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REVISION OF THE GENUS *TITANOCARCINUS* (DECAPODA: BRACHYURA: XANTHOIDEA) WITH TWO NEW GENERA AND ONE NEW SPECIES

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A B S T R A C T

The brachyuran genus *Titanocarcinus* A. Milne-Edwards, 1864, is rediagnosed and restricted to six species. It is referred to the Tumidocarcinidae Schweitzer, 2005, based upon characters of the sternum, male pleon, and dorsal carapace, along with the closely related *Lobonotus* A. Milne-Edwards, 1864. Several species that had been referred to *Titanocarcinus* are herein referred to other genera, including two new ones, *Nitotacarcinus* and *Lathahypossia*, or to other families in indeterminate genera. One new species is described from the lowermost Eocene of Spain, *Titanocarcinus decor*. *Titanocarcinus* as currently defined ranged from the Cretaceous to Eocene in northern and central Europe. *Lobonotus* is known only from the Eocene of North and Central America.

Introduction

Numerous species have been referred to *Titanocarcinus* A. Milne-Edwards, 1864, since it was originally named to embrace several species from the Cretaceous and Paleogene of Europe. The genus was originally designated as a ''Cancérien'', similar to the ''Galénides'' (A. Milne-Edwards, 1864) and was subsequently referred to the Xanthidae sensu lato (e.g., Glaessner, 1969) or the Pilumnidae Samouelle, 1819, of the Xanthoidea MacLeay, 1838 (Schweitzer et al., 2004). Like many other fossil xanthoid genera, such as *Zanthopsis*, *Xanthilites*, *Lobonotus*, *Glyphithyreus*, and *Palaeograpsus*, each of which has recently been revised (Schweitzer, 2003, 2005; Karasawa and Schweitzer, 2004; Schweitzer and Karasawa, 2004; Schweitzer et al., 2004), the definition of *Titanocarcinus* has become so broad during the nineteenth and twentieth centuries as to be meaningless.

Lőrenthey and Beurlen (1929) and Vía (1969) have previously noted that *Titanocarcinus* embraced a wide variety of forms. Förster (1970: 248) discussed the genus, and following Beurlen (*in* Lőrenthey and Beurlen, 1929) suggested that there were at least two broad subgroups within it, a granular form and a smoother form. He provided a list of included species at that time, questioning the inclusion of several that have since been removed or are removed herein (Förster, 1970: 248). Busulini et al. (1984) also acknowledged the heterogeneity of the genus and noted its similarities with *Lobonotus* A. Milne-Edwards, 1864. Müller (1993: 18) suggested that ''probably all Neogene and most or all Paleogene species'' referred to *Titanocarcinus* should be assigned to other xanthoid genera, with which Feldmann et al. (1998) concurred. In addition, there have been suggestions that *Titanocarcinus* and *Lobonotus* are synonymous (Collins and Morris, 1978; Schweitzer et al., 2002, 2004). Herein, we evaluate all species referred at one time or another to *Titanocarcinus*, reassess their generic position, and as it happens, concur with Müller's (1993) conclusion.

Evaluation of species referred to *Titanocarcinus* is hampered by the fact that the type material of the type species and some other taxa named by A. Milne-Edwards in 1864 cannot be located. Unfortunately, A. Milne-Edwards (1864) did not list the repository for his specimens of *Titanocarcinus serratifrons*, the type species, or for other species described in the same paper. The type material of *Lobonotus sculptus*, also described by A. Milne-Edwards in 1864, was noted as being deposited in the 'museum of the Geological Society of London' (p. 40), and in fact, the holotype (NHM In. 28287) is housed in The Natural History Museum (London). Neither the types of the type species nor other species of *Titanocarcinus* are listed in the register of type and illustrated specimens of fossil Crustacea deposited in The Natural History Museum (London) (Morris, 1980). Similarly, the types for *Titanocarcinus* spp. have not been located in the Muséum National d'Histoire Naturelle in Paris (A. Rage; A. Garassino, personal communication) or in any other museum in Belgium or The Netherlands. Thus, the original description and plates of the type species, *T. serratifrons*, must be used to construct a generic definition for *Titanocarcinus*, as the types of *T. serratifrons* appear to be lost.

Institutional abbreviations.—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; E,

Magyar Állami Földtani Intézet (Hungarian Geological Survey), Lőrenthey Collection, Budapest, Hungary; IRSNB MI, Institut Royal des Sciences Naturelles de Belgique, Mesozoic Invertebrates (Koninklijk Belgisch Instituut voor Natuurwetenschappen), Brussels, Belgium; MAB, Oertijdmuseum De Groene Poort, Boxtel, The Netherlands; MGSB, Museo Geológico del Seminario de Barcelona, Spain; MGUH, Geological Museum, Copenhagen, Denmark; NHM In., The Natural History Museum, London, England; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

SYSTEMATICS

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Xanthoidea MacLeay, 1838
Family Tumidocarcinidae Schweitzer, 2005

Included Genera.—*Baricarcinus* Casadío et al., 2004; *Lobonotus* A. Milne-Edwards, 1864; *Nitotacarcinus* new genus; *Paratumidocarcinus* Martins-Neto, 2001; *Pulalius* Schweitzer et al., 2000; *Titanocarcinus* A. Milne-Edwards, 1864; *Tumidocarcinus* Glaessner, 1960; *Xanthilites* Bell, 1858.

Diagnosis.—See Schweitzer (2005).

Remarks.—Recognition of the new species of *Titanocarcinus*, *T. decor*, described below, makes it possible to refer the genus to the Tumidocarcinidae. The well-preserved sterna and pleons on specimens of that species possess diagnostic features of the family including fused sternites 1 and 2 with no evidence of a suture; a deep suture between sternites 2 and 3; a deep, medially interrrupted suture between sternites 3 and 4 with lateral notches; a deep groove extending anteriorly from the sterno-pleonal cavity, merging with the sutures between sternites 3 and 4 to form a Y-shaped groove; sternite 4 with deep longitudinal grooves parallel to lateral margins; all male pleonal somites free; and the male pleon filling the entire space between the coxae of the fifth pereiopods.

The genus also conforms in most regards to the diagnosis for the family (Schweitzer, 2005), in possessing a carapace about 80 percent as long as wide and widest at the penultimate anterolateral spine about half the distance posteriorly on the carapace; a longitudinally vaulted carapace, especially in the anterior one-third; a four-lobed front; rimmed orbits; anterolateral margins with four spines; and arcuate epibranchial regions. The only difference from the family diagnosis is that *Titanocarcinus* possesses two orbital fissures and has a fronto-orbital width of two-thirds to three-quarters the maximum carapace width, whereas all other species within the family have either no or one fissure and a fronto-orbital width of about half the maximum carapace width (Schweitzer, 2005). Characters of the sternum and pleon have been judged by neontologists to be more conservative than those of the dorsal carapace, which can vary widely within one family (see for example, the Pilumnidae and the Xanthidae MacLeay, 1838, sensu stricto). The judgement that sternal and pleon characters are more conservative undoubtedly is based upon the fact that these areas of the crab's morphology are linked to reproductive structures, which are also judged to be conservative evolutionarily (Ng, 1987). For example, the gonopores are on the sternum, and the gonopods are on the pleon. Thus, based upon the sternal characters, we have judged that the best placement for *Titanocarcinus* at this time is the Tumidocarcinidae, even though the two dorsal carapace characters (orbital fissures and fronto-orbital width ratio) do differ from other members of the family.

The only other family to which *Titanocarcinus* might be referred is the Pilumnidae, in which it has been placed previously (Karasawa and Schweitzer, 2004). Members of that family are quite variable in their dorsal carapace ornamentation and aspects of the sternum and male pleon. The carapace length achieves 90 percent or more the maximum carapace width in the Calmaniinae Števčić, 1991; Eumedoninae Dana, 1853; and Halimedinae Alcock, 1898, excluding *Titanocarcinus* from those subfamilies. Many pilumnid subfamilies can accommodate the general carapace shape, orbital ornamentation (two fissures, fronto-orbital width two-thirds to three-quarters maximum carapace width), and anterolateral ornamentation of *Titanocarcinus* (Pilumninae Samouelle, 1819; Galeninae A. Milne-Edwards, 1862; Rhizopinae Stimpson, 1858), but notably, in pilumnids, the male pleon covers most of sternite 4, reaching to the anterior edge of the coxa of the first pereiopod (Davie, 2002). In *Titanocarcinus decor* new species, the only taxon in which this character is visible, the male pleon reaches only to the posterior edge of the coxa of the first pereiopod as seen in the Tumidocarcinidae. Again, note that features of the sternum and pleon have been judged to be more conservative than dorsal carapace characters; thus, *Titanocarcinus* seems to be best accommodated in the Tumidocarcinidae.

Lobonotus also has been referred recently to the Pilumnidae (Schweitzer et al., 2004). The placement of *Lobonotus* is somewhat problematic. The holotype of *L. mexicanus* Rathbun, 1930 (USNM 371096) displays a male pleon that appears to cover the entire space between the coxae of the fifth pereiopods and the eighth somite does not appear to be visible (Rathbun, 1930, pl. 1.3), although slight displacement of the somites and small amounts of sediment on the specimen itself do not permit this observation to be made with absolute certainty. The dorsal carapace conforms to the diagnosis for the Tumidocarcinidae in most regards except that, as in *Titanocarcinus*, the orbits bear two fissures and the fronto-orbital width occupies two-thirds to three-quarters the maximum carapace width. Members of the Pilumnidae do not exhibit the deep Y-shaped groove pattern on the sternum nor the deep longitudinal groove on sternite 4 typical of the Tumidocarcinidae and seen in both *Lobonotus* and *Titanocarcinus*. Thus, we refer *Lobonotus* to the Tumidocarcinidae until better sternal material can be collected to confirm observations made based upon the holotype of *L. mexicanus*.

Lobonotus A. Milne-Edwards, 1864

Lobonotus A. Milne-Edwards, 1863, pl. 10, fig. 4, 1864, p. 39. Rathbun, 1930, p. 2, pl. 1; Stenzel, 1935, p. 382-385, fig. 1, pl. 14, figs. 1-4; Glaessner, 1969, p. R518, fig. 326, 12a, 12b; Schweitzer et al., 2002, p. 19, fig. 21; Karasawa and Schweitzer, 2004, p. 150; Schweitzer et al., 2004, p. 105.

Archaeopilumnus Rathbun, 1919, p. 177, pl. 7, figs. 10-13.

Titanocarcinus A. Milne-Edwards, 1864 (part). Blow and Manning, 1996, p. 24, pl. 5, fig. 5.

Table 1. All species at one time referred to *Titanocarcinus* and their current status.

Species	Current status	Comments
T. serratifrons A. Milne-Edwards, 1864 (type)	*Titanocarcinus*	Belongs by definition as the type species; types have not been located.
Dromiopsis briarti Forir, 1887	*Titanocarcinus*	Type is in Brussels
Titanocarcinus decor new species	*Titanocarcinus*	Types are deposited in MGSB
Panopeus faxeensis von Fischer-Benzon, 1866	*Titanocarcinus*	Location of types unknown
T. raulinianus A. Milne-Edwards, 1864	*Titanocarcinus*	Types have not been located
Panopeus subellipticus Segerberg, 1900	*Titanocarcinus*	Type is in Geological Museum, Copenhagen
T. aculeatus Busulini et al., 1984	*Lathahypossia* new genus of Eriphiidae sensu lato	Holotype is located in the Museo di Storia Naturale di Venezia
Glyphithyreus bituberculatus Collins and Jakobsen, 2004 [imprint 2003]	*Nitotacarcinus* new genus of Tumidocarcinidae	Discussion herein
T. elegans Lőrenthey and Beurlen, 1929	*Montezumella* Rathbun, 1930	
T. pulchellus A. Milne-Edwards, 1864	*Haydnella* Müller, 1984, in Xanthidae sensu stricto	Müller (1984) reports type as lost; we similarly have not found it
T. purdyi Blow and Manning, 1996	*Lobonotus*	Types are in the United States National Museum of Natural History, Washington, D.C.
T. subovalis Ristori, 1896	*Chlinocephalus* Ristori, 1886, within the Goneplacidae, Euryplacinae	Pliocene of Italy; holotype in Invertebrate Palaeontological Collections, Museum of Geology and Palaeontology, University of Florence, Italy (Delle Cave, 1981)
T. vulgaris Glaessner, 1928	Holotype to *Pilodius* Dana, 1851, within the Xanthidea sensu stricto; paratypes and other material to *Haydnella steiningeri* Müller, 1984 and *Xantho moldavicus* (Yanakevich, 1977)	See Müller, 1984
T. kochi Lőrenthey, 1898	Pilumnidae	Upper Eocene of Hungary; types are deposited in Magyar Állami Földtani Intézet (Hungarian Geological Survey), Lőrenthey Collection, Budapest
T. reisi Böhm, 1891	Hepatidae; types must be examined for generic level placement. There are two different forms illustrated and described in the original work. Both are probably referable to the Hepatidae	Types are deposited in the Bayerische Staatssammlung für Paläontologie und historische Geologie, München
Xantho edwardsi Sismonda, 1846	Xanthoidea sensu lato	Referred to *Titanocarcinus* by A. Milne-Edwards (1864); type deposited in Natural History Museum in Turin, Italy
T. euglyphos Bittner, 1875	Xanthoidea sensu lato	See Feldmann et al. (1998) for additional description and illustrations
T. sismondae A. Milne-Edwards, 1864	Xanthoidea sensu lato	Types possibly in Natural History Museum in Turin, Italy
T. sculptus Ristori, 1891	Atelecyclidae, Cheiragonidae, or Pirimelidae?	Pliocene of Italy; types are apparently in Museo dei Fisiocritici, Siena
Cancer verrucosus Schafhäutl, 1851	Palaeoxanthopsidae	More complete material must be collected; location of types not known
T. mamillatus Secretan, 1964	Incertae sedis	More complete material must be collected; types in Muséum National d'Histoire Naturelle, Paris
T. meridionalis Secretan, 1961	Incertae sedis	Upper Cretaceous of Morocco; repository of types and specimen numbers not given
T. polonicus Fraaye, 1994	Incertae sedis	The holotype is deposited in Oertijdmuseum De Groene Poort, Boxtel, The Netherlands
T. zoellneri Bachmayer and Mundlos, 1968	Incertae sedis	Types are in Heimatmuseum Helmstedt

Glyphithyreus Reuss, 1859 (part). Feldmann et al., 1998, p. 13, figs. 17, 18.

Eohalimede Blow and Manning, 1996 (part). Blow and Manning, 1997, p. 177, fig. 2; Blow and Manning, 1998, p. 409.

Plagiolophus Bell, 1858 (part). Rathbun, 1935, p. 94, pl. 21, fig. 23.

Type Species.—*Lobonotus sculptus* A. Milne-Edwards, 1864, by original designation (= *Archaeopilumnus caelatus* Rathbun, 1919) (Miocene).

Other Species.—*Lobonotus bakeri* (Rathbun, 1935), as *Plagiolophus* (Eocene); *L. brazoensis* Stenzel, 1935 (Eocene); *L. mexicanus* Rathbun, 1930 (Eocene); *L. natchitochensis* Stenzel, 1935 (Eocene); *L. purdyi* (Blow and Manning, 1996), as *Titanocarcinus* (Eocene); *L. sandersi* (Blow and Manning, 1998), as *Eohalimede* (Eocene); *L. sturgeoni* (Feldmann et al., 1998), as *Glyphithyreus* (Eocene).

Diagnosis.—Male pleonal somites free, completely covering space between coxae of fifth pereiopods; sternite 8 not visible in ventral view. For remainder, see Schweitzer et al. (2004).

Occurrence.—Eocene-Miocene of North America and the Caribbean.

Material Examined.—USNM 371096, *Lobonotus mexicanus*, holotype; USNM 371574, *L. bakeri*, holotype.

Remarks.—All species of *Lobonotus* were recently evaluated and the genus restricted to only American forms (Schweitzer et al., 2004). Herein we consider *Lobonotus* and *Titanocarcinus* as separate genera based upon the shorter anterolateral margins in *Lobonotus* and especially the well-developed lateral extensions of the cardiac region in all species of *Lobonotus*. Such extensions do not exist in *Titanocarcinus*. In addition, the position of maximum width occurs well in advance of mid-length in *Lobonotus* (Schweitzer et al., 2004), while in *Titanocarcinus*, it is at mid-length or slightly posterior to it. Thus, there is an overall difference in carapace shape between the two genera, clearly suggesting that they be maintained as separate from one another.

Based upon its possession of a short anterolateral margin, a position of maximum width in advance of mid-length, and lateral extensions of the cardiac region, *Titanocarcinus purdyi* Blow and Manning, 1996, is herein referred to *Lobonotus*. *Lobonotus* ranges from Eocene to Miocene in age, and is known from the Atlantic and Gulf Coastal Plain of North America, the Caribbean, and Baja California Sur. The similarity of *Lobonotus* to *Titanocarcinus* suggests that it may well be derived from the latter.

Titanocarcinus A. Milne-Edwards, 1864

Titanocarcinus A. Milne-Edwards, 1863, pl. 9, fig. 3, pl. 10, fig. 4, 1864, p. 31. Glaessner, 1969, p. R522, fig. 330, 3; Karasawa and Schweitzer, 2004, p. 151, fig. 2.

Panopeus H. Milne Edwards, 1834, p. 403 (part). Von Fischer-Benzon, 1866, p. 29-30, pl. 2, figs. 4-6; Segerberg, 1900, p. 378-380, pl. 9, figs. 9-11, 14.

Leptoides Collins, Fraaye, and Jagt, 1995, p. 203, fig. 12G.

Glyphithyreus Reuss, 1859, p. 4, pl. 2, figs. 1-3 (part). Collins and Jakobsen, 2004 [imprint 2003], p. 74, fig. 6, pl. 5, figs. 1-5.

Type Species.—*Titanocarcinus serratifrons* A. Milne-Edwards, 1864, by page precedence in the original paper.

Other Species.—*Titanocarcinus briarti* (Forir, 1887), as *Dromiopsis* and later as *Leptoides*; *Titanocarcinus decor* new species; *T. faxeensis* (von Fischer-Benzon, 1866), as *Panopeus*; *T. raulinianus* A. Milne-Edwards, 1864; *T. subellipticus* (Segerberg, 1900), as *Panopeus*.

Diagnosis.—Carapace wider than long, maximum carapace length about 80-85 percent maximum carapace width, widest at position of last anterolateral spine, about half the distance posteriorly on carapace; regions well marked by deep grooves; regions granular; moderately vaulted longitudinally.

Frontal margin axially notched, granular, usually with blunt protuberances or spines on either side of notch and at inner orbital angles; frontal width about 30 percent maximum carapace width; orbits semi-circular, with thick rim, two orbital fissures positioned near outer-orbital angle, sometimes with a spine between fissures, fronto-orbital width between two-thirds and three-quarters maximum carapace width; anterolateral margin with four spines excluding outer-orbital spine, second and third spines generally largest, fourth often very reduced, spines well-separated from one another; posterolateral margin convex, as long as or shorter than anterolateral margin; posterior margin thickly rimmed.

Epigastric region well defined, inflated; protogastric regions very inflated, usually with longitudinal groove separating anterior portion into two lobes; anterior projection of mesogastric region smooth, extending to a point level with the epigastric regions; metagastric and urogastric regions not well differentiated, depressed; cardiac region inflated; hepatic regions inflated; intestinal region depressed; branchial regions subdivided into epi-, meso-, and metabranchial regions, epibranchial region particularly well defined, composed of an inner and outer lobe.

Sternum ovate, sternites 1-2 fused, no evidence of suture; sternites 2 and 3 separated by complete, uninterrupted suture; sternites 3 and 4 with suture expressed as deep groove; sternite 4 with grooves parallel to lateral margins which appear to be fused episternites from sternite 3; sternites 3 and 4 with longitudinal, axial groove which is extension of sterno-pleonal cavity, portion of this groove on sternite 4 and grooves separating sternites 3 and 4 forming Y-shaped groove pattern on sternum; sternite 8 not visible in ventral view. Male pleon with all somites free, completely covering space between coxae of fifth pereiopods.

Occurrence.—Cretaceous-Eocene.

Remarks.—Careful examination of the original description of the genus, type species, and other taxa referred to *Titanocarcinus* (A. Milne-Edwards, 1864) suggests that it should be restricted only to six species, listed here. The other species at some time referred to it are herein removed to other genera or families or are regarded as incertae sedis until type material can be examined (Table 1). Because the type material for the type species of *Titanocarcinus* has not yet been located, we have restricted the definition of the genus quite severely, basing it upon the original description and obvious features in the illustrations. There are no known topotypes or neotypes of *T. serratifrons*. Even with a rather restricted definition, the genus embraces several species ranging in age from Cretaceous to Eocene and is known from northern and central Europe, displaying a North Atlantic or Tethyan distribution.

Müller (1984) referred *Titanocarcinus pulchellus* (Fig. 1I) to *Haydnella* Müller, 1984; we concur. He also reported the type of that species as being lost, and we have similarly been unable to locate that specimen, collected from the middle Cenozoic of Maine-et-Loire, France (A. Milne-Edwards, 1864). The holotype of *Titanocarcinus vulgaris* Glaessner, 1928, was referred provisionally by Müller (1984) to *Pilodius* Dana, 1851, within the Xanthidae sensu stricto, based upon dorsal carapace characteristics. Müller (1984) based his new species *Haydnella steiningeri* on Glaessner's (1928) paratypes of *T. vulgaris* and placed other material later referred to *T. vulgaris* within *Xantho moldavicus* (Yanakevich, 1977). We concur.

Several species described from Italy have been referred to *Titanocarcinus*. Ristori's (1896) *Titanocarcinus subovalis* (Fig. 1F) is similar to species of *Chlinocephalus* Ristori, 1886, in possessing a carapace that is about as long as wide and having very closely spaced, small orbits as well as prominent swellings on the branchial regions, a narrow sterno-pleonal cavity that reaches to the anterior of sternite four, and weak transverse ridges on the branchial regions (Ristori, 1896, pl. 12, fig. 3). Thus, it is referred to *Chlinocephalus*,

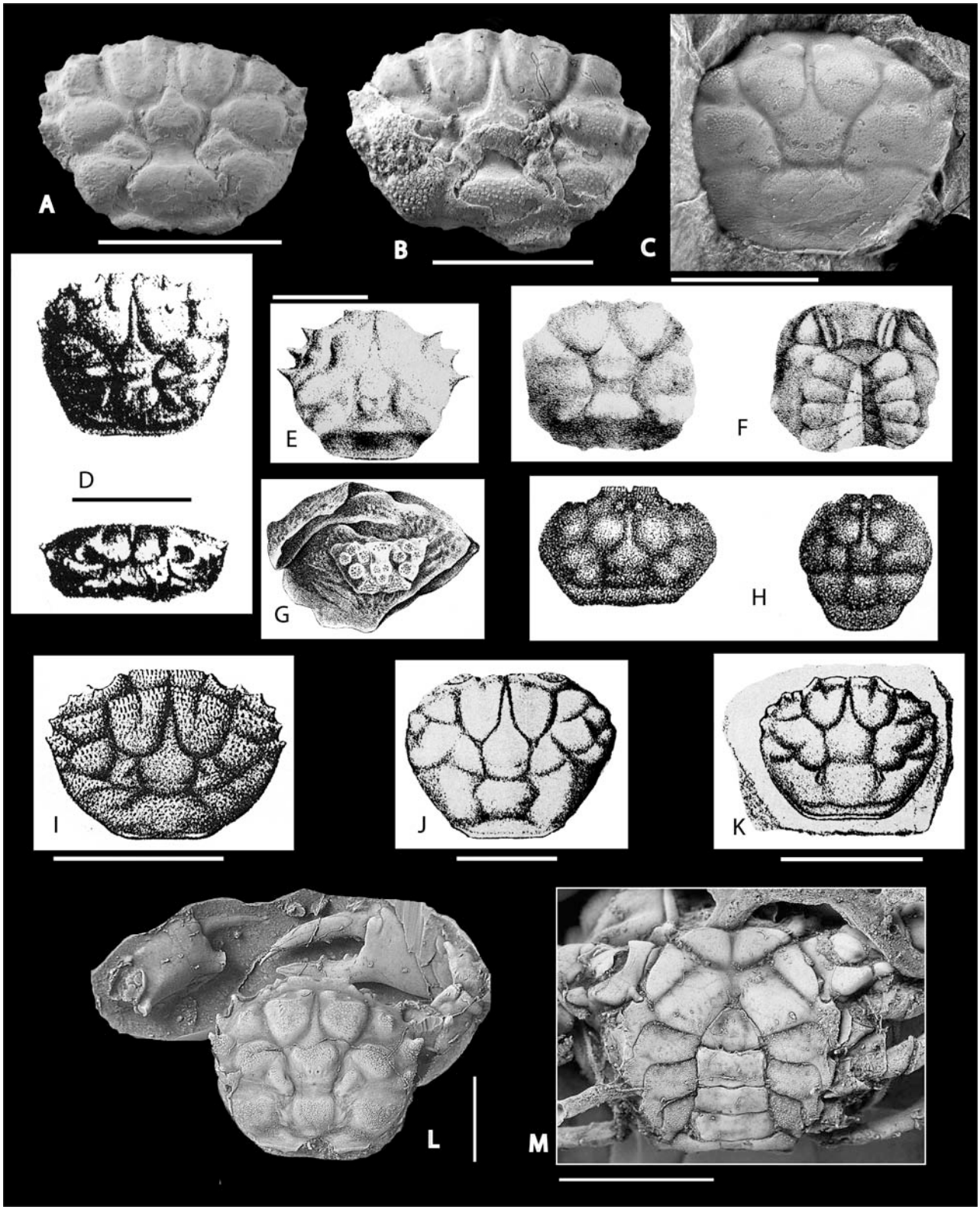

Fig. 1. Selected species referred earlier to *Titanocarcinus* and previously or herein removed. Species illustrated here are generally from old and/or obscure publications not subject to copyright and in general difficult to obtain. A, "*Titanocarcinus*" *euglyphos* Bittner, 1875, CM 36031, from the Eocene Castle Hayne Formation; B, "*Titanocarcinus*" *euglyphos* Bittner, 1875, CM 36033, from the Eocene Castle Hayne Formation; C, "*Titanocarcinus*" *kochi* Lőrenthey, 1898, Exaflex® cast of syntype E289; D, "*Titanocarcinus*" *euglyphos* Bittner, 1875, digital image from original publication, pl. 2, fig. 6; E, "*Titanocarcinus*" *sculptus* Ristori, 1891, digital image from original publication, pl. 1, fig. 2; F, "*Titanocarcinus*" *subovalis* Ristori, 1886, digital image from original publication, pl. 12, figs. 3, 4; G, *Cancer verrucosus* Schafhäutl, 1851, digital image from original publication, pl. 22, fig. 29; H, "*Titanocarcinus*" *reisi* Böhm, 1891, digital image from original publication, pl. 1, figs. 4, 5; I, *Haydnella pulchellus* (A. Milne-Edwards, 1864), digital

within the Euryplacinae Stimpson, 1871, of the Goneplacidae MacLeay, 1838 (Karasawa and Kato, 2003).

Xantho edwardsi (Sismonda, 1846) (Fig. 1K) from the Miocene of Italy was later placed in *Titanocarcinus* by A. Milne-Edwards (1864). A. Milne-Edwards (1864: 35) described this species as being poorly preserved, lacking cuticle so that it is not possible to determine whether it originally possessed more than three anterolateral spines and the nature of those anterolateral spines and dorsal carapace ornamentation, if any. It differs from other species of *Titanocarcinus* in possessing only three anterolateral spines (excluding the outer-orbital spines) and short anterolateral margins. In addition, the position of maximum width is well in advance of mid-length, not typical of other *Titanocarcinus*. Thus, we remove the species from the genus, placing it within the Xanthoidea sensu lato, until better preserved material can be recovered. A. Milne-Edwards (1864) also described *T. sismondae* (Fig. 1J) from Miocene rocks from a hill in Turin, Italy. It lacks one of the key features of *Titanocarcinus*, two orbital fissures, and possesses three anterolateral spines instead of four as in every other species. In addition, the anterolateral margins in *T. sismondae* are much shorter than those of other species of *Titanocarcinus*, and are much shorter than the posterolateral margins, not seen in species of *Titanocarcinus*. For now we refer this species to the Xanthoidea sensu lato until type material can be examined, probably deposited in the Natural History Museum in Turin, based upon the fact that the specimens of *T. edwardsi* (Sismonda, 1846), described by A. Milne-Edwards in the same paper, are deposited there. However, A. Milne-Edwards (1864) did not actually specify the location of the types of *T. sismondae*.

Another species described from the Pliocene of Italy, *Titanocarcinus sculptus* Ristori, 1891 (Fig. 1E) is clearly not referable to *Titanocarcinus*, as suggested by Garassino et al. (2004). That species is about as long as wide (L/W = 0.93) and has three long, sharp anterolateral spines, a morphology not seen in any species of *Titanocarcinus*. In addition, the overall conformation of carapace regions and the angular, hexagonal carapace shape are unlike any species of *Titanocarcinus*. Therefore, Garassino et al. (2004) suggested that it is a junior synonym of *Chlinocephalus demissifrons* Ristori, 1886, and that the specimen may be a juvenile stage of that species. *Titanocarcinus sculptus* (Fig. 1E), at least in terms of overall carapace shape, is reminiscent of crabs of the families Atelecyclidae Ortmann, 1893; Cheiragonidae Ortmann, 1893; or Pirimelidae Alcock, 1899, but the specimens will need to be examined to confirm the placement of this enigmatic taxon.

The Late Cretaceous *Titanocarcinus reisi* Böhm, 1891 (Fig. 1H), cannot be retained within the genus, based upon its possession of a narrow carapace and short tri-lobed anterolateral margin which is granular anteriorly. None of these features are accommodated by *Titanocarcinus*, and can be better embraced by several fossil members of the Hepatidae, as defined in Schweitzer and Feldmann (2000a). Another form was also referred to *T. reisi* (Böhm, 1891: 43, pl. 1, fig. 5); that specimen also appears to be best referred to the Hepatidae based upon the narrow carapace and short anterolateral margins. It is much narrower than the specimen illustrated by Böhm (1891) in his figure 4; thus, the two do not appear to be congeneric.

Titanocarcinus kochi Lőrenthey, 1898, from the Eocene of Hungary, was originally described as being similar to *T. sismondae* and *T. edwardsi* (Lőrenthey, 1898: 55), neither of which can be referred to the genus. Examination of casts of the syntypes of *Titanocarcinus kochi* (E289) (Fig. 1C) indicates that, although it possesses some similarities with *Titanocarcinus* in carapace size and shape, it cannot be retained in *Titanocarcinus* because it lacks an epibranchial region separated into two parts and appears to lack orbital fissures, each diagnostic of *Titanocarcinus*. It must be stated that the preservation of the syntypes is not exceptional, and the front, orbits and anterolateral margins are damaged or obscured on both specimens. Thus, it seems that the specimens are best referred to the Pilumnidae, because the lack of the two diagnostic features mentioned excludes them from *Titanocarcinus*.

The Eocene species *Titanocarcinus euglyphos* (Fig. 1A, B, D) was originally described as differing from typical members of the genus in the nature of the front (Bittner, 1875: 95). That species has a front with six spines, an inner, blunt pair and two outer, sharp pairs. The outer-most of these are the inner-orbital spines. No other members of *Titanocarcinus* have six frontal spines; all are four-lobed, including the inner-orbital spines or lobes. The other aspects of the dorsal carapace as described conform in general to the description of *Titanocarcinus*, but the six-lobed front suggests that the species might be better placed within the Pilumnidae. Unfortunately, the illustration of the holotype (Bittner, 1875, pl. 2, fig. 6) does not show the front well, and the specimens referred to the species by Feldmann et al. (1998) all have broken fronts (CM 36031-36035), so it will be necessary to examine the type material to place this species into a genus.

Titanocarcinus meridionalis Secretan, 1961, from the Upper Cretaceous of Morocco cannot be retained within the genus. It possesses what appear to be five anterolateral spines not including the outer orbital spines and two posterolateral spines, neither of which is consistent with the definition of *Titanocarcinus*. In addition, the carapace is longer than wide and bears marked swellings on the branchial regions. These swellings, the well-defined anterolateral spines, and the well-defined orbits are reminiscent of the Palaeoxanthopsidae, but the longer than wide carapace and posterolateral spines are not typical of that family. Careful

←

image from A. Milne-Edwards, 1863, pl. 9, fig. 2; J, "*Titanocarcinus*" *sismondae* A. Milne-Edwards, 1864, digital image from A. Milne-Edwards, 1863, pl. 10, fig. 2; K, *Xantho edwardsi* Sismonda, 1846, digital image from A. Milne-Edwards, 1863, pl. 10, fig. 3; L, *Nitotacarcinus bituberculatus* (Collins and Jakobsen, 2004 [imprint 2003]), holotype, MGUH 26794, dorsal carapace; M, *Nitotacarcinus bituberculatus* (Collins and Jakobsen, 2004 [imprint 2003]), paratype, MGUH 26797, male sternum and pleon. L and M reproduced with permission from Bulletin of the Mizunami Fossil Museum. Scale bars = 1 cm. Images for which there are no scale bars are those for which size of original specimens is unknown.

evaluation of type material will be necessary to place this species within a family.

Titanocarcinus zoellneri Bachmayer and Mundlos, 1968, from the Oligocene of Germany, was described as being densely granular overall, with poorly preserved anterolateral margins that bear spines, and well-developed carapace regions (Bachmayer and Mundlos, 1968: 672). The front and orbits were not described. The protogastric regions have longitudinal ridges parallel to the anterior process of the mesogastric region (Bachmayer and Mundlos, 1968, pl. 8), unlike species of *Titanocarcinus*. The apparently poor preservation of the material makes it difficult to place this species within a genus, but it appears to differ substantially from *Titanocarcinus*.

Some of the species assigned to *Titanocarcinus* are not referable to a genus or family based on the incomplete nature of the original material. *Titanocarcinus verrucosus* (Schafhäutl, 1851) (Fig. 1G) was originally referred to *Cancer* and later placed in *Titanocarcinus* by Glaessner (1929). That species is known only from the posterior one-third of the carapace, which is ornamented with large, granular, spherical swellings (Schafhäutl, 1851, pl. 22, fig. 29; von Meyer, 1863, pl. 16, fig. 16), not seen in *Titanocarcinus*. This ornamentation is reminiscent of genera within the Palaeoxanthopsidae Schweitzer, 2003, to which we refer it, but more complete material, with the orbits and anterolateral margins preserved, will be necessary to place this Eocene species in a genus.

Titanocarcinus mamillatus Secretan, 1964, is very badly weathered, so the nature of the anterolateral margins is not discernible. The configuration of carapace regions is similar to that seen in *Titanocarcinus*, and the front appears to be axially notched; however, the fronto-orbital width is considerably narrower compared to the maximum width (50%) (Secretan, 1964, pl. 20, figs. 1, 2) than that seen in other species of *Titanocarcinus* (66-75%). The development of regions is in fact similar to other xanthoid families known from the Cretaceous, such as the Palaeoxanthopsidae; thus, the placement of the Cretaceous *T. mamillatus* must await collection of more complete material. The Danian species *Titanocarcinus*? *polonicus* Fraaye, 1994, is too fragmentary to confirm its generic placement.

Titanocarcinus serratifrons A. Milne-Edwards, 1864
Fig. 2J

Titanocarcinus serratifrons A. Milne-Edwards, 1864, p. 33, pl. 9, fig. 3, pl. 10, fig. 4.

Diagnosis.—Carapace not much wider than long, L/W about 0.80; front straight with weak notch axially; frontal width about 30 percent maximum carapace width; anterolateral margins with four spines, third largest, first and fourth smallest; carapace regions ornamented with small tubercles.

Description (modified from the original French with additions from illustrations in square brackets).—Carapace weakly inflated in front, very depressed posteriorly; little widened, maximum width of dorsal carapace not much longer than length, [L/W about 0.80, position of maximum width about half the distance posteriorly on carapace]. Front straight, not extending beyond orbital angles, finely crenulate, lightly notched axially, notch continues as a groove merging with the mesogastric region, [frontal width about 30 percent maximum carapace width]. [Orbits rimmed, with two orbital fissures; outer orbital angle small, barely projecting; fronto-orbital width about 70 percent maximum carapace width]. Anterolateral margins with four spines clearly separated from one another, [spines granular]; first small, second slightly larger, third largest of all, fourth same size of first. Posterolateral margin straight, same length as anterolateral margin.

Gastric regions strongly marked and lobate. Epigastric regions raised and covered with small granulations which are also very numerous on protogastric regions. Mesogastric region almost smooth, with scattered tubercles, continuing to a point level with frontal region. Separation between metagastric and urogastric regions hardly visible; cardiac region large, almost smooth; hepatic regions swollen, delimited by deep grooves and ornamented with granules.

Pterygostomial regions crossed by branchial and branchio-hepatic grooves, which extend underneath. Suborbital margin with fissure at extremity of which is small tooth.

Measurements.—Carapace width = 10 mm; carapace length = 8 mm (from A. Milne-Edwards, 1864).

Types.—Unknown.

Occurrence.—Late Cretaceous near Ciply, Mons Basin (southern Belgium), Tuffeau de Saint Symphorien that can be correlated with the lower Maastricht Formation of The Netherlands.

Remarks.—The occurrence of *Titanocarcinus serratifrons* is based on A. Milne-Edwards' (1864: 32) description of the species in association with a very common species of *Dromilites*, which is now known to be *Dromiopsis mosae* Collins et al., 1995, from the Saint Symphorien Chalk. The description and illustrations of this species, because it is the type species of the genus, are the basis upon which we have framed the definition of the genus.

Titanocarcinus briarti (Forir, 1887)
Fig. 2C-G

Dromiopsis briarti Forir, 1887, p. 49, pl. 2, figs. 8, 9.
Titanocarcinus briarti (Forir, 1887). Beurlen, 1928, p. 160.
Leptoides briarti (Forir, 1887). Collins, Fraaye, and Jagt, 1995, p. 203, fig. 12G.

Diagnosis.—Carapace hexagonal, wider than long, L/W about 0.77; front with deep axial notch; frontal width about 39 percent maximum carapace width; outer-orbital spine short; anterolateral margin with four spines, third largest, second and fourth similar in size; carapace grooves deep; two swellings near orbital rim.

Description (modified from the original French with additions from illustrations in square brackets).—[Dorsal carapace hexagonal, wider than long, maximum carapace length about 77 percent maximum carapace width], slightly convex transversely, very strongly convex longitudinally with the exception of the posterior region which is nearly flat; surface smooth. Frontal region divided axially by deep

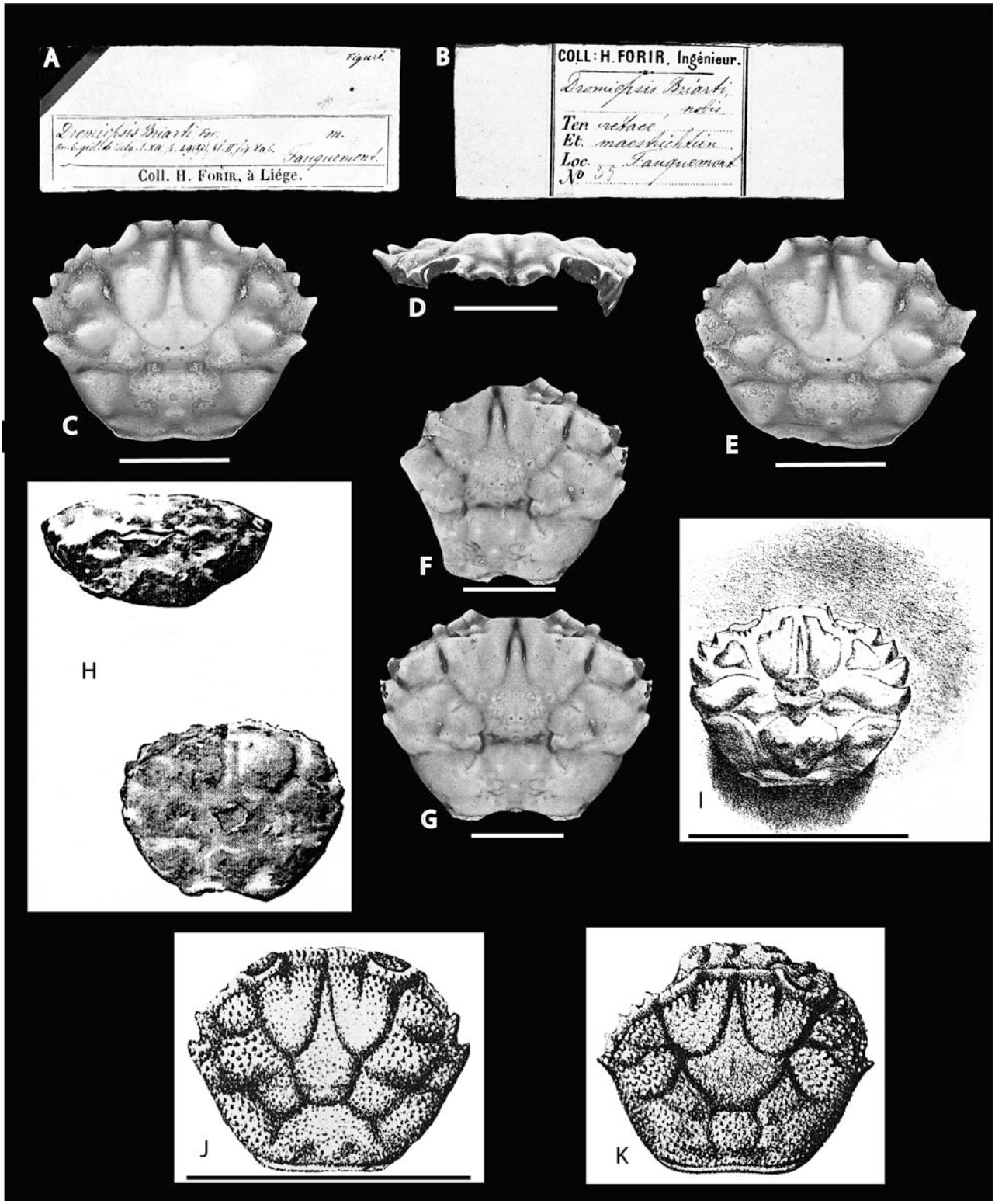

Fig. 2. Species herein referred to *Titanocarcinus* sensu stricto. A, original label of Forir's holotype of *Titanocarcinus briarti* (Forir, 1887); B, original label of Forir's holotype of *Titanocarcinus briarti* (Forir, 1887); C-E, *Titanocarcinus briarti*, holotype, IRSNB MI 11011, C, reconstruction created by reflecting right side of carapace, D, anterior view of carapace, E, dorsal carapace of holotype; F, G, *Titanocarcinus briarti*, MAB k. 1034, F, dorsal carapace and G, reconstruction created by reflecting right side of carapace; H, *Titanocarcinus subellipticus* (Segerberg, 1900), digital image from Segerberg, 1900, pl. 9, fig. 14; I, *Titanocarcinus faxeensis* (von Fischer-Benzon, 1866), digital image from von Fischer-Benzon, 1866, pl. 2, fig. 4; J, *Titanocarcinus serratifrons* A. Milne-Edwards, 1864 (type species), digital image from A. Milne-Edwards, 1863, pl. 9, fig. 5; K, *Titanocarcinus raulinianus* A. Milne-Edwards, 1864, digital image from A. Milne-Edwards, 1863, pl. 9, fig. 3. Scale bars for C-G = 5 mm; scale bars for I and J = 1 cm. Images for which there are no scale bars are those for which size of original specimens is unknown.

longitudinal groove, terminating in axial notch on frontal margin. [Frontal width about 39 percent maximum carapace width, frontal margin with very small blunt protuberances on either side of axial notch and very small swellings at inner-orbital angle.]

[Orbits shallow, semi-circular, rimmed, directed weakly anterolaterally, with two orbital fissures positioned near outer-orbital angle;] outer orbital spine short, directed forward; [fronto-orbital width about 75 percent maximum carapace width].

[Anterolateral margin with four spines not including the outer-orbital spine, increasing in size from spines 1 to 3, third largest, spines 1 to 3 directed anterolaterally; fourth spine same size as second, directed laterally.] Posterolateral margins lightly convex centrally, forming angle of about 35 degrees with axis of carapace, entire. Posterior border short, straight.

Surface of cephalothorax divided into three principal parts by two transverse grooves that do not extend onto ventral part of carapace. The posterior groove [= groove separating epibranchial region from mesogastric region + urogastric region] separates the posterior region [= mesobranchial, metabranchial, cardiac, and intestinal regions] from the median region [= hepatic, epibranchial, and metagastric regions] and the anterolateral region [= frontal, epigastric, protogastric, and mesogastric regions]. Posterior groove extends in straight line from margin toward axis, normal to axis, dividing abruptly in two depressions about one-third the distance axially to enclose pentagonal cardiac region; cardiac region depressed anteriorly [this is really the urogastric region], inflated posteriorly, with three protuberances, of which third is less elevated than other two, forming posterior angle of pentagon. Posterolateral regions [= mesogastric region] lanceolate, lightly inflated, delimited anteriorly by posterior groove and posteriorly by lenticular intestinal regions [= metagastric + intestinal regions].

Median area of carapace, placed between the two grooves, contains postmedian region [= metagastric] and branchial region [= hepatic + epibranchial regions]. Metagastric region trapezoidal, lightly inflated anteriorly, depressed posteriorly. Epibranchial region divided into two parts by deep transverse [longitudinal] depression, this feature dominates this species. Hepatic region with straight zone bearing three of the already mentioned anterolateral spines. Anterior groove or cervical groove [actually not truly the cervical groove] deep, beginning from outer-orbital spine, forming an angle of about 30 degrees to axis, then recurving in U-shape to post-median region. Mesogastric region with anterior projection, delimited exteriorly by deep grooves which separate it from protogastric and epigastric regions; posteriorly lenticular, broadened, and inflated. Protogastric regions strongly developed, very inflated, terminating at strongly elevated epigastric regions.

Measurements.—Maximum carapace length = 10 mm; maximum carapace width = 13 mm; posterior width = 6 mm (Forir, 1887).

Material.—The holotype (Fig. 2C-E) was originally deposited in the Université d'Etat à Liège in Belgium. Apparently, sometime during the early twentieth century, that material was borrowed by Victor Van Straelen at the Institut Royal des Sciences Naturelles de Belgique (Koninklijk Belgisch Instituut voor Natuurwetenschappen) in Brussels and remained there, unbeknownst to anyone. It was rediscovered there, glued to a board (Fig. 2A, B), by one of us (JWMJ) and now will remain in the collections there under the catalog number IRSNB MI 11011, for easier access to researchers. Other material is deposited in the Oertijdmuseum De Groene Poort, Boxtel, The Netherlands (Collins, et al., 1995).

Occurrence.—Maastrichtian of The Netherlands.

Remarks.—This species was originally described from the Cretaceous of The Netherlands based upon a fairly well-preserved specimen that either lacks exocuticle or is a mold of the interior, as it was described as being completely smooth (Forir, 1887). It is now known that the specimen was collected from the higher part of the Maastricht Formation. Outer layers of the cuticle often possess much of the obvious ornamentation, and if they are lost, the specimen may appear considerably smoother (Waugh et al., 2004). All other species of the genus are quite granular.

Forir (1887) originally referred the species to *Dromiopsis* Reuss, 1859, and it was later placed in *Titanocarcinus* (Beurlen, 1928). The species is clearly not referable to *Dromiopsis*, a member of the Dynomenidae Ortmann, 1892, because members of that family have poorly developed orbits with no fissures; a triangular, downturned front; and deeply incised cervical and branchiocardiac grooves, which *D. briarti* lacks. Subsequently, Collins et al. (1995), based upon an additional specimen (Fig. 2F, G) collected from the Meerssen Member of the Maastricht Formation, which is the highest part of the formation, erected the new genus *Leptoides* to accommodate *Dromiopsis briarti*. At that time, the location of the holotype of *Dromiopsis briarti* was not known; it was reported to have been deposited at the Université d'État à Liège in Belgium, but was not there at the time of Collins et al.'s (1995) work. Subsequently, one of us (JWMJ) has located the holotype in Brussels.

Comparison of the holotype of *Dromiopsis briarti* (Fig. 2C-E) and the specimen referred to that species and illustrated by Collins et al. (1995) (Fig. 2F, G) suggests that they are conspecific and are best referred to *Titanocarcinus*. The holotype of *Dromiopsis briarti* possesses the key features that unite the genus *Titanocarcinus*, including a notched front, rimmed orbits with two fissures, four anterolateral spines with the third being largest, well-developed epigastric regions, epibranchial regions well separated into two segments, and a position of maximum width at about mid-length. The specimen illustrated by Collins et al. (1995) is broken but possesses a rimmed orbit with two fissures, four anterolateral spines of which the third is largest, epibranchial regions well-separated into two segments, and a position of maximum width at about mid-length, indicating that it is also best placed in *Titanocarcinus*. The only major difference between the holotype of *Titanocarcinus briarti* and the specimen illustrated by Collins et al. (1995) is the presence of two large nodes near the orbit in the latter. However, because the differences are perhaps most likely due to differential weathering of the two specimens, it seems most prudent at

this time to refer that specimen to *Titanocarcinus briarti*. The differences could also be due to sexual dimorphism or developmental differences between the individuals, which have been documented within related families (Guinot, 1989; Schweitzer and Feldmann, 2000b). In addition, both were collected from the uppermost Maastricht Formation in The Netherlands. Thus, *Leptoides* becomes a junior synonym of *Titanocarcinus*.

Titanocarcinus faxeensis (von Fischer-Benzon, 1866)
Fig. 2I

Panopeus faxeensis von Fischer-Benzon, 1866, p. 29, pl. 2, figs. 4-6. Segerberg, 1900, p. 376, pl. 9, figs. 9-11.
Titanocarcinus faxeensis (von Fischer-Benzon, 1866). Jakobsen and Collins, 1997, p. 98, pl. 3, fig. 2.
Titanocarcinus subellipticus (Segerberg, 1900). Jakobsen and Collins, 1997, p. 98, pl. 3, fig. 1.

Diagnosis.—Carapace pentagonal, wider than long, L/W = 0.85; front with four spines including inner-orbital spines; frontal width about 30 percent maximum carapace width; orbit with inner-, intra-, and outer-orbital spines; anterolateral margin with four spines, fourth smallest; cardiac region with three swellings.

Description (modified from the original German with additions from illustrations in square brackets).—Cephalothorax almost five-sided in outline, [wider than long, maximum length about 85 percent maximum width]; carapace steeply vaulted anteriorly, remainder almost flat. Front broad, axially notched, downturned, with four spines, outer two very sharp [= inner-orbital spines], inner two indistinct, [frontal width about 30 percent maximum carapace width]. Orbits elliptical, upper orbital rim with two fissures, these help define three orbital spines, the median of which is smallest, [fronto-orbital width about two-thirds maximum carapace width]; outer-orbital angle produced into a spine, below it a gap, from this a shallow oblique channel trending axially. Suborbital margin with two small spines, one near gap, other near inner-suborbital angle.

Anterolateral margin curved, with four triangular spines; of these, fourth smallest. Posterolateral margins nearly straight. [some of original description not translated]. Posterior part of the mesogastric region elliptical, nearly twice as wide as long, with clear muscle scars discernible; anterior process of mesogastric region sword-shaped, elongate, posteriorly with two small tubercles. Urogastric region a deep depression, on it a weakly elevated, almost heart-shaped swelling, little broader than mesogastric region. Cardiac region almost heart-shaped, large, with three blunt elevations. Intestinal region forming a rim along posterior margin, interrupted medially by tip of cardiac region.

Protogastric regions when combined together have outline of an urn, large, strongly vaulted, delimited by deep grooves. Hepatic region triangular, distinctly delimited, one side of which is parallel to anterolateral margin.

One shallow groove, originating at base of fourth anterolateral spine, dividing branchial region in two parts [anteriormost is outer lobe of epibranchial region, posterior-most remainder of branchial region], bifurcating approximately half the distance axially between cardiac region and lateral margin, forming rhombic-shaped swelling anterior to front of cardiac region [this is inner lobe of epibranchial region].

Measurements.—8.2 mm long, 9.6 mm wide (from von Fischer-Benzon, 1866).

Types.—Location unknown; possibly lost.

Occurrence.—Danian of Denmark.

Remarks.—This species is retained in *Titanocarcinus* based upon its possession of a four-lobed front occupying about 30 percent the maximum carapace width; a fronto-orbital width about two-thirds the maximum carapace width; two orbital fissures; four anterolateral spines, with the fourth smallest; and well-defined carapace regions and grooves. This species was not described as possessing the granular ornament of other taxa, but the illustrations suggest that it was originally described from a steinkern in which such ornamentation would not be preserved. The specimens illustrated by Jakobsen and Collins (1997), which appear to be conspecific and are here both referred to *T. faxeensis*, are indeed granular as in the type species and other taxa.

Titanocarcinus raulinianus A. Milne-Edwards, 1864
Fig. 2K

Titanocarcinus raulinianus A. Milne-Edwards, 1863, pl. 9, figs. 3, 4, 1864, p. 37.

Diagnosis.—Carapace wider than long, L/W about 0.80; regions ornamented with large granules; front nearly straight with axial notch; frontal width about 25 percent maximum carapace width; anterolateral margin with four spines, second and third strongest, fourth smallest.

Description (modified from the original French with additions from illustrations in square brackets).—Carapace little widened, [maximum carapace length about 80 percent maximum carapace width]; a line passing through lateral angles divides it into two equal portions; regions distinct, remarkable by large granulations ornamenting inflated parts of carapace. Front little advanced, straight, weakly notched axially [about 25 percent maximum carapace width]. Upper orbital margin rimmed, with two fissures, [fronto-orbital width about 70 percent maximum carapace width]. Anterolateral margins longer than posterolateral margins; divided into four spines not including outer-orbital spines; first small; second and third strong, flattened, triangular, almost equal in size; fourth smallest. Gastric region delimited by deep grooves; subdivided into epigastric regions which are very inflated anteriorly and separated from protogastric regions by longitudinal groove which does not extend posteriorly. Mesogastric region with prolonged anterior projection extending almost to the front, confluent posteriorly with metagastric region which is hardly separated from urogastric region; cardiac region enlarged posteriorly; each of these regions granulose. Hepatic regions inflated, tubercles larger than on other regions. Branchial regions composed of epi-, meso-, and metabranchial regions, epibranchial region with granulations stronger than on branchial regions.

Measurements.—Maximum carapace width of small individuals = 31 mm; maximum carapace length of small individuals = 25 mm; in large individuals, maximum carapace width = 60 mm; maximum carapace length = 49 mm (A. Milne-Edwards, 1864: 39).

Types.—Unknown.

Occurrence.—Eocene of France, Hungary, Italy (Glaessner, 1929). The report from the Eocene of Hungary (Lőrenthey, 1898, 1902) should be confirmed.

Remarks.—The species is placed in *Titanocarcinus* based upon possessing all of the key features of the genus. The specimen illustrated by Lőrenthey (1902) is similar in many regards to the types figured by A. Milne-Edwards (1864), but the anterolateral spines are more projected laterally and the position of maximum width lies in advance of mid-length. That particular specimen should be examined to determine if it indeed should be referred to *T. raulinianus*.

Titanocarcinus subellipticus (Segerberg, 1900)
Fig. 2H

Panopeus subellipticus Segerberg, 1900, p. 379, pl. 9, fig. 14.
Titanocarcinus subellipticus (Segerberg, 1900). Secretan, 1961, p. 45.

Diagnosis.—Carapace elliptical, wider than long, L/W about 0.80; frontal width about 30 percent maximum carapace width; orbit with two fissures, intra-orbital spine, and broad outer-orbital spine; anterolateral margins with four short spines; regions inflated.

Description (modified from the original Swedish with additions from illustrations in square brackets).—Steinkern with almost elliptical circumference, anteriorly strongly downturned, remainder of carapace only weakly arched; carapace width greater than carapace length, [L/W = 0.80; position of maximum width about half the distance posteriorly on carapace]. [Frontal width about 30 percent maximum carapace width.] Orbit oval, upper orbital margin interrupted by two incisions, between them a short, sharp spine; wide outer-orbital angle a small spine, delineated from suborbital margin by clear gap; [fronto-orbital width about 70 percent maximum carapace width]; suborbital margin with inner- and outer-orbital spines, within the margin a notch so that there is an additional, small, but especially sharp, pointed intra-suborbital spine.

Anterolateral margins almost the same in length as the posterolateral margins; anterolateral margins bearing up to four short, obscurely-pointed spines. Posterior border almost straight [appears distinctly concave in Segerberg, 1900, pl. 9, fig. 14]. Regions especially evident, almost all similarly well marked and separated by deep, broad grooves. Epigastric region merging with protogastric region. Hepatic region unusually well developed, rounded. Mesogastric region and urogastric region together forming a pentagon with forward-projecting point. Cardiac region elevated, long, pentagonal, marked laterally and posteriorly by broad furrows. Epibranchial regions broad, inner-axial lobe of epibranchial region lower [than lateral portion]. Meso- and metabranchial lobes [not differentiated], trapezoidal.

Measurements.—Maximum carapace width = 20 mm, maximum carapace length = >16 mm (rostrum is broken) (Segerberg, 1900: 379).

Types.—Only one example from Fakse (Segerberg, 1900), deposited in the Geological Museum, University of Copenhagen, Denmark.

Occurrence.—Danian of Denmark.

Remarks.—The species is referred to *Titanocarcinus* based upon its possession of all of the diagnostic characters. It lacks the granular ornamentation seen in some species, but as in *T. subellipticus*, this may be because the specimen originally described appears to be a steinkern.

Titanocarcinus decor new species
Figs. 3, 4

Diagnosis.—Carapace subhexagonal, wider than long, L/W about 0.84; regions ornamented anteriorly with large pearly tubercles; frontal margin straight with U-shaped axial notch; blunt intra-orbital protuberance between orbital fissures; anterolateral margins with four spines, third largest, first smallest; regions well delimited by grooves.

Description.—Dorsal carapace subhexagonal in outline, trapezoidal in posterior portion; wider than long, maximum carapace length about 84 percent maximum carapace width, which is at level of fourth anterolateral spine, at about longitudinal midline; nearly flat transversely, moderately convex longitudinally; surface and outline densely granulate, with larger beaded tubercles in anterior half. Front not exceeding inner-orbital angle; delimited by shallow, oblique depression at corner; margin straight, finely granulated; with deep, axial, U-shaped notch; frontal width about 30 percent maximum carapace width. Orbits oblique, with a raised rim, margin densely granulated, with two deep incisions and blunt denticle in between which are positioned closer to outer orbital spine, fronto-orbital width about 70 percent maximum carapace width.

Anterolateral margin gently arched, shorter than posterolateral margin; with four acute, forward-directed, granular spines excluding outer-orbital spine; anterior two spines smaller; third largest; fourth somewhat smaller than third. Posterolateral margins converging posteriorly, nearly straight, slightly noded at central portion, forming an angle of approximately 135 degrees with posterior margin. Posterior margin short, somewhat shorter than fronto-orbital width, nearly straight, faintly concave axially, delimited by thin, delicately granular rim.

Dorsal regions well defined by lobes and grooves. Gastric regions divided; epigastric region stretched anteriorly, merging posteriorly with protogastric region, which is longer than broad, swollen, covered by large granules at anterior portion, where shallow and short longitudinal furrow separates it from epigastric region. Anterior mesogastric extension very thin, long, bounded by epigastric region; posterior mesogastric lobe broad; gastric pits present. Metagastric region not well differentiated. Urogastric region very depressed. Cardiac region subpentagonal, with bluntly rounded apex directed posteriorly. Intestinal

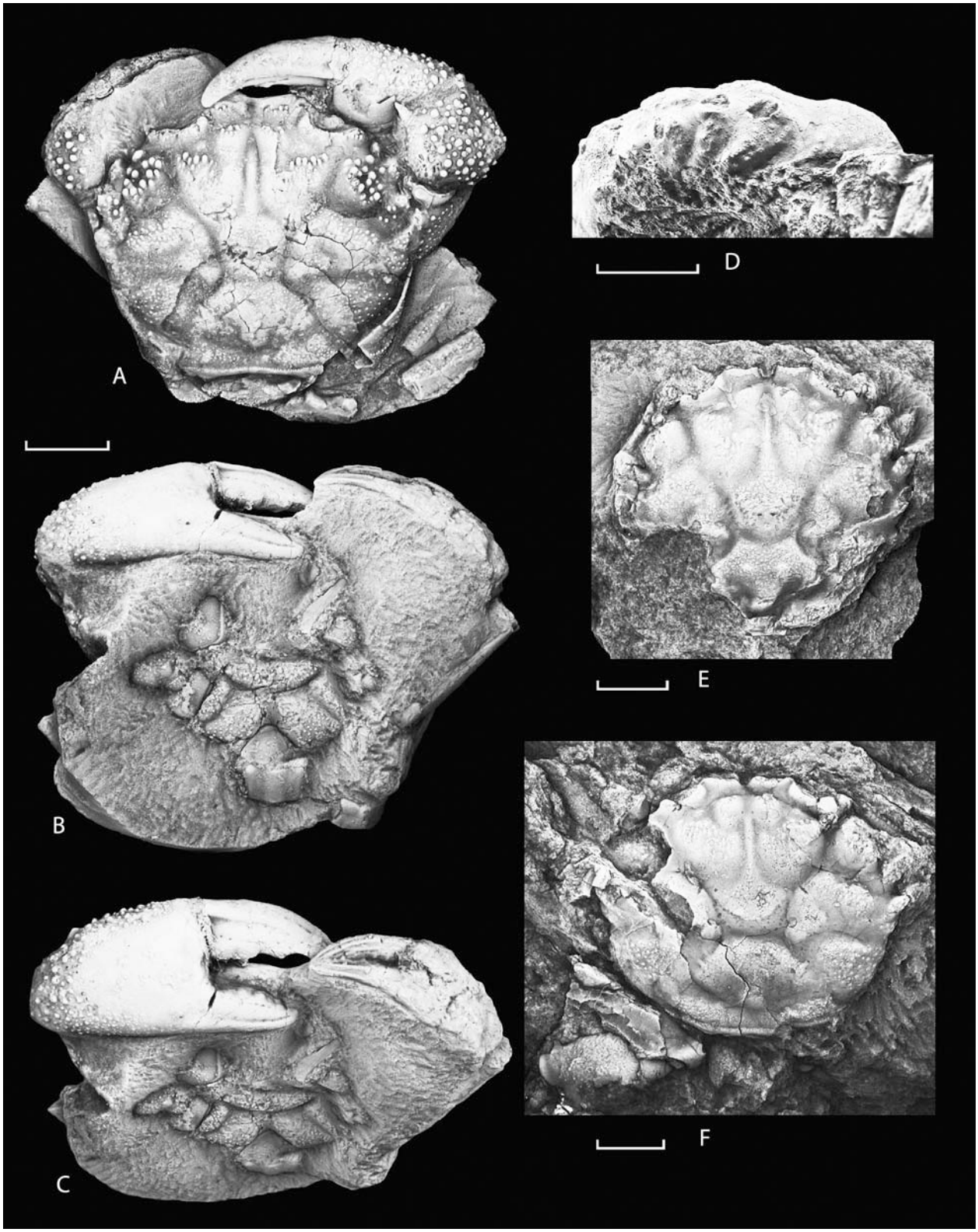

Fig. 3. *Titanocarcinus decor* new species. A, B, C, holotype, MGSB68395; D, paratype MGSB68579aa; E, paratype MGSB68420aa; F, paratype MGSB68420ab. Scale bars = 5 mm.

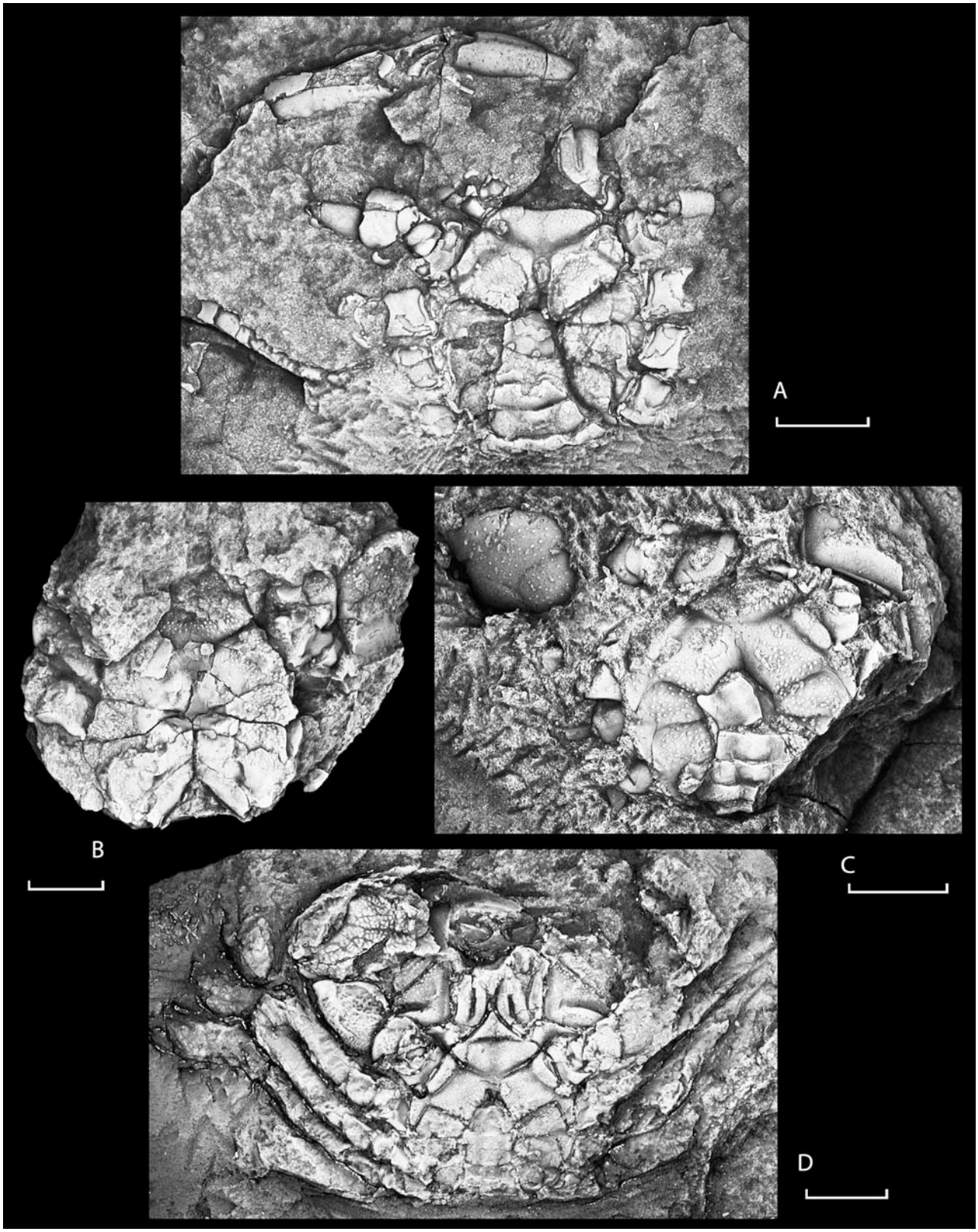

Fig. 4. *Titanocarcinus decor* new species. A, paratype MGSB68420ad; B, paratype MGSB68420ag; C, paratype MGSB68420ae; D, paratype MGSB68420af. Scale bars = 5 mm.

region axially depressed, interrupting transverse ridge close to posterior margin. Hepatic region oblique, noticeably inflated, covered by dense, beaded tuberculation. Epibranchial region large, arched, divided into two portions; remainder of branchial region undifferentiated, very large, inflated centrally to position of posterolateral margin; all regions clearly delimited by deep, broad grooves. Distinct transverse furrow, extending to lateral margins, separates branchial regions and gastric regions from cardiac region; furrow about one third the total carapace length anteriorly from posterior margin.

Pterygostomial region sculptured by short, pronounced ridges and furrows, ridges blunt, densely granulated, originating at each anterolateral spine. Third maxillipeds, covering entire buccal cavity; exopod of third maxilliped much longer than wide; endopod somewhat longer than wide, with deep longitudinal sulcus, basis triangular. Bases of antennae large, subtriangular, transversely disposed under front and completely filling space.

Sternum longer than wide; male sternites 1 and 2 fused, forming a triangle with sharp apex; very deep, continuous suture between sternites 2 and 3; from marginal notch, deep oblique furrow extends between sternites 3 and 4, forming Y-shape with axial pleonal cavity; sternite 4 with oblique furrows, parallel and close to lateral margins. Sternite 5 directed laterally, upper margin parallel to suture of sternites 3 and 4; sternites 6 and 7 directed posteriorly. Sternite 8 covered by male pleon, wide, transversely narrow, visible in specimen number MGSB68420ag (Fig. 4B) in which pleon is absent, forming angle of about 80° to axis. All sternites densely and uniformly covered by granules.

Male pleon with all somites free; somites 1 and 2 of similar size; somite 3 largest, wider than all other segments, completely covering space between coxae of fifth pereiopods, sternite 8 not visible; somites 4-6 decreasing in width to telson; somite 6 longest, only somewhat wider than long, margins nearly straight, upper angles rounded, somewhat projecting; telson triangular, nearly reaching imaginary line at level of lowermost portion of coxae of first pereiopods.

Chelae distinctly unequal. Major cheliped of male massive, palm broadly convex at outer and inner surface, upper and lower margins rounded and densely granular; fingers stout, bearing robust denticles on occlusal surface; dactylus with dorsal and ventral carinae; fixed finger with deep sulcus along lower margin. Minor cheliped much smaller and slender, fingers delicate, strongly carinate, with long furrows. Carpus large, globular, bearing rounded tubercles, with long, acute inner and dorsal spine; merus short, robust; coxae of first pereiopods articulating with basi-ischium which are not fused with merus; last four pereiopods flattened and densely granulated, only fragmentarily preserved.

Measurements.—Measurements (in mm) taken on the dorsal carapace of *Titanocarcinus decor* new species: Holotype, MGSB68395, maximum carapace width = 18.6 mm; maximum carapace length = 15.6 mm. Paratype, MGSB68579ac, the largest specimen available, maximum carapace width = 22.2 mm, maximum carapace length = 18.7 mm.

Material.—Holotype, MGSB68395, paratypes MGSB 68420aa-ag, deposited in the Museo Geológico del Seminario de Barcelona (Spain). Additional material, including the remains of several ventral surfaces, incomplete dorsal carapaces, and external molds, are also housed in the Museum (MGSB68579aa-af, MGSB68580aa-ai).

Etymology.—From the Latin adjective decor, meaning magnificent, grateful.

Occurrence.—Lower Eocene (upper Ilerdian to lower Cuisian interval) Roda Formation (Cuevas-Gozalo et al., 1985). Collected near Bacamorta (Huesca, Spain), about 2 kilometers northeast from the small village, on the south bank of the ravine named Barranco de Bacamorta, at lat. 42°21′41.6″N, long. 0°25′02.5″E.

Remarks.—The main dorsal and ventral features of the carapace in *Titanocarcinus decor* new species, major dorsal carapace measurements and proportions, the outline of the carapace and arrangement of regions, the pterygostomial groove pattern, and the lateral spines and fronto-orbital structure make it possible to assign the new Spanish species to the genus *Titanocarcinus*. The peculiar beaded ornamentation on the dorsal surface of the carapace possess a pearly luster and are nearly three-dimensional, resting like spheres on the dorsal carapace surface, unique among species of the genus. In addition, the shape and granulation of the anterolateral spines, the characteristic inflated and oblique hepatic region, and the grooves that distinctly mark the regions are also diagnostic features for the species and distinguish *Titanocarcinus decor* from all the other forms assigned to the genus. *Titanocarcinus serratifrons* is smaller in size, and differs in having more anteriorly advanced protogastric regions, more triangular hepatic lobes which are placed closer to the epibranchial regions, and a different shape and length of the anterolateral spines, the fourth being the smallest, than are seen in *T. decor*. *Titanocarcinus briarti* has clear upper and lower prominences in the metabranchial region and more rounded gastric grooves than *T. decor*; it also differs in not having a sharp tooth between the orbital fissures as does *T. decor* and possesses a V-shaped axial notch on the frontal margin and a distinctly longer third lateral spine than does *T. decor*. *Titanocarcinus faxeensis* differs in having a more triangular hepatic region with its apex directed inward, a metagastric region distingushed from the mesogastric region, and sharp triangular spines, the fourth being the smallest, all of which differ from *T. decor*. *Titanocarcinus raulinianus* is larger in size, with broader mesogastric regions, and it possesses inclined anterior margins of the protogastric regions, differing from *T. decor*. *Titanocarcinus subellipticus*, similar in size to *T. decor*, has a less hexagonal carapace outline, being more subelliptical as the species name indicates, and has a more rounded, nearly semicircular, gastric groove than in *T. decor*. It also differs in the general dorsal ornamentation, which is more uniform, and in the shape and length of lateral spines, which are stouter and more granular in *T. decor*.

Several specimens of *Titanocarcinus decor* are preserved with a complete pleon and sternum, which appear to be very similar to those of *Nitotacarcinus bituberculatus* new genus and combination, described below, in which the major difference is a deeper longitudinal furrow in the axis of

sternite 3 in the latter, which is typical among members of the same family.

The new taxon is unique among the species of *Titanocarcinus* in possessing well-preserved sterna and pleon. Dorsal features are similar to the type species of *Titanocarcinus* in most regards, differing in such characters as the size of the anterolateral spines and the degree of inflation of regions, which are species-level characters among the Brachyura. Thus, we are confident of our referral of the species to *Titanocarcinus*.

Nitotacarcinus new genus

Glyphithyreus Reuss, 1859 (part). Collins and Jakobsen, 2004 [imprint 2003], p. 74, text-fig. 6, pl. 5.

Titanocarcinus A. Milne-Edwards (1864) (part). Karasawa and Schweitzer, 2004, p. 152, fig. 2.

Type and Sole Species.—*Glyphithyreus bituberculatus* Collins and Jakobsen, 2004 [imprint 2003], by monotypy.

Diagnosis.—as for species.

Description.—as for species.

Etymology.—The genus name *Nitotacarcinus* is an anagram of the genus name *Titanocarcinus*, to which it appears closely related. The gender is masculine.

Remarks.—*Glyphithyreus bituberculatus* was moved to *Titanocarcinus* based upon its possession of a notched front, rimmed orbits with two fissures, and well-developed carapace regions, including an epibranchial region separated into two lobes (Karasawa and Schweitzer, 2004). This species differs from other species of *Titanocarcinus* in having a very reduced fourth anterolateral spine, which is actually a swelling; more slender chelae with longer fingers; a pterygostomial region with a long groove and ridge, unlike those seen in *Titanocarcinus*; a front projecting beyond the inner-orbital angles; and a more rounded posterior half of the carapace, such that the carapace itself appears more equant, suggesting that the species must be assigned to a different genus. *Glyphithyreus bituberculatus* differs from other species of *Glyphithyreus* in lacking square, forward-directed orbits and carapace regions developed such that they form transverse ridges on the dorsal carapace. Thus, we herein place *Glyphithyreus bituberculatus* into a new genus, *Nitotacarcinus*. The new genus is placed within the Tumidocarcinidae, based upon the diagnostic characters of the well-preserved male sternum and pleon in this species.

Nitotacarcinus bituberculatus (Collins and Jakobsen, 2004 [imprint 2003]) new combination
Fig. 1L, M

Glyphithyreus bituberculatus Collins and Jakobsen, 2004 [imprint 2003], p. 74, text-fig. 6, pl. 5.

Titanocarcinus bituberculatus (Collins and Jakobsen, 2004 [imprint 2003]). Karasawa and Schweitzer, 2004, p. 152, fig. 2.

Emendation to Diagnosis.—Sternum ovate, sternites 1-2 fused, no evidence of suture; sternites 2 and 3 separated by complete, uninterrupted suture; sternites 3 and 4 with suture expressed as deep groove; sternite 4 with grooves parallel to lateral margins which appear to be fused episternites from sternite 3; sternites 3 and 4 with longitudinal, axial groove which is extension of sterno-pleonal cavity, portion of this groove on sternite 4 and grooves separating sternites 3 and 4 forming Y-shaped groove pattern on sternum; sternite 8 not visible in ventral view. Male pleon with all somites free, completely covering space between coxae of fifth pereiopods. Remainder as in Karasawa and Schweitzer (2004).

Emendation to Description.—Sternum ovate, sternites 1-2 fused, no evidence of suture; sternites 2 and 3 separated by complete, uninterrupted suture; sternites 3 and 4 with suture expressed as deep groove; sternite 4 with grooves parallel to lateral margins which appear to be fused episternites from sternite 3; sternites 3 and 4 with longitudinal, axial groove which is extension of sterno-pleonal cavity, portion of this groove on sternite 4 and grooves separating sternites 3 and 4 forming Y-shaped groove pattern on sternum; sternite 8 not visible in ventral view. Male pleon with all somites free, completely covering space between coxae of fifth pereiopods. See Collins and Jakobsen (2004 [imprint 2003]) and Karasawa and Schweitzer (2004) for remainder.

Types.—Geological Museum, University of Copenhagen.

Occurrence.—Eocene of Denmark.

Remarks.—The species is well represented and illustrated (Collins and Jakobsen, 2004 [imprint 2003]) by numerous specimens. Thus, critical characters of the male sternum and pleon were available for study. This species has recently been well-illustrated (Collins and Jakobsen, 2004 [imprint 2003], p. 74, text-fig. 6, pl. 5; Karasawa and Schweitzer, 2004, p. 152, fig. 2).

Family Eriphiidae MacLeay, 1838, sensu lato

Lathahypossia new genus

Titanocarcinus A. Milne-Edwards, 1864 (part). Busulini, Tessier, and Vicentin, 1984, p. 119, fig. 1, pls. 1-3; De Angeli and Beschin, 2001, p. 42, fig. 36.

Type and Sole Species.—*Titanocarcinus aculeatus* Busulini, Tessier, and Vicentin, 1984, by monotypy.

Diagnosis.—Carapace transversely ovate, much wider than long, maximum carapace length about 75 percent maximum carapace width, widest at anterolateral angle. Front bilobed, medially notched, with three strong supplementary spines on each side of notch; frontal width about 30 percent maximum carapace width; long spine present between frontal margin and supraorbital angle. Upper orbital margin spinose, with sharp spine and two upper orbital fissures laterally; inner-orbital and outer-orbital spines well developed; lower orbital margin with four spines; orbit not closed; fronto-orbital width about 55 percent maximum carapace width. Basal article of antenna not reaching front. Anterolateral margin moderately convex, with six or seven irregular spines. Posterolateral margin gently convex, rimmed, tuberculate. Posterior margin about 35 percent maximum carapace width, rimmed, tuberculate. Carapace regions well defined, ornamented with coarse granules on elevated surfaces. Chelipeds strongly heterochelous, spinose. Fingers

slender, elongate, black in color; dactylus of major cheliped with basal, molar tooth; occlusal surface of fixed finger of major cheliped serrated on distal half. Palm and merus of both chelipeds ornamented with row of prominent spines on upper and outer surfaces. Propodus, carpus, and merus of pereiopods two through five spinose, spines strong on dorsal margin of propodus and carpus. Thoracic sternum moderate in width; episternal markings on thoracic sternite four absent; sternite eight not visible in ventral view. Male pleon with all free somites, filling entire space between coxae of pereiopods five.

Etymology.—*Lathahypossia* is an anagram of *Hypothalassia* Gistel, 1848; feminine gender.

Remarks.—*Titanocarcinus aculeatus* from the Eocene of Italy (Busulini, Tessier, and Vicentin, 1984) cannot be retained within *Titanocarcinus* because in *T. aculeatus*, the front, orbits, and anterolateral margins of the dorsal carapace and pereiopods one through five are spinose. These spines are absent in *Titanocarcinus*. The fronto-orbital width of *Lathahypossia* is narrower (55 percent maximum carapace width) than species of *Titanocarcinus* (66-75 percent). *Titanocarcinus* is characterized by deep episternal markings on sternite four, not seen in *Lathahypossia*. Therefore, it is clear that *T. aculeatus* must be moved to a new genus.

Lathahypossia exhibits many superficial similarities to the extant *Hypothalassia* Gistel, 1848. Both genera have spinose anterior carapace margins and pereiopods and do not have episternal markings on thoracic sternite four. However, *Lathahypossia* differs from *Hypothalassia* in that the carapace is much wider than long and is ornamented with coarse granules without sharp spines on the dorsal regions. The front of *Lathahypossia* has three supplementary spines on each side of the median notch, whereas the number of supplementary spines in *Hypothalassia* is only two.

Hypothalassia previously had been placed in the family Eriphiidae sensu lato (Ng et al., 2001; Davie, 2002; Sakai, 2004; and others). Most recently, Karasawa et al. (2005) showed, based upon cladistic analysis, that *Hypothalassia* belongs to an independent lineage within the superfamily Eriphioidea (their Platyxanthidae + [*Hypothalassia* + [Eriphiidae + Pseudoziidae + Oziidae]] clade) and suggested that *Hypothalassia* warrants its own family (Karasawa and Schweitzer, 2006). In the present work, we place *Hypothalassia* and *Lathahypossia* within the Eriphiidae sensu lato based upon Ng et al. (2001) and Davie (2002).

Discussion

K/P Boundary Implications

The referral of *Titanocarcinus* to the Tumidocarcinidae extends the geologic range of the family into the Cretaceous. Thus, the family survived the Cretaceous/Paleogene (K/P) boundary events. This is not a surprising discovery. During the Cretaceous, the only known Cretaceous genus within the family, *Titanocarcinus*, was known from northern European localities, including the Maastrichtian of Belgium and The Netherlands, and was subsequently known from the Danian of Denmark. This type of pattern has been termed "the historical Danian problem" in the literature (Kauffman and Harries, 1996: 18; Schweitzer and Feldmann, 2005: 24), in which taxa in high-latitude regions display low levels of extinction across the K/P boundary, and which is already well documented for Cretaceous and Danian arthropods of Denmark and Sweden (Ekdale and Bromley, 1984; Collins and Jakobsen, 1994; Fraaije, 2003). Thus, the hypotheses of Schweitzer and Feldmann (2005), that the effects of the K/P events may not have been as geographically widespread as often stated and that the decapods were certainly not as broadly impacted as other groups, are upheld by the geologic range of both *Titanocarcinus* and the Tumidocarcinidae.

Paleobiogeography

Schweitzer (2005) hypothesized that the Tumidocarcinidae displayed an amphitropical distribution, based upon the genera referred to the family at that time. The assignment of *Titanocarcinus* and *Lobonotus* to the family changes that interpretation somewhat. The family appears to have originated in northern Europe, based upon our current understanding, and subsequently dispersed to the Americas, probably via ocean currents or continental shelves in the incipient Atlantic Ocean, by the Eocene. Note also that by the Eocene, Tumidocarcinidae was well established in the mid- to high-latitudes in the Southern Hemisphere; thus, its distribution was amphitropical by Eocene time. A possible dispersal pathway to achieve such a distribution would be logically via the Tethys Seaway.

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References

Alcock, A. 1898. The Family Xanthidae: The Brachyura Cyclometopa, Part I: Materials for a Carcinological Fauna of India, No. 3. Journal of the Asiatic Society of Bengal 67 (II:1): 67-233.

———. 1899. The Families Portunidae, Cancridae and Corystidae: The Brachyura Cyclometopa, Part II: Materials for a Carcinological Fauna of India, No. 3. Journal of the Asiatic Society of Bengal 68 (II:1): 1-104.

Bachmayer, F., and R. Mundlos. 1968. Die tertiären Krebse vom Helmstedt bei Braunschweig, Deutschland. Annalen des Naturhistorischen Museums in Wien 72: 649-692, pls. 1-15.

Bell, T. 1858. A Monograph of the fossil malacostracous Crustacea of Great Britain, Pt. I, Crustacea of the London Clay. Palaeontographical Society Monograph, London. 44 pp.

Beurlen, K. 1928. Die fossilen Dromiaceen und ihre Stammesgeschichte. Paläontologische Zeitschrift 10: 144-183.

Bittner, A. 1875. Die Brachyuren des vicentinischen Tertiärgebirges. Denkschriften der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe 34: 63-106, pls. 1-5.

Blow, W. C., and R. B. Manning. 1996. Preliminary descriptions of 25 new decapod crustaceans from the middle Eocene of the Carolinas, U.S.A. Tulane Studies in Geology and Paleontology 29: 1-26.

———, and R. B. Manning. 1997. A new genus, *Martinetta*, and two new species of xanthoid crabs from the middle Eocene of the Carolinas, U.S.A. Tulane Studies in Geology and Paleontology 29: 1-26.

———, and ———. 1998. *Eohalimede sandersi*, the correct name for the species described as *Eohalimede saundersi* Blow & Manning, 1997 (Crustacea: Decapoda: Xanthidae). Proceedings of the Biological Society of Washington 111: 409.

Böhm, J. 1891. Die Kreidebildungen des Fürbergs und Sulzbergs bei Siegsdorf in Oberbayern. Palaeontographica 38: 1-106, pls. 1-5.

Busulini, A., G. Tessier, and M. Vicentin. 1984. *Titanocarcinus aculeatus* nuova specie di brachiuro nell'eocene del Veneto (Crustacea, Decapoda). LAVORI-Società Veneziana di Scienze Naturali 9: 107-117.

Casadío, S., A. De Angeli, R. M. Feldmann, A. Garassino, J. L. Hetler, A. Parras, and C. E. Schweitzer. 2004. New decapod crustaceans (Thalassinidea, Galatheoidea, Brachyura) from the middle Oligocene of Patagonia, Argentina. Annals of Carnegie Museum 73: 25-47.

Collins, J. S. H., and S. L. Jakobsen. 1994. A synopsis of the biostratigraphic distribution of the crab genera (Crustacea, Decapoda) of the Danian (Palaeocene) of Denmark and Sweden. Bulletin of the Mizunami Fossil Museum 21: 35-46.

———, and ———. 2004 [imprint 2003]. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark. Bulletin of the Mizunami Fossil Museum 30: 63-96.

———, and S. F. Morris. 1978. New lower Tertiary crabs from Pakistan. Palaeontology 21: 957-981.

———, R. H. B. Fraaye, and J. W. M. Jagt. 1995. Late Cretaceous anomurans and brachyurans from the Maastrichtian type area. Acta Palaeontologica Polonica 40: 165-210.

Cuevas-Gozalo, M., M. E. Donselaar, and S. D. Nio. 1985. Eocene clastic tidal deposits in the Tremp-Graus Basin (Provs. of Lérida and Huesa). 6th European Regional Meeting I.A.S., Lérida, Guidebook Excursion no. 6: 215-266.

Dana, J. D. 1851. On the classification of the Cancroidea. American Journal of Science and Arts 12 (34): 121-131.

———. 1853. A review of the classification of Crustacea, with reference to certain principles of classification. In, United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, 1842 Under the Command of Charles Wilkes, U.S.N., 13: 1395-1592. Philadelphia: C. Sherman.

Davie, P. J. F. 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda Anomura, Brachyura. In, A. Wells and W. W. K. Houston (eds.), Zoological Catalogue of Australia, 19.3B. CSIRO Publishing, Melbourne, Australia. 641 pp.

De Angeli, A., and C. Beschin. 2001. I crostacei fossili del territorio Vicentino. Natura Vicentina 5: 5-54.

Delle Cave, L. 1981. Catalogue of type specimens in the Invertebrate Palaeontological Collections of the Museum of Geology and Palaeontology of the University of Florence. (Italy). Crustacea, Decapoda. Atti della Società Toscana di Scienze Naturali, Memorie, Serie A 88: 43-50.

Ekdale, A. A., and R. G. Bromley. 1984. Sedimentology and ichnology of the Cretaceous-Tertiary boundary in Denmark: implications for the causes of the terminal Cretaceous extinction. Journal of Sedimentary Petrology 54: 681-703.

Feldmann, R. M., K. L. Bice, C. Schweitzer Hopkins, E. W. Salva, and K. Pickford. 1998. Decapod crustaceans from the Eocene Castle Hayne Limestone, North Carolina: paleoceanographic implications. The Paleontological Society Memoir 48 (Supplement to Journal of Paleontology, 72). 28 pp.

Fischer-Benzon, R. von. 1866. Über das relative Alter des Faxekalkes und über die in demselben vorkommenden Anomuren und Brachyuren. Kiel: Schwers'sche Buchhandlung. 30 pp., pls. 1-5.

Forir, H. 1887. Contributions à l'étude du système crétacé de la Belgique. Annales de la Societé Géologique de Belgique 14: 25-56, pls. 1, 2.

Förster, R. 1970. Zwei neue brachyure Krebse aus dem Paläozän des Haunsberges nördlich von Salzburg. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 10: 241-252.

Fraaye, R. H. B. 1994. Early Paleocene crabs (Crustacea, Decapoda) from the Middle Vistula Valley, Central Poland. Acta Geologica Polonica 44: 261-266, pls. 1, 2.

Fraaije, R. H. B. 2003. Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. Contributions to Zoology 72: 119-130.

Garassino, A., A. De Angeli, L. M. Gallo, and G. Pasini. 2004. Brachyuran and anomuran fauna from the Cenozoic of Piedmont (NW Italy). Atti della Società Italiana di Scienze naturali e del Museo civico di Storia naturale in Milano 145: 251-281.

Gistel, J. 1848. Naturgeschichte des Thierreiches für höhere Schulen bearbeitet. Hoffmann'sche Verlags-Buchhandlung, Stuttgart. 216 pp., 32 pls.

Glaessner, M. F. 1928. Die Dekapodenfauna des österreichischen Jungtertiärs. Jahrbuch der Geologischen Bundesanstalt 78 (1-2): 161-219, pls. 3, 4.

———. 1929. Crustacea Decapoda, 464 pp. In, F. J. Pompeckj (ed.), Fossilium Catalogus, I. Animalia. W. Junk, Berlin.

———. 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. New Zealand Department of Scientific and Industrial Research, New Zealand Geological Survey, Palaeontological Bulletin 31: 5-79.

———. 1969. Decapoda, pp. R400-R566, R626-R628. In, R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part R, Arthropoda 4. Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.

Guinot, D. 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. Compte Rendu de l'Académie des Sciences, Paris, Serie D 285: 1049-1052.

———. 1989. Le genre *Carcinoplax* H. Milne Edwards, 1852 (Crustacea, Brachyura: Goneplacidae). pp. 265-345. In, J. Forest (ed.), Résultats des Campagnes MUSORSTOM. Vol. 5 Mémoires du Muséum National d'Histoire Naturelle, (A)144.

Jakobsen, S. L., and J. S. H. Collins. 1997. New middle Danian species of anomuran and brachyuran crabs from Fakse, Denmark. Bulletin of the Geological Society of Denmark 44: 89-100.

Karasawa, H., and H. Kato. 2003. The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records. Paleontological Research 7: 129-151.

———, and C. E. Schweitzer. 2004. Revision of the genus *Glyphithyreus* Reuss, 1859 (Crustacea, Decapoda, Brachyura, Xanthoidea) and recognition of a new genus. Paleontological Research 8: 143-154.

———, and ———. 2006. A new classification of the Xanthoidea sensu lato (Crustacea: Decapoda: Brachyura) based on phylogenetic analysis and traditional systematics and evaluation of all fossil Xanthoidea sensu lato. Contributions to Zoology, 75: 23-72.

———, ———, and H. Kato. 2005. Phylogenetic analysis of Xanthoidea *sensu lato* (Decapoda: Brachyura), fossil and recent, using adult morphological characters. p. 132. In, Books of Abstracts, Sixth International Crustacean Congress, Glasgow, Scotland, UK, 18-22 July 2005.

Kauffman, E. G., and P. J. Harries. 1996. The importance of crisis progenitors in recovery from mass extinction. pp. 15-39. In, M. B. Hart, (ed.), Biotic Recovery from Mass Extinction Geological Society Special Publication 102, London.

Latreille, P. A. 1802-1803. Histoire naturelle, générale et particulière, des crustacés et des insectes. Vol. 3. F. Dufart, Paris, France. 467 pp.

Lórenthey, E. 1898. Beiträge zur Decapodenfauna des Ungarischen Tertiärs. Természetrajzi Füzetek 21: 1-133, pls. 1-9.

———. 1902. Neuere Beiträge zur Tertiären Decapodenfauna Ungarns. Mathematische und Naturwissenschaftliche Berichte aus Ungarn 18: 98-120, pls. 1, 2.

———, and K. Beurlen. 1929. Die fossilen Decapoden der Länder der Ungarischen Krone. Geologica Hungarica, Series Palaeontologica 3: 421 pp., 16 pls.

MacLeay, W. S. 1838. On the Brachyurous Decapod Crustacea brought from the Cape by Dr. Smith, pp. 53-71. In, A. Smith (ed.), Illustrations of the Annulosa of South Africa; consisting chiefly of the Objects of Natural History Collected during an Expedition into the Interior of South Africa, in the Years 1834, 1835, and 1836; fitted out by the Cape of Good Hope Association for Exploring Central Africa. Smith, Elder, and Company, London.

Martins-Neto, R. G. 2001. Review of some Crustacea (Isopoda and Decapoda) from Brazilian deposits (Paleozoic, Mesozoic, and Cenozoic) with descriptions of new taxa. Acta Geologica Leopoldensia 34 (52/53): 237-254.

Meyer, H. von. 1863. Tertiaere Decapoden aus den Alpen, von Oeningen und dem Taunus. Palaeontographica 10: 147-178, pls. 16-19.

Milne Edwards, A. 1862-1865. Monographie des crustacés de la famille cancériens. Annales des Sciences Naturelles, Zoologie, Series 4, 18 (1862): 31-85 pl. 1-10; 20(1863):273-324, pl. 5-12; Series 5, 1(1864):31-88, pl. 3-9; 3(1865):297-351, pl. 5-10.

Milne Edwards, H. 1834. Histoire Naturelle des Crustacés comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux. Libraire Encyclopédique de Roret, Imprimerie et Fonderie de Fain, Paris, 468 pp., Atlas, 32 pp., 42 pls.

Morris, S. F. 1980. Catalogue of the type and figured specimens of fossil Crustacea (excl. Ostracoda), Chelicerata, Myriapoda and Pycnogonidae in the British Museum (Natural History). Trustees of the British Museum (Natural History), Great Britain. 53 pp., 3 pls.

Müller, P. 1984. Decapod Crustacea of the Badenian. Geologica Hungarica, series Palaeontologica 42: 1-317.

———. 1993. Neogene decapod crustaceans from Catalonia. Scripta Musei Geologici Seminarii Barcinonensis 225: 1-39.

Ng, P. K. L. 1987. The Indo-Pacific Pilumnidae II. A revision of the genus *Rhizopa* Stimpson, 1858, and the status of the Rhizopinae Stimpson, 1858 (Crustacea, Decapoda, Brachyura). Indo-Malayan Zoology 4: 69-111.

———, C.-H. Wang, P.-H. Ho, and H.-T. Shih. 2001. An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). National Taiwan Museum Special Publication Series 11: 1-86.

Ortmann, A. E. 1892. Die Decapoden-Krebse der Strassburger Museums. V. Theil. Die Abteilungen Hippidae, Dromiidae, und Oxystomata. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie, und Biologie der Thiere 6: 532-588, pl. 26.

———. 1893. Abtheilung: Brachyura (Brachyura genuina Boas), II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Die Decapoden-Krebse der Strassburger Museums, VII. Theil. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie, und Biologie der Thiere 7: 411-495, pl. 17.

Rathbun, M. J. 1919. West Indian Tertiary decapod crustaceans, pp. 159-184, pls. 1-9. In, T. W. Vaughn, (ed.), Contributions to the Geology and Paleontology of the West Indies. Carnegie Institution of Washington Publication No. 291, Washington, D.C.

———. 1930. Fossil decapod crustaceans from Mexico. Proceedings of the United States National Museum 78: 1-10, pls. 1-6.

———. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. Geological Society of America, Special Paper 2. 160 pp.

Reuss, A. 1859. Zur Kenntnis fossiler Krabben. Denkschriften der kaiserlichen Akademie der Wissenschaften zu Wien 17: 1-90, pls. 1-24.

Ristori, G. 1886. I Crostacei Brachyiuri e Anomuri del Pliocene Italiano. Bollettino della Società Geologica Italiana 5: 93-119.

———. 1891. Contributo alla fauna carcinologica del Pliocene Italiano. Atti della Società Toscana di Scienze Naturali, Memorie 11: 1-25, pl. 1.

———. 1896. Crostacei neogenici di Sardegna e di alcune altre località Italiane. Bollettino della Società Geologica Italiana 15: 504-513, pl. 12.

Sakai, K. (ed.). 2004. Crabs of Japan. World Biodiversity Database CD-ROM Series. Biodiversity Center of ETI, Amsterdam and UNESCO-Publishing, Paris.

Samouelle, G. 1819. The entomologist's useful compendium; or an introduction to the knowledge of British Insects. Thomas Boys, London. 496 pp.

Schafhäutl, K. E. 1851. Geognostische Untersuchungen des südbayerischen Alpengebirges. Geognostische Untersuchungen der Bayerischen Lande, unter Leitung des Conservators Dr. Schafhäutl, 1. Beitrag. 206 pp., 44 pls. München: Literarisch-artistische Anstalt.

Schweitzer, C. E. 2003. Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura). Journal of Paleontology 77: 1107-1128.

———. 2005. The genus *Xanthilites* Bell and a new xanthoid family (Crustacea: Decapoda: Brachyura: Xanthoidea): new hypotheses on the origin of the Xanthoidea Macleay, 1838. Journal of Paleontology 79: 277-295.

———, and R. M. Feldmann. 2000a. New species of calappid crabs from Western North America and reconsideration of the Calappidae de Haan sensu lato. Journal of Paleontology 74: 230-246.

———, and ———. 2000b. New fossil portunids from Washington, USA, and Argentina, and a re-evaluation of generic and family relationships within the Portunoidea Rafinesque, 1815 (Decapoda: Brachyura). Journal of Paleontology 74: 636-653.

———, and ———. 2005. Decapod crustaceans, the K/P event, and Palaeocene recovery, pp. 17-53. In, S. Koenemann and R. A. Jenner, (eds.), Crustacea and Arthropod Relationships. Taylor and Francis Group, New York.

———, and H. Karasawa. 2004. Revision of *Amydrocarcinus* and *Palaeograpsus* (Decapoda: Brachyura: Xanthoidea) with definition of three new genera. Paleontological Research 8: 71-86.

———, R. M. Feldmann, and P. Gingerich. 2004. New decapods (Crustacea) from the Eocene of Pakistan and a revision of *Lobonotus* A. Milne-Edwards, 1864. Contributions of the Museum of Paleontology, University of Michigan 31: 89-118.

———, ———, G. Gonzáles-Barba, and F. J. Vega. 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico, and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. The Paleontological Society Memoir 59 (Supplement to Journal of Paleontology, 76). 43 pp.

———, ———, A. B. Tucker, and R. E. Berglund. 2000. Eocene decapod crustaceans from Pulali Point, Washington. Annals of Carnegie Museum 69: 23-67.

Secretan, S. 1961. Une nouvelle espèce de Xanthides au Maroc: *Titanocarcinus meridionalis* nov. sp. Notes du Service Géologique du Maroc 20: 39-57.

———. 1964. Les crustacés décapodes du Jurassique supérieur et du Crétacé de Madagascar. Mémoires du Muséum National d'Histoire Naturelle, (C) 14: 224 pp., 20 pls.

Segerberg, K. O. 1900. De anomura och brachyura dekapoderna inom Skandinaviens Yngre krita. Geologiska Föreningens i Stockholm Förhandlingar 22: 347-387, pls. 7-9.

Sismonda, E. 1846. Descrizione dei pesci e dei crostacei fossili del piemonte. Memorie della Reale Accademia delle Scienze di Torino, Serie Seconda 10: 88 pp., 3 pls.

Stenzel, H. B. 1935. Middle Eocene and Oligocene decapod crustaceans from Texas, Louisiana, and Mississippi. The American Midland Naturalist 16: 379-400.

Števčić, Z. 1991. Note on some rare and aberrant Australian crabs. Beagle, Records of the Northern Territory Museum of Arts and Sciences 8: 121-134.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit W. Stimpson. Pars. V. Crustacea Ocypodoidea. Proceedings of the Academy of Natural Sciences, Philadelphia 10: 93-110.

———. 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L. F. de Pourtalès, Assist. U. S. Coast Survey. Bulletin of the Museum of Comparative Zoology at Harvard College 2: 109-160.

Vía, L. 1969. Crustáceos Decápodos del Eoceno español. Pirineos 91-94: 479 pp.

Waugh, D. A., R. M. Feldmann, R. S. Crawford, S. L. Jakobsen, and K. B. Thomas. 2004. Epibiont preservational and observational bias in fossil marine decapods. Journal of Paleontology 78: 961-972.

Yanakevich, A. N. 1977. Middle Miocene Reefs of Moldavia. Ministry of Public Education of Moldavia, Soviet Socialist Republic, Kishinev, Moldavia, 100+ pp. [in Russian].

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