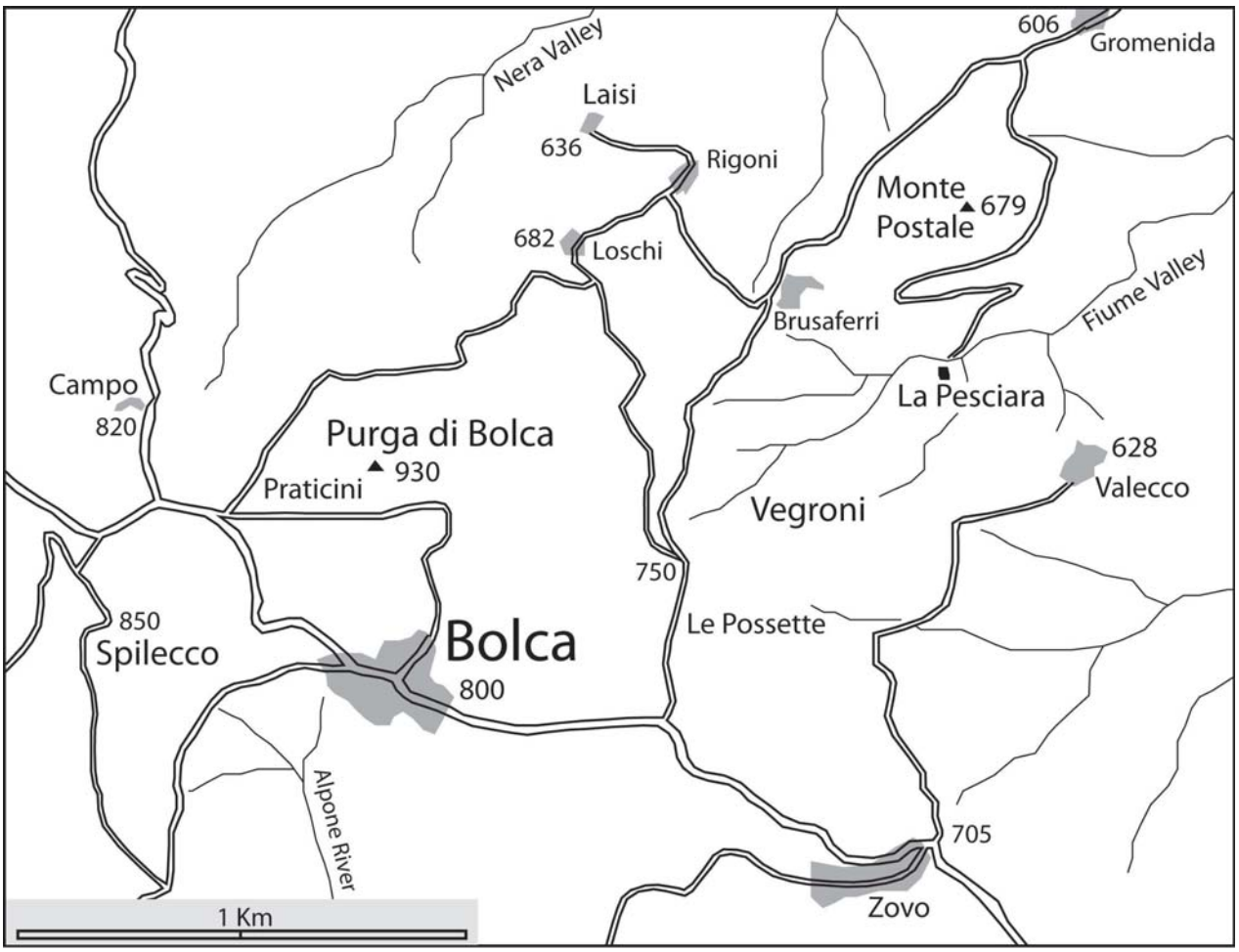

Fig. 1 - Location map of the main fossiliferous sites cropping out in the surroundings of Bolca (Verona).

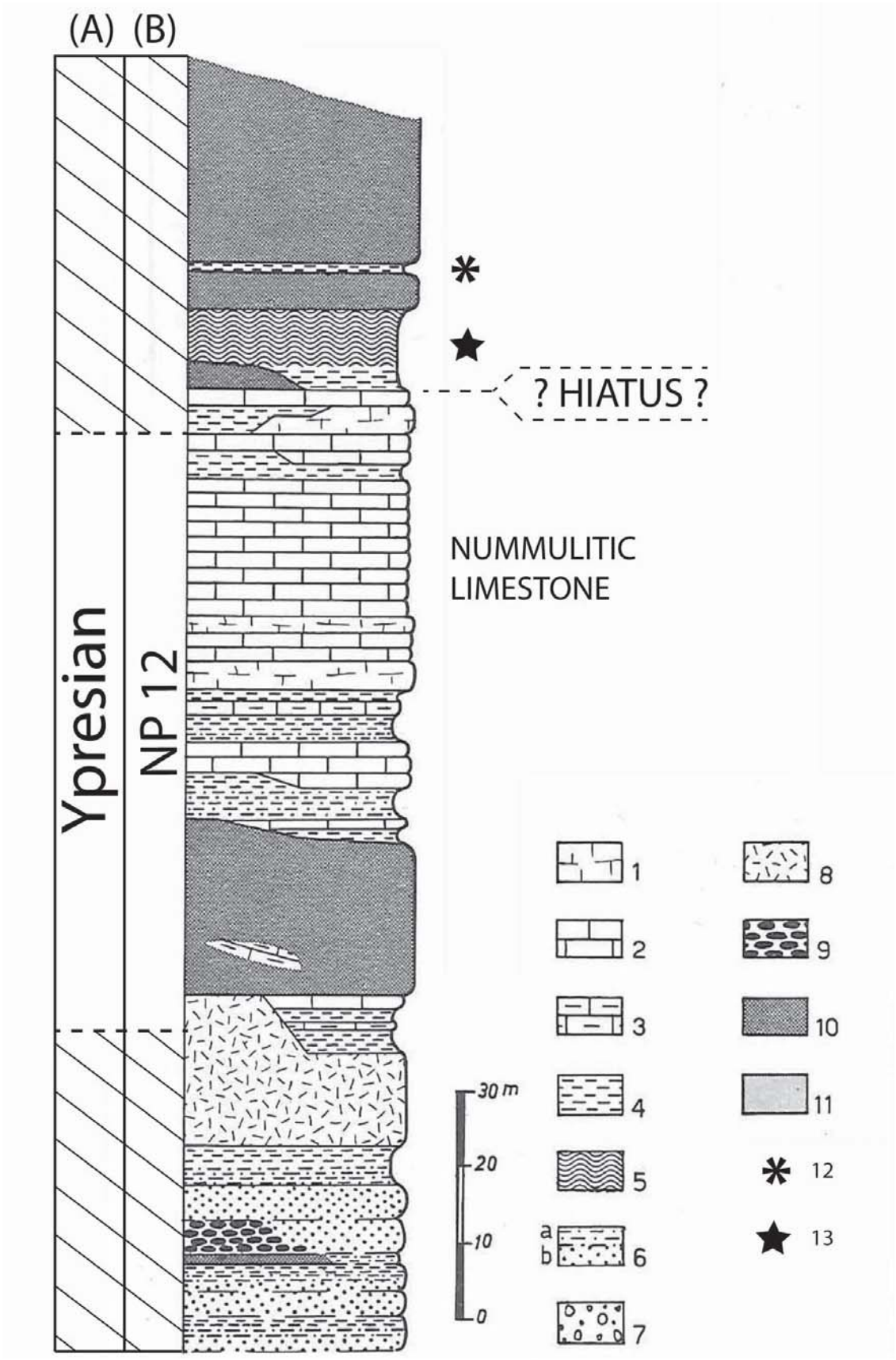

Fig. 2 - Stratigraphic log of the north-western slope of the Purga di Bolca (modified from Barbieri & Medizza, 1969). Legend: 1) Reefal limestones with algae; 2) Nummulitic limestones; 3) Marls and marly limestones with nummulites; 4) Clayey marls and volcanic clays; 5) Clays, silts and lignites; 6) Chaotic volcanoclastic rocks; 7) Chaotic, extra diatremic explosive breccias; 8) Chaotic hyaloclastites; 9) Basaltic pillow lavas; 10) Subaqueous basaltic lavas flows; 11) Sub-aerial basaltic lavas flows; 12) Vertebrate remains; 13) Plant remains. A) Chronostratigraphy; B) Calcareous Nannofossil Zonation of Martini (1971) based on data of Barbieri & Medizza (1969).

Later, Fabiani (1915), Malaroda (1954) and Barbieri & Medizza (1969) detailed the series exposed along the northern side of Purga di Bolca (Fig. 2). According to the most recent study, Ypresian (Lower Eocene) nummulitic limestones, firmly dated with calcareous nannofossils (Fig. 2), are overlaid by clays, silts and lignitic beds with vertebrates and mollusks, followed by tuffaceous layers with palms. The entire succession is interrupted and capped by volcanic rocks (Barbieri & Medizza, 1969; Fig. 2). We must underline, however, that according to Giuseppe Cerato (1860-1928) four distinct fossiliferous horizons existed: two with reptiles and two with plants (Fabiani, 1912; p. 212). The freshwater or brackish sediments of the sites near Bolca testify the ephemeral emersion of islands, probably linked with the intense volcanism which repeatedly occurred in the area during the Early and Middle Eocene (Barbieri & Medizza 1969; Antonelli et al., 1990). The age of the fossiliferous beds is quite debated: Fabiani (1915) referred them to the "Auversian" (=Bartonian), whereas Malaroda (1954) proposed a middle-late Lutetian age. Finally, Barbieri & Medizza (1969) ascribed these problematic beds to the "Cuisian". In the 19th century, various authors correlated the palm-bearing beds of Vegroni and Praticini with the Oligocene beds cropping out in various localities of the Vicenza Province (e.g., Massalongo, 1858a, b; Molon, 1867; Nicolis, 1884). The entire continental succession of Bolca is clearly in need of a modern stratigraphic revision.

The reptile fauna

Mostly from the lignitic beds of Purga di Bolca, several fossil reptiles have been found, namely crocodiles, freshwater turtles, and a snake (Lioy, 1865, 1896; De Zigno, 1889, 1890; Negri, 1892; Sacco 1895; Fabiani 1912, 1914, 1915; Bergonioux, 1954; Kotsakis, 1977, 1978, 1984). The bulk of the discoveries and most descriptions of those fossils dates back to the second half of the 19th century, when in the Bolca area the lignites were actively excavated by members of the Cerato family.

The only snake so far discovered here is an ophidian which De Zigno described for the first time in 1890, introducing the new species *Coluber ombonii*. This unique specimen, incomplete and scarcely preserved, was discovered in the "marls" associated to the lignite beds of the Purga and, at present, is housed in the Museo di Geologia e Paleontologia dell'Università di Padova.

The crocodilian fossil fauna from Bolca (Figs 3a-c), described for the first time by Lioy (1865) and Sacco (1895), consists of about ten specimens; some of them are almost complete and finely preserved. Lioy (1865) erected the new species "*Crocodilus*" *vicetinus* (sometimes misspelled as "*vicentinus*") for a more than two meters long individual. Years later, the holotype was figured for the first time by Sacco (1895) and then redescribed in detail by Fabiani (1912). This latter provided also data on the stratigraphic position of that fossil, reporting that it was found on the north-western side of Monte Purga, at about 850 m a.s.l., near Col della Battaglia. Unfortunately, the holotype of *C. vicetinus* was completely destroyed during the Second World War, but replicas are housed in the Museo di Geologia e Paleontologia dell'Università di Padova, in the Museo dei Fossili di Bolca and in the Museo Naturalistico Archeologico di Vicenza (Fig. 3c).

Sacco in 1895 described five other more or less complete specimens found in the lignites of Bolca. He ascribed three of them to *C. vicetinus* and one, lacking the head and the tail, to *Crocodylus* cf. *vicetinus*. For the fifth and largest individual, about two meters long, he established the new species *"Crocodilus" bolcensis*. The holotype of the species is currently housed in the Museo di Storia Naturale di Torino, while another specimen attributed to the same taxon is exposed in Padova.

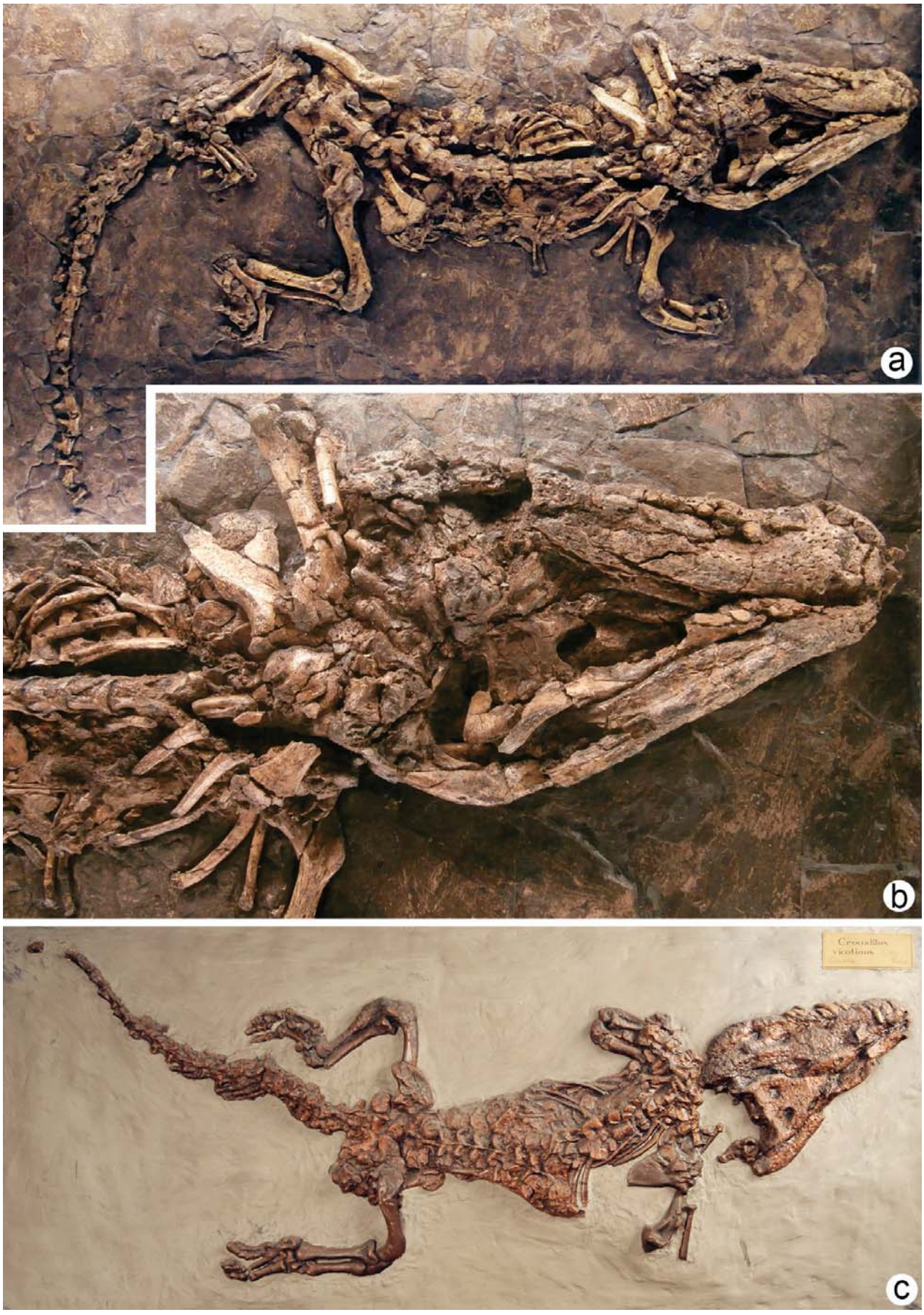

Fig. 3 - a) *Asiatosuchus* ?*depressifrons*. Lenght 135 cm. Complete skeleton in ventral view. MCSNV V.7097. b) Detail of the skull of the specimen. c) *Crocodylus vicetinus* Lioy, 1865. Replica of the holotype destroyed during the Second World War. MGP-PD 27568. Museo di Geologia e Paleontologia dell'Università di Padova

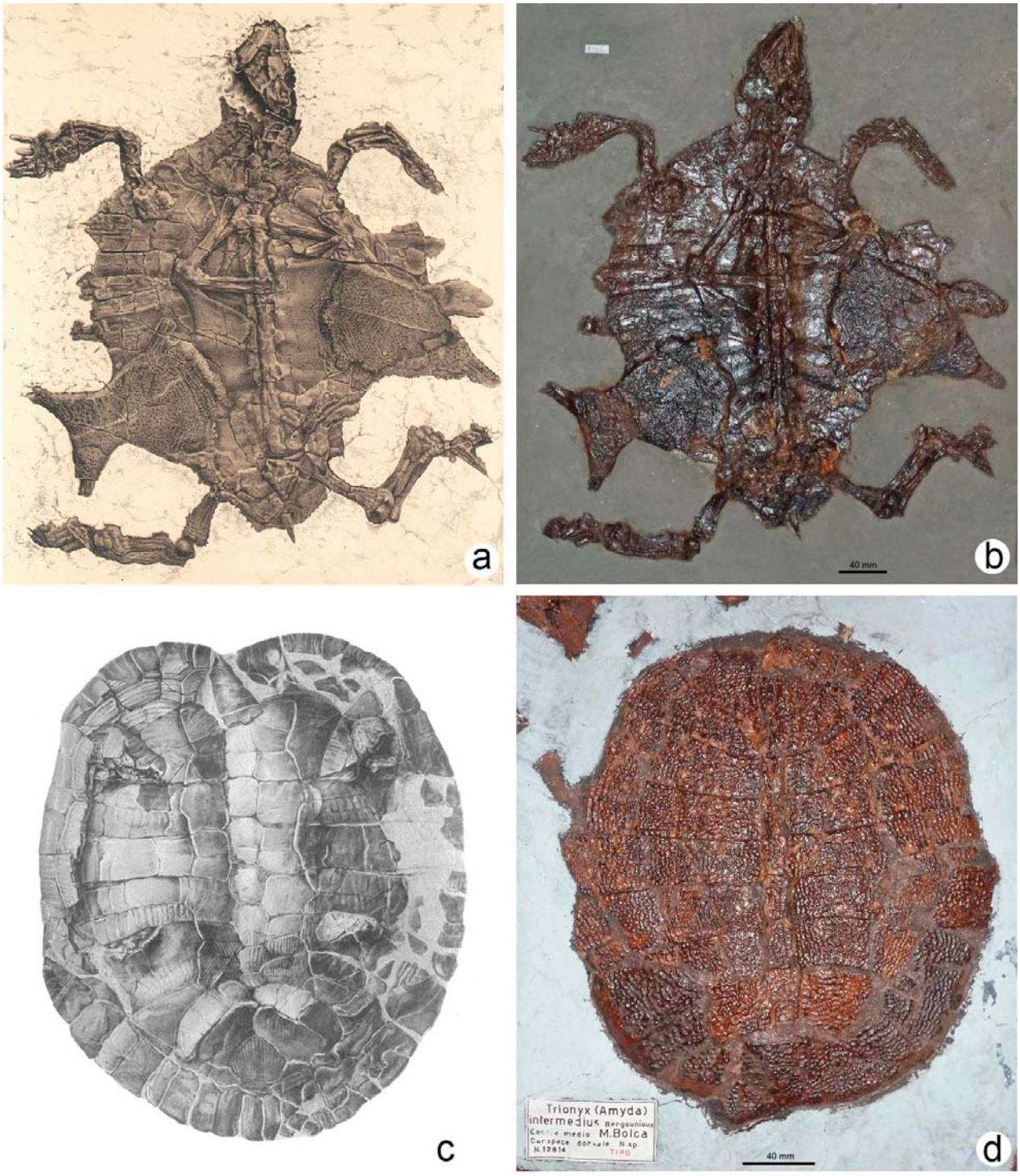

Fig. 4 - a) Holotype of *Trionyx gemmellaroi* Negri 1892 (from Negri, 1892; Plate I). b) The holotype of *Trionyx gemmellaroi* Negri 1892. MGP-PD 5157; c) *Neochelys capellinii* (De Zigno, 1889) (from De Zigno, 1889; Plate I); d) *Trionyx intermedius* Bergounioux 1954. Holotype. MGP-PD 12814. According to Kotsakis (1977), *Trionyx gemmellaroi* and *T. intermedius* are synonymous of *T. capellini* Negri 1892.

The last specimen recovered from the Monte Purga is a complete skeleton unearthed in 1946 and currently on exhibition at the Museo Civico di Storia Naturale di Verona (Figs 3a, b). In 1966 Berg (p. 65) gave a brief description of this individual, referring it to the genus *Asiatosuchus* on the basis of the long mandibular symphysis, but sometimes it is cited in literature as *Crocodylus vicetinus* (e.g., De Zanche & Mietto, 1977; Medizza, 1980; Viohl, 2008). Kotsakis et al. (2005) later ascribed this specimen to *A. ?depressifrons* (Figs 3a, b).

The fossil crocodiles from Bolca have been the subject of several revisions which led to the identification of no less than four different genera, namely *Asiatosuchus*, *Hassiacosucus* (= *Allognathosuchus), Pristichampsus* and *Diplocynodon* (Berg, 1966; Vasse, 1992; Rauhe & Rossmann, 1995; Rossmann; 1998, Kotsakis et al., 2004). This taxonomic richness reflects an evident morphological and possibly ecological diversification comparable to that of crocodiles faunas of others famous Eocene European *Lagerstätten*, such as Messel and Geiseltal.

The taxonomic status of Bolca material is still unclear and much debated (see for instance Del Favero, 1999; Delfino & Smith, 2008; Brochu, 2012). Further studies are needed in order to elucidate the taxonomy and the paleoecology of this exceptional crocodilian record.

The first chelonians were described by De Zigno (1889) and Negri (1892). De Zigno erected *Emys capellinii* for an almost complete carapace of a freshwater pleurodiran turtle (Fig. 4c), currently assigned to the genus *Neochelys* Bergounioux, 1954 (Kotsakis, 1978). In 1892, Negri described for the first time the rich fauna of trionychidae from Bolca, introducing three new species: *Trionyx gemmellaroi*, *T. capellinii,* and *T. affinis,* based on material housed in the Museo di Geologia e Paleontologia dell'Università di Padova (Fig. 4). Later Sacco (1894) published a study regarding five other specimens of *Trionyx* from the same locality, attributing them to a new variety of *T. capellinii*.

The rich chelonian fauna of Bolca (Fig. 4) was later revised by Bergounioux (1954) and, more recently, by Broin (1977) and Kotsakis (1978, 1986). The latter author made a systematic revision of the entire material, concluding that in Bolca there are only two species of turtles: *Neochelys capellinii* (De Zigno, 1889) and *Trionyx* (*Amyda*) *capellinii* Negri, 1892 (Fig. 4). Both *Neochelys* and *Trionyx* are abundant and widely recorded freshwater (or brackish) forms in the Paleogene of Europe (Kotsakis, 1986; Perez Garcia & Lapparent de Broin, 2013). In particular *Trionyx* is a softshell turtle, whose living relatives are carnivorous and inhabit tropical or subtropical swamps (Kotsakis, 1986).

The invertebrates

Omboni (1886) described a badly preserved coleopteran (*Dytiscus* or *Hydrophylus*) fossilized in a "shaly lignite" from Bolca, likely recovered in the Purga or nearby sites. According to Malaroda (1954) and Barbieri & Medizza (1969), ostracods ("*Cypris"*) are common in the reptile-bearing beds. The most common invertebrates of the "Purga series" are, however, freshwater and terrestrial mollusks reported from the plant-bearing beds (Fabiani, 1915). Malaroda (1954) listed the following taxa: *Helix damnata*, *Cyclotus obtusicosta*, *Melanopsis vicetina* and *Planorbis muzzolonicus*.

The flora

Massalongo (1858a, b; 1861) and De Visiani (1864) described several fossil plants from Vegroni and surrounding localities, most of them belonging to palms with flabellate leaves (e.g., *Latanites*) and pinnate leaves as *Hemiphoenicites* and *Geonomites* (Figs 5a, b). Fiore (1931) reported the occurrence of fungi (*Discomycetes*, *Pyrenomycetes*, and *Deuteromycetes*) on a specimen of *Latanites* likely recovered at Vegroni or surroundings and, one year later, described new species of *Latanites* based on specimens discovered at Vegroni and Praticini (Fiore, 1932). From Praticini, Fiore also reported the occurrence

Fig. 5 - a) *Geonomites saturnia* De Visiani, 1864. Vegroni, near Bolca. Holotype. MGP-PD 904V. b) *Latanites* sp. Purga di Bolca. Both specimens are housed in the "Palm Hall" of the Museo di Geologia e Paleontologia dell'Università di Padova.

of leaves of *Salix* sp. and *Populus* sp. and erected the new taxa *Castanea integra* and *Fagus silvatica* var. *praticinensis* (Fiore, 1936a, b). Fossil palms from Bolca are presently housed in several Italian and foreign museums (Fig. 5).

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Excursion guidebook CBEP 2014-EPPC 2014-EAVP 2014-Taphos 2014 Conferences
The Bolca *Fossil-Lagerstätten*:
A window into the Eocene World
(*editors* C.A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi & R. Zorzin)

10. The Spilecco site

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The Spilecco locality (Fig. 1) is mainly known for its contribution to the regional stratigraphy since Fabiani (1912) erected the "Spilecciano" stage to fill the gap between the Cretaceous Scaglia Rossa and the alleged Middle Eocene "Calcari nummulitici". For the most complete description of the "Spilecciano" in its type locality (the Spilecco hill) we refer to Barbieri & Medizza (1969) and to Medizza (1980). Based on calcareous nannofossil data of Barbieri & Medizza (1969), the succession ranges the NP 9

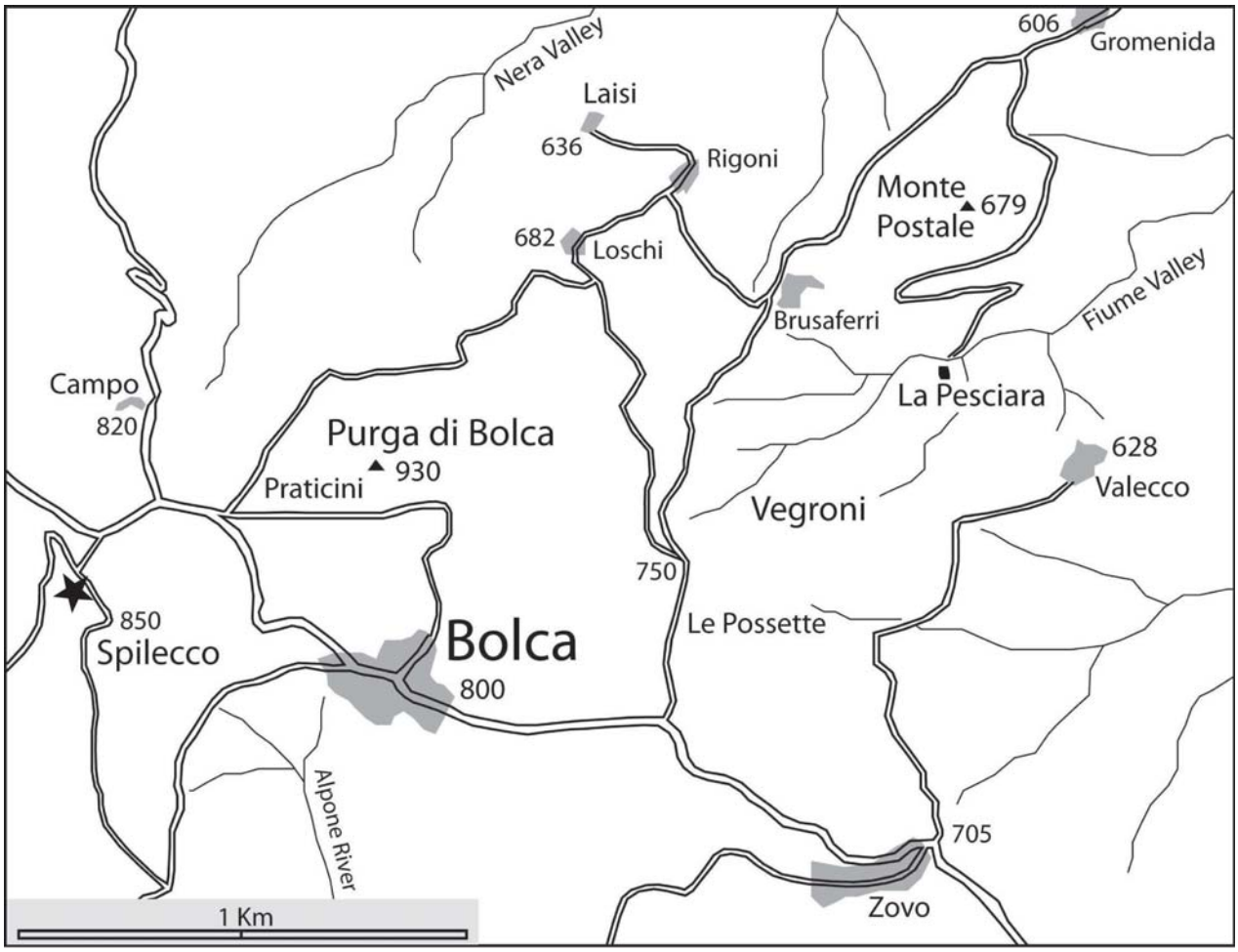

Fig. 1 - Sketch map indicating the position (star) of the Spilecco outcrops near Bolca (Verona).

(Thanetian)-NP 12 (Ypresian) Zones, lacking completely the NP 11 (Fig. 2). The Lower Paleocene is only represented within some burrows into the uppermost part of the Scaglia Rossa, filled in by sediments with Danian planktonic foraminifera (Barbieri & Medizza, 1969). The starting of shallow-water sedimentation in this area (and in the whole Lessini Shelf) is testified by the resedimented periplatform deposits with larger foraminifera,

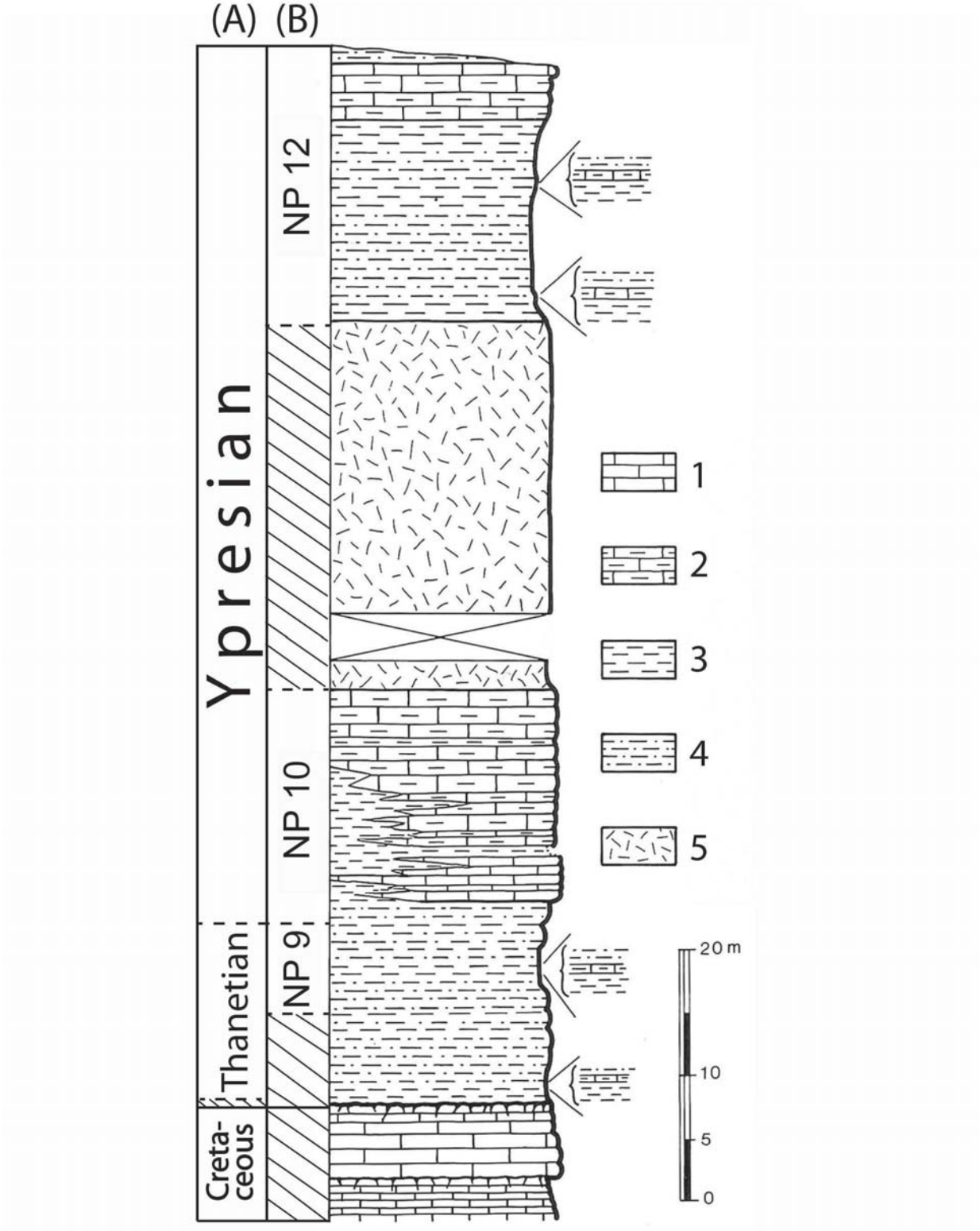

Fig. 2 - Reconstruction of the succession of Spilecco Hill (modified after Medizza, 1980). Based on previous data of Barbieri & Medizza (1969) Legend: 1) Limestones; 2) Clayey limestones and calcareous marls; 3) Clayey marls and volcanic clays; 4) Bedded volcaniclastic rocks; 5) Hyaloclastites. A) Chronostratigraphy; B) Calcareous Nannofossil Zonation of Martini (1971) based on data of Barbieri & Medizza (1969).

crinoids, brachiopods, and shark teeth, ascribed to the SBZ 7 (Trevisani & Papazzoni, 2003), NP 10, and P5 (Barbieri & Medizza, 1969), or lower Ypresian.

At present, only the uppermost part of the gray-green limestones with planktonic foraminifera and the characteristic reddish marly limestones with macrofossils and larger foraminifera still crop out. They approximately correspond to the NP 9-NP 10 portion of the stratigraphic column in Fig. 2.

The invertebrates

In the reddish marly limestones, the most abundant invertebrates are the larger foraminifera. They include *Nummulites bolcensis*, *N. spileccensis*, *N. oppenheimi*, *N. pernotus*, *Assilina custugensis*, *Discocyclina tenuis*, *Orbitoclypeus multiplicatus*, *O. munieri*, *O. schopeni*, *Asterocyclina taramellii*. *N. bolcensis* and *N. spileccensis* are endemic species, rarely recorded out of the type locality and needing a taxonomic revision (Trevisani & Papazzoni, 2003).

The crinoids are quite abundant in the reddish marly limestones. The most characteristic taxa are *Conocrinus suessi, Conocrinus thorenti* and *Holopus spileccense* (e.g., Massalongo, 1850; Fabiani, 1915; Manni, 2005). *H. spileccense* is a very rare species and it is only known from the "Spilecciano" rocks of Spilecco (Manni, 2005).

The echinoid remains are also common. Based on two spines, Dames (1878) erected the species *Cidaris spileccensis*, subsequently cited by Fabiani (1915).

The brachiopods are the most characteristic macrofossils from Spilecco and have been studied for the first time by Abramo Massalongo (1850), who described two species from the site: "*Terebratula" bolcensis* and "*T". polymorpha*. Massalongo figured the two species in his plate 19 of the never published "Compendium Faunae et Florae fossilis Bolcensis". These taxa have been later described in more detail and figured by Davidson (1870). According to Fabiani (1913) and Altichieri (1992), the brachiopods occurring at Spilecco are *Erymnaria bolcensis*, *E. polymorpha*, "*Terebratula*" *fumanensis*, and, dubitatively, *Terebratulina striata* (Figs 3a-g).

Braga (1968) studied the bryozoans from the reddish marly limestones of Spilecco. The assemblage is dominated by *Quadricellaria* sp., *Sertella beaniana*, *Entalophora* cf. *macrostoma*, *Filisparsa* sp., *Idmonea* sp., *Tervia* sp., and *Ceriopora* sp. Such bryofauna is the oldest so far recovered in the Paleogene of the Veneto region and shares significant affinities with Upper Cretaceous-Paleocene bryofaunas of the Northern basins (Braga, 1968). Based on larger foraminifera and byrozoan content, the author hypothesized a depositional depth of one hundred meters for the "red marls" of Spilecco.

Massalongo (1850) and Fabiani (1915) listed the following mollusks from Spilecco: *Terebellum*, *Cypraea*, *Helix*, *Crassatella*, and the nautiloid *Aturia ziczac*. At Spilecco also solitary corals occur, ascribed by Massalongo (1850) to "*Turbinolia"*.

The vertebrates

In the reddish marly limestones from Spilecco the shark teeth are quite common (Fig 3h-l). They were reported since the 19th century (e.g., Massalongo, 1850; Bassani, 1876; D'Erasmo, 1922) and the most updated taxonomical list can be found in Roccaforte et al. (1994): *Ginglymostoma* cf. *serra*, *Carcharias hopei*, *C. macrota*, *Isurus* cf. *mantelli*, *Lamna obliqua*, *Mustellus spileccensis*, *Notidanus serratissimus.*

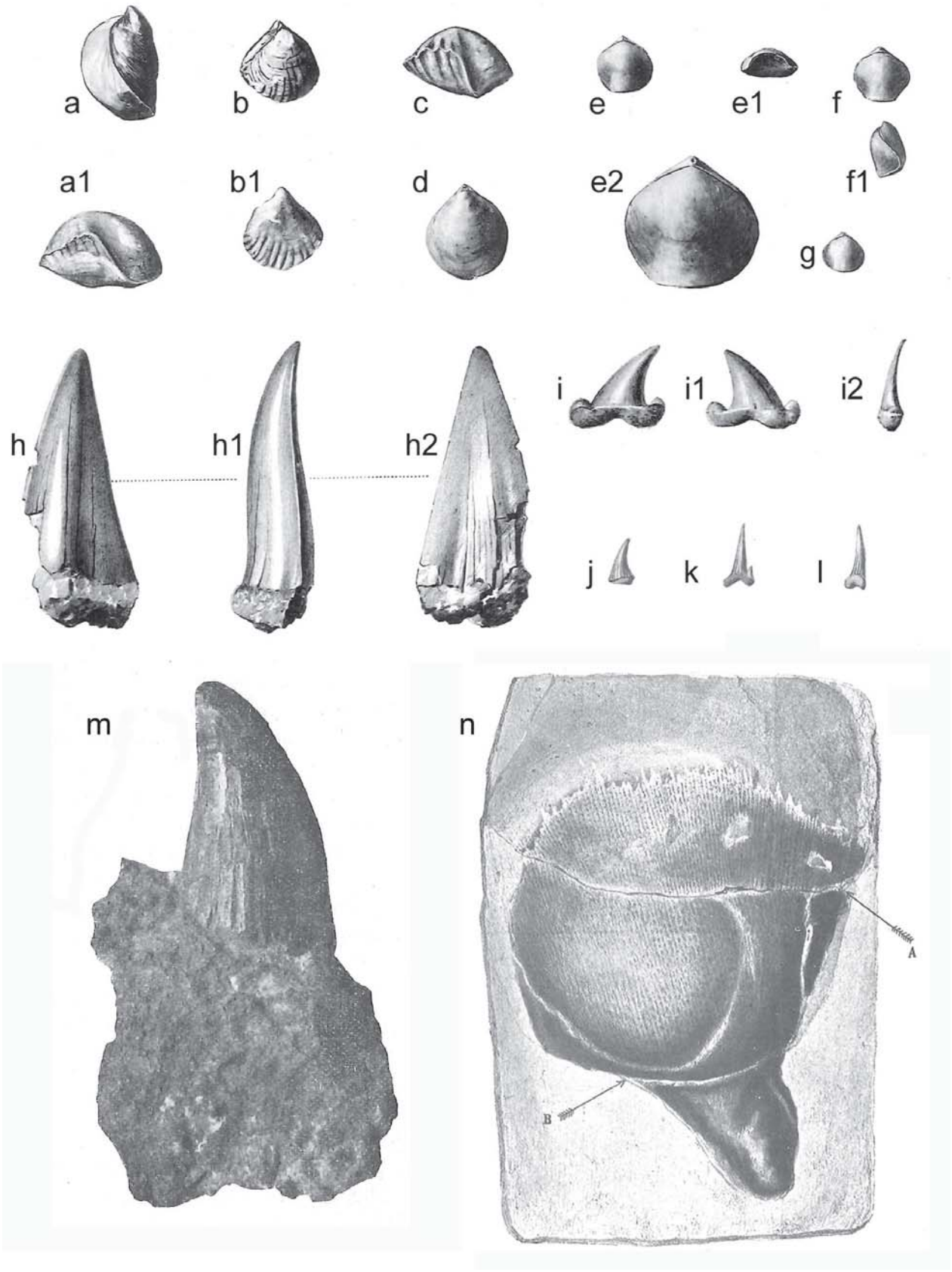

Fig. 3 - Some macrofossils from the "Spilecciano" of Spilecco. Brachiopods: a-d) *Erymnaria polymorpha* (Massalongo, 1850); e-g) *Erymnaria bolcensis* (Massalongo, 1850). Shark and reptile teeth: h) *Isurus* cf. *mantelli* (Agassiz, 1833-1844); i) *Lamna obliqua* (Agassiz, 1833-1844); j-l) *Carcharias macrota* (Agassiz, 1833-1844). m) The supposed mosasaurian tooth from Spilecco. Approximate height of the specimen ca. 4 cm. Green algae: n) *Avrainvilleopsis cyathiformis* (Massalongo 1855-1856) Forti, 1926. Approximate height of the specimen ca. 13 cm. [All the figures are excerpts from original illustrations of Nicolis (1907), Fabiani (1913), D'Erasmo (1922) and Forti (1926)].

From Spilecco an alleged crocodilian tooth is reported by Medizza (1980) and Kotsakis et al. (2004). This specimen (Fig. 3m) has been originally referred to a mosasaur (Nicolis, 1907 p. 36-37), but the early Paleogene age of the Spilecco succession led later authors to discard the mosasaurian nature of the fossil. Such controversy is still unsolved, waiting for a careful taxonomic and micropaleontological investigation of the fossil.

The flora

Massalongo (1855-1856) described the occurrence of several "algae" at Spilecco, most of them controversial and more likely referable to ichnofossils, such as *Halimedopsis tuna* and *Spartophycos funalis* (Massalongo, 1859; Forti, 1926; Fiore, 1936). Forti (1926) revised *Cylindrites cyathiformis* Massalongo, erecting the new genus *Avrainvilleopsis* (Fig. 3n), which is compared to the recent udoteacean green alga *Avrainvillea*.

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