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Article

Eocene decapod faunas from the Konservat-Lagerstätten laminites of "Pesciara" (Bolca, Verona) and Monte Postale (Altissimo, Vicenza) in northeast Italy: a review and update

Giovanni Pasini, Alessandro Garassino, Antonio De Angeli, Matúš Hyžný, Luca Giusberti, and Roberto Zorzin

With 17 figures and 1 table

Abstract: An updated systematic review of the Eocene decapod crustacean species from the laminites of the historical Konservat-Lagerstätten of "Pesciara" (Bolca, Verona) and Monte Postale (Altissimo, Vicenza) in northeast Italy, originally reported by Secrétan (1975), is presented. In addition, species recorded by subsequent authors are also discussed and their taxonomic assignment updated, resulting in a compilation, as complete as possible, of taxa known to date from both localities. Finally, several newly collected specimens are evaluated taxonomically and added to the list. Our review suggests seven taxa to be valid, namely *Penaeus bolcensis* Secrétan, 1975, *Justitia desmaresti* (Secrétan, 1975), *Scyllarides bolcensis* De Angeli & Garassino, 2008, *Enoplonotus armatus* A. Milne-Edwards, 1860, *Archaeocypoda veronensis* Secrétan, 1975, *Lophopanopeus bolcensis* (Secrétan, 1975) nov. comb., and *Eotrachynotocarcinus airaghii* Beschin, Busulini, De Angeli & Tessier, 2007. Our re-evaluation of the material of *Protaxius eocenicus* Secrétan, 1975 and *Protaxius* sp. has led to the erection of a new genus *Bolcacalliax*. One form is left in open nomenclature, *Portunus* sp., two forms, *Eriphia* sp. and *Macropipus ovalipes* Secrétan, 1975 are considered as problematic taxa, and a single indeterminate specimen constitutes the first record of a representative of the superfamily Majoidea Samouelle, 1819. In addition, *Lophoranina maxima* Beschin, Busulini, De Angeli & Tessier, 2004, previously recorded from the Lutetian, is now reported from the late Ypresian, extending back its stratigraphic range. Finally, the systematic position of ?*Parsacus cristatus* (Förster, 1984), still unresolved, is briefly discussed. Based on our update of the taxonomy, some preliminary remarks on the taphonomy of the entire crustacean assemblage and palaeoenvironment of "Pesciara" and Monte Postale laminites are provided.

Key words: Crustacea, Decapoda, early Eocene, late Ypresian, taphonomy.

1. Introduction

The Eocene Lagerstätten of Bolca in northeast Italy, known since the 16th century, are famous worldwide for their extraordinarily well-preserved and highly diverse fish fauna (> 200 species), documenting the rise of marine teleost groups that predominate in modern faunas, such as acanthomorphs, and representing an early "modern" coral reef assemblage (Carnevale et al. 2014; Marramà et al. 2016; Friedman & Carnevale 2018). During the last four decades, extensive taxonomic studies have explored the diversity of the main teleost lineages from Bolca and recently some broader overviews of fish faunas have been published (e.g., Bannikov 2014; Carnevale et al. 2014; Marramà et al. 2018). The fish have been subject of studies for centuries, overshadowing the so-called "minor fauna" (Sorbini 1980; Sorbini 1999) that mostly comprises terrestrial and marine arthropods, jellyfishes, annelids, molluscs, and lophophorates

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(Omboni 1886; Alessandrello 1990; Mellini & Quaggiotto 1999; Trevisani et al. 2005; Trevisani & Ragazzi 2013; Giusberti et al. 2014; Friedman & Carnevale 2018). Crustaceans, although rather rare, are undoubtedly one of the more conspicuous components of the "minor fauna" at Bolca; however, they have been mostly neglected by scholars for over two centuries. The main purpose of the present study is to update and critically revise the systematics of the Eocene decapod crustacean species of Bolca in order to evaluate the single comprehensive study of this group by Secrétan (1975) based upon the current concepts.

2. Historical background

2.1. Earliest records of crustaceans from Bolca

The first report on the generic presence of fossil "crabs" in the laminites of Bolca dates back to the second half of the 17th century. Don Paolo Silvio Boccone (1697) noted, through the Venetian citizen Cesare Cordis: "*In una Montagna tra'l Territorio di Verona e Vicenza, nella villa di Bolca, poco lontano dal luogo, detto Saline* (oggi San Mauro di Saline) *un miglio lontano dà Vestena nova* (oggi Vestenanova)*, si trovano Pietre bianche. . . .a Lastre una sopra l'altra . . . . Trà esse, si può dire, che in ogn'una si trovi stampato ed indurito dentro parte di sotto, e parte di sopra qualche Pesce, . . . granchi, e simili,. . . "* (Translated: In a hill between Verona and Vicenza, in Bolca village, not very far from the locality called Saline [today San Mauro di Saline], some kilometres from Vestena nova (today Vestenanova), there are some white stones . . . in overlapping slabs . . . Among these, it is possible to find several flattened and hardened fishes . . . crabs, and such alikes). This documents for the first time the correct source of the fossil fishes in Verona area, which had been mentioned briefly ever since the 16th century (for a full documentation, reference is made to Guerra 2014: 101, 123).

Faujas de Saint-Fond (1804: pl. 1, fig. 5) was the first to illustrate a decapod crustacean from Bolca (Fig. 1A). The specimen was probably one of the "*quatre empreintes de petits crabes*" (four imprints of small crabs) donated in 1803 by the Conte Gazola of Verona to the Muséum national d'Histoire naturelle of Paris (Brignon 2019: 30, 64, Annexe 1, Document 17). This historical specimen has not been traced in the collections of the Paris Museum and is probably lost (S. Charbonnier pers. comm. 2018).

2.2. The first carcinological studies

In a rather informal manner, Desmarest (1817, 1822) recorded several decapod crustaceans (palinurids) from Bolca, assigning these to *Palinurus* Weber, 1795. Later, Catullo in a private letter (dated 1854) to Professor Naumann of Leipzig, also "mentioned and briefly described four palinurids from Bolca" (Giusberti et al. 2015: 111). The first formal description of a crustacean from Bolca was that by Münster (1842), who erected the species "*Squilla*" *antiqua* (= *Lysiosquilla antiqua*), the holotype of which is probably lost (Secrétan 1975; De Angeli & Beschin 2006). In the mid-19th century, the palaeobotanist Abramo Massalongo (1824–1860) developed an interest in the "minor fauna" of Bolca and in a paper devoted to annelids (Massalongo 1855) he listed 19 crustacean taxa, including a palinurid that he referred to as "*Palinurus Desmarestii* Zigno", a name previouly coined, but never published, by Achille De Zigno for a specimen of his private collection (Garassino & Novati 2001; Giusberti et al. 2015). Moreover, another decapod crustacean simply listed as "*Udora* ?*Faujassii*" (Massalongo 1855: 33), presently housed in the collections of the Museo di Geologia e Paleontologia dell'Università di Padova, was illustrated in the unpublished *Compendium* (see *Penaeus bolcensis*, listed below).

Subsequently, A. Milne-Edwards (1860: 247, pl. 7, figs. 1, 1a) reported and figured a single specimen, possibly part of Massalongo's Collection, from "Monte Bolca", ascribed to *Enoplonotus armatus*. This was the first decapod species to be formally named (see below).

2.3. Massalongo's "Compendium Faunae et Florae Fossilis Bolcensis"

In a paper on annelids from Bolca Massalongo (1855: 30) mentioned his intention to publish a comprehensive study on crustaceans and other fossils from Bolca, entitled "*Compendium Faunae et Florae Fossilis Bolcensis*". Such a monograph never appeared, but twenty plates were printed, albeit never published (De Visiani 1861; Giusberti et al. 2015). The sole surviving copy of these unpublished plates, with the year "1854" handwritten and the title, is now kept

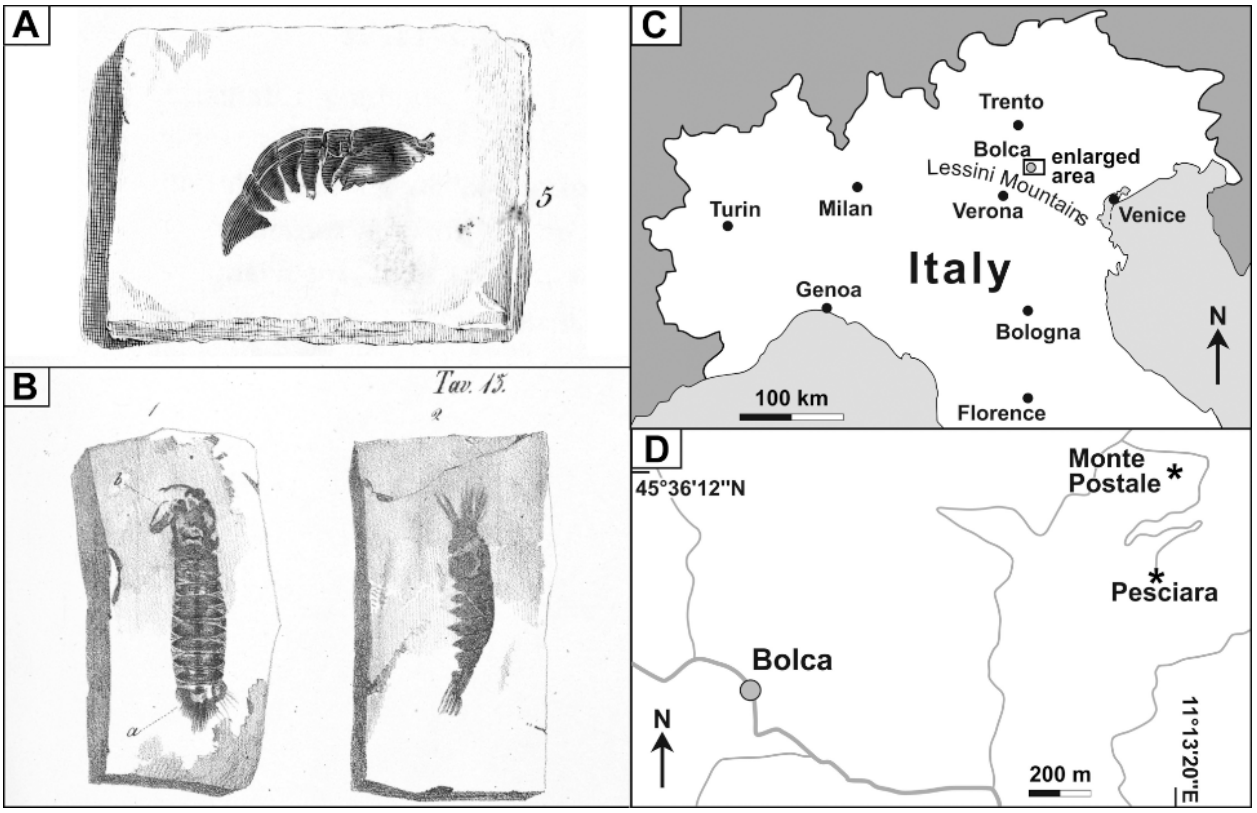

Fig. 1. A – The first illustration of a decapod crustacean from Bolca, as figured by Faujas de Saint-Fond (1804: pl. 1, fig. 5) and subsequently ascribed to "*Udora*? *faujassii*" by Massalongo (1855). **B** – Excerpt from the unpublished plate 15 of the "*Compendium Faunae et Florae Fossilis Bolcensis*" of A. Massalongo illustrating a mantis shrimp ("*Squilla deperdita*") and a penaeid shrimp ("*Udora*? *faujassii*") from Bolca (see Massalongo 1855: 33). **C, D** – Map of the fossiliferous localities of "Pesciara" and Monte Postale in the surroundings of the village of Bolca (Verona, northeast Italy). From Vescogni et al. (2016).

in the Biblioteca dell'Orto Botanico dell'Università di Padova (Giusberti et al. 2015). This has been re-examined for the purposes of the present work. Plates 12–18 are devoted to crustaceans and illustrate several penaeids, brachyurans, and stomatopods from Bolca (Fig. 1B), whereas plate 7 illustrates "lumbricarians" and an isopod. Several crustacean names listed in Massalongo (1855: 32, 33), amongst them seven new undescribed taxa and other taxa left in open nomenclature, are specifically referred to plates and figures of the planned "*Compendium*". Plate 12, for instance, illustrates the spiny lobster *Palinurus Desmarestii* (= *Justitia desmaresti*; see Giusberti et al. 2015: fig. 1.A), which has long confounded nomenclatural history (only recently disentangled by Garassino & Novati (2001) and Giusberti et al. (2015). Handwritten notes on the plates of Massalongo's *Compendium* document that several illustrated specimens came from the private collections of De Zigno and Massalongo, and some of them were identified during research for the present paper in the collections of the Museo di Geologia e Paleontologia dell'Università di Padova and Museo di Storia Naturale di Verona. Some of Massalongo's plates are included herein, in association with the original specimen, as identified.

2.4. The last two centuries

More than a century after the list of crustaceans published by Massalongo (1855), Secrétan (1975) carried out the first and last extensive study of decapod crustaceans from Bolca, based on the specimens housed in the collections of the Museo di Storia Naturale di Verona, the Museo di Geologia e Paleon-

tologia dell'Università di Padova, the Muséum national d'Histoire naturelle of Paris, and the Museo di Storia Naturale di Milano. Her monograph lists isopods, stomatopods, and decapods; eight new taxa were erected. Later, Förster (1984) recognized for the first time a scyllaroid from Bolca, referring it to a new species, *Parribacus cristatus*. At the end of the millenium, studies on crustaceans were resumed, but in most cases these represented only partial reviews or involved descriptions of new taxa (Garassino & Novati 2001; De Angeli & Beschin 2006; De Angeli & Garassino 2008; Giusberti et al. 2014; Beschin et al. 2015; Giusberti et al. 2015; Haug & Rudolf 2015; Vonk et al. 2015; Robin et al. 2018).

3. Geological and stratigraphical context

The village of Bolca is located in the eastern Lessini Mountains, in the province of Verona (northeastern Italy). Around Bolca, there are at least six main Eocene fossiliferous sites that have yielded the historically famous marine and terrestrial faunas and floras, as summarized in Papazzoni et al. (2014) and Friedman & Carnevale (2018) (Fig. 1C, D).

The most famous source of extraordinarily well-preserved fish is the Konservat-Lagerstätte known as "Pesciara" (Fig. 2A–C). This is a large limestone olistolith (a few hundred square metres) embedded within dark volcanic deposits and made up of *c.* 20 m of alternating fossiliferous laminites and "barren" coarse-grained biocalcarenites and biocalcirudites with molluscs and foraminifera (Papazzoni & Trevisani 2006). Most fish, other rare vertebrates, plants, and invertebrates come from five levels of laminites, and mainly the first, second and fifth levels have yielded the majority of fossils. The fifth level is no longer exposed because it has been excavated completely during the last four centuries (Papazzoni & Trevisani 2006). Based on larger foraminifera (alveolinids) and calcareous nannofossil content, this site has been assigned to zone SBZ 11 of Serra-Kiel et al. (1998) and zone NP14 of Martini (1971) or zone CNE 6 of Agnini et al. (2014), corresponding to a late Ypresian age (Papazzoni & Trevisani 2006; Papazzoni et al. 2017).

The other fish-bearing site is Monte Postale (Fig. 2D–F), which crops out to the north of "Pesciara" and belongs to the province of Vicenza (Altissimo). Its complex succession consists of more than 130 m of limestones showing significant lateral facies changes from fine-grained limestones (including fish- and plant-bearing laminites) to massive coralgal limestones representing a bioconstructed facies (Vescogni et al. 2016; Papazzoni et al. 2017). At least three intervals of fossiliferous laminites with fishes, plants, and invertebrates have been recognised (Papazzoni et al. 2017). In addition to fish and plants, the site is also renowned for its molluscan fauna, coming from the uppermost beds of the succession (Dominici 2014; Papazzoni et al. 2017). A recent integrated study of calcareous nannofossils and alveolinids from Monte Postale allowed the entire section to be assigned to zone CNE 5 of Agnini et al. (2014) and zone SBZ 11 of Serra-Kiel et al. (1998), corresponding to a late Ypresian age and spanning an interval between *c.* 50.5 and 48.96 Myr. (Papazzoni et al. 2017). According to available data, the uppermost portion of Monte Postale can possibly be correlated with the "Pesciara" limestones (Papazzoni et al. 2017). Recent taphonomic, palaeoecological and sedimentological studies have outlined the depositional environments of the laminites at "Pesciara" and Monte Postale (Marramà et al. 2016; Vescogni et al. 2016; Friedman & Carnevale 2018). "Pesciara" illustrates a low-energy basin with permanent bottom dysoxia or anoxia in a peri-reefal system that was strongly influenced both by coastal and pelagic environments, whereas the Monte Postale laminites originated in a "lagoon" with at least periodic anoxic conditions at the bottom and surrounded by coralgal buildups with peri-reefal areas densely vegetated by seagrass beds and mangroves.

4. Material

The studied specimens are preserved as poorly mineralised, flattened and compressed bodies on the surfaces of the laminated calcilutites of "Pesciara" and Monte Postale fossiliferous layers. In many cases the bodies are preserved as part and counterpart, usually articulated or as incomplete moults, in dorsal-ventral (mainly brachyurans) or lateral (commonly penaeids) views. Excluding the achelatans (palinuroids and scyllaroids) that possess a hard well-mineralised exoskeleton, other decapod crustaceans, mainly penaeids and brachyurans, are usually poorly preserved, making their study and interpretation difficult.

The best-preserved examples, in which the main morphological characters are visible, have been selected from the type material and figured specimens. Most of the studied specimens, housed in historical collections, have been labelled and reported as coming from the generic "Monte Bolca". However, this is not an official toponym since "Monte Bolca" simply does not exist (Papazzoni et al. 2014). It must be noted, however, that several authors of

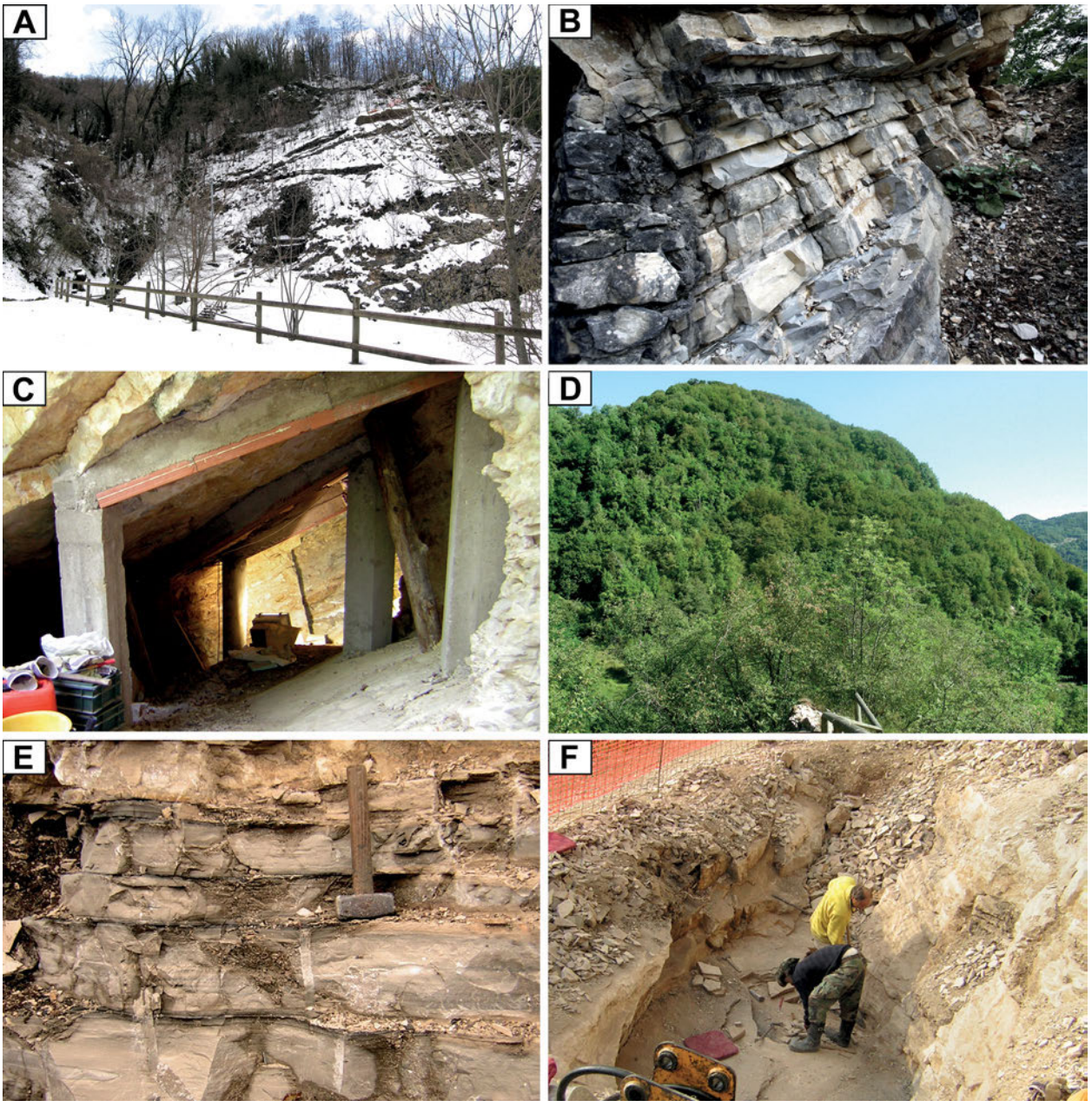

Fig. 2. The “Pesciara” and Monte Postale sites. **A** – View of the “Pesciara” site. **B** – Close-up of the fossiliferous layers at “Pesciara”. **C** – Recent excavation within “Pesciara” (“upper quarry”). **D** – View of the Monte Postale site. **E** – Close-up of the laminated layers at Monte Postale. **F** – Recent excavation at Monte Postale (2009).

the 19th-century, such as De Zigno (1874 a, b), used the term "Monte Bolca" in the sense of "Pesciara" and clearly separated this site from Monte Postale. Based on the lithology of the slabs that contain the fossils, we have provided, where possible, a more appropriate identification of the type species localities, differentiating "Pesciara" (Bolca, Verona) and Monte Postale (Altissimo, Vicenza), respectively.

Finally, some species have been redescribed based upon new specimens that were discovered during the 11 field trips carried out by the Museo Civico di Storia Naturale di Verona in "Pesciara" and Monte Postale: 219 complete and incomplete decapod crustaceans have been collected between 1999 and 2011; 54 from "Pesciara" and 165 from Monte Postale. Unfortunately, for the greater part, these specimens are too poorly preserved or fragmentary to establish their systematic position and assignment.

Abbreviations: CMC: Cerato Collection, Bolca (Verona); GBA: Geologische Bundesanstalt (Geological Survey), Vienna (Austria); MB.A: Museum für Naturkunde der Humboldt-Universität, Berlin (Germany); MCSNV, IG VR, and MCSNV Cr: Museo Civico di Storia Naturale di Verona; MFB and MFB IG: Museo dei Fossili, Bolca (Verona); MGP-PD: Museo di Geologia e Paleontologia dell'Università di Padova; NHMW: Naturhistorisches Museum Wien, Vienna (Austria); MNHN: Muséum national d'Histoire naturelle, Paris (France); MSNM: Museo di Storia Naturale di Milano; MSNVE: Museo di Storia Naturale di Venezia; G1: first gonopod; 3mxp: third maxilliped; P1–P5: pereiopods 1–5; s1–s5: pleonal somites 1–5.

5. Systematic palaeontology

5.1. Review of decapod crustaceans recorded by Secrétan (1975)

Order Decapoda Latreille, 1803
Suborder Dendrobranchiata Bate, 1888
Infraorder Penaeidea De Haan, 1840
Surfamily Penaeoidea Rafinesque, 1815
Family Penaeidae Rafinesque, 1815

Genus *Penaeus* Fabricius, 1798

Type species: *Penaeus monodon* Fabricius, 1798, by subsequent designation by Latreille (1810).

Included fossil species: see Schweitzer et al. (2010: 11).

Penaeus bolcensis Secrétan, 1975
Figs. 3, 4A, B

Udora bolcensis? De Zigno [*in schedis*].
*1975 *Penaeus bolcensis*. – Secrétan, pp. 327–330, figs. 4–6, pls. 2–6.
1999 *Penaeus bolcensis*. – Beschin & Garassino, p. 194.
2006 *Penaeus bolcensis*. – De Angeli & Garassino, p. 7.
2010 *Penaeus bolcensis*. – Schweitzer et al., p. 11.
2011 *Penaeus bolcensis* aut *obtusus*. – Cerato, p. 126 (text figure).
2014 *Penaeus* sp. – Giusberti et al., p. 79, fig. 4c.
2016 *Penaeus bolcensis*. – Quaggiotto & De Angeli, p. 29.

Original diagnosis by Secrétan (1975: 329): Carapace finement granuleuse. Crête longitudinale médiane bifide postérieurement. Rostre recourbé vers le haut, muni de sept dents au moins sur son bord supérieur et de quatre ou cinq sur le bord inférieur. Ecaille antennaire presque aussi longue que le rostre. Troisième péréiopode plus long et plus robuste que les autres. Quatre premiers segments abdominaux aux extrémités pleurales pointues. Sixième pléonite plus long que les precedents.

Literal translation in modern terms: Carapace finely granulated. Dorsal median carina bifid posteriorly. Rostrum directed upwards, with seven suprarostral teeth and four or five subrostral teeth. Scaphocerite as long as the rostrum. P3 longer and stronger than the others. s1–s4 pleura pointed ventrally. s6 longer than the others.

Type material: Holotype MCSNV 100–100bis (part and counterpart); MCSNV F2, M01, M04, 110, 112–112bis (part and counterpart); 114; MGP-PD 6794–6797 (part and counterpart) (De Zigno Collection), MGP-PD 10.094.

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Additional material: MCSNV 70034, 70035, T486; MSNVE 6302–6304, 6306–6308; MFB IG 24505, CMC3 [this specimen was also illustrated by Cerato (2011: 126) as *Penaeus bolcensis* auct *obtusus* and later by Giusberti et al. (2014: 79, fig. 4 c), as *Penaeus* sp.]; MGP-PD 12547, 12548.

Remarks: Secrétan (1975: 327) described the morphological features preserved in each of the specimen she studied which she tentatively considered to belong to the same taxon, and listed in her diagnosis the main characters based on the best-preserved, complete specimen, designated holotype. Based upon additional specimens we provided herein an emended description for this species.

The specimen MGP-PD 6794 (Fig. 4A) has an old label, stating "*Udora bolcensis*? De Zigno", a *nomen in schedis*. The same specimen was named *Udora* ?*Faujassii* by Massalongo (1855: 33) and illustrated in plate 13 (fig. 2) of his unpublished *Compendium* (Fig. 4B).

Emended description: Carapace – Carapace subtriangular with convex ventral margin narrowing frontally; dorsal margin straight; rimmed posterior margin slightly sinuous, overlapping partially s1; elongate serrated rostrum slightly turned upwards, poorly preserved distally, with 5? dorsal

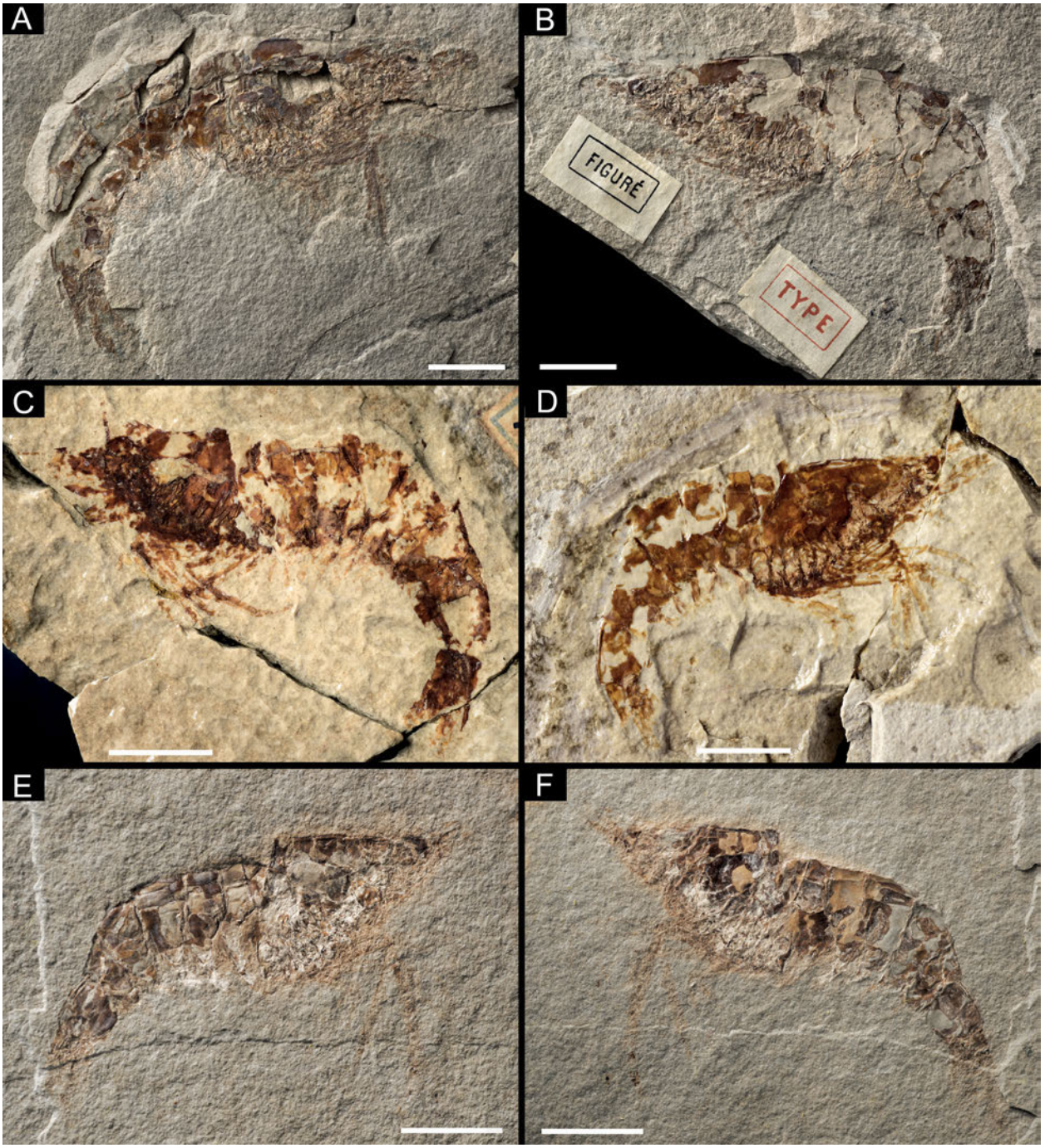

Fig. 3. *Penaeus bolcensis* Secrétan, 1975. **A, B** – Holotype, MCSNV 100–100bis (part and counterpart). **C** – MGP-PD 12547. **D** – MGP-PD 10904. **E, F** – CMC3 (part and counterpart). Specimens in C and D were immersed in alcohol prior to photography. Scale bars equal 10 mm.

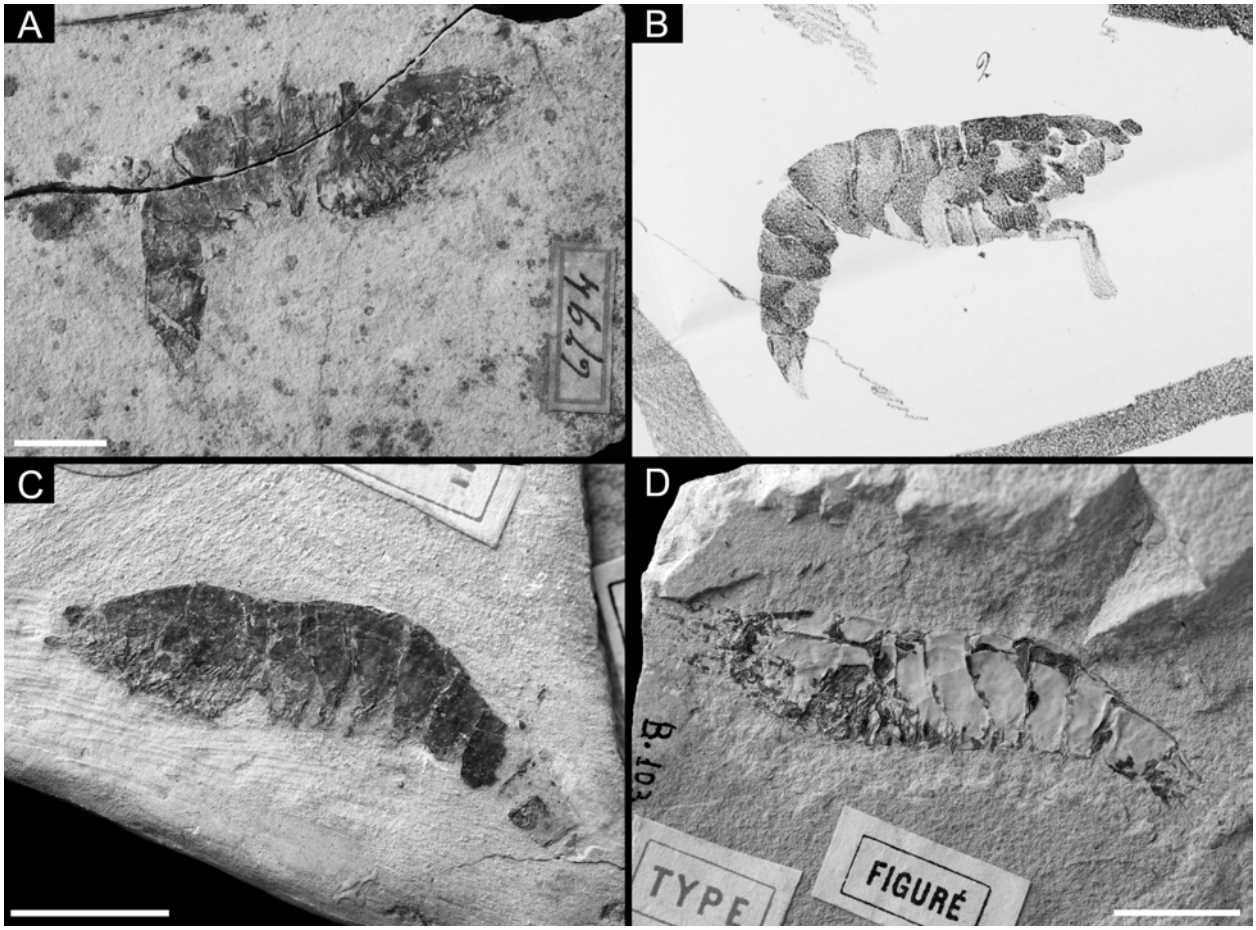

Fig. 4. A – *Penaeus bolcensis* Secrétan, 1975, MGP-PD 6794 (De Zigno Collection). **B** – Excerpt from "*Compendium Faunae et Florae Fossilis Bolcensis*", Massalongo's unpublished plate 13, illustrating MGP-PD 6794. **C** – ?*Penaeus obtusus* Secrétan, 1975, Holotype, MCSNV 106. **D** – ?*Pseudobombur nummuliticus* Secrétan, 1975, Holotype, MCSNV 103. Scale bars equal 10 mm.

pointed teeth frontally directed, decreasing distally, and at least 3 ventral teeth; postrostral dorsal thin carina; short antennal spine; short shallow cervical groove convex posteriorly; deep rounded ocular incision. Pleon – subrectangular s1–s5 increasing in size posteriorly; s1–s5 terga straight and smooth; triangular-shaped s1–s5 smooth pleurae; subsquare s6 rimmed dorsally and ventrally; subtriangular pointed telson; telson shorter than uropods. Cephalic appendages – Rounded stalked eye; antennae and antennulae not preserved; elongate slender scaphocerite, as long as the rostrum. Thoracic appendages – Elongate 3mxp, exceeding the rostrum length; P1–P2 not preserved; slender P3–P5, with elongate carpus and propodus; chelate P3 slightly longer than P4–P5; achelate P4–P5 decreasing in length posteriorly. Pleonal appendages – Subsquare protopod, bearing two multi-articulate flagella; uropodal endopod and exopod poorly preserved; uropodal exopod slightly longer than endopod; diaresis not observed.

Discussion: According to Pérez Farfante & Kensley (1997), the typical characters of *Penaeus* are as follows: rostrum with supra- and subrostral teeth; presence of cervical, orbito-antennal and hepatic grooves; strong hepatic and antennal spines; telson with a deep median groove; antennule flagella shorter than carapace.

In conclusion, based upon our review of the type material, additional specimens, and the main generic characters, we consider *P. bolcensis* to be a valid species of *Penaeus*.

?*Penaeus obtusus* Secrétan, 1975
Fig. 4C

*1975 *Penaeus obtusus*. – Secrétan, pp. 330–332, figs. 7–9, pls. 7–10.
1999 *Penaeus obtusus*. – Beschin & Garassino, p. 194.

2006 *Penaeus obtusus*. – De Angeli & Garassino, p. 7.
2010 *Penaeus obtusus*. – Schweitzer et al., p. 11.
2014 *Penaeus obtusus*. – Giusberti et al., p. 82.
2016 *Penaeus obtusus*. – Quaggiotto & De Angeli, p. 29.

Original diagnosis by Secrétan (1975: 332): Carapace très finement granuleuse. Région tergale légèrement infléchie antéro-postérieurement. Crête médiane bifide postérieurement. Sillon cervical peu profond. Ecaille antennaire courte. Trois premiers segments abdominaux avec extrémités pleurales pointues. Pleuron du quatrième pléonite arrondi, celui du cinquième subrectiligne. Sixième pléonite plus long, au bord inférieur droit.

Literal translation in modern terms: Carapace very finely granulated. Posterior region of carapace slightly antero-posteriorly curved. Dorsal median carina bifid posteriorly. Shallow cervical groove. Short scaphocerite. s1–s3 pleurae pointed ventrally. s4 rounded pleura. s5 pleura nearly straight. s6 longer with straight inferior margin.

Type material: Holotype MCSNV 106; MCSNV 101–101bis (part and counterpart), 102–102bis (part and counterpart), 104, 105, 111–111bis (part and counterpart), 113, 115, 118, 120, 121, 122.

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphic age: Early Eocene (late Ypresian).

Discussion: Our review of the type series has not allowed to identify the main characters of *Penaeus*, such as indicated by Pérez Farfante & Kensley (1997), thus questioning the systematic validity of *P. obtusus*. Indeed the characters mentioned in the original diagnosis of the species by Secrétan (1975) are not diagnostic, but found amongst most of the species assigned to the Penaeidae. Therefore, based on the present review, we question the assignment of *P. obtusus* to *Penaeus* and, in fact, we consider it a questionable penaeid.

Genus ?*Pseudobombur* Secrétan, 1975

Type species: *Pseudobombur nummuliticus* Secrétan, 1975, by monotypy.

Included fossil species: *Pseudobombur nummuliticus* Secrétan, 1975.

?*Pseudobombur nummuliticus* Secrétan, 1975
Fig. 4D

*1975 *Pseudobombur nummuliticus*. – Secrétan, pp. 332–335, figs. 9, 10, pl. 11, figs. 1–3; pl. 12, fig. 2.
1999 *Pseudobombur nummuliticus*. – Beschin & Garassino, p. 194.
2006 *Pseudobombur nummuliticus*. – De Angeli & Garassino, p. 7.
2010 *Pseudobombur nummuliticus*. – Schweitzer et al., p. 11.
2014 *Pseudobombur nummuliticus*. – Giusberti et al., p. 82.

Original diagnosis by Secrétan (1975: 334): Céphalothorax court et massif orné d'une crête longitudinale médiane bifurquée postérieurement. Abdomen massif également, en continuité avec la ligne du cephalothorax. Structure identique des cinq premieres pléonites, aux bords antérieur et postérieur subparallèles. Pas d'elargissement des pleurons dont le bord inférieur est subrectiligne. Sixième segment allongé, marquee d'une crête longitudinale.

Literal translation in modern terms: Cephalothorax short and broad, with a dorsal longitudinal median carina bifid posteriorly. Broad pleon, aligned with the midline of the carapace. s1–s5 equal in size, with subparallel anterior and posterior margins. Square pleurae, not enlarged laterally, with straight inferior margin. Elongate s6, with a longitudinal carina.

Type material: Holotype MCSNV 103; B II (erroneously recorded by Secrétan as F5. 2), 108, 109.

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Discussion: Based on the original diagnosis by Secrétan (1975) and our review of the type material, we have not been able to identify diagnostic characters useful to justify the placement of *Pseudobombur* within the Penaeidae. Moreover, her statement that the representatives of this genus have a similar arrangement of the pleonal somites, identical pleural margins, and general shape of the cephalothorax with *Bombur* Münster, 1839, a poorly known genus from the Middle Triassic and Upper Jurassic of Europe, appears arbitrary (Secrétan 1975: 338). Indeed, Van Straelen (1925: 101) already pointed out the problems surrounding recognition of this genus as based on the poor state of preservation of the known specimens, assigning it tentatively to the Caridea on account of the strong angle between s2–s3, typical of many carideans, although Förster (1967: 172) considered *Bombur* to be a juvenile stage of *Hefriga* Münster, 1839.

Our re-examination of the holotype of *P. nummuliticus* has revealed that the dorsal midline of the carapace was erroneously interpreted by Secrétan (1975) as a median bifid carina due to the slight displacement of the carapace that occurred during the fossilisation process. Alhough rounded pleurae on pleonal somites are typical of the Penaeidae, the character by itself is not sufficient to justify assignment of the studied specimens to a new genus. Finally, rostrum, cephalic spines, and grooves are not identifiable due to the poor state of preservation of the carapace.

In conclusion, we can observe that the lack of diagnostic characters of the type material of *P. nummuliticus* questions the systematic validity of this genus within the Penaeidae. Only additional well-preserved specimens may resolve the systematic position of this dubious genus.

Infraorder Axiidea de Saint Laurent, 1979
Family Callianassidae Dana, 1852b
Subfamily Eucalliacinae Manning & Felder, 1991

Genus *Bolcacalliax* Hyžný nov.

Type species: *Protaxius eocenicus* Secrétan, 1975, by monotypy and present designation.

Diagnosis: Carapace lacking dorsal oval; chelipeds (P1) subchelate, unequal, similar; merus with serrated lower margin; propodus rectangular; fixed finger very short, stump-like; dactylus unarmed, approximately three times longer than index; telson wider than long, subrectangular in outline, with rounded posterolateral margins.

Etymology: The name is a combination of Bolca, in reference to the type area, combined with *Calliax*. Gender: feminine.

Discussion: In *Bolcacalliax* n. gen. the *linea thalassinica* is straight and extends the entire length of the carapace. Such a *linea thalassinica* is present in representatives of several families of the infraorder Gebiidea de Saint Laurent, 1979, i.e., namely Axianassidae Schmitt, 1924; Laomediidae Borradaile, 1903; and Thalassinidae Latreille, 1831, whereas within the infraorder Axiidea de Saint Laurent, 1979, it is present only in members of the Callianassidae Dana, 1852b and Ctenochelidae Manning & Felder, 1991 (Dworschak et al. 2012). In *Bolcacalliax* n. gen., the pleon is much longer than the carapace and s1 and s2 seem to be only lightly sclerotised. Additionally, pleonal tergopleura are much reduced. Such a combination of characters is present in the Callianassidae and Ctenochelidae (Poore 2004; Dworschak et al. 2012), whereas many axiideans have pleura that are acutely angled (Dworschak et al. 2012). The combination of P1 (cheliped) carpus as high as propodus and merus with straight upper margin is present only in the Callianassidae and in some ctenochelids (*sensu* Manning & Felder 1991). In representatives of the Callianideidae Kossman, 1880 the distal margin of the carpus is often as high as the proximal margin of the propodus; however, the merus is ovoid in outline and its upper margin is strongly arched (Poore 1997; Poore 2015). Moreover, the propodus is often higher distally in the Callianideidae, which is not the case in *Bolcacalliax* n. gen. Representatives of the Ctenochelidae have a distinct hook on the lower margin of the P1 merus (Manning & Felder 1991); in *Bolcacalliax* n. gen., however, the lower margin of the merus is serrated. In *Bolcacalliax* n. gen., the uropodal exopod bears a secondary lobe (dorsal plate), which is a typical character of the Callianassidae; the uropodal exopod is simply ovate in representatives of the Ctenochelidae (Poore 2004; Dworschak et al. 2012).

Based upon the above discussion, the assignment of *Bolcacalliax* n. gen. to the Callianassidae is undoubted. However, the new genus possesses a subchelate state of both P1, i.e., a short index in combination with an elongate dactylus. Subchelate P1 are commonly present in the Thalassinidae (Ngoc-Ho & de Saint Laurent 2009) and Upogebiidae (Ngoc-Ho 2003; Dworschak et al. 2012), but within the Callianassidae only *Calliax* de Saint Laurent, 1973 has an elongate dactylus that is longer than the index and it is present only in the minor chela (Ngoc-Ho 2003; Hyžný & Gašparič 2014). There are more similarities to extant representatives of the Eucalliacinae Manning & Felder, 1991: *Bolcacalliax* n. gen. has subequal and similar P1, which are also present in *Eucalliax* Manning & Felder, 1991 and *Calliaxina* Ngoc-Ho, 2003 (Ngoc-Ho 2003; Hyžný 2012; Hyžný & Gašparič 2014), and the minor chela is reminiscent of the one in *Calliax* as mentioned above. In *Bolcacalliax* n. gen., the telson is wider than long and subrectangular in outline with rounded posterolateral margins, and hence similar to that in representatives of *Calliaxina* and *Eucalliax* (Poore & Griffin 1979; Heard 1989; Ngoc-Ho 2003; Dworschak 2006). Based on the characters that are shared with the taxa mentioned above, *Bolcacalliax* n. gen. is herein assigned to the Eucalliacinae.

Bolcacalliax eocenica (Secrétan, 1975)
Figs. 5–8

*1975 *Protaxius eocenicus*. – Secrétan, pp. 343, 344, pl. 16, figs. 1, 2, 5.
1975 ?*Protaxius* sp. – Secrétan, pp. 344, 345, fig. 11.
2006 *Protaxius eocenicus*. – Garassino & De Angeli, p. 17.
2010 *Protaxius eocenicus*. – Schweitzer et al., p. 42.
2014 *Protaxius eocenicus*. – Giusberti et al., p. 82.
2016 *Protaxius eocenicus*. – Emmerson, p. 371.

Original diagnosis by Secrétan (1975: 344): Céphalothorax à branchiostèges minces, de forme ovoide. Orbites profondes à la base d'un rostre triangulaire. Chélipedes égaux, subchéliformes. Propode et carpe peu distincts l'une de l'autre à leur articulation qui est rectiligne. Deuxième et cinquième segments abdominaux à décrochements pleuraux, ornés de lignes et des crètes. Sixième pléonite plus long que les precedents.

Literal translation in modern terms: Lateral or dorsolateral part of carapace narrow and oval. Deep orbits at level of triangular rostrum. Chelipeds equal in size and subchelate. Propodus and carpus articulation straight. s2 and s5 pleurae with carinae. s6 longer than the previous ones.

Revised diagnosis: As for genus.

Holotype: MCSNV B4-B5 (part and counterpart), individual preserved in dorsal view with both chelipeds (left chela being the major one), cephalothorax and pleon.

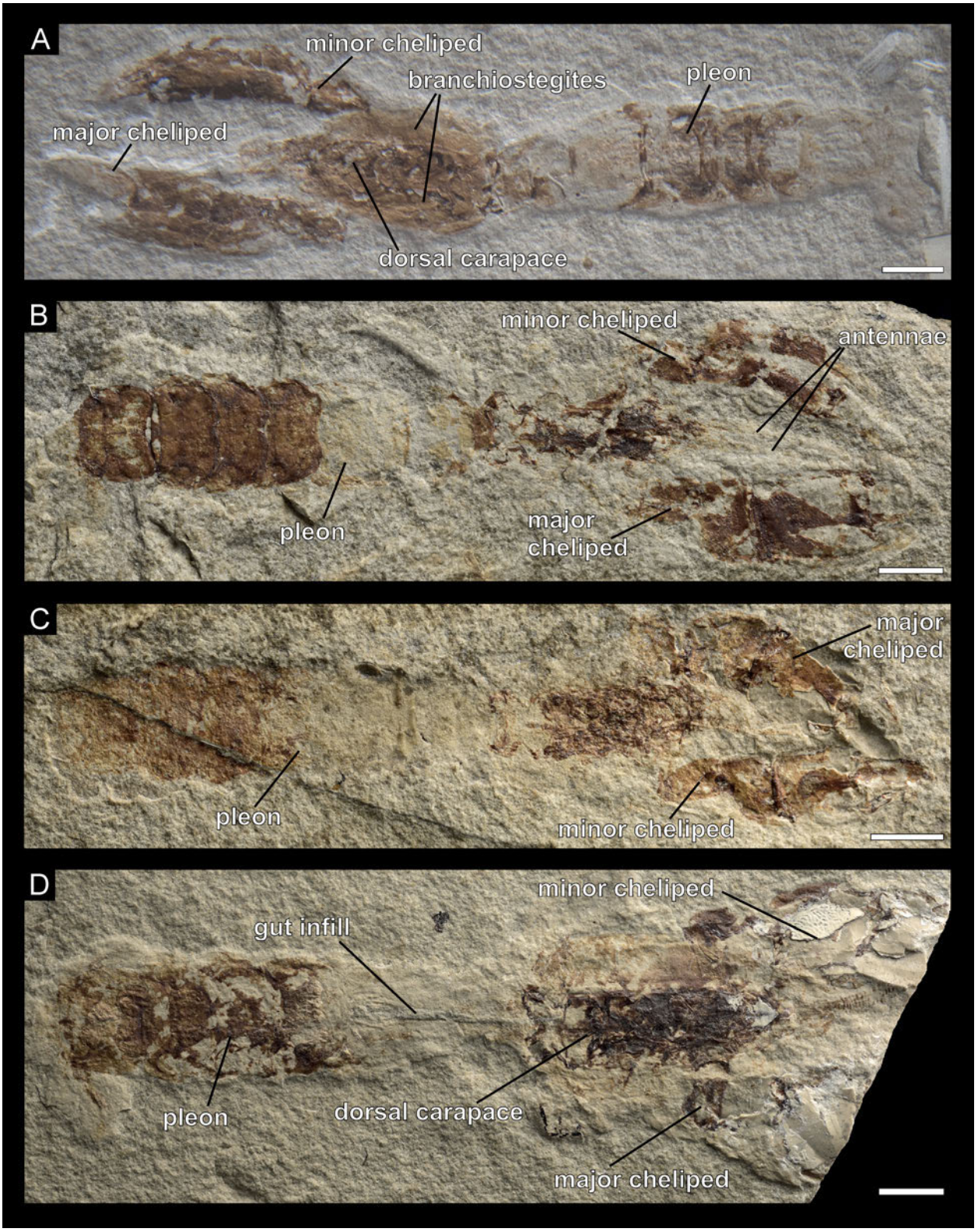

Fig. 5. *Bolcacalliax eocenica* (Secrétan, 1975). **A** – Holotype, MCSNV B5 (counterpart). **B** – MGP-PD 10.905. **C** – MGP-PD 12.545. **D** – MCSNV Cr 59. Scale bars equal 5 mm.

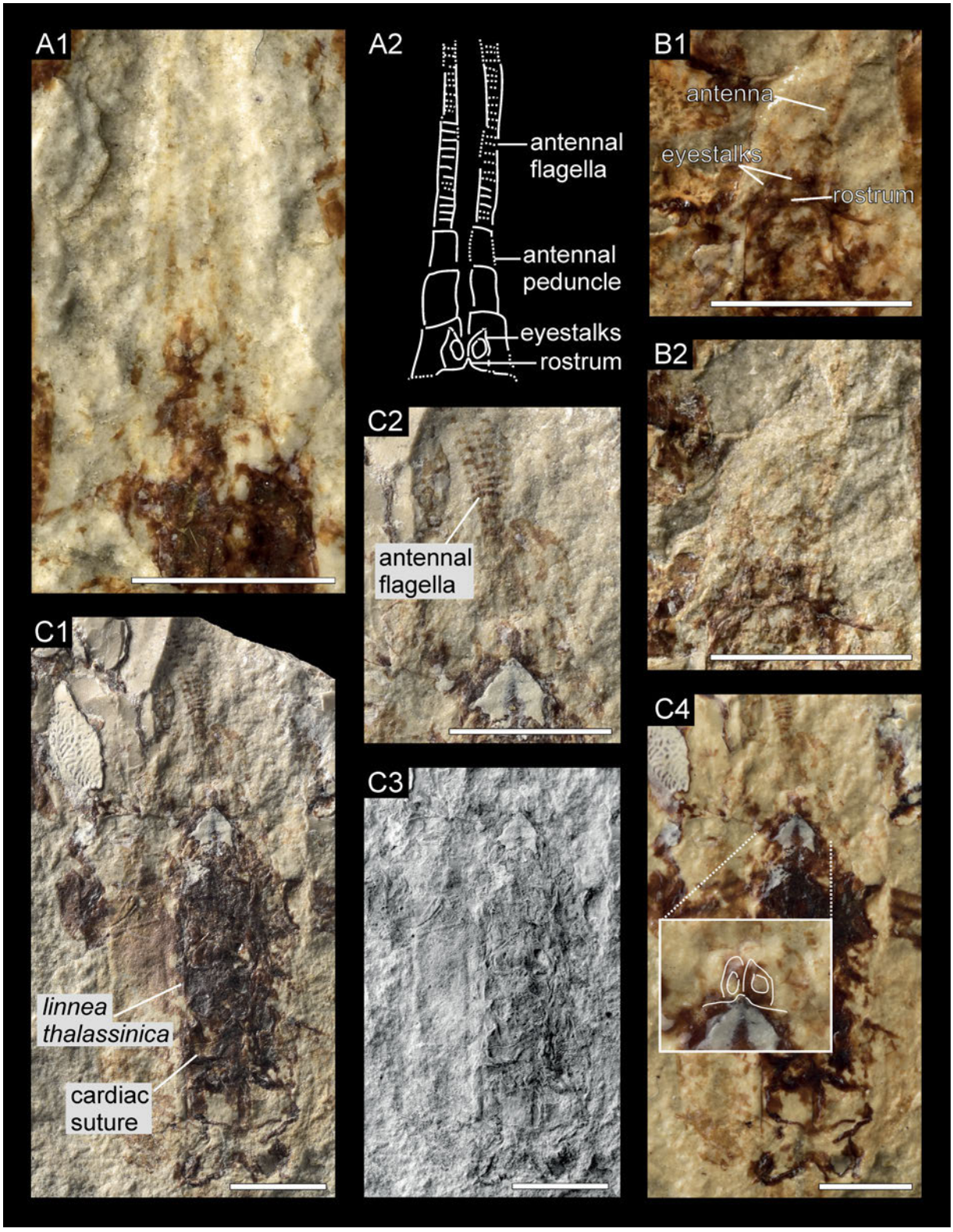

Fig. 6. *Bolcacalliax eocenica* (Secrétan, 1975). **A** – Cephalic appendages and the carapace front of MGP-PD 10.905. **B** – MGP-PD 12.545. **C** – Carapace and cephalic appendages of MCSNV Cr 59. Specimens in A1, B1 and C4 were immersed in alcohol prior to photography. Specimen in C3 was whitened with ammonium chloride prior to photography. Scale bars equal 5 mm.

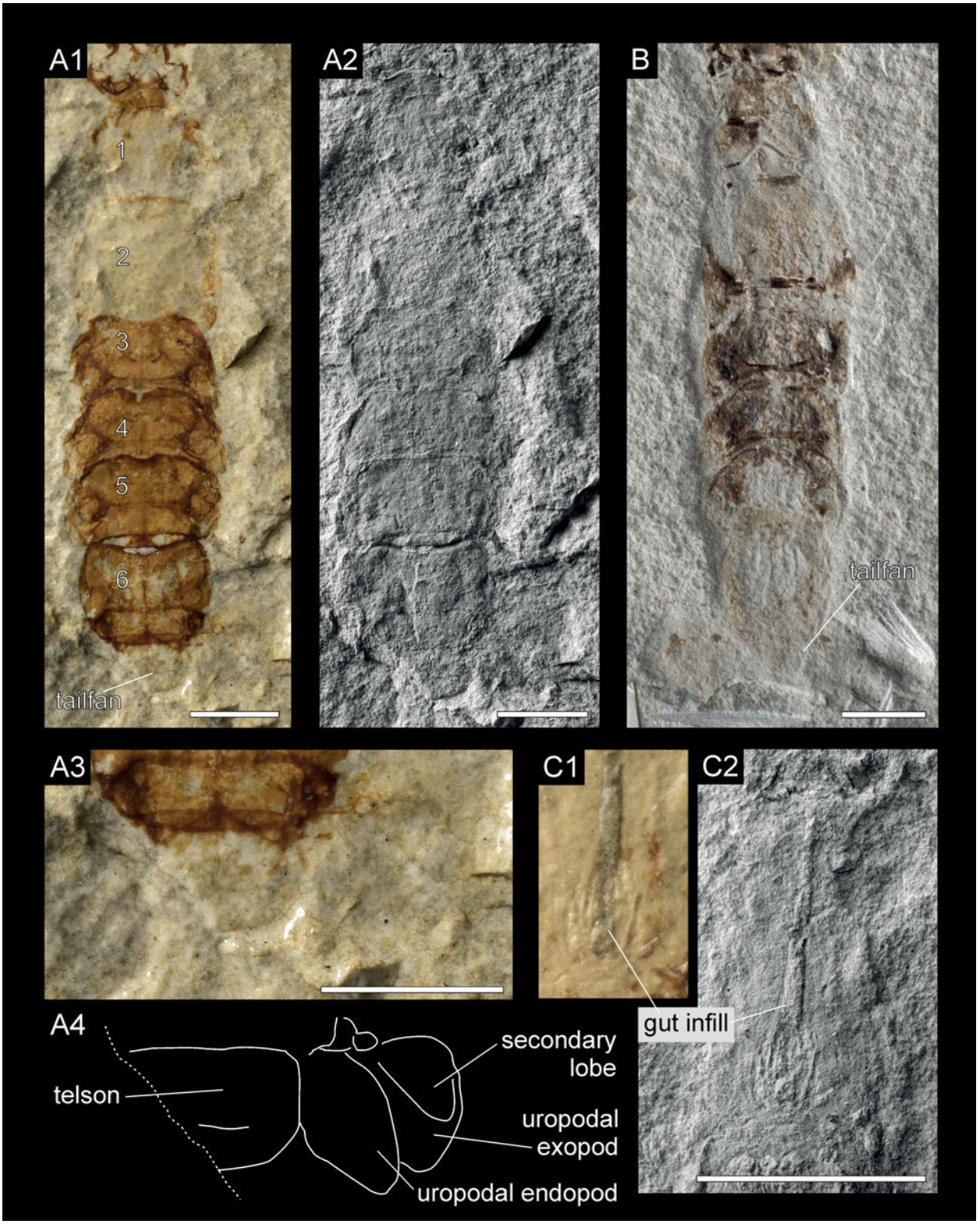

Fig. 7. *Bolcacalliax eocenica* (Secrétan, 1975). **A** – Pleon of MGP-PD 10.905, (A1–A3) with details of tailfan (A3–A4). **B** – Pleon of the holotype, MCSNV B5 (counterpart). **C** – Gut infill of MCSNV Cr 59. Specimens in A1, A3, and C1 were immersed in alcohol prior to photography. Specimens in A2 and C2 were whitened with ammonium chloride prior to photography. Scale bars equal 5 mm.

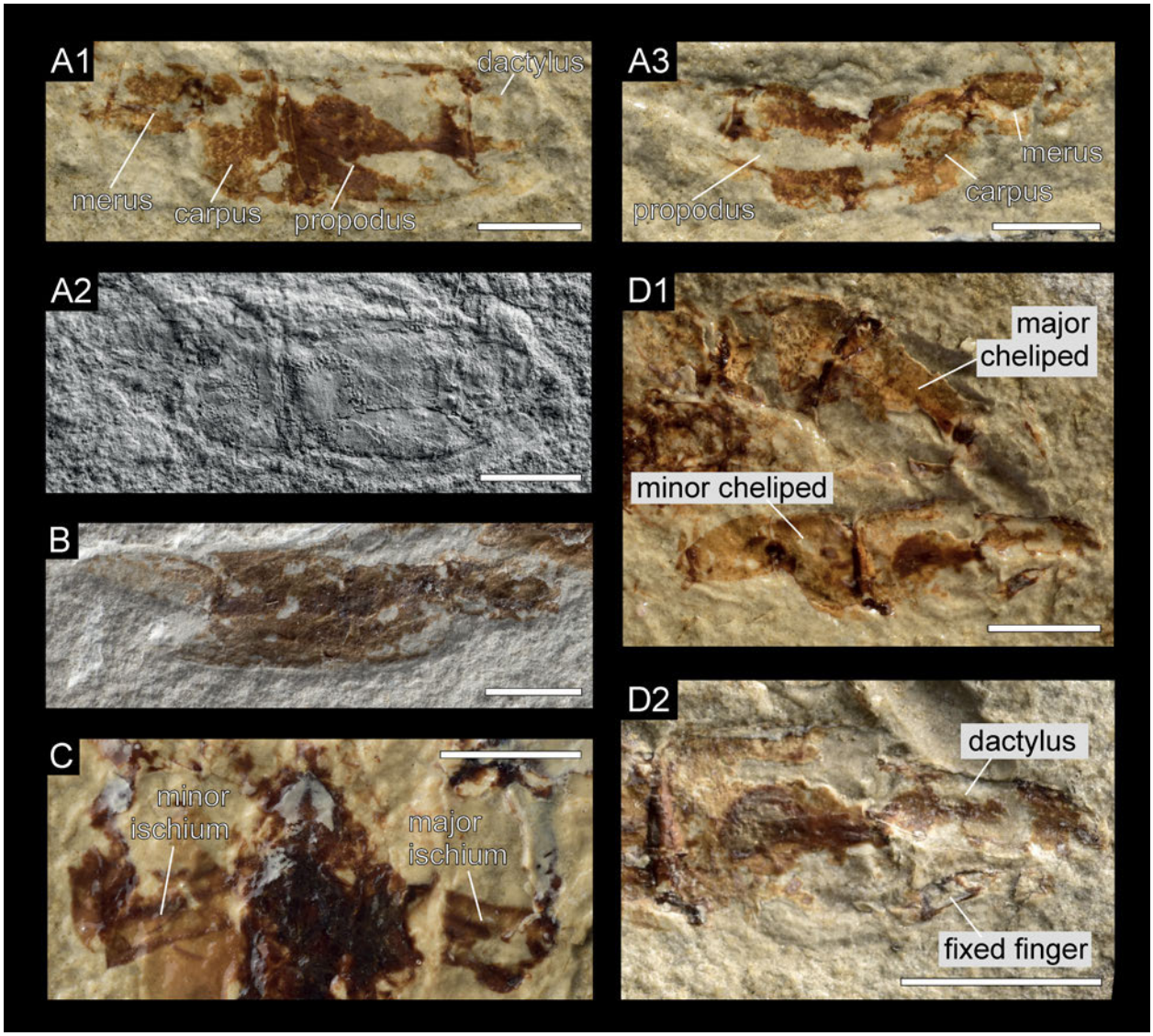

Fig. 8. *Bolcacalliax eocenica* (Secrétan, 1975). **A** – Chelipeds of MGP-PD 10.905, including major cheliped (A1, A2) and minor cheliped (A3). **B** – Major cheliped of the holotype, MCSNV B5 (counterpart). **C** – Ischia of major and minor chelipeds of MCSNV Cr 59. **D** – Chelipeds of MGP-PD 12.545, with detail of minor chela (D2). Specimens in A1 A3, C and D1 were immersed in alcohol prior to photography. Specimen in A2 was whitened with ammonium chloride prior to photography. Scale bars equal 5 mm.

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Additional material: MGP-PD 10.905 (?*Protaxius* sp. *sensu* Secrétan 1975), individual preserved in dorsal view with both chelipeds (right chela being the major one), cephalothorax and pleon. MGP-PD 12.545 (?*Protaxius* sp. *sensu* Secrétan 1975), individual preserved in dorsal view with both chelipeds (left chela being the major one), cephalothorax and pleon. MCSNV Cr 59, individual preserved in dorsal view with partially preserved chelipeds (right one being the major), cephalothorax and pleon, including the gut content.

Description: Carapace – Dorsally, carapace slightly longer than s1 and s2 combined; frontal margin of carapace with narrow triangular rostrum; rostrum acute terminally; rostrum extending to one-third of visible length of eyestalks in dorsal view; carapace lacking dorsal oval, cardiac promi-

nence, and dorsal carina; cervical groove distinct, disjunct near *linea thalassinica*; *linea thalassinica* strong, parallel to midline of carapace; cardiac suture in median posterior half of carapace distinct, continuous across midline of carapace. Pleon – Pleon long; dorsal length ratio (along midline) of s1 to s6 1.0, 1.4, 0.8, 0.8, 0.8, 1.0; s2 longest, s3–s5 distinctly shorter than s2; s6; telson wider than long, subrectangular in outline, with rounded posterolateral margins; uropod with endopod suboval, overreaching telson; exopod subtriangular, with secondary lobe. Cephalic appendages – Eyestalks approximately three times longer than wide; pigmented region distinct at midlength of dorsal basal articles of antennular peduncles approximately 1.5 times longer than eyestalks. Thoracic appendages – Chelipeds (P1) unequal, similar, with major and minor chela strongly developed; major cheliped ischium and merus with serrated lower margin; merus two times longer than high; carpus 1.5 times higher than long, proximo-lower margin rounded; propodus rectangular, as long as or longer than high; index very short, stump-like, armed with small teeth; dactylus straight, unarmed, robust, approximately three times longer than index; minor cheliped similar to and slightly smaller than major cheliped.

Discussion: Secrétan (1975) described *Protaxius eocenicus* based on a single specimen, whereas she retained two additional specimens (MGP-PD 10.905, 12545, from "Monte Bolca") in open nomenclature as ?*Protaxius* sp. *Protaxius* was erected by Beurlen (1930) for several Jurassic species previously interpreted as *Callianassa*, with the following diagnostic characters: P1 (chelipeds) robust, slightly asymmetric, manus elongate, fingers short; index distinctly shorter than dactylus; s1 slighly reduced, nearly as large as s2; pleurae of s1–s6 (tergopleurae) rectangular, slightly rounded, well developed. Secrétan (1975) assigned her new species to *Protaxius* although many of these characters actually are not present in the studied specimens; indeed, s2 is much larger than s1 and pleurae are reduced. Moreover, *Callianassa isochela* Woodward, 1876, type species of *Protaxius*, differs greatly from *Protaxius eocenicus* in other aspects as well. *Callianassa isochela* has no *linea thalassinica*, the P1 merus has arched upper and lower margins without distinct serration and the uropodal exopod is simply ovate without a secondary lobe. Therefore, *Protaxius eocenicus* is removed herein from *Protaxius*.

Based on detailed analysis of the original material recorded by Secrétan (1975), we have been able to redescribe the species and identify the characters that differentiate from all callianassid genera, fossil or extant, known to date. *Protaxius eocenicus* is considered the type and sole species of the newly erected genus *Bolcacalliax* n. gen.

Finally, one of the additional specimens (MCSNV Cr 59) preserves a gut infill. This suggests that the individual is a corpse, not a moult. This conclusion is further supported by the articulation between pleon and cephalothorax. This mode of preservation actually is seen in all studied specimens of *Bolcacalliax eocenica* suggesting that all of them represent corpses rather than moults.

Infraorder Achelata Scholtz & Richter, 1995
Family Palinuridae Latreille, 1802

Genus *Justitia* Holthuis, 1946

Type species: *Palinurus longimanus* H.-M. Edwards, 1837, by original designation.

Included fossil species: *Justitia desmaresti* (Secrétan, 1975), *J. vicetina* Beschin, De Angeli & Garassino, 2001.

Justitia desmaresti (Secrétan, 1975)
Fig. 9

Selected synonyms:

1855 *Palinurus Desmarestii* Zigno *in litt*. – Massalongo, p. 32 [*nomen nudum*].
*1975 *Palinurus desmaresti*. – Secrétan, pp. 339, 340, pl. 12, fig. 1; pl. 13, figs. 1–5; pl. 14, figs. 1–4; pl. 15, figs. 1–4; pl. 16, figs. 3, 4.
2001 *Justitia desmaresti*. – Garassino & Novati, p. 259, figs. 1–7.
2014 *Justitia desmaresti*. – Giusberti et al., p. 82, fig. 5.
2014 *Justitia desmaresti*. – De Angeli & Garassino, p. 11.
2015 *Justitia desmaresti*. – Giusberti et al., pp. 116, 118, figs. 1A, B, 3 [*cum syn.*].
2018 *Justinia* (sic) *desmaresti*. – Friedman & Carnevale, fig. 3c.

Emended diagnosis by Giusberti et al. (2015: 116): Two strong supraorbital spines; deep median cervical groove; dorsal region of carapace adorned by small imbricate scales; three transverse parallel grooves on s2-s5.

Lectotype: MCSNV 23 as designated by Giusberti et al., 2015) (illustrated by Secrétan 1975: pl. 12, fig. 1; Giusberti et al. 2015: fig. 3).

Paralectotypes: MCSNV 89 (Secrétan 1975: pl. 13, fig. 2), MCSNV 90bis (Secrétan 1975: pl. 13, fig. 3; it is the counterpart of MCSNV 23), MCSNV 93 (Secrétan 1975: pl. 14, fig. 1), MCSNV 95 (Secrétan 1975: pl. 14, figs. 2–4).

Additional material: CMC I.G. 132590–132605 (part and counterpart), CMC 6 (previously illustrated by Cerato 2011: 76); MCSNV 17–17bis, MCSNV CR 17, 18, MO2, 19, 20, 23B, 24, 25–25bis, 91–91bis, 92, 94; MGP-PD: 6804, 7747C-7450C, 7448C-7449C; MFB IG 91130; MSNM i22867; MSNVE 4927, 6298; MNHN. FA51537 (Conte Gazola Collection); NHMW 1853/XXVII/59–1853/XXVII/60; GBA 2010/275/0053 (former coll. no. 2319).

Type locality: "Pesciara" (Bolca, Verona).

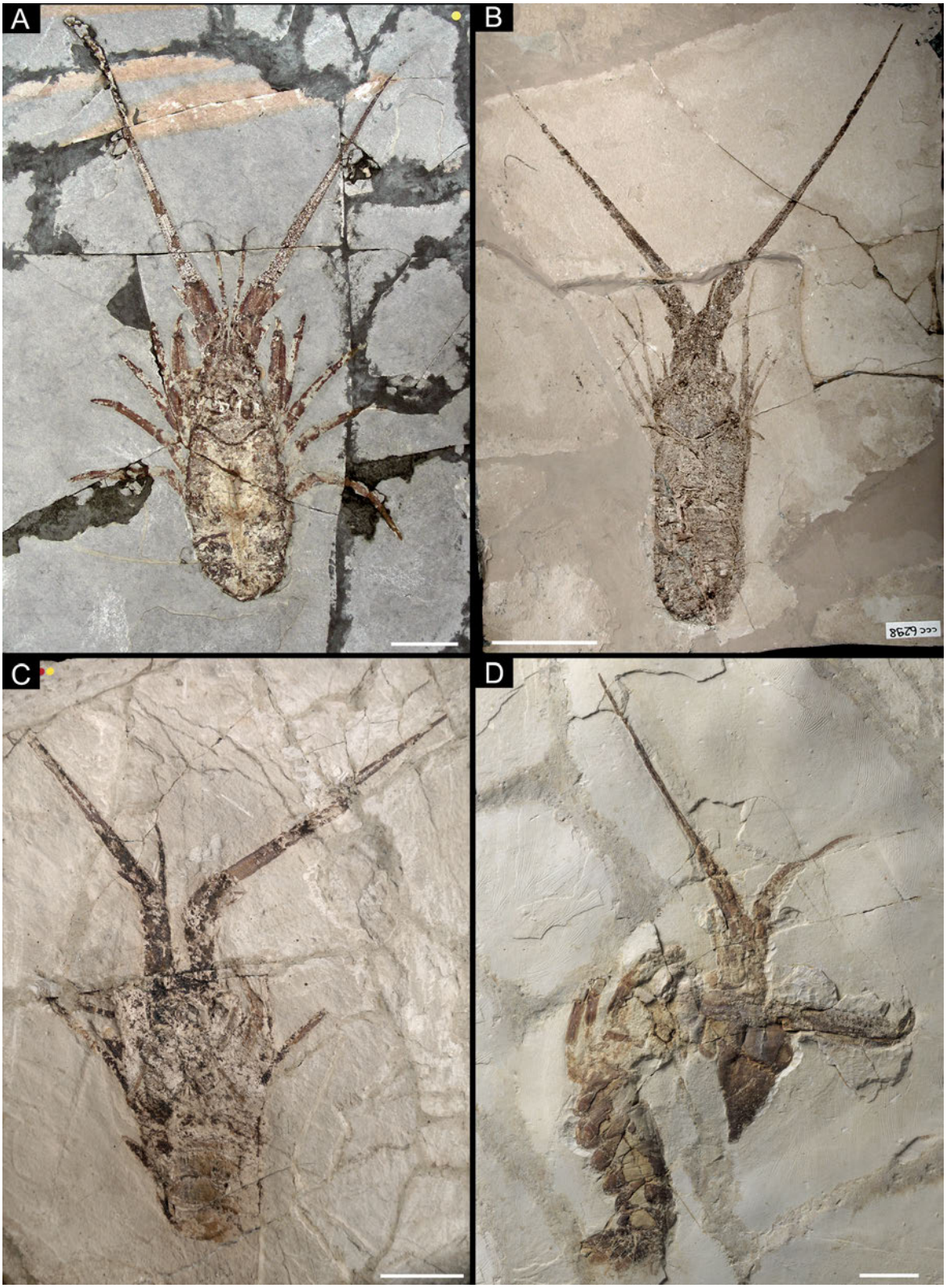

Fig. 9. *Justitia desmaresti* (Secrétan, 1975). **A** – Lectotype, MCSNV 23. **B** – MSNVE 6298. **C** – MCSNV 91, the specimen originally illustrated by Massalongo in his unpublished *Compendium* (see Giusberti et al. 2015). **D** – MFB IG 91130. Scale bars equal 50 mm.

Stratigraphical age: Early Eocene (late Ypresian).

Description: See Giusberti et al. (2015).

Discussion: Secrétan (1975: 339) was the first to describe *Palinurus desmaresti* formally; it had previously been erroneously assigned to De Zigno (1915). Later, Garassino & Novati (2001) revised and redescribed the species, listing it as *Justitia desmaresti* (Massalongo, 1854). Finally, Giusberti et al. (2015) assigned the authorship of *Justitia desmaresti* to Secrétan (1975) (for a full discussion, reference is made to Giusberti et al. 2015: 116). According to Garassino & Novati (2001) and Giusberti et al. (2015), *Justitia desmaresti* is a valid species of the genus.

Infraorder Brachyura Latreille, 1802
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Portuninae Rafinesque, 1815

Genus *Enoplonotus* A. Milne-Edwards, 1860

Type species: *Enoplonotus armatus* A. Milne-Edwards, 1860, by monotypy.

Included fossil species: *Enoplonotus armatus* A. Milne-Edwards, 1860.

Enoplonotus armatus A. Milne-Edwards, 1860
Fig. 10

*1860 *Enoplonotus armatus*. – A. Milne-Edwards, pp. 247, 248, pl. 7, figs. 1, 1a.
1915 *Enoplonotus armatus*. – Fabiani, p. 284.
1929 *Enoplonotus armatus*. – Glaessner, p. 149.
1929 *Enoplonotus armatus*. – Lőrenthey & Beurlen, p. 170.
1975 *Enoplonotus armatus*. – Secrétan, p. 359, pl. 21, figs. 1, 2.
2006 *Enoplonotus armatus*. – De Angeli & Garassino, p. 57.
2008 *Enoplonotus armatus*. – Karasawa et al., pp. 110, 126.
2010 *Enoplonotus armatus*. – Schweitzer et al., p. 108.
2014 *Enoplonotus armatus*. – Giusberti et al., p. 82.

Remarks: A. Milne-Edwards (1860) did not provide a diagnosis for this species, describing only the main characters of the dorsal surface of the carapace. Our re-examination of the specimen described by Secrétan (1975) has revealed that this is the same sample that was described by A. Milne-Edwards (1860) and thus the type of the species. Here we provide an emended diagnosis and an emended description based on our review of the single specimen available.

Emended diagnosis: Carapace subpentagonal, wider than long; front protruded beyond orbits, with six lobes; supraorbital margin continuous, with median fissure; anterolateral margin with four large spines (except the extraorbital spine); fourth anterolateral spine (= epibranchial spine) strongly elongate directed outwards, with at least 10 small spines on the upper margin and smooth lower margin; posterolateral margin slightly concave and smooth; regions indistinct; deep cervical groove.

Holotype: MCSNV M1-M2 (part and counterpart).

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Emended description: Carapace subpentagonal, wider than long; front slightly protruding beyond orbits, with six lobes (including the inner orbital lobe); wide and shallow orbits; supraorbital margin continuous, with median fissure; short extraorbital spine; short anterolateral margin with four spines (except the extraorbital spine); first pointed anterolateral spine protruding backwards; second pointed anterolateral spine protruding outwards; third mushroom-shaped anterolateral spine protruding outwards; fourth anterolateral spine (= epibranchial spine) strongly elongate, pointed distally, carinate dorsally, and protruding outwards; fourth anterolateral spine with at least 10 small spines equal in size on the upper margin and smooth lower margin; posterolateral margin slightly concave and smooth; straight rimmed posterior margin as long as the frontal margin; regions indistinct; deep cervical groove, delimiting meso-, meta-, and urogastric regions; ornamentation of dorsal surface of carapace with large and small tubercles uniformly arranged in longitudinal lines.

Discussion: This species was first recorded and figured by A. Milne-Edwards (1860: 247, 248; pl. 7, figs. 1, 1a) based on a single specimen in Massalongo's collection. The specimen probably was part of his original private collection, later acquired from his heirs, by the Verona municipality for the Museo Civico di Storia Naturale di Verona. Secrétan (1975: 359: pl. 21, figs. 1, 2) reported a specimen as belonging to *E. armatus* based on the following characters: carapace wider than long, deep, arcuate branchiocardiac depressions, numerous spines on the anterolateral margins, and an extremely long epibranchial spine, with serrate upper margin. The specimen also shows an incomplete P5, which appears to be rather stylised in the drawing provided by A. Milne-Edwards. Therefore, based on

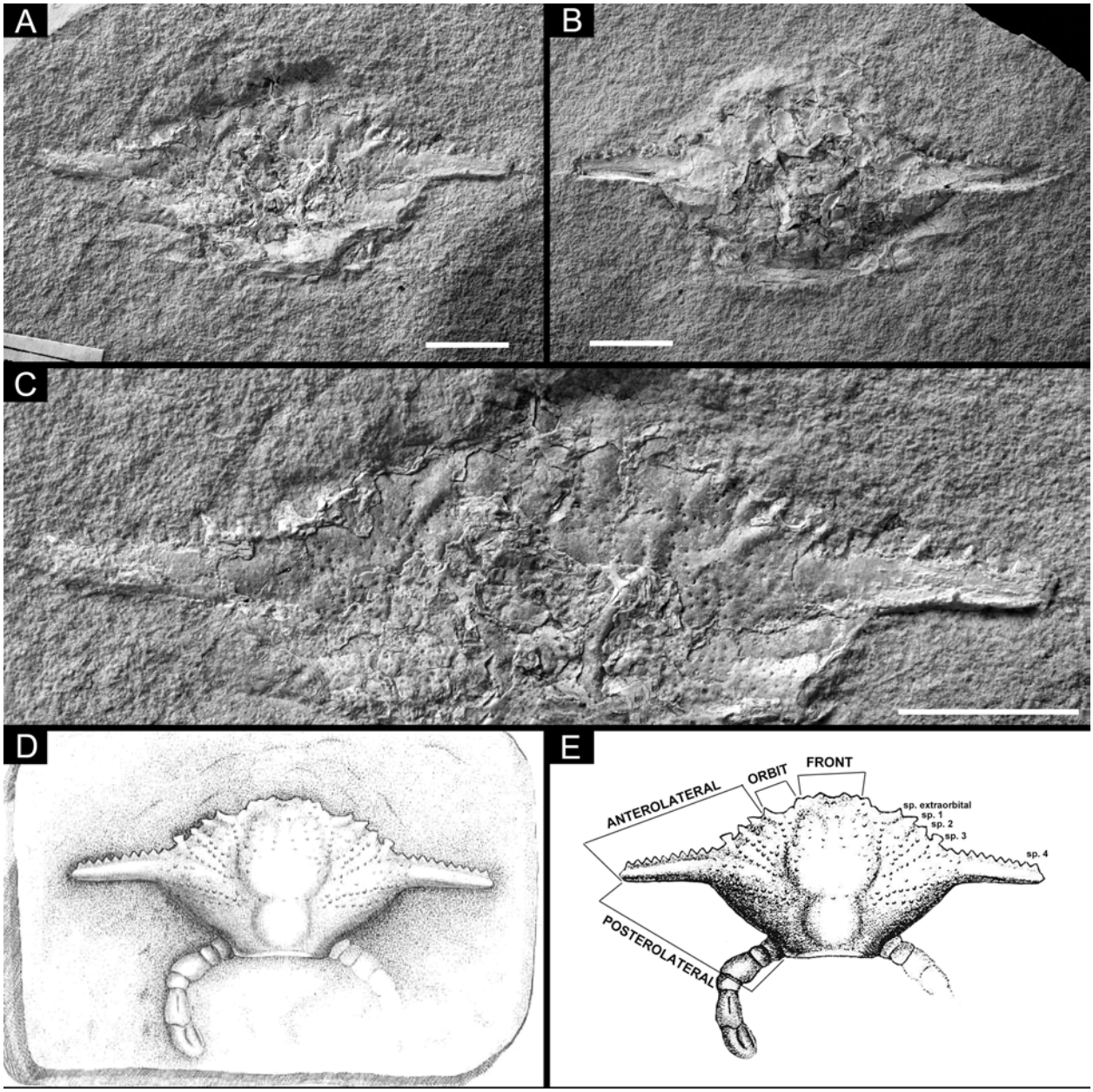

Fig. 10. *Enoplonotus armatus* A. Milne-Edwards, 1860. **A, B** – Holotype, MCSNV M1-M2 (part and counterpart). **C** – MCSNV M1, close-up of the front and anterolateral margins. **D** – A. Milne-Edwards' plate 7 (fig. 1, 1a), illustrating the holotype. **E** – Reconstruction of the carapace. Scale bars equal 10 mm.

A. Milne-Edwards' description and illustration, the specimen described by Secrétan should be considered the original of A. Milne-Edwards. Schweitzer & Feldmann (2002: 951) pointed out the peculiar distinctive features of the monospecific *Enoplonotus* A. Milne-Edwards, 1860, as having "*rows of small tubercles that extend in oblique lines from the anterolateral margin towards the axis of carapace*" and "*the long lateral spine of Enoplonotus is serrate along its entire length*". Karasawa et al. (2008: 110) suggested to place *Enoplonotus* within the Portunidae *sensu lato*, as based upon the spiny anterolateral margin and carapace that is wider than long, until better-preserved material is recovered that would allow the true systematic position of this genus to be determined. However, based on the diagnosis of the Portuninae provided by Karasawa et al. (2008: 108) and the emended description of *Enoplonotus* (present work), we argue that this genus does fit some of the diagnostic characters of the subfamily, such as a carapace that is markedly wider than long, a front which corresponds to about one-quarter of the maximum carapace width, forwardly directed orbits, and an anterolateral margin generally with spines, the last one (= epibranchial spine) usually notably longer than others.

In conclusion, *Enoplonotus* can be included definitively within the Portuninae.

Superfamily Xanthoidea MacLeay, 1838
Family Panopeidae Ortmann, 1893
Subfamily Panopeinae Ortmann, 1893

Genus *Lophopanopeus* Rathbun, 1898

Type species: *Xantho bella* Stimpson, 1860, by original designation.

Included fossil species: See Schweitzer et al. (2010: 122).

Lophopanopeus bolcensis (Secrétan, 1975) n. comb.
Fig. 11

Cancer bolcensis De Zigno [*in schedis*].

1855 *Cancer Zignii*. – Massalongo, p. 32 [*nomen nudum*].

*1975 *Panopeus bolcensis*. – Secrétan, pp. 359–362, fig. 19, pl. 22; pl. 23, figs. 3, 4.

2006 *Panopeus bolcensis*. – De Angeli & Garassino, p. 69.

2010 *Panopeus bolcensis*. – Schweitzer et al., p. 122.

2010 *Panopeus bolcensis*. – Gatt & De Angeli, p. 1338.

2011 *Eriphia?* sp. – Cerato, p. 112.

2014 *Panopeus bolcensis*. – Giusberti et al., p. 82.

2018 *Panopeus bolcensis*. – Beschin et al., p. 192.

Original diagnosis by Secrétan (1975: 361): Céphalothorax sub-oval trasversal. Front large, droit et incisé. Orbites larges et peu profondes. Bords latéro-antérieurs élargis, garnis de dents au nombre de trois au moins. Bord latéro-postérieur renflé, lisse et fuyant, bord postérieur étroit et rectiligne. Péréiopodes longs et robustes.

Literal translation in modern terms: Carapace suboval transversely. Wide, straight front. Orbits wide and shallow. Anterolateral margin with at least 3 teeth. Posterolateral margin bulged and smooth. Posterior margin narrow and straight. Pereiopods long and strong.

Type material: Lectotype, designated herein, MGP-PD 6793–6803 (part and counterpart); two paralectotypes MNHN 18, MCSNV Cr 51–52 (part and counterpart) (erroneously recorded by Secrétan as MCSNV 100–100bis).

Note: Specimen MGP-PD 6793–6803 has old labels stating, "*Cancer Bolcensis*? Zigno". The same specimen was named *Cancer Zignii* (*nomen nudum*) by Massalongo (1855: 32) and figured in plate 13 (fig. 1) of his unpublished *Compendium*.

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Additional material: CMC4 (previously illustrated as *Eriphia*? sp. by Cerato (2011: 112).

Emended description: Carapace – Carapace subhexagonal, wider than long, length about three-quarters of width, maximum width at junction between antero- and posterolateral margins; regions well defined by deep grooves; surface of regions coarsely granular; carapace flattened transversely and longitudinally; frontal margin broad, frontal width about one-third of maximum width; front extended slightly beyond orbits; front bilobed medially, lobes rounded, separated by a median fissure; frontal margin concave between inner orbital angle and medial lobes; narrow round orbits, directed forwards; rimmed supraorbital margin with two fissures; intraorbital spine well developed; convex inner orbital angle well distinct from the front; anterolateral margin weakly convex with 4 spines (excluding extraorbital spine); small 1st spine less developed outwards; triangular 2nd–3rd spines well developed outwards; smaller 4th spine on anterolateral angle; smooth posterolateral margin weakly convex; short posterior margin strongly convex and rimmed; gastric regions without transverse, discontinuous ridges; rectangular epigastric region slightly inflated, with a distinctly inflated, rounded bulge on each side; protogastric region inflated centrally and weakly depressed anteriorly, ornamented with small tubercles, anterior and inner margin nearly straight, outer and posterior margins convex; mesogastric region narrow anteriorly, lateral margins of anterior process nearly straight; region broadened distally, distal portion pentagonal, margins nearly straight; urogastric region weakly defined; pentagonal cardiac region markedly broader than urogastric region; intestinal region flattened,

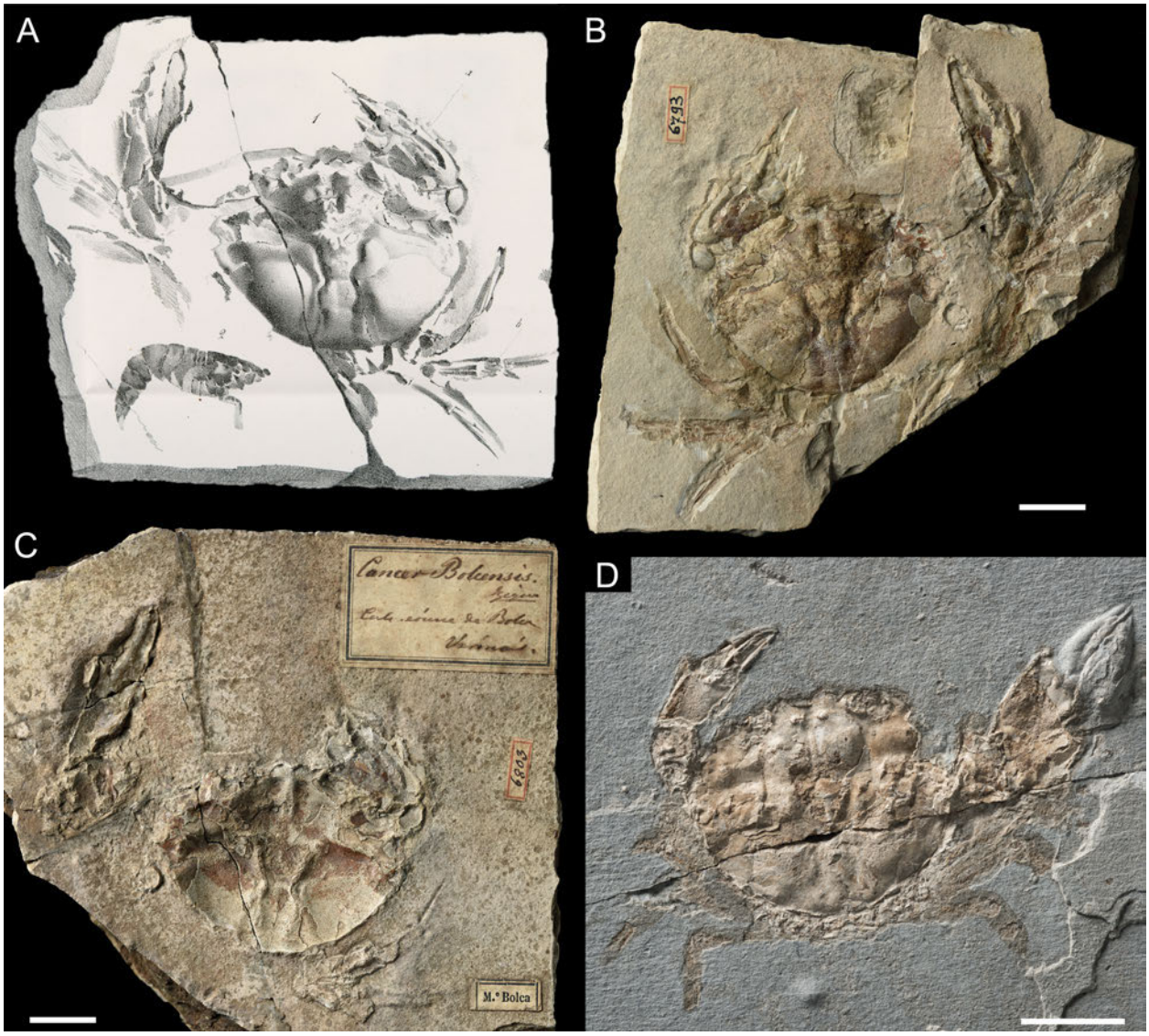

Fig. 11. *Lophopanopeus bolcensis* (Secrétan, 1975) n. comb. **A** – "*Compendium Faunae et Florae Fossilis Bolcensis*", Massalongo's unpublished plate 13, illustrating MGP-PD 6793 (lectotype, part). **B, C** – Lectotype MGP-PD 6793–6803 (part and counterpart). **D** – CMC4. Scale bars equal 20 mm.

not well developed; hepatic region weakly inflated centrally and without transverse, discontinuous ridges; epibranchial region inflated centrally and ornamented with small tubercles; mesobranchial region slightly inflated, ornamented with tubercles, merged with flattened metabranchial region. Thoracic appendages – Chelipeds (P1) heterochelous, with surface strongly granular; P1 palm longer than high, bulbous, with upper and lower margins slightly convex; P1 index and dactylus equal in size; P1 index, with straight smooth lower margin; occlusal margin of P1 index with molariform teeth; P1 dactylus, with smooth upper margin slightly concave; occlusal margin of P1 dactylus not visible; P1 dactylus more distinctly hooked at tip than that of index; P2–P5 elongate and narrow, with surface strongly granular; P2–P5 meri much longer than high, with straight upper and lower margins; P2–P5 carpi longer than high, with straight upper and lower margins; P2–P5 propodi with a longitudinal median tuberculate ridge; P2–P5 dactyli pointed.

Discussion: According to Manning (*in* Schweitzer 2000: 730) "Panopeus sensu lato, *is a diverse and speciose genus, which may actually be comprised of taxa referable to numerous closely related genera*". Moreover, Schweitzer (2000: 730) pointed out that "*differentiation of panopeid genera is based upon features that do not preserve in fossils*". Casadío et al. (2005: 167) provided a diagnosis of *Panopeus*

as follows, *"Carapace wider than long, length usually about two-thirds to three-quarters maximum carapace width; regions fairly well delimited, sometimes with transverse, discontinuous ridges or with granules on anterior half; anterolateral margins convex, shorter than posterolateral margins, with four spines excluding outer-orbital spine, outer-orbital spine coalesced with first anterolateral spine, remainder of anterolateral spines usually well-delineated; angle between anterolateral and posterolateral margins between 100 and 120 degrees, especially in fossil forms; fronto-orbital width more than half maximum carapace width; front about 30 percent maximum carapace width, with median notch, separated from inner orbital rim by a notch, may be produced beyond orbits; orbital margin with two open notches. Chelipeds unequal in males and females; merus with superior subterminal tooth; carpus with tooth at inner angle; fingers acute. Male genital openings coxal*".

Based upon the generic diagnosis, the lack of transverse, discontinuous ridges on hepatic and gastric regions and the spiny anterolateral margin, it follows that the studied specimens do not belong to *Panopeus*.

The general shape of the front, the narrow orbits, the spiny anterolateral margins, and the dorsal regions that are well-marked by grooves but lack transverse, discontinuous ridges on hepatic and gastric regions allow this material to be referred to *Lophopanopeus*, a genus previously recorded from the middle Eocene strata at Rossi quarry (Monte di Malo, Vicenza) by Beschin et al. (1998).

Superfamily Dorippoidea MacLeay, 1838
Family Dorippidae MacLeay, 1838

Genus *Archaeocypoda* Secrétan, 1975

Type species: *Archaeocypoda veronensis* Secrétan, 1975, by monotypy.

Included fossil species: *Archaeocypoda veronensis* Secrétan, 1975.

Archaeocypoda veronensis Secrétan, 1975
Fig. 12

1855 *Gonoplax ?*spec. indet. – Massalongo, p. 33.
1972 *Plagiolophus ellipticus*. – Sorbini, pl. 27, fig. 1.
*1975 *Archaeocypoda veronensis*. – Secrétan, pp. 363–369, figs. 21, 22, pl. 23, fig. 2; pls. 24, 25.
2005 *Archaeocypoda veronensis*. – Casadío et al., p. 175.
2006 *Archaeocypoda veronensis*. – De Angeli & Garassino, p. 79.
2010 *Archaeocypoda veronensis*. – Schweitzer et al., p. 79.
2014 *Archaeocypoda veronensis*. – Giusberti et al., p. 82, fig. 6d.
2016 *Archaeocypoda veronensis*. – Marramà et al., p. 7, fig. 7D.

Remarks: When introducting *Archaeocypoda*, with *A. veronensis*, as the type species, Secrétan (1975) failed to provide a generic diagnosis. Our review of the type series and additional material allows to establish an emended diagnosis for this poorly known genus.

Emended diagnosis: Suboval carapace; straight front with a shallow median fissure; supraorbital margin continuous; antero- and posterolateral margins smooth; metagastric region with two distal lateral tubercles; cardiac region with two median lateral tubercles; undifferentiated branchial regions; weak cervical groove; branchiocardiac groove absent; P1 heterochelous.

Type material: Holotype, MSNM i4563a, b (*ex* 45–45bis) (part and counterpart); Paratype, MSNM i4564 (*ex* i46), Paratype MCSNV 103–104 (part and counterpart).

Remarks: Specimens MCSNV 101, 102 noted by Secrétan (1975: 363) to belong to the type material are probably lost (L. Giusberti pers. obs. 2018). Specimen MCSNV 104 was illustrated by Massalongo in plate 16 of his unpublished *Compendium* and listed as "*Gonoplax*? spec. indet." in Massalongo (1855: 33). Specimen MCSN 97 was originally figured by Sorbini (1972) as "*Plagiolophus ellipticus*".

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Additional material: MSNVE 6310.

Emended description (based mainly on the holotype MSNM i4563, paratype MCSNV 103–104 female, and paratype MSNM i4564 male): Carapace – Suboval carapace slightly wider than long; relatively broad straight front with a shallow median fissure; front not protruding beyond orbits; postfrontal region bearing two paired elevate, short transverse ridges; wide deep orbits spoon-shaped; supraorbital margin continuous; extraorbital spine apparently absent; antero- and posterolateral margins rounded and smooth; long straight posterior margin slightly convex laterally for articulation with P5 basis; protogastric region slightly depressed medially; piriform meso- and metagastric regions; metagastric region with two distal lateral tubercles; urogastric region depressed; pentagonal cardiac region with two median lateral tubercles; wide flat intestinal region; branchial region undifferentiated; weak cervical groove; branchiocardiac groove absent; dorsal surface of carapace covered by small granules arranged uniformely. Male thoracic sternum and pleon – Sternum with smooth surface; sternites 1–4 completely fused, forming one plate without traces of sutures; sutures between sternites 4–8 medially interrupted; no trace of peg or tubercle on sternite 5 (one depressed pit on both lateral sides in female); sternopleonal cavity deep; elongate triangular and smooth pleon; s3–s5 probably fused; subtrapezoidal s6; triangular telson with round tip; G1 elongate, basal part broadest, median and distal parts slender, tubular, slightly curved distally. Thoracic appendages – P1 heterochelous; left P1 chela

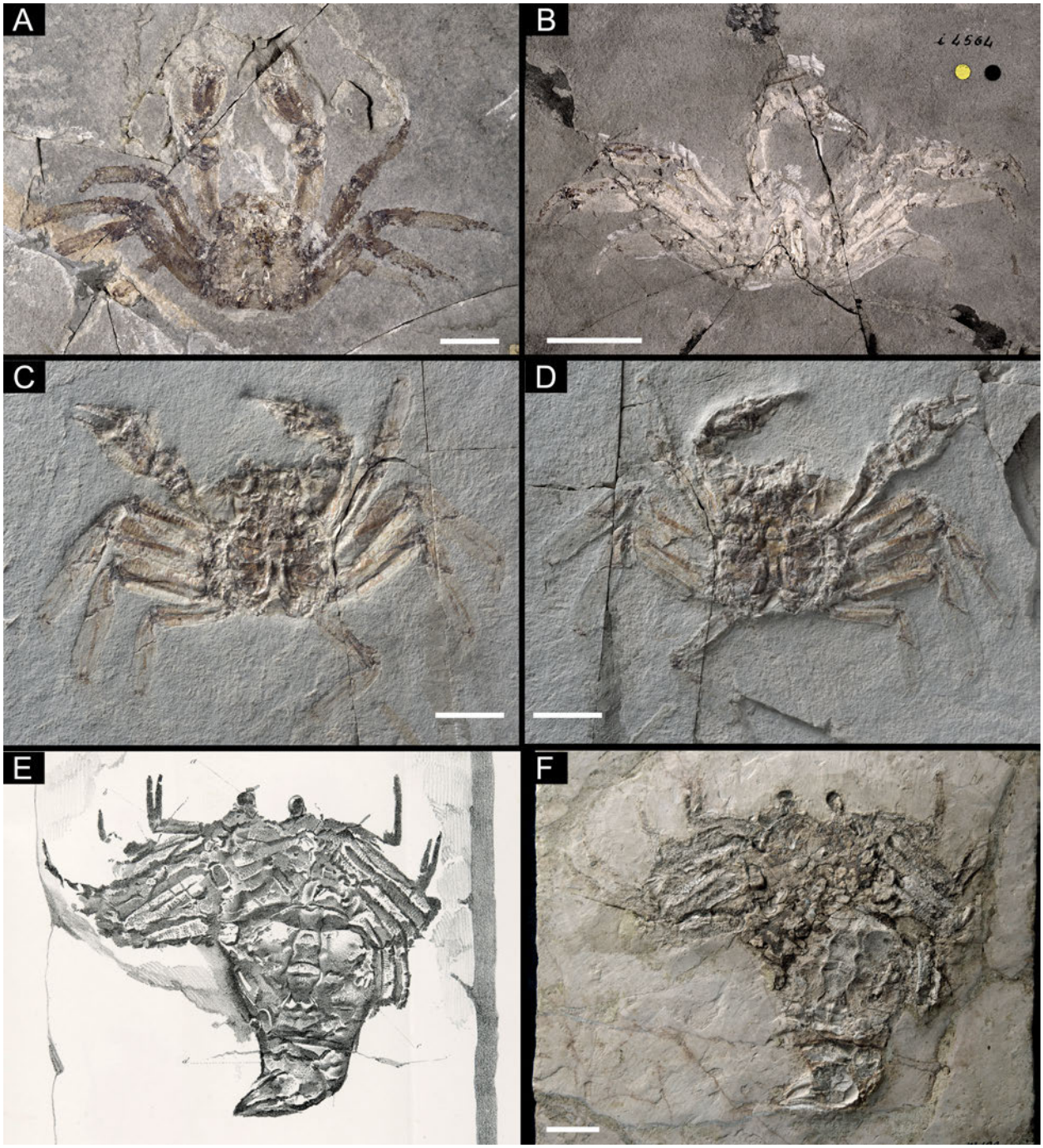

Fig. 12. *Archaeocypoda veronensis* Secrétan, 1975. **A** – Holotype, MSNM i4563a, b (*ex* 45–45bis). **B** – Paratype, MSNM i4564 (*ex* i46). **C, D** – MCSNV 97–97bis (part and counterpart). **E** – "*Compendium Faunae et Florae Fossilis Bolcensis*", Massalongo's unpublished plate 16, illustrating MCSNV 104. **F** – Paratype, MCSNV 104 (counterpart). Scale bars equal 20 mm.

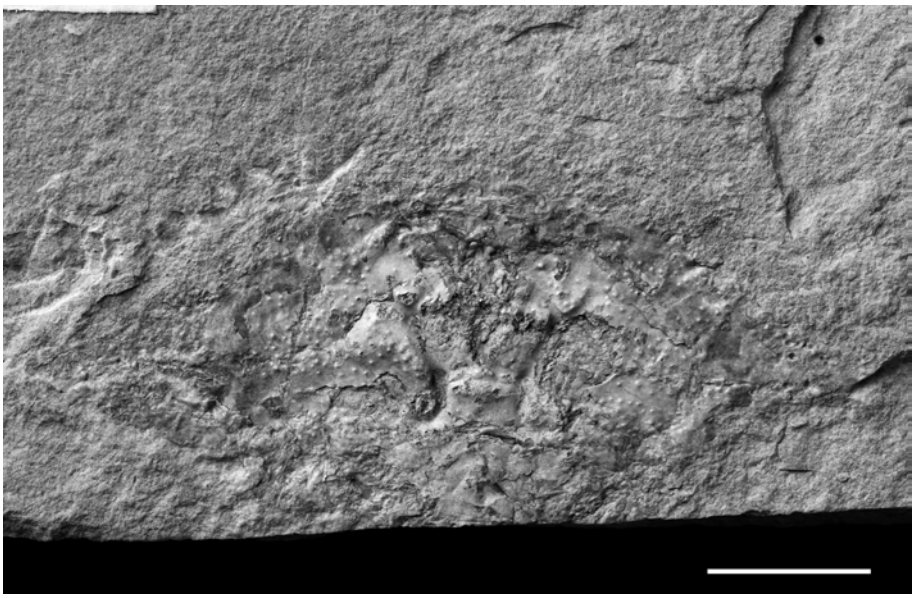

Fig. 13. *Portunus* sp., MCSNV M3. Scale bar equals 10 mm.

stouter than right P1 chela; elongate P1 merus with a strong distal outer spine at level of articulation with P1 carpus; subsquare P1 carpus; upper and lower margins of P1 palm smooth; P1 index and dactylus equal in size slightly curved distally; occlusal margin of P1 index with molariform teeth decreasing in size distally; occlusal margin of P1 dactylus slightly serrate; P1 elements covered by small granules uniformely arranged; elongate P2-P5, with pointed and gently curved dactylus; P5 slightly shorter than P2–P4; P2–P5 merus, carpus, and propodus longitudinally and medially carinate.

Discussion: According to Casadío et al. (2005: 175) *Archaeocypoda* should not be considered an ocypodid. Indeed, with regard to "*the rounded carapace, deep orbits, and relatively broad front*" the species may be better considered as "*a member of the Dorippidae* MacLeay, *1838*", as proposed by Schweitzer et al. (2010: 79). Proxy characters and the shape of the dorsal regions allow to exclude this species from the ocypodids. However, in dorsal view, paratype (MSNV 103–104) unfortunately has a very compressed carapace that does not allow a reliable reconstruction of the frontal outline, an important character useful for a more definitive systematic assignment. Therefore, according to Casadío et al. (2005) and Schweitzer et al. (2010) we prefer to keep *Archaecypoda veronensis* as a questionable dorippid. Only the discovery of better-preserved specimens can allow to resolve the systematic position of this taxon.

5.2. Specimens reported in open nomenclature by Secrétan (1975)

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815

Portunus sp.
Fig. 13

1975 *Portunus* sp. – Secrétan, p. 358, pl. 21, fig. 3.

Material: MCSNV M3.

Locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Discussion: Based on our review of the sole and poorly preserved specimen, the carapace appears wider than long, subhexagonal in shape, with a ridged and curved epibranchial region and an inner portion that is rather inflated; the mesogastric region is divided into two portions and appears swollen; the urogastric region is ridged, horizontally; deep grooves are present between the epibranchial and the gastric regions; the front looks as having small teeth; the anterolateral margin has numerous spines, the last one (= epibranchial spine) is longer than the previous ones. Despite the poor preservation, this specimen is clearly a portunoid, probably close to *Portunus*, as suggested by Secrétan (1975) and recently by P. Artal (pers. comm. 2018). Only specimens with complete front and complete anterolateral margins can resolve the correct systematic assignment of this specimen, now left in open nomenclature.

5.3. Species recorded by subsequent authors

Achelata Scholtz & Richter, 1995
Neoscyllarida J. T. Haug, Audo, Charbonnier, Palero, Petit, Abi Saad & C. Haug, 2016

Genus *Parsacus* Garassino, Bahrami, Yazdi & Vega, 2014

Type species: *Parsacus eocenicus* Garassino, Bahrami, Yazdi & Vega, 2014, by monotypy.

Included fossil species: *Parsacus eocenicus* Garassino, Bahrami, Yazdi & Vega, 2014.

?*Parsacus cristatus* (Förster, 1984)
Fig. 14

*1984 *Parribacus cristatus*. – Förster, pp. 62–64, fig. 2.
2001 *Parribacus cristatus*. – Garassino & Novati, pp. 251, 252, 258.
2007 *Parribacus cristatus*. – Webber & Booth, pp. 36–38, 397, fig. 2.5.
2007 *Parribacus cristatus*. – Vega et al., p. 408.
2014 *Parribacus cristatus*. – Giusberti et al., pp. 78, 82.
2014 *Parsacus cristatus*. – Garassino et al., p. 49, fig. 5 H.
2015 *Parsacus*? *cristatus*. – Haug & Rudolf, p. 114, figs. 1, 2.

Holotype: MB.A 88.

Type locality: Monte Postale (Altissimo, Vicenza).

Stratigraphical age: Early Eocene (late Ypresian).

Additional material: MGP-PD 10.029–10.030 (part and counterpart) (De Zigno Collection), 10.032–10.033 (part and counterpart) (De Zigno Collection), MGP-PD 12822 (Omboni Collection); MFB IG 135621–135622 (part and counterpart); MCSNV 67296–67297 (part and counterpart).

Discussion: Förster (1984) recorded *Parribacus cristatus* based upon one specimen from "Monte Bolca" or "Monte Postale" (exact provenance unclear, two different original labels reporting both localities). Later, Garassino et al. (2014) revised the systematic position of this species, assigning it to a new genus. Subsequently, Haug & Rudolf (2015) reinvestigated this species using macro-fluorescence imaging, revealing new characters indicating that the specimen clearly represented a nisto larval stage. This conclusion hampers not only the systematic assignment of this species, but also the comparison with fossil and extant forms since we would then compare non-corresponding stages. For this reason the systematic position of this species is still open and, as suggested by Haug & Rudolf (2015), for the time being the most effective way is to refer to it as ?*Parsacus cristatus*.

Remarks: Specimens MGP-PD 10.029–10.030 and 10.032–10.033 from the De Zigno Collection housed in the Museo di Geologia e Paleontologia dell'Università di Padova have been erroneously mislabelled as coming from the Jurassic Lagerstätte of Solnhofen, southern Germany (L. Giusberti pers. obs. 2018).

Genus *Scyllarides* Gill, 1898

Type species: *Scyllarus aequinoctialis* Lund, 1793, by original designation.

Included fossil species: see Schweitzer et al. (2010: 47).

Scyllarides bolcensis De Angeli & Garassino, 2008
Fig. 15A

*2008 *Scyllarides bolcensis*. – De Angeli & Garassino, pp. 173, 174, 176, figs. 5–7.
2010 *Scyllarides bolcensis*. – Schweitzer et al., p. 47.
2014 *Scyllarides bolcensis*. – Giusberti et al., pp. 78, 82.

Original diagnosis by De Angeli & Garassino (2008: 173): Carapace highly vaulted, without lateral cervical incision; carapace without postorbital spine; carapace with a strongly marked median ridge; grooves of carapace rather indistinct; inner orbital margin smooth; median ridges on abdominal somites hardly noticeable.

Holotype: MCSNV 69353.

Type locality: Monte Postale (Altissimo, Vicenza).

Stratigraphical age: Early Eocene (late Ypresian).

Description: See De Angeli & Garassino (2008).

Discussion: De Angeli & Garassino (2008) described *Scyllarides bolcensis* from the laminites of Monte Postale (Altissimo, Vicenza). Based on direct observation of the holotype, *S. bolcensis* is considered to be as a valid species within the Neoscyllarida (= crown-group Scyllaridae) *sensu* Haug et al. (2016).

Dromiacea incerta sedis

Genus *Eotrachynotocarcinus* Beschin, Busulini, De Angeli & Tessier, 2007

Type species: *Eotrachynotocarcinus airaghii* Beschin, Busulini, De Angeli & Tessier, 2007, by monotypy.

Included species: *Eotrachynotocarcinus airaghii* Beschin, Busulini, De Angeli & Tessier, 2007.

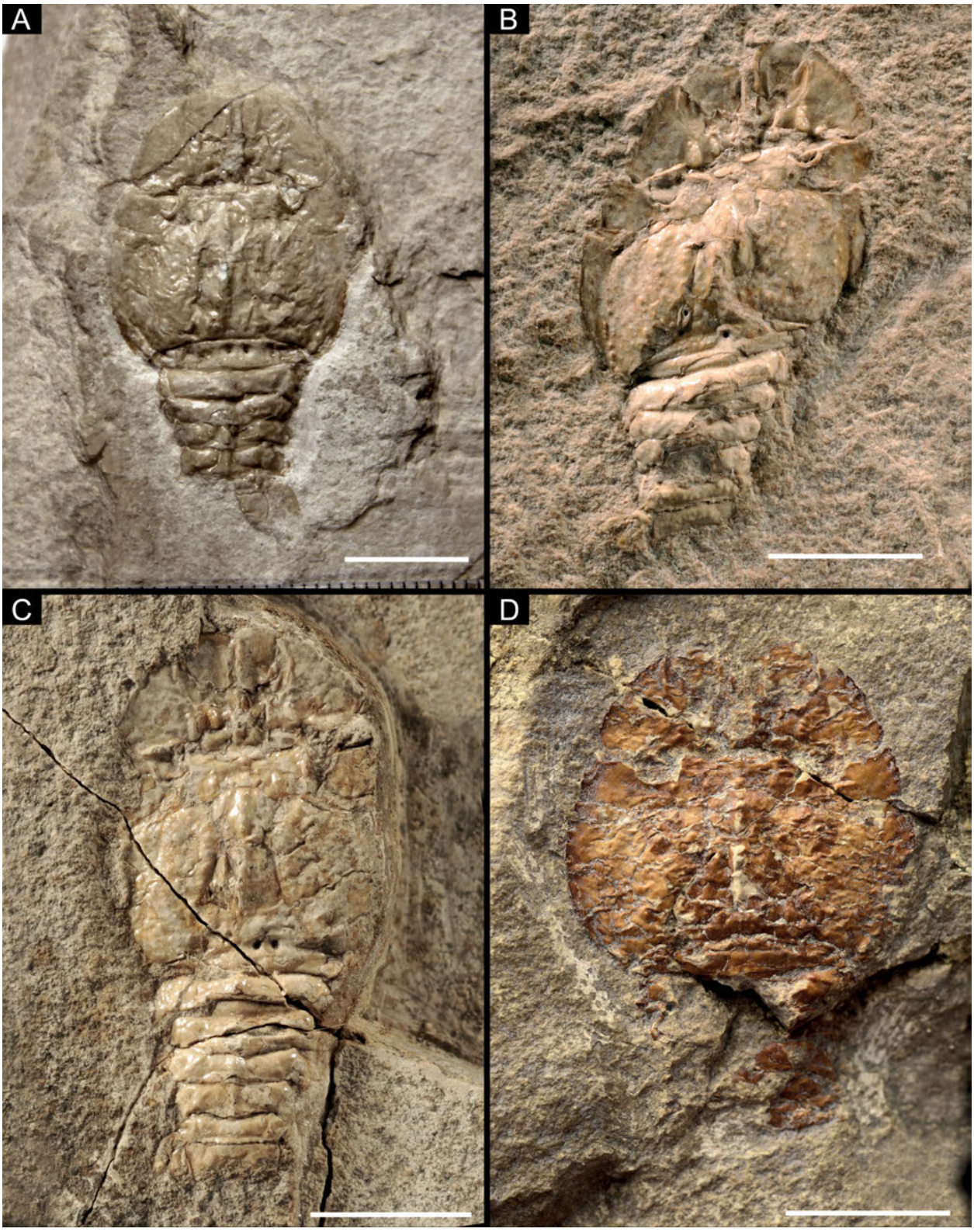

Fig. 14. ?*Parsacus cristatus* (Förster, 1984). **A** – Holotype, MB.A 88. **B** – MGP-PD 10029 (De Zigno Collection). **C** – MGP-PD 10033 (De Zigno Collection). **D** – MGP-PD 12822 (Omboni Collection). Scale bars equal 10 mm.

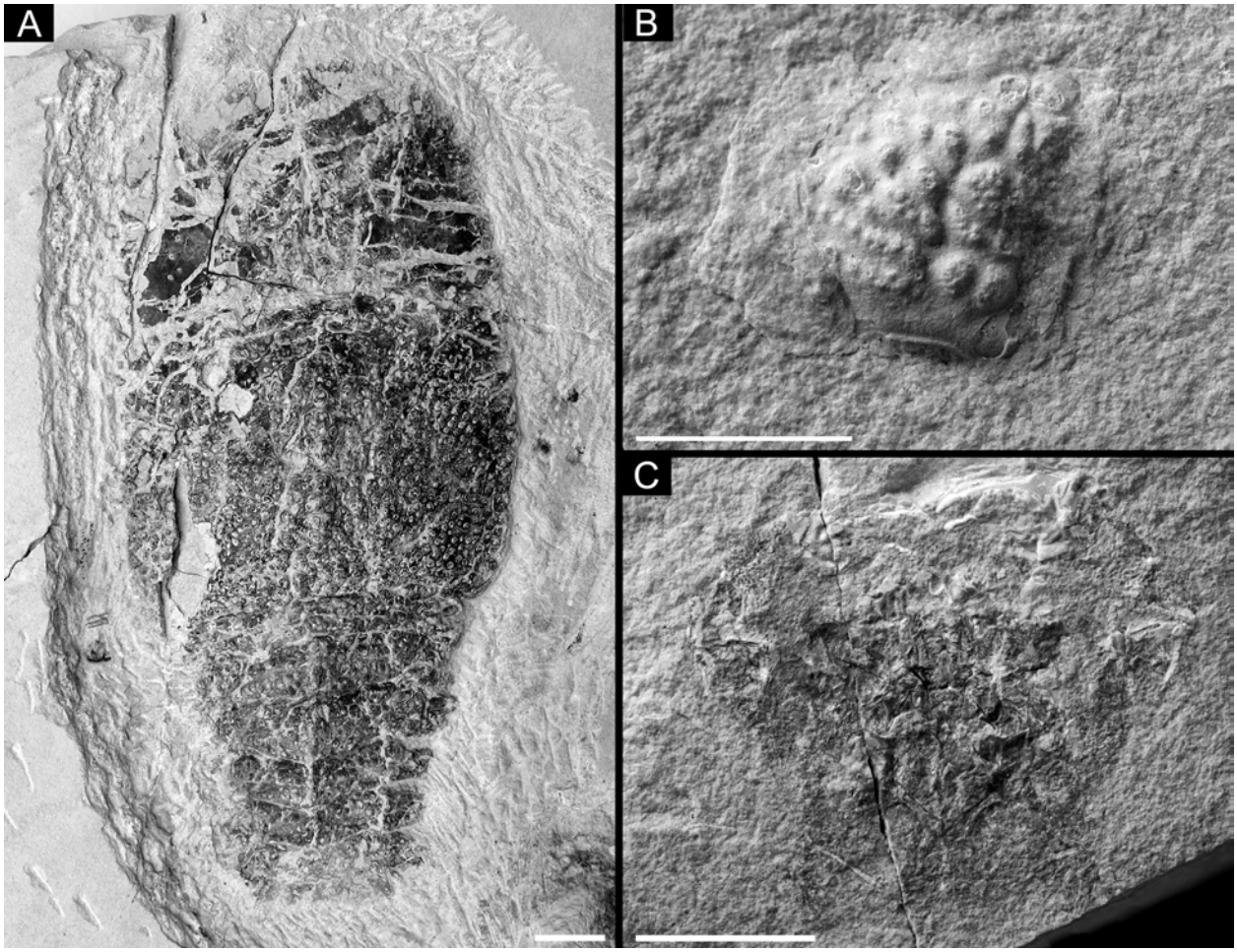

Fig. 15. A – *Scyllarides bolcensis* De Angeli & Garassino, 2008, Holotype MCSNV 69353. **B** – *Eotrachynotocarcinus airaghii* Beschin, Busulini, De Angeli & Tessier, 2007, MCVR 94552 (part). **C** – ?*Eriphia* sp., MCSNV 4. Scale bars equal 10 mm.

Eotrachynotocarcinus airaghii Beschin, Busulini, De Angeli & Tessier, 2007
Fig. 15B

**Eotrachynotocarcinus airaghii*. – Beschin, Busulini, De Angeli & Tessier, p. 25, pl. 2 , figs. 7–9.
2010 *Eotrachynotocarcinus airaghii*. – Schweitzer et al., p. 66.
2011 *Eotrachynotocarcinus airaghii*. – Tessier et al., p. 215, fig. 3.5.
2015 *Eotrachynotocarcinus airaghii*. – Beschin et al., p. 65, pl. 2, fig. 5.
2016 *Eotrachynotocarcinus airaghii*. – Beschin et al., p. 75, fig. 77, pl. 9, fig. 4.

Original diagnosis by Beschin et al. (2007: 25): Carapace subheptagonal, weakly convex, wider than long with the largest width on the posterior third; front having two lamellae divided by a median sinus; orbits large; anterolateral margins long, lobate, ending with a tooth; regions well defined with many swellings; meso-, metagastric, and cardiac regions with a longitudinal median groove; cervical groove almost transversal, engraved; three transverse grooves on the branchial regions; brief transverse ridge on metabranchial regions.

Material: MCSNV 94552–94553 (part and counterpart).

Locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Description: See Beschin et al. (2007).

Discussion: This species described by Beschin et al. (2007) from Gecchelina (Monte di Malo, Vicenza), has subsequently been recorded from the laminites of "Pesciara" (Bolca), based upon a single carapace without the right margin

(Beschin et al. 2016: 75, fig. 77). Although the specimen is incomplete and preserved as an inner cast, the main distinctive characters of the dorsal ornamentation allow to confirm the assignment of the studied specimen to this species.

5.4. Problematic taxa

Brachyura incertae sedis

?*Eriphia* sp.
Fig. 15C

1975 *Eriphia*? sp. – Secrétan, p. 362, fig. 20, pl. 23, fig. 1.

Material: MCSNV 4.

Locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Discussion: The specimen is a poorly preserved, small carapace, in ventral view, partially preserving both the granulated chelae and robust dactyli. Secrétan (1975: 362, 363, fig. 20) described this specimen and provided an interpretative line drawing, comparing it tentatively to *Eriphia*. The specimen lacks, however, the main characters of that genus, such as the rimmed frontal margin and the spiny anterolateral margins. Moreover, the missing dorsal ornamentation, dactyli that are more elongate and less robust than those of *Eriphia*, and the geological age question the hypothetical assignment to this genus advocated by Secrétan (1975: 363). In conclusion, due to the impossibility to observe substantial proxy character of the body, the specimen is herein referred to as an indeterminate brachyuran.

?*Macropipus ovalipes* Secrétan, 1975
Fig. 16

*1975 *Macropipus ovalipes*. – Secrétan, pp. 348–356, figs. 12–18, pls. 17–20.
2006 *Macropipus ovalipes*. – De Angeli & Garassino, p. 57.
2010 ?*Macropipus ovalipes*. – Schweitzer et al., p. 107.
2014 *Macropipus ovalipes*. – Giusberti et al., p. 82.
2018 *Macropipus ovalipes*. – Pasini et al., p. 72.

Type material: Holotype MCSNV 8 (Secrétan 1975: fig. 12c; pl. 17, fig. 3); MGP-PD 6800, 6801 (De Zigno Collection); MSNM i4565-4566 (part and counterpart) recorded as 47 and 95 (Secrétan 1975: pl. 17, figs. 1, 2); MCSNV NS Cr 1 (Secrétan 1975: pl. 18, fig. 2); MCSNV 2–2bis (part and counterpart) (Secrétan 1975: fig. 16a; pl. 19, figs. 1, 2); MCSNV 3 (Secrétan 1975: pl. 20, fig. 1); MCSNV 6–6bis (part and counterpart) (Secrétan 1975: fig. 12a; pl. 20, fig. 3); MCSNV 9 (Secrétan 1975: fig. 12b; pl. 20, fig. 4); MCSNV 11 (Secrétan 1975: fig. 15b; pl. 20, fig. 2); MCSNV 12 (Secrétan 1975: fig. 15a; pl. 20, fig. 5); MCSNV 15 (Secrétan 1975: pl. 18, fig. 1); Cr 7, Cr 13 (illustrated by Secrétan 1975: fig. 14) could not be found in the MCSNV collection.

Remarks: Secrétan (1975: 347) recorded six specimens in the MGP-PD collections: 6800, 6801, 6802, 6895–6898 (part and counterpart), and 6896. Specimens MGP-PD 6802, 6895, and 6896 were not recovered in the collections of Museo di Geologia e Paleontologia dell'Università di Padova (L. Giusberti pers. obs. 2018).

Type locality: "Pesciara" (Bolca, Verona).

Stratigraphical age: Early Eocene (late Ypresian).

Additional material: MSNVE 4581, 4582, 6301; MGP-PD 6798.

Remarks on the type material: Among about thirty specimens available, only some have been chosen as type series of this species by Secrétan, based upon their state of preservation (see updated list above). Our review of these specimens has allowed to update and point out some substantial remarks on Secrétan's original descriptions, as follows:

MCSNV NS Cr 1: Based upon the picture and line drawings in Secrétan (1975: figs. 12d, 13 a–c; pl. 18, fig. 2), we can state that this specimen is a female in ventral view, preserving the complete spatulate left P5, a typical character of representatives of the swimming crabs within the Portunidae. However, this specimen is now lost, so that we have not been able to verify the presence of the extraorbital and anterolateral spines and the spatulate left P5 that Secrétan (1975: 349) noted.

MCSNV 2–2bis (part and counterpart): specimen in ventral view, having a partial, straight unarmed frontal margin, granulated ornamentation, incomplete left chela slightly larger than the right, incomplete elongate P1–P4, and P5 with short, flattened, and enlarged merus and twisted carpus, but lacking the propodus and the dactylus. The morphology of P5 is such that it could be speculated that could this was used in swimming.

MCSNV 3: specimen in ventral view, having left chela with elongate, dentate pointed dactylus curved distally and partial shorter index, thoracic petaloid sternites 4–8 well preserved, granulated dorsal inner surface with coarse pits (possibly corresponding to rounded granules on the carapace surface), P1–P4 elongate, P5 not preserved.

MCSNV 6–6bis (part and counterpart): specimen in dorsal view, having straight frontal margin, lateral margins poorly preserved, short straight posterior margin, dorsal surface with small coarse, rounded granules, with some possible elevated ?tubercles on the anterior part, indent regions poorly preserved, well-marked V-shaped gastric groove, delimiting the cardiac regions, legs not preserved. MCSNV 8: specimen in dorsal view, having subtrapezoidal, granulated carapace (as preserved), frontal margin almost straight,

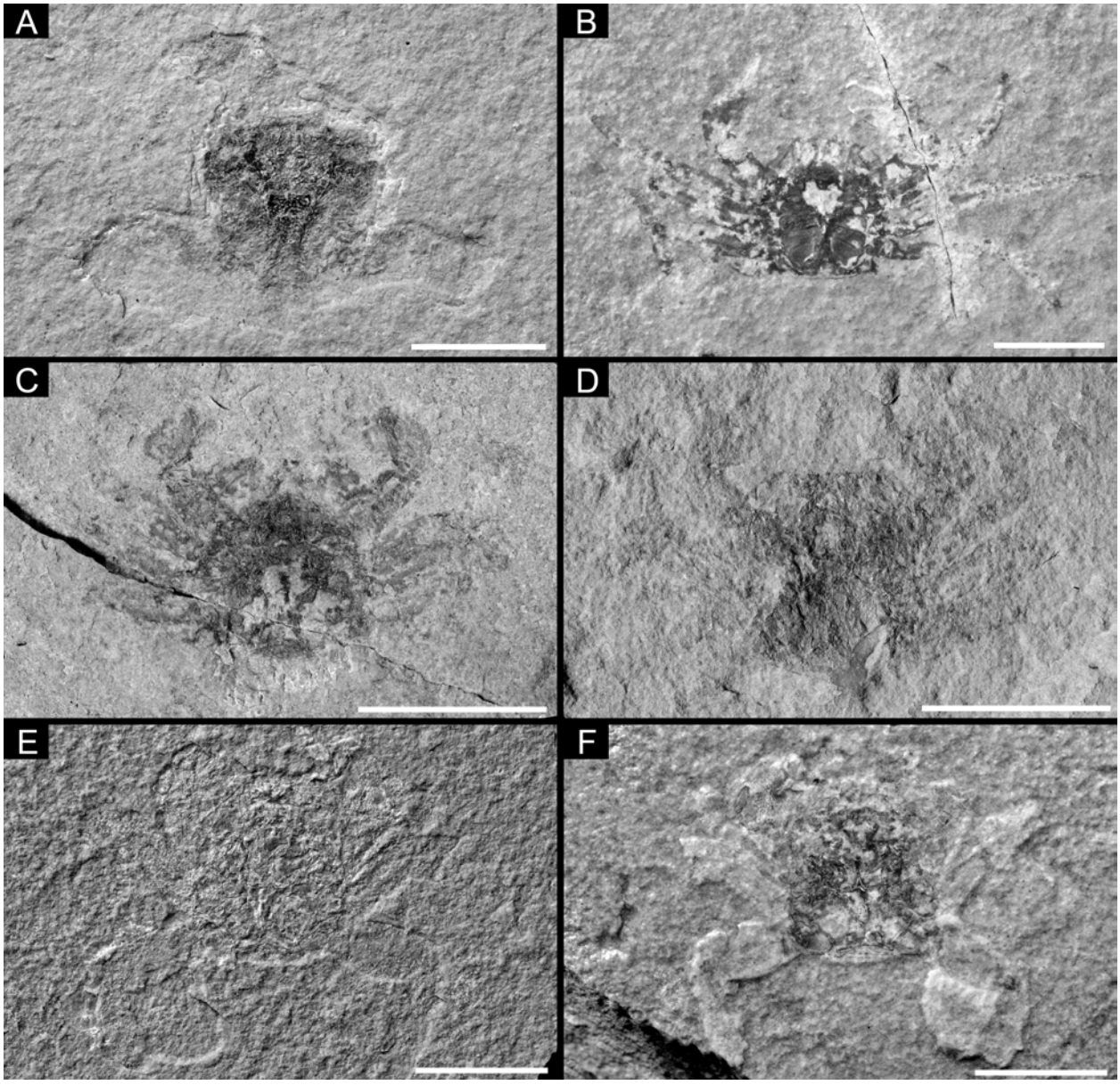

Fig. 16. ?*Macropipus ovalipes* Secrétan, 1975. **A** – Holotype, MCSNV 8. **B** – MCSNV 3. **C, D** – MSNM 4565–4566 (part and counterpart). **E, F** – MCSNV 2–2bis (part and counterpart). Specimens in A and F were immersed in alcohol prior to photography. Scale bars equal 10 mm.

continuous (*vs* "*median frontal incision*", Secrétan 1975: 349), anterolateral margin poorly preserved without spines or teeth (*vs* Secrétan 1975: 349, fig. 12c), posterolateral margins converging to the posterior margin shorter than the frontal, curved, V-shaped branchial groove, and poorly preserved P5.

MCSNV 9: male specimen in ventral view, having straight frontal margin (*vs* "*median frontal incision*", Secrétan 1975: 349), outline of carapace not preserved, elongate P1–P4, wide flattened P5 merus, subrectangular pleonal sternites 1–5 similar in size and shape.

MCSNV 11: poorly preserved specimen in dorsal view, having straight frontal margin and granulated dorsal ornamentation.

MCSNV 12: specimen partially exposed in dorsal view, having straight front margin, possible right ?extraorbital pointed spine forwardly directed, carapace surface (as preserved) covered with small rounded grains and alternating

elevated tubercles on the anterior-postfrontal regions, thoracic sternites partially exposed on the posterior part of the body, legs poorly preserved.

MSNM i4565-4566 (recorded as 47 and 95 by Secrétan 1975: pl. 17, figs. 1, 2) (part and counterpart): female specimen in ventral view, having straight continuous frontal margin, anterolateral convex margin unarmed (as preserved) mainly covered by chelipeds coxa and ambulatory legs, chelipeds short with subglobular palms equal in size, slender, elongate P1–P4, with pointed triangular elongate dactylus, P5 with merus, carpus and poorly preserved propodus wide, flattened and short, most probably ending in a paddle-like dactylus.

Finally, specimens MCSNV 15 (ventral view), MCSNV Cr 7 and MCSNV Cr 13 (incomplete chelipeds) have not been discussed in detail herein, because they show the same characters described in the above-mentioned specimens.

Discussion: Secrétan (1975: 347) based this species on about thirty small-sized specimens, but failed to provide a specific diagnosis. Due to the poor preservation of this material, the species has been described based on the morphological characters visible on a single specimen, designated as holotype. The assignment to *Macropipus* Prestandrea, 1833 relied mainly on a single specimen which preserved a complete articulated P5 with a paddle-like dactylus (MCSNV NS Cr 1 – Secrétan 1975: 350, fig. 1a–c; pl. 18, fig. 2), today lost. According to Koch & Ďuriš (2016: 124), *Macropipus* has, based on the typical characters of *M. tuberculatus* (Roux, 1830), a front with three distinct sharp teeth, with the median tooth more pointed than lateral ones, a distinctive granulation over the whole carapace and distinctive elevated regions, a serrated anterolateral margin with the 5th anterolateral spine larger than the others, and P5 with broadly lanceolate dactylus and with a clearly visible median carina. After a careful examination of the type material we confirm that *M. ovalipes* clearly has a straight non-serrate frontal margin, as pointed out by Secrétan (1975: 353), non-serrated anterolateral margins (as preserved), and probably a single postorbital spine. Most of the specimens are preserved in ventral view and those that are exposed dorsally (MCSNV 8, 11, 12) the ornamentation is not clearly visible due to the compression of the small and weak carapaces, usually admixed with exposed ventral parts.

In conclusion, our inability to distinguish the characters described by Secrétan (1975) calls assignment of these specimens to *Macropipus* into question. Moreover, there is no diagnostic character that could support the generic status of the present form. Therefore, we consider it to be an indeterminate brachyuran.

Remarks: Although Secrétan (1975) tentatively assigned all the studied specimens to the Portunidae, it is possible to postulate that several of these had straight unarmed frontal margin, ?subsquare carapace, short P1 chelipeds, and more or less evident P5 with broadly lanceolate dactyli. These could belong to a new fossil taxon within the grapsoid Varunidae H.-M. Edwards, 1853, which contains extant representatives showing with comparable proxy characters.

5.5. New records

Superfamily Raninoidea De Haan, 1839
Family Raninidae De Haan, 1839
Genus *Lophoranina* Fabiani, 1910

Lophoranina maxima Beschin, Busulini, De Angeli & Tessier, 2004
Fig. 17A–C

Material: MCSNV Cr 55–56 (part and counterpart); IG VR 27697–27698 (part and counterpart).

Locality: "Pesciara" (Bolca, Verona) and Monte Postale (Altissimo, Vicenza).

Stratigraphical age: Early Eocene (late Ypresian).

Description: One specimen (MCSNV Cr 55–56) poorly preserved frontally, in dorsal view, crushed and compressed dorsoventrally, preserving both chelipeds; one very incomplete carapace (IG VR 27697–27698) is crushed into three fragments partially overlapping, lacking the frontal margin.

Discussion: The carapace ornamentation with transverse tegulated rims is typical of *Lophoranina*. Specimen, MCSNV Cr 55–56 is large sized: it preserves the chelipeds with propodus having the lower margin with three spines (except the index); the dorsal carapace surface has transverse granulate rims; the dorsal anterior rims have the median part convex anteriorly, whereas the posterior rims are more or less straight or interrupted and convex posteriorly; the anterolateral margin has two sharp spines.

According to Beschin et al. (2004, 2011) this specimen is assigned to *Lophoranina maxima*, first recorded from the Lutetian of "Main" quarry of Arzignano (Vicenza) and Ciupio di San Giovanni Ilarione (Verona). Specimen IG VR 27697–27698 is highly incomplete and the dorsal ornamentation has transverse granulate rims as the previous specimen. Probably also this specimen can be assigned to *Lophoranina maxima.* Both specimens are assigned to *L. maxima* rather than to *L. marestiana* (König, 1825), usually common in the Ypresian-Lutetian of Veneto region, because the latter is not only smaller, but also differs from *L. maxima* in having the lower margin of the cheliped with five spines (except the index), a lesser number of tranverse rims convex posteriorly, and the second anterolateral spine bifid.

Remarks: Massalongo (1855: 33) reported the occurrence of a raninid from "Monte Bolca", ascribed to "*Ranina Aldrovandi*". It is unclear if such report relies or not on MCSNV Cr 55–56, the specimen coming from old historical excavations at "Pesciara" and presently housed in the collections of Museo Civico di Storia Naturale di Verona.

Superfamily Majoidea Samouelle, 1819
Family Majidae Samouelle, 1819

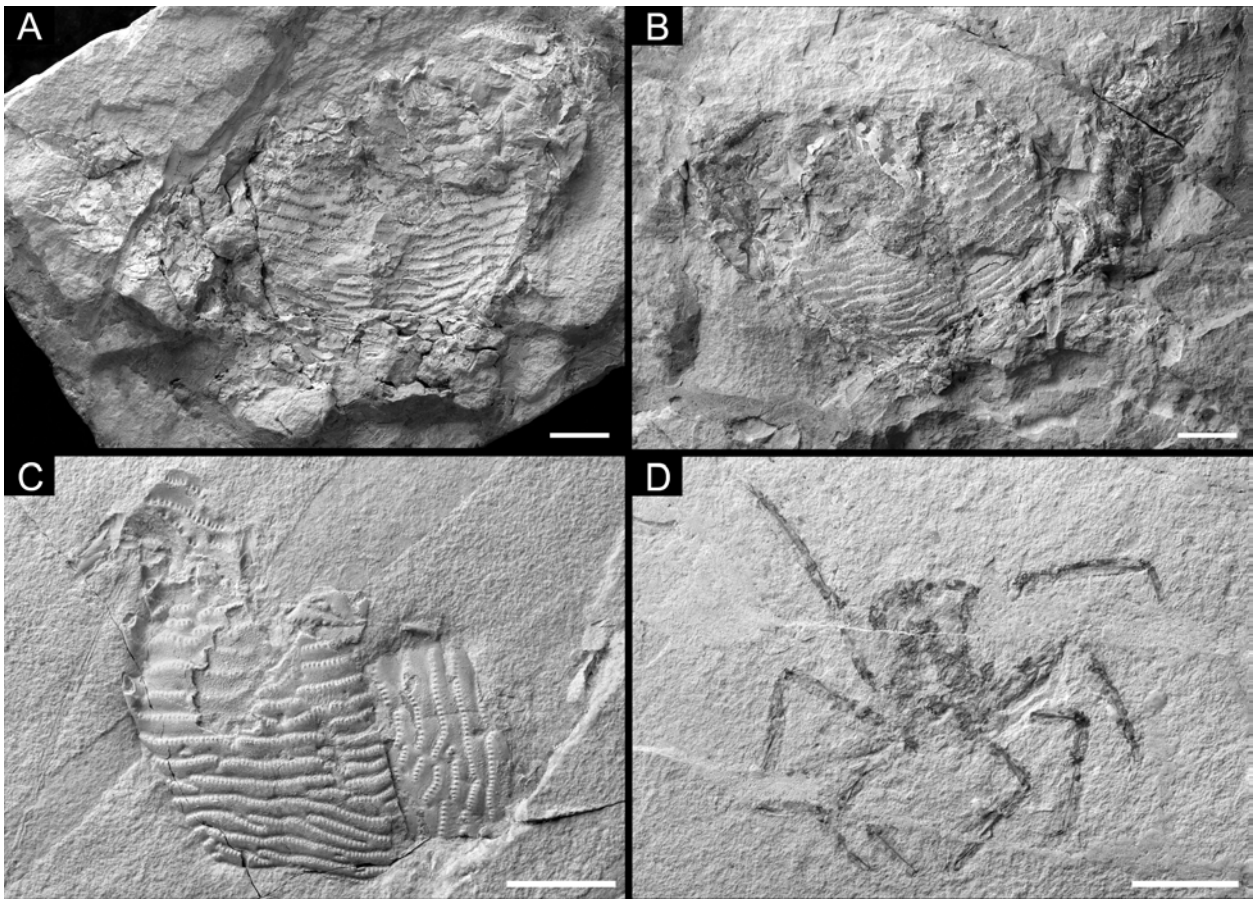

Fig. 17. A, B – *Lophoranina maxima* Beschin, Busulini, De Angeli & Tessier, 2004, MCSNV Cr 55–56 (part and counterpart). **C** – *Lophoranina maxima* Beschin, Busulini, De Angeli & Tessier, 2004, IG VR 27697 (part). **D** – Superfamily Majoidea Samouelle, 1819, family, genus, and species indeterminate, IG VR 67295. Scale bars equal 20 mm.

Genus and species indeterminate
Fig. 17D

2016 *Archaeocypoda veronensis*. – Marramà et al., p. 7, fig. 7D.

Locality: Monte Postale (Altissimo, Vicenza).

Stratigraphical age: Early Eocene (late Ypresian).

Material: IG VR 67295–67498 (part and counterpart).

Remark: The counterpart is nowadays kept in the MFB collections.

Description: A single specimen dorsoventrally preserved in part and counterpart from the 2004 digs at the Monte Postale, pertains to a spider crab generically. Like the majority of decapod crustaceans from the laminites of the "Pesciara" – Monte Postale sites, the carapace of this specimen is poorly preserved and compressed, showing parts of the dorsal carapace mixed in with the pleonal structures, whereas the original body margin shape is scarcely visible. The specimen preserves shorter chelipeds with elongate slender incomplete chelae, all arranged in life posture and the four elongate walking legs with a curved pointed dactylus. The body has the typical pyriform shape, rounded and larger posteriorly and narrower frontally. The frontal margin is poorly preserved with a rostral spine (visible on the right side of the front) and part of the orbit with the inner orbital spine. Elongate 3mxp, protruding frontally, ending with a curved, short pointed dactylus.

Discussion: The general carapace shape, with rounded, poorly convex posterior margin, the presence of one rostral spine on the right side of the front, the presence of the inner orbital spine, the short chelipeds, and the elongate walking legs are proxy characters typical of the Majidae Samouelle, 1819, resembling those of some representatives of the Inachinae McLeay, 1838. However, the in-

ability to identify other main distinctive dorsal, frontal, and orbital characters of the carapace does not allow substantial generic and specific comparisons. Therefore we prefer to leave the specimen in open nomenclature.

6. The crustacean assemblage: environmental and taphonomic remarks

Recently Marramà et al. (2016) have provided new insights into the palaeoecology and taphonomy of the fish assemblages of the "Pesciara" and Monte Postale, based upon quantative analysis of findings coming from the 1999–2011 controlled excavations. Although that particular study does not include details on invertebrates, it has strongly improved our knowledge of the palaeoecology and palaeoenvironment of the Bolca Konservat-Lagerstätte, and has provided a useful step for some preliminary remarks on the significance of the decapod crustacean assemblage.

We point out here that the total number of specimens for each species recorded to date from both sites is too low to provide any quantitative significant analysis for understanding the real composition of the decapod crustacean assemblage. Moreover, most of the studied specimens come from historical collections or from recent "non-supervised" excavations, lacking detailed stratigraphic data and records of their distribution according to distinct fossiliferous beds. Therefore, only some generic behavioural and environmental observations on their taphonomy are possible.

According to Secrétan (1975), the poor state of preservation of decapod crustaceans, i.e, usually compressed, and only rarely preserved three-dimensionally, renders their taxonomic evaluation difficult or even impossible. Specimens originate from levels in a random manner, commonly in part and counterpart. No schooling behaviour or mass mortality events have been reported to date from either site.

The penaeids are the commonest decapod crustaceans at both sites. They are usually poorly preserved, having a weakly calcified exoskeleton, with the body strongly laterally compressed and incomplete carapaces lacking the cephalic appendages. Indeed, only few specimens from "Pesciara" have been assigned to *Penaeus bolcensis*, based upon the present re-evaluation. However, penaeids must certainly have been more differentiated and widespread in the shallow subtropical waters around both the "Pesciara" and Monte Postale basins.

Although the brachyurans have more heavily mineralised carapaces and chelae than penaeids, they are also insufficiently preserved, with the carapace strongly crushed, compressed dorso-ventally or overlapped with ventral regions, seldom complete, mostly preserved in ventral view, with chelipeds and legs usually partially preserved or lost. Some specimens show the ventral shield twisted and exposed posteriorly (?moult).

In several specimens only the thoracic appendages are in a life-like position, especially those from the "Pesciara" or with the chelipeds directed forwards frontally (e.g., MSNM i4564, MSNV 97) suggesting the presence of a possible moderate current at the bottom of the basin.

Only achelatans show a slightly better state of preservation at both sites, which is a result of their harder and thicker exoskeletons.

Moreover, we point out that the rare preservation of decapod crustacean bodies contrasts with the "*high quality preservation*" (Marramà et al. 2016: 13) that has been observed for a great number of fish and non-crustacean invertebrates from "Pesciara".

Indeed, "Pesciara" laminites are considered to have been deposited in an "intraplatform basin in which anoxic conditions at the bottom and development of the biofilm acted as promoters of high-quality fossil preservation" (Marramà et al. 2016: 13). These conditions do not appear to have been conductive to preservation of decapod crustacean bodies, maybe due to the unfavourable chemistry on the bottom of the basin. Most crustacean specimens, due to the relative disarticulation of the body, suggest that they pertain to moults, whereas others seem to have been transported after death, with some defacement disarticulation of the organisms prior to final burial.

The presence of several benthic stomatopods and uncommon axiidean shrimps (exhibiting fossorial behaviour), usually completely preserved in the laminites of "Pesciara" does not match the anoxic conditions present at the bottom of the basin. This could most probably suggest that these specimens were trasported in some way from a nearby platform prior to death.

In contrast, the Monte Postale laminites reflect on the contrary a different depositional context "likely deposited close to an emerged coastal area characterized by mangroves' seagrass, and coral reefs, with high degree of disturbance producing prominent disgregation of the fish remains… suggesting at least periodic aerobic conditions at the bottom" (Marramà et al. 2016: 13). This hypothesised palaeoenvironment explains better the state of preservation of the fauna assemblage of Monte Postale, as well as the decapod

crustacean assemblage, including benthic, swimming, and reefal decapod genera.

In conclusion, based upon our re-evaluation, it is not possible to present a clear reconstruction of the taxonomic diversity and distribution of the decapod crustacean assemblage from the "Pesciara" – Monte Postale Konservat-Lagerstätte, but a few preliminary observations can be made. The low number of identifiable specimens does not correspond with the high palaeodiversity suspected for the palaeoenvironments at both sites. The decapod crustacean assemblages appear to be quite similar (considering also the specimens not identified at the species level), excluding the presence of some species more strictly linked to a reefal environment (as at Monte Postale), whereas the fish fauna shows clear differences between both sites (Marramà et al. 2016). The majority of recorded taxa suggests that the decapod crustacean species inhabited the platform or nearshore environments. The conditions at the bottom of the "Pesciara" basin that allowed a near-perfect preservation of the fossil fish fauna appear not to have favoured the preservation of carbonate exoskeleton of crustaceans. No clear evidence of predation on any decapod crustacean specimens has been reported, except for a single specimen from "Pesciara" (CMC4, *Lophopanopeus bolcensis*), which shows a strange, deep fracture along the right anterolateral carapace margin that possibly is a result of a bite of a supposed fish predator. Moreover, in comparison with the higher number of specimens reported from the "Pesciara", the poor record from Monte Postale does not appear to represent the real variety and distribution of the decapod crustacean fauna in the basin. This likely reflects also more intense excavations at "Pesciara" over the years, in contrast to the occasional and intermittent digs at Monte Postale.

Finally we point out the (apparent) absence of representatives of anomurans (e.g., Paguroidea) amongst the decapod crustacean faunas at both sites due to probably the unfavourable environment (dysoxic/anoxic) at the bottom of both basins.

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Addresses of the authors:

Alessandro Garassino (corresponding author), Research Adjunct, Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92354, USA;
e-mail: alegarassino@gmail.com

Giovanni Pasini, Via Alessandro Volta 16, 22070 Appiano Gentile (Como), Italy;
e-mail: giovannialdopasini@gmail.com

Antonio De Angeli, Associazione Amici del Museo Zannato, Piazza Marconi 15, 36075 Montecchio Maggiore (Vicenza), Italy;
e-mail: antonio.deangeli@alice.it

Matúš Hyžný, Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, Bratislava, Slovakia;
e-mail: hyzny.matus@gmail.com

Luca Giusberti, Department of Geosciences, University of Padua, Via Gradenigo 6, 35131 Padua, Italy;
e-mail: luca.giusberti@unipd.it

Roberto Zorzin, Museo Civico di Storia Naturale di Verona, Lungadige Porta Vittoria 9, 37129 Verona, Italy;
e-mail: roberto.zorzin@comune.verona.it

Table 1. Complete and updated list of decapod crustacean species (Isopoda, Stomatopoda, and Decapoda) with distribution in the laminites of the "Pesciara" (left column) – Monte Postale (right column) Konservat-Lagerstätten, based upon recent and present reviews. The systematics of stomatopod and isopod crustacean fauna have recently been discussed by De Angeli & Garassino (2008), Vonk et al. (2015), and Robin et al. (2018), respectively.

	"Pesciara"	Monte Postale
Order Isopoda Latreille, 1817		
Genus *Cirolana* Leach, 1818		
Cirolana acuticauda (Secrétan, 1975)	X	–
Cirolana titanophila Robin, Marramà, Vonk, Kriwet & Carnevale, 2018	X	–
Genus *Dynamenella* Hansen, 1905		
Dynamenella veronensis (Secrétan, 1975)	X	X
Order Stomatopoda Latreille, 1817		
Genus *Lysiosquilla* Dana, 1852a		
Lysiosquilla antiqua (Münster, 1842)	X	X
Genus *Pseudosquilla* Dana, 1852a		
Pseudosquilla lessinea De Angeli & Garassino, 2008	–	X
Infraorder Axiidea de Saint Laurent, 1979		
Genus *Bolcacalliax* nov.		
Bolcacalliax eocenica (Secrétan, 1975)	X	–
Order Decapoda Latreille, 1803		
Genus *Penaeus* Fabricius, 1798		
Penaeus bolcensis Secrétan, 1975	X	–
Genus *Justitia* Holthuis, 1946		
Justitia desmaresti (Secrétan, 1975)	X	–
Genus *Scyllarides* Gill, 1898		
Scyllarides bolcensis De Angeli & Garassino, 2008	X	–
Genus *Archaeocypoda* Secrétan, 1975		
Archaeocypoda veronensis Secrétan, 1975	X	–
Genus *Eotrachynotocarcinus* Beschin, Busulini, De Angeli & Tessier, 2007		
Eotrachynotocarcinus airaghii Beschin, Busulini, De Angeli & Tessier, 2007	X	–
Genus *Enoplonotus* A. Milne-Edwards, 1860		
Enoplonotus armatus A. Milne-Edwards, 1860	X	–
Genus *Lophopanopeus* Rathbun, 1898		
Lophopanopeus bolcensis (Secrétan, 1975) n. comb.	X	–
Genus *Lophoranina* Fabiani, 1910		
Lophoranina maxima Beschin, Busulini, De Angeli & Tessier, 2004	X	X