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Piacenzian (Pliocene) decapod crustacean faunules from northwest Belgium*

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*** In commemoration of Frans J. De Meuter (1936-2003)**

Abstract

From strata assigned to the Oorderen Member (Lillo Formation; Piacenzian, Pliocene), as exposed in recent harbour works (Verrebroekdok, Deurganckdok) near Kallo (Antwerp area, NW Belgium), eleven species of anomurans and brachyurans are described, including one new genus and three new species (*Ebalia jacqueshermani* sp. nov., *Metacarcinus tenax* sp. nov., and *Pliopirimela deconincki* gen. nov. and sp. nov.). *Galathea dispersa* Bate, 1859 is described from the fossil record for the first time, and Gripp's (1967) revision of *Micromithrax holsatica* Noetling, 1881 and reassignment to the genus *Corystes* is corroborated. Comparisons are made with extant North Sea crabs and with assemblages of Miocene (Langhian-Early Serravallian) age from Hungary.

Key words: Crustacea, Decapoda, Pliocene, Kallo, Belgium, new taxa

Introduction

Despite the fact that in Belgium strata of Cainozoic age are widely distributed and regularly exposed in road cuttings and harbour extension works, records of decapod crustaceans from these deposits are surprisingly scanty. The most complete, albeit outdated, listing of Paleogene and Neogene crabs and lobsters is still that by van Straelen (1921; see also 1924). In comparison to the Neogene (see below), there are numerous records of taxa of Paleogene age (Eocene and Oligocene in particular), documenting, for instance, nephropids and geryonids from the Boom Formation (Rupelian, Oligocene) (Stainier, 1887; Stainier and Bernays, 1899). More recent papers referring to and/or describing Cainozoic decapod crustacean taxa from Belgium are those by Janssen and Müller (1984), Feldmann and Dhondt (1991), Collins and Smith (1993), Verheyden (2002) and van Bakel et al. (2000, 2003a, b, in prep.).

As far as Pliocene taxa are concerned, van Straelen (1921, pp. 126-127) listed all pre-1920 records of decapod crustacean remains from the Antwerp area. From the 'étage Scaldisien', corresponding to the Kattendijk and Lillo formations in current usage (see Buffel et al., 2001), Cogels (1874) recorded fragmentary chelipeds, while Delheid (1895) mentioned a fairly large number of chelipeds and carapace fragments collected during excavation of the America dock. Lastly, Mourlon (1880) recorded the presence of *Cancer* in the Pliocene of Belgium, but failed to indicate its stratigraphic provenance. The current whereabouts of this material is unknown; to our knowledge, systematic treatments have never appeared in print subsequently.

To this meagre Pliocene record we here add two anomuran and nine brachyuran taxa, all from the Kallo area (province of Antwerpen, Belgium). These comprise one new genus and three new species (*Ebalia jacqueshermani* sp. nov., *Metacarcinus tenax* sp. nov., and *Pliopirimela deconincki* gen. nov. and sp. nov.).

Localities and stratigraphy

Near Kallo and Doel, on the western bank of the River Schelde (Scheldt) (Antwerp city area; Fig. 1), harbour extension works provide large-scale outcrops of strata of Pliocene age on a regular basis. Both the works themselves and the sand dumps nearby have been

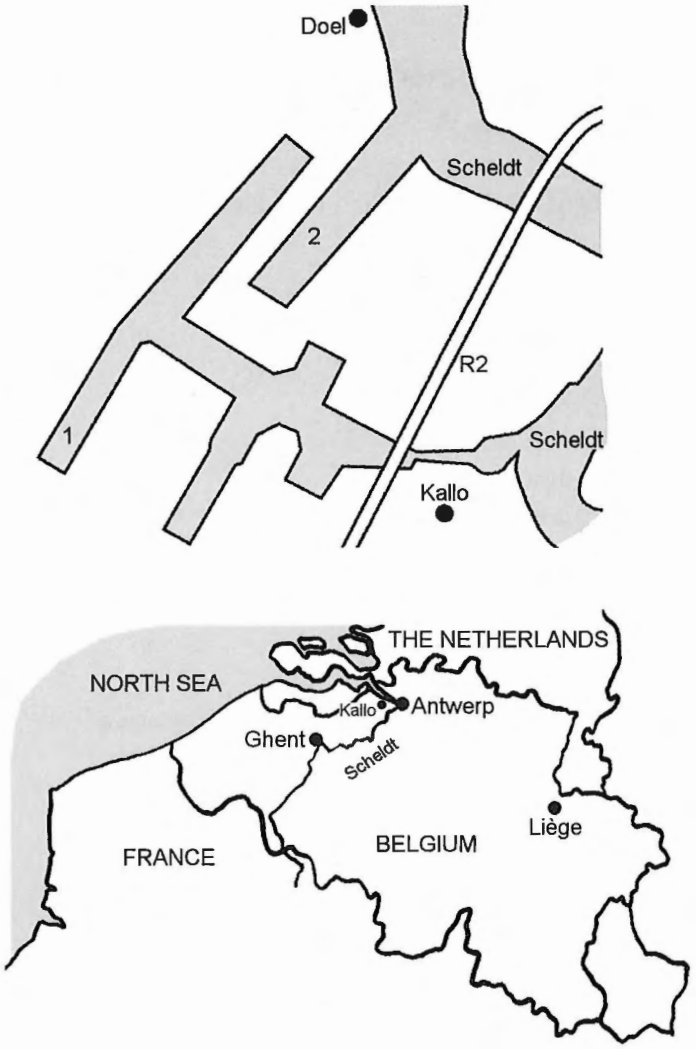


Fig. 1. Schematic map showing the location of the Verrebroekdok (1) and the Deurganckdok (2) near Kallo (Antwerp city area); R2 = ring road around Antwerp.

screened meticulously over recent years by a group of people (see Acknowledgements). The decapod crustacean material collected there, which is well-documented stratigraphically, forms the basis of the present study.

Material before us is both from the Verrebroekdok, west of Kallo, and from the Deurganckdok, south of Doel (Fig. 1). Both these temporary exposures have recently been described by Marquet (2002), to which paper reference is made. All anomuran and brachyuran species recorded below are from the Oorderen Member of the Lillo Formation (Fig. 2), and the majority of them from the so-called *Atrina* level (or *Atrina* bed; see Marquet, 2002, table 1) within this unit.

The Oorderen Member (Oorderen Sands, sensu de Meuter & Laga, 1977) comprises fine, glauconitic shelly sands, with three major compact shell layers, with the lower portion of the unit being greyish brown and homogeneous, and the upper portion darker grey and (very) clayey. On benthic foraminifer evidence, de Meuter and Laga (1977) referred the Oorderen Member to their *Elphidiella hannai-Cribrononion excavatum* Assemblage Zone (BFN 6), which corresponds to subzone FA 2 of the *Elphidiella hannai-Cribrononion excavatum* Zone (FA) as used on adjacent Dutch territory (Doppert et al., 1979). This correlates part of the Lillo Formation (Oorderen, Kruisschans and Merksem members) with the Oosterhout Formation in the Dutch stratigraphic scheme, of Late Pliocene age (Doppert et al., 1979, table 1).

Nuyts (1990) studied benthic foraminiferal assemblages from the Oorderen Member exposed in a temporary outcrop (Vrasenedok), and noted that the occurrence of numerous specimens of the genus *Cribrononion* and a sudden increase of *Elphidiella hannai* were typical of a shallow, high-energy environment with much sediment displacement and highly variable parameters, such as temperature and salinity. In

My	International chronostratigraphic units		Lithostratigraphy		
	Pleistocene	Calabrian		Sand suppletion Late Quaternary deposits	
1.8					
		Gelasian		Merksem Member ?	
2.6					
		Piacenzian	Lillo Formation	Kruisschans Member	
	Pliocene			Oorderen Member	*Angulus benedeni* level *Cultellus* level *Atrina* level basal crag
				Luchtbal Member	
3.6					
		Zanclean	Kattendijk Formation	Kattendijk Member	
5.3					
	Miocene	Messinian			

Fig. 2. Litho- and chronostratigraphy of Pliocene strata exposed during harbour extension works at the Verrebroekdok and Deurganckdok (modified after Buffel et al., 2001; Marquet, 1998, 2002).

addition, the low p/b ratio (planktonic/benthic foraminifera) suggests a nearshore environment as does the low number of species *vs* number of specimens. The gradual increase in *Elphidium* within the Oorderen Member may signify an environmental change, since this genus is characteristic of a shallow-water niche, more particularly of hypersaline tidal zones and lagoons, close to the coastline. The shallow-water setting of the Oorderen Member is illustrated by molluscan faunas as well. Vervoenen (1995, p. 71) noted for the *Atrina* level within this unit the influence of periodic storms and a maximum water depth of 20 to 30 metres (see below).

On the basis of dinoflagellate cysts from the borehole Kalmthout, northeast of Antwerp, Louwye and Laga (1998) dated the Kattendijk and Lillo formations as Zanclean to Piacenzian (see also Laga et al., 2002).

Systematic palaeontology

To denote the repositories of material described in the present paper, the following abbreviations are used:

EW E. Wille Collection, Wuustwezel-Gooreind (Belgium);
MAB Oertijdmuseum de Groene Poort, Boxtel, the Netherlands;
MNHN Muséum national d'Histoire naturelle, Paris, France;
RGM Nationaal Natuurhistorisch Museum (Naturalis), Leiden, the Netherlands (formerly Rijksmuseum van Geologie en Mineralogie).

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Galatheoidea Samouelle, 1819
Family Galatheidae Samouelle, 1819
Subfamily Galatheinae Samouelle, 1819
Genus *Galathea* Fabricius, 1793

Galathea dispersa Bate, 1859

(Pl. 4, Figs. 3-5)

Material: A single specimen (EW.9500); a partial carapace with associated fragmentary appendages, an eye stalk and a left chela, from the sediment fill of a large gastropod of the genus *Scaphella*, from the *Atrina* level (Oorderen Member), Verrebroekdok.

Remarks: Until now, this species was unknown from the fossil record. While carapace features are identical to those of extant material, the chela in the fossil specimen is somewhat more robust. Several dozens of *G. dispersa* in lot RGM 19518 have been examined and these show a fairly strong allometric growth of the chela. The Pliocene specimen is larger than the extant material studied, which may explain this difference.

Superfamily Paguroidea Latreille, 1802
Family Paguridae Latreille, 1802
Genus *Pagurus* Fabricius, 1775

Pagurus bernhardus (Linné, 1758)

Material: A left-hand fixed finger with part of digital margin preserved (MAB k.2367) from the *Atrina* level (Oorderen Member), Deurganckdok. Evidence of former pagurid occupation of gastropod shells, as described in detail by Walker (1992), comes in the form of wear marks on a large specimen of *Scaphella lamberti* (EW. 9501) from the *Atrina* level (Oorderen Member, Verrebroekdok) and of bryozoan overgrowth of a small, unidentified gastropod shell (MAB k.2368), from an unknown level within the Lillo Formation (Deurganckdok).

Remarks: Considered conspecific is material recorded by Bell (1921) as *Eupagurus* sp. from the Coralline and Red crags (Pliocene, Pleistocene) and overlying Pleistocene strata at several localities in England (see also Holthuis, 1949; Collins, 2002). Holthuis (1949, pp. 58-59, pl. 1, fig. 1) recorded *P. bernhardus* from Lower Pleistocene ('Icenian') deposits penetrated in boreholes at Maassluis, Dordrecht and Ginneken (the Netherlands).

Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Leucosioidea Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Subfamily Ebaliinae Stimpson, 1871
Genus *Ebalia* Leach, 1817

Ebalia cranchii Leach, 1817

(Pl. 1, Figs. 1-6)

Material: A male carapace preserving with ventral parts (S. Mermuijs Collection), an unregistered carapace in the J. Herman Collection, a carapace with the right anterolateral margin damaged (MAB k.2400), a female abdomen (MAB k.2370), and a right propodus with articulated carpus collected from the sediment fill of a larger gastropod (*Scaphella*; MAB k.2371). All specimens are from the Oorderen Member, Deurganckdok.

Remarks: Extant material of *E. cranchii* (RGM collections, Leiden), recently examined by us, reveals distinct differences in carapace morphology which may be ascribed to sexual dimorphism and intraspecific variation. Male morphotypes are characterised by a distinctly bilobed posterior carapace margin and clusters of tubercles scattered over their carapace regions, whereas in females the posterior margin is barely bilobed to continuous, and the carapace much smoother than in males. The present specimens represent both male and female carapaces, and fit the specific variation displayed by the examined material well.

Bloklander (1953) recorded a carapace and an abdomen from the sediment fill of a Pliocene gastropod shell collected at Ellewoutsdijk, province of Zeeland (the Netherlands), currently in the RGM collections (Leiden).

***Ebalia jacqueshermani* sp. nov.**

(Pl. 2, Figs. 4-7)

Diagnosis: Small-sized *Ebalia*, carapace suboctagonal in outline, front projecting, orbits large, carapace entirely covered in simple granules.

Etymology: The species is named after Dr. J. Herman (Institut royal des Sciences naturelles de Belgique, Brussels), in recognition of his much appreciated efforts to document the Pliocene of the Antwerp area in great detail, both stratigraphically and palaeontologically.

Material: Holotype is MAB k.2372, a ?male carapace; paratype is MAB k.2373, a ?female carapace; both from an unknown level within the Oorderen Member, Deurganckdok.

Description: ?Male carapace suboctagonal in outline, length equalling maximum carapace width; front projected, bilobed. Orbitofrontal margin occupying 41% of maximum carapace width, which is situated at about 47% of carapace length from the front. Orbits large, bluntly rounded, directed slightly outwards with sharp outer orbital angle not reaching level of front, inner orbital margins slightly concave. Orbital margin with two fissures, the inner one deep, directed axially, and the outer faint, short, running parallel with anterolateral margin.

Anterolateral margins divided into two gently rounded parts by a medial indentation, anterior portion sloping more strongly than posterior portion. Posterolateral margins long; first portions short, weakly converging, second portions long, strongly converging with same angle as opposite anterolateral margins, posterior weakly concave towards blunt posterior corners. Posterior margin slightly narrower than orbitofrontal margin, faintly bilobed.

Axial portion of carapace elevated, anterior elevation bifurcated towards frontal lobes. Cardiac region strongly elevated into rounded bump, branchiocardiac grooves weakly developed, linked by weak, rounded depression between urogastric and cardiac regions. Lateral carapace margins flattened. Carapace surface entirely covered with crowded, evenly sized simple granules.

?Female carapace has orbits narrower than ?male carapace, on account of straightened axial sides, front roughly bifid owing to blunt medial emargination. Anterolateral margins divided into two gently rounded parts by medial indentation, forming a more continuous, more rounded entity than in ?male carapace. Posterior margin gently curved, slightly wider than orbitofrontal margin, indented at transition to posterolateral margins.

Remarks: In general, decapod crustaceans are rare in the fossil record, which explains why, in those cases in which but one or a few specimens are available, the description and differentiation of fossil crabs may turn out risky, since sexual dimorphism and/or allometric growth cannot be properly evaluated (see e. g. Müller, 1979; Fraaye, 1996). Awaiting the discovery of additional material, preferably with sternal features preserved, we here consider the present two morphotypes to be conspecific, and reflect the sexual dimorphism reported previously for the genus *Ebalia*. In *E. cranchii* (see above), sex may be determined from the carapace width and the shape of its posterior margin. In the holotype of *E. jacqueshermani* sp. nov., this is bilobed and narrower than in the paratype, indicating the former to be the male.

In overall size, shape of the front and possession of relatively large orbits, *Ebalia jacqueshermani* sp. nov. most closely resembles *E. oersi* Müller, 1979 (p. 279, pl. 13, figs. 1-3; see also Müller, 1984, p. 69, pl. 43, figs. 3-7, ? 8) from the 'Badenian' (= Langhian and Early Serravallian, Miocene; see Harzhauser et al., 2002, fig. 1) of Hungary. We have examined some casts of this species, kindly supplied by Dr. P. Müller (Geological Institute of Hungary, Budapest), which show a wide variation in carapace shape and ornament; yet, *E. jacqueshermani* sp. nov. does not fall within this range. In *E. oersi* the front is less projected than in *E. jacqueshermani* sp. nov., and the lateral margins in the former meet under an acute angle, whereas the lateral corner is blunt in the latter. In *E. jacqueshermani* sp. nov. only the cardiac region is clearly elevated, while its Miocene congener has a much more bumpy carapace with well-differentiated regions. *Ebalia jacqueshermani* sp. nov. is easily distinguished from *E. cranchii* (see above) in having large-sized orbits, a wide orbitofrontal margin and less elevated branchial and cardiac regions.

Ebalia vanstraeleni Bachmayer, 1953 (p. 243, pl. 2, figs. 1, 4, 4a) from the Tortonian (Upper Miocene) of Austria and *E. multiangulata* Müller, 1993 (p. 11, figs. 5a-g) from the Langhian (lower Middle Miocene) of Catalonia (Spain) are both easily distinguished from *E. jacqueshermani* sp. nov. on account of their strongly areolated carapaces, the shape of the lateral corner, the notched frontal margin and the relatively smaller orbits.

In size, *E. jacqueshermani* sp. nov. resembles the extant *Ebalia edwardsii* Costa, 1838, but in this carapace width greatly exceeds length.

***Ebalia tumefacta* (Montagu, 1808)**

(Pl. 1, Fig. 7; Pl. 2, Figs. 2, 3)

Material: A partial female carapace (immature) (MAB k.2375), a female abdomen (MAB k.2374), and a male one (EW.9507), all from the sediment fill of larger gastropods of the genera *Scaphella* and *Neptunea*, collected from the *Atrina* level (Oorderen Member), Deurganckdok.

Remarks: The partial, immature carapace is undoubtedly that of a female, and fits the intraspecific range of variation well. For the present paper, we have examined extant specimens of *E. tumefacta* (MNHN, lots B.19966 [4 specimens] and B.19961 [2 specimens]). Mature females have excessively swollen branchial regions; in addition, carapace width exceeds length. In contrast, carapace length in mature males exceeds width, on account of more slanting lateral margins, and more concentrated tumid regions; such specimens appear close to *E. cranchii*. Immature female carapaces are characterised by gently sinuous carapaces.

Superfamily Majoidea Samouelle, 1819

Family Majidae Samouelle, 1819

Subfamily Majinae Samouelle, 1819

Genus *Maja* Lamarck, 1801

***Maja squinado* (Herbst, 1788)**

(Pl. 3, Figs. 1, 2, 5-12)

Material: A well-preserved carapace preserving ventral side (EW.9502), a frontal portion of a carapace (MAB k.2376), and a large-sized right carpus (MAB k.2377), all collected from sand dumps near docks, 1 metre above the *Atrina* level (Oorderen Member), Deurganckdok. A left dactylus (MAB k.2379) and a left fixed finger (MAB k.2378) are from undefined levels within the Oorderen Member (Verrebroekdok), while a merus of a limb (MAB k.2380) is from an undefined level within the Oorderen Member (Deurganckdok).

Remarks: Holthuis (1949, p. 66, pl. 2, figs. 23-25) recorded *M. squinado* from Middle Pliocene ('Scaldisian') and Lower Pleistocene ('Icenian') deposits penetrated in boreholes at Biggekerke (Walcheren), Vlissingen, Schouwen and Bergen op Zoom (the Netherlands), as well as washed ashore at de Kaloot (Zuid-Beveland) and dredged from the Westerschelde.

Superfamily Corystoidea Samouelle, 1819

Family Corystidae Samouelle, 1819

Genus *Corystes* Latreille, 1802

Remarks: Noetling (1881, p. 363, pl. 20, fig. 2) described a new genus and species of oxyrhynchid crab, *Micromithrax holsatica*, from an erratic sandstone boulder found at Segeberg (Schleswig-Holstein, northern Germany). This sandstone is the so-called 'Holsteiner Gestein', of Early Miocene (Burdigalian) age (see Janssen & Gürs, 2002). The specimen illustrated by Noetling is a small pyriform carapace with a tube-like front and swollen, tubercular carapace regions, which he assumed was closest to the Majidae ('Majaceen'), and which he thought showed a certain resemblance to the genus *Mithrax* A. Milne-Edwards.

Much later, Gripp (1964) described a new species, *Corystes bernhardi*, from the Miocene of Schleswig-Holstein, and illustrated a small, yet complete, carapace, lacking cuticle. When having gained access to Noetling's type of *Micromithrax holsatica* (collections of the Humboldt-Universität, Berlin), Gripp (1967) could not help but notice that Noetling's original figure was a clear case of 'artist's impression'. He discussed the types of this and of his own species, and concluded that they were conspecific, with the name *holsatica* having priority. Gripp treated *Micromithrax* as a junior synonym of *Corystes*, a conclusion with which we concur.

Several later authors (Glaessner, 1969; Feldmann and Wilson, 1988), seemingly unaware of Gripp's (1967) redescription, accepted and discussed the genus *Micromithrax*, and even assigned (Feldmann and Wilson, 1988) a new species from the Eocene of Antarctica, ? *M. minisculus*, to it, albeit with a query. This small carapace does indeed resemble Noetling's original figure, yet probably represents a genus of majid, and thus cannot be assigned to *Corystes*.



Fig. 3. Type specimen of *Micromithrax holsatica* Noetling, 1881 (Museum für Naturkunde, Humboldt-Universität Berlin, unregistered; photograph by Waltraud Harre). Scale bar equals 5 mm.

Having now restudied Noetling's original specimen (see Fig. 3), and with Gripp's illustrations (1964, p. 123, pl. 21, fig. 8) and the newly discovered material from the Pliocene of Kallo before us, we subscribe to Gripp's decision to reassign *Micromithrax holsatica* to *Corystes*. The bifurcated front, broadly ovate orbits, appearance of carapace regions and tubercles, and form and placement of anterolateral and posterior marginal spines are all in support of such an assignment.

When discussing *Corystites latifrons* (Lőrenthey in Lőrenthey and Beurlen, 1929), Müller (1984, p. 75) noted that this species showed similarities to *Micromithrax holsaticus* [*sic*] and to the extant genus *Jonas* Jacquinot and Lucas, 1853. Unfortunately, the type specimen of *Corystites latifrons* is lost and so far no additional specimens have been collected (P. Müller, pers. comm., 2002). Of note in this species are the division and shape of the carapace regions, and the placement of the primary tubercles on the anterior regions, which features all correspond favourably to those of *Corystes holsaticus*, as here interpreted. For this reason, placement of *Corystites latifrons* in the Corystidae would appear to be correct. The most notable differences between *Corystites latifrons* and *Corystes holsaticus* are: five lateral-marginal spines in the former *vs*

three in the latter, and the presence of more tumid gastric regions, resulting in a more depressed frontal region in the former. *Corystites latifrons* may have given rise to corystid crabs of the genera *Jonas* and *Gomeza* Gray, 1831, which is why we think *Corystites* should be retained as a separate genus.

Corystes holsaticus (Noetling, 1881)

(Pl. 4, Figs. 1, 2, 6-8)

1881 *Micromithrax holsatica*; Noetling, p. 363, pl. 20, fig. 2.
1964 *Corystes bernhardi*; Gripp, p. 123, pl. 21, fig. 8.

Material: A partial carapace (MAB k.2381), a median portion of a carapace (MAB k.2382), a complete carapace (EW.9503), and a large portion of another one (EW.9504), all from the *Atrina* level (Oorderen Member), Verrebroekdok.

Description: Carapace ovoid, longer than wide, maximum width (inclusive of lateral spines) at 84% of carapace length, front projected, bifid, with sharply triangular anteriorly directed spines.

Carapace tumid in longitudinal section, semi-circular in transverse section. Fronto-orbital width 60% of greatest carapace width, orbits directed anteriorly, elliptical, deepest towards carapace axis and marked by a short, distinct orbital fissure; inner orbital corners slightly projected beyond outer orbital teeth, forming the base of a noded, concave arch leading to broad, sharp, triangular frontal teeth. Orbital margin indented in front of sharp outer orbital teeth, entire orbitofrontal border distinctly beaded.

Anterolateral margin divided into strongly concave portion starting at outer orbital teeth, leading to straight, slightly convergent part with three lateral teeth. Anteriormost teeth strong, curved, directed forwards and outwards. Medial teeth smallest, less curved than anteriormost, and positioned closer to anterior than to posterior lateral teeth. Third pair of anterolateral teeth directed outwards, and forming the greatest carapace width at 54% of the maximum carapace length from the anterior border. Posterolateral margin gently convex, at a quarter of its total length from the posterior it shows a small spiniform tooth. Posterior corners sharp, posterior margin straight, thickened, and relatively narrow (47% of maximum carapace width).

Carapace regions distinctly separated by grooves, moderately vaulted. Frontal region plain, epigastric regions small, tumid, at same vertical level as deepest point of orbits, clamping a weak median sulcus originating at the base between the frontal teeth. Mesogastric region narrowly triangular anteriorly, posteriorly it widens and bears a median tubercle. Protogastric regions large, angular, with large medial tubercle and a smaller one next to the narrow anterior mesogastric process. Grooves axially bounding the hepatic regions broad, non-granular. Subhepatic regions with a sharp central spine (see arrow in Pl. 4, Fig. 2), which is visible in dorsal and lateral view. Urogastric regions weakly vaulted, only laterally well differentiated, with large axial tubercle. Cardiac region slightly broader than urogastric region, hexagonal with two tubercles at the same vertical level near the carapace axis. Intestinal region small, subpentagonal with the apex touching the posterior margin, narrow. Epibranchial and mesobranchial regions each with a strong medial elevation leading to a tubercle, metabranchial region large, with an indistinct vertical tumidity halfway.

Entire carapace surface crowded with fine sharp tubercles, the majority slightly anteriorly directed.

Remarks: In carapace outline, ornament, division and elevation of carapace regions, and placement of lateral spines, the present specimens closely resemble Gripp's illustration (1964, pl. 21, fig. 8) as well as Noetling's type (see Fig. 3). Yet, there are some differences with its Miocene congener. The Kallo material has a denser tuberculation scattered all over the carapace. Specimens of extant *Corystes cassivelaunus* (Pennant, 1777) reveal a tuberculation that varies in intensity, irrespective of sex and ontogenetic stage, as seen in juveniles, males and females in the MAB and RGM collections. Noetling's and Gripp's specimens are much smaller than those described here, which might explain this difference in ornament. The distinctly triangular, flattened rostral teeth do not show properly in earlier illustrations of *Corystes holsaticus*. Gripp's specimen lacks cuticle, while new photographs of the type of *Micromithrax holsatica* (see Fig. 3) clearly show these teeth to have broken off at the base. Thus, the well-preserved specimens from the Pliocene of Kallo reveal this feature for the first time; the same holds true for the circular orbits. The delicate orbital margin is poorly preserved but in Noetling's type and in Gripp's specimen. Awaiting the discovery of additional, well-preserved material from the Miocene of northern Germany, it appears best in our view, to refer the Pliocene 'population' to *C. holsaticus*. This taxon differs from its only extant relative, *C. cassivelaunus*, in having a dense granulation, more distinctly divided carapace regions, a more tumid carapace in longitudinal section and more widely triangular rostral teeth. In *C. cassivelaunus*, the second anterolateral tooth is reduced to a blunt node (see Adema, 1991, fig. 48), and the subhepatic spine is absent. *Corystes holsaticus* has primary tubercles on the anterior and median carapace regions, a feature not seen in *C. cassivelaunus*.

Family Cancridae Latreille, 1802
Subfamily Cancrinae Latreille, 1802
Genus *Cancer* Linné, 1758

Cancer cf. *pagurus* Linné, 1758

(Pl. 5, Figs. 1-9)

Material: A single, complete juvenile carapace (EW.9504) and the right-hand half of an average-sized carapace (MAB k.2383), both from the *Atrina* level (Oorderen Member), Verrebroekdok; an articulated right carpus, propodus and dactylus of a juvenile specimen (MAB k.2384), an articulated left-hand carpus, propodus and dactylus of average size (MAB k.2399) and a large-sized right-hand propodus with articulated carpus (EW.9505), all from the Oorderen Member, Deurganckdok; a right-hand dactylus (MAB k. 2401) and a right-hand fixed finger (MAB k.2385), from an unknown level within the Oorderen Member, Deurganckdok.

Description: Adult carapace morphology and features of both juvenile and adult chelipeds agree well with extant *Cancer pagurus* examined by us. However, the juvenile carapace (EW.9504) shows features that diverge from this range of variation. The three medial frontal lobes are accurately evenly sized, in contrast to extant material, and the V-shaped depression just posterior of the medial lobe is not observed in this Pliocene specimen. Moreover, the frontal lobes extend beyond the level of the outer orbital corners, and the anterolateral margin lobes are less curved anteriorly and less noded posteriorly, forming a more continuous margin than in extant *C. pagurus*. In transverse section, EW. 9504 is continuously curved with no medial plain, in contrast to extant specimens.

Remarks: Amongst specimens of extant *C. pagurus* that we have examined for the present paper, there is just one which comes close to EW.9504. This is RGM D.43709, an exuvia, most probably beach-dried, of a juvenile. This specimen also has more tumid cross sections and deformed lateral and orbital margins. It shows clear signs of having dried rapidly, with cracks over its carapace and a strongly folded posterior margin. In contrast, EW.9504 does not show such features at all, although the adult morphology should also be taken into consideration. The right-hand half of an adult carapace (MAB k.2383) has an incomplete frontal region, which means that specific assignment is impossible and conspecificity with the Late Miocene *C. parvidens* Collins and Fraaye, 1991 or the Early/Middle Pliocene *C. vancalsteri* van Bakel, Jagt and Fraaije, 2003a cannot be entirely ruled out.

Cancer pagurus has been recorded from Lower Pleistocene ('Icenian') strata in boreholes at Dordrecht, Dubbeldam-Prinsenheuvel, Dongen and Roosendaal as well as dredged from the Westerschelde (the Netherlands; see Holthuis, 1949) and from the Pliocene (Coralline, Walton and Butleyan crags) of southeast England (Bell, 1897; Holthuis, 1949).

Genus *Metacarcinus* A. Milne Edwards, 1862

***Metacarcinus tenax* sp. nov.**

(Pl. 6, Figs. 4-6)

Diagnosis: Medium-sized *Metacarcinus*, carapace subpentagonal in outline, wider than long, widest across ninth anterolateral teeth. Lateral margins with noded teeth bearing rimmed edge, front projecting beyond orbits, with broadly rounded teeth. Carapace regions slightly vaulted, median part elevated, granular ornament more distinct here.

Etymology: From Latin *tenax* (adj.), meaning tenacious or stubborn, in reference to recent fieldwork sessions in the Kallo area, often under adverse weather conditions, carried out by a group of palaeontologists led by Dr. J. Herman.

Material: Holotype, and sole specimen known, is MAB k.2386, from the *Atrina* level (Oorderen Member), Deurganckdok.

Description: Carapace length from tip of median orbitofrontal tooth to posterior margin approximately 74% of maximum width, front projected, trifid, with rounded anteriorly directed teeth, median tooth slightly narrower than submedian, clearly separated from adjacent pair by axially directed, distinct, closed fissures. Submedian teeth separated from blunt inner orbital teeth by broadly triangular interspace with indistinct fissure. Fronto-orbital width approximately 35% of total carapace width, orbits relatively small, elliptical, deepest towards outer orbital corners, lateral sides of inner orbital teeth thickened, extended into supraorbital margin which bears two long closed fissures, first at deepest point of orbit, and one near outer orbital angle which is on a lower vertical level than are the inner orbital teeth. Frontal teeth and orbital margins granular.

Anterolateral margins long, strongly curved with teeth alternating in size from broad to narrow, becoming more noded and spiniform towards lateral corner which is formed by tips of ninth anterolateral teeth, and situated at approximately 65% of carapace length from the front. Individual teeth separated by distinct, deep, closed fissures.

Posterolateral margins weakly concave with two gently rounded, blunt teeth bearing tubercular margin, separated from each other by a weak notch, second tooth obscure, having tubercular margin which sinuously passes into rest of posterolateral margin, which posteriorly curves axially, becoming fainter.

Posterior margin slightly smaller in width than orbitofrontal part, with vaulted margin. Carapace regions weakly vaulted, crowded with fine granules, indistinctly separated by broad, shallow, less granulate depressions. Hepatic regions indistinct, protogastric regions large, ovate, bounding the less vaulted, narrowly triangular mesogastic region which effaces posteriorly into a median elevation. Cardiac region roundly triangular, metabranchial and epibranchial regions swollen, intestinal region not clearly differentiated.

Remarks: In general carapace outline, placement and ornament of anterolateral spines, and division and elevation of carapace regions, the new species closely resembles *Metacarcinus borealis* (Stimpson, 1859), an extant species from the east coast of North America. In *M. borealis*, the median frontal tooth is distinctly smaller and sharper than in *M. tenax* sp. nov., the adjacent pair of teeth slope laterally to a broader and more rounded interspace, not having the weak incision that is seen in *M. tenax* sp. nov. The outer orbital angle in *M. borealis* is sharper and more anteriorly directed than in *M. tenax* sp. nov.; the anterolateral margin is less convex, resulting in a proportionally broader carapace with a longer, less concave posterolateral margin. The lateral incisions appear to be more open in *M. borealis*, even ending in a pit near the greatest carapace width, a feature not seen in *M. tenax* sp. nov.

The present species was recorded by van Bakel et al. (2000) as probably ancestral to *Cancer bellianus* Johnson, 1861. However, no extant material had been examined at that time, and the conclusion relied solely on illustrations supplied by Nations (1975).

Note, however, that in the caption of Nations' figure 38, *C. bellianus* and *M. borealis* have been inadventently exchanged. Figure 38/1-2 represent *M. borealis*, not *C. bellianus*, which is illustrated in Figure 38/3-4.

Isolated fingers of *Lobocarcinus sismondai* (von Meyer, 1843), recorded by Holthuis (1949, p. 61, pl. 1, figs. 5-9, as *Cancer deshayesii* A. Milne-Edwards, 1861 [*sic*]) from Lower Pleistocene ('Icenian') deposits at Schouwen (province of Zeeland, the Netherlands) are probably conspecific with either *C. bellianus* or *M. tenax* sp. nov. *Lobocarcinus sismondai* has recently been recorded with certainty from the Pleistocene deposits at Parma, Italy (Garassino and Fornaciari, 2000). Pliocene records include also England (Bell, 1921; Collins, 2002).

Family Pirimelidae Alcock, 1899

Genus *Pliopirimela* gen. nov.

Type species: *Pliopirimela deconincki* sp. nov., by monotypy.

Etymology: With reference to its stratigraphic age (Pliocene).

Diagnosis: Carapace subpentagonal in outline, front projecting with distinct median tooth, anterolateral margins serrated, central carapace regions well differentiated.

Remarks: The trilobate front with a pronounced median tooth, the toothed anterolateral margin and the shape of the carapace favour assignment of the new genus to the Pirimelidae. It may be considered to be closely related to both *Pirimela* Leach, 1816 and *Trachypirimela* Müller, 1974. *Pliopirimela* gen. nov. differs from these two genera in having non-sawtooth-shaped anterolateral teeth, in lacking a distinct cervical furrow, and in showing a tuberculate carapace surface. Other pirimelids possess a distinct, deeply depressed front, a feature not seen in *Pliopirimela* gen. nov.

Carapace shape and nature of the anterolateral margins are most closely similar to *Pirimela loerentheyi* (Müller, 1974) (p. 122, pl. 2, figs. 4, 5, as '*Carcinus' lőrentheyi*; see also Müller, 1984, p. 78, pl. 60, figs. 3-5), whereas the vaulted median carapace regions may be compared favourably to *Trachypirimela grippi* (Müller, 1974) (see Müller, 1984, p. 79, pl. 61, figs. 1-6), both from the 'Badenian' (= Langhian and Early Serravallian, Middle Miocene) of Hungary. The orbitofrontal margin in the Pliocene genus closely resembles that of the extant *Pirimela denticulata* (Montagu, 1808) (see Adema, 1991, fig. 52), although the frontal spines are more slender and acute in the latter.

***Pliopirimela deconincki* sp. nov.**

(Pl. 6, figs. 1-3)

Diagnosis: As for genus.

Etymology: The trivial name honours Luc De Coninck (Nieuwkerken-Waas, Belgium), who collected and kindly donated the holotype.

Material: Holotype is MAB k.2387 (ex De Coninck Colln), a near-complete carapace from the *Atrina* level (Oorderen Member), Verrebroekdok.

Description: Carapace subpentagonal in outline, slightly wider than long (length c. 21 mm, width c. 23 mm); greatest carapace width at lateral corners which are positioned approximately 44% of maximum carapace length from the front; very convex in longitudinal cross section and convex and irregular in transverse cross section.

Orbitofrontal width approximately 48% of maximum carapace width. Front projecting, trifid with sharp, pronounced median tooth, extending well beyond orbits. Adjacent pair of frontal teeth subdued, much smaller than median tooth, situated close to inner orbital bulges. Orbits small, subelliptical, with sharp, finely serrated edge, axially raised. Two faint fissures are present on the sloping margin towards the outer orbital tooth; orbital margin between those fissures gently curved into two minute lobes.

Anterolateral margin curved, with five teeth, the outer orbital tooth and the lateral corner included. Outer orbital tooth smallest, anteriorly directed. Successive three teeth evenly sized, becoming more outwardly directed towards the lateral corner, which is formed by the fifth and largest, outwardly directed tooth. Posterolateral margin straight, with sharp, beaded margin fading posteriorly.

Posterior margin slightly broader than orbitofrontal margin, sinuous with rounded lateral corners, marked by faintly beaded, thickened margin.

Carapace regions clearly defined in central portion of carapace, subdued in anterior portion. Intestinal region not clearly differentiated, swollen, depressed axially. Cardiac region distinctly separated by broad grooves, anterior portion strongly elevated in blunt, granular tooth, posterior portion with faint swelling. Urogastric region more clearly separated from cardiac region than from mesogastric region by narrow, shallow grooves. Two setal pits are at the base of an anteriorly positioned granular boss. Mesogastric region with convex posterior margin and narrow anterior process, effacing between protogastric regions. Posterior portion subpentagonal with central granular boss. Protogastric regions subcircular, weakly differentiated axially, anteriorly faintly differentiated by orbitofrontal depression. Hepatic region triangular, raised. Epibranchial and mesobranchial regions with sharp granular tooth axially and anteriorly, which together form a vertically curved elevation.

Carapace entirely covered with small, anteriorly directed tubercles. Tubercles are smallest at the front and most distinct in median regions.

Family Portunidae Rafinesque, 1815

Subfamily Polybiinae Ortmann, 1893

Genus *Liocarcinus* Stimpson, 1870

***Liocarcinus holsatus* (Fabricius, 1798)**

(Pl. 2, Fig. 1; Pl. 3, Figs. 3, 4)

Material: A complete juvenile carapace from the sediment fill

of a large *Scaphella* (EW.9506), three partial juvenile carapaces from the sediment fill of a *Neptunea* (MAB k.2388a-c), a left-hand juvenile articulated carpus, propodus and dactylus from the sediment fill of a large unidentified gastropod (EW.9509), two left-hand dactyli (MAB k.2390, k.2391), a left-hand fixed finger (MAB k. 2392), three right-hand dactyli (MAB k.2393, k.2394, k.2395), two right-hand fixed fingers (MAB k.2396, k.2397), and a right-hand propodus (MAB k.2398), all from the *Atrina* level (Oorderen Member), Deurganckdok.

Remarks: Isolated fingers of this species have been described from Lower Pleistocene ('Icenian'), Riss I and Riss-Würm Interglacial ('Eemian') deposits in the Netherlands (Gravendeel, Moerdijk, Haamstede, Bergen) by Holthuis (1949, p. 65, pl. 2, figs. 18-22) and from the Pleistocene of England (Bell, 1921; Holthuis, 1949). In their preliminary report, Van Bakel et al. (2000) referred to the present material as *L. marmoreus* (Leach, 1814) (see Adema, 1991, p. 154, fig. 61), a species closely related to *L. holsatus*. D'Udekem d'Acoz (1999) reassigned this species to *Polybius* Leach, 1820, although most authors apply *Liocarcinus* instead.

Discussion

Of special note is the fact that many of the crab specimens described above have been collected from the sediment fill of larger gastropods (e. g. *Scaphella, Neptunea, Galeodea*, and *Atractodon*). Two examples in particular need to be mentioned: a specimen of *Galathea dispersa* preserving limbs, an eye stalk as well as a chela, and a fragile carapace with associated left chela of *Liocarcinus holsatus*. In both cases it may be assumed that, in view of their fragility, these remains did not undergo extended *post-mortem* displacement, neither were they washed into empty gastropod shells. It is quite likely that these animals used the gastropods for shelter. Remarkable in this respect is the presence of three (partial) carapaces of *L. holsatus* within a single gastropod shell; since these specimens are of different size, the possibility that they represent various moulting stages of the same individual can be ruled out.

Of the nine genera here listed, seven (*Galathea, Pagurus, Ebalia, Maja, Metacarcinus, Cancer*, and *Liocarcinus*) also occur in the 'Badenian' (Middle Miocene) of Hungary; of the two remaining taxa ancestral taxa occur there (*Pirimela* and *Trachypirimela* for *Pliopirimela* gen. nov.; *Corystites*? for *Corystes*) (see Müller, 1984). None of the taxa on record from Hungary and NW Belgium are identical at the species level. *Corystes holsaticus* is the only species which is also known from the Miocene of northern Germany. With the exception of *Pliopirimela* gen. nov., which in Recent faunas is replaced by *Pirimela*, all genera survive in the North Sea to the present day (see Christiansen, 1969; Ingle, 1980; Adema, 1991), and seven (*Galathea dispersa, Pagurus bernhardus, Ebalia cranchii, E. tumefacta, Maja squinado, Cancer pagurus* and *Liocarcinus holsatus*) appear to have remained unchanged since Late Pliocene times.

As stated above, Vervoenen (1995) noted for the Oorderen Member, and the *Atrina* level in particular, a maximum water depth of 20 to 30 metres, as based on molluscan and sedimentary evidence. The crab material available to us substantiates this estimate, using data supplied by Adema (1991). Those data also include records of habitat preference, which, with caution, can also be used for the Pliocene faunules. Present-day *Ebalia cranchii*, distributed from the west coast of Norway and Sweden to Denmark, Great Britain, the North Sea, the English Channel and further south, to Senegal and inclusive of the Mediterranean, occurs from the tidal zone down to depths of 110 metres, but most records from the southern North Sea are from between 20 and 50 metres, generally occurring on more or less firm bottoms with coarse sand and/or shell grit, but occasionally also on clayey bottoms. A similar habitat is reported for *E. tumefacta* (tidal zone to depths of 155 metres, and in southern North Sea between 20 and 40 metres; hardened bottoms with rocks, shell hash, gravel and coarse sand and less frequently on fine sand, mud and clay).

Maja squinado, occurring from the tidal zone to depths of 70 metres, apparently prefers bottoms with rocks or sand. Its current distribution is the west coast of Scotland to the coast of Guinea, the Canary Islands and the Mediterranean; finds in the North Sea are incidental. *Corystes cassivelaunus* (tidal zone to depths of 100 metres, in southern North Sea between 20 and 60 metres), lives in clean sandy bottoms, hidden during the day, being active night predators. Its food consists of small crustaceans, molluscs and bristle worms, and lesser amounts of echinoderms and algae. Current distribution is the south coast of Norway to SW Sweden, Denmark, NW Germany, Great Britain, the Netherlands, Belgium, France, Portugal and the Mediterranean.

Pirimela denticulata (tidal zone to depths of 200 metres) occurs on sand, either mixed with shell hash or not, but also between algae and sea grass, while *Cancer pagurus* (tidal zone to depths of 300 metres) prefers sandy and/or rocky bottoms. This species is susceptible to low temperatures and favours a salinity of at least 15 promille; it is slow moving, active at night and carnivorous, preferring mainly molluscs and echinoderms. It is an eastern Atlantic species, ranging from Norway to Portugal, but rare in the Mediterranean. *Liocarcinus holsatus* is distributed from the tidal zone to depths of 100 metres (in the southern North Sea mostly between 0 and 40 metres), and lives on bottoms of sand, shell hash and rocks, but preferring clean sand to dig into. This is a fairly good swimmer, swift and aggressive, carnivorous, and an active hunter. Its food comprises crustaceans, worms and echinoderms; predators include cod and flatfish. Current distribution is from Iceland to northern Norway to south to southern Portugal and the Canary Islands.

In preferred habitat (bottom conditions, depth) and food requirements, there is thus a good correspondence between extant North Sea Basin crab species and Pliocene conspecific forms. This would also seem to hold true for predators (cod in particular).

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Explanation of Plate 1

Ebalia cranchii Leach, 1817

Figs. 1-4. Male specimen (S. Mermuijs Colln), in frontal (1), right lateral (2), dorsal (3) and ventral (4) view. Scale bar equals 2 mm.

Fig. 5. MAB k.2371 (ex F. Smet Colln), right propodus with articulated carpus. Scale bar equals 1 mm.

Fig. 6. MAB k.2370 (ex E. Wille Colln), female abdomen. Scale bar equals 1 mm.

Ebalia tumefacta (Montagu, 1808)

Fig. 7. MAB k.2375 (ex E. Wille Colln), immature female specimen, dorsal view of carapace. Scale bar equals 2 mm.

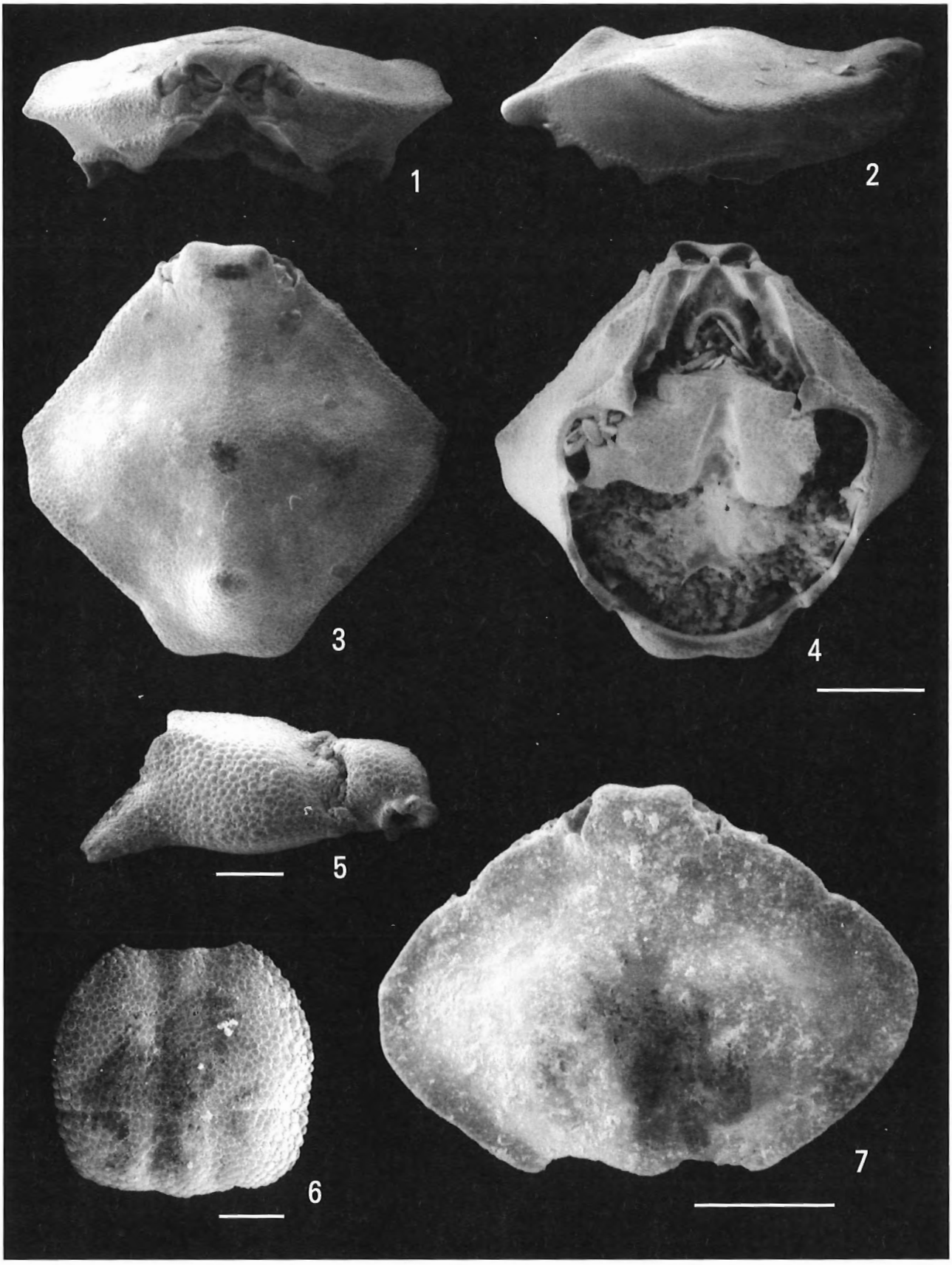

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Plate 2

Liocarcinus holsatus (Fabricius, 1798)

Fig. 1. EW.9506, juvenile specimen, dorsal view of carapace. Scale bar equals 2 mm.

Ebalia tumefacta (Montagu, 1808)

Fig. 2. MAB k.2374 (ex F. Smet Colln), female abdomen.

Fig. 3. EW.9507, male abdomen. Scale bar equals 2 mm.

Ebalia jacqueshermani sp. nov.

Fig. 4. MAB k.2373 (ex E. Wille Colln), paratype, a ?female specimen, dorsal view of carapace.

Figs. 5-7. MAB k.2372 (ex E. Wille Colln), holotype, a ?male specimen, in frontal, dorsal and right lateral view, respectively. Scale bar equals 1 mm.

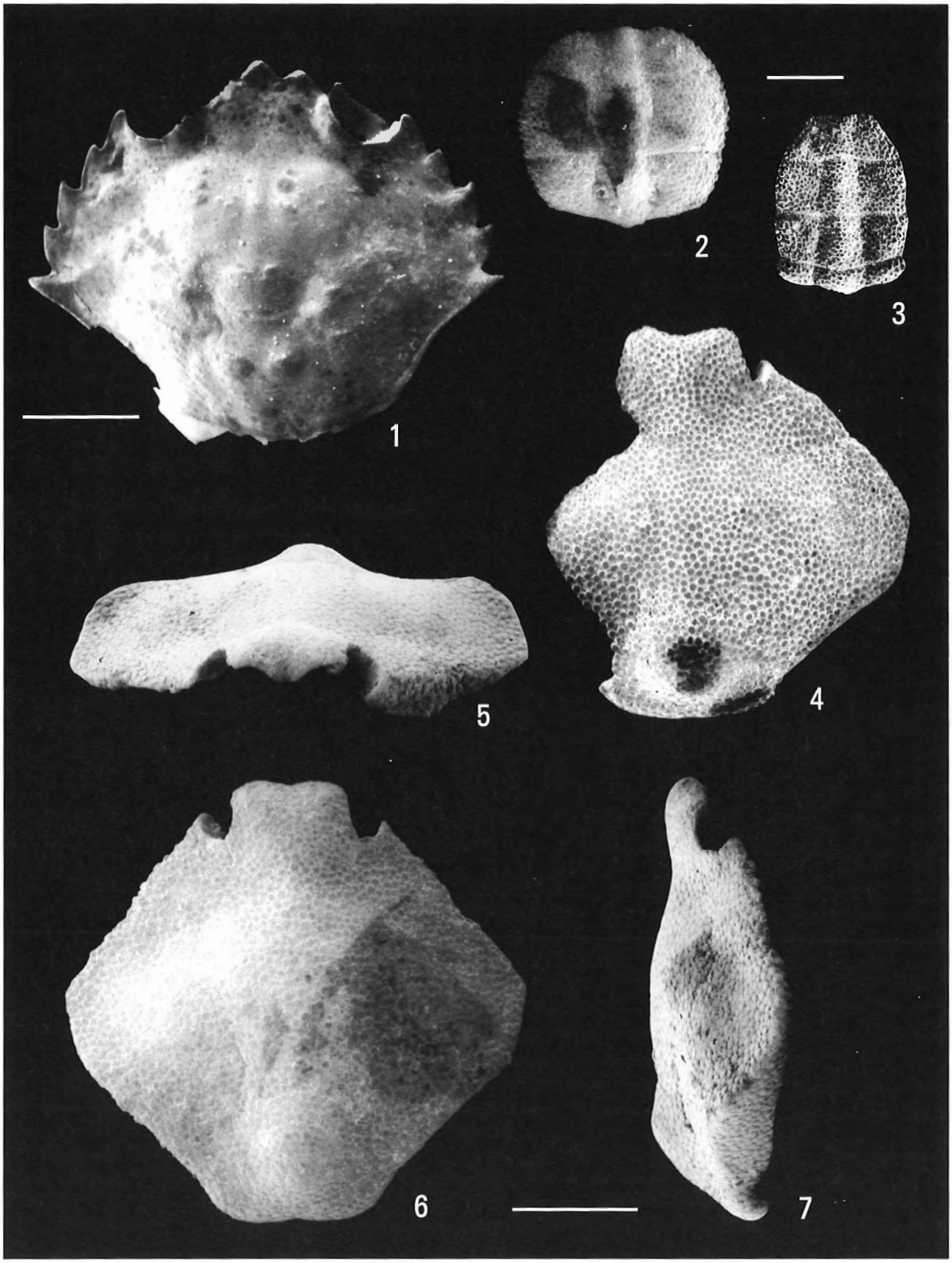

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Plate 3

Maja squinado (Herbst, 1788)

Figs. 1-2. MAB k.2377 (ex E. Wille Colln), top and outer view of right carpus. Scale bar equals 5 mm.

Figs. 5-6. MAB k.2378 (ex E. Wille Colln), top and outer view of left fixed finger. Scale bar equals 5 mm.

Figs. 7-8. MAB k.2378 (ex E. Wille Colln), inner and outer view of left dactylus. Scale bar equals 5 mm.

Figs. 9-12. EW.9502, female carapace, in frontal, right lateral, dorsal and ventral view, respectively. Scale bar equals 10 mm.

Liocarcinus holsatus (Fabricius, 1798)

Figs. 3-4. MAB k.2398 (ex E. Wille Colln), top and outer view of right propodus. Scale bar equals 5 mm.

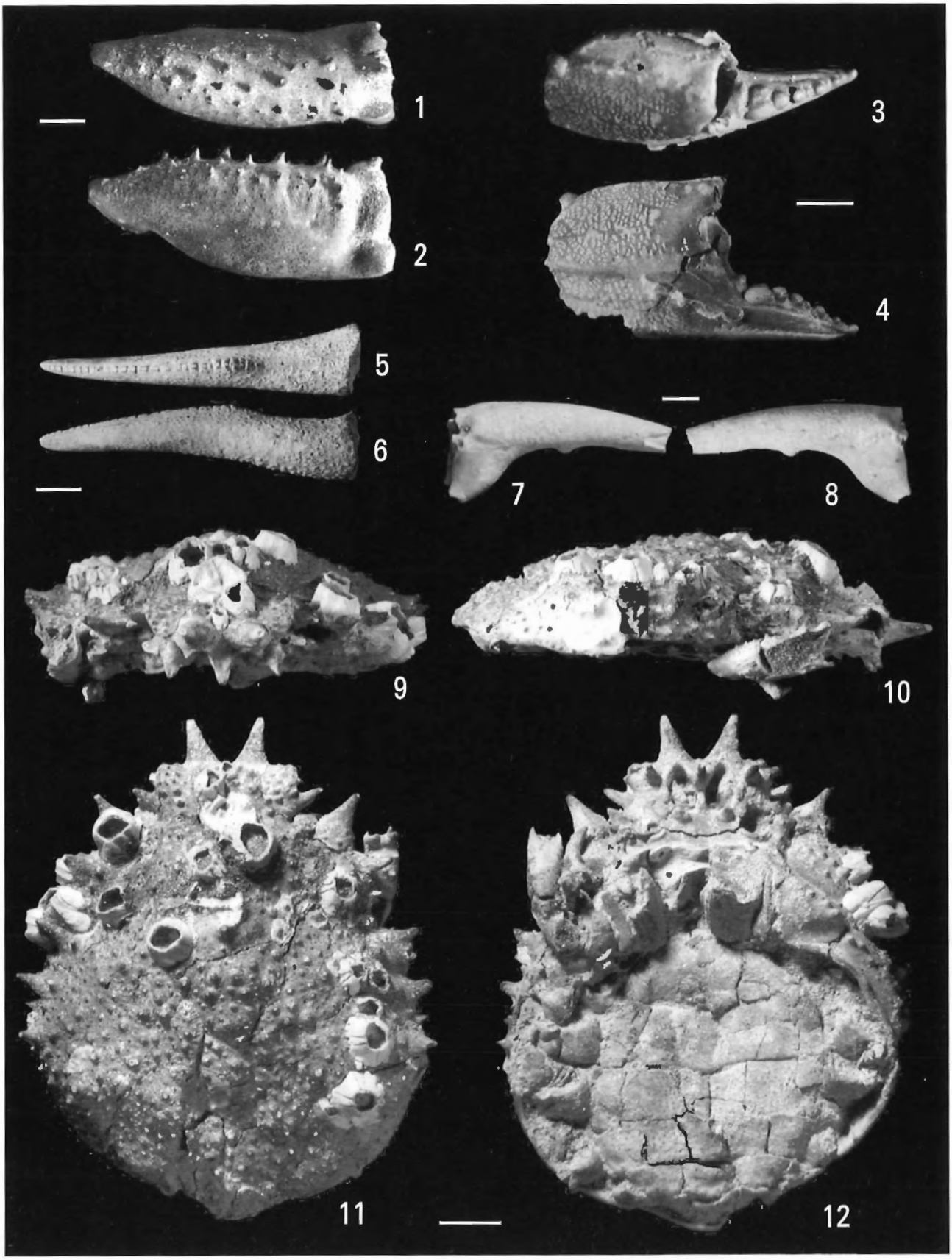

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Plate 4

Corystes holsaticus (Noetling, 1881)

Figs. 1-2. MAB k.2381 (ex E. Wille Colln), dorsal and right lateral view of carapace (arrow indicates subhepatic spine). Scale bar equals 5 mm.

Figs. 6-8. EW.9503, carapace in frontal, dorsal and right lateral view, respectively. Scale bar equals 5 mm.

Galathea dispersa Bate, 1859

Figs. 3-5. EW.9500, outer and top view of chela (3, 4) and dorsal view of partial carapace (5) found associated. Scale bar equals 5 mm.

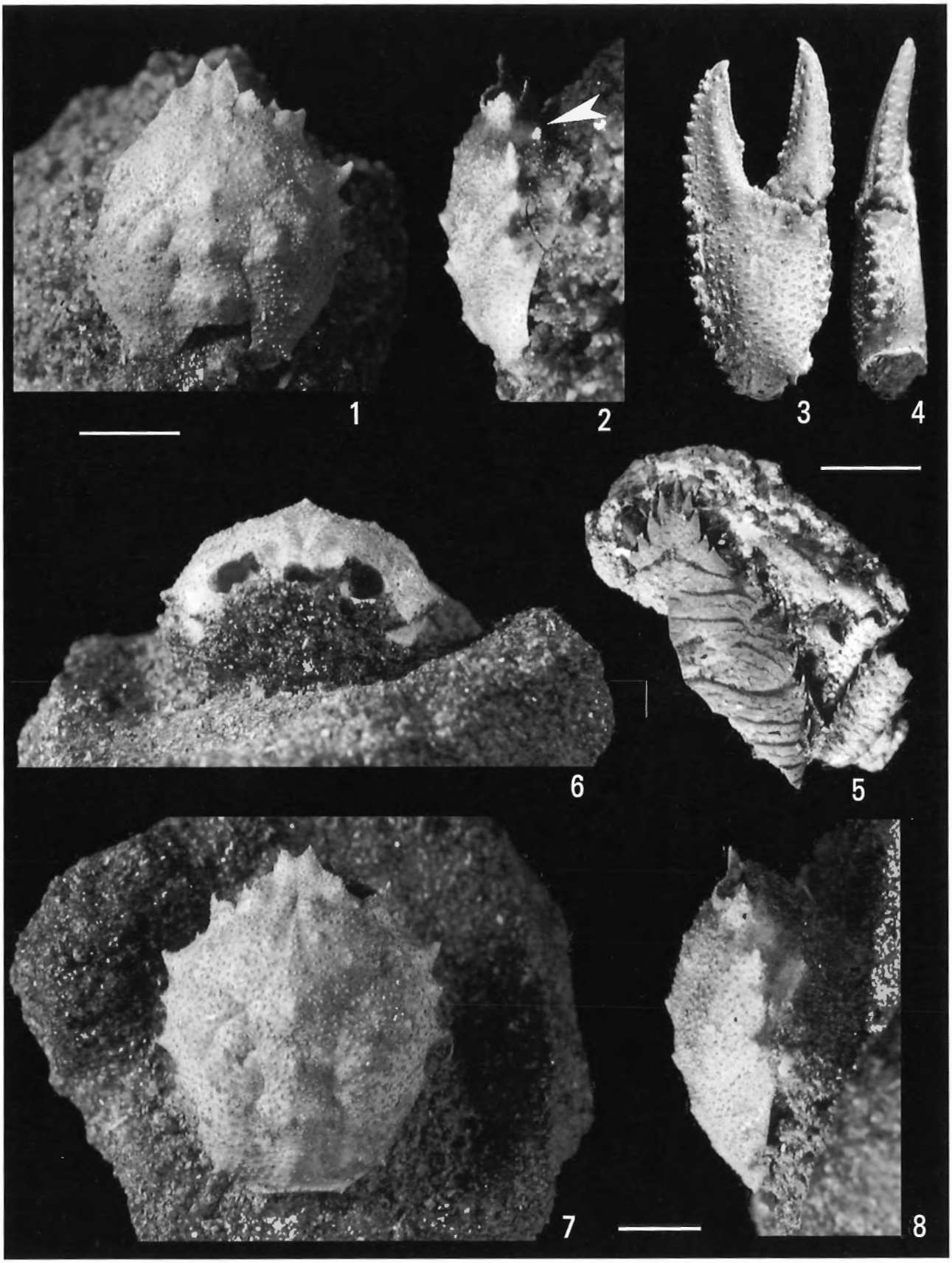

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Plate 5

Cancer cf. *pagurus* Linné, 1758

Figs. 1-2. EW.9505, outer and inner view of right propodus with articulated carpus. Scale bar equals 10 mm.

Fig. 3. MAB k.2383 (ex E. Wille Colln), dorsal view of right-hand half of carapace. Scale bar equals 10 mm.

Fig. 4. MAB k.2399 (ex E. Wille Colln), outer view of left-hand chela with articulated carpus. Scale bar equals 5 mm.

Figs. 5-6. MAB k.2384 (ex E. Wille Colln), top and outer view of right chela with articulated carpus of juvenile specimen, respectively. Scale bar equals 5 mm.

Figs. 7-9. EW.9504, frontal, dorsal and right lateral view of juvenile carapace, respectively. Scale bar equals 10 mm.

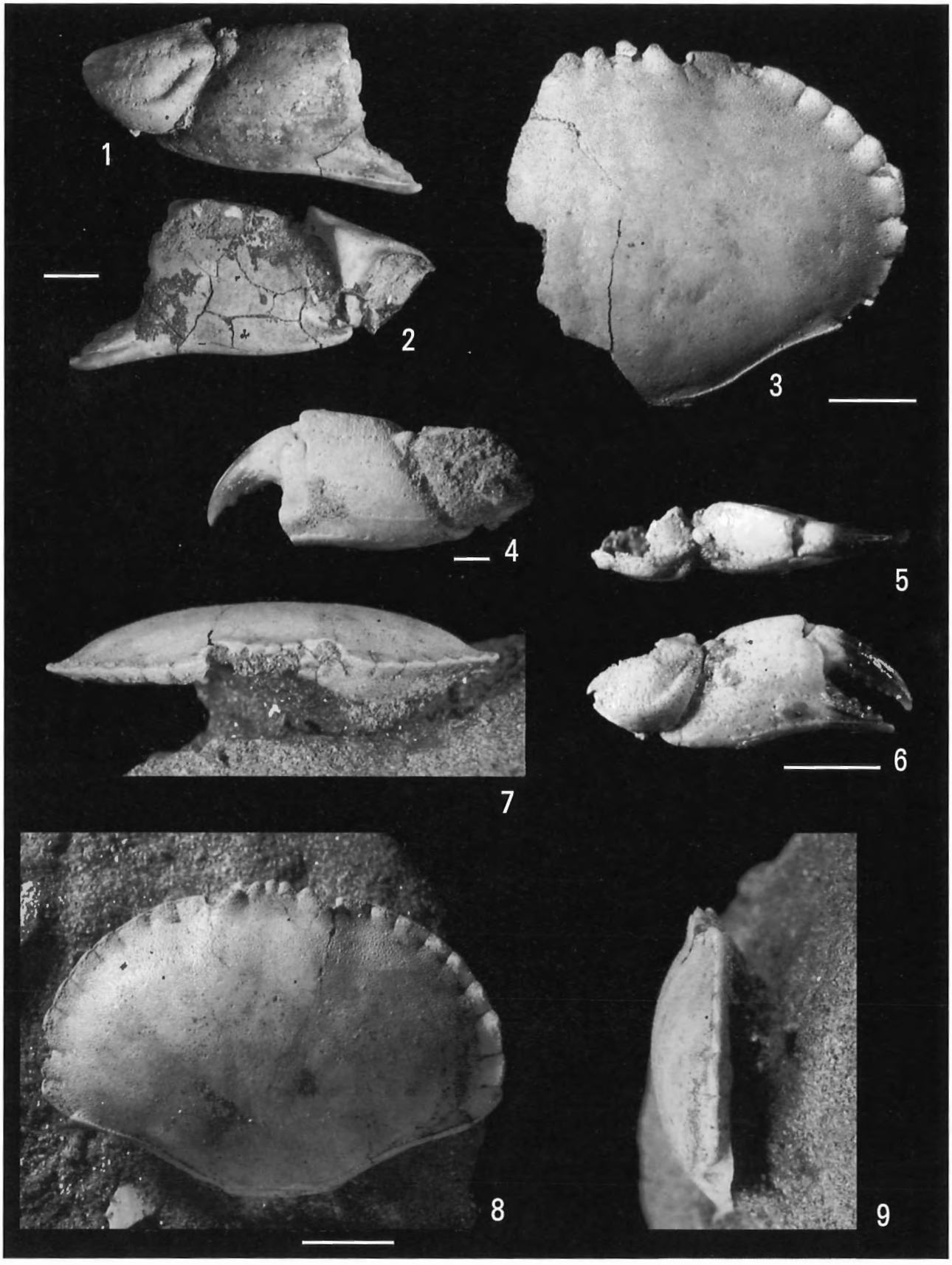

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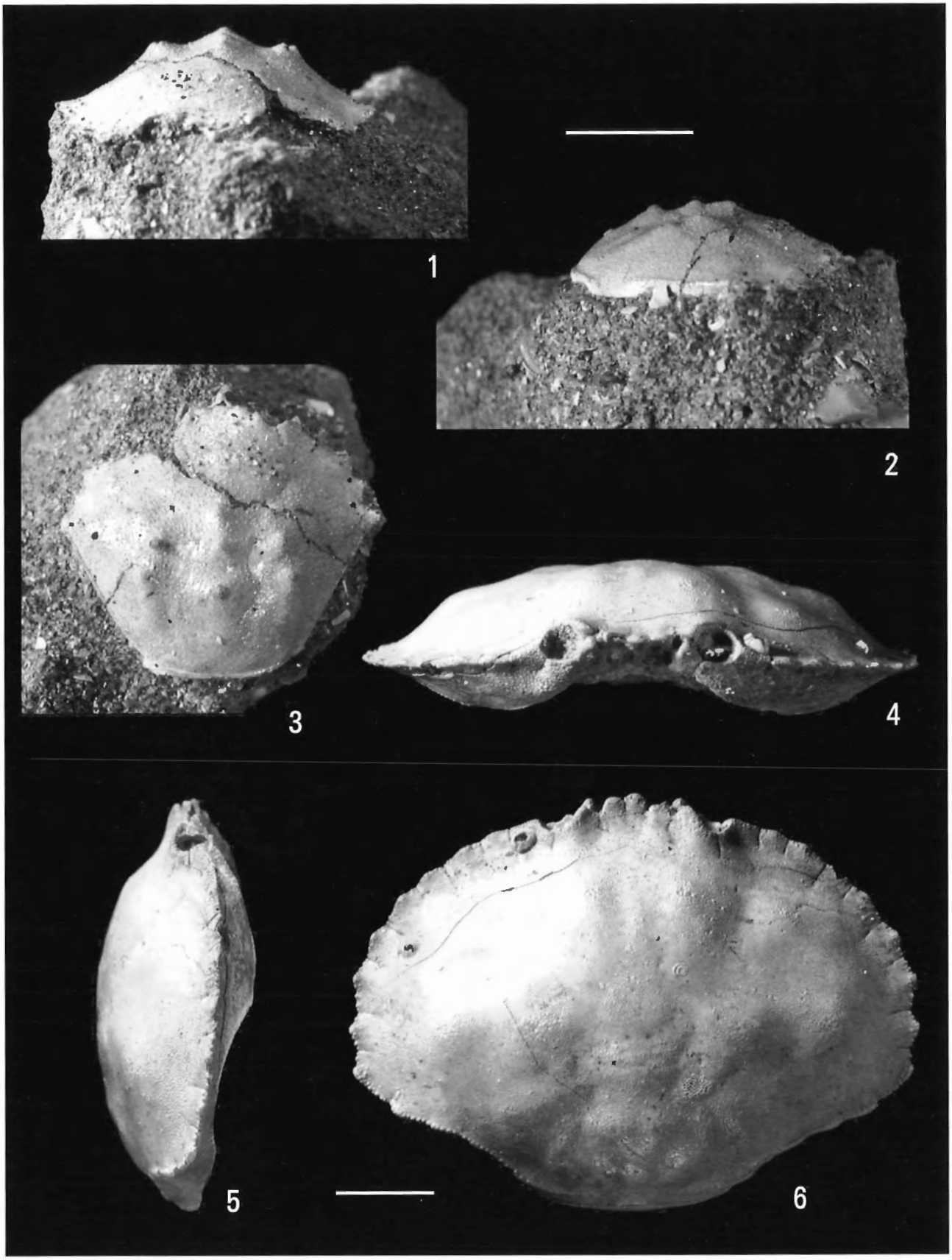
Plate 6

Pliopirimela deconincki gen. nov. and sp. nov.

Figs. 1-3. MAB k.2387 (ex L. De Coninck Colln), holotype, carapace in frontal, right lateral and dorsal view, respectively. Scale bar equals 10 mm.

Metacarcinus tenax sp. nov.

Figs. 4-6. MAB k.2386 (ex E. Wille Colln), holotype, carapace in frontal, right lateral and dorsal view, respectively. Scale bar equals 10 mm.


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