

NECROCARCINUS ORNATISSIMUS FORIR, 1887, AND *PREHEPATUS WERNERI* FRAAYE & COLLINS, 1987 (UPPER MAASTRICHTIAN, THE NETHERLANDS) REVISITED, WITH NOTES ON OTHER CRETACEOUS DYNOMENID CRABS (DECAPODA, BRACHYURA)

BY

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ABSTRACT

The recently traced type specimens of decapod crustaceans erected by H. Forir from the Upper Cretaceous (upper Maastrichtian) of southern Limburg and Liège (southeast Netherlands, northeast Belgium) include *Necrocarcinus ornatissimus*, a species based on a single left claw. This species is shown to be conspecific with another claw-based taxon from the same area and stratigraphic level, *Prehepatus weneri* Fraaye & Collins, 1987. *Necrocarcinus ornatissimus* is thought to be a dynomenid.

RÉSUMÉ

Les spécimens types de crustacés décapodes récemment découverts et décrits par H. Forir du Crétacé supérieur (Maastrichtien supérieur) du sud du Limbourg et de Liège (sud-est Pays-Bas, nord-est Belgique), comprennent *Necrocarcinus ornatissimus*, une espèce décrite à partir d'une seule pince gauche. Il est montré que cette espèce est conspécifique de *Prehepatus weneri* Fraaye & Collins, 1987, taxon du même niveau stratigraphique, décrit également d'après la pince. Il est proposé de rattacher *N. ornatissimus* aux Dynomenidae.

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INTRODUCTION

During the last two decades, the upper portion of the Maastricht Formation (Emael, Nekum, and Meerssen members; latest Maastrichtian, *Belemnitella junior* and *Belemnella (Neobelemnella) kazimiroviensis* cephalopod zones) in the type area of that unit, has yielded rich and diverse decapod crustacean faunas (Collins et al., 1995; Fraaye, 1996a, b, 1997; Fraaye & Van Bakel, 1998; Jagt et al., 2000; Swen et al., 2001; Fraaije, 2002, 2003; Van Bakel et al., 2003; Fraaije et al., 2008). With the exception of some raninid taxa, most of this material comprises isolated remains of carapaces and dissociated chelae, some of which may actually represent moults. In general, complete specimens are exceedingly rare. The consistent association of claws with certain types of carapaces may be used to infer conspecificity of some of these, in particular necrocarcinids (paranecrocarcinines). In a few cases, subsequent finds of well-preserved material have substantiated such interpretations.

Forir (1887b: 169, 172 [51, 54], pl. 7 fig. 7a-d) described an isolated left claw from ‘la couche à bryozoaires de l’étage maestrichtien supérieur (danien) de la Montagne St-Pierre à Maestricht’ as a new species, *Necrocarcinus ornatissimus*. In current lithostratigraphic terminology, this would correspond to one of the bryozoan-rich intervals of the lower/middle Meerssen Member (Maastricht Formation). Despite several attempts during recent years (P. J. Felder, pers. comm.), Forir’s original material could not be traced at the Université d’État (Liège) where it was stated to have been deposited. In November 2003, the first author came across two collection trays in the basement of the Institut royal des Sciences naturelles de Belgique (Brussels), containing most of Forir’s labelled originals (fig. 1A-F). It appears that the late Victor Van Straelen had borrowed this material, but failed to return it. Additional specimens in Forir’s Collection, e.g., a xanthoid and additional dromioids (Forir, 1887a, c, 1889), have been described in detail elsewhere (Schweitzer et al., 2007a) or will be revised shortly (Jagt et al., work in progress).

A left claw similar to *N. ornatissimus* was recorded one hundred years later under the name of *Prehepatus weneri* by Fraaye & Collins (1987) from the same stratigraphic unit, but at a different locality (the former Blom quarry, Berg en Terblijt), a few kilometres east of Maastricht. However, those authors failed to mention Forir’s (1887b) paper. Subsequently, Collins et al. (1995: 169) stated that, ‘The last-named species [= *Necrocarcinus ornatissimus*] has a superficial resemblance to *Prehepatus weneri* Fraaye & Collins, 1987’. Now that the type of *N. ornatissimus* has been traced, it can be demonstrated beyond doubt that *P. weneri* is a junior synonym.

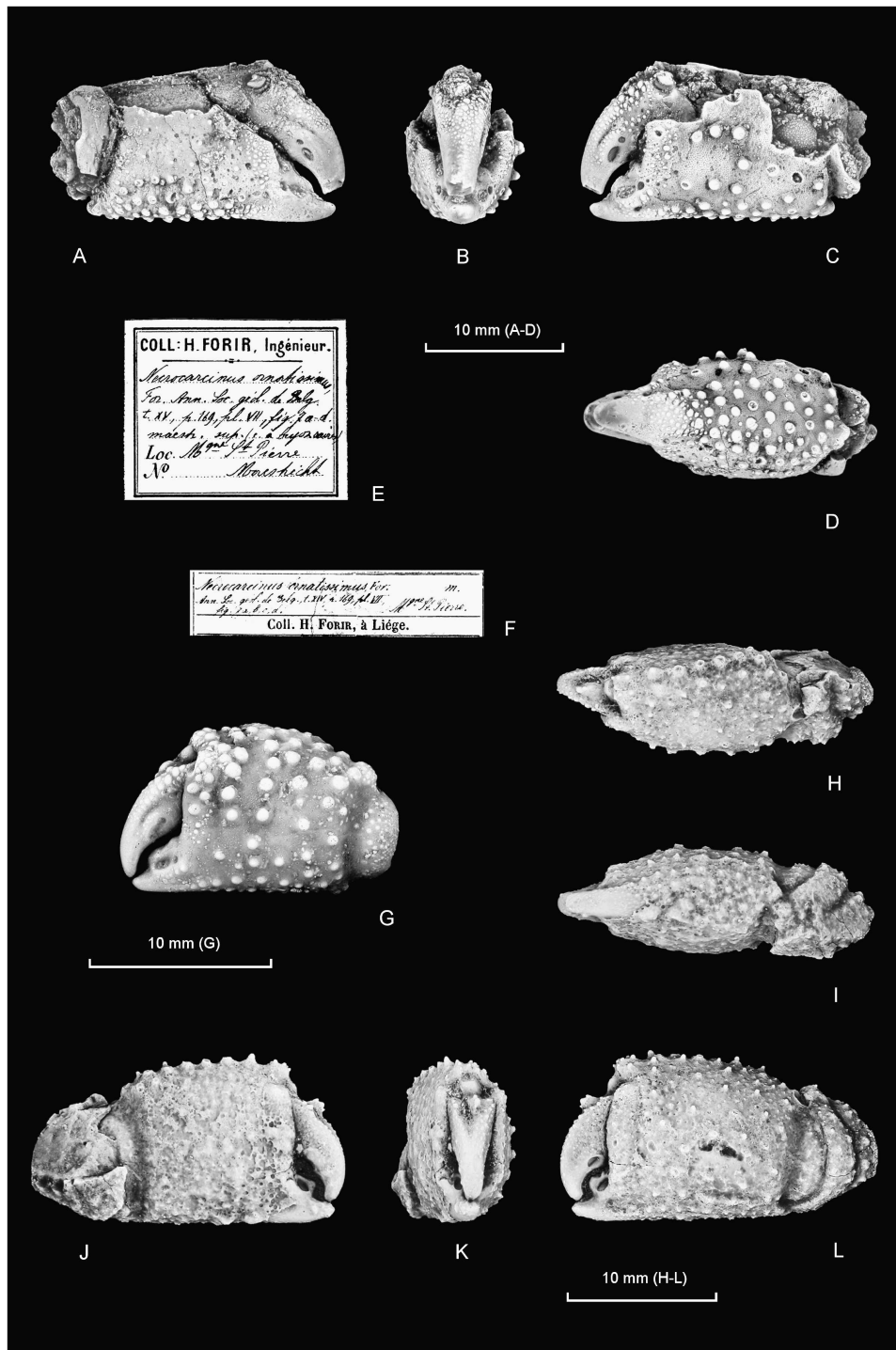


Fig. 1. Cretaceous dynomenid claws, assignable to the 'form genus' *Roemerus* Bishop, 1983; A-F, *Roemerus ornatissimus* (Forir, 1887b), holotype (IRScNB MI 11005) of *Necrocarcinus ornatissimus*, with original labels in Forir's handwriting; lower/middle Meerssen Member (Maastricht Formation), St Pietersberg, south of Maastricht (Netherlands); G, *Roemerus ornatissimus* (Forir, 1887b), holotype (MAB k. 1007) of *Prehepatus weneri* Fraaye & Collins, 1987; lower/middle Meerssen Member (Maastricht Formation), former Blom quarry, Berg en Terblijt (Netherlands); H-L, *Roemerus* sp. (MGSB 68.581), lower Aptian, Morella (Castellón, Spain).

Numerous carapaces and isolated chelae of necrocarcinids (paranecrocarcinines) have been collected from the upper Maastricht Formation (Nekum and Meerssen members, in particular) as to cast serious doubts over either a necrocarcinid or calappid nature of *N. ornatissimus* (see fig. 2). Moreover, a literature search and examination of newly acquired fossil material from northern Spain, made us reflect on the possibility that this, and other, claw-based species represented dynomenids rather than necrocarcinids. Previous authors (e.g., Förster, 1968; Wright & Collins, 1972) already hinted at this. The fact that ‘necrocarcinid’ claws appear consistently associated with dynomenid carapaces throughout the Lower and Upper Cretaceous can thus no longer be ignored. Some of these isolated claws have unfortunately been formally named, as in the case of associated carapaces. So long as specimens preserving chelae are not forthcoming, it is proposed here to use parataxonomy for such cases, by using the ‘form genus’ *Roemerus* Bishop, 1983 (type species, by original designation, *R. robustus* Bishop, 1983). This taxon, from the lower Albian (Lower Cretaceous) Glen Rose Limestone of central Texas, originally regarded as a paguroid claw, is here interpreted as a dynomenid, which may be conspecific with the co-occurring, carapace-based species, *Trachynotocarcinus naglei* (Bishop, 1983), originally referred to the genus *Palaeodromites* A. Milne-Edwards, 1865 (see Collins & Donovan, 2007: 62). Vega et al. (2006: 331, fig. 6.7) subsequently recorded *R. robustus* from the Sierra Madre Formation, a lower Albian plattenkalk facies, in Chiapas (southeast Mexico). Given that the specimen preserved similar-sized left and right chelae, these authors considered it to be a diogenid hermit crab.

Additional evidence that claws of a type similar to *Roemerus robustus* are in fact dynomenid rather than paguroid (diogenid) or necrocarcinid, comes from still unpublished early Aptian and Maastrichtian material from Castellón and Navarra, Spain (*Roemerus* sp. and *Graptocarcinus texanus* Roemer, 1887; see figs. 1H-L, 3), from collections briefly exhibited by Àlex Ossó during the Third Symposium on Mesozoic and Cenozoic Decapod Crustaceans at Milan (May, 2007) and from specimens from the Cenomanian of northern France (*Graptocarcinus* sp.; fig. 4E-H), contained in the L. de Putter Collection, Axel, Netherlands (casts are MAB k. 2545 and k. 2546). Previous records of so-called necrocarcinid claws (i.e., assigned to *Necrocarcinus*) are invariably associated with dynomenid carapaces of the genera *Palaeodromites* (= *Cyphonotus* [sensu Bell, 1863]; *Distefania* Checcia-Rispoli, 1914), *Graptocarcinus* Roemer, 1887, and *Trachynotocarcinus* Wright & Collins, 1972.

It appears that on such features as size, ornament, development of fixed and movable fingers plus the presence or absence of ovate depressions in

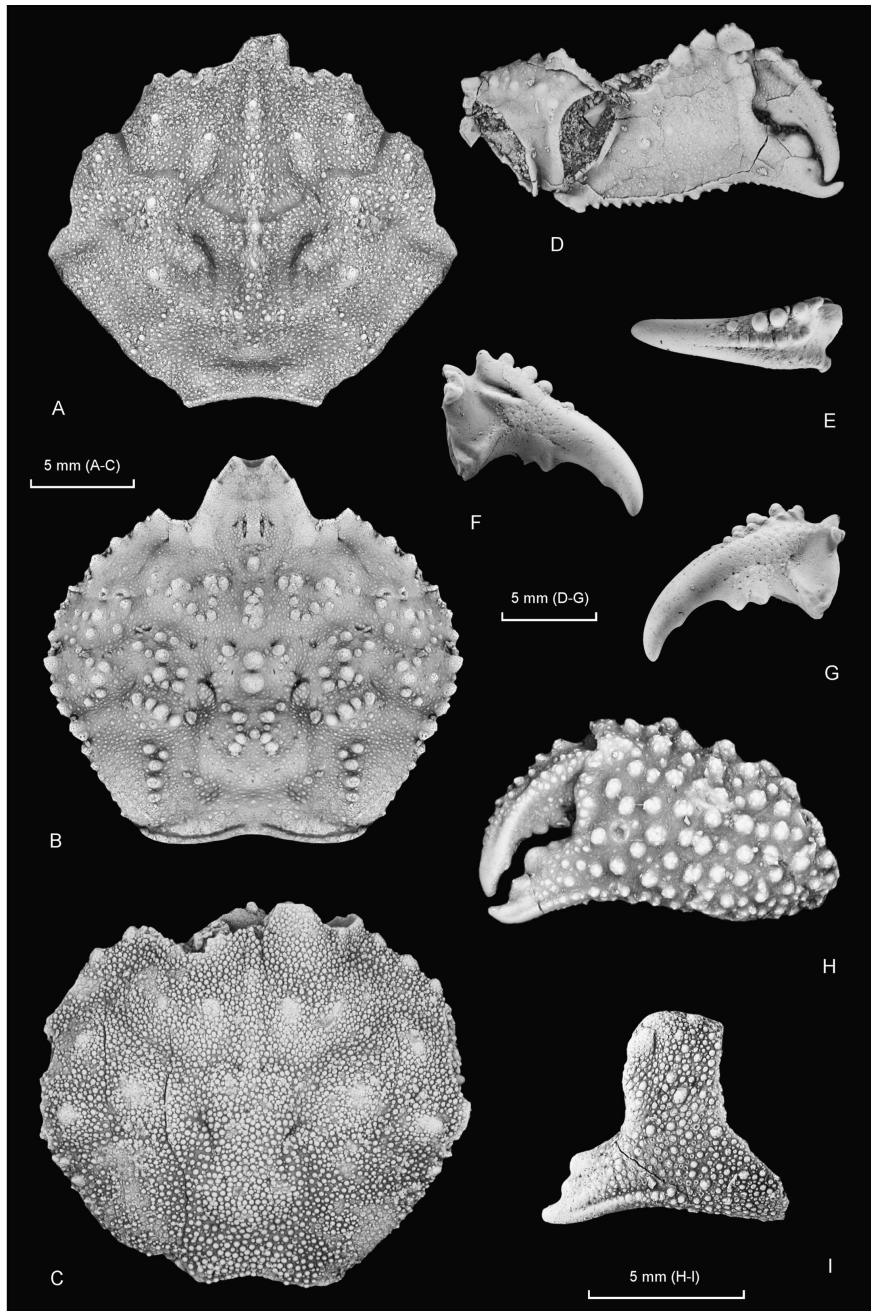


Fig. 2. Necrocarcinids (paranecrocarcinines) and orithopsid from the Maastricht Formation (Emael, Nekum, and Meerssen members; see also Collins et al., 1995; Fraaije, 2002) in the Maastrichtian type area; A, *Orithopsis angelicus* (Fraaije, 2002), carapace (MAB k. 2548, composite photograph); B, D, H, *Paranecrocarcinus quadriscissus* (Noetling, 1881) (= *Dromiopsis ubaghsi* Forir, 1887c), carapace MAB k. 2549 and two left chelae (NHMM JJ 6737 and MAB k. 0720, respectively), in inner and outer respect, respectively; C, I, *Paranecrocarcinus vanbirgeleni* Fraaije, 2002, holotype (MAB k. 2278) carapace, and referred fragmentary left chela (MAB k. 2550), respectively; E-G, '*Pseudomicippe granulosa* (Bosquet MS) Pelseneer, 1889', isolated left dactylus (holotype, IRScNB MI 10670), here held to be conspecific with *Paranecrocarcinus quadriscissus* (see fig. 3D, H). All specimens coated with ammonium chloride prior to photography.

TABLE I

Dynomenid claws, previously assigned to the genera *Necrocarcinus*, *Prehepatus*, and *Roemerus*, linked to associated dynomenid carapaces in the same faunal assemblages (data from Bosquet, 1854; Forir, 1887b; Fritsch & Kafka, 1887; Gründel, 1974; Bishop, 1983; Fraaye & Collins, 1987; Collins et al., 1995; Collins & Dieni, 1996; Collins & Donovan, 2007); *Forir (1887b: 165 [47], pl. 7 fig. 5a, b) assumed claws associated with a partial carapace which he named *Dromiopsis gigas* to be conspecific

Claw-based taxa	Carapace-based taxa
<i>Necrocarcinus avicularis</i> Fritsch in Fritsch & Kafka, 1887	(<i>Cancer?</i>) <i>modestus</i> (?= <i>Graptocarcinus texanus</i> ; see Wright & Collins, 1972)
<i>Roemerus ornatissimus</i> (Forir, 1887b) (= <i>Prehepatus weneri</i> Fraaye & Collins, 1987)	<i>Stephanometopon granulatum</i> Bosquet, 1854
<i>Necrocarcinus woodwardi</i> [sensu Gründel, 1974]	<i>Palaeodromites incertus</i> (Bell, 1863)
<i>Necrocarcinus woodwardi</i> [sensu Bell, 1863]	<i>Palaeodromites incertus</i> (Bell, 1863) <i>Trachynotocarcinus sulcatus</i> (Bell, 1863)
<i>Roemerus robustus</i> Bishop, 1983	<i>Trachynotocarcinus naglei</i> (Bishop, 1983)
Pagurinae gen. indet.	<i>Graptocarcinus bellonii</i> Collins & Dieni, 1996
<i>Dromiopsis gigas</i> Forir, 1887b*	<i>Dromiopsis gigas</i> Forir, 1887b

both dactylus and fixed finger (see below), species might be based on isolated dynomenid chelae here assigned to the ‘form genus’ *Roemerus*, but we have refrained from introducing new taxa (for available names, see table I) and hope other authors will follow our example. It has previously been noted (e.g., Collins, 1999) that isolated crab claws are notoriously difficult to identify, but that ‘educated guesses’ regarding association with carapaces have at times proved correct. We can only hope for finds of more or less complete specimens with claws preserved in every example referred to below. Until that time, we prefer to use parataxonomy for those taxa that have already been described on the basis of isolated cheliped material. In those cases where chelae are found attached to carapaces, we propose carapace-based names take priority over those erected on the basis of isolated chelae.

SYSTEMATIC PART

Abbreviations used to denote the repositories of specimens referred to in the text are as follows: ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; GSCM, Georgia Southern College Museum, Statesboro, Georgia, U.S.A.; MAB, Oertijdmuseum De Groene Poort, Boxtel, Nether-

lands (formerly Museum de Ammonietenhoeve, Boxtel); MGSB, Museo Geológico del Seminario de Barcelona, Barcelona, Spain; MNB, Museum für Naturkunde, Berlin, Germany; MNH-UABCS, Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Mexico; NHMM, Natuurhistorisch Museum Maastricht, Maastricht, Netherlands (with collection letter codes: JJ — J. W. M. Jagt; RD — R. W. Dortangs); SDSNH, San Diego Natural History Museum, San Diego, California, U.S.A.; UT, University of Texas, Austin, Texas, U.S.A.

Superfamily DROMIOIDEA De Haan, 1833

Family DYNOMENIDAE Ortmann, 1892

‘Form genus’ **Roemerus** Bishop, 1983

Type species. — *Roemerus robustus* Bishop, 1983: 42, pl. 3 figs. 20-31, text-fig. 8G, by original designation; lower Albian Glen Rose Limestone, Blanco and Kendall counties, Texas. The holotype, left claw (UT 45704), and one paratype, left propodus (SDSNH 23662), have been described by Bishop (1983).

Diagnosis. — ‘Chelae elongate, similar, with rectangular palm, outer face transversely convex, inner flat. Carpal and dactyl articulations perpendicular to lower margin, which is straight except for convexity below base of fixed finger. Fingers short and turned slightly inward. Fixed finger has at least 1 proximal tooth. Tip of movable finger overlaps fixed finger in smaller claws and closes onto outer edge of tip in large claws. Surface sparsely covered with large, low granules which become numerous and prominent on lower edge. The upper surface surmounted by a low, oblique ridge accentuated on the proximal inner face by a few low granules and becoming less conspicuous as it runs toward the top center of the distal margin of the claw’ (Bishop, 1983: 42).

Remarks. — As here understood, the ‘form genus’ *Roemerus* comprises only those forms that have oval depressions (for setae; see below) in both dactylus and fixed finger (fig. 1). It appears that this ‘form genus’ can be linked to carapaces of *Palaeodromites*, while forms without such oval depressions belong to *Graptocarcinus* or some closely allied dynomenid.

Roemerus ornatissimus (Forir, 1887b) (fig. 1A-G)

Necrocarcinus ornatissimus Forir, 1887b: 169 [51], pl. 7 fig. 7a-d.

Prehepatus weneri Fraaye & Collins, 1987: 549, figs. 1, 2; Collins et al., 1995: 198, fig. 11c-g.

Types. — The holotype, by monotypy, of *N. ornatissimus*, left claw (IRScNB MI 11005) (fig. 1A-D; original labels, see fig. 1E, F). The holotype of *P. weneri*, by original designation,

left claw (MAB k. 0017) (fig. 1G); paratypes, fragmentary right fixed finger (MAB k. 0018) and fragmentary right movable finger (MAB k. 0019).

Material examined. — In addition to the types of both taxa, several isolated left claws and movable fingers (MAB k. 1037-k. 1038, NHMM JJ 12653, NHMM JJ 13264, NHMM RD unregistered), as well as a left cheliped (MAB k. 2547, leg. J. W. M. Jagt) are available.

Description. — Left manus subrectangular in outline; upper margin slightly depressed proximally, outer surface being moderately convex longitudinally, transversely, passing sharply into broad, gently rounded upper surface; broad furrow separating finely granular carpal articulation from remainder of manus; straight distal margin bordered on upper surface by row of fine granules, which become larger, sparser on outer surface where bounded by short, vertical groove and anteriormost tubercle of 3 rows of 4 large tubercles, each forming strongly curved line; above these, less regularly arranged tubercles give way to crowded granules on upper surface; below, row of 6 tubercles, followed by straight row of 9 or 10 decreasing in size distally, terminating at margin halfway along fixed finger, joined at an angle by median one of 3 rows of fine granules on fixed finger, uppermost lining base of occlusal teeth on opposing margin; several other tubercles scattered among transverse rows, some tending to form longitudinal rows; lower margin weakly concave to straight, more or less in line with the fixed finger, with row of 7 or 8 tubercles decreasing in size distally. Fixed finger about one-third of manus length; deep depression occurring below second of 2 large cusps on opposing margin; moderately curved moveable finger with narrow, granular tubercle proximally; of 3 granular ridges, the lowermost, strongest issuing from articulating facet, continuing almost to tip; shallow ovate depression, ridged above, coincident with depression below proximal cusp on fixed finger; both depressions found on inner faces as well, all with perforated floor.

Discussion. — Fraaye & Collins (1987) originally referred this claw type to the otherwise exclusively North American, claw-based genus *Prehepatus* Rathbun, 1935 (p. 47; type species, by original designation, *P. cretaceus* Rathbun, 1935), as the first and only European representative. Rathbun (1935: 47) interpreted *P. cretaceus* as a calappid, differing from others, ‘in [...] the palmar portion bent horizontally to form an upper surface’. In the absence of carapaces preserving such claws, it is difficult to assign them correctly, but Schweitzer et al. (2007b: 32) discussed this matter in detail, and favoured placement within the Hepatidae Stimpson, 1871, at least for the time being. To date, six species have been assigned to *Prehepatus*, all from North and Central America, as follows:

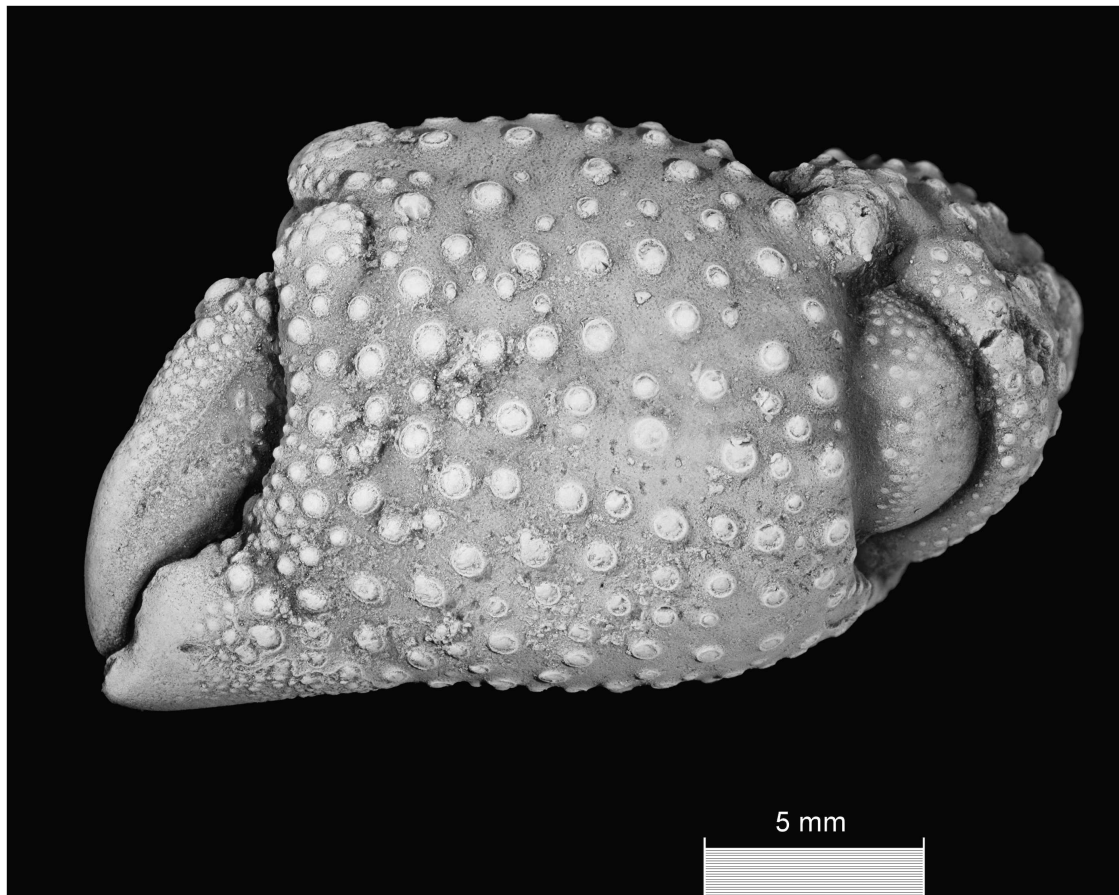


Fig. 3. *Graptocarcinus texanus* (Roemer, 1887), Maastrichtian, Puerto de Urbasa (Navarra, Spain), MGSB 28.148b.

1. *Prehepatus cretaceus* Rathbun, 1935 (p. 47, pl. 11 figs. 29, 30), from the Duck Creek Limestone (upper Albian) of Grayson County, Texas (holotype UT 211). Rathbun (1935: 47) opined that, 'The dactylus, "*Pseudomicippe*" *granulosa* Pelseneer may belong to the same genus as the species above described' [= *P. cretaceus*]. We disagree, and rather consider *Pseudomicippe granulosa* to be conspecific with *Paranecrocarcinus quadriscissus* (see below, and figs. 2D-H, 3).
2. *Prehepatus pawpawensis* Rathbun, 1935 (p. 48, pl. 11 figs. 26-28), from the Pawpaw Shale (upper Albian; see Kennedy, 2004) of Tarrant County, Texas (holotype is an unregistered specimen in UT collections).
3. *Prehepatus dilksi* Roberts, 1962 (p. 183, pl. 89 fig. 2), from the Merchantville Formation (latest Santonian to mid-Campanian; see Miller et al., 2004) of Burlington County, New Jersey (holotype ANSP 19728).
4. *Prehepatus hodgesi* Bishop, 1983 (p. 50, pl. 3 figs. 1-19; text-figs. 8F, 11, 12), from the Glen Rose Limestone (lower Albian) of Blanco and Kendall counties, Texas (holotype SDSNH 23655).

5. *Prehepatus harrisi* Bishop, 1985 (p. 1029, figs. 1.1-1.5, 2.1-2.9), from the Coon Creek and Prairie Bluff formations (lower-middle Maastrichtian) of Union County, Mississippi (holotype GSCM 1686). This species has subsequently been recorded from the lower Maastrichtian of northeast Mexico by Vega et al. (1995: 247, figs. 3.1, 3.2).
6. *Prehepatus mexicanus* Schweitzer et al., 2007b (p. 33, figs. 2.10, 2.11), the sole Cenozoic member, from the Eocene of Baja California Sur (northwest Mexico) (holotype MNH-UABCS/Ba10-8).

Bishop (1985: 1031; see also Bishop, 1986) recognized two lineages in Mid- and Late Cretaceous *Prehepatus*, one containing species with triangular claws, such as *P. hodgesi*, *P. harrisi* and *P. pawpawensis*, confined to the Gulf Coastal Plain of the United States, the other with more quadrate claws (i.e., *P. cretaceus*, *P. dilksi*) occurring in the Gulf Coastal and northern Atlantic Coastal plains.

All these forms differ considerably from the claw type represented by *R. ornativissimus* in that they are more triangular, of smaller size, with differently shaped fixed and movable fingers (notably lacking elongate-oval pits or depressions on opposing faces, and a tendency to become more or less spatulate), and with an oblique, rather than (near-)straight manus/carpal articulation. For that reason, hepaticids can be ruled out for *Roemerus*.

Records of carapaces preserving appendages and/or venters are extremely sparse (compare Schweitzer et al., 2003; Larghi, 2004) amongst necrocarcinids. However, of two species of the Paranecrocarcininae Fraaije, Van Bakel, Jagt & Artal, 2008 from the Maastrichtian type area, associations of carapaces and chelae are so consistent that the latter may safely be taken to belong here (fig. 2; see also Fraaije, 2002). Of the third species, originally referred to *Necrocarcinus* (see Fraaije, 2002), but now placed in the Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 (see Guinot, Vega & Van Bakel, 2008: 27), only carapaces are so far known. These taxa are (see fig. 2A-I):

1. *Paranecrocarcinus quadriscissus* (Noetling, 1881) (p. 368, pl. 20 fig. 4a, b; holotype MNB A.239), inferred to be from the Meerssen Member (Maastricht Formation) of Valkenburg aan de Geul, southern Limburg (the Netherlands).
2. *Paranecrocarcinus vanbirgeleni* Fraaije, 2002 (p. 916, figs. 1.3, 3.1, 3.2; holotype MAB k. 2278), from the lower Meerssen Member (Maastricht Formation) of the ENCI-HeidelbergCementGroup quarry (Maastricht).

3. *Orithopsis angelicus* (Fraaije, 2002) (p. 914, figs. 1.1, 2, as *Necrocarcinus angelicus*; holotype MAB k. 1008), from the middle Meerssen Member (Maastricht Formation) of the same quarry.

Although still not found connected with carapaces, claws of the first two species differ considerably from *R. ornatissimus* (compare Collins et al., 1995, fig. 11A, B; Fraaije, 2002, figs. 3.8, 3.9). The ‘species’ *Pseudomicippe granulosa* (Bosquet MS) Pelseneer, 1886 (p. 170, fig. 6; holotype IRScNB 10670), as based on a single left movable finger from the upper Maastrichtian of the St Pietersberg area, south of Maastricht (compare fig. 2E-G), is here considered conspecific with *Paranecrocarcinus quadriscissus*, and thus unrelated to the majine genus *Pseudomicippe* Heller, 1861 (see Ng et al., 2008).

With such differences in claw morphology, paranecrocarcinines can also be ruled out, as can necrocarcinines, for that matter, demonstrated by a comparison with a late Albian specimen of *Necrocarcinus labeschii* which preserves a near-complete left claw (fig. 4A-D). Outline, ornament, merus/carpal articulation and size and shape of fixed and movable fingers are different to *R. ornatissimus*, and can easily be distinguished from claws of *Cenomanocarcinus* as well (see Breton & Collins, 2007, fig. 4).

PREVIOUS RECORDS OF CRETACEOUS ‘NECROCARCINID’ CHELAE

Several examples of comparable ‘necrocarcinid’ claws in the literature refer to dynomenids. Bell (1863: 21, pl. 5 fig. 4) illustrated a claw from the lower Cenomanian Greensand of Wiltshire (southwest England), which he assigned to a new species, *Necrocarcinus woodwardii*, noting the claw of ‘*N. inflatus*’ (= *Cenomanocarcinus inflatus*) had ‘the same general aspect’. That this is in error is clearly seen when comparing Bell’s illustration with that in Breton & Collins (2007, fig. 4). It is instead much closer to dynomenid claws here referred to the ‘form genus’ *Roemerus*. Moreover, on the basis of carapaces, the dynomenids *Palaeodromites incertus* and *Trachynotocarcinus sulcatus* have been recorded from these levels (see Wright & Collins, 1972: 9, 13).

Schlüter (in Von der Marck & Schlüter, 1868: 298) referred with a question mark to an isolated claw from the lower Turonian of the Bochum area (northern Germany) as ‘*Necrocarcinus woodwardi* Bell?’, noting that it resembled the claw illustrated by Bell (1863, pl. 5 fig. 4). Schlüter (1879: 609, pl. 17 fig. 3) referred to this specimen as *Necrocarcinus* sp. n. This is also best referred to *Roemerus* sp. until such time that it can be positively assigned to a dynomenid carapace.

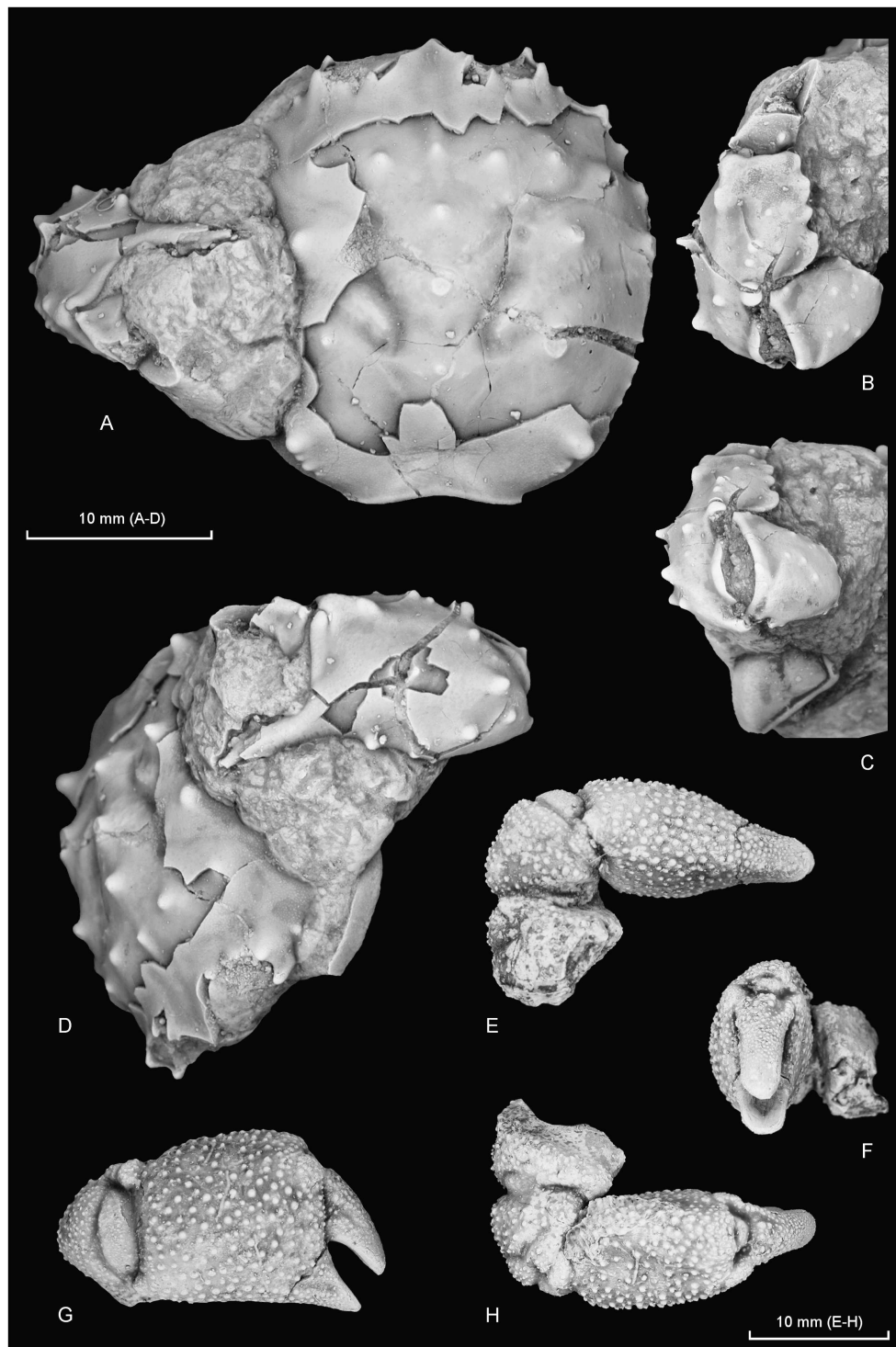


Fig. 4. Mid-Cretaceous necrocarcinid and dynomenid; A-D, *Necrocarcinus labeschii* (J. A. [Eudes-] Deslongchamps, 1835), upper Albian, Escalles, northern France (MAB k. 2549 [cast]), carapace with associated left claw, of a type similar to that of *Cenomanocarcinus inflatus* Van Straelen, 1936 (see Breton & Collins, 2007, fig. 4); E-H, *Graptocarcinus* sp., lower Cenomanian, Escalles, northern France (MAB k. 2546); note the lack of pits on opposing faces in the fixed and movable fingers.

Fritsch (in Fritsch & Kafka, 1887) assigned two ‘species’, both based on isolated claws, to *Necrocarcinus* Bell, 1863. *Necrocarcinus avicularis* Fritsch (in Fritsch & Kafka, 1887: 47, pl. 10 figs. 2a-f, 10-12), of Cenomanian age from the localities Zbyslav and Kamajk (Bohemia, Czech Republic), was distinguished from taxa known at the time on account of a more roundish shape and finer ornament. *Necrocarcinus perlatus* Fritsch (in Fritsch & Kafka, 1887: 47, pl. 10 fig. 14), from the younger (?Turonian) Priesener Schichten at Černodol, near Laun (Bohemia), was based on a claw with very short fingers and relatively large tubercles. For the time being, the first of these ‘species’ would also be best assigned to the ‘form genus’ *Roemerus*, especially so since it co-occurred with a dynomenid carapace, (*Cancer?*) *modestus* Fritsch (in Fritsch & Kafka, 1887: 49, pl. 10 fig. 12), which Wright & Collins (1972: 54) questionably synonymized with *Graptocarcinus texanus* Roemer, 1887. The status of the second ‘species’ is not certain, and without having seen the original specimen, we cannot discuss this matter further (see below).

Mertin (1941: 156, 240, pl. 8 fig. 15) recorded a single claw as *Necrocarcinus* sp. from the basal ‘Untersenon’, possibly lower Santonian of Heudeber, east of Halberstadt (eastern Germany), which could also represent a dynomenid claw, but the photograph leaves much to be desired. The fine granular ornament appears distinctive, but without having seen the original nothing more can be said.

Förster (1968: 183-185, pl. 13 figs. 5, 6) discussed and illustrated a number of what he referred to as ‘Necrocarcininae-Scheren’. He noted that finds of still-connected claws and carapaces of necrocarcinids were extremely rare, and that he only knew of such instances for *N. labeschii*, *N. woodwardii* and *Cenomanocarcinus vanstraeleni*. The last-named species is now referred to its own family, Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008. Despite this drawback, previous authors named several species on the basis of isolated claws, mostly with reference to *N. labeschii* from the ‘Gault’ (Albian) of England, which revealed such a typical claw shape. Förster (1968) rightly pointed out that assignment to genera was problematic, especially when the very different claws of *C. vanstraeleni* were considered. In addition to taxa referred to above, Förster (1968) listed *N. woodwardii* [sensu Schlüter, 1879: 608, pl. 17 fig. 2], from the Cenomanian of northern Germany, *Necrocarcinus* sp. [sensu Schlüter, 1879: 609, pl. 17 fig. 3], from the lower Turonian of northern Germany, *N. franconicus* Lehner, 1937 (p. 214, pl. 19 figs 21, 22), from the lower Turonian of southern Germany, *N. cf. senoniensis* [sensu Mertin, 1941: 239, pl. 8 fig. 14], from the upper Campanian of northern

Germany. These records, as well as earlier ones from the Lower Cretaceous of France and Switzerland, as noted by Förster (1968) (e.g., *Gebia controversa* de Tribolet, 1874: 657, pl. 15 figs. 1-5, Valanginian, western Switzerland; *Gebia muensteri* Robineau-Desvoidy, 1849: 137, pl. 5 fig. 17, Hauterivian, central France) should be revised in order to determine if they can be linked to co-occurring dynomenid carapaces. Förster (1968: 185) also suggested that *N. perlatus* was not a necrocarcinid claw, but that in shape and ornament there was a close match with *Caloxanthus formosus* (A. Milne-Edwards, 1864; Cenomanian, France). Of especial note is Förster's (1968: 185) observation that, '[. . .] denn eine Reihe kretazischer Dynomeniden dürfte ähnlich gebaute Scheren besessen haben. Da bisher jedoch nur bei *Necrocarcinus* Funde im Zusammenhang mit dem Carapax vorliegen, sollen diese charakteristischen Scheren vorerst weiterhin als *Necrocarcinus*-Scheren geführt werden'. This translates as, '[. . .] because a number of Cretaceous dynomenids are likely to have had similarly built chelae. Given that so far only finds in association with carapaces are known for *Necrocarcinus*, such characteristic chelae could still be referred to as *Necrocarcinus* chelae in the future']. We agree with Förster's observation.

Gründel (1974: 90, pl. 4 figs. 1, 2) recorded a claw assigned to *Necrocarcinus woodwardi* Bell, 1862 [sic] from the *plenius* Zone (uppermost Cenomanian; 'Klippenfazies' near Plauen, eastern Germany) and added the dynomenid, *Palaeodromites incertus* (Bell, 1863) (see Gründel, 1974, pl. 3 fig. 3), from the same stratigraphic level and area.

Collins & Dieni (1996: 70, figs. 2/1, 2, 4) recorded a new dynomenid species, *Graptocarcinus bellonii*, from Cenomanian rudist limestones in north-east Italy. An associated claw, interpreted by these authors as 'Pagurinae genus indet'. (Collins & Dieni, 1996, figs. 2/3, 5, 6) is remarkably close to *Roemerus* and other dynomenid claws illustrated in the literature. It is here assumed that these forms are identical to each other.

Necrocarcinus ornatissimus and *P. weneri*, as well as material described in the literature and on recently acquired, mostly unpublished specimens, are also associated to dynomenids, and to *Palaeodromites* and *Graptocarcinus* in particular (see figs. 1H-L, 3; tables I, II). The use of the 'form genus' *Roemerus* is proposed here for such claws, so long as finds of carapaces preserving claws are lacking for *Palaeodromites* in particular.

McLay (1999) briefly commented on fossil dynomenid genera, while Guinot (2008: 20, 21) was of the opinion that the genus *Diaulax* Bell, 1863 was a dynomenid, and that the family Diaulacidae Wright & Collins, 1972 (see also

TABLE II

Cretaceous dynomenid crabs (from Wright & Collins, 1972; Förster, 1975; Via Boada, 1981; Collins et al., 1995; Collins & Dieni, 1996; Breton & Collins, 2007; Jagt et al., 2007; Guinot, 2008; Jagt et al., work in progress); *originally recorded by Collins et al. (1995) from the Maastrichtian type area (Maastricht, Netherlands); subsequent studies have shown that this material actually came from the upper Maastrichtian (Saint-Symphorien Calcarene Formation) of the Mons Basin, southern Belgium

Genus and species	Stratigraphic and geographic range
<i>Diaulax feliceps</i> Wright & Collins, 1972	middle-upper Albian; England
<i>Diaulax millerae</i> Bishop, 1992	lower Campanian; Delaware
<i>Diaulax oweni</i> (Bell, 1850) (= <i>carteriana</i> Bell, 1863)	lower Albian-middle Cenomanian; England
<i>Diaulax roddai</i> Bishop, 1983	lower Albian; Texas
<i>Diaulax yokoi</i> Collins, Kanie & Karasawa, 1993	Santonian; Japan
<i>Dromiopsis mosae</i> Collins, Fraaye & Jagt, 1995*	upper Maastrichtian; Belgium
<i>Dromiopsis praelaevious</i> Collins, Fraaye & Jagt, 1995	upper Maastrichtian; Netherlands
<i>Dromiopsis</i> cf. <i>rugosa</i> (Von Schlotheim, 1820)	upper Campanian; Germany
<i>Dromiopsis</i> sp.	upper Campanian; Belgium
<i>Graptocarcinus bellonii</i> Collins & Dieni, 1996	Cenomanian; Italy
<i>Graptocarcinus maastrichtensis</i> Fraaye, 1996b	upper Maastrichtian; Netherlands
<i>Graptocarcinus muiri</i> Stenzel, 1944	Aptian; Mexico
<i>Graptocarcinus texanus</i> Roemer, 1887	?Albian, lower-middle Cenomanian; Texas, England, Spain, Czech Republic, Mexico
<i>Palaeodromites autissiodorensis</i> (Van Straelen, 1936)	Hauterivian-Aptian; France
<i>Palaeodromites centrosus</i> (Van Straelen, 1940)	Cenomanian; Spain
<i>Palaeodromites crypticus</i> Jagt, van Bakel & Fraaije, 2007	lower-middle Cenomanian; Belgium
<i>Palaeodromites himerensis</i> (Checchia-Rispoli, 1914)	Cenomanian; Sicily
<i>Palaeodromites incertus</i> (Bell, 1863)	lowermost-upper Cenomanian; England, France, Germany, Austria
<i>Palaeodromites octodentatus</i> A. Milne-Edwards, 1865	Hauterivian; France
<i>Palaeodromites sinuososulcatus</i> Wright & Collins, 1972	lower Albian; England
<i>Palaeodromites transiens</i> Wright & Collins, 1972	upper Albian-lower Cenomanian; England, Spain
<i>Stephanometopon granulatum</i> Bosquet, 1854	upper Maastrichtian; Netherlands, Belgium
<i>Trachynotocarcinus naglei</i> (Bishop, 1983)	lower Albian; Texas
<i>Trachynotocarcinus sulcatus</i> (Bell, 1863)	lower-upper Cenomanian; England, France

Collins et al., 1993) was perhaps best treated as a subfamily, close to, or possibly synonymous with, the Metadynomeninae. *Diaulax* currently comprises five Mid- to Late Cretaceous species, two from England, one from Japan and two from the United States. Finds of carapace-associated chelae are known in four of these (table II), showing them to be of a general dynomenid aspect, but to differ quite considerably from those here assigned to *Roemerus*. *Diaulax carteriana* Bell, 1863, the type species by monotypy, is a junior subjective synonym of *Platypodia oweni* Bell, 1850, as discussed by Wright & Collins (1972: 56). It is known from the lower Albian to middle Cenomanian. Wright & Collins, 1972 (p. 58, pl. 10 fig. 1a, b) described the chelae of *D. oweni* ‘[. . .] equal and a little shorter than the carapace. The hand has a tumid outer surface and a flat palm, slightly excavate at the rear end. The fingers are about a third of the length of the hand; the fixed finger is reflexed; a groove lined with pits for hairs runs along the upper margin of the movable finger. The carpus is half as long as the hand, the outer surface very convex with a shallow longitudinal depression. The convex outer surfaces of hand and wrist have, in large Cenomanian specimens, many small distinct well-spaced tubercles tending to a linear arrangement but they are absent or only weakly developed in Cambridge Greensand specimens. The merus is large, with slightly convex outer and flat inner surface; there are a few large granules on the posterior margin, but the upper surface has minute close flat granules like those on the cephalothorax’. The chelae of *D. feliceps* (Wright & Collins, 1972: 59, pl. 10 figs. 2-6), from the middle and upper Albian of Kent, England, were characterized as, ‘The surface ornament is as in *Diaulax oweni* and the same fine ornament covers the inflated untuberculate chelae’. Collins et al. (1993: 297) added that, ‘The median furrow on the carpus is common to both *D. oweni* and *D. feliceps*, but only *D. feliceps* has a groove on the propodus, that of *D. oweni* being ornamented by longitudinal rows of granules continued onto the carpus’.

Claws of *D. millerae* (see Bishop, 1992: 559, fig. 1A), from the lower Campanian of the United States Atlantic Coastal Plain, were described as, ‘[. . .] approximately equal; merus stout; carpus pentagonal, moderately sized; propodus short and high, strongly granulate (at least on inner face); dactylus long, narrow, and strongly curved downward [. . .]’. Those of *D. yokoi* Collins, Kanie & Karasawa, 1993 from the Santonian of Japan (see also Karasawa et al., 2006), were typified as follows (Collins et al., 1993: 297), ‘The propodus of the cheliped is trapezoidal in lateral view, with the basal margin about one-third longer than the dorsal and interdigital margins. There is a wide convexity in the basal margin at the base of the stout, moderately deflexed, slightly

inturned fixed finger. The interdigital margin is nearly straight and bounded by a shallow groove and a wide, deep groove bounds the carpal articulation which is rather more oblique in the left chela, the right and left propodus have the finely granulated lateral surface smoothly rounded and have an incipient furrow extending parallel to the dorsal margin, but it is closer to the midline in the right chela. The slender dactylus is about as long as the fixed finger. The carpus is a little shorter than the propodus, rounded triangular in section and the strongly convex lateral surface is smooth with a median furrow'. In short, claws of *Diaulax* differ from those here referred to *Roemerus* in details or ornament and in structure of fixed and movable fingers, which both lack ovate depressions.

Stratigraphic range. — *Roemerus ornatissimus* appears to be confined to the upper Nekum and Meerssen members (Maastricht Formation) in southern Limburg and contiguous Belgian territory, and the range of the dynomenid *Stephanometopon granulatatum* Bosquet, 1854 (p. 137, pl. 10 fig. 12a, b, non 12c) is much the same. The holotype carapace fragment (IRScNB 10652), since damaged, was illustrated by Bosquet (1854) together with a claw. This claw (Bosquet, 1854, pl. 10 fig. 12c) undoubtedly belongs to a different form, perhaps a species of *Dromiopsis* Reuss, 1859, which is known from the same levels (*D. praelaevious* Collins, Fraaye & Jagt, 1995) (see table II).

MORPHOLOGY OF CHELAE

The claws of the 'form genus' *Roemerus* have a distinctive morphology, which can be linked to their mode of feeding. The genera *Graptocarcinus* and *Palaeodromites* are considered dynomenids on the basis of carapace outline and areolation, groove system as well as construction of lateral margins and orbitofrontal area (see also McLay, 1999: 434). Their remains are found in reefal or near-reefal deposits, like extant descendants. Dynomenids are interpreted as one of the most ancient families, with an impressive record from the Upper Jurassic onwards (Guinot, 2008: 3). The wide range of cheliped morphology undoubtedly reflects different feeding habits (see McLay, 1999). Dynomenid chelipeds generally differ from those of dromiids, as a result of their different ecology. Dromiids camouflage their bodies, hence their common name 'sponge crabs' (see, e.g., McLay, 1993; Guinot et al., 1995; Guinot & Tavares, 2003; Van Bakel et al., 2009). Normally dromiids are larger than dynomenids; the latter often hide and live in coral crevices. In many dynomenids, the propodus/carpus and carpus/merus articulations show a

bulge. There is no opening between these articles when bent. This modification is likely to serve as protection for the arm when moving through coral colonies or during feeding.

The cheliped fingers of dynomenids show particular setal modifications. Dynomenids are filter feeders and their diet apparently consists of food obtained by sieving fine sediment, or perhaps coral mucus (McLay, 1999: 428). They have clumps of stiff setae at the inner and outer margins of both fixed and movable fingers, which collectively close the space between the fingers and form a sieving device. McLay (1999: 449) observed that, ‘... *D. praedator* show that these setae help to sift out food particles which are passed to the third maxillipeds’. This ‘sieving screen’ was observed by McLay (1999: 476, 484, 490) in several extant species (e.g., *Dynomene hispida* (Latreille, in Milbert, 1812), *D. praedator* A. Milne-Edwards, 1879 and *D. filholi* Bouvier, 1894). The modified articulation of the propodus and carpus, and the clumps of setae on both sides of the fingers, can be considered characteristic of the Dynomenidae (see fig. 1A-F, H-L). These distinct characters have not been observed in fossil dromiid or necrocarcinid crabs, but are seen in all ‘species’ here assigned to the ‘form genus’ *Roemerus*.

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