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Eubrachyuran crabs (Brachyura, Decapoda) from the early Eocene coral reef mounds of the Serraduy Formation (Southern Pyrenees, Huesca, Spain)

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Abstract

A highly diversified fauna of brachyurans is described from the lower Eocene Serraduy Formation of Huesca, northeastern Spain. Fifteen new and first-reported taxa of brachyurans are described including three new genera, ten new species, and five taxa in open nomenclature. New taxa include: *Carpilius feldmanni* n. sp., *Ceronnectes rugosus* n. sp., *Eohexapus simplex* n. sp., *Galenopsis ossoi* n. sp., *Matutsalen rotundus* n. gen. n. sp., *Microboschettia elegans* n. gen. n. sp., *Parhalimede antiqua* n. sp., *Locomius parthenopimimus* n. gen. n. sp., *Liocarcinus tridentatus* n. sp., and *Xanthilites robustus* n. sp. Five additional genera have been recognized from fragmented material only including *Alponella* sp., *Lovaroides* sp., *Paromola* sp., ?*Rhinolambrus* sp., and ?*Spinirostrimaia* sp. Moreover, based on new specimens, we provide new data on *Ilerdapatiscus guardiae* and *Aragolambrus collinsi.* New information supports previous considerations about reef settings that are comparable to modern reef ecosystems as environments of diversified decapod crustaceans in the early Eocene.

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Non-technical Summary

Brachyurans or true crabs are a dominant group of arthropods in modern ecosystems with a long fossil record. High diversity settings (hot spots) yielding crabs include modern reefs like those from the Indo-Pacific and the Caribbean. Understanding ancient reef-like hot spots is challenging especially because they have some physical environmental conditions (high energy, low sedimentation rates) that do not favor preservation. The Ramals outcrop in the Eocene Serraduy Formation (about 53 million years old) of Huesca, northeastern Spain is an exception, and it hosts a great diversity of invertebrates including decapod crustaceans. Herein we report from this exceptional locality 15 new or first-reported taxa of brachyurans including three new genera, ten new species, and five taxa in open nomenclature. Some of the crab taxa are the first ones reported in Spain and some represent the oldest occurrence of modern families of crabs.

Introduction

Modern coral reef ecosystems, which are among the most diverse habitats globally (Moberg and Folke, 1999; Roberts et al., 2002; Knowlton et al., 2010; Hurley et al., 2016), were fully established by the Eocene (Pomar et al., 2017). Modern mesophotic coral reefs, like those found in the Serraduy Formation, occur in the deeper parts of the photic zone, ranging from 30 to 150 meters in depth (i.e., Hinderstein et al., 2010; Hurley et al., 2016).

Fossil invertebrates from these habitats are difficult to sample and quantify especially because they usually are subjected to taphonomic conditions that do not favor preservation (Klompmaker et al., 2015). Decapod crustaceans from the coral reef mounds from the Serraduy Formation are an exception, because facies distribution and general transgressive trends with rapid sedimentary pulses favored preservation of reef inhabitants, which were transported to and accumulated in the forereef facies (Ferratges et al., 2021a). Consequently, 44 taxa of decapod crustaceans have been preserved in different states of preservation (Artal and Vía, 1989; Artal and Castillo, 2005; Artal and Van Bakel 2018a, b; Ferratges et al., 2019, 2021a, b, 2022; Artal et al., 2022; Ferratges, 2022; Table 1).

Two previous contributions focused on the study of dromioid crabs (Artal et al., 2022) and paguroids (Ferratges et al., 2022). However, heterotrematous crabs are the most diverse group of decapods and remained undescribed (Table 1). This paper focusses on the descriptions of new and newly reported species of brachyurans (excluding Raninoidea).

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Table 1. Updated table with Ramals outcrop decapod crustacean diversity. Species in bold are described in this work or recognized for the first time; *taxa only known in this outcrop as isolated chelipeds

Superfamily	Family	Subfamily	Taxon
Axiidea de Saint Laurent, 1979 (Infraorder)	Callianassidae Dana, 1852		*Callianassidae indet.
	Ctenochelidae Manning and Felder, 1991	Ctenochelinae Manning and Felder, 1991	**Ctenocheles* cf. *cultellus* (Rathbun, 1935)
Paguroidea Latreille, 1802	Diogenidae Ortmann, 1892		**Clibanarius isabenaensis* Ferratges et al., 2022
			**Parapetrochirus serratus* Ferratges et al., 2022
			**?Petrochirus* sp.
	Annuntidiogenidae Fraaije, van Bakel, and Jagt, 2017		**Paguristes perlatus* Ferratges et al., 2022
	Calcinidae Fraaije, van Bakel, and Jagt, 2017		**Dardanus balaitus* Ferratges et al., 2022
			**Eocalcinus veteris* Ferratges et al., 2022
	Paguridae Latreille, 1802		**?Pagurus* sp.
			**Anisopagurus primigenius* Ferratges et al., 2022
Dromioidea De Haan, 1833	Dromiidae De Haan, 1833	Basinotopinae Karasawa, Schweitzer, and Feldmann, 2011	*Mclaynotopus longispinosus* Artal, Ferratges, van Bakel and Zamora, 2022
		Dromiinae De Haan, 1833	*Torodromia elongata* Artal, Ferratges, van Bakel and Zamora, 2022
		Sphaerodromiinae Guinot and Tavares, 2003	*Basidromilites glaessneri* Artal et al., 2022
			Basidromilites sp.
	incertae sedis		?*Basinotopus* sp.
	Dynomenidae Ortmann, 1892	Paradynomeninae Guinot, 2008	*Kromtitis isabenensis* Artal et al., 2022
			Sierradromia gladiator Artal et al., 2022
Homoloidea De Haan, 1839	Homolidae De Haan, 1839		***Paromola* sp.**
Raninoidea De Haan, 1839	?Orithopsidae Schweitzer et al., 2003		?*Necrocarcinus* sp. (in preparation)
	Lyreididae Guinot, 1993		?*Lyreidus* sp. (in preparation)
	Raninidae De Haan, 1839	Cyrtorhininae Guinot, 1993	*Cyrtorhina ripacurtae* Artal and Castillo, 2005
		Raninoidinae Lőrenthey in Lőrenthey and Beurlen, 1929	?*Ranina* sp. (in preparation)
			Quasilaeviranina sp. (in preparation)
		Rogueinae Karasawa et al., 2014	?*Doraranina* sp. (in preparation)
Aethroidea Dana, 1851	Aethridae Dana, 1851		*Ilerdapatiscus guardiae*, Artal and Van Bakel, 2018a
?Cancroidea Latreille, 1802	Family indet.		***Locomius parthenopimimus* n. gen. n. sp.**
	Cancridae Latreille, 1802	*Cancrinae* Latreille, 1802	***Ceronnectes rugosus* n. sp.**
Carpilioidea Ortmann, 1893	?Arabicarcinidae Schweitzer and Feldmann, 2017		***Matutsalen rotundus* n. gen. n. sp.**
	Carpiliidae Ortmann, 1893		***Carpilius feldmanni* n. sp.**
			Eocarpilius ortegai Artal and van Bakel, 2018b
			Oscacarpilius rotundus Artal and van Bakel, 2018b
	Tumidocarcinidae Schweitzer, 2005		***Xanthilites robustus* n. sp.**
Goneplacoidea MacLeay, 1838	Euryplacidae Stimpson, 1871		***Alponella* sp.**
Hexapodoidea Miers, 1886	Hexapodidae Miers, 1886		***Eohexapus simplex* n. sp.**
Parthenopoidea MacLeay, 1838	Parthenopidae MacLeay, 1838	Dairoidinae Števčić, 2005	*Aragolambrus collinsi* Ferratges, Zamora, and Aurell, 2019
		Parthenopinae MacLeay, 1838	***?Rhinolambrus* sp.**

(*Continued*)

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Table 1. (*Continued*)

Superfamily	Family	Subfamily	Taxon
Pilumnoidea Samouelle, 1819	Pilumnidae Samouelle, 1819		***Galenopsis ossoi* n. sp.**
Majoidea Samouelle, 1819	Majidae Samouelle, 1819	?Majinae Samouelle, 1819	**?*Spinirostrimaia* sp.**
Portunoidea Rafinesque, 1815	Carcinidae MacLeay, 1838	Polybiinae Paul'son, 1875	***Microboschettia elegans* n. gen. n. sp.**
			***Lovaroides* sp.**
			***Liocarcinus tridentatus* n. sp.**
	Geryonidae Colosi, 1923		*Pyrenicola pyrenaica* (Artal and Vía, 1989)
Xanthoidea MacLay, 1838	Panopeidae Ortmann, 1893	Eucratopsinae Stimpson, 1871	*Glyphithyreus almerai* Artal and van Bakel, 2018b
	Xanthidae MacLeay, 1838		***Parhalimede antiqua* n. sp.**

True crabs or brachyurans are ubiquitous members of modern reef communities and are present in many trophic niches (Plaisance et al., 2011), being among the most representative groups in benthic communities (Hurley et al., 2016). Many of the modern families of crabs originated at least in the Eocene (i.e., Brösing, 2008; Tsang et al., 2014; Schweitzer and Feldmann, 2015). Thus, the present work provides additional taxa informing about the first occurrence of the genera *Carpilius*, *Ceronnectes*, *Eohexapus*, *Galenopsis*, *Parhalimede*, *Liocarcinus*, *Alponella*, and *Lovaroides*.

Locality, material, and methods

Locality. The material described herein was collected from the early Eocene (middle Ypresian) Serraduy Formation of the Tremp-Graus Basin. The material was collected from an outcrop that exposes the transition between the reef limestones and the overlying Riguala Marls at a locality known as "Barranco de Ramals" (see Ferratges et al., 2021a, for further information). All specimens were collected from the same levels described in Ferratges et al. (2021a, 2022) and Artal et al. (2022), to which further reference is made.

Material. More than 1000 specimens of brachyuran crabs (357 in MPZ and about 700 in MGSB) that have been revised from the studied outcrop belong to 20 genera and species (included in 15 families), 14 of which are new or reported for the first time, with 10 new species formally named (Table 1). The specimens were prepared physically using a Micro Jack 2 air scribe (Paleotools; Brigham, UT, USA) and prepared chemically in some cases using potassium hydroxide (KOH). The specimens were then photographed dry and coated with ammonium chloride sublimate. Detailed photography of the carapace surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a macro, 60-mm lens.

Repositories and institutional abbreviations. The specimens are deposited in the Museo Geológico del Seminario de Barcelona (MGSB) and the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ). The material deposited in MPZ was collected under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón). The material deposited in MGSB was collected in the early 1980s and is housed within the historical collection of the Seminario Conciliar de Barcelona.

Systematic paleontology

Order **Decapoda** Latreille, 1802
Infraorder **Brachyura** Latreille, 1802
Section **Eubrachyura** de Saint Laurent, 1980
Superfamily **Aethroidea** Dana, 1851
Family **Aethridae** Dana, 1851
Genus ***Ilerdapatiscus*** Artal and van Bakel, 2018a

Type species. Ilerdapatiscus guardiae Artal and van Bakel, 2018a, by original designation.

Ilerdapatiscus guardiae Artal and van Bakel, 2018a
Figure 1

2018a *Ilerdapatiscus guardiae* Artal and van Bakel, p. 5, fig. 1-2.
2021a *Ilerdapatiscus guardiae*; Ferratges et al., p. 11, fig. 7L.

Holotype. A complete carapace (MGSB 75460).

Emended diagnosis. Modified from the original diagnosis of Artal and van Bakel (2018a). Carapace subcircular, broader than long; maximum width in anterior portion; front narrow, with small medial incision, marked axial depression; orbits small, with two small supraorbital fissures; anterolateral margins arched, with seven small lobes; posterolateral margins convex, bearing notable hemispherical mesobranchial swelling and small metabranchial node; posterior margin concave, shorter than frontal margin; dorsal surface with eight hemispherical swellings; three gastric, four branchial, and one cardiac; mesobranchial region with hemispherical swelling situated at posterolateral margin. Sternum narrow, transversely subelliptical. Sterno-pleonal cavity narrow; sternites 1–4 fused, subtriangular, with protruding episternite 4; sternites 7–8 extremely narrow. Chelipeds homochelous, robust, external side of palm covered by rows of tubercles.

Material examined. Forty-six specimens in MPZ and 75 in MGSB. Specimen MGSB 77611 preserves ventral portions. Measurements: W 20 mm, L 21 mm. Specimen MGSB 75462 with attached cheliped.

Remarks. Recently prepared specimens showing ventral features allow the original diagnosis to be emended to include ventral aspects. These ventral features confirm assignation to Aethridae (see Ng et al., 2008, p. 44–45; Beschin and De Angeli, 2017, p. 24).

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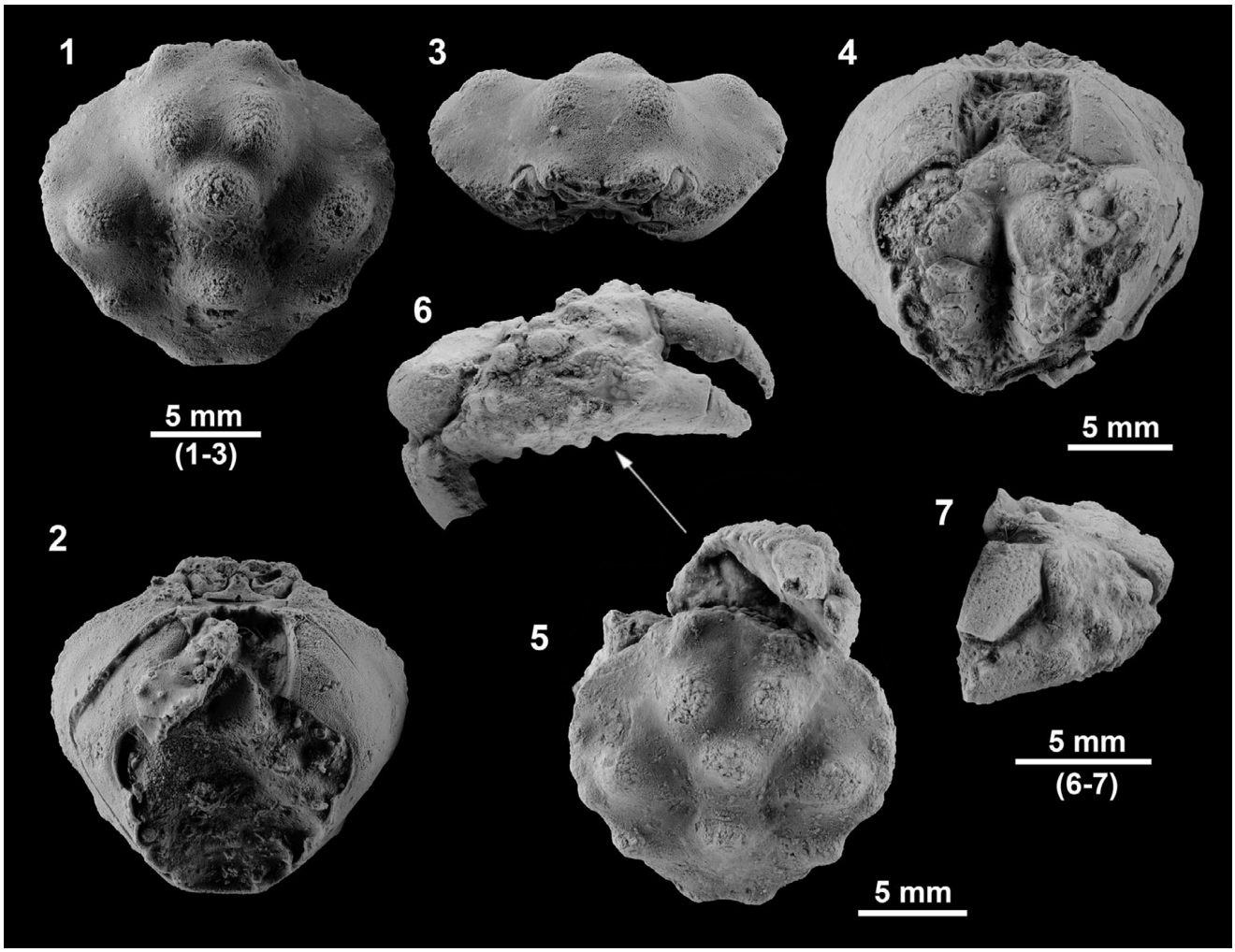

Figure 1. (**1–7**) *Ilerdapatiscus guardiae* Artal and van Bakel, 2018a, MPZ 2021/39 in dorsal (**1**), ventral (**2**), and frontal (**3**) views; (**4**) MGSB 77611 ventral view with sternum; (**5, 6**) MGSB 75462 (**6**) dorsal view with chelipeds, (**7**) right cheliped in oblique lateral view; (**7**) MGSB 75462 left cheliped in oblique frontal view.

Some isolated chelipeds (Fig. 1.5, 1.6) have been assigned to this taxon based on a partially articulated specimen, a carapace with attached remains of chelipeds, and the similarity of these chelipeds to those of other fossil genera assigned to the Aethridae (i.e., Vía, 1959; De Angeli and Beschin, 1999; Beschin and De Angeli, 2017).

Superfamily **Cancroidea** Latreille, 1802
Family indet.
Genus ***Locomius*** new genus

Type species. Locomius parthenopimimus n. gen. n. sp., by monotypy.

Diagnosis. As for the type species, by monotypy.

Etymology. The name refers to its fan shape, which calls to mind the 1980s pop music group "Locomia", in arbitrary combination of letters. Gender masculine.

Remarks. Locomius n. gen. shows certain morphological characteristics that seem typical of cancroids, including a subhexagonal outline of the carapace, being wider than long; the front with protruding teeth; raised orbits, with two notable supraorbital fissures; arched anterolateral margins; anterolateral margins divided into flat lobes separated by notches; strongly concave posterolateral margins converging backwards; dorsal regions well defined by swellings (Schram and Ng, 2012; Schweitzer and Feldmann, 2019; Karasawa and Takahashi, 2020; Poore and Ahyong, 2023).

Some fossil genera that present characteristics very similar to *Locomius* n. gen., including *Eogarthambrus* De Angeli, Garassino, and Alberti, 2010, and *Mesolambrus* Müller and Collins, 1991 (see Schweitzer et al., 2020), have been assigned to the family Parthenopidae due to their subtriangular morphology, but parthenopids have a strongly differentiated frontal margin, and differentiated fronto-orbital margin. In the case of *Eogarthambrus*, the only difference is the much wider outline of the carapace and the presence of four broad and armed teeth in the anterolateral margin, and the orbits directed more obliquely (see De Angeli, Garassino, and Alberti, 2010, fig. 1-3). Recently, Ferratges et al. (2023b) carried out a phylogenetic analysis to clarify parthenopoid relationships, which included several fossil taxa traditionally assigned to this group. The results obtained suggested that taxa very similar to *Locomius* n. gen., such as *Eogarthambrus*, might be included within Cancroidea. We follow that classification.

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Locomius parthenopimimus new species
Figures 2, 3.1–3.5

Type material. Five specimens, the holotype, a complete carapace, is MGSB 77604; and four paratypes: MGSB 77605a–c and MPZ 2021/35.

Diagnosis. Sub-hexagonal carapace, wider than long, L/W ratio about 0.8, steeply downturned anteriorly; quadrilobed front, with two medial protruding teeth; small orbits, slightly obliquely directed, raised supraorbital margin, with two deep fissures; anterolateral margin with four lobes flattened dorsoventrally; concave posterolateral margins, convergent; strongly swollen dorsal regions, well defined by shallow grooves and raised swellings.

Description. Carapace subhexagonal, fan-shaped in outline, wider than long, L/W ratio about 0.8, maximum width at 3/4 of its length; dorsal surface longitudinally convex, steeply downturned anteriorly. Front with four lobes, narrow, slightly extended beyond orbits, with four lobes and median incision, the two medial more protruding, with blunt tip and directed forward. Orbits elliptical, anterolaterally directed, orbital margin markedly raised, with two supraorbital indentations; outer-orbital spine not well developed. Fronto-orbital margin occupying about 45% of the maximum width of carapace. Anterolateral margins broadly convex, with four dorso-ventrally flattened lobes separated by fissures. Posterolateral margins shorter, concave, connecting to anterolateral margins by acute angle. Posterior margin short, nearly straight. Dorsal regions strongly swollen and raised, subdivided in portions and bounded by shallow grooves. Epigastric region small, defined by elongated ridges. Protogastric and mesogastric regions large, strongly swollen and raised. Hepatic region small, depressed, only covered with irregular granules. Epi- and mesobranchial regions differentiated, defined by oblique swellings. Cardiac region large, elongated, subpentagonal in shape. Dorsal grooves numerous, most of them shallow, the branchiocardiac groove deep. Dorsal surface of carapace strongly ornamented, densely covered by small granules and irregular tubercles. Manus of cheliped short; lateral surface with three granular ridges and scattered tubercles; upper margin with four short spines; ventral margin concave. Fingers short and robust. The chelae tentatively assigned to this taxon are robust, with divergent upper and lower margins, five strong spines in the upper margin; outer surface with three tubercles and three subtle longitudinal ridges; inner surface smooth (Fig. 4.4, 4.5).

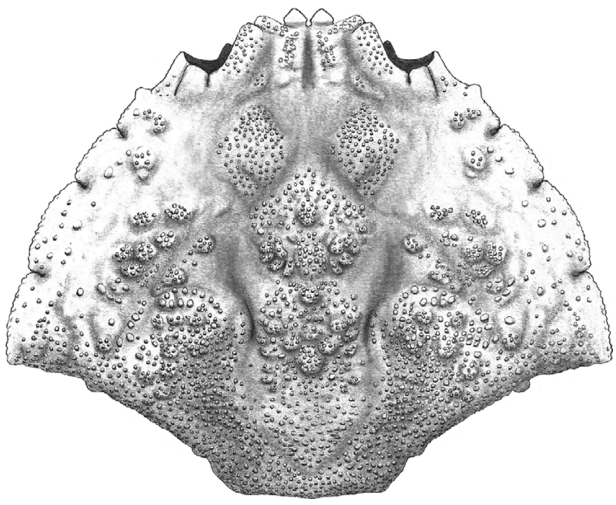

Figure 2. Idealized reconstruction of the carapace of *Locomius parthenopimimus* n. gen. n. sp.

Etymology. The name "*parthenopimimus*" refers to the triangular morphology of the carapace, which resembles that of parthenopoids.

Other material examined. Three isolated chelipeds in MGSB, and two in MPZ (MPZ 2024/80, MPZ 2024/81).

Remarks. Locomius parthenopimimus n. gen. n. sp. shows important similarities with *Eogarthambrus guinotae* De Angeli, Garassino, and Alberti, 2010; however, the carapace is less laterally expanded and in the anterolateral margin shows four teeth instead five as *E. guinotae.* The fossil species *Ramacarcinus lineatuberculatus* (Beschin, Busulini, and Tessier in Beschin et al., 2016a) from the early Eocene of Italy has a similar morphology to *Locomius* n. gen. with a wide frontal margin, with an incision in the middle frontal area and four lobes (including intraorbital ones); supraorbital margin rimmed, robust, granulated and with two fissures; anterolateral margins long, convex, endowed with flat teeth, separated by notches; convergent and concave posterolateral margins; short straight posterior margin; dorsal regions defined by smooth furrows ornamented with tubercles (see Beschin et al., 2016a, t.11, figs. 1a,. 44; De Angeli and Ceccon, 2016, p. t.5–6, fig. 11). However, in the anterolateral margin, *R. lineatuberculatus* has five bifid or trifid teeth (excluding the extraorbital one) instead of four finely serrated teeth as in the new species *Locomius parthenopimimus* n. gen. n. sp.; dorsal surface with different ornamentation, and not distributed in alignments.

Family **Cancridae** Latreille, 1802
Genus ***Ceronnectes*** De Angeli and Beschin, 1998

Type species. Cancer böckhii Lőrenthey, 1897, by original designation.

Fossil species included. Ceronnectes boeckhi (Lőrenthey, 1897), *C. granulosa* (Feldmann et al., 1998, ?*C. pusillinus* (Secrétan in Plaziat and Secrétan, 1971), and *C. rugosus* n. sp.

Ceronnectes rugosus new species
Figure 3.6–3.9

Type material. Two almost complete carapaces, one holotype (MGSB 88653) and one paratype (MGSB 77592).

Diagnosis. Carapace subhexagonal, L/W ratio 0.85 maximum width at level of last anterolateral spine, about two-thirds of carapace length; dorsal regions delimited by grooves; surface ornamented with small irregular granules. Orbits broad, with two weak supraorbital fissures. Anterolateral margins arched, with four irregular, flattened lobes.

Description. Carapace subhexagonal, with fan-shaped outline; longitudinally slightly vaulted, somewhat more vaulted transversely; wider than long, L/W ratio 0.85; maximum width at level of last

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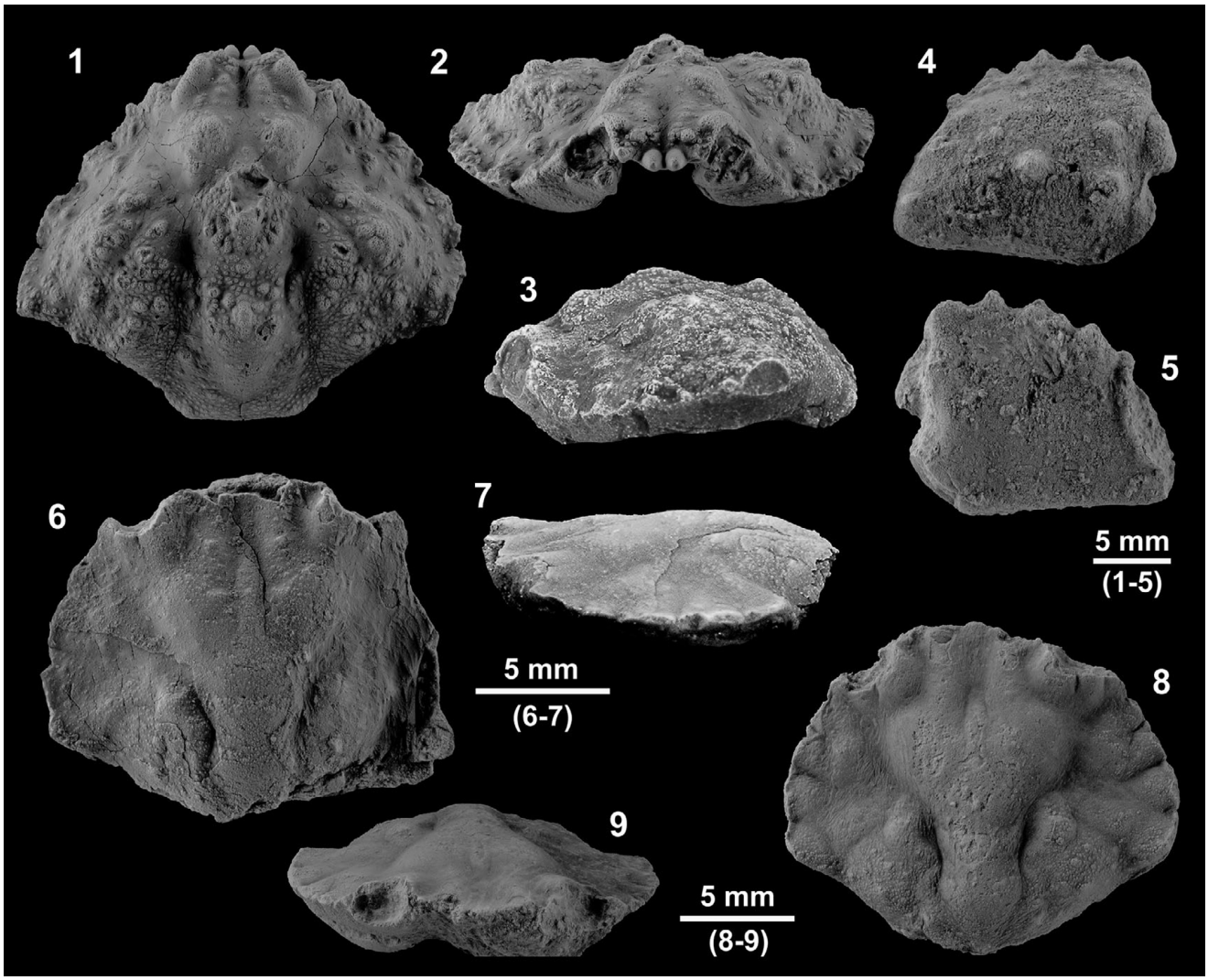

Figure 3. (**1–5**) *Locomius parthenopimimus* n. gen. n. sp. (**1, 2**) Holotype (MGSB 77604) in dorsal (**1**) and (**2**) frontal views; (**3**) lateral view of paratype MGSB 77605a; (**4, 5**) MPZ 2024/80 right cheliped (specimen), in lateral view of outer side (**4**) and inner side (**5**). (**6–9**) *Ceronnectes rugosus* n. sp. in dorsal (**6**), left lateral (**7**), and frontal (**9**) views of paratype (MGSB 77592) and dorsal view (**8**) of holotype (MGSB 88653).

anterolateral spine, about two-thirds of its length. Frontal margin not well preserved. Orbits relatively broad; supraorbital margin with two weak supraorbital fissures; outer orbital spine acute and subtriangular. Fronto-orbital margin occupying about 73% of carapace width. Anterolateral margins arched, longer than posterolateral margins, bearing four irregular, different by size, flattened lobes. Posterolateral margins nearly straight, slightly concave, very convergent posteriorly. Posterior margin narrow, not completely preserved. Dorsal regions well defined, gently swollen. Gastric process large; epigastric lobes elongated, swollen; protogastric lobes broad, swollen, delimited by shallow grooves; mesogastric region scarcely differentiated from the urogastric region, only slightly swollen, with the anterior extension relatively broad and swollen. Urogastric region weakly defined by a horizontal row of granules. Cardiac region large, swollen, barely distinct from gastric lobe, bounded by relatively deep grooves. Hepatic regions flattened, delimited from gastric regions by the gastro-hepatic groove. Epibranchial ridge arched, reaching the last anterolateral tooth. Dorsal surface of carapace covered by irregular granules, some of them unevenly grouped, conferring the appearance of a wrinkled dorsal surface.

Etymology. The specific epithet refers to the coarse texture of the dorsal carapace surface.

Remarks. The Eocene *Ceronnectes boeckhi* (Lőrenthey, 1897) is the most similar taxon, but it has a more subhexagonal outline of carapace with wider appearance; orbits with two deep, well-marked supraorbital fissures; anterolateral margins with four lobes of similar size; posterolateral margins being concave, the dorsal regions more elongated; dorsal surface smoother, with absence of noticeable granules (De Angeli and Beschin, 1998; Beschin et al., 2016b, fig. 43, t. 8, f. 9). *Liocarcinus* Stimpson, 1871, *Macropipus* Prestandrea, 1833, and *Polybius* Leach, 1829, three genera with apparently similar dorsal features and outline as *Ceronnectes*, have been assigned to Portunoidea (Schweitzer et al., 2021), and mainly differ by the absence of anterolateral nodes that are bounded by noticeable indentations, which is a diagnostic character in the Cancroidea.

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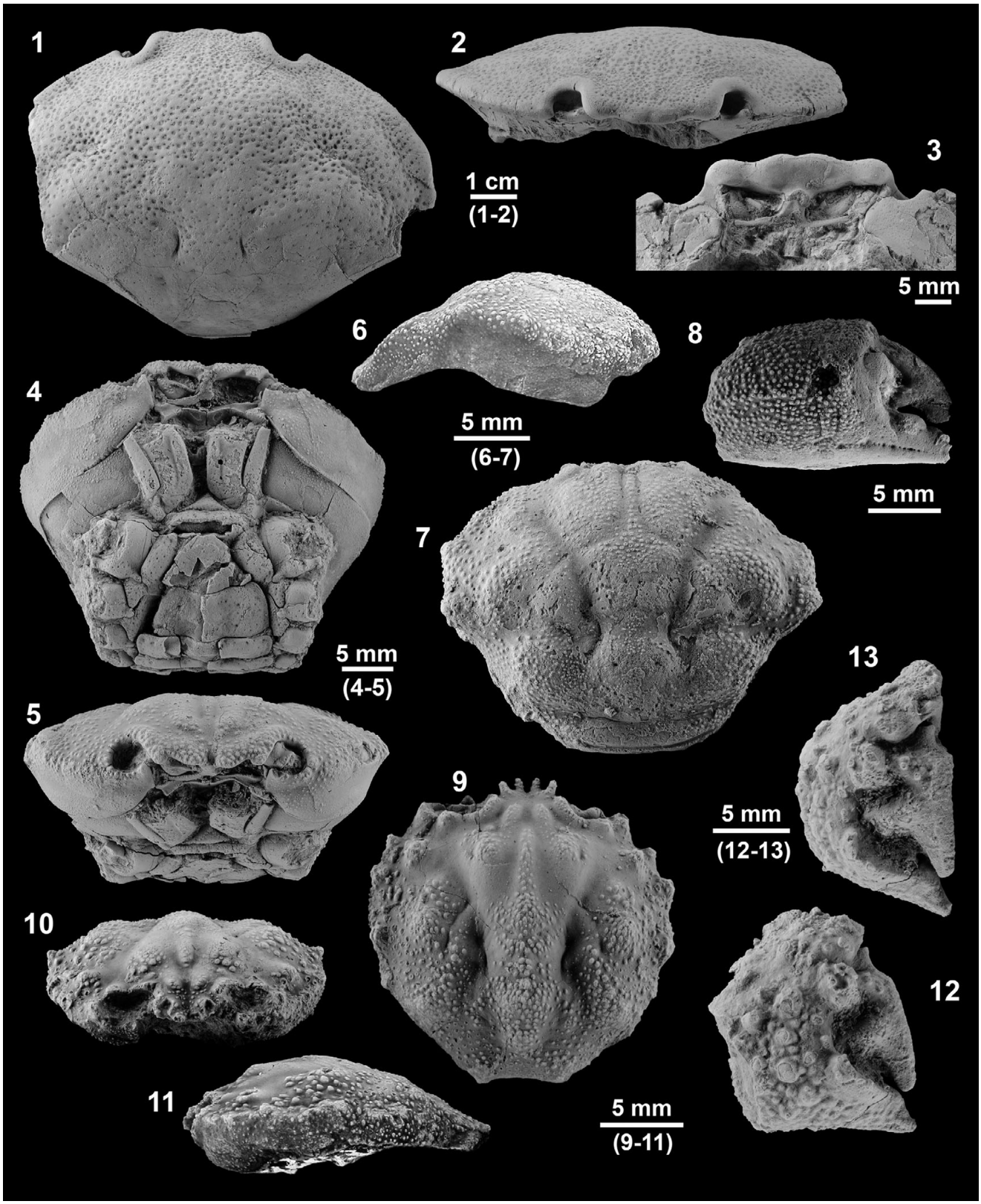

Figure 4. *Carpilius feldmanni* n. sp. (**1–3**) holotype (MPZ 2024/82) in (**1**) dorsal, (**2**) frontal, and (**3**) detail of the ventral side of frontal margin. *Xanthilites robustus* n. sp. (**4–8**) holotype (MGSB 75446) in ventral (**4**), frontal (**5**), and lateral (**6**) views; paratype (MPZ 2021/44) in dorsal view (**7**); right cheliped (specimen MPZ 2024/84), in lateral view of outer side (**8**). (**9–13**) *Matutsalen rotundus* n. gen. n. sp. (**9–11**) Holotype (MGSB 75463) in dorsal (**9**), lateral (**11**), and frontal(**10**) views; (**12, 13**) right cheliped (MPZ 2021/40), (**12**) in lateral view of outer side and (**13**) oblique frontal view.

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Superfamily **Carpilioidea** Ortmann, 1893
Family ?**Arabicarcinidae** Schweitzer and Feldmann, 2017

Remarks. Due to the morphology of the rounded carapace, shape of the orbits, and general outline of the carapace, all of which are very similar to *Eomatuta* and *Arabicarcinus*, we tentatively assign *Matutsalen* n. gen. to the family Arabicarcinidae Schweitzer and Feldmann, 2017 (see Beschin et al., 2019).

Genus ***Matutsalen*** new genus

Type species. *Matutsalen rotundus* n. gen. n. sp., by original designation.

Diagnosis. See species diagnosis.

Etymology. The generic name refers to the family Matutidae with which it shares several superficial similarities, in combination with "Matusalén" as the man who is claimed to have lived the longest life, referring to their ancestral condition. Gender masculine.

Remarks. *Matutsalen* n. gen. shows similarities with the fossil genus *Eomatuta* De Angeli and Marchiori, 2009, in the general outline of the carapace, shape of the orbits, and front with four lobes, and narrow concave posterior margin, with one small tubercle on each side. However, *Eomatuta* is easily distinguished from *Matutsalen* n. gen. in having continuous lateral margins, without spines, the dorsal surface completely covered with dense and large granulation, and dorsal regions very slightly marked. *Matutsalen* n. gen. and *Arabicarcinus* Schweitzer and Feldmann, 2017, from the Coniacian Cretaceous of Saudi Arabia, exhibit similarities in the oval shape of the carapace, a front with four lobes, moderately large and subrectangular orbits, and a concave posterior margin. However, they present clear differences: *Arabicarcinus* has continuous lateral margins without spines, a punctate dorsal surface with low relief and poorly defined regions, sinuous orbits, and rimmed posterior margin.

The fossil genus *Szaboa* Müller and Galil, 1998, included in the family Matutidae De Haan, 1835, has a very similar outline of the carapace with *Matutsalen* n. gen., but shows differences in the morphology of the dorsal regions, which are more marked in the new genus; the shape and size of the anterolateral spines, which are more robust in the new genus; the frontal margin without prominent tubercles in *Szaboa*; and the posterior margin convex instead of concave as in *Matutsalen* n. gen.

Matutsalen n. gen. shows morphological similarities with fossil and modern *Ashtoret* Galil and Clark, 1994, and the modern genera *Matuta* Weber, 1795, *Izanami* Galil and Clark, 1994, and *Mebeli* Galil and Clark, 1994, (all included in the family Matutidae), including: (1) general shape of the carapace with a slightly convex surface; (2) shape of the frontal margin, with front divided into four and orbits very angled in the internal supraorbital margins; (3) convexity of the anterolateral margins; and (4) narrow posterior margin. However, *Matutsalen* n. gen. shows strong conical spines on the anterolateral margins; lacks the long lateral spines, typical of modern genera; and lacks the smooth and porcelain appearance of modern genera, with dorsal regions well defined and granulated.

The chelipeds assigned to *Matutsalen* n. gen. show the typical characteristics of calappoids: laterally compressed, without ornamentation on the inner side; outer surface tuberculate; a ridge with several spines on the upper margin; and a movable finger with a molariform expansion that separates it from the base of the dactylus. Furthermore, the curvature of the inner margin of the chelipeds fits with the anterior lower part of the carapace (see Ferratges et al., 2021a, fig. 7O; Fig. 1.10, 1.11). All these characteristics of *Matutsalen* n. gen. are ambiguous and its inclusion either in Calappoidea De Haan, 1833, or Carpilioidea Ortmann, 1893, is problematic.

Matutsalen rotundus new species
Figures 4.9–4.13, 5

Type material. Four specimens, the holotype, a near-complete carapace, is MGSB 75463, and three paratypes: MGSB 75464a, MGSB 75464b, and MPZ 2021/34.

Diagnosis. Carapace subcircular, convex surface, almost as wide as long; frontal margin with four lobes, orbits suboval, with two supraorbital fissures and a fissure in the infraorbital margin; lateral margins convex, with three spines and one posterior tubercle; posterior margin narrow and concave; dorsal regions well defined; the posterior two-thirds of the carapace covered by granules.

Description. Carapace almost as long as wide, subcircular shape, L/W ratio about 0.98, maximum width at one-half of its length; dorsal surface longitudinally and laterally convex, steeply downturned anteriorly; broad fronto-orbital margin, occupying 63% of the carapace width. Front narrow, extended beyond orbits, with median incision and two lobes directed slightly ventrally on each side. The middle part of the frontal region is furrowed by a longitudinal depression. Orbits large, elliptical, oriented forward; supraorbital margin raised, with two supraorbital fissures; anterolateral margins convex, with three conical spines, the first two directed anteriorly, the third oriented laterally, perpendicular to the axis. Posterolateral margins less convex than anterolateral margins; bearing a blunt spine. Narrow posterior margin, slightly concave, with a small protrusion on each side. Dorsal regions well defined by swellings and shallow grooves. Frontal region with longitudinal depression. Gastric regions swollen, elongated. Hepatic region small, with a strong protuberance. Branchial regions divided in portions, defined by oblique inflations. Cardiac region elongated. Intestinal region depressed. Dorsal surface ornamented with irregular granulations, more abundant in the posterior two-thirds

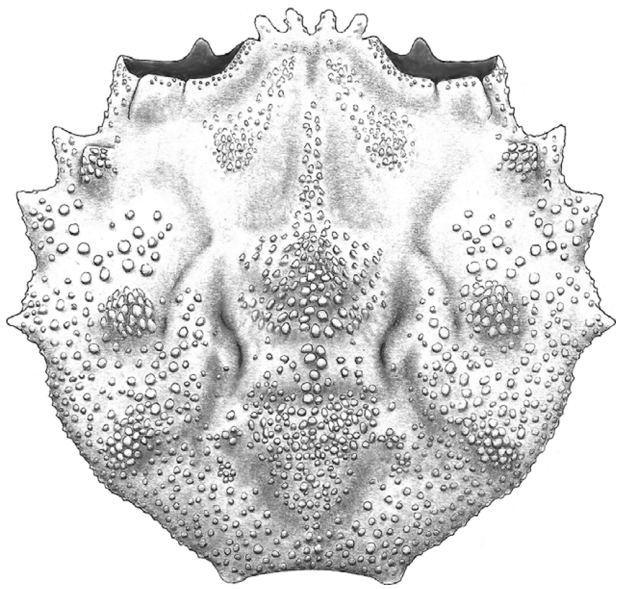

Figure 5. Idealized reconstruction of the carapace of *Matutsalen rotundus* n. gen. n. sp.

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(Figs. 1.7, 2). The chelipeds assigned to this genus (Fig. 1.10, 1.11) present the typical structure of the calappoids, with an expansion in the occlusal margin of dactyl. The upper margin of the propodus is provided with a highly developed crest forward oriented; outer surface of the palm is ornamented with irregular granulations; fixed finger short and turned obliquely downwards, the occlusal margin has small, rounded teeth; the dactyl is long and robust, with the upper margin decorated with granulations. Ventral parts not preserved.

Etymology. "*rotundus*" is given in the masculine form to agree with the gender of the genus, and refers to the rounded shape of the carapace.

Remarks. Matutsalen rotundus n. gen. n. sp. shows a morphology similar to *Eomatuta granosa* De Angeli and Marchiori, 2009. However, it differs in some aspects: frontal margin divided into four lobes that are very accentuated in the new taxon; anterolateral margins of the new taxon have five teeth, the first being that of the postorbital margin; dorsal regions much more clearly defined in the new species; and dorsal surface of the new taxon mostly covered with tubercles in the posterior part and on the tips of the dorsal regions only, not homogeneously covered with rounded tubercles as in *E. granosa.*

Family **Carpiliidae** Ortmann, 1893
Genus ***Carpilius*** Leach in Desmarest, 1823

Type species. Cancer maculatus Linnaeus, 1758, by monotypy.

Fossil species included. Carpilius cantellii De Angeli and Alberti, 2020; *C. convexus* (Forskål, 1775) (also extant); *C. corallinus* (Herbst, 1783) (also extant); *C. feldmanni* n. sp.; *C. maculatus* (Linnaeus, 1758) (also extant); C. *petreus* Beschin et al., 2007.

Carpilius feldmanni new species
Figure 4.1–4.3

Type material. The holotype, a near-complete, slightly compressed carapace, is MPZ 2024/82.

Diagnosis. Carapace ovate, wider than long, vaulted longitudinally, smooth surface, with small- to medium-size pits on anterior two-thirds, poorly defined regions. Front with central bilobed projection. Circular, rimmed and smooth orbits. Convex anterolateral margin. Nearly straight posterior and posterolateral margins. Cheliped smooth, manus about as long as high; fingers short, thick, with one blunt tooth.

Description. Carapace transversely oval, vaulted, wider than long, L/W ratio 0.68; regions not defined, maximum width about two-thirds of its length. Frontal margin with four blunt lobes (quadrilobate). Orbits sub-circular; inner and outer orbital spines blunt. Fronto-orbital margin occupying about 43% of carapace width. Anterolateral margins arched, longer than the posterolateral margins, entire. Posterolateral margins nearly straight. Posterior margin narrow, rimmed. Dorsal regions not defined, only the branchiocardiac grooves are well marked. Dorsal surface with small- to medium-size pits on anterior two-thirds of the carapace. Proepistome subtriangular, with rounded apex, antennular fossettes rhomboidal.

Etymology. The specific epithet honors Dr. Rodney Feldmann, in recognition of his considerable contributions to the crustacean paleontological record.

Remarks. The general shape, dorsal ornamentation, and the main characters of the new material fit the general diagnosis of the extant and extinct *Carpilius* (see Schweitzer et al., 2018). However, *C. feldmanni* n. sp. has a narrower fronto-orbital margin, and the branchiocardiac grooves are deeper than other species. The fossil species *C. petreus* is slightly reminiscent of the general outline of the carapace of the new species; however, it is more rounded than that of the new species and the morphology of the frontal margin is different, more downward oriented, and with more marked protuberances in *C. petreus* (see Beschin et al., 2007, t. 5, ff. 7a, b, 8a, b, 2016b, fig. 45. t. 9, ff. 3A, B). The fossil species *C. cantellii* De Angeli and Alberti, 2020, from the late Eocene of Italy, can be differentiated mainly in its more rounded outline (less laterally expanded), wider posterior margin, less marked branchiocardiac grooves, and the pits of its carapace are larger and are distributed over the entire surface, unlike the new species. *Carpilius feldmanni* n. sp. represents the oldest record of the genus *Carpilius.*

Family ***Tumidocarcinidae*** Schweitzer, 2005
Genus ***Xanthilites*** Bell, 1858

Type species. Xanthilites bowerbanki Bell, 1858, by original designation.

Fossil species included. Xanthilites bowerbanki Bell, 1858, *X. robustus* n. sp., *X. interpunctus* Schafhäutl, 1863.

Xanthilites robustus new species
Figure 4.4–4.8

2017 *Xanthilites bowerbanki*, Ferratges, p. 53, fig. 13 B, C.
2021a *Xanthilites* sp. Ferratges et al., p 11, fig. 7S.

Type material. Four specimens, the holotype (MGSB 75446) preserves the ventral portion, and three paratypes; MGSB 75447 a–c, and MPZ 2021/44.

Diagnosis. Carapace subhexagonal, wider than long, widest at position of epibranchial node. Frontal margin downturned, straight from dorsal view, bearing four lobes. Orbits small, rimmed, with two supraorbital fissures. Anterolateral margin bearing two blunt nodes. Posterolateral margin somewhat concave. Posterior margin with thin rim. Dorsal regions well defined by gentle swellings and shallow grooves. Mesobranchial region weakly separated from posterior regions. Dorsal surface densely covered by granules. Sternum broad, subtriangular, with arched lateral margins. Sternites 3 and 4 with elongated horizontal and oblique swellings. Female pleon broad, subtriangular; telson triangular, sixth pleonal segment subrectangular, large. Coxae of pereiopods and third maxillipeds large.

Description. Carapace subhexagonal in outline, wider than long, L/W ratio about 0.77, widest at position of the last anterolateral spine, about 50% of carapace length. Carapace vaulted in both directions. Front broad, straight from dorsal view, with a small axial indentation, strongly downturned; frontal margin with four blunt lobes. Orbits small, anterolaterally directed, orbital margin rimmed, granulated. Anterolateral margins arched and shorted than posterolateral; first portion broadly arched, last portion bearing two blunt nodes. Posterolateral margins converging posteriorly, slightly concave. Posterior margin rimmed, somewhat longer than the frontal margin. Dorsal regions well defined by broad, gentle swellings and weak, shallow grooves. Epigastric regions defined by

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small swellings and numerous granules. Protogastric regions large, subtrapezoidal in shape. Mesogastric region large, subpentagonal, weakly differentiated posteriorly; anterior extension extremely narrow, elongated. Hepatic region slightly swollen. Epibranchial region large, slightly swollen, scarcely divided, the anterior portions of branchial region separated from the metabranchial by a shallow depression. Cardiac region somewhat swollen, subtriangular inverted in shape. Intestinal region flattened. Dorsal surface of carapace densely granulated, except the dorsal grooves and depressions, which are smooth. A well-defined hepatogastric groove runs obliquely along the carapace, merging with the gastrobranchial and the branchiocardiac grooves; the cervical groove not defined. Ventral portions of carapace narrow, elongated, with scarce granules. Pterygostomial region large, arched, devoid of granulation. Sternum large, subtriangular, with arched lateral margins. Sternites 1–2 small subtriangular, fused. Sternites 3–4 large, fused, sternite 3 horizontal swollen; sternite 4 oblique, swollen; sternite 5 scarcely visible, sternites 6–8 covered by female pleon. Episternites 4 and 5 subtriangular, well developed. Upper portion of the antennular space, below the front, strongly ridged. Basal segment of antennule subtriangular. Proepistome subtriangular, with rounded apex. Epistome robust, subrectangular, with rounded corners and medial sulcus. Buccal frame subtrapezoidal. Maxilipeds 3 large, stout, endopod with elongated sulcus in the middle, exopod long, narrow. Sternopleonal cavity large, relatively deep. Female telson large, subtriangular; pleonal segment 6 subrectangular, large, pleomeres 3–5 free, narrow. Coxae of pereiopods large, subrectangular. Chela short robust, palm short globular, densely granulated, carpopropodial articulation oblique; dactylus with long and robust occlusal protuberance.

Etymology. "robustus" referring to its robust constitution.

Other material examined. About 57 near-complete carapaces (MGSB 75447), 36 additional incomplete carapaces in MPZ (MPZ 2024/83), and one specimen figured in Ferratges, 2017 (p. 52–53, fig. 27-B, pl. 13 B, C); there are about 10 isolated chelipeds in MGSB.

Remarks. The type species *Xanthilites bowerbanki* differs from the new species in several features. It has a wider frontal margin with larger indentations, strongly downturned, and features four blunt nodes. In *X. bowerbanki*, the frontal margin projects farther beyond the orbits, with four spinous processes visible in dorsal view and a V-shaped axial notch. In contrast, *X. robustus* n. sp. has orbits that are less rimmed and raised. The anterolateral margins bear two blunt nodes, separated by a vertical portion. In *X. bowerbanki*, these margins present two arched lobes and two more projecting, spinous processes.

The dorsal regions are gently swollen, moderately marked, and less subdivided in portions in *Xanthilites robustus* n. sp., whereas they are more swollen, strongly marked, and subdivided in portions in *X. bowerbanki.* The meso-, proto-, and epigastric regions are more tumid in *X. bowerbanki*, and the mesogastric region is smaller, more inflated, and bounded posteriorly by a deep groove. The urogastric region is just a depression behind the mesogastric region in the new species, whereas it is swollen and subtrapezoidal in shape in *X*, *bowerbanki.* The hepatic region is scarcely defined in the new species, while it is larger and more swollen in *X. bowerbanki.* The dorsal grooves are also more evident, deeper in *X. bowerbanki*, and weakly defined in the new species. The sternum also shows some notable differences: sternites 3–4 are swollen and elongated in the new species, but they are flatter and more defined by a deep oblique and longitudinal medial depression, described as a Y-shaped groove by Schweitzer (2005) in *X. bowerbanki.* The epistome bears three arched indentations in the lower margin in *X. bowerbanki*, whereas it is robust and subrectangular in *X. robustus* n. sp. The chelae are short, globular, stout, and densely granulated in the new species, whereas they are more elongated and less ornamented in *X. bowerbanki*; the fingers are short and robust, with a strongly elongate occlusal protuberance in the dactylus, and only one low, robust protuberance in the occlusal margin of the fixed finger in *X. robustus* n. sp., whereas they are thinner and more elongated, with more numerous and less robust occlusal protuberances in *X. bowerbanki* (Bell, 1858; Schweitzer, 2005).

Superfamily **Goneplacoidea** MacLeay, 1838
Family **Euryplacidae** Stimpson, 1871
Genus ***Alponella*** Beschin et al., 2016a

Type species. Alponella paleogenica Beschin et al., 2016a, by original designation.

Fossil species included. Alponella paleogenica Beschin et al., 2016a; *Alponella* sp.

***Alponella* sp.**
Figure 6.4

Description. Carapace subhexagonal to subcircular, slightly wider than long, longitudinally convex. Front broad, protruding, downturned, with median groove; frontal margin almost straight. Orbits wide, slightly raised, with orbital margin entire. Anterolateral margins short, convex, not well preserved; posterolateral margins longer, convex. Dorsal regions scarcely defined.

Material examined. One incomplete specimen, MPZ 2024/85.

Remarks. The specimen is included in the genus *Alponella* because of its subhexagonal carapace, slightly wider than long; shape of the frontal margin; and the rounded shape and oblique position of the orbits. The only other species is *A. paleogenica* Beschin et al., 2016a, from the early Eocene of Italy, but *Alponella* sp. can be differentiated by its less marked dorsal regions and a less elongated outline of the carapace; the front is flat, without inflations; and the orbits are only weakly rimmed. For contrast, the Italian species presents a frontal margin with two strongly swollen lobes, the orbits are notably rimmed, and the dorsal regions are more evident, with gentle inflations and weak grooves (Beschin et al., 2016a). With only one incomplete carapace, we assign this taxon to the genus *Alponella*, keeping it in open nomenclature.

Superfamily **Hexapodoidea** Miers, 1886
Family **Hexapodidae** Miers, 1886
Genus ***Eohexapus*** De Angeli, Guinot, and Garassino, 2010

Type species. Eohexapus albertii De Angeli, Guinot, and Garassino, 2010, by original designation.

Fossil species included. Eohexapus albertii De Angeli, Guinot, and Garassino, 2010; *E. simplex* n. sp.

Eohexapus simplex new species
Figure 6.1–6.3

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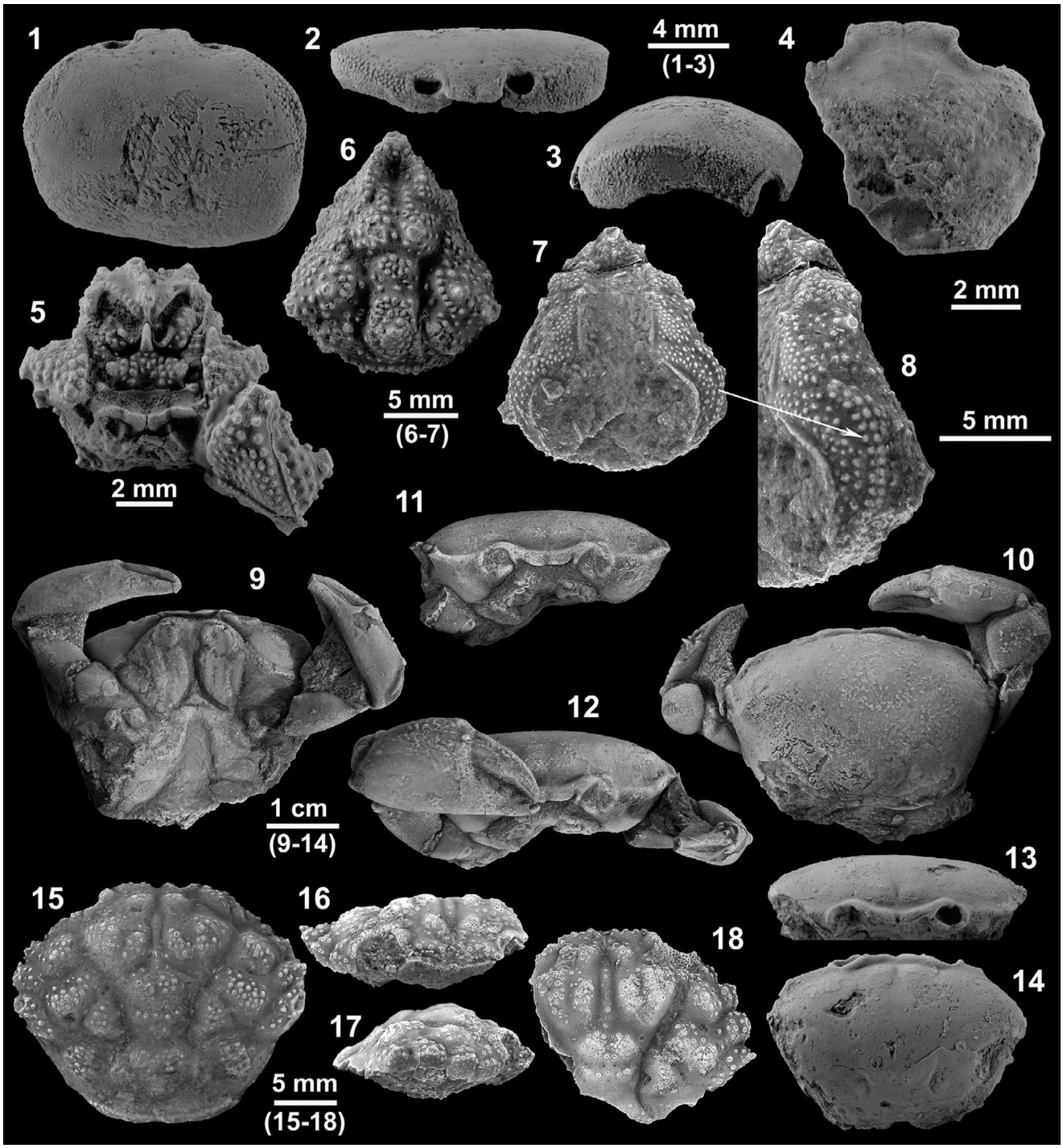

Figure 6. (**1–3**) *Eohexapus simplex* n. sp., holotype (MGSB 77607) in dorsal (**1**), frontal (**2**), and left lateral (**3**) views. (**4**) *Alponella* sp. in dorsal view (MPZ 2024/85). (**5–8**) *Aragolambrus collinsi* Ferratges, Zamora, and Aurell, 2019, (MPZ 2024/86) detail of frontal ventral view (**5**) with epistoma and antennular pits; (**6**) dorsal view of MGSB 75458; ventral view (**7**) and (**8**) detail of the pterigostomial region with the ridge of tubercles (MGSB 75459). (**9–14**) *Galenopsis ossoi* n. sp. (**9–12**) MGSB 75439 in ventral (**9**), dorsal (**10**), and frontal views without and with chelipeds (**11, 12** respectively); frontal (**13**) and dorsal (**14**) views of the paratype MGSB 75440. (**15–18**) *Parhalimede antiqua* n. sp. holotype (MGSB 75465) in dorsal view (**15**), and paratype MPZ 2024/87 in frontal (**16**), right lateral (**17**), and dorsal views (**18**).

Type material. Only one complete carapace, the holotype MGSB 77607.

Diagnosis. Carapace subrectangular, frontal margin downturned, nearly straight. Orbits small, directed forward. Anterolateral margins short, broadly arched, bearing numerous granules. Posterolateral margins subparallel, slightly convergent backwards. Posterior margin long, slightly convex. Lateral sides of carapace vertical, bearing numerous granules. Dorsal regions of carapace poorly defined.

Description. Carapace wider than long, subrectangular; dorsal surface convex longitudinally, smooth, without deep cervical and branchiocardiac grooves; arched, short, branchio-cardiac depressions;

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mesogastric and cardiac regions poorly defined by shallow grooves. Surface ornamented by spaced pits, anterior margins of carapace and lateral sides with dense granulation. Front depressed, narrow, downturned, extending beyond orbits, widened distally, sulcate; margin straight in frontal view. Orbits reduced and rounded; supraorbital border rounded, weakly rimmed; upper orbital margin sinuous; anterolateral margin convex, ornamented with small granules; posterolateral margins subparallel, somewhat convergent backwards, posterior portion with rimmed, large, concavity; wide posterior margin, slightly convex. Lateral margins convex, vertical; posterior portion with large concavity for the insertion of last pereiopods.

Etymology. "*simplex*", due to the simplicity of its carapace.

Remarks. Despite the complete preservation of dorsal characters, including the fronto-orbital construction, in absence of ventral characters and chelipeds, or more numerous specimens, we include this new taxon in the genus *Eohexapus*. Both *E. simplex* n. sp. and the Italian taxon *E. albertii*, share a subrectangular outline of carapace; with short, broadly arched anterolateral margins, bearing granules; slightly arched and somewhat convergent posterolateral margins; and a long weakly convex posterior margin. The new taxon presents a more subquadrate outline of the carapace; a nearly straight frontal margin; anterolateral margin and the lateral sides are densely covered by notable granules; and short, arched, well-marked branchiocardiac grooves. For contrast in the Italian species, the outline is more subrectangular, being notably wider; the frontal margin is bilobed from dorsal view, with both lobes slightly swollen; in frontal view the margin exhibits a thin rim; the anterior portion of lateral margins is visibly rimmed; the granulation over the dorsal carapace and vertical sides is smaller and differently distributed; the dorsal surface exhibits two big, rounded depressions close to the cardiac region. The fossil species *Stevea cesarii* Beschin et al., 1994, is very similar, but shows a different outline of the carapace, subtrapezoidal instead of subrectangular, with the lateral margins divergent backwards; the orbits are strongly rimmed; the posterior margin is more convex and presents a notable rim. Other fossil genera assigned to the Hexapodidae exhibit still more notable differences (see De Angeli, Guinot, and Garassino, 2010).

Superfamily **Parthenopoidea** MacLeay, 1838
Family **Parthenopidae** MacLeay, 1838
Subfamily **Dairoidinae** Števčić, 2005
Genus ***Aragolambrus*** Ferratges, Zamora, and Aurell, 2019

Type species. *Aragolambrus collinsi* Ferratges, Zamora, and Aurell, 2019, by original designation.

Aragolambrus collinsi Ferratges, Zamora, and Aurell, 2019
Figures 6.5–6.8, 7

2019 *Aragolambrus collinsi* Ferratges, Zamora, and Aurell, fig. 4.
2021a *Aragolambrus collinsi*; Ferratges et al., p. 11, fig 7 M.

Holotype. An almost complete carapace preserving chelipeds (MPZ-2019/210).

Emended diagnosis. Carapace subtriangular to pentagonal, longer than wide; orbits inflated; regions inflated; epibranchial margin slightly expanded. Projected frontal margin, triangular, with interorbital depression. Exorbital angle acute. Anterolateral margins almost straight; gastro-orbital notch present. Hepatic margin distinct with small spine, not continuous with epibranchial region. Hepatobranchial notch present, distinct. Epibranchial margin convex, angled at last epibranchial spine; posterolateral margin converging backward. Dorsal surface densely tuberculated with non-coalescent mushroom-shaped tubercles. Proto-, meso-, and metagastric regions differentiated, without ridge; protogastric region is most developed. Hepatic region inflated, slightly lower than epibranchial, gastric regions. Epibranchial region without continuous diagonal ridge. Epistome densely ornated. Pterygostomial ridge present. Subepibranchial region narrow, tuberculate. Epimeral line bordered by numerous small tubercles. Cheliped manus outer margin with 3–5 teeth, triangular in shape and widely spaced; inner margin composed by only three ornamented tubercles; outer side covered with tubercles of variable size (diagnosis modified from Ferratges et al., 2019).

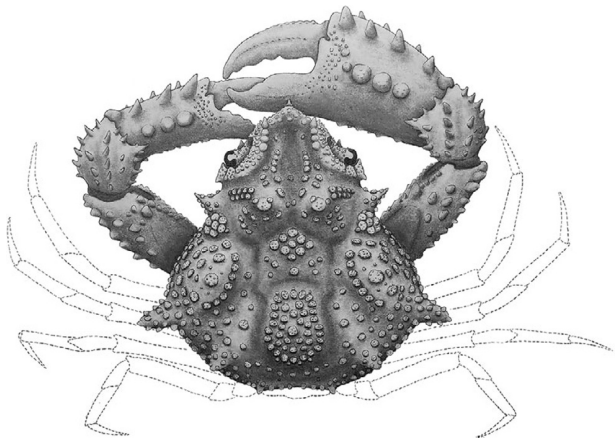

Figure 7. Reinterpreted and idealized reconstruction of *Aragolambrus collinsi* Ferratges, Zamora, and Aurell, 2019, based on the new material.

Material examined. Five specimens in MGSB. Two of them represent complete carapaces (MGSB 75458; MGSB MGSB 75459; and some remains (MPZ 2024/86), and MGSB 77610a–c.

Remarks. The new material studied allows further characters to be included in the original diagnosis proposed by Ferratges et al. (2019); especially those from the ventral view of the carapace. In addition, the new data observed in the new material was used in Ferratges et al. (2023b) to clarify the systematic position of *Phrynolambrus* Bittner, 1893. The obtained results suggest a close position of both genera that are included in the subfamily Dairoidinae Števčić, 2005.

Superfamily **Pilumnoidea** Samouelle, 1819
Familia **Galenidae** Alcock, 1898
Subfamily **Halimedinae** Alcock, 1898
Genus ***Parhalimede*** Beschin et al., 2016b

Type species. *Parhalimede ornata* Beschin et al., 2016b by original designation.

Fossil species included. *Parhalimede antiqua* n. sp., *P. ornata* Beschin et al., 2016b.

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Parhalimede antiqua new species
Figure 6.15–6.18

Type material. Eleven specimens, the holotype MGSB 75465, and 10 paratypes MGSB 75466a–c, MGSB 75467a–c, MPZ 2021/41, MPZ 2024/87, MPZ 2024/88, MPZ 2024/89.

Diagnosis. Carapace subhexagonal, strongly convex, wider than long; frontal margin sulcate medially, with two rows of granulated ridges; small, rimmed, anterolaterally directed orbits; short and acute outer-orbital spine; convex anterolateral margins, with four granulated blunt nodes, last one spinous; posterolateral margin longer, slightly convex, without spines; posterior margin straight, finely rimmed, corners slightly rounded. Dorsal regions subdivided in portions, raised, swollen, tip of regions densely granulated.

Description. Carapace subhexagonal in outline, strongly convex in longitudinal and transverse sections; wider than long, maximum width at level of last anterolateral spine, L/W ratio about 0.81. Frontal margin nearly straight, slightly sulcate medially; with two rows of parallel granules and two small medial lobes when seen from frontal view. Orbits small, somewhat raised and rimmed, bearing two barely perceptible supraorbital fissures; short and acute outer-orbital spine. Fronto-orbital margin occupying about 62% of carapace width. Anterolateral margins slightly arched, convex, with four blunt, stout nodes covered by granules, the last one sometimes more spinous and protruding; posterolateral margin longer, nearly straight, only slightly convex, without spines. Posterior margin nearly straight, only somewhat convex, finely rimmed, corners slightly rounded. Dorsal regions well defined, divided into numerous portions, large, strongly raised, swollen, bearing numerous big granules. Epibranchial regions subcircular, situated close to the frontal margin; epigastric regions with a medial longitudinal groove; mesogastric region relatively small, transversely subelliptical in shape, with narrow, long, anterior extension. Hepatic region large, strongly swollen, obliquely positioned. Urogastric region defined by a horizontal ridge of granules. Epibranchial region divided into three portions; postbranchial regions defined by a large swelling. Cardiac region broad, subpentagonal, with five rounded swellings. Intestinal region flattened, barely distinct from cardiac lobe. Dorsal grooves numerous, defined as narrow and shallow depressions.

Etymology. "*antiqua*" referring to the fact that it is the oldest representative of the genus.

Remarks. The new taxon has important similarities with *Parhalimede ornata* Beschin et al., 2016b, from the early Lutetian of Italy, such as the general outline, similar fronto-orbital construction, rather similar anterolateral margins, and the shape and distribution of dorsal regions. Nevertheless, the new species exhibits a more subhexagonal outline of the carapace, strongly convex in both directions; the front is straighter and only slightly sulcate; the orbits bear nearly imperceptible incisions; the anterolateral margins bear only four stout, blunt nodes, covered with granules, in some remains the fourth node is somewhat more spinous but few protruding; the posterolateral margins are clearly straight and devoid of granules, tubercles, or spines; the posterior margin is finely rimmed; the dorsal regions are larger, more raised, and swollen, with narrower depressions between them.

Family **Pilumnidae** Samouelle, 1819
Genus ***Galenopsis*** Milne-Edwards, 1865

Type species. *Galenopsis typica* Milne-Edwards, 1865, by original designation.

Fossil species included. *Galenopsis crassifrons* Milne-Edwards, 1865, *G. depressa* (Milne-Edwards, 1872), *G. murchisoni* Milne-Edwards, 1865, *G. ossoi* n. sp.; *G. pustulosa* (Milne-Edwards, 1865), *G. ristorii* Checchia-Rispoli, 1905, *G. schopeni* Checchia-Rispoli, 1905, and *G. similis* Bittner, 1875.

Galenopsis ossoi new species
Figure 6.9–6.14

Type material. Three specimens, the holotype is MGSB 75439 (measurements: W, 49 mm, L, 28 mm) and the paratypes are 75440a, b.

Diagnosis. Carapace subtrapezoidal, wider than long; frontal margin downturned, rimmed, with relatively deep posterior groove; orbits subcircular, strongly rimmed; anterolateral margins rimmed, with single arched lobe and two blunt nodes; posterolateral margins straight; posterior margin notably concave. Cheliped surface smooth, heterochelous, with the right bigger; occlusal margins of right cheliped with blunt molariform teeth; fingers of left cheliped thin, elongated, without occlusal teeth.

Description. Carapace subtrapezoidal in shape, wider than long, widest at position of the last anterolateral node, L/W ratio about 0.67; convex longitudinally, less convex transversely. Front strongly downturned, nearly straight, slightly sulcate medially, rimmed, with a deep posterior groove when seen from dorsal view; broad, with two notable arched lobes bounded laterally by thin, acute spines when seen from frontal view. Orbits small weakly arched from dorsal view, outer-orbital corner with spinous appearance; orbits subcircular, closed, from frontal view; supraorbital margins entire, strongly rimmed; fronto-orbital width occupying about 45% of maximum carapace width. Anterolateral margin short, arched, strongly rimmed, with three lobes, first of which immediately behind orbit, gently arched; the two posterior lobes are stout, robust, blunt nodes. Posterolateral margins longer than anterolateral, nearly straight converging backwards. Posterior margin wide, concave, with a thin rim. Dorsal regions not well differentiated; epigastric region small, with strong swellings directed forwards. Only weak, arched, branchiocardiac grooves are defined in some specimens. Dorsal surface smooth. Chelipeds smooth, without ornamentation; strongly marked heterochely. Large right chela, palm robust, globular oval in cross section. Robust fingers, with blunt molariform teeth. Left chela smaller, more elongate; fingers elongated, thin, without strong denticles. Buccal frame subhexagonal; endostome large, stout, bearing a longitudinal groove; exostome elongate. Sternum wide, subtriangular, with long base. Sternites 1–2 subtriangular, fused, with thin and elongate apex; sternites 3–4 fused, with large episternite 4; sternite 5 horizontal, with rounded lateral corner; sternites 6–7 narrow, obliquely situated.

Etymology. Honoring Àlex Ossó, a prolific author on decapod systematics.

Remarks. The new taxon shares the main characters assigned to the genus *Galenopsis*, such as the carapace expanded laterally, wider than long; orbits small; anterior part bowed, but the front edge rises so as to form a rather thick, beaded rim that continues to the anterolateral margins; anterolateral margins slightly trilobate and shorter than posterolateral ones; and posterolateral margins almost straight; dorsal regions poorly marked (see Milne-Edwards, 1875). *Galenopsis depressa* has a concave posterior margin that is straight in the new species (see Beschin et al., 2018). In addition, *Galenopsis ossoi* n. sp. presents on the

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anterolateral margin a first arched lobe, a second rather protruding node and a posterior stout but blunt node, whereas *G. depressa* exhibits the two first lobes as gently arched, and the posterior node spinous, strongly protruding. The posterolateral margins are more straight in the new species, less convergent posteriorly, with a less marked lateral angle. The new taxon has a more elongated outline than *G. crassifrons*, and a smooth dorsal surface, not covered with small pits. Other differences are illustrated in Ferratges et al. (2020) in which the anterolateral nodes are defined by two gently arched lobes and a posterior protruding, spinous, node. It is also easily distinguishable from *G. similis* because it has a less prominent frontal margin, a more oval outline, and orbits oriented forwards.

Superfamily **Majoidea** Samouelle, 1819
Family **Majidae** Samouelle, 1819
Subfamily **?Majinae** Samouelle, 1819
Genus ***Spinirostrimaia*** Beschin et al., 2012

Type species. *Micromaia margaritata* Fabiani, 1910, by original designation.

Fossil species included. *Spinirostrimaia margaritata* (Fabiani, 1910); *S. echinata* Ferratges et al., 2023a.

?*Spinirostrimaia* sp.
Figure 8.11

Description. Carapace pyriform (not totally preserved). Lateral margins convex, notched by the cervical groove. Dorsal regions ornamented with pearl-shaped tubercles (probably broken spines); carapace regions well defined by relatively shallow grooves; axial regions elevated above other regions. Proto- and mesogastric regions inflated; meta- and urogastric regions narrower than mesogastric and cardiac regions; hepatic region inflated; branchial regions wide; epi- and mesobranchial regions inflated, poorly differentiated by a shallow groove; metabranchial region slightly depressed; cardiac region inflated; branchiocardiac grooves deep. Posterior margin not preserved.

Material examined. One incomplete specimen (MGSB 88654).

Remarks. The studied material cannot be assigned on the species level because the specimen lacks important diagnostic elements such as orbits and pseudorostrum. However, the specimen can be assigned questionably to *Spinirostrimaia* based on the elongate carapace general outline, and distribution of dorsal regions (see diagnosis in Beschin et al., 2012) with a similar morphology in the preserved dorsal regions (gastric, hepatic, branchial, and cardiac regions).

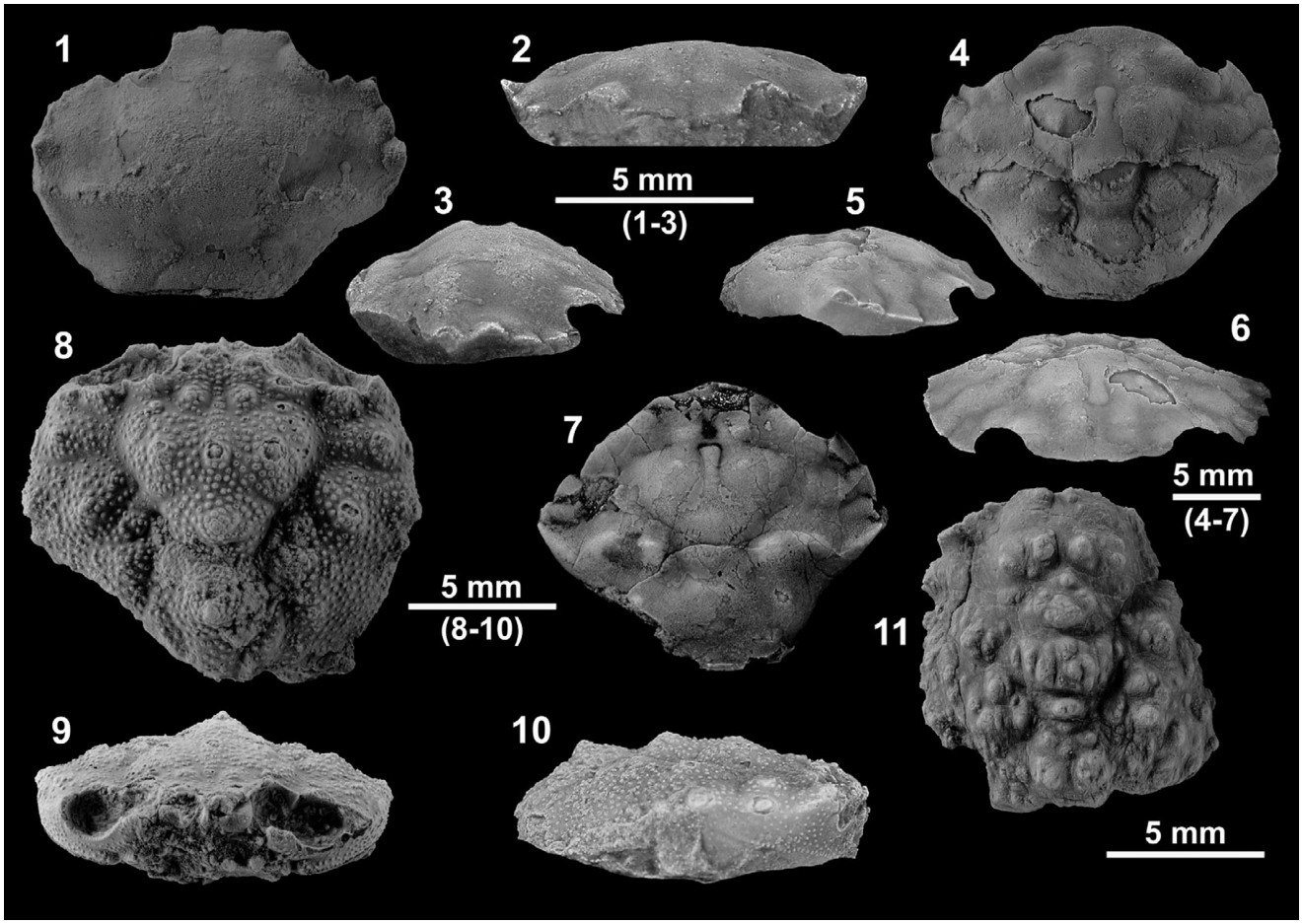

Figure 8. (**1–3**) *Lovaroides* sp. MGSB 77613a in dorsal (**1**), frontal (**2**), and right lateral (**3**) views. (**4–7**) *Liocarcinus tridentatus* n. sp. holotype (MGSB 75448) in dorsal (**4**), lateral (**5**), and oblique frontal (**6**) views; (**7**) paratype MGSB 75449 in dorsal view. (**8–10**) *Microboschettia elegans* n. gen. n. sp. holotype (MGSB 77609) in frontal (**8**), dorsal (**9**), and lateral (**10**) views. ?*Spinirostrimaia* sp. (**11**) in dorsal view (MGSB 88654).

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Superfamily **Portunoidea** Rafinesque, 1815
Family **Carcinidae** MacLeay, 1838
Subfamily **Polybiinae** Paul'son, 1875
Genus ***Microboschettia*** new genus

Type species. *Microboschettia elegans* n. gen. n. sp. by monotypy.

Diagnosis. As for the type species by monotypy.

Etymology. The generic name refers to the small size, together with *Boschettia*, the most similar genus.

Remarks. The fossil genus *Boschettia* Busulini et al., 2003, shows similarities with the new genus in the general shape of the carapace, frontal margin, orbits, and dorsal ornamentation. However, *Boschettia* presents a shorter frontal margin, broader orbits, strongly granulated dorsal surface and a very long fourth anterolateral spine, all of which precludes a congeneric relationship with *Microboschettia* n. gen (see Busulini et al., 2003, pl. 4, fig. 2).

Microboschettia elegans new species
Figure 8.8–8.10

Type material. Two specimens; the holotype MGSB 77609, the paratype MGSB 77614.

Diagnosis. Carapace subquadrate, nearly wider than long; frontal margin with four lobes, projecting beyond orbits; orbits large, with two notches, well-developed suborbital spine, visible from dorsal view; anterolateral margin short, with two spines, last largest, outwardly directed; posterolateral margin convex, with small spine just behind last anterolateral spine. Dorsal regions well defined by swellings and spinous tubercles on tip of gastric, cardiac, and branchial regions. Cardiac region largest, strongly swollen, bearing protruding tip. Dorsal grooves defined by shallow depressions. Lateral portion of cervical groove horizontal. Dorsal regions densely covered by noticeable granules.

Description. Carapace subquadrate, moderately vaulted; nearly as wide as long, maximum width at level of last anterolateral spine, L/W ratio about 0.9. Frontal margin broad, slightly projecting beyond orbits, not completely preserved, with four spines, occupying about 25% of the total width of carapace. Orbits large, broad, with two differentiated portions; supraorbital margin divided into three lobes by two supraorbital fissures; the two inner-orbital lobes are small, slightly spinous, the intra-orbital lobe is nearly straight, the outer-orbital tooth large, stout, subtriangular; suborbital tooth extremely developed, subtriangular, first portion of the supraorbital margin finely rimmed, bearing two small lobes. Fronto-orbital margin about 0.8 of carapace width. Anterolateral margins slightly arched, shorter than the posterolateral margins, bearing two small conical spines, the posterior the largest, directed outwards. Posterolateral margins broadly convex, longer than the anterolateral, convergent posteriorly, bearing a small concavity in the lower corner, at position of the fifth pereiopod. Posterior margin not preserved. Mesogastric region well defined, large, swollen, subdivided in portions, bounded by shallow grooves, bearing eight pointed tubercles on tip of regions, mesogastric region the largest and more swollen, subpentagonal in shape, with a notably protruding tip; horizontal gastric slits are present in the lower portion of the mesogastric region; urogastric lobe transversely narrow, separated anteriorly by the cervical groove, which is horizontal in the lateral portion. Cardiac region large, subpentagonal in shape, strongly swollen, bearing a prominent tubercle on tip. Intestinal region flattened, barely distinct from cardiac lobe. Hepatic regions swollen, bearing a pointed tubercle, delimited from branchial regions by the cervical groove, delimited from gastric regions by the gastrohepatic groove. Dorsal surface of carapace and the vertical lateral sides are densely and uniformly covered by notable granules of similar size.

Etymology. "*elegans*" referring to its elaborate appearance.

Remarks. *Boschettia giampietroi* Busulini et al., 2003, from the middle Eocene of Italy shows similarities with the new species in the general shape of the carapace, similar construction of fronto-orbital margin, orbits, similar distribution of dorsal regions, ornamentation and similar spines in the lateral margin (see Busulini et al., 2003, pl. 4, fig. 2). However, *Microboschettia elegans* n. gen. n. sp. is easily distinguishable in having a much more subquadrate carapace and smaller size; the frontal margin is somewhat broader; broader orbits, which exhibit a clearly differentiated supraorbital margin, with different shape and distribution of intraorbital projections; the outer orbital tooth is large, stout, and subtriangular; the anterolateral margins have less developed spines, with only two small, short, conical nodes. The posterior margin is not totally preserved in the new taxon.

Genus ***Lovaroides*** Beschin et al., 2016b

Type species. *Lovaroides elegans* Beschin et al., 2016b, by original designation.

Fossil species included. The type species is the only species included.

***Lovaroides* sp.**
Figure 8.1–8.3

Description. Carapace subhexagonal, wider than long, L/W ratio about 0.75, maximum width at position of the last anterolateral tooth, vaulted in longitudinal and transverse sections. Frontal margin broad, nearly straight, with four small lobes, the two axial ones more protruding. Orbits large, anterolaterally directed, without apparent supraorbital fissures, outer orbital spine reduced. Small and oblique indentation between orbits and frontal margin. Fronto-orbital margin about 66% of the maximum width; anterolateral margin arched, short, bearing three subtriangular teeth, excluding the outer orbital. Posterolateral margin arched, bearing a small spine. Posterior margin not well preserved. Dorsal regions poorly defined. Gastric regions broad, large, only gently swollen, similarly swollen posterior portion of the branchial region and cardiac region. Cervical and branchiocardiac grooves shallow, weakly defined. Dorsal surface of carapace smooth.

Material examined. Two incomplete carapaces, MGSB 77613a, b.

Remarks. The new material shows several similarities with the type species, *Lovaroides elegans*, in the outline of the carapace, frontal margin with four small lobes, the two medial somewhat more developed; orbits broad, entire, without supraorbital fissures; anterior margins with similar teeth; and dorsal regions of carapace weakly defined. However, the two species present notable differences: the new material exhibits a straighter frontal margin, with the two axial lobes more prominent; the anterolateral margin bears

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three flattened, triangular spines; the carapace presents a subhexagonal outline, being wider than the type species; the gastric, mesobranchial, and cardiac regions are scarcely inflated; and the dorsal grooves are weakly defined. The Italian species, *L. elegans*, presents a much more subcircular outline of the carapace; the frontal margin is more sinuous, with smaller axial lobes; the lateral nodes are spinous, conical, and not contiguous, with space between them; the gastric, epibranchial and cardiac regions are well defined, swollen; and the dorsal grooves are shallow but better defined (Beschin et al., 2016b). The similarities and distinctions with other genera were discussed in Beschin et al. (2016b). *Prealpiplax lessinea* Beschin, Bussulini, and Tessier, 2016, and *Corallioplax exigua* Beschin, Busulini, and Tessier, 2016, have similar anterolateral margins, with the same number of teeth, the penultimate the largest, and a similar carapace outline. However, they show a different morphology and distribution of dorsal regions, anterolateral spines more pointed, and a clearly different frontal margin wider, straighter and less prominent (see Beschin et al., 2016a, p. 144–146., pl. 19).

Genus ***Liocarcinus*** Stimpson, 1871

Type species. *Portunus holsatus* Fabricius, 1798, by original designation.

Fossil species included. *Liocarcinus corrugatus* (Pennant, 1777) also extant; *L. depurator* (Linnaeus, 1758) also extant; *L. holsatus* (Fabricius, 1798) also extant; *L. kuehni* (Bachmayer, 1953); *L. marmoreus* (Leach, 1816) also extant; *L. oligocenicus* (Paucă, 1929); *L. oroszyi* (Bachmayer, 1953); *L. praearcuatus* Müller, 1996; *L. pusillus* (Leach, 1816) also extant; *L. rakosensis* (Lőrenthey in Lőrenthey and Beurlen, 1929); *L. priscus* Beschin et al., 2016b.

Liocarcinus tridentatus new species
Figure 8.4–8.7

Type material. Two almost complete carapaces in MGSB; holotype MGSB 75448; paratype MGSB 75449.

Diagnosis. Carapace subhexagonal, wider than long, maximum width at level of last anterolateral spine, about half of carapace length. Frontal margin advanced, large, broadly arched. Orbits wide; supraorbital margin without notches or fissures. Anterolateral margins arched, armed with three subtriangular teeth. Posterolateral margin longer, concave. Posterior margins straight. Dorsal regions defined by shallow grooves. Anterior extension of mesogastric process well marked, spatula-shaped, bounded by deep groove. Epibranchial swelling well marked, arched.

Description. Carapace subhexagonal in outline, moderately vaulted; wider than long, maximum width at level of last anterolateral spine, L/W ratio about 0.77. Frontal margin large, slightly advanced, broadly arched, entire. Orbits broad, without supraorbital fissures, anterolaterally directed, outer orbital teeth robust, subtriangular. Fronto-orbital margin occupying about 64% of maximum carapace width. Anterolateral margins arched, shorter than the posterolateral margins, armed with three robust subtriangular teeth, forwardly directed. Posterolateral margins slightly concave, elongated, convergent posteriorly. Posterior margin straight, finely rimmed. Dorsal regions well defined, gently swollen, bounded by shallow grooves. Mesogastric region transversely subelliptical; anterior extension of the mesogastric region elongated, spatula-shaped, with straight tip, bounded by a deep groove. Protogastric regions large, swollen. Epigastric regions subcircular, connected with the protogastric region. Urogastric region arched. Hepatic region slightly swollen, elongated, delimited from branchial regions by the cervical groove, delimited from gastric regions by the gastrohepatic groove. Epibranchial ridge well marked, arched, reaching the last anterolateral tooth; meso- and metabranchial regions inflated, large. Cardiac region broad, subpentagonal. Intestinal region flattened, barely distinct from cardiac lobe. Dorsal surface of carapace smooth, without ornamentation.

Etymology. "*tridentatus*", referring to the three teeth in the anterolateral margins.

Remarks. *Liocarcinus tridentatus* n. sp. has a frontal margin entirely arched, like in fossil species *L. priscus* and the modern *L. navigator* (Herbst, 1794). However, the new taxon is clearly distinct in having a much broader and advanced frontal margin; complete orbits, without supraorbital fissures; anterolateral margins with only three teeth; different posterolateral margins, without the large concavity for the insertion of the last pereiopods, the anterior extension of the mesogastric process spatula-shaped, bounded by deep grooves. *Liocarcinus priscus* exhibits a less broad and advanced frontal margin; orbits with two supraorbital fissures; anterolateral margins with four teeth, excluding the outer orbital; posterolateral margins with a strong concavity in the lower corner for the insertion of the last pereiopods; anterior mesogastric process narrow and pointed.

Indeterminate and isolated chelipeds
Figure 9

Remarks. In addition to the great diversity of decapod crustaceans found, a large number of isolated chelae have been observed. Some of them can be assigned to brachyuran taxa such as *Aragolambrus collinsi* Ferratges, Zamora, and Aurell, 2019; *Pyrenicola pyrenaica* (Artal and Vía, 1989) (see Artal and Ossó, 2024); *Eocarpilius ortegai* Artal and van Bakel, 2018b; *Oscacarpilius rotundus* Artal and van Bakel, 2018b; *Ilerdapatiscus guardiae* Artal and van Bakel, 2018a; *Locomius parthenopimimus* n. gen. n. sp.; *Xanthilites robustus* n. sp.; and various Dromioidea such as: *Mclaynotopus longispinosus* Artal et al., 2022; and *Kromtitis isabenensis* Artal et al., 2022 (see Artal et al., 2022).

However, some of the isolated chelae cannot be included in any known species (Fig. 9). For example, some elongated specimens (MGSB 75468) resemble the material described by Ferratges et al. (2021b) from the Roda Formation, assigned to the genus *Paromola* Wood-Mason in Wood-Mason and Alcock, 1891, collected four kilometers from the studied outcrop in the present work (Fig. 9.9–9.11). One isolated right propodus (MGSB 77606) is tentatively assigned to the genus ?*Rhinolambrus* Milne-Edwards, 1878 (Parthenopinae) due to its elongated morphology, with tubercles distributed in three rows, situated in the lower, upper, and inner margins, and its slightly triangular section. The mentioned characters are typical in Parthenopinae as described and illustrated by different authors (i.e., Tan and Ng, 2007, and references herein), and show similarities with modern species of the genus *Rhinolambrus*.

Final remarks

The remarkable site of Ramals has provided a great diversity of decapod crustaceans (see Table 1). In addition, its exceptional

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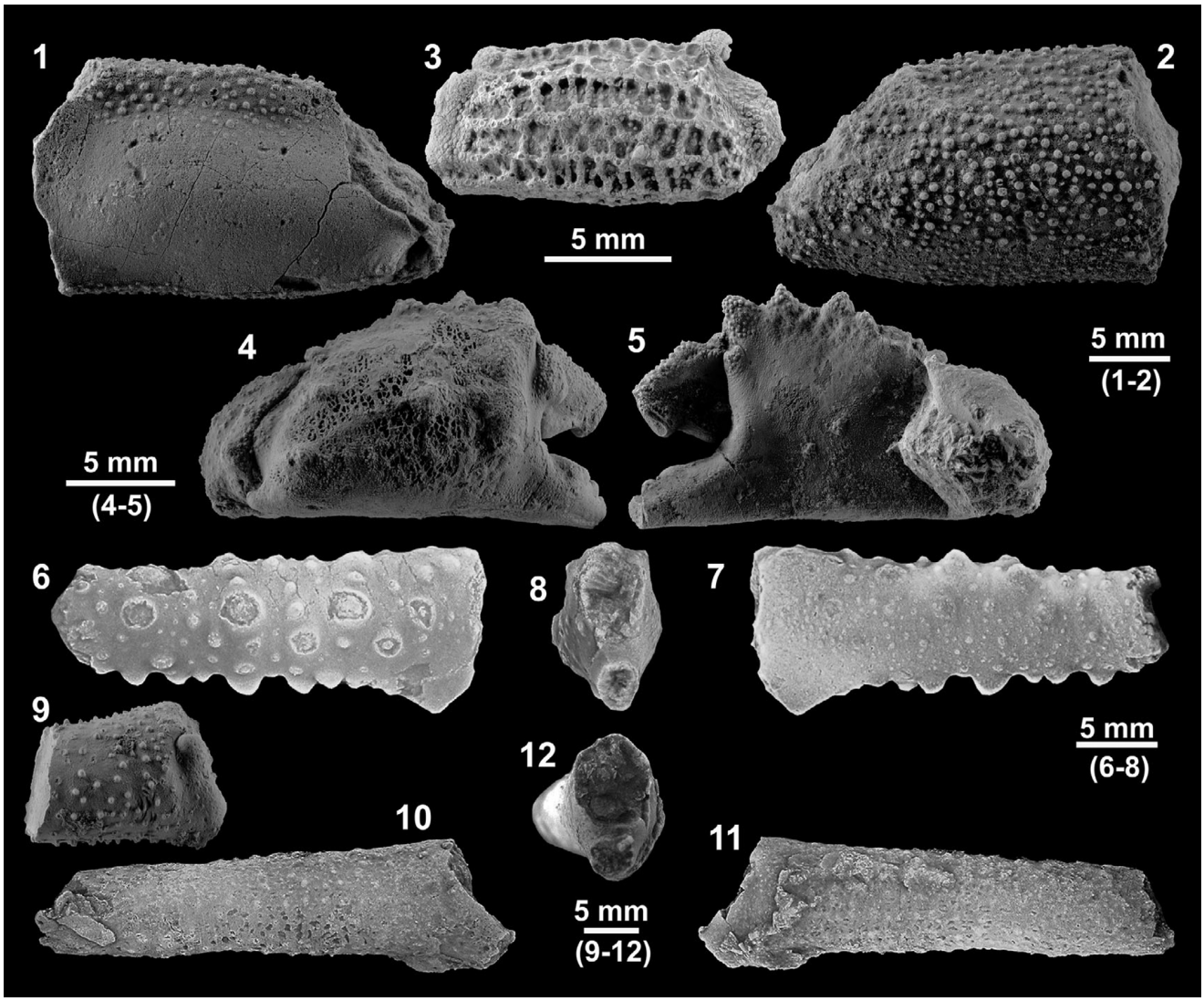

Figure 9. Isolated chelipeds from the studied outcrop. (**1–5**) Indeterminate chelipeds. (**6–8**) isolated manus of ?*Rhinolambrus* sp. in outer side (**6**), inner side (**7**), and frontal (**8**) views (MGSB 77606). (**9–12**) *Paromola* sp. in inner (**9, 10**), outer (**11**), and frontal (**12**) views; (**9**) MPZ 2024/90, (**10, 12**) MGSB 75468.

exposure and state of preservation of fossils allowed controlled sampling, which has made it possible to interpret the distribution of these species within the same environment (Ferratges et al., 2021a). This sole outcrop concentrates the greatest diversity of associated decapod crustaceans for the Eocene of the Iberian Peninsula and is one of the most diverse worldwide locations for this period, having 44 different species (including the taxa described here) to date, in addition to some remains that could not be assigned to any of the described taxa.

Considering the quantitative data presented by Ferratges et al. (2021a), decapod crustaceans were common components in these early Eocene reef assemblages. The most important contribution of this site is that some of the taxa represent the oldest records in some genera of modern families (Cancridae; Carpiliidae; Parthenopidae). These records have important implications for molecular clock calibrations (Luque et al., 2023) and the understanding of modern hot spots of decapod crustaceans.

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Competing interests. The authors declare no competing interests.

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