

Late Oligocene decapod crustaceans from the Trbovlje Formation of Slovenia, with a description of two new species of hymenosomatid crabs

Rok Gašparič, Matúš Hyžný, Tomaž Hitij, and Aleš Šoster

ABSTRACT

From the Oligocene (Chattian) marls of the Trbovlje Formation, exposed at the Neža locality, Slovenia, a brachyuran crab (Malacostraca: Brachyura) association consisting of three taxa is described. The material presented here includes as many as 15 near-complete crab specimens from the Upper Oligocene of Slovenia does not only allow direct comparison with extant hymenosomatids, but the identification of important diagnostic characters permit classification of the fossils in question within extant genera, i.e., *Halicarcinus* White, 1846, and *Lucascinus* Poore, Guinot, Komai, and Naruse, 2016. The newly erected species, *Halicarcinus popeius* sp. nov. and *Lucascinus trifailensis* sp. nov., are considered herein the first reliable occurrences of the family Hymenosomatidae MacLeay, 1838, in the fossil record. Previously reported occurrence of hymenosomatid crabs from the Cretaceous of Brazil is disputed herein. The hymenosomatid association from the Neža locality is accompanied with the portunid crab, *Necronectes* cf. *melchioni* A. Milne-Edwards, 1860, documented by an incomplete claw.

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Key words: Chattian; Malacostraca; Brachyura; Hymenosomatidae; Portunidae Palaeoecology

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INTRODUCTION

Representatives of the eubrachyuran crab family Hymenosomatidae MacLeay, 1838, are sometimes called “false spider crabs”, referring to their superficial resemblance to “true spider crabs” of the superfamily Majoidea Samouelle, 1819. In fact, the fossils of hymenosomatid crabs presented herein were first recognized as belonging to majoid spider crabs (Kovalchuk et al., 2023). Hymenosomatids are small eubrachyurans with only a lightly mineralised exoskeleton (Lucas, 1981), thus having a very low fossilization potential (Klomp maker et al., 2017, and references therein). Their relative absence in the fossil record was attributed to their small size, flat body, and poorly calcified carapace (Guinot, 2011, p. 46). This is likely connected to collection bias, rather than poor fossilization potential, as their remains are easily overlooked, due to their size. Because the recently published alleged occurrence of fossil hymenosomatid crabs from the Cretaceous of Brazil (Mendes et al., 2022) is disputed herein (see further below), the present occurrence from the Upper Oligocene of Slovenia

is considered as the first and so far the only known report of fossil Hymenosomatidae.

Decapod occurrences in Oligocene and lower Miocene fish beds (i.e., laminated marls yielding exceptionally preserved articulated fish fauna) of the Central and primarily Eastern Paratethys have been recognized since the beginning of the twentieth century (Paučá, 1929; Smirnov, 1929). These occurrences have recently been reassessed by Hyžný et al. (2022) and Kovalchuk et al. (2023).

In the present contribution we describe well-preserved decapod specimens from the upper Oligocene fish beds of the Trbovlje Formation, Slovenia. Previously reported occurrence of decapods from the respective formation includes a single specimen of the xanthoid panopeid *Glyphithyreus sulcatus* (Beurlen, 1939) (Hyžný et al., 2020).

GEOLOGICAL SETTINGS

Decapod specimens were collected from the locality “Neža” (GPS coordinates: 46°08'56"N, 15°04'03"E) situated halfway between towns of Hrastnik and Trbovlje (Figure 1). Fossil-bearing Oligocene beds crop out in an abandoned coal

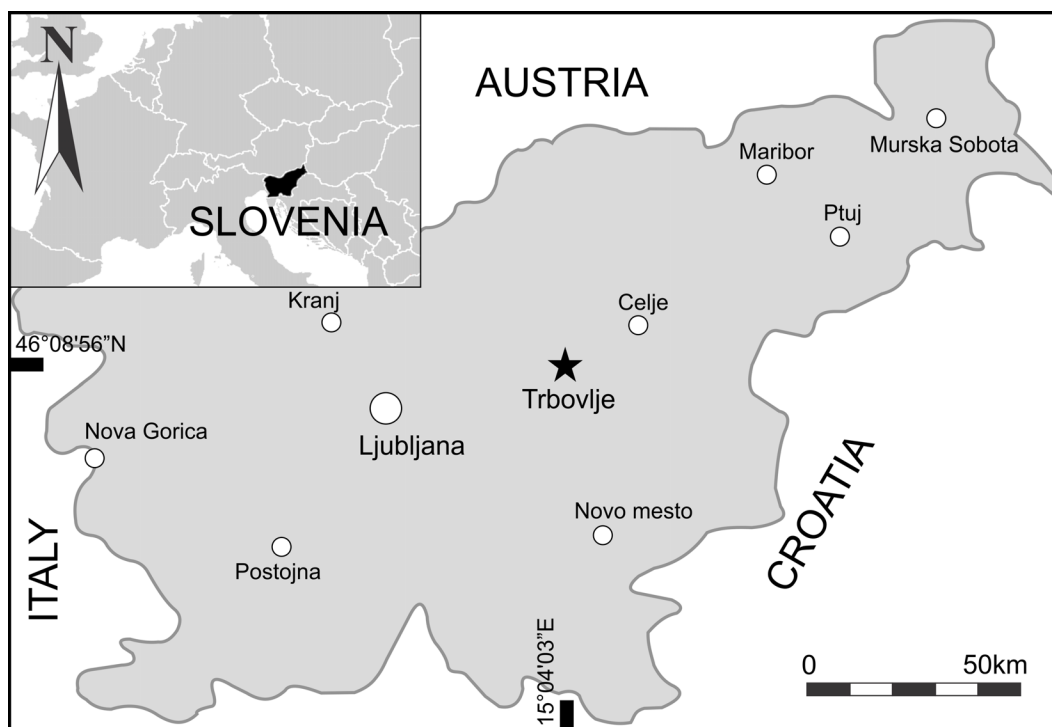


FIGURE 1. Simplified geographical map of Slovenia showing (marked with star) the fossiliferous locality “Neža” near Trbovlje.

mining pit, which has been restored and now represents an outdoor activity area. The wider area was intensively mined for lignite (brown coal) over the last two centuries and has been well researched (Bittner, 1884; Petrascheck, 1952; Kuščer, 1967; Jelen et al., 1992; Placer, 1999; Hafner, 2000). The Cenozoic sequence starts with the upper Oligocene Trbovlje Formation, which discontinuously overlies Triassic rocks. Basal horizons comprise conglomerates and sandstones, grading upwards into greyish coloured marls and marly limestones. An economically important coal seam occurs within the marly beds (Bechtel et al., 2004) and palynological analysis has identified species of Cupressaceae within the main coal seam (Bruch, 1998; Križnar, 2000) with a likely transition to reed marshes in the upper part. The marls and marly limestones above the coal layer are fossiliferous, yielding a diverse fish fauna (Bittner, 1884; Križnar, 2015; Križnar and Lorencon, 2021), crustaceans (Buckeridge et al., 2020; Kovalchuk et al., 2023; herein), molluscs (Bittner, 1884), as well as abundant plant remains (Lorencon, 2019). A late Oligocene (Chattian) age has been confirmed by radiometric dating of interbedded tuff layers (Odin et al., 1994). A grey marine clay of the Sivica Formation occurs on top of the fossiliferous beds; above this the sequence grades into lenses of fine-grained clastic rocks, particularly sandstones and conglomerates of the lower Miocene Govce Formation (Hafner, 2000).

MATERIAL AND METHODS

Due to the abundance of fossil fish remains, the “Neža” locality was frequently visited by private collectors in the recent years, resulting in discovery of several decapod specimens. Therefore, a detailed bed by bed sampling was done within the available 2m thick sequence. An area of approximately 1 m² was excavated and all fossils on the beds were documented. Fossil remains of fish and flora occur throughout the section with varying frequency. Additionally, four mass accumulations of fish remains (probably a mass mortality event) were identified at different levels within the section, as well as two beds from which the presented decapod specimens originated (Figure 2).

The present study is based on 15 specimens of near-complete crabs and a single large claw. The specimens were prepared and studied under a Leica EZ 4D stereomicroscope. Photographs were taken with a digital camera Nikon Zfc equipped with Micro NIKKOR 40mm f/2.8G lens. Photographs were subsequently developed in Photo-

shop CS6 to correct for light, contrast, and colour where needed. The large claw specimen was further prepared as a latex cast and whitened with sublimate of ammonium chloride prior to photography. Selected near-complete specimens were documented under SEM ThermoFischer Scientific Quattro S. Micrographs were acquired in low vacuum mode with an accelerating voltage of 15 kV and a spot size of 3.5 in backscattered electron imaging mode using the annular CBS detector. Samples were coated with a thin film of amorphous carbon to ensure electrical conductivity. Measurements of the specimens were made with digital calipers under the stereomicroscope. The reference of size is given as maximum carapace width, which is mostly at the level of the posterior part of carapace. The rostrum is included in measurements of carapace length. Walking leg length is measured from the longest leg, usually the second pereopod (P2).

Abbreviations

Abbreviations of dorsal carapace characters used in the illustrations are as follows: CW – Carapace width, CL – Carapace length, P1L – Cheliped length, P2L – Pereopod P2 length. Repository acronyms: MNHN.F – Collection de Paléontologie, Muséum national d’Histoire naturelle, Paris, France. RGA/SMNH – Slovenian Museum of Natural History, Ljubljana, Slovenia (R. Gašparič Collection).

SYSTEMATIC PALAEOONTOLOGY

Order DECAPODA Latreille, 1802
 Infraorder BRACHYURA Latreille, 1802
 Superfamily HYMENOSOMATOIDEA
 MacLeay, 1838

Family HYMENOSOMATIDAE MacLeay, 1838
 Genus *HALICARCINUS* White, 1846

Type species. *Cancer planatus* Fabricius, 1775, by original designation.

Remarks. Hymenosomatidae MacLeay, 1838, comprises 24 genera and over 130 species (Poore et al., 2016) of which *Halicarcinus* White, 1846, was the most diverse and morphologically heterogeneous. Poore et al. (2016) have revised *Halicarcinus* and reassigned the species to seven genera to accommodate the diversity previously encompassed in the genus. Currently *Halicarcinus* includes seven species characterised by the complete hymenosomian groove, well-developed epistome, rostrum developed as median tubercle with paired pseudorostral elements, strongly curved

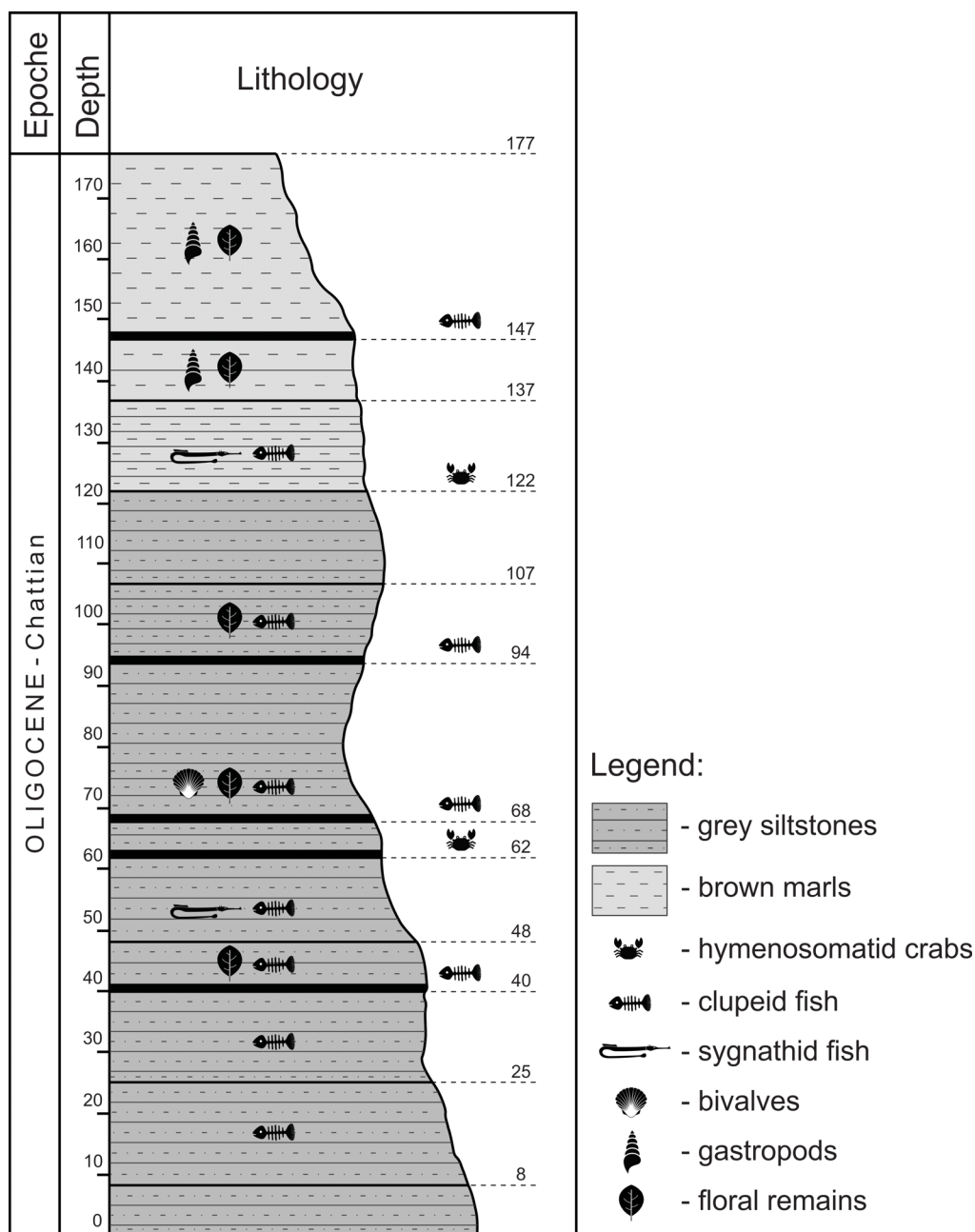


FIGURE 2. Lithostratigraphic section showing exposed strata at the “Neža” locality. Depths on the right indicate the fish fauna mass mortality layers (marked with a fish icon) and layers with fossil hymenosomatid crabs, which are marked with a crab icon.

gonopod 1, pleomeres 1-5 free, pleomere 6 fused to telson (pleotelson), pereopodal dactylar teeth shorter than in other genera, and propodi of male chelipeds frequently swollen and barrel-like (Naruse and Komai, 2009; Poore et al., 2016).

Halicarcinus popeius sp. nov.
 Figures 3, 4A-D, 5A-C

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2023 Majoidea gen. et sp. indet. – Kovalchuk et al., p. 5, figs. 2E, F.

Etymology. The species name originates from a Latinised name of the cartoon character Popeye, the sailor man. A fictional character who, despite the diminutive stature, possesses strong, bulging forearms, reminiscent of the chelipeds of the new species.

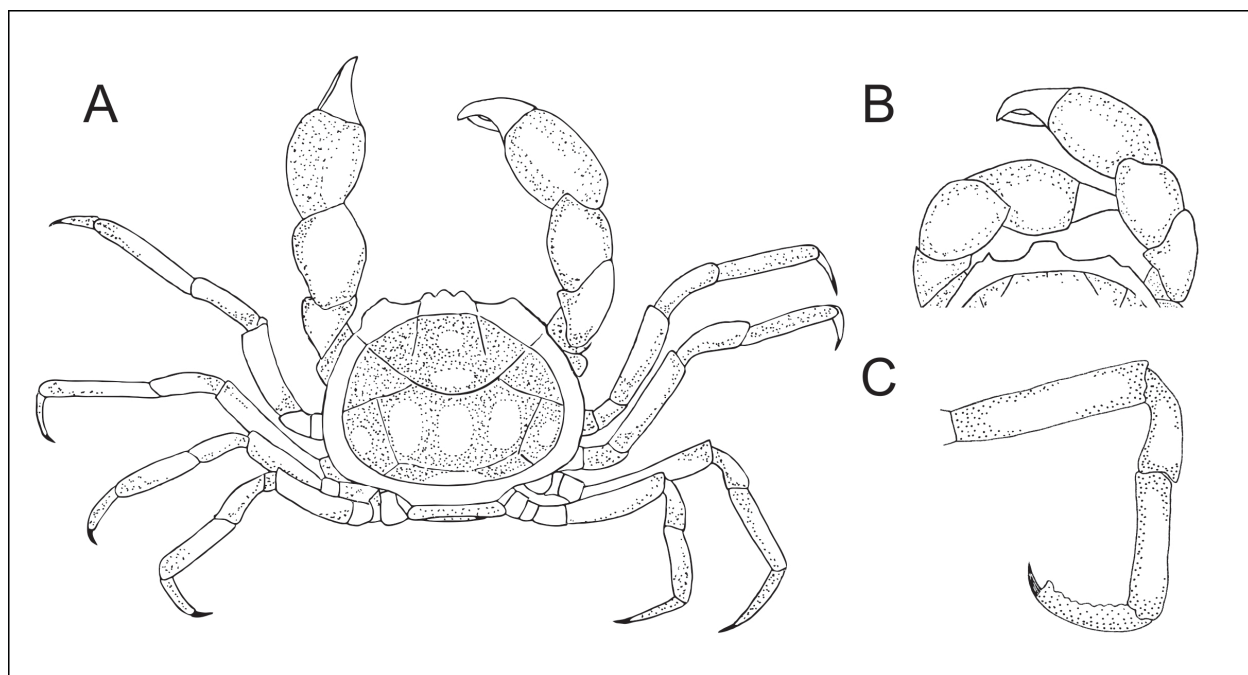


FIGURE 3. *Halicarcinus popeius* sp. nov., schematic reconstruction. A. Carapace in dorsal view; B. Detailed view of second type of rostrum and robust chelipeds (male); C. Third pereopod (P3) with detailed view of dactylus.

Diagnosis. Carapace oval, wider than long, surrounded by a wide rim. Trilobate to trapezoid rostrum; length not extending as far as eyes. Eyes on short, stout eyestalks; extending beyond rostrum. Anterolateral corners forming a rounded postocular projection; either as rounded lobe or a pair of forward pointing teeth. Lateral side of carapace rounded; almost vertical posteriorly; with a concavity at posterolateral margin. Dorsal carapace with continuous gastro-cardiac groove, forming a hexagonal cardiac region. Chelipeds massive in males, sub-equal, homomorph, with swollen barrel-like propodus; more slender in females. Both fingers long, occluding with a gape; no dentation of the occlusal margin. Pereopods very long and slender. Dactylus broad, distinctively curved, tip composed of two developed, sub-equal, teeth; ventral edge armed by a row of blunt tubercles.

Type material. Holotype is RGA/SMNH 6377-6378 (part and counterpart) (Figure 4A), paratypes are RGA/SMNH 6373-6374 (part and counterpart) (Figure 4B, 6C), RGA/SMNH 6371-6372 (part and counterpart), RGA/SMNH 6369-6370 (part and counterpart), RGA/SMNH 6385-6386 (part and counterpart) (Figures 4C, 5A) and RGA/SMNH 2041 (Figures 4D, 5B). Other specimens are RGA/SMNH 2039-2040 (part and counterpart), RGA/SMNH 6375-6376 (part and counterpart), RGA/SMNH 6381-6382 (part and counterpart) and RGA/

SMNH 6389-6390 (part and counterpart). Measurements are given in Figure 7, Table 1 and Table 2.

Type locality. Trbovlje, Slovenia.

Description. Carapace oval, wider than long (CL/CW = 0.82–0.93) (Table 1), surrounded by a wide hyemosian rim. Trilobate to trapezoid rostrum; wide and short; width approx. 0.1–0.2 times carapace width; length not extending as far as eyes (Figure 5A). Lobes close together; sub equal in length; median lobe slightly bigger than the other two, sometimes not differentiated and forming a single trapezoidal rostrum (Figure 4B). Eyes on short, stout eyestalks; extending beyond rostrum (Figure 5A). Anterolateral corners rounded, forming a rounded postocular projection; either as rounded lobe or a pair of forward pointing teeth. Lateral side of carapace rounded; almost vertical posteriorly; with a concavity at posterolateral corner (Figure 4A-D).

Dorsal carapace with continuous gastro-cardiac groove, extending concavely from one side of hyemosian rim to the other; forming a hexagonal cardiac region (Figure 4A, D). Frontal region trapezoidal; not differentiated from gastric region posteriorly. Hepatic and prebranchial regions small; triangular. Postbranchial region square; separated from cardiac region by the thoracic groove. Cardiac region ornamented by three longitudinally oval

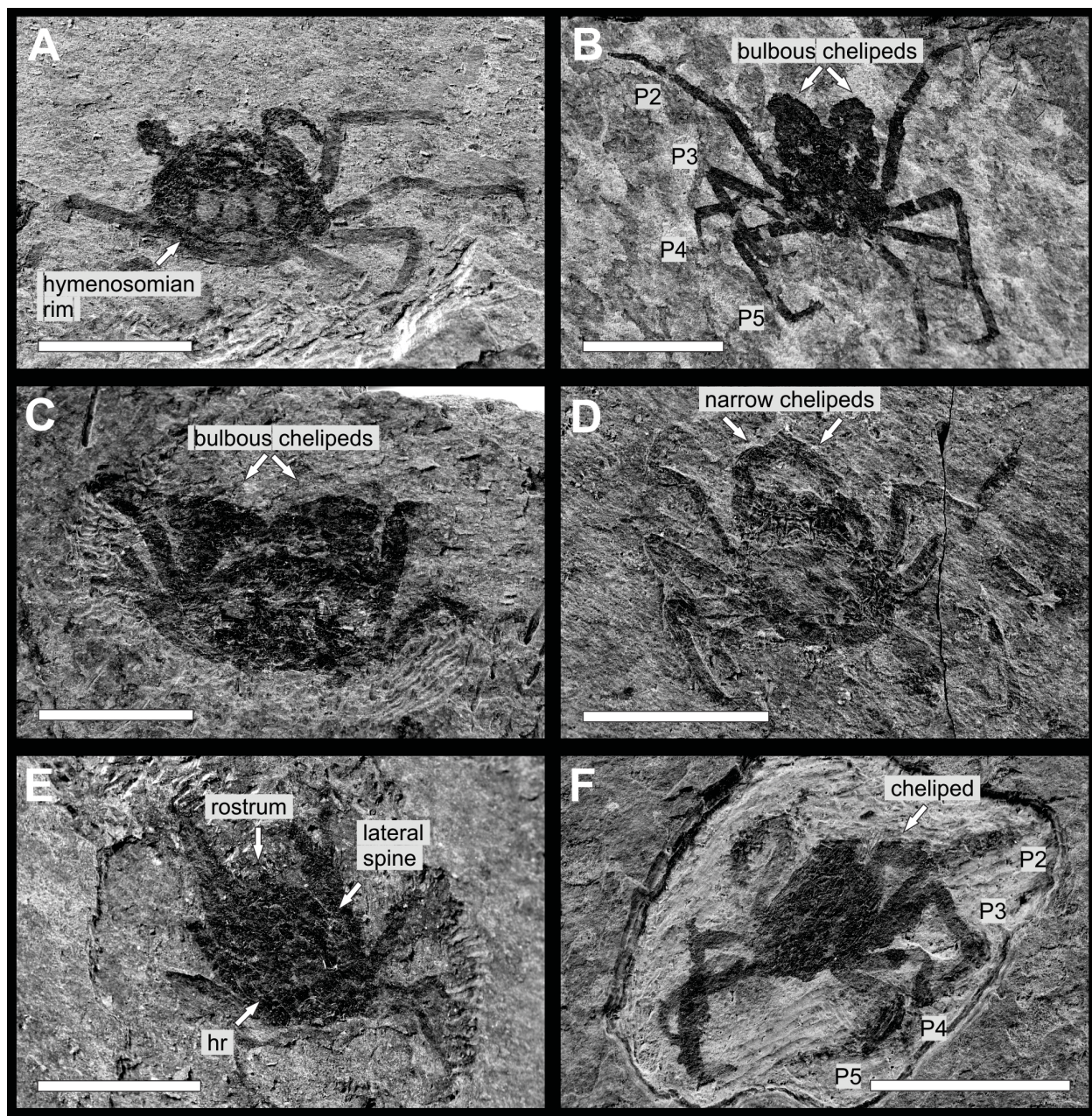


FIGURE 4. *Halicarcinus popeius* sp. nov. (A–D) and *Lucascinus trifailensis* sp. nov. (E, F): A. RGA/SMNH 6377, dorsal, (holotype), visible hymenosomian rim (hr) and coloration patterns; B. RGA/SMNH 6373, dorsal, (paratype), male with well-preserved chelipeds and pereopods (P2–P5); C. RGA/SMNH 6385, dorsal, (paratype), male with bulbous chelipeds; D. RGA/SMNH 2041, ventral, (paratype), female with missing sternum; E. RGA/SMNH 6384, dorsal, (holotype), indicated rostrum and hymenosomian rim (hr); F. RGA/SMNH 6391, dorsal, (paratype), elongated chelipeds and well preserved pereopods (P2–P5). All scale bars equal 5 mm.

areas of brighter colour (Figure 4A); smaller oval coloration of dorsal carapace also in gastric region, anteriorly of gastro-cardiac groove; crescent-shaped coloration of carapace at posterior border.

Chelipeds massive, with swollen barrel-like propodus (Figure 4A, C); length approx. 1.1–1.7 times of carapace length; slighter in females.

Ischium short; merus slightly longer than wide; carpus longer than merus, swollen with rounded margins, almost as broad as long; manus greatly inflated, margins rounded and convex. Both fingers long, occluding with a gape; no dentation of the occlusal margin observable. Pereopods very long and slender (Figure 4B, Table 2), almost same

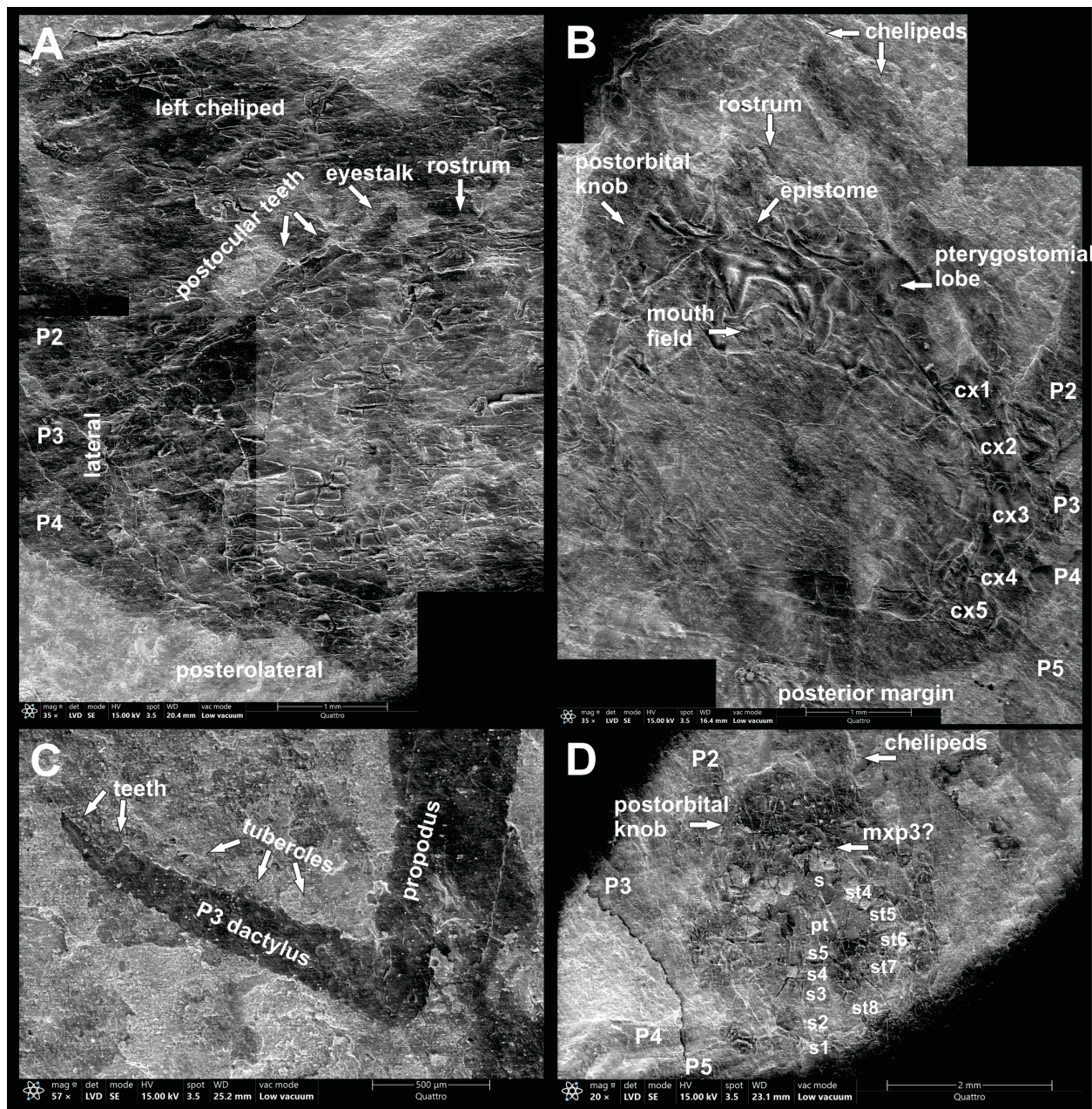


FIGURE 5. Scanning electron photomicrographs of *Halicarcinus popeius* sp. nov. (A–C) and *Lucascinus trifailensis* sp. nov. (D): A. RGA/SMNH 6385, details of anterior and left lateral border in dorsal view, pereopods (P2–P5), (composite of several photomicrographs); B. RGA/SMNH 2041, ventral side with missing sternum, details of anterior margin and buccal cavity, coxa of pereopods (cx2–cx5), pereopods (P2–P5), (composite of several photomicrographs); C. RGA/SMNH 6373, detailed view of pereopodal (P3) dactylus; D. RGA/SMNH 6387, ventral side with male pleon, pereopods (P2–P5), abdominal somites (s1–s5), pleotelson (pt), sternites (st4–st8), sternal shield (s), third maxilliped (mxp3). Scale bars indicated on the photomicrographs.

length, approx. 2.0–3.5 times of carapace length. Ischium very short; merus longest; carpus about one-thirds as long as merus; propodus almost as long as merus. Dactylus shorter than the propodus, broad, distinctively curved, tip composed of two developed, sub-equal, teeth; ventral edge armed by a row of blunt tubercles (Figure 5C).

Remarks. *Halicarcinus popeius* sp. nov. is the first fossil representative of the genus. Thus, by the general habitus it would be most similar to *Halicarcinus quoyi* (H. Milne Edwards, 1853), with which it shares a wider than long carapace with broad rim, a trilobed rostrum, shape of pereopodal dactyli and strongly swollen, bulbous propodi of male cheli-

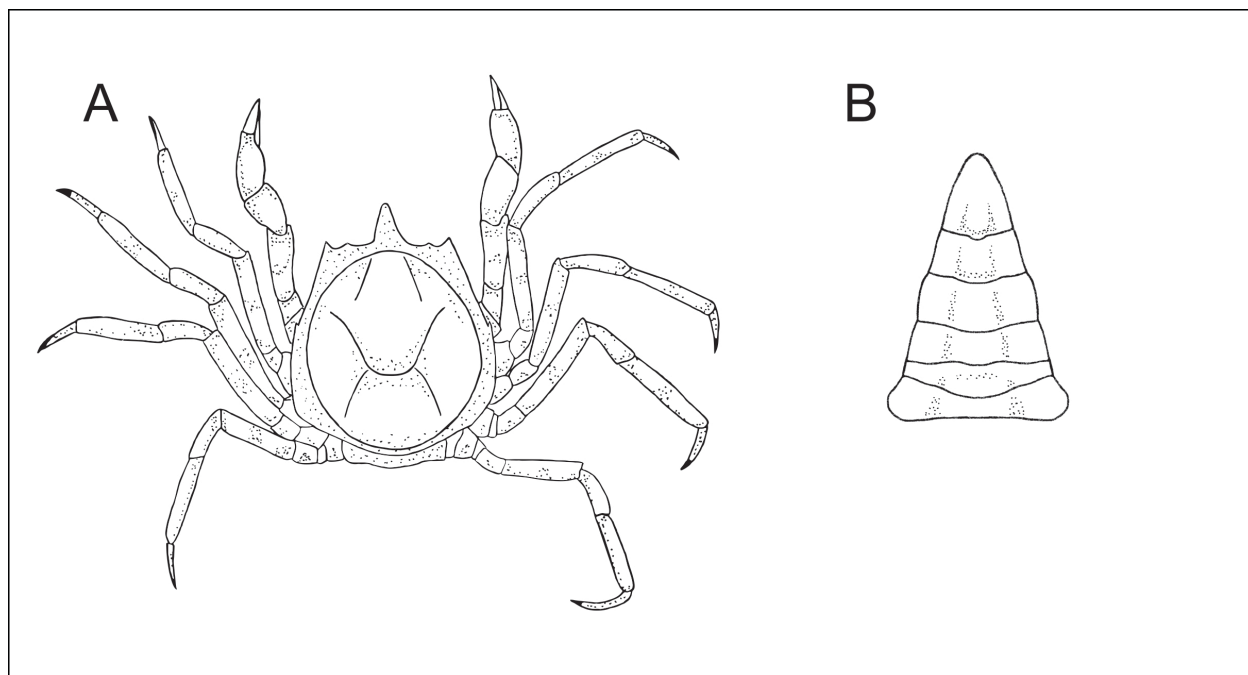


FIGURE 6. *Lucascinus trifailensis* sp. nov., schematic reconstruction. A. Carapace in dorsal view; B. Detailed view of male pleon.

ped. The new fossil species differs from *H. quoyi* in possessing postorbital projections at anterolateral corners of carapace and in development of dorsal carapace regions, especially wide hexagonal cardiac region. Additionally, we recognize heterogeneity in development of rostra within the fossil material, which can be explained as intraspecific variations or possible sexual dimorphism. Lucas (1981) previously recognized that the shape and relative length of the rostrum within *Halicarcinus* are sometimes sexually dimorphic, although such variations were not reported in *Halicarcinus quoyi*.

Range. Late Oligocene (Chattian).

Occurrence. To date, known only from the type locality.

Genus *LUCASCINUS*

Poore, Guinot, Komai, and Naruse, 2016

Type species. *Halicarcinus bedfordi* Montgomery, 1931, by original designation.

Remarks. Poore et al. (2016) erected a genus *Lucascinus* and transferred to it three species: *Lucascinus bedfordi* (Montgomery, 1931) (originally as *Halicarcinus*); *Lucascinus coralicola* (Rathbun, 1909) (originally as *Rhynchoplax*) and *Lucascinus keijibabai* (Takeda and Miyake, 1971) (originally as *Rhynchoplax*). The species within *Lucascinus* differ from *Rhynchoplax* mostly by pos-

sessing a male pleon with free somites 1-5, plus telson, and additionally from *Halicarcinus* by their elongated chelipeds and triangular plate-like rostrum (Poore et al., 2016).

Lucascinus trifailensis sp. nov.

Figures 4E-F, 5D, 6

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Etymology. The species name refers to old name for coal mining town of Trbovlje (Trifail). Trbovlje is Slovenia's tenth-largest town and closest to the type locality of new species.

Diagnosis. Carapace trapezoid, longer than wide, fully surrounded by a rim. Rostrum formed as a long triangular plate. Postocular anterior margin sinuous; defined by a postocular tubercle and a more pronounced tooth at anterolateral corner of the carapace. Lateral side of carapace almost straight; diverging posteriorly; with a single projection near base of cheliped. Posterior border of carapace sinuously rounded. Dorsal carapace with visible gastro-cardiac groove and posteriorly developed thoracic grooves. Frontal region trapezoidal; not differentiated from gastric posteriorly. Cardiac region simple and posteriorly not bordered. Male pleon triangular; pleonal somites 1-5 free; somite 1 widest. Chelipeds long; propodus elongated and slightly swollen. Fingers short. Pereopods very long and slender; almost same length. Dactylus short, curved, teeth not observed.

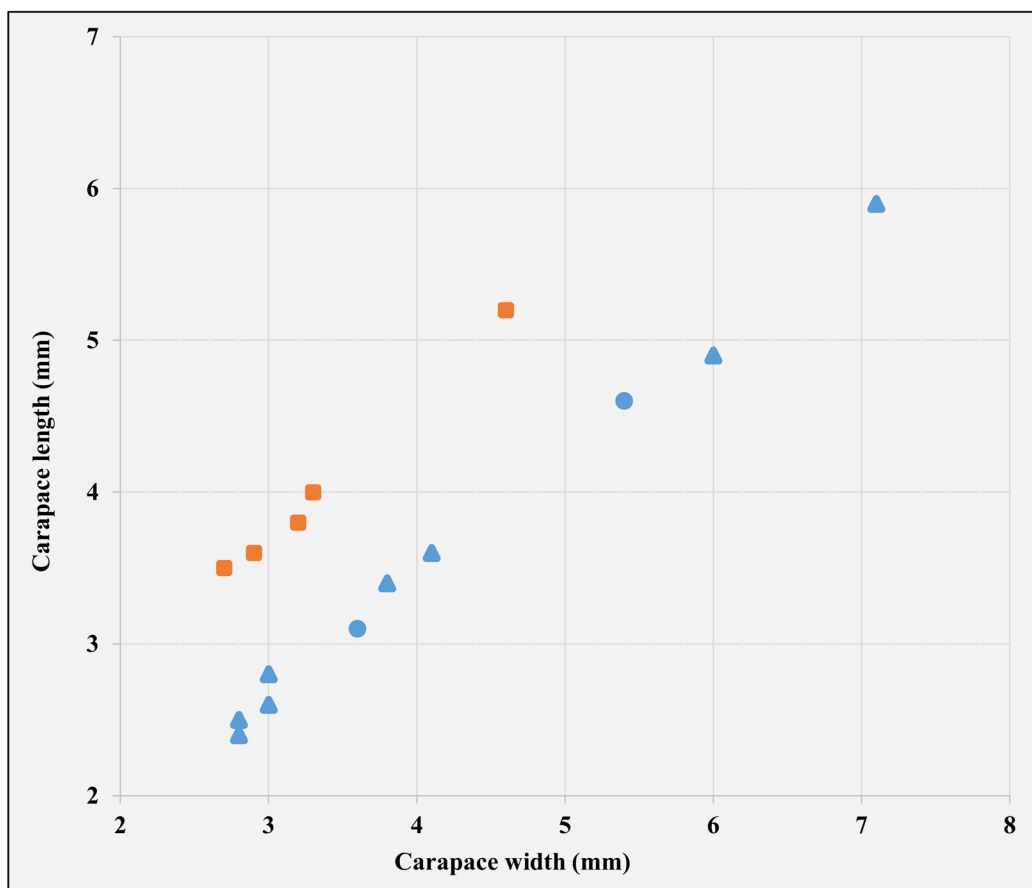


FIGURE 7. Carapace length vs. maximum carapace width of hymenosomatid specimens from the “Neža” locality. *Halicarcinus popeius* sp. nov. are marked in blue triangles (circles when trapezoid rostrum), *Lucascinus trifailensis* sp. nov. specimens are marked with orange squares. All measurements in mm.

TABLE 1. Carapace length (CL) and carapace width (CW) measurements of hymenosomatid specimens from the “Neža” locality. All measurements in mm.

Taxon	Specimen No.	CL (mm)	CW (mm)	CL/CW
<i>Halicarcinus popeius</i> sp. nov.	RGA6369/6370	2.4	2.8	0.86
<i>Halicarcinus popeius</i> sp. nov.	RGA6381/6382	2.5	2.8	0.89
<i>Halicarcinus popeius</i> sp. nov.	RGA6375/6376	2.6	3.0	0.87
<i>Halicarcinus popeius</i> sp. nov.	RGA6389/6390	2.8	3.0	0.93
<i>Halicarcinus popeius</i> sp. nov.	RGA6373/6374	3.1	3.6	0.86
<i>Halicarcinus popeius</i> sp. nov.	RGA2039/2040	3.4	3.8	0.89
<i>Halicarcinus popeius</i> sp. nov.	RGA2041	3.6	4.1	0.88
<i>Halicarcinus popeius</i> sp. nov.	RGA6377/6378	4.6	5.4	0.85
<i>Halicarcinus popeius</i> sp. nov.	RGA6385/6386	4.9	6.0	0.82
<i>Halicarcinus popeius</i> sp. nov.	RGA6371/6372	5.9	7.1	0.83
<i>Lucascinus trifailensis</i> sp. nov.	RGA6387/6388	3.5	2.7	1.30
<i>Lucascinus trifailensis</i> sp. nov.	RGA6392	3.6	2.9	1.24
<i>Lucascinus trifailensis</i> sp. nov.	RGA6391	3.8	3.2	1.19
<i>Lucascinus trifailensis</i> sp. nov.	RGA6379/6380	4.0	3.3	1.21
<i>Lucascinus trifailensis</i> sp. nov.	RGA6383/6384	5.2	4.6	1.13

TABLE 2. Pereopod measurements of hymenosomatid specimens from the “Neža” locality. Cheliped (P1), Pereopod (P2-P5), dactylus (dac), propodus (pro), carpus (car), merus (mer), ischium (isc). All measurements in mm.

Taxon		<i>Haliscarcinus popeius</i> sp. nov.															
Specimen No.		RGA 6369/6370	RGA 6381/6382	RGA 6375/6376	RGA 6389/6390	RGA 6373/6374	RGA 2039/2040	RGA 2041	RG A6377/6378	RGA 6385/6386	RGA 6371/6372	RGA 6387/6388	RGA 6392	RGA 6391	RGA 6379/6380	RGA 6383/6384	
Cheliped - P1 (mm)	dac	1.1	0.5	0.9	—	1.7	1.0	0.8	—	1.8	2.2	0.5	—	0.6	—	1.2	
	pro	2.4	1.2	1.7	—	3.1	2.1	1.4	—	3.3	3.6	1.1	—	1.5	—	1.8	
	car	0.8	0.4	0.7	—	1.8	0.6	0.7	—	1.6	1.7	0.6	—	0.5	—	0.9	
	mer	0.5	—	—	—	0.7	0.5	0.5	—	—	1.6	0.6	—	0.7	—	0.8	
	isc	—	—	—	—	—	0.3	—	—	—	0.8	—	—	—	—	—	
Pereopod - P2 (mm)	dac	1.3	0.3	—	—	1.6	—	—	—	—	—	0.5	—	—	—	—	
	pro	1.6	1.0	—	—	1.9	—	—	2.3	—	—	2.1	—	2.4	—	2.1	
	car	0.9	0.3	—	—	1.1	0.5	0.9	1.3	—	1.7	0.6	—	0.6	—	0.5	
	mer	2.3	1.3	2.1	1.8	2.5	1.5	1.9	2.2	2.6	2.5	1.6	—	2.1	2.2	1.8	
	isc	0.3	0.1	0.2	0.2	0.7	0.2	0.3	0.5	0.4	0.7	0.2	—	0.3	0.3	0.3	
Pereopod - P3 (mm)	dac	—	—	—	—	1.3	—	—	—	—	—	0.6	—	1.0	—	—	
	pro	—	1.5	—	—	2.1	—	—	2.3	—	—	2.0	—	2.2	—	—	
	car	—	0.4	0.9	—	1.4	—	1.1	1.6	—	—	0.7	—	0.8	0.6	0.6	
	mer	2.3	1.6	2.0	1.9	2.3	1.8	2.3	2.4	3.0	2.8	1.5	—	2.0	2.3	1.9	
	isc	0.4	0.2	0.3	0.2	0.4	0.3	0.4	0.4	0.4	0.6	0.2	—	0.3	0.3	0.2	
Pereopod - P4 (mm)	dac	—	—	—	—	1.3	—	0.9	—	—	—	—	1.5	1.0	—	—	
	pro	—	1.4	1.7	—	2.3	—	2.0	—	—	—	1.2	2.5	2.1	—	—	
	car	—	0.3	0.8	—	1.1	0.6	0.9	—	—	1.0	0.4	0.7	0.5	0.5	0.7	
	mer	2.5	1.5	2.0	—	2.6	1.8	2.3	2.1	—	2.2	1.1	2.3	1.8	2.0	1.8	
	isc	0.3	0.2	0.3	—	0.4	0.3	0.3	0.4	—	0.4	0.1	0.3	0.2	0.2	0.3	
Pereopod - P5 (mm)	dac	—	0.4	—	—	1.3	—	—	—	—	—	—	0.6	1.0	—	0.5	
	pro	—	1.1	1.8	—	2.4	—	—	—	—	—	—	2.0	2.1	—	2.1	
	car	—	0.3	0.5	—	1.5	0.5	—	—	—	—	—	0.5	0.6	0.5	0.5	
	mer	—	0.9	2.0	—	2.4	1.5	1.7	—	—	—	0.9	1.4	1.5	1.5	1.3	
	isc	—	0.2	0.2	—	0.3	0.2	0.2	—	—	—	0.1	0.3	0.2	0.2	0.2	

Type material. Holotype is RGA/SMNH 6384-6383 (part and counterpart) (Figure 4E); paratypes are RGA/SMNH 6391 (Figure 4F), RGA/SMNH 6387-6388 (part and counterpart) (Figure 5D), RGA/SMNH 6379-6380 (part and counterpart) and RGA/SMNH 6392. Measurements are given in Figure 7, Table 1 and Table 2.

Type locality. Trbovlje, Slovenia.

Description. Carapace trapezoidal, longer than wide (CL/CW = 1.13–1.30) (Table 1), fully surrounded by a hymenosomian rim (Figure 4E - F). Rostrum formed as a long triangular plate; twice as

long as wide; width approx. 0.1–0.15 times carapace width (Figure 5D). Postocular anterior margin sinuous; defined by a postocular tubercle and a more pronounced tooth at anterolateral corner of the carapace. Lateral side of carapace slightly convex; almost straight; diverging posteriorly; with a single projection near base of cheliped. Posterior border of carapace sinuously rounded (Figure 4F).

Dorsal carapace with visible gastro-cardiac groove and posteriorly developed thoracic grooves. Frontal region trapezoid; not differentiated from gastric posteriorly. Cardiac region simple and

posteriorly not bordered (Figure 4E). Male pleon triangular; pleonal somites free; somite 1 widest, with rounded convex lateral sides; rest of the somites with straight and anteriorly converging lateral margins; pleotelson much longer than wide, triangular, with rounded apex (Figure 5D).

Chelipeds long; length approx. 0.85-1.0 times of carapace length. Ischium short; merus and carpus longer than wide; propodus elongated and lightly swollen. Fingers shorter than manus. Pereopods very long and slender (Figure 4F, Table 2); length approx. 1.9-2.3 times of carapace length, P3 and P4 longest. Ischium short; merus almost as long as propodus, carpus less than one third of merus; propodus longest, but narrower than the merus. Dactylus short, curved, teeth not observed.

Remarks. *Lucascinus trifailensis* sp. nov. is the first fossil representative of the genus and among extant species most closely resembles *Lucascinus bedfordi* (Montgomery, 1931). The shared similarities between the fossil and extant species are in ornamentation of dorsal carapace and the shape of a triangular rostrum. However, *Lucascinus trifailensis* sp. nov. has a narrower carapace, with distinct sinuous shape of the anterior margin, defined by a small postocular tubercle, and a more pronounced tooth at the anterolateral corner of the carapace. Additional spinose projection is located at lateral margin, near the base of cheliped, which is typical for *Lucascinus* (Poore et al., 2016), but much less pronounced in *Lucascinus trifailensis* sp. nov. Such combination of characters has not been observed in any of the extant species. However, we prefer to use the most parsimonious way and include the fossil species in the closest extant genus.

Range. Late Oligocene (Chattian).

Occurrence. To date, known only from the type locality.

Superfamily PORTUNOIDEA Rafinesque, 1815

Family PORTUNIDAE Rafinesque, 1815

Genus *NECRONECTES* A. Milne-Edwards, 1881

Type species. *Necronectes vidalianus* A. Milne-Edwards, 1881, by original designation.

Necronectes cf. *michelini* A. Milne-Edwards, 1860
Figure 8A-D

Material. A single “crusher” chela (RGA/SMNH 5009-5010) preserved as an imprint. Measurements: length of propodus = 53.6 mm; maximum height of manus = 31.9 mm; length of dactylus = 31.0 mm.

Description. Chela robust. Manus trapezoidal to suboval in outline; upper and lower margin arched and converging proximally; surface appears smooth, without indication of spines on distal margin at dactylus articulation. Fingers long and stout; as long as manus. Fixed finger robust; occlusal margin with four large molariform teeth, followed by several smaller conical teeth distally; first and second proximal teeth joined; fingertip curved upwards. Dactylus stout, curved forward; with rounded upper margin; strong proximal knob-like flattened molariform tooth followed by six rounded conical teeth of different sizes; strongly curved fingertip.

Remarks. The original cuticle has been dissolved and the massive fingers are preserved as hollow imprints. Therefore, some details cannot be observed in the studied specimen. However, after preparing the latex cast, the preserved features of the chela are sufficient to assign the material to *Necronectes* A. Milne-Edwards, 1881. Observed important taxonomic characters include lack of distal spines on manus at position of dactylus articulation and rounded upper margin of manus, which are the key characters for an assignment to *Necronectes*, and differentiate it from closely related *Scylla* De Haan, 1833 (Ossó and Gagnaisson, 2019). The herein presented specimen strongly resembles *Necronectes michelini* Milne-Edwards, 1860, from the Miocene of France (Figure 8E-F), somewhat differing in well-developed proximal molariform teeth on fixed finger and dactylus. Given similarities in preserved specimen, the stratigraphic span and geographic distribution of *N. michelini*, it is also possible that the occurrence reported here, from the upper Oligocene of Slovenia, belongs to this species. Nevertheless, we refrain to assign it to *N. michelini* because of insufficient preservation of diagnostic features on the manus and absence preserved carapace remains. Due to the fragmentary preservation we leave the specimen in open nomenclature.

Range. Late Oligocene (Chattian).

Occurrence. *Necronectes* is a well-known genus known from a number of Oligocene and Miocene occurrences (Schweitzer et al., 2006; Luque et al., 2017; Hyžný and Dulai, 2021). *Necronectes michelini* A. Milne-Edwards, 1860, has so far been reported from the middle Miocene of France (Ossó and Gagnaisson, 2019) and the middle Miocene of Hungary (Lórentthey and Beurlen, 1929).

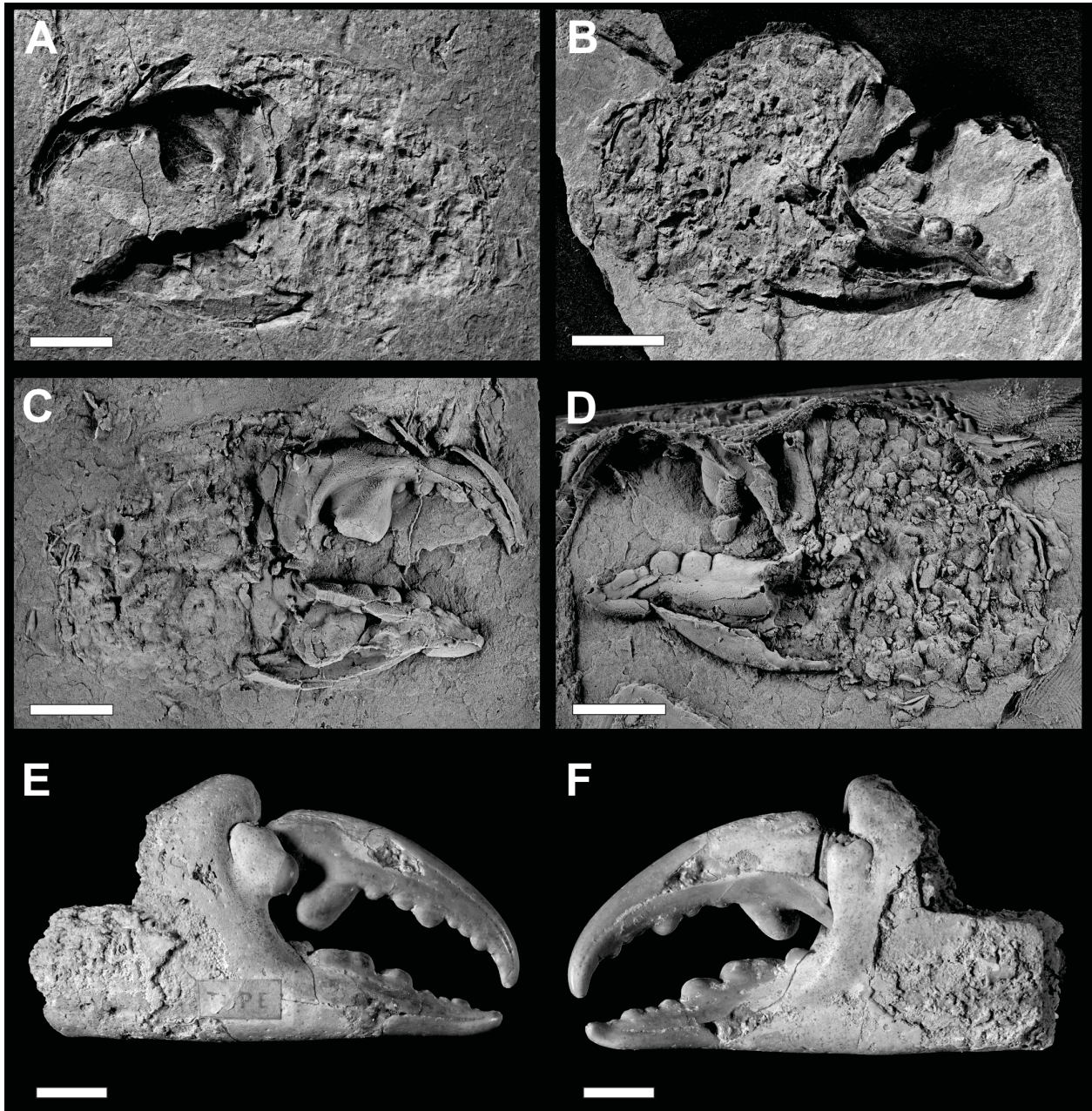


FIGURE 8. *Necronectes cf. michelini* Milne-Edwards, 1860 (A–D) and *Necronectes michelini* Milne-Edwards, 1860 (E, F): A. RGA/SMNH 5009, imprint of the outer side of chela; B. RGA/SMNH 5010, imprint of the inner side of chela; C. RGA/SMNH 5009, whitened latex cast; D. RGA/SMNH 5010, whitened latex cast; E. MNHN.F.R03775, (paralectotype), outer side of chela; F. MNHN.F.R03775, (paralectotype), inner side of chela. All scale bars equal 10 mm. Photos A and D: RECOLNAT (ANR-11-INBS-0004) - Jocelyn FALCONNET – 2017.

DISCUSSION

Fossil Hymenosomatidae

The present occurrence of hymenosomatid crabs from the upper Oligocene of Slovenia is considered the first reliable report of the respective family in the fossil record. Mendes et al. (2022) reported several small, incomplete, distorted dorsal

carapaces from the Lower Cretaceous of NE Brazil and assigned them to three newly erected species within two newly erected genera belonging to a newly erected subfamily Eureotropisinae within the family Hymenosomatidae. Unfortunately, the preservation of their material lacking diagnostic synapomorphies of the family Hymenosomatidae does not warrant the attribution of the Brazilian material

to the respective family. The carapaces of Mendes et al. (2022) are relatively featureless, and their comparison with any extant brachyuran higher taxa is difficult at best. Moreover, the longitudinal dorsal ridge of Eureotropisinae crossing the entire or nearly entire carapace as shown by Mendes et al. (2022) is not present in any known brachyuran taxon (Ng et al., 2008; Davie et al., 2015). Thus, the affinities of the Eureotropisinae remain obscure.

Taphonomy

Despite the relatively low fossilization potential of hymenosomatid crabs, due to their small size and weakly mineralized cuticle, the studied specimens from the Trbovlje Formation are always preserved fully articulated but compressed. The assessment of taxonomical characters is further complicated by what appears to be a thin layer of carbonized film covering the carapace obscuring the details, and in some cases even the exact outline of the carapace. This can possibly be contributed to the carbonization of the biofilm layer and organic matter that covered the dorsal carapace and camouflaged the hymenosomatids in their environment (Melrose, 1975).

The complete and articulated mode of preservation of hymenosomatid crabs indicates, that they likely represent corpses or a mix of corpses and moults (compare with Hyžný et al., 2022). Specimens would have been quickly buried in-situ, without any or a minimum post-mortem transportation or disturbance, and under calm, but rapid depositional conditions (Klompaker et al., 2017).

The claw of a portunid crab *Necronectes* sp. is disarticulated, with pereopod fragments observed close by, which suggests that it is parautochthonous or even allochthonous, and was transported before burial by mild currents.

Palaeoenvironment

Extant hymenosomatid crabs are ecologically very diverse, inhabiting marine, estuarine, and even freshwater environments (Melrose, 1975; Guinot and Richer de Forges, 1997; Guinot and Mazincourt, 2020). Oligocene fish beds of the Paratethys are interpreted as deposited in various depositional settings, from deeper marine, with anoxic bottom conditions, and fast sedimentation

rates, to possibly shallower costal settings or open lagoonal settings (Kovalchuk et al., 2023).

We conclude, that the late Oligocene fauna from the Neža locality inhabited a shallow marine, near shore facies. High influx of organic detritus based on rich plant remains, but calm environment without strong currents that would significantly disturb post-mortem taphocoenosis. The shallow depth is supported by the present ichthyofauna, which apart from predominant specimens of clupeid fish, consists of sygnathid and centriscid species having a bathymetrical preference for shallow near-shore bottoms with seagrass meadows (Ahnesjö and Craig, 2011; Nelson et al., 2016). Such interpretation of palaeoenvironment fits well with the presence of hymenosomatid crabs, as most extant species inhabit shallow water environment.

CONCLUSIONS

Two newly described species of the family Hymenosomatidae represent the first reliable occurrence of the family in the fossil record. *Halicarcinus popeius* sp. nov. and *Lucascinus trifailensis* sp. nov. are the first fossil representatives of the genera *Halicarcinus* and *Lucascinus*. The poor fossil record of the group is partly due to the fragile nature of hymenosomatid exoskeleton and their poor preservation potential, due to the lack of fossiliferous localities with calm depositional near shore facies, and because of the minute size of specimens also due to the presence of collecting bias. Shallow water, near shore environmental setting, similar as is inhabited by most extant hymenosomatid species, is reconstructed based on associated fauna.

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