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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)

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

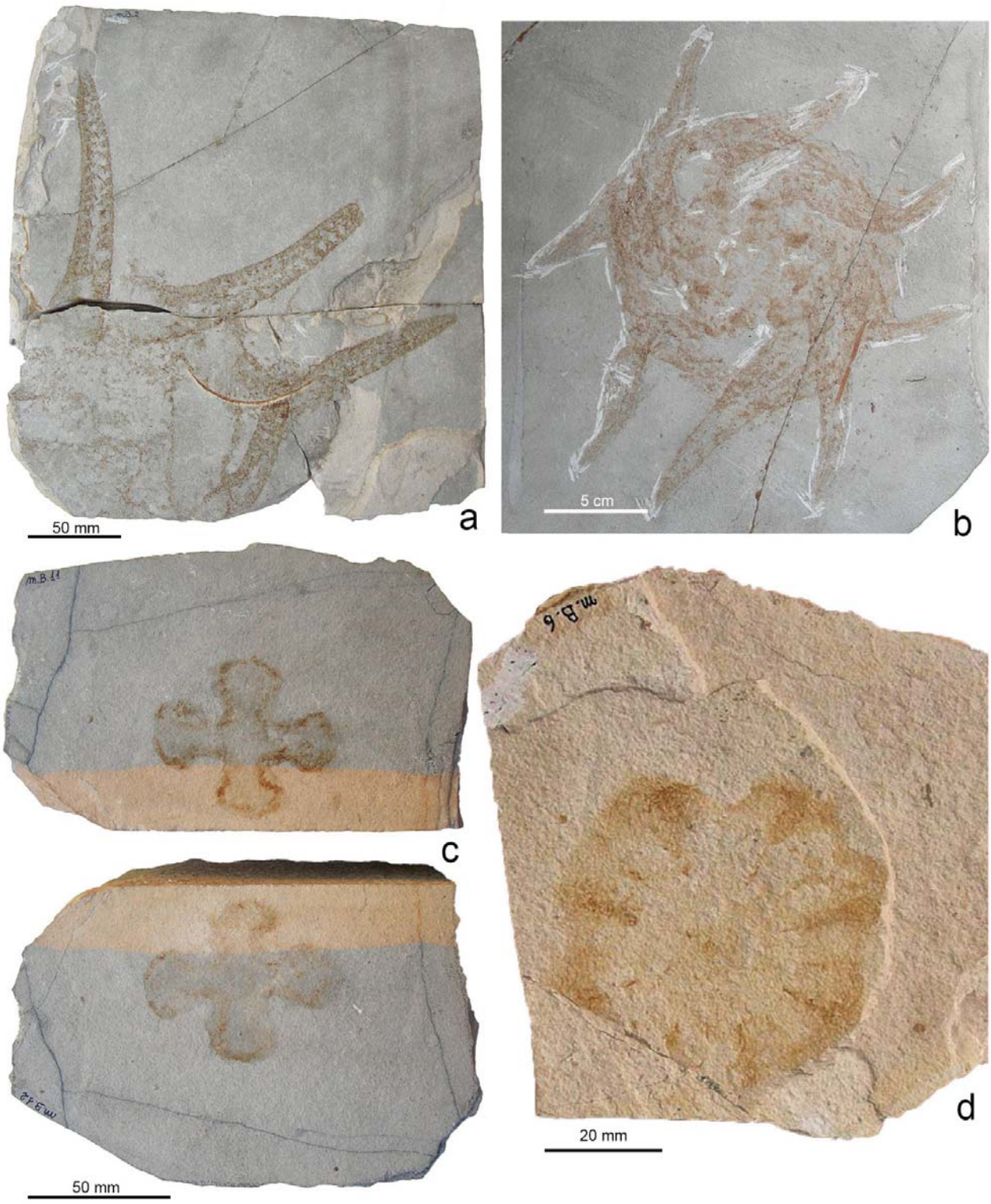

Fig. 1 - Medusae. a) *Simplicibrachia bolcensis* Broglio Loriga & Sala Manservigi 1973. Holotype. MCSNV m.B.2. b) *Simplicibrachia bolcensis* Broglio Loriga & Sala Manservigi 1973. Paratype. MCSNV m.B.1. c) Undetermined scyphomedusa. MCSNV m.B.11-12. d) Possible ephyra of scyphomedusa (aff. *Chrysaora*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

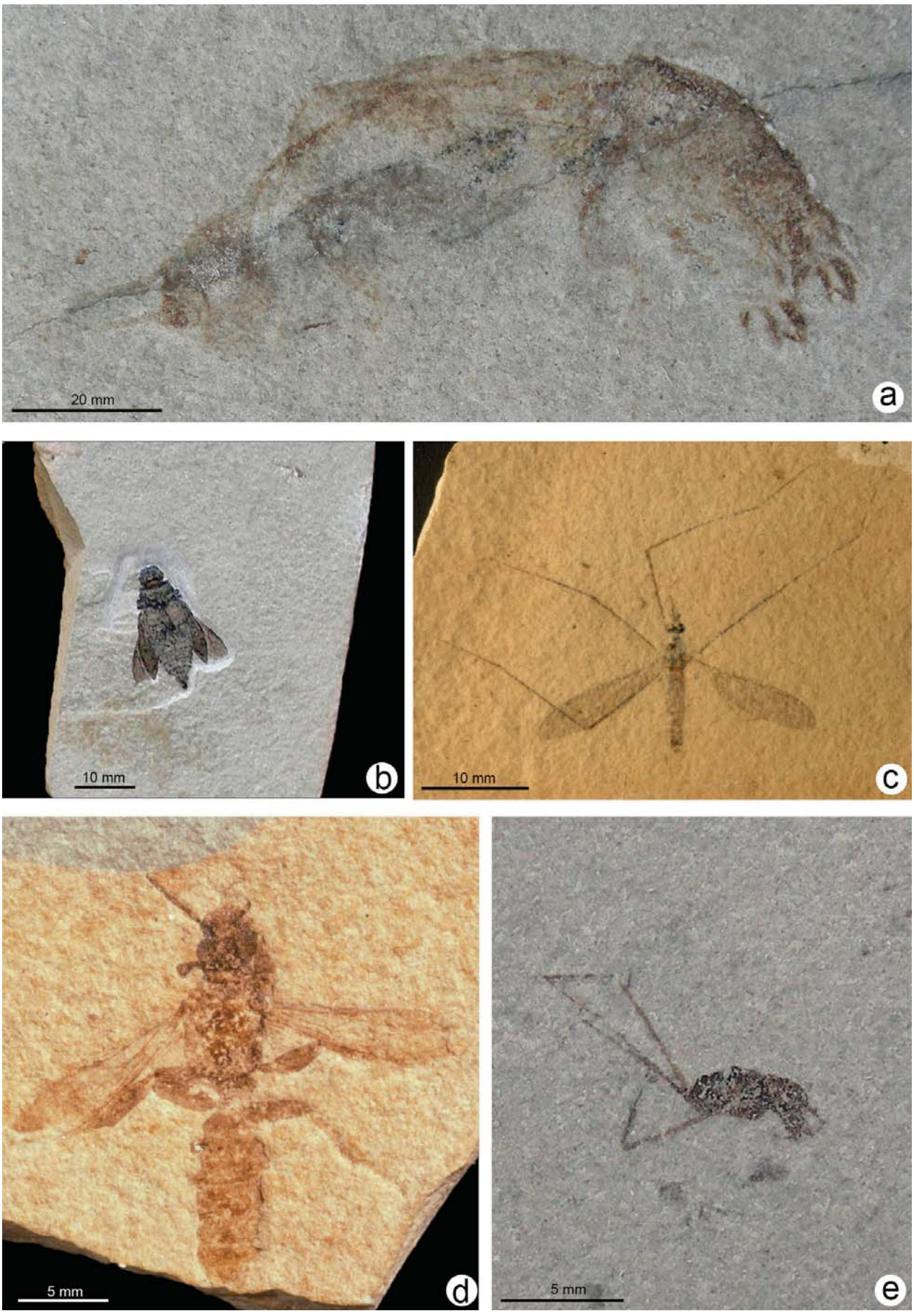

Fig. 2 - Insects. a) *Gryllotalpa tridactylina* Secretan 1975a. Holotype. MCSNV 24517. b) Coleopter MCSNV i.B.20. c) Mosquito (Diptera). MCSNV i.B.8. d) Hymenopteran MCSNV i.c.2NS. e) *Halobates ruffoi* Andersen et al. 1994. MCSNV I.G. 24527.

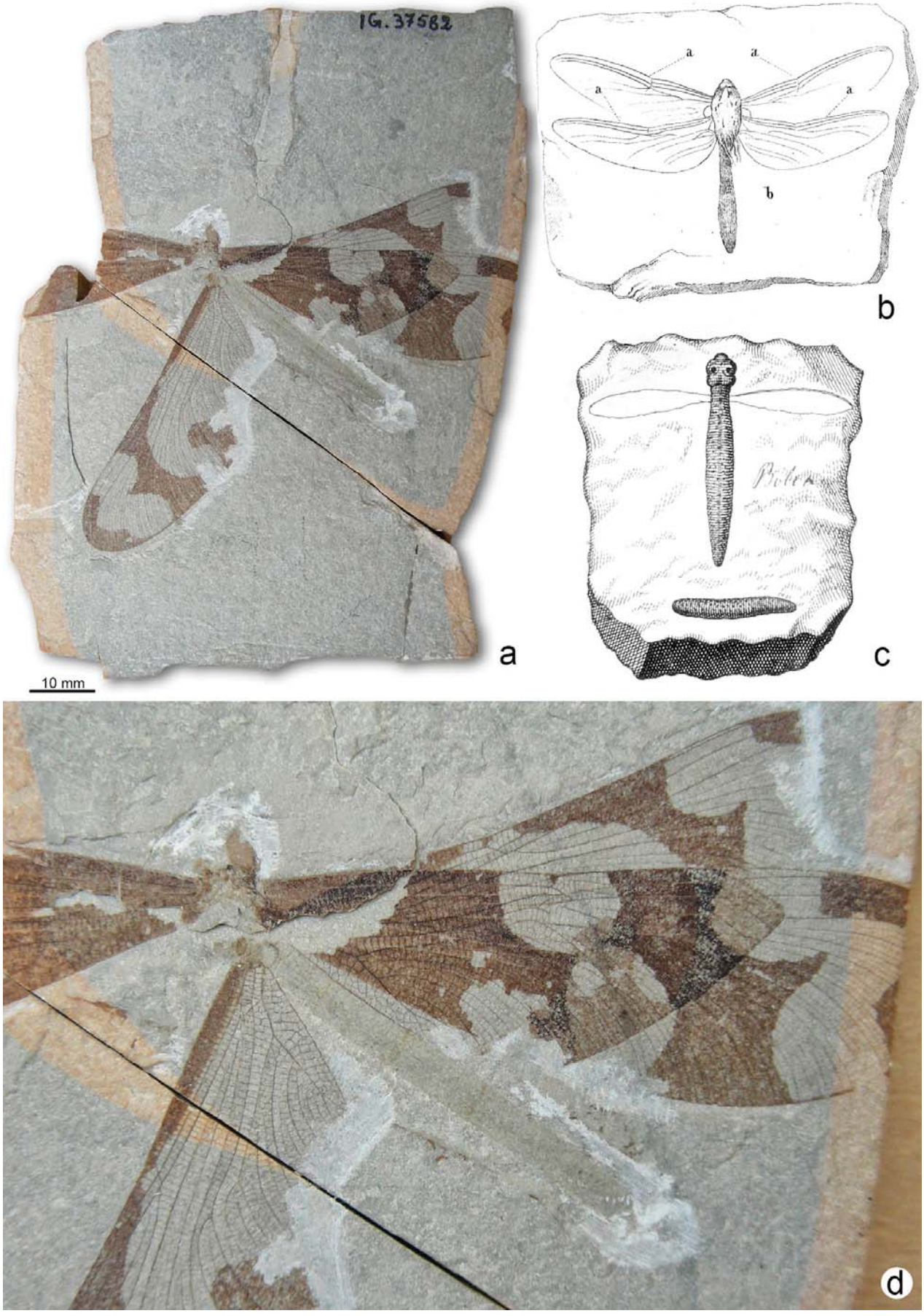

Fig. 3 - Insects. a) The damselfly *Bolcathore colorata* Gentilini 2002. Holotype. MCSNV I.G. 37582. b) *Cordulia*? *scheuchzeri* Massalongo 1856 [excerpt from Massalongo (1856, Plate II, Fig. 7)]. c)The dragonfly figured by Scheuchzer (1709), probably a Tipulomorpha. d) Detail of the holotype of *Bolcathore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

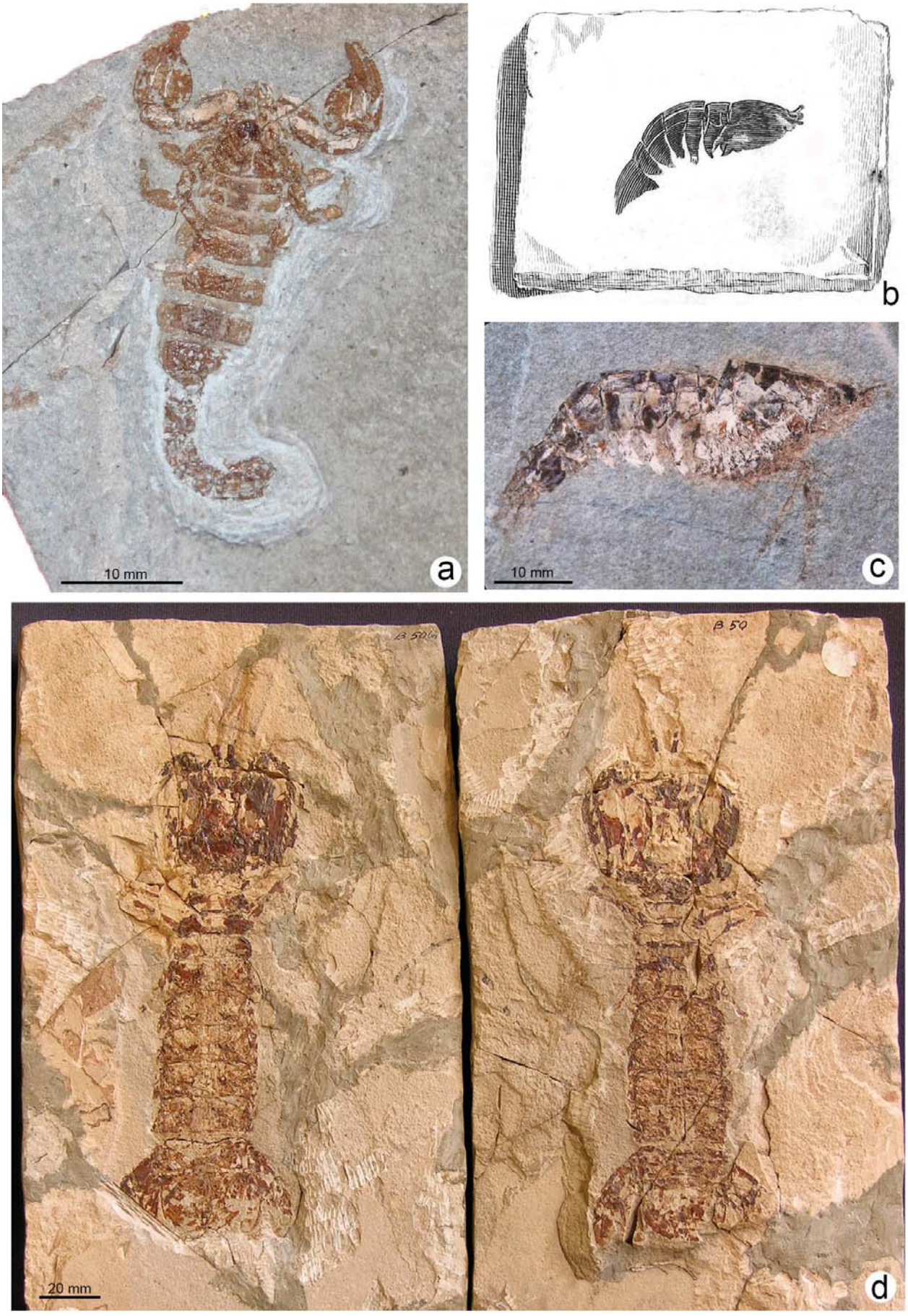

Fig. 4 - Arachnids and crustaceans. a) Scorpion. Cerato collection. b) The first illustration of a crustacean from Bolca, possibly a penaeid [excerpt from Faujas de Saint-Fond (1804, Plate I, Fig. 5)]. c) *Penaeus* sp. Cerato collection. d) *Lysiosquilla antiqua* (Münster 1842). MCSNV B50 and 50bis.

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

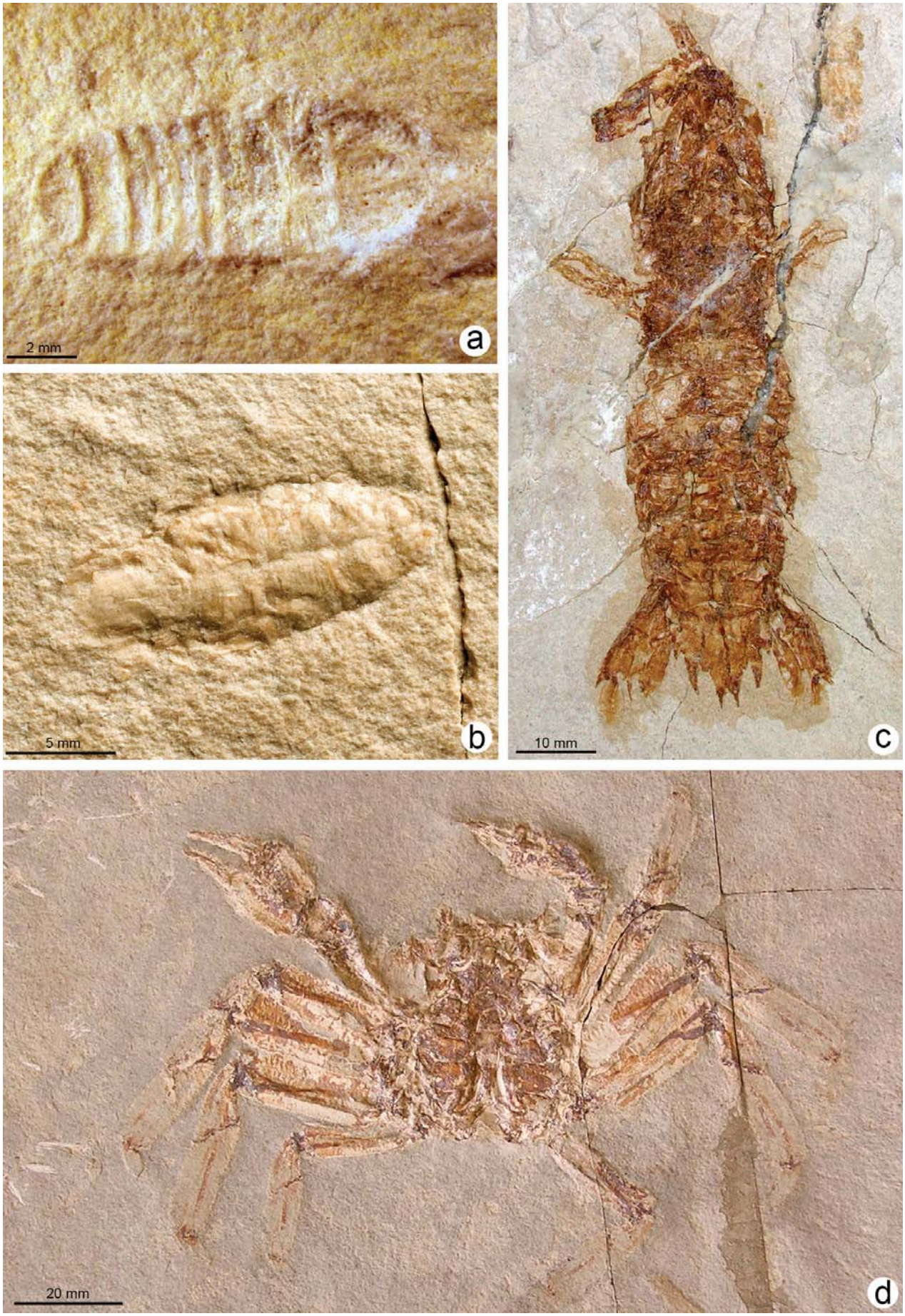

Fig. 6 - Crustaceans. a) *Heterosphaeroma veronensis* Secretan 1975a. Holotype. MCSNV Cr.14. b) *Palaega* sp. MGP-PD 31433. c) *Pseudosquilla lessinea* De Angeli & Garassino 2008. Holotype. MCSNV I.G. VR 67497. d) *Archaeocypoda veronensis* Secretan 1975a. MCSNV n. 97.

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).

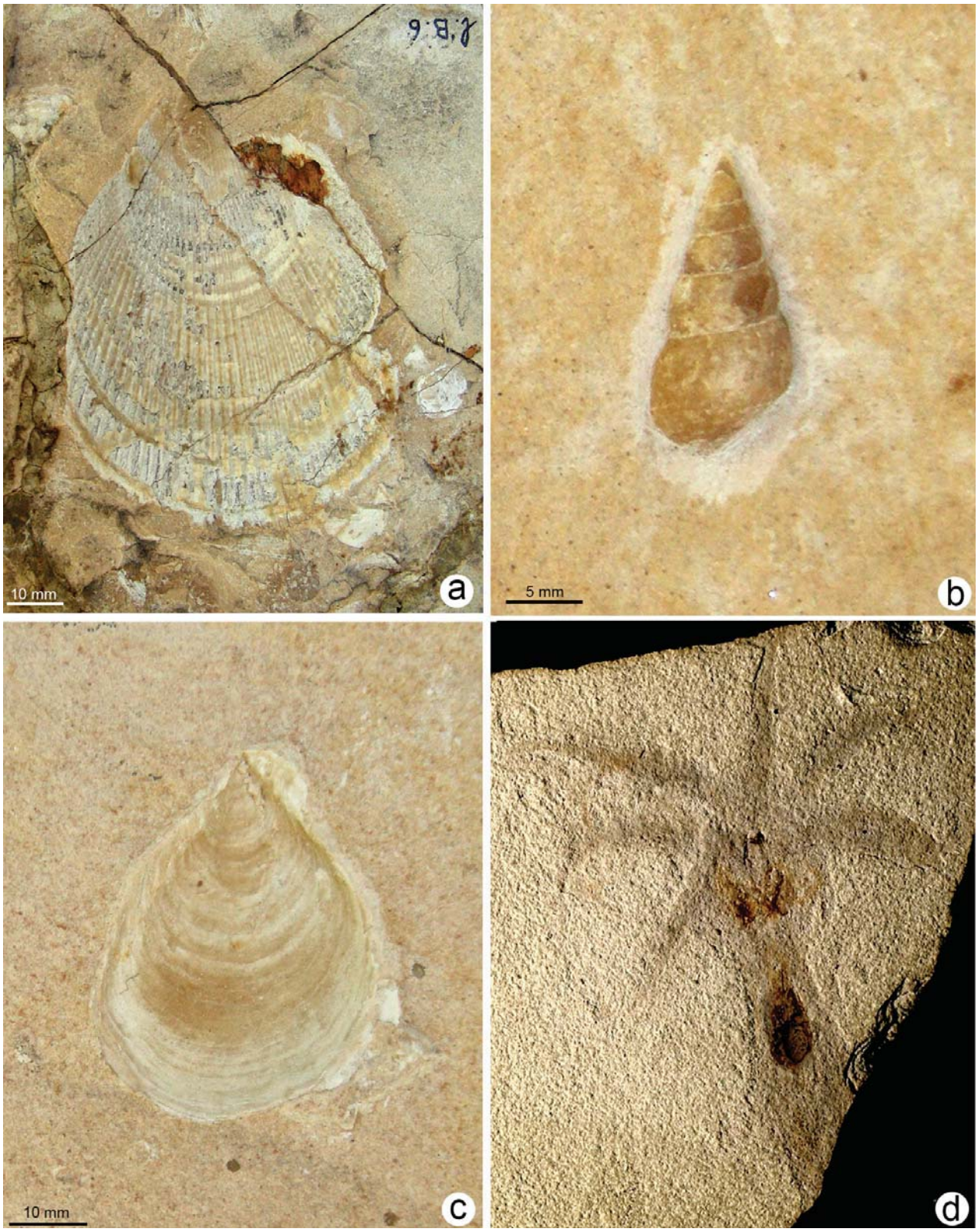

Fig. 7 - Mollusks. a) *Lima* (*Ctenoides*) cf. *papillifera* Bayan 1870. Imprint. MCSNV l.B.6. b) *Dialopsis incompleta* (Deshayes 1861). MCSNV l.B.9. c) Mytilidae. MCSNV 145139. d) Teuthoid. MGP-PD 31434. Maximum length of the specimen about 10 cm.

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*.

Acknowledgements

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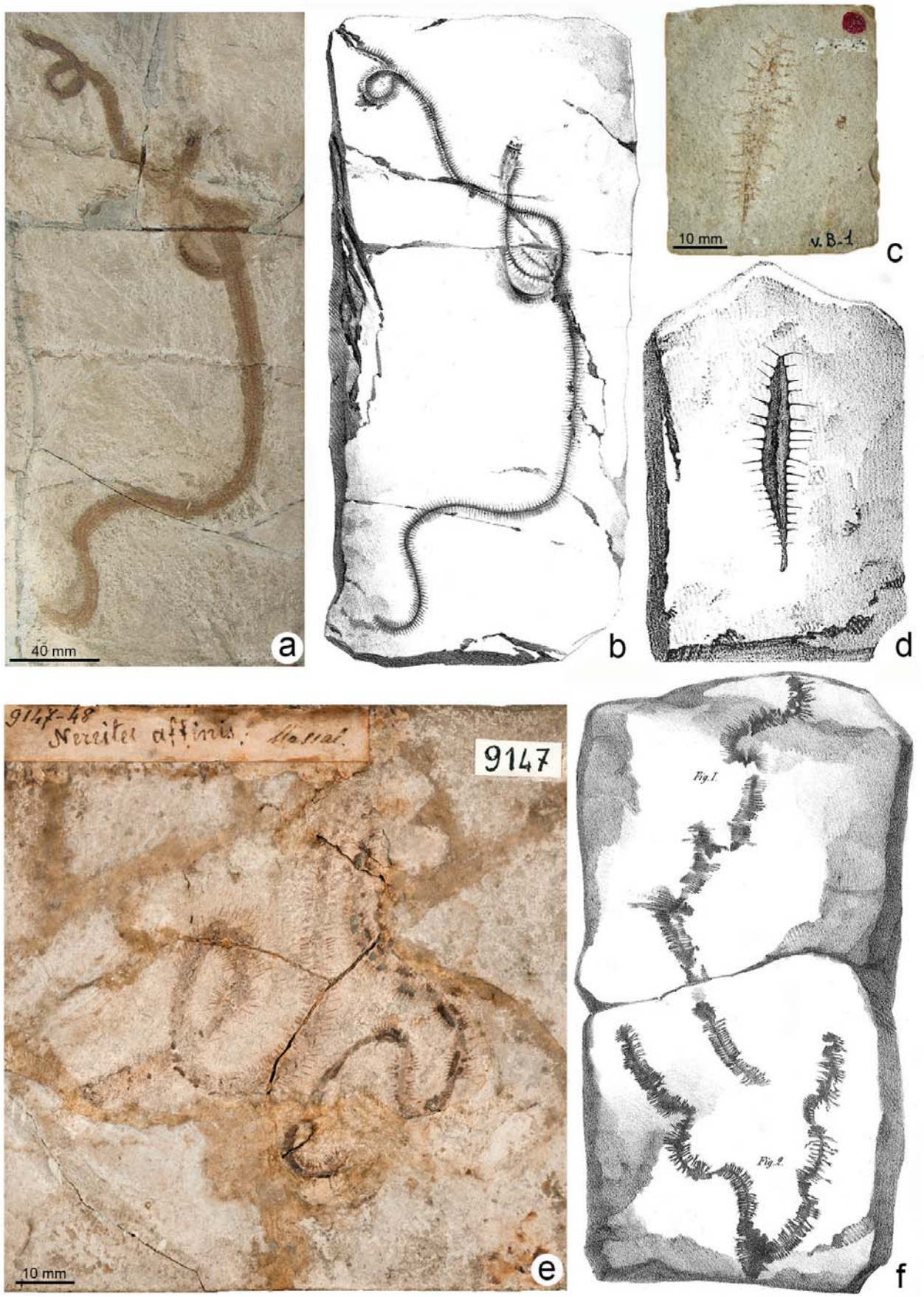

Fig. 8 - Polychaete worms. a) *Eunicites gazolae* (Massalongo 1855). Holotype. MCSNV v.B.5. b) The holotype of *Eunicites gazolae* [excerpt from Massalongo (1855, Plate I)]. c) *Siphonostomites hesionoides* (Massalongo 1855) Holotype. MCSNV v.B.1. d) The holotype of *Siphonostomites hesionoides* [excerpt 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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