



***Lophoranina maxima* Beschin, Busulini, De Angeli & Tessier, 2004 (Decapoda Brachyura, Raninidae) from Lower Eocene laminites of the “Pesciara di Bolca” (Verona, northeast Italy)**

***Lophoranina maxima* Beschin, Busulini, De Angeli & Tessier, 2004 (Decapoda Brachyura, Raninidae) iz spodnjeeocenskih laminiranih apnencev “Pesciara di Bolca” (Verona, severovzhodna Italija)**

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Ključne besede: raki, deseteronožci, tafonomija, paleogen, Sredozemlje

Abstract

The sole specimen of a raninid crab found to date in the Lower Eocene Fossil-Lagerstätte of the “Pesciara di Bolca” (Verona, northeast Italy) and referred to *Lophoranina maxima*, is described. Results of a CT analysis of this specimen and of a study of its cuticle are discussed.

Izvleček

Opisan je edini primerek raninidne rakovice, ki je bila do sedaj najdena v spodnjeeocenskih apnencih znanega nahajališča “Pesciara di Bolca” (Verona, severovzhodna Italija) in pripada vrsti *Lophoranina maxima*. Predstavljeni so rezultati CT analize primerka in analiza kutikule oklepa.

Introduction

Among representatives of the so-called “minor fauna” from the Lower Eocene Fossil-Lagerstätte called “La Pesciara” (Bolca, Vestenanova, Verona, northeast Italy; Fig. 1) abundant specimens of malacostracan crustaceans have been found; these are referred to the Isopoda, Decapoda and Stomatopoda. Most of these are housed in the collections of the Natural History Museum in Verona, the Fossil Museum at Bolca, the University of Padua and the Natural History Museum in Milan. After incomplete analyses published during the 19th century, they were studied in detail by Secretan (1975). Amongst brachyurans she described species of the families Macropipidae Stephenson & Campbell, 1960, Portunidae Rafinesque, 1815, Panopeidae Ortmann, 1893, Eriphiidae MacLeay, 1838 and, probably, of the

Ocypodidae Rafinesque, 1815. Since then some of these remains have been revised and additional specimens recovered. Vonk et al. (2015) studied the Isopoda, while additional papers dealt with stomatopods (see Giusberti et al., 2014). Finally, Pasini et al. (2019a, b) thoroughly revised the crustacean fauna from this area.

The sole specimen of the genus *Lophoranina* Fabiani, 1910a from the “Pesciara” laminites (Fig. 2) is on display in the permanent exhibition of the Natural History Museum in Verona. Despite easy access to this fossil it has never been analysed in full. The reason why it was not included in her study by Secretan (1975) is unknown: at that time, it certainly was already housed in the palaeontological collections of the Veronese museum. It was recorded for the first time by Beschin et al. (2011) as *Lophoranina marestiana*



Fig. 1. Location of the “Pesciara di Bolca” site (modified after Beschin et al., 2016b).

(König, 1825), but not described. Later, Zorzin et al. (2019) referred it to *Lophorantina maxima* and this attribution has subsequently been confirmed by Pasini et al. (2019b). This note presents a detailed description and analysis of this particular individual.

Geological setting of the “Pesciara di Bolca”

The Bolca area, with its famous Fossil-Lagerstätten of the “Pesciara” and Monte Postale, is located in the eastern part of the Lessini Mountains at an altitude of about 800 metres above sea

level near the watershed between the high Alpone Valley (Vestenanova, Verona) and the Chiampe Valley (Altissimo, Vicenza). This territory is part of the Southern Alpine tectonic unit; in a general geological framework it is constituted mainly by volcanic rocks and secondarily by small outcrops of carbonate rocks of Cretaceous–Paleogene age that rest on the so-called Trento Platform palaeogeographical unit. During the Middle Jurassic it formed a structural high between the Lombard and Belluno lateral basins; later it completely subsided and up to the Paleocene it assumed the character of a pelagic plateau with marine sedimentation. During Alpine Orogeny this area responded rigidly to tectonic stresses and was broken up into blocks. Some of these rose up to shallow sea conditions; on these small carbonate platforms came into existence. Afterwards they built a unique structure called the Lessini Shelf (Bosellini, 1989).

Important faults produced during the Paleocene and Early and Middle Eocene activated volcanic cycles with emissions of great amounts of basic lavas, mostly submarine, associated with extensional tectonics (Piccoli, 1965, 1966). Late Eocene volcano-tectonic activity resulted in the opening of the Alpone-Agno graben or semigraben, a wide and lengthy depression delimited to the west by the Castelvetro Fault and to the east by the Schio-Vicenza fault system. During quiescent phases of volcanism in the Early and Middle Eocene, carbonate sediments and marls were cyclically laid down in this graben (Barbieri et al., 1991; Zampieri, 1995). Despite intense magmatic activity, a rich fauna, represented by crustaceans,



Fig. 2. Panoramic view of the “Pesciara” site.

bivalves, gastropods, echinoids and other macrobiota inhabited the sea floor. Fossils are perfectly preserved and particularly abundant within the Eocene tuffites cropping out in the Chiampo Valley and in the Roncà area (central and southern Alpone Valley): they have been studied with great interest since the 18th century.

Tectonic stresses produced fragile responses on the calcareous rocks with the isolation of a series of blocks bounded by faults; some of these collapsed as olistolithes in the basin (Barbieri & Zampieri, 1992; Zampieri, 1995). This is the case for the “Pesciara” outcrop which is made up of a series of Lower Eocene calcareous strata, about 19 metres thick, and completely surrounded by volcanoclastic rocks (Papazzoni & Trevisani, 2006).

Fossils recovered from the “Pesciara”, mostly fish and plants, are preserved in five successive horizons made of extremely fine-grained, thinly laminated limestones that are interbedded with detrital calcareous levels that yield invertebrate remains, mostly larger foraminifera, bivalves and gastropods. This succession of fine- and coarse-grained limestones testifies to cyclic phases of different environmental conditions.

The environment of the “Pesciara” is characterised by deposition of calcareous muds within an intra-platform basin, in which anoxic bottom conditions and a microbial film that developed on corpses enabled perfect preservation of its rich and diverse fossil fauna (Marramà et al., 2016; Friedman & Carnevale, 2018). The presence of coral reefs that are similar to the ones observed along the coasts of the present-day St. Croix Island (Caribbean Sea) cannot be excluded, at least along the outer margin of the “Pesciara” lagoon (Beschinn et al., 2017).

The “Pesciara” is the most famous and important Eocene Fossil-Lagerstätte in Italy. Excavations since the 16th century, and particularly those in the 2000s on the instigation of the Museum of Natural History in Verona, have allowed to recover not only a great number of fish (Bosellini et al., 2014), but also remains of reptiles and birds and a rich “minor fauna”. The latter comprises crustaceans (malacostracans and ostracods), scorpions, bivalves, cephalopods, gastropods, brachiopods, bryozoans, worms, corals, jellyfish and foraminifera.

Material and methods

The specimen studied here exposes the carapace in dorsal view as well as both chelipeds and is preserved as two slabs (width about 245 mm; length about 195 mm); it is housed in the collec-

tions of the Natural History Museum in Verona (Museo Civico di Storia Naturale di Verona), under registration numbers CR 55 and CR 56.

CR 55 is the negative (Figs. 3a, b), CR 56 the positive (Figs. 4a, b). CR 56 was computed tomography (CT) scanned and its cuticle was studied with the use of a stereoscopic microscope (Leica M165C).

Systematic palaeontology

Order Decapoda Latreille, 1802
 Infraorder Brachyura Linnaeus, 1758
 Section Podotremata Guinot, 1977
 Subsection Gymnopleura Bourne, 1922
 Superfamily Raninoidea De Haan, 1839
 Family Raninidae De Haan, 1839
 Genus *Lophoranina* Fabiani, 1910a

Type species: *Ranina marestiana* König, 1825, by original designation.

Lophoranina maxima Beschinn, Busulini, De Angeli & Tessier, 2004
 1983 *Lophoranina reussi*; Busulini et al., p. 61, pl. 2, fig. 1 (*non* Woodward, 1866).
 1988 *Lophoranina* cf. *reussi*; Beschinn et al., p. 185, fig. 8, pl. 5, fig. 1; pl. 8, figs 1-4; pl. 9, fig. 1.
 2004 *Lophoranina maxima* Beschinn, Busulini, De Angeli & Tessier, p. 110, text-figs. 1, 2; pl. 1, figs. 1-3; pl. 2, figs. 1, 2.
 2006 *Lophoranina maxima*; De Angeli & Garrassino, p. 35.
 2010 *Lophoranina maxima*; Schweitzer et al., p. 73.
 2011 *Lophoranina marestiana*; Beschinn et al., p. 38 (*pars*).
 2011 *Lophoranina maxima*; Beschinn et al., p. 46, text-fig. 9, pl. 4, fig. 1.
 2019 *Lophoranina maxima*; Zorzin et al., p. 97, figs. 1, 2.
 2019b *Lophoranina maxima*; Pasini et al., p. 261, fig. 17A, B.

Measurements (in mm): Carapace: maximum width ~ 95; posterior width ~ 50; length > 85. Right carpus: height ~ 20. Right propodus: maximum length ~ 50; maximum height ~ 35. Right dactylus: length ~ 30; height ~ 10.

Description (based on both positive and negative): Subovate carapace, dorsoventrally compressed and strongly damaged in both anterior and posterior parts; only right part of wide fronto-orbital margin preserved with a strong and

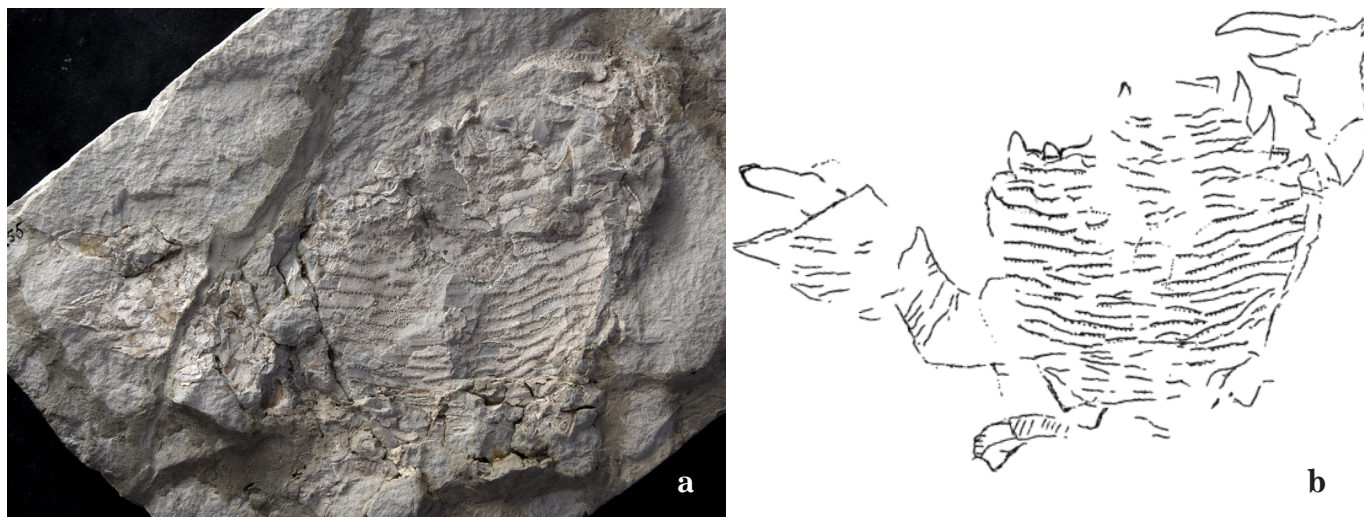


Fig. 3. CR 55, negative (maximum width 95 mm), in photograph (a) and line drawing (b).

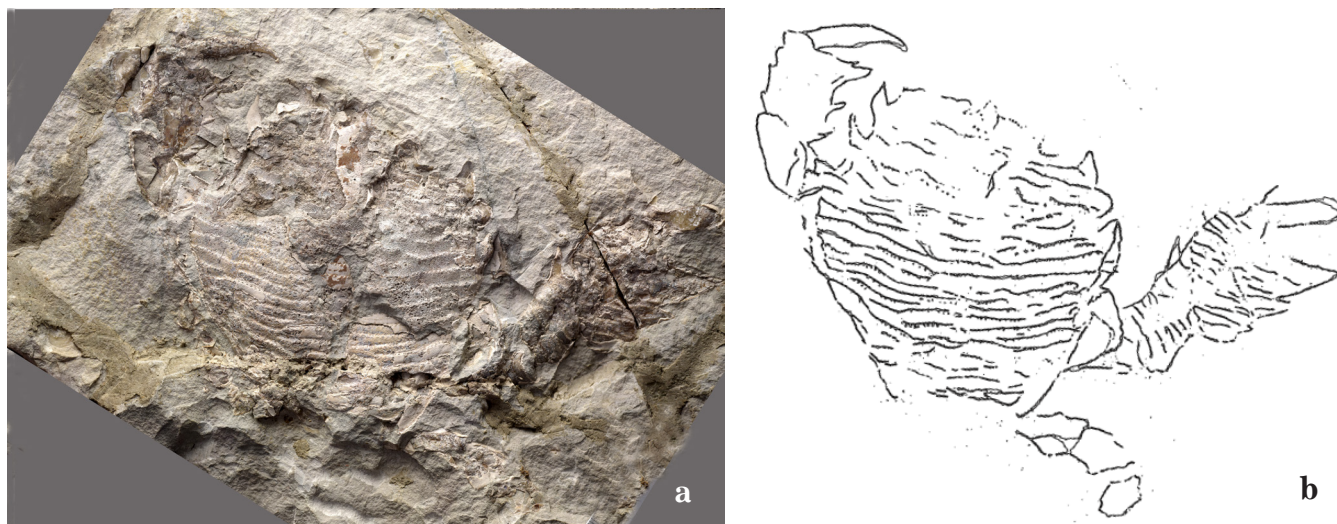


Fig. 4. CR 56, positive part (maximum width 95 mm), in photograph (a) and line drawing (b).

pointed lateral tooth and a supraorbital tooth defined by two fissures (Fig. 5a). Lateral margins convergent; almost completely preserved and appearing double because of separation of upper and lower part of carapace during fossilisation (Fig. 5b). In anterior part of right margin, traces of two large teeth visible; two spiny large teeth can be observed on left margin (Fig. 5c) linked to a fragment of carapace that was thrown forwards probably during fossilisation and so dislocated from original position. Rear part of right lateral margin showing granulated rim (Fig. 5d). Posterior margin, that should have been narrower than fronto-orbital margin, is lacking. Dorsal ornament with at least 21 subparallel transverse terraces, well preserved mainly in intermediate part of carapace, where terraces are nearly continuous from one side to the other, while rear ones appear interrupted. As far as can be seen,

the frontal area was short. On terraces, bases of small spines that constituted them are visible as regularly spaced, tiny pits.

In median anterior part, there is a structure recognised as the sternal plate using CT scanning (Fig. 6b); it shows some weak transverse terraces that probably are traces of ornament of carapace impressed on it.

Both chelipeds are preserved: left one is settled near carapace, almost in anatomical position and covered with matrix; right one outstretched and shows propodus and carpus; both large, stout, covered with subparallel transverse ridges. Carpus appears almost squarish with a spine on upper distal angle; propodus shows a spine on upper margin and three spines on lower margin (including fixed finger); dactylus is long and sickle-shaped. Distal part of right fifth pereopod with paddle-like dactylus.

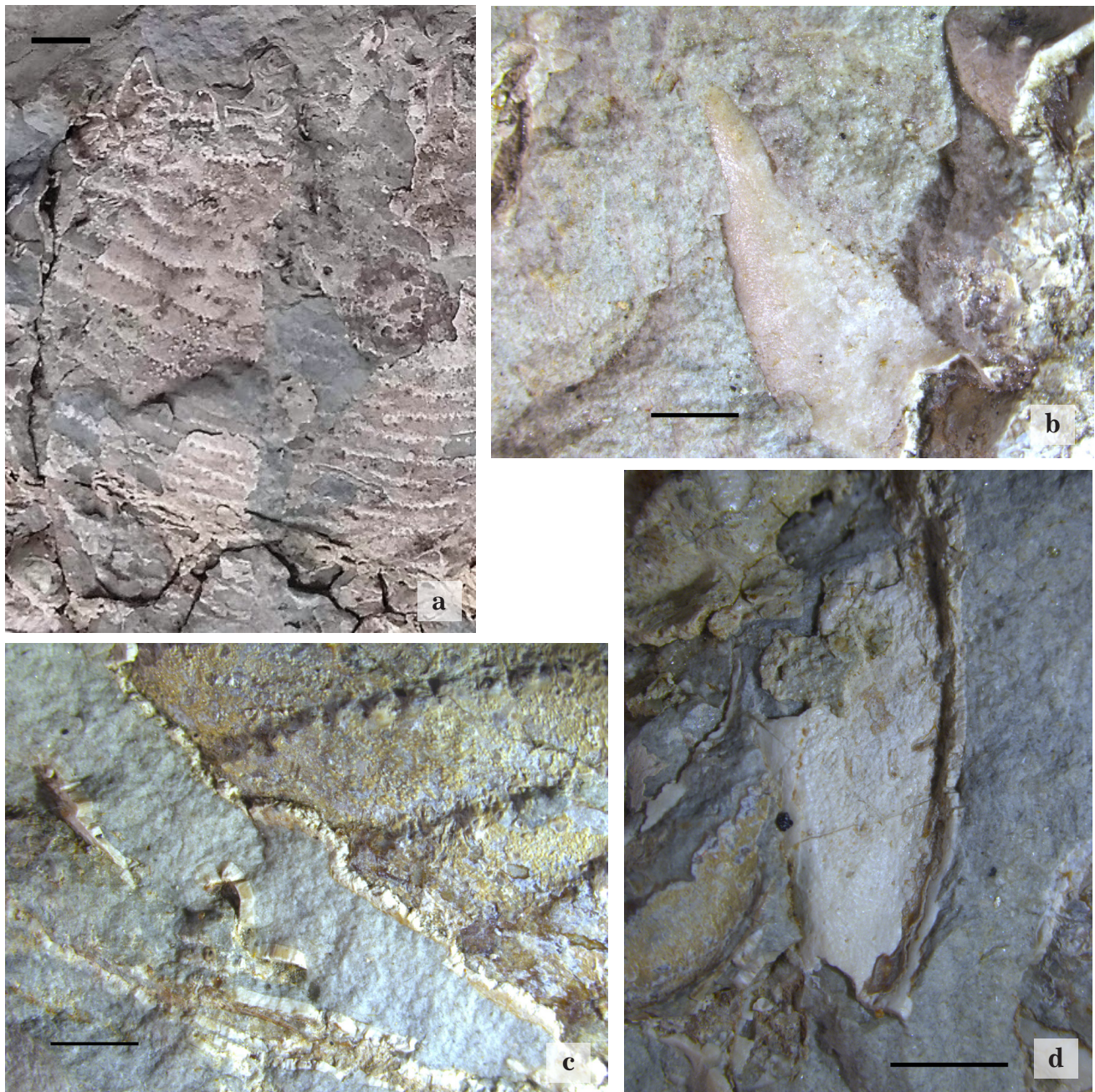


Fig. 5. Details of carapace: A. CR 55 (negative), right orbital and lateral margins (scale bar equals 10.0 mm); B. CR 56, double left posterolateral margin (scale bar equals 2.8 mm); C. CR 56, left anterolateral tooth (scale bar equals 2.5 mm); D. CR 56, right posterolateral margin (scale bar equals 4.0 mm).

Distribution: *Lophoranina maxima* has previously been recorded only from Lutetian (Middle Eocene) rocks at Main Quarry (Arzignano-Vicenza) and Case Pozza di San Giovanni Ilarione (Verona). It is now recognised in Ypresian (Lower Eocene) levels in the “Pesciara di Bolca” (Verona) and, according to Pasini et al. (2019b), also at Monte Postale.

Discussion

Fabiani (1910a; see also Fabiani, 1910b) erected the genus *Lophoranina* to accommodate species that had previously been included in *Ranina* Lamarck, 1801, but showed transverse terraces

composed of tiny, forwardly inclined spines on the dorsal carapace surface. This extinct genus has a worldwide distribution and a stratigraphical range from the Eocene to the Miocene. In Veneto (northeast Italy), representatives of *Lophoranina* are highly characteristic of Eocene levels of volcanoclastic origin and include numerous species such as *L. avesana* (Bittner, 1883), *L. bittneri* (Lörenthey, 1902), *L. laevifrons* (Bittner, 1875), *L. marestiana* (König, 1825), *L. maxima*, *L. reussi* (Woodward, 1866), *L. straeleni* Vía Boada, 1959 and, probably, *L. aldrovandii* (Ranzani, 1818) (see Beschin et al., 1988, 2011, 2016a). The structure of the dorsal terraces and the large

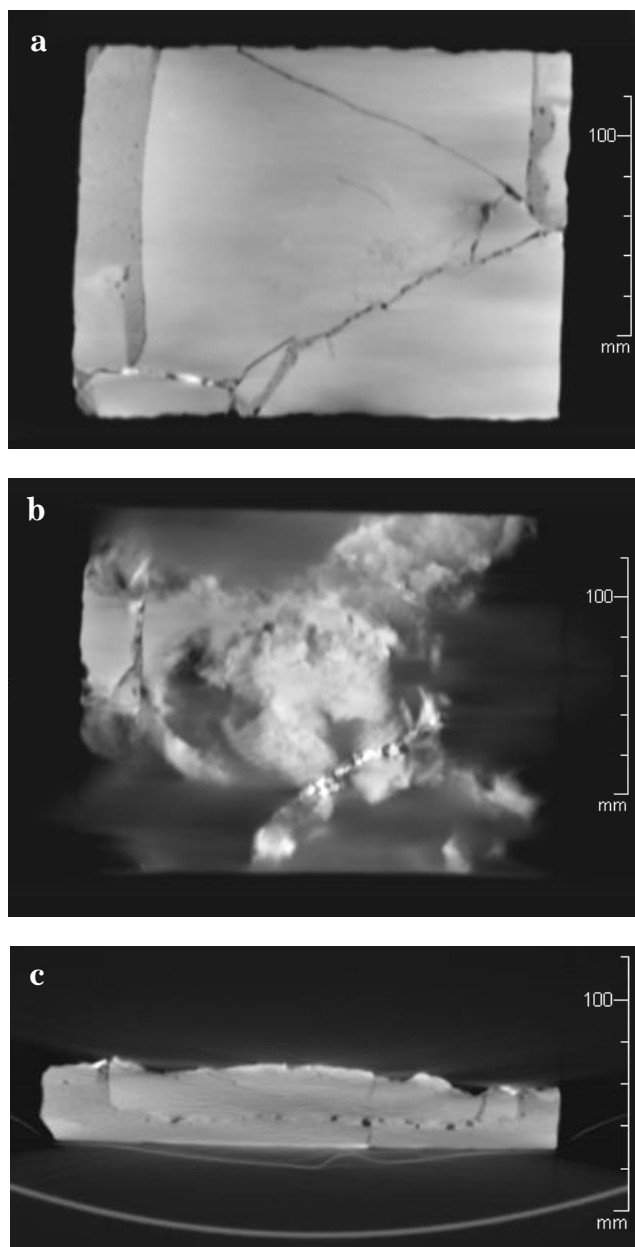


Fig. 6. CR 56. A. CT coronal reconstruction of the slab under the specimen (depth 20.1 mm); B. CT coronal reconstruction showing the specimen (depth 8.6 mm); C. CT axial scan (81 mm from the anterior margin of the slab).

carapace size, the short fronto-orbital region, the position and number (two) of anterolateral spines, the relatively short propodus of chelipeds with only three spines on the lower margin, all suggest that specimen CR 55/56 belongs to *Lophorantina maxima*. As far as comparisons with other large-sized species of *Lophorantina* are concerned, *L. avesana* has fewer ridges on the dorsal surface but these are more continuous and form a general anterior concavity; moreover, the anterolateral spines are spatulate rather than spiny, and the propodus of the cheliped is longer with a dentate lower margin. *Lophorantina mar-estiana* has a longer fronto-orbital area, more regular ridges, less acute anterolateral spines

that are situated more anteriorly, the propodus of the cheliped with six spines (including the fixed finger) on the lower margin. The differences with the other species are greater.

Our CT analysis of specimen CR 56 (positive) has revealed that the matrix piece in which the specimen is preserved was broken into four main pieces along three straight fractures (Fig. 6a). One fracture cuts the specimen in the rear part of the carapace and a second one runs through the propodus of the right cheliped (Fig. 4a).

During restoration, fragments were fixed with a thick cement on a calcareous slab (in its turn divided into two parts) as a reinforcement (total thickness about 37 mm) (Fig. 6c). This preparation method was applied to fossils found in the “Pesciara” during the 1930s (Massimo Cipriano Cerato, pers. comm., 2019; the Cerato family of Bolca are the owners of the “Pesciara” site, where excavations have been ongoing for about two centuries, and during the last fifty years under supervision of the Museum of Natural History in Verona). Hence, specimens CR 55/66 of *Lophorantina maxima* was presumably collected during those years. The CT axial scan shows that the frog crab is almost completely dorsoventrally flattened and produced only a weak relief of the surface of the slab. The CT coronal reconstruction shows the outline of the carapace with a thick fracture in its rear part and the collapsed cardiac part; a small shield-shaped structure in the anterior part is reminiscent of the sternal plate (Fig. 6b); it was probably dislocated during fossilisation.

The general preservation of this specimen confirms observations made by Secretan (1975), who noted that the crustaceans found in the “Pesciara” were almost flattened and lost any reliefs, their outlines being “confused” and part of the cuticle removed and dislocated.

Cuticle is preserved mainly in specimen CR 55 (negative): it shows almost the entire carapace cuticle in its inner, deeper part (Fig. 5a). In specimen CR 56 (positive) only a few shreds of the cuticle can be seen. An analysis using a stereoscopic microscope detected thick cuticle in a natural cross section along the lateral margins of the carapace and at the tip of the dactylus, and revealed details of the deep structure of the finger. As can be seen in Figure 7a, the preserved cuticle in its upper margin is composed of a thick endocuticle that shows undulate laminations in its deep portion; each undulation corresponds to a small globular swelling in the amorphous filling of the dactylus surmounted

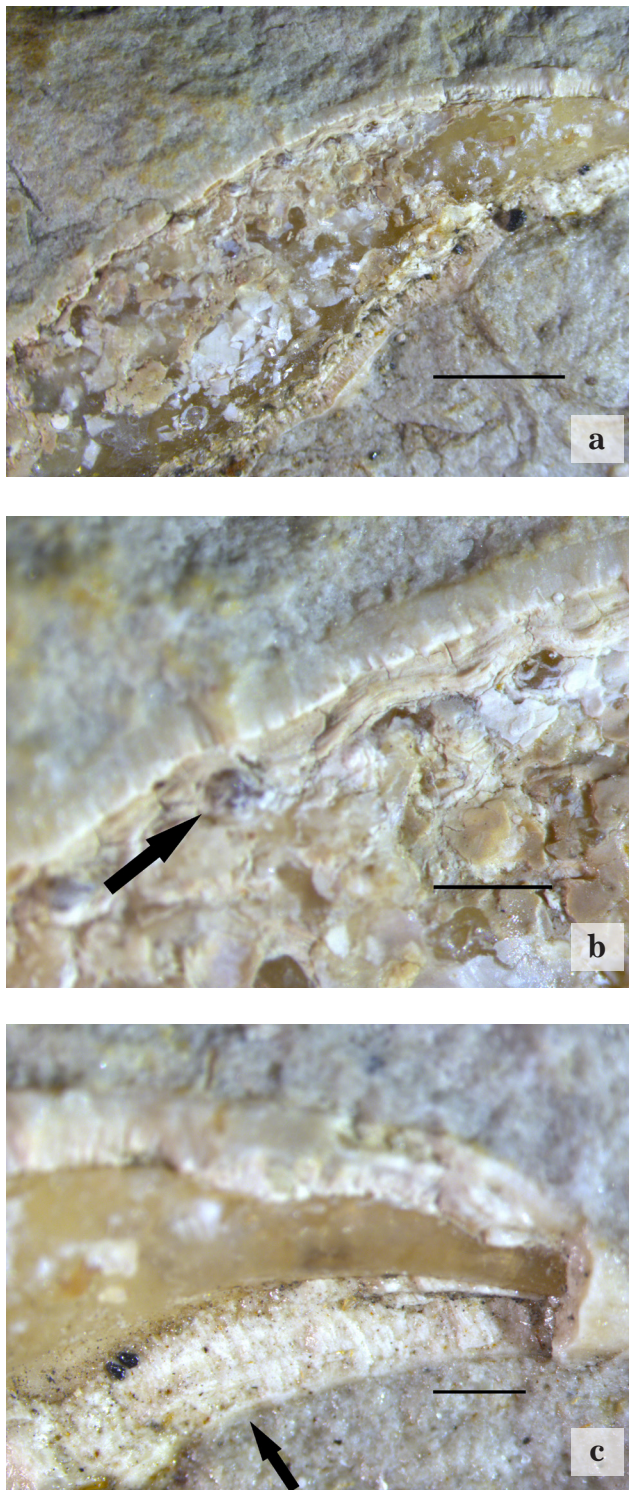


Fig. 7. CR 56. A. distal part of left dactylus (scale bar equals 4.0 mm); B. cuticle of dactylus: the arrow indicates a globular swelling associated with a tegumental canal (scale bar equals 1.0 mm); C. tip of left dactylus: the arrow indicates the exocuticle (scale bar equals 1.0 mm).

by a possibly tegumental canal (i.e., a vestige of a mechanoreceptive sensillum or a tegumental gland) (Fig. 7b) (Waugh et al., 2009a, b; Davie et al., 2015). On the lower margin of the dactylus, a fragmentary exocuticle can be observed as well (Fig. 7c).

The presence of a crab with burrowing habits may appear improbable in a palaeoenvironment that has generally been considered as anoxic, but many fish and also crustaceans found in the “Pesciara” were benthic species. Our analysis also aimed at determining whether or not this particular specimen was a moult or a corpse. Most of the individuals of *Lophoranina* in volcanoclastic rocks in Veneto are moults (in open moult position, or Salter’s position). The particular preservation of the specimen found in the “Pesciara” laminites does not allow this to be determined; however, the position of the chelipeds and the collapsed cardiac region suggest that it could be a corpse (Bishop, 1986). The good condition of the lower cuticle layer is in agreement with this hypothesis, although Waugh et al. (2009a) pointed out that this feature does not allow to determine with certainty the nature of a specimen in fossil material.

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