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A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata)

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Abstract

Abundant fossil material of extinct brachyurans has revealed morphological details hitherto rarely used in palaeontological studies. Detailed comparisons between extant and extinct material have been carried out, with an emphasis on thoracic sternum, abdomen and appendages. Documented for the first time is the unique character of Raninoidea De Haan, 1839, their 'gymnopleurity', which is not found in their predecessors, the Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929. Palaeocorystidae, together with four other families (Camarocarcinidae Feldmann, Li & Schweitzer, 2008; Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008; Necrocarcinidae Förster, 1968 **emend.**; and Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a **emend**.), is assigned here to the superfamily Palaeocorystoidea, of similar rank to Raninoidea. Both Raninoidea and Palaeocorystoidea are afforded a subsection rank and referred to as subsection Raninoidia De Haan, 1839 **emend**. New or emended diagnoses are provided for all higher taxonomic levels, and all members of Raninoidia are listed in an appendix. A unique abdominal holding structure, the double peg, is described for the first time. Its gradual evolution is documented and the phylogenetic implications are discussed. Comparative morphology of the thoracic sternum, abdominal holding structures, the sternum-pterygostome configuration, respiratory physiology and spermathecae, all reveal polarities of the raninoidian clade. The configuration of the sternum with the pterygostome, which is related to body strength and respiratory physiological efficiency, differs significantly between the two superfamilies, Raninoidea showing a derived condition. An evolutionary lineage, leading from Palaeocorystidae, via Lyreididae to Raninidae is recognised, and an intermediate form, *Marylyreidus punctatus* **n. comb.**, is discussed. Several hitherto unknown structures in extant raninoids, an obstruction system for the abdomen and a telson protection valve, are documented. The cryptic spermathecal apertures of raninoids, so far barely understood, are re-examined and compared to those of palaeocorystoids. The phylogeny of Podotremata, often debated in the recent literature, is discussed anew on the basis of these observations. A position of Raninoidea within Eubrachyura, recently claimed by several authors, cannot be maintained, an observation supported by documentation of the basal condition of Raninoidia. A new basal lyreidid clade, Marylyreidinae **n. subfam.**, is erected, whereas new genera and species include *Antonioranina* **n. gen.** (Cyrtorhininae), *Bournelyreidus teodorii* **n. gen., n. sp.** (Lyreidinae), *Cenocorystes bretoni* **n. sp.** (Palaeocorystidae), *Cenomanocarcinus cantabricus* **n. sp.** (Cenomanocarcinidae), *Eosymethis aragonensis* **n. gen., n. sp.** (Symethinae), *Eucorystes iserbyti* **n. sp.**, *Eucorystes navarrensis* **n. sp.** (both Palaeocorystidae), *Ferroranina tamilnadu* **n. gen., n. sp.** (Palaeocorystidae), *Joeranina gaspari* **n. gen., n. sp.** (Palaeocorystidae), *Marylyreidus* **n. gen.** (Marylyreidinae **n. subfam.**), *Paranecrocarcinus balla* **n. sp.** (Paranecrocarcininae), *Symethoides monmouthorum* **n. gen., n. sp.** (Symethinae) and *Vegaranina* **n. gen.** (Ranininae). Several raninoid and palaeocorystoid genera are revised, and emended diagnoses given.

Key words: Crustacea, Decapoda, Brachyura, Podotremata, Raninoidia, Palaeocorystoidea, Raninoidea, Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae, Orithopsidae, Palaeocorystidae, revision, comparative morphology, back-burrowing, burying, respiration, abdominal holding, spermatheca, evolution, phylogeny, new subfamily, new genera, new species, Cretaceous, Paleogene.

Introduction

The fossil record of the superfamily Palaeocorystoidea Lőrenthey *in* Lőrenthey & Beurlen, 1929 **emend.**, dates back to the Lower Cretaceous (Hauterivian, 136.4–130 Ma); the clade went extinct during the Oligocene (Paleogene, 33.9–23.03 Ma). Currently, more than 90 species are recorded as members of the superfamily. Palaeocorystoids show clear podotreme traits that do not differ much from those of basal Podotremata Guinot, 1977, except for their adaptations to a burying mode of life, and they evidently represent the sister group of Raninoidea De Haan, 1839.

The Raninoidea ranges from the late Albian (103–99 Ma) to the present day and includes a large number of living and fossil representatives (see Appendix). The extant Raninoidea was hitherto considered to comprise but a single family, Raninidae, with six subfamilies (Ahyong *et al.* 2007: 584; 2009: vii, 135, as section Raninoida; Ng *et al.* 2008: 42; 2010: 213, as superfamily Raninoidea; De Grave *et al.* 2009: 5, 7, 28, table 1, as section Raninoida; Ng *et al.* 2009: 16, fig. 5, as section Raninoida; Karasawa *et al*. 2011: 549, as section Raninoida). There is therefore a rather high diversity of opinions for a relatively small number of taxa, i.e. 12 genera and 46 species. In fossil assemblages, a considerably larger number of taxa are known (De Grave *et al.* 2009: table 1). A total of 182 fossil species (see Appendix) in 38 genera (Table 7) are listed here, not counting the species or genera placed in *incertae sedis.* The number of fossil species is therefore four times the number of extant species.

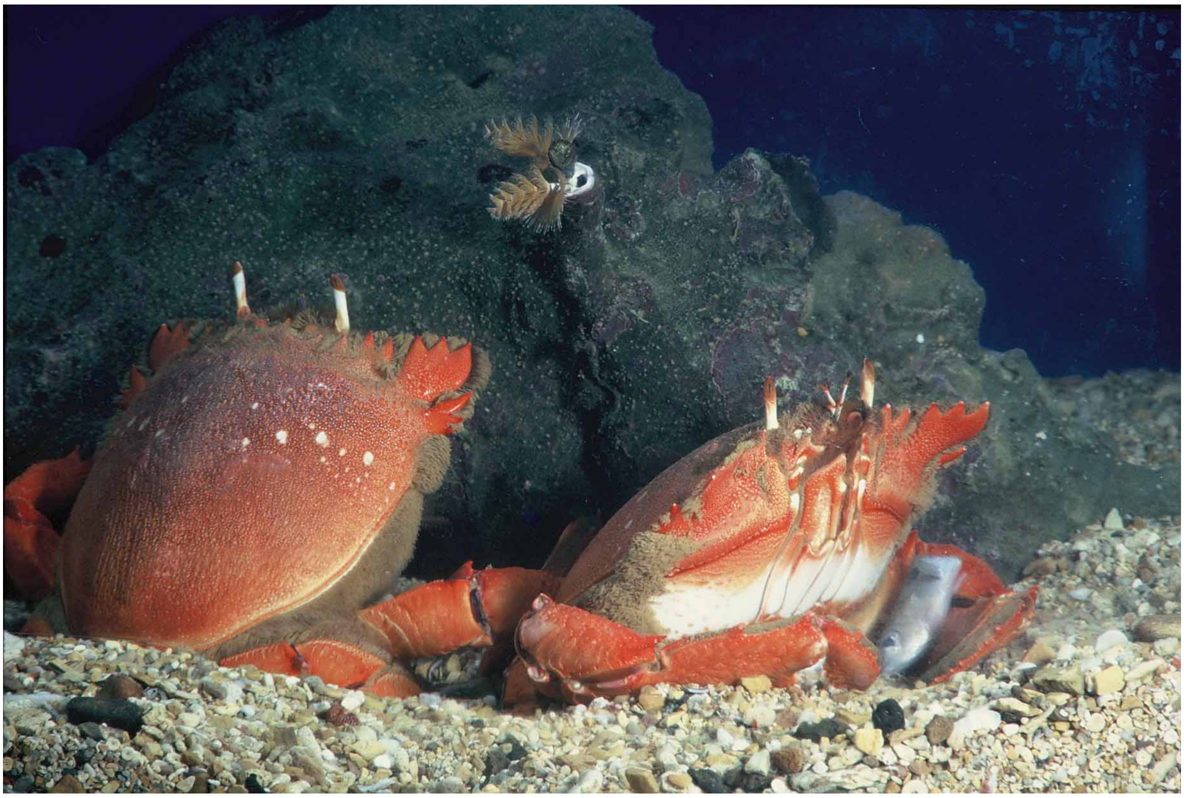


FIGURE 1. *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), half buried. Photograph by R. Catala-Stucki (1972) in aquarium, Nouméa, New Caledonia.

The relative paucity of modern raninoid taxa, coupled with their presence in nearly all oceans, provides strong evidence that they are best regarded as relict faunas. The long survival rate of raninoids over geological time is probably associated with their adaptability to employ different mechanisms for respiration (see Bourne 1922b), and their functional morphology that are related to back burrowing (i.e., body shape, modified pereiopods, cuticle microstructure). These adaptations can be traced from the earliest fossil members to the present-day representatives.

The Lyreidinae Guinot, 1993, is here elevated to the rank of family, while all remaining raninoideans are referred to Raninidae. The family includes two subfamilies, Lyreidinae and Marylyreidinae **n. subfam.** The Raninidae **emend.** is here understood to comprise five subfamilies, viz. Cyrtorhininae Guinot, 1993, Notopodinae Serène & Umali, 1972, Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929, Ranininae De Haan, 1839, and Symethinae Goeke, 1981 (Tables 1, 2). Members of the subfamilies Cyrtorhininae and Symethinae have unique morphologies that easily distinguish them from the other raninoideans. The interrelationships of Raninidae, as shown herein, must be regarded as preliminary and beyond the scope of the present paper. A revision of extant Raninoidea is in preparation by M. Tavares (pers. comm., 2010). This text on extant Raninoidea is thus only a critical examination of the main raninoid features, based mostly on Bourne (1922b) and on our own comparative work on fossil and modern taxa. The aim of this examination is to combine the distinctive data sets locked in the extremely diverse patterns displayed by extant taxa with the stratigraphic (temporal) component based on fossil evidence.

As expected, fossil brachyurans provide unique sets of morphological data, which complement our understanding of higher-level taxa. The importance of fossils in phylogenetic reconstructions and the major problems caused by integration of fossil data in neontological evolutionary biology and classification schemes has been well established (see Hennig 1966; Nelson 1978; Patterson 1981; Wiley 1981; Novacek 1992; Goujet & Tassy 1997; Grantham 2004). Simultaneous analysis of both fossil and extant (terminal) taxa will certainly contribute to phylogenetic reconstructions, as well as provide information on the sequence and timing of evolutionary changes.

TABLE 1. Proposed classification of the subsection Raninoidia De Haan, 1839 **emend.** (exclusively fossil taxa are indicated by †).

- Superfamily †Palaeocorystoidea Lőrenthey in Lőrenthey & Beurlen 1929 **new status**
  - Family †Camarocarcinidae Feldmann, Li & Schweitzer, 2008
  - Family †Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008
  - Family †Necrocarcinidae Förster, 1968
    - Subfamily †Necrocarcininae Förster, 1968
    - Subfamily †Paranecrocarcininae Fraaije, Van Bakel, Jagt & Artal, 2008
  - Family †Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003
  - Family †Palaeocorystidae Lőrenthey in Lőrenthey & Beurlen 1929 **new status**
- Superfamily Raninoidea De Haan, 1839
  - Family Lyreididae Guinot, 1993 **new status**
    - Subfamily Lyreidinae Guinot, 1993
    - Subfamily †Marylyreidinae **n. subfam.**
  - Family Raninidae De Haan, 1839
    - Subfamily Ranininae De Haan, 1839
    - Subfamily Notopodinae Serène & Umali, 1972
    - Subfamily Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen 1929
    - Subfamily Cyrtorhininae Guinot, 1993*
    - Subfamily Symethinae Goeke, 1981*

**Preliminary rank*

The infraorder Brachyura Latreille, 1802, within the order Decapoda Latreille, 1802, is here treated as comprising two sections, Podotremata Guinot, 1977 and Eubrachyura de Saint Laurent, 1980. In adopting the preliminary arrangement proposed by Guinot et al. (2008), four subsections can be distinguised in section Podotremata, viz. Dromioidia De Haan, 1833 (= Dromiacea De Haan, 1833, **emend.**), Homoloidia De Haan, 1839, Cyclodorippoidia Ortmann, 1892, and Raninoidia De Haan, 1839 (Table 2; Guinot, Tavares & Castro in press).

While the monophyly of the section Eubrachyura and its two subsections, Heterotremata Guinot, 1977, and Thoracotremata Guinot, 1977, is supported by a substantial body of data, the monophyly of Podotremata has been seriously questioned by several authors, primarily on molecular analyses and the taxon has even been considered ‘untenable’ (Ahyong *et al.* 2007: 576, 581). Based on adult morphology, the monophyly of Podotremata was also doubted by Scholtz & McLay (2009) and Karasawa *et al.* (2011). We disagree with their outcome. New evidence and arguments presented here merit the recognition of Podotremata as a monophyletic taxon (see *Phylogeny of the Raninoidia* below; Guinot, Tavares & Castro in press). The Raninoidia (as well as Cyclodorippoidia) was considered as a separate section in the classification of living and fossil crabs by De Grave *et al.* (2009: 28, as Raninoida), but as subsection of Eubrachyura by Martin & Davis (2001: 74) and Schweitzer *et al.* (2010: 70). There is clearly no consensus among current workers over the precise position of the Raninoidea, and is probably a result of different interpretations of the fundamental morphological traits. While the inclusion of the Raninoidia (and Cyclodorippoidia) in the Podoremata is recently debated, removal of these two groups is unjustified on morphological grounds and the palaeontological record. It would also raise new and unresolved problems (see *Phylogeny of the Raninoidia* below).

The status of Raninoidea is therefore a focal point in a better understanding of the Brachyura. A complete picture of the evolutionary history of the long-existing and complex raninoidian clade is therefore of prime importance. Such a picture can only be obtained by incorporating fossil taxa into the phylogenetic context of extant relatives. New data are here documented to explore the effects of combining morphological traits of both modern and extinct taxa. Up to this study, the distinctive features of Palaeocorystidae have not been recognised, which is why they have always been considered only as a subfamily of Raninidae. It is surprising to see that previous authors failed to notice, for instance, the absence of exposed pleurites in the palaeocorystids. The palaeocorystids have a unique set of features that places them among several unusual, extinct raninoidian families, here assembled for the first time in a separate superfamily, Palaeocorystoidea, placed at the root of Raninoidia (see *Phylogeny of the Raninoidia* below). The present in-depth study of extinct raninoidians has now led to a better understanding of their taxonomic position, phylogenetic relationships and evolutionary pathways.

It should be pointed out that Raninoidea was included in Eubrachyura by Martin & Davis (2001: 74) and Schweitzer *et al.* (2010: 70, the Palaeocorystinae being a subfamily of Raninidae). However, such a position cannot be substantiated and is, in fact, completely untenable (see *Phylogeny of the Raninoidia* below). Raninoidian crabs are true podotremes: female and male gonopores are situated on the appendages on P3 and P5 coxae, respectively, thus exhibiting the generalised condition (as in other Decapoda) (Fig. 39D); a paired spermatheca is present (Fig. 57C, D), unconnected with the oviducts and showing a basic structure similar to that of other primitive crabs, i.e. lying within endosternite 7/8. Other authors accept this observation and most retain them in Podotremata (see Ng *et al.* 2008). In Palaeocorystoidea, the spermathecal aperture is also at the extremity of the sternal suture 7/8, corresponding to a paired spermatheca at this level, a condition unique to Podotremata (Guinot & Tavares 2001: fig. 10A–D, F–J). However, the position of the spermathecal aperture of Raninoidia is modified (Gordon 1963; Hartnoll 1979) as a result of extreme narrowing of the body, including the thoracic sternum, initiated by the highly specialised burying (see *Modifications for a burying mode of life* below).

TABLE 2. Proposed revised classification of Brachyura Latreille, 1802 (extant taxa only).

Section Podotremata Guinot, 1977
Subsection Dromioidia De Haan, 1833 (= Dromiacea De Haan, 1833)
Superfamily Homolodromioidea Alcock, 1900
Family Homolodromiidae Alcock, 1900
Superfamily Dromioidea De Haan, 1833
Family Dromiidae De Haan, 1833
Subfamily Dromiinae De Haan, 1833
Subfamily Hypoconchinae Guinot & Tavares, 2003
Subfamily Sphaerodromiinae Guinot & Tavares, 2003
Family Dynomenidae Ortmann, 1892
Subfamily Acanthodromiinae Guinot, 2008
Subfamily Dynomeninae Ortmann, 1892
Subfamily Metadynomeninae Guinot, 2008
Subfamily Paradynomeninae Guinot, 2008
Subsection Homoloidia De Haan, 1839
Family Homolidae De Haan, 1839
Family Latreilliidae Stimpson, 1858
Family Poupiniidae Guinot, 1991
Subsection Cyclodorippoidia Ortmann, 1892
Superfamily Cyclodorippoidea Ortmann, 1892
Family Cyclodorippidae Ortmann, 1892
Subfamily Cyclodorippinae Ortmann, 1892
Subfamily Xeinostomatinae Tavares, 1992
Family Cymonomidae Bouvier, 1897
Family Phyllotymolinidae Tavares, 1998
Subsection Raninoidia De Haan, 1839
Superfamily Raninoidea De Haan, 1839
Family Lyreididae Guinot, 1993 **new status**
Family Raninidae De Haan, 1839
Subfamily Ranininae De Haan, 1839
Subfamily Notopodinae Serène & Umali, 1972
Subfamily Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929
Subfamily Cyrtorhininae Guinot, 1993*
Subfamily Symethinae Goeke, 1981*
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977**
Subsection Thoracotremata Guinot, 1977**

**Preliminary rank*
***Here not divided further*

The fossil record provides indisputable data that Podotremata was much more diverse than extant faunas indicate. While Ng *et al.* (2008) listed 10 extant podotreme families, De Grave *et al.* (2009: table 1) noted, in both extant and fossil faunas, 18 families (assigned to three sections: Dromiacea, Raninoida and Cyclodorippoida). The brachyuran evolutionary tree appears complex and deep, with a large number of ancient branching events (with, most probably, also unknown extinct lineages). Several recently discovered fossil primitive crabs, currently under study, confirm such a hypothesis. Some newly discovered Cretaceous dromioidian crabs with well-preserved ventral morphology will shed new light on the taxonomic position of several genera and families. In addition, new and well-preserved material of Etyidae is currently being studied by us, and characters described by Guinot & Tavares (2001) may be complemented for a better understanding of the phylogenetic position of this family. All these new fossil data must be taken into account in an attempt to reconstruct a more complete podotreme phylogeny than was hitherto possible.

Presented here is a detailed morphological study of members of the subsection Raninoidia De Haan, 1839 **emend.**, as well as a taxonomic review and phylogenetic analysis of the group, using a combination of morphological data for both extant and extinct taxa. The incompleteness of the fossil record has substantially hindered our understanding of the superfamily Raninoidea, but the extensive material available on hand in the present study effectively overcomes this hurdle. Nearly all fossil taxa have been examined, several new ones discovered and named, and a number of transitional forms recognised. In addition, and for the first time, numerous specimens representing different families have been prepared in order to expose ventral structures. In this way, various previously unknown morphological details have been collected. Comparative morphology of combined fossil and extant raninoid taxa has led to a hypothesis on the polarity of the abdominal holding mechanism, configuration of the thoracic sternum, partial exposure of thoracic pleurites and modification of respiratory physiology, all of which are related to a marked specialisation for a burying mode of life. The incorporation of extinct taxa into the phylogenetic context of their modern relatives has led to a more complete picture of the evolutionary history of the long-existing clade Raninoidia.

As a result, a new classification is proposed for raninoidian crabs. The Palaeocorystinae Lőrenthey *in* Lőrenthey & Beurlen, 1929, is elevated to the rank of superfamily, Palaeocorystoidea Lőrenthey *in* Lőrenthey & Beurlen, 1929 **new status**. The subsection Raninoidia **emend.** is divided into two superfamilies, namely the exclusively extinct Palaeocorystoidea **new status** and Raninoidea De Haan, 1839, which comprises both fossil and extant taxa. The Palaeocorystoidea embraces five families: Camarocarcinidae Feldmann, Li & Schweitzer, 2008 **emend.**, Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008, Necrocarcinidae Förster, 1968 **emend.**, Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a **emend.** and Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929 **new status**. Raninoidea is here divided into two families: Lyreididae Guinot, 1993b **new status** and Raninidae De Haan, 1839 **emend.** (Table 1). The numerous taxonomic changes proposed are listed in the Appendix, which lists all members of Raninoidia, with stratigraphic distribution and geographic occurrence, synonymy and references.

Material and methods

Preparation of specimens. Specimens were mechanically prepared under a LOMO MBS-10 stereomicroscope, using needles and scalpels. Needles were manually sharpened with a grinding pad. Pneumatic airscribes of a type designed specifically for delicate cleansing under a microscope were used: Micro-jack #2 and #3 of Paleotools, Inc. A selection of specimens was prepared specifically to reveal novel features, or to complement descriptions. In cases where more than a single specimen retained the abdomen, but the thoracic sternum was not exposed in any specimen, some abdomens were prepared away to expose details of the sternum such as the spermathecae, or the abdominal holding system. Specimens to be cast were first thoroughly cleansed so that any cuticle remains were removed in order to to expose the natural external mould, which could provide additional data after casting.

Moulding. Specimens were impregnated with woodglue (EN204-D3) dissolved in water, to increase rigidity. Subsequently they were treated with releasing wax to facilitate rubber to flow over the finest details, prevent micro air bubbles, and release the original specimen from the mould after the silicone rubber had set. Tin-cured silicone rubber was applied in a thin, transparent film blown with an airgun to prevent micro air bubbles from contacting the surface.

Photography. Specimens were coated with ammonium chloride, photographed using a Nikon digital SLR in aperture priority, Micro-nikkor 60 mm macro lens, and, in several occasions, extension tubes. A copy stand was used, and a Euromex coldlight source for illumination. In some cases a polyurethane cast or silicone mould (of the original negative imprint) was used. Post-processing was done in Paint Shop Pro or Photoshop; curves were adjusted for white balance and contrast, the sharpness slightly enhanced with an 'unsharp mask'. The original background was erased with selecting tools, to ensure an even, black background.

Morphological descriptions. For suprageneric taxa, primitive ones are treated first before derived ones, whereas genera and species are listed in alphabetical order.

Descriptions of the ventral surface are made with the crab seen in ventral view; in a lower level for sternites 1–3 thus means these sternites lie deeper.

Comparison of cuticle microstructures has proved very useful, with the constructive work of Waugh *et al.* (2009) as a guide. The terminology used by those authors is adopted here; for description and discussion of fungiform, inclined and upright nodes, pits, setal pits and perforations, reference is made to Waugh *et al.* (2009: fig. 1). The anterior thoracic sternites are often described as 'crown shaped' or 'diamond shaped'. The difference between these is that the former term covers those types in which only the apex is pointed or angular, whereas the latter is employed to refer to those with three anterior pointed or angular corners.

The numbering of thoracic elements may cause confusion when they are used for non-homologous parts. Secretan-Rey (2002: 85, 86) defined the axial skeleton as follows:

> '*Le squelette axial céphalothoracique ne comprend ni les éléments insegmentés (carapace et épimère branchiostégial), ni les appendices. Il se compose des sclérites simples externes ventraux (ou sternites), dorsaux (ou tergites) (lorsqu'ils n'ont pas été 'absorbés' par la carapace), des sclérites simples externes latéraux (ou pleurites) et des sclérites doubles qu'ils émettent à l'intérieur du corps, ou phragmes endosternaux et endopleuraux.*' [The axial cephalothoracic skeleton does not include either unsegmented elements (carapace and branchiostegal epimere) or appendages. It is composed of simple external sclerites, either ventral (sternites) or dorsal (tergites) (if they have not been 'absorbed' into the carapace), of simple external lateral sclerites (pleurites) and of double sclerites that are emitted from the interior of the body, or endosternal and endopleural phragmae].

The '*sclérites simples externs latéraux (ou pleurites)*' of Secretan-Rey (2002) correspond to the 'epimera' (or 'epimeral walls') of Bourne (1922b: 37, 38) and of earlier authors (e.g., Pearson 1908) or even of modern ones (e.g., Feldmann & Schweitzer 2010). The pleurites are covered in the normal brachyuran condition. Some of them, pleurites 5 to 7, are uncovered, thus becoming exposed in Raninoidea, hence the group name 'Gymnopleura' was used by Bourne (1922b). Here used is '**exposed pleurites'** for the externally exposed and highly calcified portion of pleurites 5 to 7 in Raninoidea. Usually, the internal portion of the pleurites is weakly calcified.

There are several ways of counting the somites of the body, plus their sternites and pleurites. Bourne (1922b) took into account an ocular somite, thus six cephalic somites in total (somites I–VI for eyestalk, antennule, antenna, mandibule, mx1 and mx2). After this, he counted the eight thoracic somites (somites VII–XIV for mxp1–mxp3, five pereiopods, P1–P5). He (Bourne 1922b: 53) assigned the thoracic sternites and pleurites (which he referred to as 'epimeres') accordingly, but named the first pair of pereiopods 'chelipeds' and referred to the walking legs as P1–P4, thus:

Somite, sternite and pleurite I for the eyestalk,
Somite, sternite and pleurite II for the antennule,
Somite, sternite and pleurite III for the antenna,
Somite, sternite and pleurite IV for the mandible,
Somite, sternite and pleurite V for mx1,
Somite, sternite and pleurite VI for mx2,
Somite, sternite and pleurite VII for mxp1,
Somite, sternite and pleurite VIII for mxp2,
Somite, sternite and pleurite IX for mxp3,
Somite, sternite and pleurite X for cheliped,
Somite, sternite and pleurite XI for P1,
Somite, sternite and pleurite XII for P2,
Somite, sternite and pleurite XIII for P3,
Somite, sternite and pleurite XIV for P4.

Secretan-Rey (2002: 91, table) employed nearly the same system; but she did not count an ocular somite (the eye is part of ‘segment 0’ in her table); thus her count differs from Bourne’s by one number. In addition, she did not distinguish the chelipeds from the other pereiopods, and used P1 for P5, as follows:

Somite, sternite and pleurite I for the antennule,
Somite, sternite and pleurite II for the antenna,
Somite, sternite and pleurite III for the mandible,
Somite, sternite and pleurite IV for mx1,
Somite, sternite and pleurite V for mx2,
Somite, sternite and pleurite VI for mxp1,
Somite, sternite and pleurite VII for mxp2,
Somite, sternite and pleurite VIII for mxp3,
Somite, sternite and pleurite IX for P1 (cheliped),
Somite, sternite and pleurite X for P2,
Somite, sternite and pleurite XI for P3,
Somite, sternite and pleurite XII for P4,
Somite, sternite and pleurite XIII for P5.

Only the eight thoracic somites are counted here, in accordance with Guinot (1977: 1050; 1979: 69) and Ng *et al.* (2008: 13), and numbered them and their sternites and pleurites as such. Instead of using P1 to P5, the term ‘cheliped’ was used for P1. For descriptive purposes, the following terms are used:

Proepistome for the septum between the antennules (i.e. antennulary sternite),
Epistome for the antennary sternite,
Endostome for the mandibular sternite,
Somite, sternite and pleurite 1 for mxp1,
Somite, sternite and pleurite 2 for mxp2,
Somite, sternite and pleurite 3 for mxp3,
Somite, sternite and pleurite 4 for P1 (cheliped),
Somite, sternite and pleurite 5 for P2,
Somite, sternite and pleurite 6 for P3,
Somite, sternite and pleurite 7 for P4,
Somite, sternite and pleurite 8 for P5.

Abbreviations

The following abbreviations are used to denote the repositories of material illustrated or referred to in the text:

AMNH	American Museum of Natural History, New York, U.S.A.
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
GAB	Gale A. Bishop Collection, housed in different institutions (see original papers for details)
GIK	Geologisches Institut der Universität zu Köln (Cologne), Germany
GSC	Geological Survey of Canada, Eastern Paleontology Division, Ottawa, Ontario, Canada
IRScNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium
MAB	Oertijdmuseum De Groene Poort, Boxtel, the Netherlands
MB	Museum für Naturkunde, Berlin, Germany
MCZ	Museo Civico ‘G. Zannato’, Montecchio Maggiore, Vicenza, Italy
MGSB	Museo Geológico del Seminario de Barcelona, Barcelona, Spain
MGUH	Geological Museum [currently Statens Naturhistorisk Museum], University of Copenhagen, Copenhagen, Denmark
MHN LM	Musée d’Histoire naturelle or ‘Musée Vert’, Le Mans, Sarthe, France

MNHN	Muséum national d’Histoire naturelle, Département Histoire de la Terre, Paris, France; and Département Milieux et peuplements aquatiques, Paris, France
NHM	The Natural History Museum, Department of Palaeontology, London, U.K.
NHMM	Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands
OUM	Oxford University Museum of Natural History, Oxford, U.K.
RME	Stiftung Ruhr Museum, Essen (Germany)
RGM	Nationaal Natuurhistorisch Museum (Naturalis), Leiden (the Netherlands)
SM	Sedgwick Museum, Cambridge, U.K.
SV	Società Veneziana di Science Naturali, Venezia, Italy
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
ZMC	Zoological Museum [currently Statens Naturhistorisk Museum], University of Copenhagen, Copenhagen, Denmark

The following abbreviations are used in the descriptions: P1, P2 coxa – pereiopod 1, coxa of pereiopod 2, etc.; mxp1, mxp2, mxp3 – first, second, third maxillipeds.

Used terminology

Abdomen: part of the body posterior to the cephalothorax, consisting of six somites (= segments) plus the telson, without tail fan; reduced and calcified, generally flexed under the body
Admedial: towards or near the medial level
Apodeme: movable invagination (appendicular) of the axial skeleton (according to Secretan-Rey 2002: 85)
Article: individual element of a crustacean appendage (not to be confused with a somite or segment of the body)
Arthrodial cavity: lateral chamber of every metamere, formed by both pleurite and sternite, in which the apodemes for the pereiopods are housed (see also Secretan-Rey 2002: 87, 91)
Axial skeleton: metamerised central skeletal structure of the body (often termed endoskeleton, endophragmal skeleton or internal skeleton)
Branchiostegite: posterior part of the carapace extending ventrolaterally over the branchial chamber
Buccal cavity: cavity in which the mouthparts lie
Buccal collar: rim or border on the pterygostome along the buccal frame (Fig. 50A, B, D), generally smooth and covered by the mxp3 exopod
Buccal frame: space enclosing the mouthparts, partly or entirely covered by the third maxillipeds
Condyle: small articular protuberance of article of the appendage fitting into a socket (named ‘gynglyme’ by H. Milne Edwards 1851: 52) [= ‘strophidium’ *sensu* Bourne (1922b: 33, footnote)]
Coxo-pleural condyle: condyle of the coxa articulating on the pleurite
Coxo-sternal condyle: condyle of the coxa articulating on the thoracic sternum
Distal: a position directed away from the element that is considered in relation (opposite of proximal)
Double peg: two teeth involved in abdominal holding situated on episternite 5, may be distally located on a short (Marylyreidinae **n. subfam.**) or long (Lyreidinae) hook-like projection (see Figs. 36F, 38B, 40C–E, 41C–F)
Endostome: bottom or floor of the buccal cavity, palate-like plate posterior to epistome; occasionally fused with side-flanges of epistome to form a water channel from and to the branchial chamber
Episternite: lateral extension of the sternite (often as pointed projection; may be more or less delimited by a ‘suture’), which bears the gynglyme receiving the condyle of the corresponding appendage (H. Milne Edwards 1834: 16, 31; 1851: 52)
Epistome: antennary sternite
Furrow: frontal carapace structures in Palaeocorystoidea
Gonopod: paired modified male abdominal appendages serving for sperm transfer
Gonopore: external opening of the oviduct or vas deferens
Groove: furrow-like structure on dorsal carapace following position of carapace regions, e.g., cervical, branchial, branchiocardiac grooves; furrow is only used here for frontal region
Gynglyme: socket receiving the articular protuberance (condyle, see above) for articulation [= ‘strophingium’ *sensu* Bourne (1922b: 33, footnote)]

Linea brachyura: often referred to as ‘pleural line’ or ‘pleural suture’, but Ng *et al*. (2008: 15) is followed for stability in terminology; the linea may be a decalcified line, and is the place of the dehiscence during exuviation

Mandible: third paired cephalic appendage and first pair of mouthparts, used to masticate food

Maxilliped: anterior paired thoracic appendage (three pairs present) modified to act as mouthparts

Milne-Edwards opening: inhalant opening in front of the cheliped or pre-chelipedal branchial opening for the flow of water to the gills

Mxp3 endopod: internal (medial) branch of the maxilliped (consisting of several articles; ischium, merus and palp)

Mxp3 exopod: lateral (admedial) branch of the maxilliped (primarily consiting of one article plus the palp, which is present (may be concealed), reduced or lost)

Orbit: paired cavity in carapace containing eyestalk

Orbital fissure or notch: slit in the orbital margin

Outgrowth on exposed pleurite: structure protruding from exposed pleurite, functioning as attachment of this to branchiostegite (‘projections’ of Bourne 1922b: 37) (Figs. 44A, B, 46A, B)

Oxystomian condition: buccal frame, endostome, mouthparts extended forwards to form pointed 'mouth', with equally extended and operculiform mxp3; openings for inhalant/exhalant current situated anteriorly

Phragma (-ae): internal double sclerite; fixed internal invagination of the skeleton, endosternal and endopleural

Pleopod: appendage of abdominal somite; the first two pleopods in males are the two pairs of gonopods

Plesiomorphic characters: an ancestral or primitive state of character

Pleuron (-a): ventral extension of tergite on each side of abdominal somite

Pleurite: single, lateral sclerite of body somite (often erroneously termed ‘epimere’)

Press-button: structure that functions as a ‘snap fastener’, typically consisting in Eubrachyura of a sternal prominence (sternite 5) and an abdominal socket (sixth abdominal somite)

Proepistome: antennulary sternite

Proximal: position nearest the element that is considered in relation (opposite of distal)

Pterygostome: ventral region of the carapace, on each side of the buccal frame

Sclerite: any hard cuticular (sclerified or calcified) plate of the skeleton constituting each somite (each metamer)

Socket (for abdominal holding): depression ventrally on sixth abdominal somite receiving a sternal prominence, the whole forming the ‘press-button’

Somite: segment of body (head, thorax, abdomen), including axial skeleton; usually with a pair of appendages; basically five somites for head, eight somites for thorax, six somites for abdomen; each somite basically consisting of dorsal tergite, ventral sternite, and lateral pleurites

Sternite: single, ventral sclerite of body somite; contiguous sternites form sternal plate, indicating basic segmentation of cephalothorax

Sterno-abdominal cavity: medial depression hollowed on the thoracic sternum, generally well delimited, generally shaped like abdomen; derived condition (i.e, typical of the Eubrachyura)

Sterno-abdominal depression: depression between the pereiopods receiving the abdomen, thus in the male the abdomen is filling the width of the sterno-abdominal depression completely; primitive condition (i.e., typical of the Podotremata, but not in Cyclodorippoidia)

Sterno-coxal depression: deeply excavated lateral depressions at the thoracic sternum corresponding with the coxae of the pereiopods that may slide inside (Guinot 1993a; Guinot & Bouchard 1998)

Subantennary lobe of the pterygostome: anteriormost portion of the pterygostome, may be demarcated by a shallow groove and pointed (Fig. 50A, B, D, F), term used by Bourne (1922b) (referred to as ‘avancée ptérygostomienne’ by Guinot 1977: fig. 7A–D; ‘pterygostomial lobe’ in Castro 2000: fig. 2B)

Suture: line indicating the zone of articulation, or of incomplete fusion, between two body somites or two articles of appendages

Synapomorphy: a trait that is shared by two or more taxa and their most recent common ancestor, whose ancestor in turn does not possess the trait

Telson protection valve: calcified, operculate plate covering the ventral side of the telson, hypothesised to prevent sand particles to enter or damage the intestine during digging and burying (Fig. 49A).

Tergite: single, dorsal sclerite of body somite

Thoracopod: limb of the thorax (8 somites), i.e., maxillipeds (1 to 3) and pereiopods (P1 to P5)

Uropod: appendage of sixth abdominal somite (in other Decapoda forming tail fan when combined with the telson); developed as dorsal plate or ventral lobe in basal crabs; socket on sixth abdominal somite is considered homologous to the uropod for abdominal locking system of Brachyura.

Nomenclature

Supra-familial names. Because the system of taxonomic levels used here differs from that used in the recent literature, for the subsection Raninoidia, the adjective 'raninoidian' is used; for the superfamilies Palaeocorystoidea and Raninoidea 'palaeocorystoid' and 'raninoid', respectively. The adjective 'raninid' is used solely for the family Raninidae.

Definition of 'emend.' with taxon names. Similar to usage in the *Treatise of Invertebrate Paleontology* (The Geological Society of America, Boulder, and The University of Kansas Press, Lawrence), the term 'emend.' is applied to denote that the name of a taxon has changed or that the definition has been 'importantly altered'. If the composition of a (higher-level) taxon changes, it does not necessarily mean that the diagnosis should be emended. Only when an important modification of the diagnosis is proposed (e.g., as a result of newly collected material), is the term 'emend.' used. This term is also applied to denote changes in the current concepts of particular groups, as with the exclusion of Lyreidinae from Raninidae.

Systematics

Infraorder Brachyura Latreille, 1802

Remarks. Guinot *et al.* (in press) is followed for the authorship of the infraorder Brachyura.

Section Podotremata Guinot, 1977

Subsection Raninoidia De Haan, 1839 emend.

Raninoidea De Haan, 1839: 102; 1841: 136.
Raninoidea—Tucker 1998: 321; Števčić 2005: 26; Waugh *et al*. 2009: 15.
Raninoidia—Guinot *et al*. 2008: 681, 712; Guinot, Tavares & Castro in press.

Superfamilies included. Palaeocorystoidea Lőrenthey *in* Lőrenthey & Beurlen, 1929 and Raninoidea De Haan, 1839 (Table 1).

Diagnosis. Female, male gonopores coxal, on P3, P5 coxae, respectively. Presence of paired spermatheca, opening either at extremity of thoracic sternal suture 7/8 (Palaeocorystoidea) or anteriorly on sternite 7, but remaining to be typically formed by separation of 2 laminae composing endosternite 7/8 (Raninoidea). Carapace typically longer than wide, elongated (all Raninoidea, Palaeocorystidae), may also be wider than long, subcircular or subhexagonal (Palaeocorystoidea, except Palaeocorystidae), variously vaulted, sometimes with axial carina. Dorsal surface with distinct or shallow cervical groove, or cervical groove faint or lacking altogether; branchiocardiac groove well defined, or shallow, may be absent. Carapace surface variable: roughly or finely granular, sometimes with transverse rows, terraced, scabrous (entirely or partially), eroded, or smooth, polished. Cuticle microstructure variable: upright nodes, fungiform nodes (Palaeocorystoidea, Symethinae), with pits, upright nodes (Lyreididae), to inclined nodes (Raninoidea, except for Symethinae). Locking system of abdomen present on sternite 5, consisting of 2 teeth, as 'double peg' (Cenomanocarcinidae, Orithopsidae, Palaeocorystidae; presumed in all Palaeocorystoidea), or as 2 teeth (a double peg) placed at extremity of projection of episternite 5 ('lyreidid hook' in Lyreididae), or lost (Raninoidea, except Lyreididae). Presence of coapted sockets on abdominal somite 6 (Lyreididae; assumed in all Palaeocorystoidea). Oxystomian condition always present, primitive in Necrocarcinidae. Mxp3 distinctly elongated, operculiform. No junction sternum/pterygostome, Milne-Edwards openings present (Palaeocorystoidea; Marylyreidinae **n. subfam.**), or sternum/pterygostome junction present, Milne-Edwards openings absent (Raninoidea, except Marylyreidinae **n. subfam.**). Respiratory system with inhalant respiratory current through posterior openings and/or frontal by modifications of cephalic appendages (Raninoidea, except Marylyreidinae **n. subfam.**), or pre-chelipedal through Milne-Edwards openings (Palaeocorystoidea; Marylyreidinae **n. subfam.**). Branchiostegite either normal (Palaeocorystoidea) or variously reduced (Raninoidea), either overhanging to variable extent region formed by exposed pleurites 5–7 (Ranininae, Raninoidinae) or not (Cyrtorhininae, Lyreididae, Notopodinae, Symethinae). Pleurites 5–7 as usual, i.e. covered by the carapace, thus completely concealed (Palaeocorystoidea) or exposed (gymnopleurity), calcified (Raninoidea), may be showing as an excavated plate. Sterno-abdominal depression present (Palaeocorystoidea) or absent (Raninoidea, except for Lyreididae in which kind of depression is formed). Abdomen of 6 free somites plus telson, with first somites in prolongation of cephalothorax, thus dorsal. Male abdomen either of usual configuration, i.e., fairly long, reaching sternite 4, entirely inserted in sterno-abdominal depression, fixed (Palaeocorystoidea), or short, unfastened (Raninoidea, except for Lyreididae). Absence of uropods as dorsal plates or ventral lobes, may be modified into sockets (Palaeocorystoidea, Lyreididae). Pleopodal formula (known only in extant Raninoidea) incomplete in males (no vestigial pleopods on somites 3–5) as well as in females (pleopod 1 absent). Gonopods either protected, concealed by abdomen (Paleocorystoidea, Lyreididae) or largely exposed in front of the short abdomen (other Raninoidea). Chelipeds variously shaped, flattened (except Symethinae), often with spines on upper, lower margins, inner surface excavated in Palaeocorystoidea. P2–P4 always, but variously, modified, with distal articles flattened, enlarged, particularly propodi, dactyli: dactyli always modified. P4 with arthrodial cavity subdorsal in position. P5 with arthrodial cavity subdorsal in position, generally reduced: more often varying from reduced to much reduced, may be filiform, with variously modified distal articles (Raninoidea, unknown in Palaeocorystoidea); may be not reduced (Ranininae **emend.**). Thoracic sternum entirely covered in width by male abdomen, nevertheless, anterior sternites exposed because of shortness of abdomen. Anterior exposed portion showing as small, narrow plate, usually crown shaped. Sternite 4 long, rather narrow (Palaeocorystoidea) or well developed, widened, as large shield, with anterior extensions towards pterygostome (Raninoidea). Sternites 5, 6 as usual (Palaeocorystoidea) or showing lateral extensions connecting thoracic sternum to exposed pleurites 5–7, passing between the P1, P2 (connection joining sternite 5 to pleurite 5), between P2, P3 (connection joining sternite 6 to pleurite 6). Sternites 6, 7 as usual (Palaeocorystoidea) or strongly narrowed (Raninoidea). Sternal suture 4/5 reduced, short, generally crescent shaped. One pair of prominences on sternite 5, being part of abdominal holding system, present (Palaeocorystoidea, Lyreididae) or lost (Raninoidea, except for Lyreididae). Sternite 8 reduced, narrow, tilted. Posterior curvature present, strong, may involve sternites 7, 8 to variable extent or only sternite 8. Spermathecal apertures either normally located at extremities of sutures 7/8, separate, not recessed (Palaeocorystoidea) or close to each other, may be practically contiguous, located in medial pit, deeply recessed (Raninoidea, except for Symethinae). Axial skeleton strongly modified (Raninoidea), unknown but supposed 'normal' (Palaeocorystoidea). Number of gills (known only in extant taxa) reduced to just 8 or 7 pairs (Symethinae).

Superfamily Palaeocorystoidea Lőrenthey *in* Lőrenthey & Beurlen, 1929 new status

Palaeocorystinae Lőrenthey *in* Lőrenthey & Beurlen, 1929: 299.

Type family. Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929, by present designation.

Families included. Camarocarcinidae Feldmann, Li & Schweitzer, 2008 **emend.**; Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008; Necrocarcinidae Förster, 1968 **emend.**; Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a **emend.,** and Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929.

Diagnosis. Carapace subcircular to subhexagonal, elongated (Palaeocorystidae); varying from flattened (Orithopsidae, Palaeocorystidae) to distinctly convex (Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae); widest at or anterior to mid-length. Epibranchial tooth varying from conspicuously strong, produced (Cenomanocarcinidae, Orithopsidae) to moderate (Necrocarcinidae, Palaeocorystidae), or obsolete (Paranecrocarcininae). Anterolateral margin with 3–6 spiniform teeth. Carapace surface may have axial, branchial ridges, tubercular or granular (Cenomanocarcinidae, Necrocarcininae *pro parte*, Orithopsidae, Palaeocorystidae *pro parte*), or with pits and weak tubercles (Camarocarcinidae). Branchiocardiac grooves well-marked, branchial groove indistinct, cervical groove distinct, or shallow (Camarocarcinidae). Interbranchial groove sometimes present. Orbits oval, large (nearly corresponding to carapace width) (Orithopsidae, Palaeocorystidae), smaller in families with more subcircular carapace outlines (Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae); supraorbital margin with 2 fissures. Rostrum sulcate (Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae, Orithopsidae) or strongly grooved (Palaeocorystidae). Post-rostral slits may be present. Posterior margin concave. Antennae posteroventral to antennules, not in line with orbits; both positioned behind orbits. Endostome with well developed exhalant channels (Cenomanocarcinidae, Necrocarcinidae, Palaeocorystidae), unknown in others. Carapace surface with upright and/or fungiform nodes, sometimes with additional pits.

Pterygostome tumid, grooved, with granular crests; anterior process distinct, projected. Branchiostegite in contact with coxae of pereiopods, thus no exposure of pleurites (no ‘gymnopleure’ condition); surface smooth or with distinct rim. Mxp3 long, elongated, coxae conspicuously large, flabelliform, curved inwards anterior to P1, not close to each other. Milne-Edwards openings present.

Chelipeds subequal, homochelous, homodontous, lower cheliped margin spinose. P2–P4 rather long, with flattened propodus, dactylus (Cenomanocarcinidae, Palaeocorystidae, unknown for others), P5 subdorsal, strongly reduced in size. Arthrodial cavities of all pereiopods opening lateroventrally.

Thoracic sternum relatively narrow, widest at sternites 4, 5, narrowed towards posterior. All sternites distinguishable. Sternites 1–4 as triangular plate, no lateral extensions between P1, P2 and between P2, P3. Sternite 4 narrow anteriorly, not appressing pterygostome. Sternite 1 inserted between mxp3, sternites 2, 3 triangular, may be crown shaped; sternite 4 long, episternite 4 as lateral plate. Sternites 4–8 separated by deep sutures; suture 4/5, 5/6 crescent shaped with anterior part vertical, markedly deeper. Sternite 8 tilted in level different than in anterior sternites. Sterno-abdominal depression shallow (Cenomanocarcinidae, Orithopsidae, Palaeocorystidae) or rather strongly excavated (Camarocarcinidae, Necrocarcinidae). Spermathecal aperture elongated, at extremety of suture 7/8 (Cenomanocarcinidae, Palaeocorystidae, unknown for others). Female gonopore small, circular, close to coxo-sternal condyle of P3 coxa.

TABLE 3. Genera included in superfamily Palaeocorystoidea Lőrenthey *in* Lőrenthey & Beurlen, 1929 **new status**.

Araripecarcinus Martins-Neto, 1987 (*incertae sedis*)
Camarocarcinus Holland & Cvancara, 1958
Campylostoma Bell, 1858
Cenocorystes Collins & Breton, 2009
Cenomanocarcinus Van Straelen, 1936
Cherpiocarcinus Marangon & De Angeli, 1997
Corazzatocarcinus Larghi, 2004 (*incertae sedis*)
Cretacocarcinus Feldmann, Li & Schweitzer, 2008
Cretacoranina Mertin, 1941
Cristella Collins & Wienberg Rasmussen, 1992 (*incertae sedis*)
Eucorystes Bell, 1863
Ferroranina **n. gen.**
Glyptodynomene Van Straelen, 1944
Hasaracancer Jux, 1971
Joeranina **n. gen.**
Marycarcinus Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a
Notopocorystes McCoy, 1849
Necrocarcinus Bell, 1863
Orithopsis Carter, 1872
Paradoxicarcinus Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a
Paranecrocarcinus Van Straelen, 1936
Protonecrocarcinus Förster, 1968
Shazella Collins & Williams, 2005
Silvacarcinus Collins & Smith, 1993

Abdomen long, wide in both sexes, reaching middle of sternite 4, covering entire width of thoracic sternum, thus in contact with coxae of pereiopods; dorsal uropods absent. Sexual dimorphism indistinct, male abdomen slightly narrower. All abdominal somites free, of equal width, with constriction between somites 1, 2. Anterior sternites 1–4 (4 partially) exposed. First abdominal somites dorsal, in prolongation with carapace; somites 1–5, or 1–6, with medial (central) spine or node, may bear additional lateral spines or nodes. Abdominal somite 1 short, somite 6 much longer than others, may have medial elevation over complete length; somite 6 with sockets. Telson large, proximal portion of telson as wide as somites, outline triangular with rounded apex.

Abdominal holding system as double peg at episternite 5 (Cenomanocarcinidae, Orithopsidae, Palaeocorystidae, unknown in others); teeth sharp in young individuals of both sexes and in males; blunt in adult females. Long socket is assumed (but not verified) at ventral side of abdominal somite 6.

Remarks. Authors have variously cited the authorship of the Palaeocorystinae as Lőrenthey, 1929; Lőrenthey & Beurlen, 1929; or Lőrenthey *in* Lőrenthey & Beurlen, 1929. In the preface of that particular work, Beurlen explained that parts I and III had been written exclusively by Lőrenthey and that he had only translated these portions from Hungarian to German. Therefore, we prefer to note authorship as Lőrenthey *in* Lőrenthey & Beurlen, 1929.

See Table 3 for genera included.

Family Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929 new status

Palaeocorystinae Lőrenthey *in* Lőrenthey & Beurlen, 1929: 299.

Type genus. *Palaeocorystes* Bell, 1863 (= *Notopocorystes* McCoy, 1849), subsequent designation by Withers (1928).

Genera included. *Cenocorystes* Collins & Breton, 2009; *Cretacoranina* Mertin, 1941; *Eucorystes* Bell, 1863; *Ferroranina* **n. gen.**; *Joeranina* **n. gen.**, and *Notopocorystes* McCoy, 1849.

Diagnosis. Carapace subhexagonal, elongated or relatively short (*Cenocorystes*), widest anterior to midlength to about anterior one-third portion; weakly arched in longitudinal direction, gently arched to convex in transverse direction. Anterolateral margin angular in cross section, with 3–6 spiniform teeth. Mesobranchial tooth smaller than anterolateral teeth. Posterolateral margin long, angular to blunt, edge granular or smooth. Posterior margin concave, narrower than orbitofrontal margin. Rostrum bifid, with 2 distal, 2 subdistal teeth, trapezoidal or narrower with concave sides, with 2 deep grooves that may extend onto carapace surface; shallow post-rostral slits may be present (*Ferroranina* **n. gen.**). Carapace surface with distinct axial carina with anteriorly directed tubercles (*Notopocorystes*); anterior half with strap-like, flat bars, sides granular or smooth (*Eucorystes*); narrow cervical groove, hepatic protuberances (*Ferroranina* **n. gen.**, *Joeranina* **n. gen.**), or without carina or areolation (*Cretacoranina*). Distinct branchiocardiac grooves always present, generally conspicuously deep; cervical groove generally distinct, but may be short (*Cretacoranina*, *Ferroranina* **n. gen.**), axially interrupted between gastric pits. General surface varying from tubercular or granular to pitted, sometimes with fungiform nodes (*Cretacoranina*, *Ferroranina* **n. gen.,** *Eucorystes* [*pro parte*]). Orbits distinctly wide, horizontally arranged, deep; supraorbital margin weakly concave, with 2 long fissures. Eyestalk short, thick, arched (*Notopocorystes stokesii*) or long, with longitudinal granular crest (*Joeranina broderipii* **n. comb.**). Antennar fossae closer to each other than antennular fossae, both situated posteroventral of orbits. Proepistome short, epistome wide, partly overhung by oxystomian ‘mouth’ formed by endostome, which is posteroventrally shaped into well-developed exhalant channels. Third article of antenna strongly enlarged, flattened, axially twisted. Carapace dorsal surface with upright and/or fungiform nodes, sometimes with additional pits (*Joeranina* **n. gen.**).

Pterygostome grooved, with blunt or rounded granular crests. Subantennary lobe of pterygostome strongly pronounced. Branchiostegite developed, joining coxae of pereiopods, thus no exposure of pleurites; surface not areolated. Mxp3 with oxystomian condition, endopodite elongated, exopodite half the length of endopodite, narrow. Mxp3 coxae large, not close to each other, intercalated between sternite 4, pterygostome, closing Milne-Edwards openings (*Eucorystes carteri*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*, *N. serotinus*, unknown in others).

Chelae homochelous, homodontous, no apparent sexual dimorphism. Palm flattened, fingers elongated, closing; upper, lower margins of propodus with anteriorly directed spiniform teeth. P1 articles with surface smooth, granular or tubercular. Distal end of merus, carpus with sharp, arched crest (*Ferroranina dichrous* **n. comb.**, *Notopocorystes stokesii*, unknown in others). P2–P4 with flattened dactylus, propodus (*Joeranina broderipii* **n. comb.**, *Ferroranina dichrous* **n. comb.**, *Notopocorystes stokesii*, unknown in others). Basis fused to ischium, with distinct suture (*Eucorystes carteri*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*, *N. serotinus*, unknown in others). Female gonopore small, circular, close to coxo-sternal condyle of P3 coxa. P5 strongly reduced (*Eucorystes carteri*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderipii* n. comb, *Notopocorystes stokesii, N. serotinus*, unknown in others).

Thoracic sternum rather narrow, nearly flat anteriorly, strongly excavated posteriorly, slightly narrowed posterior portion (*Cretacoranina schloenbachi*, *Eucorystes carteri*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*, *N. serotinus*). Slightly wider in females, covered in width by abdomen in both sexes, thus not visible laterally, exposed only anteriorly between telson, mxp3. Sternites 1, 2 may be at distinctly lower level than sternite 3, or sternites 1, 2 distinguishable from sternite 3, but not clearly at lower level. Short, distinct depression between sternite 3, anterior corner of sternite 4 (*Eucorystes carteri*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*, *N. serotinus*). Sternite 4 immediately broadening posterior to sternite 3 (*Eucorystes carteri*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*, *N. serotinus*). Episternite 4, anterior portion of sternite 5 slightly widened; not intercalated between P1, P2. Sternite 5 (episternite 5) with 2 close-set locking teeth. Sternite 8 elongated, narrow, strongly tilted (*Eucorystes carteri*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*, *N. serotinus*). Sutures 4/5–6/7 lateral, crescent shaped, lateral portion roughly horizontal, longitudinal portion deep. Suture 7/8 long, arched anteriorly (*Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*). Spermathecal apertures at extremities of sutures 7/8, well separated, large, oval, margin raised (*Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii*). Arthrodial cavities evenly spaced, ventrolaterally directed. Medial line absent in females, present in males at sternite 8.

Abdomen with sexual dimorphism indistinct, all abdominal somites free in both sexes, only slightly narrower in males than in females. Abdomen in both sexes occupying complete width of sterno-abdominal depression, thus in contact with pereiopod coxae. Abdomen rather long, telson reaching sternite 4, thus thoracic sternum exposed between telson, mxp3. First somites in prolongation of carapace, thus visible dorsally. Somites 1, 2 restricted between P5 coxae; somite 6 long. All abdominal somites with raised axial part; somites may have central tooth.
Abdominal holding system by double peg on episternite 5. Teeth sharp in young individuals of both sexes and males; blunt in adult females. No locking structures on pereiopod coxae.

Genus *Cenocorystes* Collins & Breton, 2009

Cenocorystes Collins & Breton, 2009: 45.

Type species. *Cenocorystes fournieri* Collins & Breton, 2009, by original designation.

Species included. *Cenocorystes bretoni* **n. sp.**, and *C. fournieri* Collins & Breton, 2009.

Material examined. *Cenocorystes bretoni* **n. sp.**: type series, see below; *C. fournieri*: MAB k. 2881, cast of holotype NHN LM 2003-1-3813, lower Cenomanian, Sables & Grès de Lamnay Formation, Les Ormeaux quarry, Chambouquet (Saint-Maixent, Sarthe, France).

Emended diagnosis. Carapace subhexagonal in outline; length, width nearly equal, widest one-third distant from front; surface fairly convex in both directions; orbitofrontal margin about three-quarters of total carapace width, orbits large, ovate, 2 long, relatively open fissures in upper orbital margins, elongated outer orbital spine; short, arched anterolateral margin with 3 well-spaced spines; 2 in front of, 1 behind cervical notch; posterolateral margin somewhat longer, slightly convex; posterior margin from straight to strongly concave; dorsal regions poorly defined, protogastric lobes may be with transverse row of 4 small tubercles (*C. fournieri*); cervical groove indistinct, incompletely defined, gastric muscle scars emphasised, gastric pits present; branchiocardiac grooves arched, short; branchial groove formed by muscle scars; dorsal surface of carapace finely granular. Pterygostome large, inflated, buccal margin concave with narrow buccal collar; mxp3 coxa large, flabelliform; endopod basis-ischium long, merus shorter, both grooved; thoracic sternum narrow, elongated, narrowing backwards, sternites 1, 2 narrowly triangular, at lower level; sternite 3 crown shaped, clearly separated from sternite 4 by oblique grooves; sternite 4 trapezoidal, episternite 4 suboval, robust, slightly extending laterally; suture 4/5 crescent shaped; sternite 5 without lateral depression; suture 5/6 crescent shaped. Arthrodial cavity of P4 tilted; P5 reduced, (sub)dorsal. Abdomen narrow, somite 1 tightly fitted between P5 coxae, somite 2 narrow.

Remarks. Collins & Breton (2009: 47) placed their new genus *Cenocorystes* in Palaeocorystidae, suggesting that it had, ‘characters in common to both *Notopocorystes* and *Cretacoranina*’. Their opinion, however, was based on *C. broderipii*, which is here transferred to *Joeranina* **n. gen.** Characters that distinguish *Cenocorystes* from all other palaeocorystids are the relatively shorter carapace, large orbits, and the long and relatively open orbital fissures. *Cenocorystes* shares the above features with Orithopsidae. *Cenocorystes*, however, differs substantially from members of that family, which have a wider carapace with a pronounced, complete cervical groove, distinct axial and branchial carinae. In addition, the lateral spines are stronger and directed outwardly. Sternite 4 is deeply grooved medially in the orithopsids *Orithopsis tricarinata* and *Silvacarcinus laurae*; this character is absent in

Cenocorystes bretoni **n. sp.** (not preserved in *C. fournieri*). It should be noted that the pterygostome of *C. bretoni* is weakly areolated for a palaeocorystoid, the branchiostegite being relatively high.

Cenocorystes is easily distinguished from *Joeranina* **n. gen.** by absence in the former of characteristic hepatic and protogastric protuberances, frontal furrows, deep and continuous cervical groove, and rimmed posterolateral margin; moreover, it has a relatively shorter carapace. *Cenocorystes* is easily distinguished from *Ferroranina* **n. gen.** by absence in the former of a post-frontal terrace and by having a shorter relative length and a gently rounded, rather than rimmed, posterolateral margin. *Cenocorystes* is also characterised by having a granular microstructure, instead of fungiform nodes in *Ferroranina* **n. gen.** This difference also separates *Cenocorystes* from *Cretacoranina*, in addition to the different carapace outline, definition of cervical groove and the architecture of the posterolateral margins. *Cenocorystes* is known exclusively from the Cenomanian of northern France and is typically found in coarse-grained sediments.

Cenocorystes bretoni n. sp.

(Fig. 2A–D)

Diagnosis. Carapace small, subhexagonal in outline, slightly longer than wide, maximum width at epibranchial spine one-third distant from front; posterior margin rimmed, strongly concave, shorter than orbitofrontal margin; dorsal regions weakly differentiated; cervical groove weakly defined, V-shaped; branchiocardiac grooves well-defined; epibranchial region with median oblique scar; cuticle granular. Pterygostome large, inflated, buccal margins concave, rimmed. Thoracic sternum narrow, elongated; sternites 1, 2 narrow, triangular; sternites 3, 4 separated by oblique grooves. Mxp3 elongated, coxae large, basis-ischium fused, grooved.

Derivation of name. In honour of Gérard Breton (Université de Rennes I, Rennes, France), who has substantially contributed to our knowledge of fossil decapods from France.

Material examined. Holotype: MAB k. 2899 (indeterminate sex); upper Cenomanian, precise level unknown; Vibraye, near Le Mans (Sarthe, northern France).

Description. Carapace small, subhexagonal in outline, slightly longer than wide (in absence of orbitofrontal margin, length measured from basis of extraorbital spine), widest approximately one-third of total carapace length from front; dorsal surface fairly convex in both directions. Orbitofrontal margin broad, front not preserved. Anterolateral margins arched, with 3 broadly based spines; 1 hepatic plus 2 epibranchial, decreasing in size posteriorly. Posterolateral margins converging backwards, sinuous, slightly concave anteriorly, slightly convex posteriorly, margin rounded; with small spine anteriorly. Posterior margin fairly concave, rimmed, narrower than orbitofrontal margin. Dorsal regions of carapace poorly differentiated. Cervical groove weakly defined, discernible at lateral margins, axially; medially interrupted by small gastric pits. Epibranchial region exhibits oblique scar in medial portion, arched muscle scars posteriorly running subparallel to cervical groove. Cardiac region large, bounded by rather deep branchiocardiac grooves. Dorsal surface of carapace densely, uniformly granular.

Pterygostome large, inflated; buccal margin concave, rimmed. Pleural suture well-defined as thin line.

Thoracic sternum narrow, not connected to pterygostome, narrowing backwards, sternites 1, 2 narrowly triangular, situated at lower level; sternite 3 crown shaped, well separated from sternite 4 by oblique grooves; sternite 4 trapezoidal, episternite 4 suboval, robust, slightly extending laterally; suture 4/5 crescent-shape; sternite 5 without lateral depression; suture 5/6 crescent-shape. P4 arthrodial cavity tilted; P5 reduced, (sub)dorsal.

Abdomen narrow, first somite broader. Mxp3 elongated, with large, flabelliform coxa; endopod basis-ischium elongated, merus shorter, strongly depressed axially.

Remarks. The new species presents the following features that allow placement in *Cenocorystes*: reduced length of the carapace, with length roughly equalling width; large orbits; weakly defined cervical groove; arched anterolateral margin with four spines directed forwardly and outwardly, gently rounded posterolateral margins. In absence of a completely preserved front in both species of the genus, the total length was taken from the base of the extraorbital spine, which is preserved in the holotypes of both. *Cenocorystes bretoni* **n. sp.** differs from the type species, *C. fournieri*, in having a more tumid dorsal carapace surface and in lacking clearly defined grooves around the hepatic anterolateral spine (Collins & Breton 2009: fig. 6) as well as four protogastric tubercles, and in having a more concave posterior margin. In addition, *C. bretoni* **n. sp.** has more distinct branchiocardiac furrows, whereas the intestinal region is better defined in *C. fournieri*.

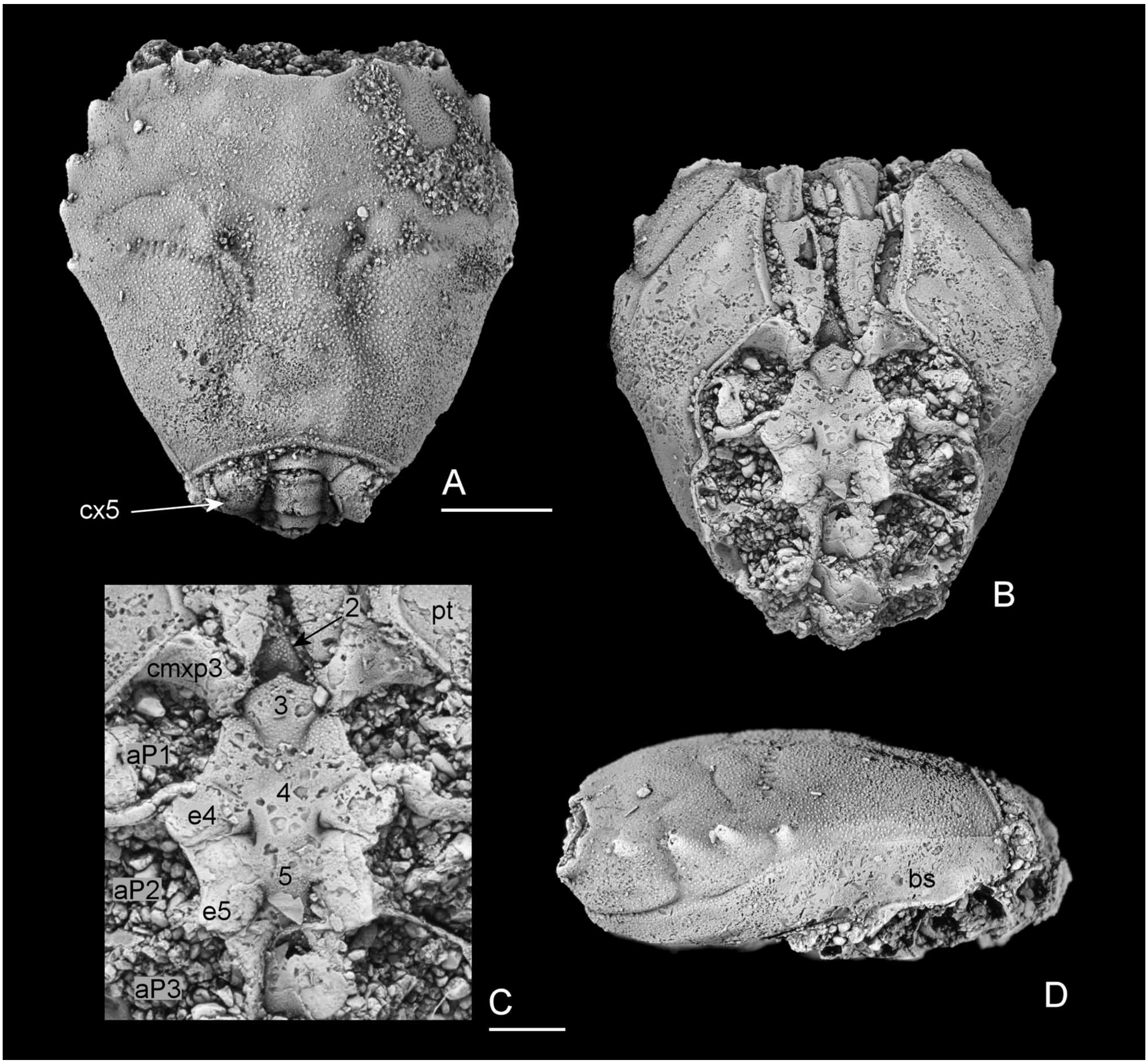


FIGURE 2. *Cenocorystes bretoni* **n. sp.** (Palaeocorystidae), MAB k. 2899 (holotype; indeterminate sex), upper Cenomanian, Vibraye near Le Mans (northern France); A, dorsal view of carapace; B, ventral view, showing thoracic sternum, abdomen and mxp3; C, detail of thoracic sternum; D, left lateral view of carapace. **2, 3, 4, 5,** thoracic sternites 2, 3, 4, 5; **aP1, aP2, aP3,** arthrodial cavities of P1, P2, P3**; br,** branchiostegite; **cx5,** P5 coxa**; e4, e5,** episternites 4, 5; **cmxp3,** coxa of mxp3; **pt,** pterygostome. Scale bars: A, B, D: 5mm; C: 2mm.

The new species, with partial ventral side preserved, reveals the thoracic sternum of *Cenocorystes* for the first time. It matches the general sternal configuration of Palaeocorystidae; differences with other genera are the rather strong grooves separating sternites 3 and 4, sternite 5 lacking a lateral depression, and sutures are more closed.

Genus *Cretacoranina* Mertin, 1941

Cretacoranina Mertin, 1941: 237.

Type species. *Raninella schloenbachi* Schlüter, 1879, by original designation.

Species included. *Cretacoranina denisae* (Secretan, 1964) [as *Notopocorystes*; Fig.10A, B], *C. fritschi* (Glaessner, 1929) [as *Notopocorystes*], *C. schloenbachi* (Schlüter, 1879) [as *Raninella*], *C. testacea* (Rathbun, 1926) [as *Raninella*] and *C. trechmanni* (Withers, 1927) [as *Ranina*].

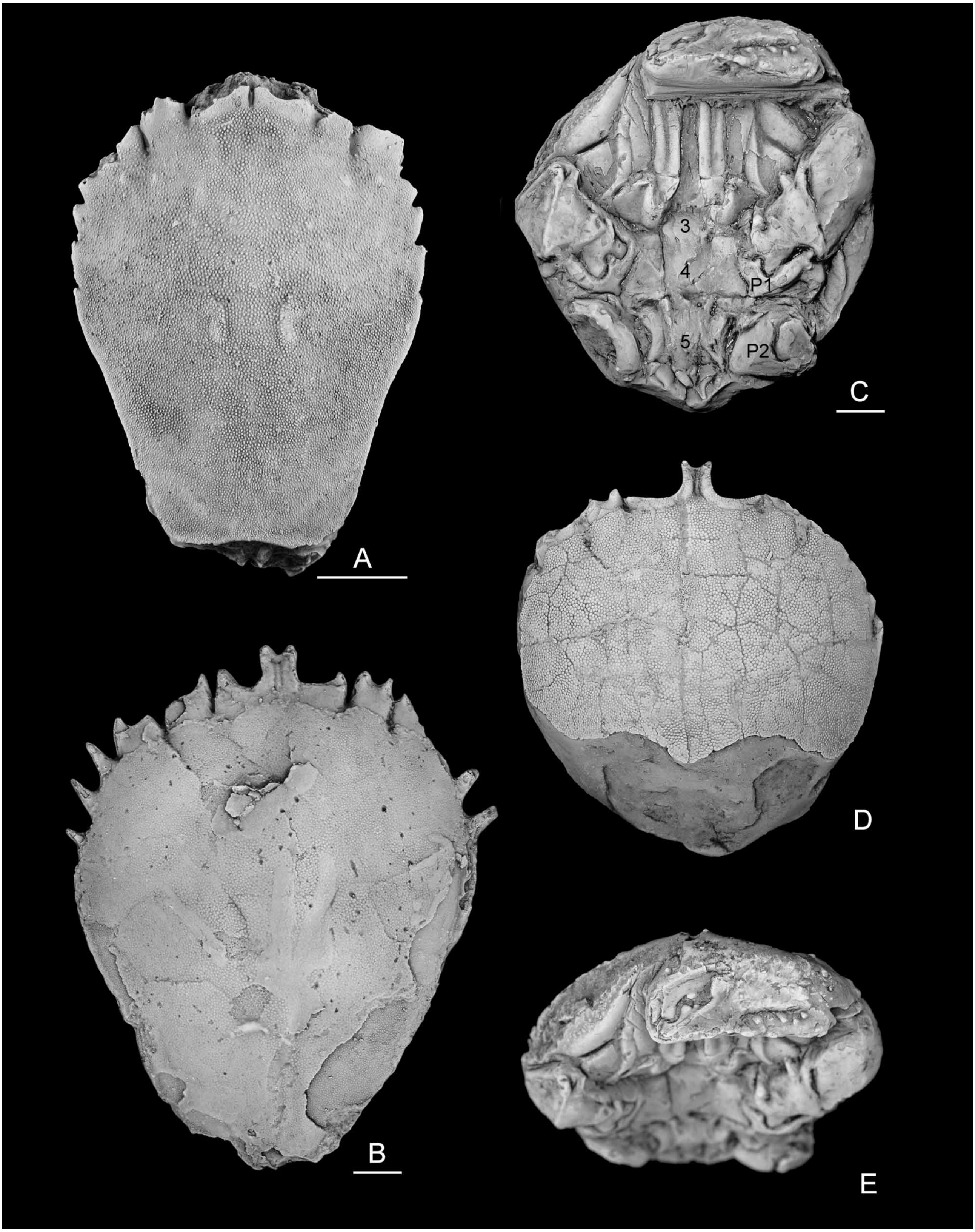


FIGURE 3. A, *Cretacoranina testacea* (Rathbun, 1926b) (Palaeocorystidae), MAB k. 2934 (cast of GAB 37-844; indeterminate sex), lower Maastrichtian, Mississippi (U.S.A), dorsal view of carapace; B, *Cretacoranina schloenbachi* (Schlüter, 1879), MAB k. 2935 (cast of RME 551.763.333 A 3963; indeterminate sex), upper Campanian, Coesfeld (northwestern Germany), dorsal view of carapace; C–E, *Cretacoranina schloenbachi* (Schlüter, 1879), MGSB75290 (indeterminate sex), Campanian, Vitoria (northern Spain), dorsal; ventral, and oblique frontal views of carapace. Ventral view shows thoracic sternum and appendages, while left cheliped is visible in E. **3, 4, 5,** thoracic sternites 3, 4, 5; **P1, P2,** pereiopods 1, 2. Scale bars: 5mm.

Material examined. *Cretacoranina denisae*: holotype, MNHN F.R03875; paratypes, MNHN F.R03876, F.R03877 and MNHN F.R03878 [as *Notopocorystes australis* Secretan, 1964]; all well-preserved carapaces, lower Campanian, Ampolipoly-Antsirasira-Behamotra, Menabe region, Madagascar (see Charbonnier *et al*. in press). *C. schloenbachi*: RME 551.763.333 A 3963 (of which MAB k. 2935 is a plaster cast), two carapaces with associated remains of chelae, upper Campanian, Coesfeld, northwest Germany; MGSB75290 (of which MAB k. 2936 is a plaster cast), incomplete carapace with associated chela, thoracic sternum and mxp3, Campanian, Puerto de Vitoria, Vitoria, province of Álava, northern Spain. *Cretacoranina* cf. *schloenbachi*: NHMM JJ 13448A-C, incomplete carapace, late Maastrichtian (*Belemnitella junior* Zone), Gulpen Formation, Vijlen Member, CPL SA-Haccourt quarry (Liège, Belgium). *C. testacea*: MAB k. 2934 (a cast of GAB 37-844; Bishop 1983b: table 1), Coon Creek Formation, lower Maastrichtian, Union County, Mississippi, U.S.A. *C. trechmanni*: holotype, NHM In. 26011, carapace with associated right chela and pereiopod, ?Campanian, between Cambridge and Catadupa, Jamaica.

Diagnosis. Carapace medium to large in size, subhexagonal in outline, widest at posteriormost lateral spine, slightly anterior to mid-length; axial carina absent; orbitofrontal margin wide, fissures deep, relatively open, orbital margin spinose; orbits large; front narrow, bifid, lateral sides concave, with axial furrows, 2 diverging distal spines, 2 weak subdistal nodes; anterolateral margins short, weakly arched, with 3 long, sharp, conical spines with narrow triangular bases; posterolateral margins longer, convex (*Cretacoranina schloenbachi* [Fig. 3B–E], *C. trechmanni*) or weakly concave (*C. testacea*; Fig. 3A), anteriorly with small spine; posterior margin weakly concave, much shorter than orbitofrontal margin; dorsal regions not defined, cervical groove absent, only discrete, short branchiocardiac grooves. Carapace surface covered by dense mosaic of fungiform nodes.

Pterygostome with blunt crests, deep grooves; buccal margin with broad buccal collar. Mxp3 elongated; coxae large, flabelliform; exopod slender, smooth; endopod basis-ischium long, with distinct longitudinal groove.

Thoracic sternum elongated, relatively wide anteriorly; sternite 3 crown shaped; sternite 4 wider than long, trapezoidal, anteriorly much wider than sternite 3; episternite 4 widened; sternites 5, 6 increasingly narrowed, with acute lateral depressions. P1 large, homochelous; upper, lower margins spinose, fingers with strong teeth.

Remarks. *Cretacoranina* was until recently used to embrace several fossil species, with Tucker (1998: table 4) and De Grave *et al.* (2009: 29) each recognising 12 species. The current generic definition is too wide, and it is proposed here to subdivide *Cretacoranina* sensu lato into *Cretacoranina* **emend.**, *Joeranina* **n. gen.**, and *Ferroranina* **n. gen.**, on the basis of dorsal carapace and sternal features (Table 4). *Cretacoranina* **emend.** is distinguished from all other palaeocorystid genera by its large size, complete absence of areolation or cervical groove on the dorsal carapace surface, weak branchiocardiac grooves, long lateral and orbital spines, short furrows confined to a narrow rostrum, and a distinctly wide sternite 4. Because of the derived carapace and sternal characters, *Cretacoranina* is here considered to be the most derived amongst palaeocorystids.

In addition to the differences mentioned above, *Cretacoranina* **emend.** is easily distinguished from *Joeranina* **n. gen.** in having a relatively wider carapace, lacking the long and deep frontal furrows, the absence of an axial carina and cuticle exhibiting a microstructure of fungiform nodes (pits and granules in *Joeranina* **n. gen.**). *Cretacoranina* **emend.** is considered closely related to *Ferroranina* **n. gen.**, both genera sharing the spinose orbital margin, cuticle microstructure and a wide sternite 4. However, *Ferroranina* **n. gen.** differs in having longer frontal furrows, which extend onto the carapace, a medially defined cervical groove and, most obviously, a clearly discernible post-frontal terrace. The front of *Cretacoranina* **emend.** also lacks distinct subdistal spines (Fig. 3B and D), which are present in *Ferroranina* **n. gen.** and *Joeranina* **n. gen.**

Members of *Cretacoranina* **emend.** are known from the Coniacian to the Maastrichtian, with records from Bohemia (Czech Republic), England, Germany, northeastern Belgium, Spain, Madagascar, Jamaica and U.S.A.

Genus *Eucorystes* Bell, 1863

Eucorystes Bell, 1863: 17.

Type species. *Notopocorystes carteri* McCoy, 1854: 118, pl. 4, fig. 3, by monotypy.

Species included. *Eucorystes carteri* (McCoy, 1854) [as *Notopocorystes*], *E. eichhorni* (Bishop, 1983a) [as *Notopocorystes* (*Eucorystes*)], *E. exiguus* (Glaessner, 1980) [*as Notopocorystes* (*Cretacoranina*)], *E. iserbyti* **n. sp.**, *E. intermedius* Nagao, 1931, *E. ligulatus* Wright & Collins, 1972 [as *Notopocorystes* (*Eucorystes*) *carteri ligulatus*], *E. navarrensis* **n. sp.,** *E. mangyshlakensis* Ilyin & Pistshikova *in* Ilyin, 2005 [as *Notopocorystes* (*Eucorystes*)], and *E. oxtedensis* Wright & Collins, 1972 [as *Notopocorystes* (*Eucorystes*)].

Material examined. *E. carteri*: NHM In. 29645-1-7 and NHM In. 29903-1-5, 12 carapaces; SM B23091, well-preserved carapace, abdomen and sternum; IRScNB unregistered, Van Straelen Collection, drawer 218, approximately 100 specimens, some with remains of abdomen, thoracic sternum and pereiopods; all from Cambridge Greensand, upper Albian, Cambridge, southern England. *E. iserbyti* **n. sp.**: type series, see below. *E. ligulatus*: holotype, SM B23137, carapace, Cambridge Greensand, upper Albian, Cambridge, southern England. *E. navarrensis* **n. sp.**: type series, see below. *E. oxtedensis*: holotype, NHM In. 60983, poorly preserved carapace; paratype, NHM In. 60984, anterior portion of carapace; both lower Albian, Coney Hill Priory Sandpit, Oxted, southern England.

TABLE 4. Distinguishing features of the palaeocorystid genera *Joeranina* **n. gen.**, *Ferroranina* **n. gen.,** and *Cretacoranina* Mertin, 1941.

Joeranina **n. gen.**	- Frontal furrows long, prominent - No post-frontal terrace discernible, only hepatic protuberance - Cervical groove complete, also laterally defined, medial portion U-shaped - Medial carina clearly defined, complete - Cuticle microstructure with granules and pits - Thoracic sternite 4 anteriorly slightly wider than sternite 3
Ferroranina **n. gen.**	- Frontal furrows slightly extended onto carapace - Distinct post-frontal terrace discernible, trilobate - Cervical groove only medially defined, medial portion V-shaped - Medial carina absent or conspicuously weak - Cuticle microstructure with fungiform nodes - Thoracic sternite 4 anteriorly much wider than sternite 3
Cretacoranina Mertin, 1941	- Frontal furrows only on rostrum - Post-frontal terrace absent; hepatic protuberance present - Cervical groove absent - Medial carina absent - Cuticle microstructure with fungiform nodes - Thoracic sternite 4 anteriorly much wider than sternite 3

Diagnosis. Carapace small, subhexagonally elongated in outline, fairly convex in transverse cross section, weakly convex longitudinally; maximum width at epibranchial spine; orbits wide, with 2 deep supramarginal fissures; front narrow to relatively broad, bifid, with 2 distal, 2 subdistal spines, distal spines may be long; axial ridge partially discontinued by swellings, grooves, may be less evident in posterior half of carapace (e.g., *Eucorystes carteri*, *E. iserbyti* **n. sp.**) or clearly visible (e.g., *E. ligulatus*, *E. navarrensis* **n. sp.**); anterolateral margins short, arched, sharp, with 2 long spines with broadly triangular base, separated by deep cervical notch; small spine behind subtle branchial notch in nearly straight posterolateral margins converging backwards, first portion sharp, posterior portion rounded; posterior margin fairly concave, narrower than orbitofrontal margin; dorsal surface of carapace areolated in anterior half by numerous raised 'strap-like' lobes, grooves; grooves relatively broad, shallow; cervical groove well defined; branchiocardiac groove relatively deep, short, arched; raised lobes flat-topped (*E. carteri*, *E. ligulatus*, *E. navarrensis* **n. sp.**) or rounded (*E. iserbyti* **n. sp.**, *E. oxtedensis*); some dorsal regions divided into separate portions; hepatic region with single small protuberance directed upwards, small additional protuberance may be present (*E. navarrensis* **n. sp.**); gastric, epibranchial lobes divided into several portions. Dorsal regions may bear upright nodes, inclined nodes, fungiform nodes, pits; surface of grooves finely pitted. Pterygostome large, with blunt crests, buccal margin concave, with broad buccal collar; thoracic sternum narrow, never in contact with pterygostome, elongated, narrowing backwards; sternites 1, 2 narrow, situated at lower level; sternite 3 subpentagonal, apex pointed downwards; deep lateral incision separating sternite 3 from 4; sternite 4 subtrapezoidal, lateral margins concave; episternite 4 extending laterally; sternite 5 laterally with short, arched grooves (*E. carteri*) or deep, acute depressions (*E. iserbyti* **n. sp.**); episternite 5 elongated, with a double peg for abdominal holding; sternite 6 narrow, episternites 6 elongated; sternites 7, 8 reduced in size, oblique; abdomen narrow, entirely covering the sternal space laterally, reaching sternite 4; all somites free, somites 1, 2 restricted for P5 coxae, somites 1–6 with raised medial portion, somites 2–5 with axial spines (*E. iserbyti* **n. sp.**); mxp3 elongated, in oxystomian condition, coxae large, flabelliform, exopod slender, endopod lanceolated; P1 long, chelae homochelous, tuberculate, outer surface of merus with sharp distal crest. P2–P4 with flattened propodus, dactylus; upper, lower margins granular. P5 strongly reduced, subdorsal.

Remarks. Bell (1863: 17) erected *Eucorystes* for *Notopocorystes carteri*, but there was little consensus about how this genus was to be defined. *Eucorystes* was treated, as was *Cretacoranina*, as a subgenus of *Notopocorystes* by Wright & Collins (1972) and Collins (1997), on account of the similar and gradational carapace morphology. These two subgenera were given generic rank by Tucker (1998: 331), a course of action that has received wide support (e.g., Haj & Feldmann 2002; Schweitzer & Feldmann 2002b; Collins 2003; Vega *et al.* 2007a; Guinot *et al.* 2008; Collins & Breton 2009; De Grave *et al.* 2009; Waugh *et al.* 2009; Schweitzer *et al.* 2010).

Eucorystes is distinguished from other palaeocorystids in that the anterior half of the carapace bears a set of raised, strap-like lobes. These lobes may be flat topped, or rounded, but are always clearly elevated from the dorsal surface. The epigastric region consists of an elongated, distinct lobe; the protogastric region bears two arched, admedial lobes, extended towards the front. The epibranchial region is subdivided into three raised lobes: the anterior portion subtriangular, the medial portion always as a raised oblique lobe directed to the marginal branchial notch, the posterior portion, also swollen, arched, bounding the cervical groove.

Although Schweitzer & Feldmann (2002b: 200) stated that strap-like ornament was 'clearly observeable' in their new species, *Eucorystes platys*, with which Schweitzer *et al.* (2003a: 24) concurred, Schweitzer *et al.* (2009b: 418, fig. 7) described new material that showed a 'muted nature of the so-called strap-like ornamentation on the dorsal carapace'. This was explained by loss of exocuticular layers in their new specimens; however, strap-like lobes in *Eucorystes* are elevated and so distinct that loss of cuticular layers will not cause the strap-like ornament to efface. The entire cuticle of *Eucorystes* is undulated (Waugh *et al.* 2009: fig. 10.3); thus, members of *Eucorystes* can be recognised whatever the degree of loss of cuticle may be (Bishop 1983a: fig. 5). *Eucorystes* and *Joeranina* **n. gen.** are considered closely related; the well-defined groove system in the latter may give the dorsal surface an areolated appearance. *Eucorystes platys* is here transferred to *Joeranina* **n. gen.** (see below).

Noteworthy is the variety of cuticle microstructures within *Eucorystes*: the dorsal surface may bear upright, inclined or fungiform nodes and/or pits. In general, cuticle microstructures are remarkably constant in genera of Raninoidia (see also Waugh *et al.* 2009), only in *Eucorystes* being substantially variable.

Eucorystes, as considered herein, ranges from the lower Albian to the Campanian; the majority of species are Albian. Records are from England, France, Spain, Switzerland, Kazakhstan, U.S.A., Australia and Japan.

Eucorystes exiguus, from the Cenomanian of Australia, was originally assigned to the 'subgenus' *Cretacoranina*, a taxonomic position that was retained by Collins (1997: table 1) and, with *Cretacoranina* elevated to generic status, by Tucker (1995: 181, 1998: table 4). The anterior carapace is areolated and gently rounded lobes are visible; the carapace of the only specimen known lacks the deep frontal furrows that are present in *Joeranina* **n. gen.**, but the presence of well-defined carapace grooves and lobes exclude it from *Cretacoranina* **emend.** Placement in *Eucorystes* is favoured pending the re-examination of the type specimen or additional material.

Eucorystes carteri ligulatus, a subspecies (Wright & Collins 1972: 82) overlooked by Tucker (1998; see also Collins 2003: 84), is here considered valid and given full species rank. The examined holotype is slightly worn, but microstructures document that the 'straps', including the branchial ones, are by no means the result of taphonomic overprint, but rather are a characteristic of this species.

Eucorystes intermedius does not show clearly raised strap-like lobes, being 'only marked by weak straps' (Collins *et al.* 1993: 302), but presents a continuous anterior mesogastric extension with arched epigastric grooves. Specimens so far illustrated are decorticated or poorly preserved; the species seems to share characters of both *Eucorystes* and *Joeranina* **n. gen.**, and better-preserved material is needed.

Eucorystes iserbyti n. sp.

(Figs. 4A–E; 5A–E)

Diagnosis. Carapace small, maximum width at level of epibranchial spine; front relatively broad, bifid, advanced, with 2 distal, 2 subdistal spines, posterior ones smaller, yet distinct; orbits large, with 2 supramarginal fissures, central portion broad, with oblique upper margin, outer orbital spine directed forwards, with robust base; anterolateral margins short, arched, with 2 spines deeply separated by cervical notch; 2 additional granular, small nodes present between extraorbital, hepatic lateral spines; regions with granular raised lobes; hepatic region with small tubercle; gastric, epibranchial lobes divided into several portions; cardiac region well-defined. Dorsal surface densely pitted, granular; raised lobes, lateral regions with inclined nodes. Sternite 3 with conspicuously narrow base; sternite 4 with axial granular tubercle; episternite 4 extended laterally, with large gynglyme; sternite 5 with medial surface flat, deep lateral depressions; episternite 5 with prominent double peg.

Derivation of name. In honour of Arne Iserbyt (Wilrijk, Belgium), who collected and donated the holotype.

Material examined. Holotype, MAB k. 2970, dorsal carapace, partial appendages, and abdomen (*ex* Arne Iserbyt Collection; male); paratype, MAB k. 2871, partial carapace with thoracic sternum (*ex* Arne Iserbyt Collection; indeterminate sex); paratype, MAB k. 2886, dorsal carapace, parts of appendages and abdomen (*ex* Yoeri Christiaens Collection; male); paratype, MAB k. 3006, dorsal carapace (*ex* Arne Iserbyt Collection; indeterminate sex); all from the middle Albian, Pargny, Haute-Marne, northern France. MNHN-B.146366, 2 partial carapaces, Albian, Fécamp, Haute-Marne, northern France.

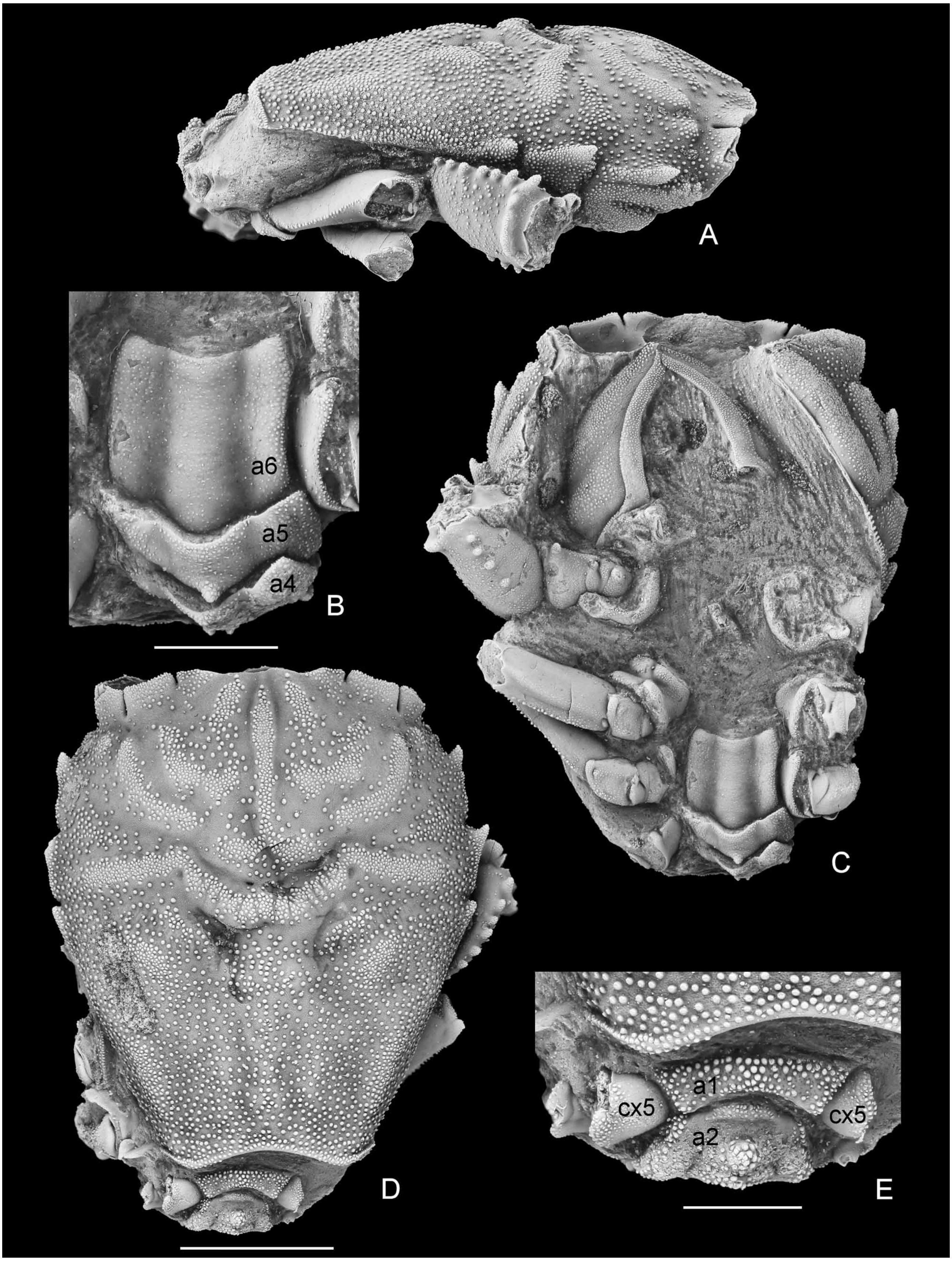


FIGURE 4. *Eucorystes iserbyti* **n. sp.** (Palaeocorystidae), MAB k. 2970 (holotype, *ex* Arne Iserbyt Collection; male), middle Albian, Pargny (northern France); A, right lateral view; B, detail of abdomen; C, ventral view; D, dorsal view of carapace; E, detail of posterior margin of carapace, first abdominal somites and P5 coxae. **a1, a2, a4, a5, a6,** abdominal somites 1, 2, 3, 5, 6; **cx5,** P5 coxa. Scale bars: A, C, D: 5mm; B, E: 2mm.

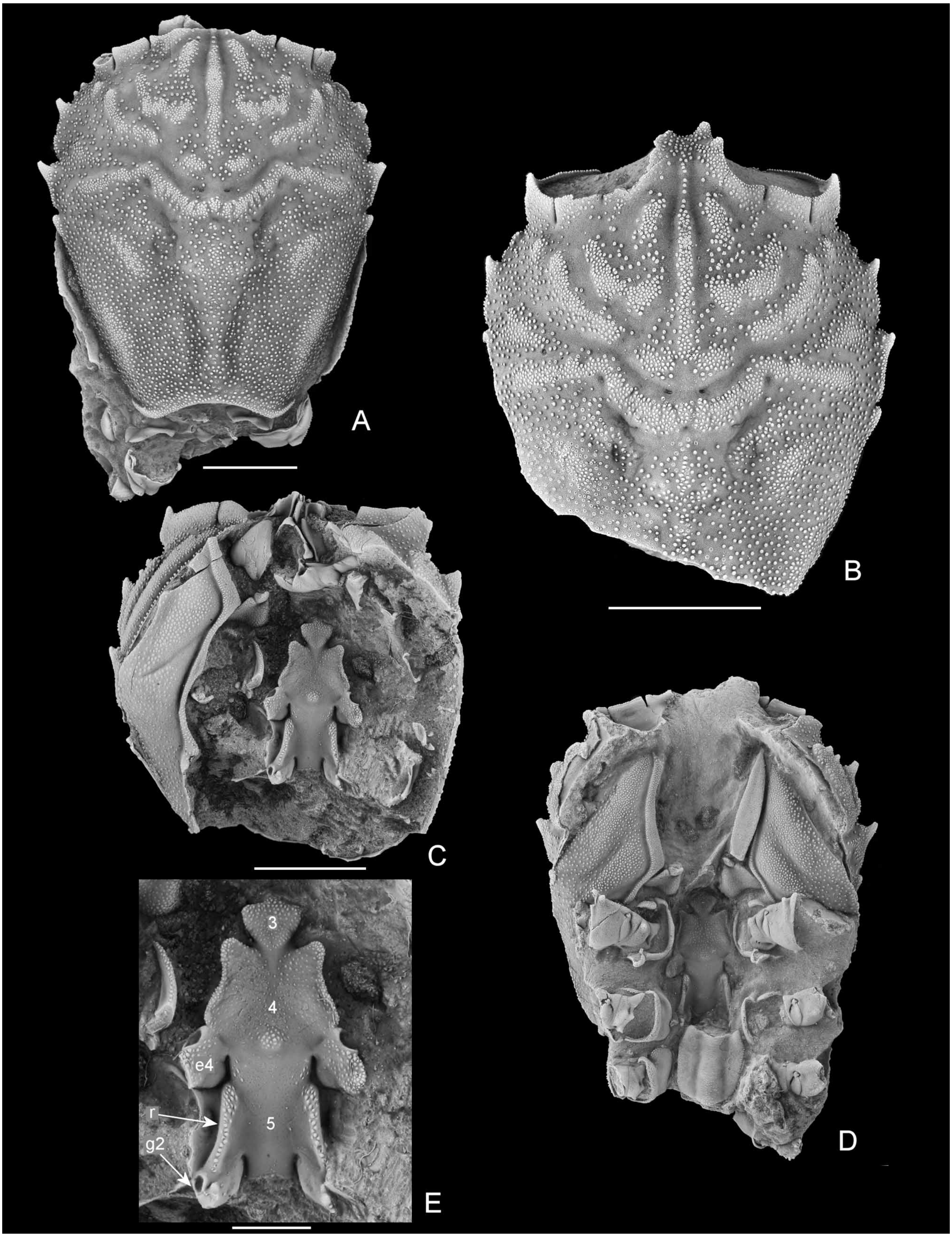


FIGURE 5. *Eucorystes iserbyti* **n. sp.** (Palaeocorystidae), middle Albian, Pargny (northern France); A, D, MAB k. 2886 (paratype, ex Yoeri Christaens Collection; male) in dorsal and ventral views, latter showing thoracic sternum, abdomen and bases of appendages; B, MAB k. 3006 (**paratype**; indeterminate sex), dorsal view of carapace; C, E, MAB k. 2871 (**paratype**; indeterminate sex), ventral view (and detail) showing thoracic sternum. **3, 4, 5,** thoracic sternites 3, 4, 5; **e4,** episternite 4; **g2,** gynglyme for P2 coxa; **r,** ridge. Scale bars: A-D: 5mm; E: 2mm.

Description. Carapace small, subhexagonally elongated in outline, weakly convex longitudinally, more so transversely. Maximum width at epibranchial spine. Front advanced, relatively broad, bifid with 2 distal, 2 subdistal spines, the latter smaller but well defined, differentiated. Orbits large, supraorbital margin divided by 2 fissures: outer ones twice the length of inner ones, supramarginal central portion with upper margin oblique. Anterior mesogastric process reaching base of rostrum. Anterolateral margins short, with hepatic spine, epibranchial spine (both with broadly triangular base), 2 granular nodes between extraorbital, hepatic spines at slightly lower level. Cervical notch deep, well defined. Posterolateral margins longer, rounded, anteriorly with small mesobranchial tooth. Posterior margin strongly concave, markedly shorter than orbitofrontal. Dorsal regions anteriorly well defined by lobes, grooves, posterior half with moderately marked, yet well-defined regions. Anterior mesogastric process narrow, long, reaching base of front. Mesogastric process broad, well defined posteriorly by a relatively deep cervical groove; gastric pits present. Protogastric region with 2 arched lobes. Epigastric lobes elongated, isolated. Hepatic region with small granular protuberance. Epibranchial region divided into 3 parts: anterior lobe with upper portion directed forwards, medial portion transverse, joining urogastric region, posterior portion obliquely directed, interrupted by cardiac groove. Urogastric region broadly arched, meeting the medial lobe of the epibranchial region. Cardiac region large, anteriorly bounded by deep branchiocardiac grooves. Intestinal region elongated, slightly inflated. Dorsal surface of carapace densely pitted, granulate, weakly inclined nodes on lobes, lateral regions. Pterygostome large, with blunt crests, buccal margin fairly concave, with broad buccal collar. Thoracic sternum elongated; sternite 3 crown shaped, conspicuously narrow at base; deep lateral incision, furrows separating sternite 3 from sternite 4; sternite 4 with axial granular tubercle; episternite 4 extended laterally, with large gynglyme; sternite 5 with deep lateral depressions, elevated granular ridge; episternite 5 elongated, somewhat raised, distally with double peg. Abdomen with all somites free, covering thoracic sternum in width in both sexes; somites 1–6 with medial portion raised; somites 2–5 with axial spines. P1 merus triangular in cross section, margins granular, upper margin spinose, distinct granular crest distally at outer surface; P2–P4 with flattened merus, upper, lower margins granulate. P5 strongly reduced, subdorsal.

Remarks. All features of carapace outline and dorsal regions in *Eucorystes iserbyti* **n. sp.** are typical of *Eucorystes*. The new species has a unique set of characters: dorsal strap-like lobes are rounded; epigastric lobes isolated; transverse mesogastric lobe directed posteriorly; lower portion of epibranchial region inflated; cardiac region inflated; intestinal region surrounded by shallow depressions; cuticle granular, laterally granules inclined.

The new species can be easily distinguished from *E. carteri* (Fig. 6A, C) from the upper Albian of southern England and from *E. navarrensis* **n. sp.** from the Albian of northern Spain (see below) by the different organisation of grooves and division in the protogastric region, in having the posterior carapace half areolated and with tumid, rather than flat-topped, lobes and a granular cuticle microstructure (upright and inclined nodes) rather than fungiform nodes. *Eucorystes mangyshlakensis*, from the lower Albian of Kazakhstan, is relatively much longer on account of a longer posterior carapace, exhibits a narrow cardiac region and has fused protogastric and epigastric strap-like lobes.

Eucorystes iserbyti **n. sp.** appears closely related to *E. oxtedensis*, a poorly known species from the lower Albian of southern England (see above), as far as carapace ornament is concerned. The holotype of the latter is rather poorly preserved; however, it does reveal certain patches with fairly well-preserved cuticle. In *E. oxtedensis* the orbitofrontal width is smaller (wide in *E. iserbyti* **n. sp.**), the carapace is distinctly tumid in transverse direction (much flatter in *E. iserbyti* **n. sp.**), epibranchial lobes are weak (distinct in *E. iserbyti* **n. sp.**), the granules on the dorsal surface are small, not inclined laterally (larger, inclined near lateral margins in *E. iserbyti* **n. sp.**), and the posterolateral margin is sharp, rimmed (rounded, rim absent, in *E. iserbyti* **n. sp.**). *Eucorystes oxtedensis* shows more basal characters than does *E. iserbyti* **n. sp.**; the smaller orbitofrontal width and the rimmed posterolateral margin of the former resemble the disposition in *Notopocorystes*.

Thoracic sterna are known in *E. carteri* and *E. iserbyti* **n. sp.**; in the latter, the sternite 3 base is notably narrow (wider in *E. carteri*); sternite 4 bears a granular tubercle on sternite 4 (absent in *E. carteri*); episternite 4 is rather narrow (more laterally extended in *E. carteri*); sternite 5 has deep, long lateral depressions (sternite 5 with short, arched lateral furrows in *E. carteri*). A prominent double peg for abdominal holding is present in the holotype; it is raised from the sternum, consists of two conical structures, the distal structure being larger, with several granules a bit lower.

Eucorystes sp. figured by Waugh *et al.* (2009: fig. 10.5) represents *E. iserbyti* **n. sp.** Former records from France and Switzerland of *E. carteri* may in fact turn out to be *E. iserbyti* **n. sp** the presence of *E. carteri* outside England has yet to be verified.

Eucorystes navarrensis n. sp.

(Fig. 6B, D)

Diagnosis. Small-sized carapace, subhexagonally elongated, maximum width at level of epibranchial spine. Dorsal surface with numerous strap-like lobes, grooves, separating dorsal regions into numerous portions. Front narrow, bifid, with 2 long, divergent spines. Narrow, rounded, salient axial carina along entire carapace axis. Dorsal regions defined by narrow, clearly flat-topped lobes; hepatic region with 2 small protuberances; mesogastric region rhombic; urogastric region V-shaped; epibranchial region subdivided. Posterior half of carapace lacking well-defined regions.

Derivation of name. From Navarra (northern Spain), the type location.

Material examined. Holotype, a dorsal carapace (MGSB75291); paratype, a dorsal carapace preserved upside down (MGSB75292a); a cast with well-preserved front (MGSB75292b), all from approximately 1.5 km northwest of the village of Alloz (Navarra), from limestones considered to be of Albian age (Instituto Geológico de España 1978).

Description. Carapace small, subhexagonally elongated in outline, maximum width at base of epibranchial region, dorsal surface weakly convex in both directions. Orbitofrontal margin wide, only partially preserved. Front narrow, bifid, with long, divergent spines. Lateral margins broadly arched, lateral spines incompletely preserved. Posterior margin strongly concave, notably shorter than orbitofrontal margin. Mesogastric region small, markedly rhombohedric in shape, well defined by furrows, anterior process narrow, ridged, not reaching base of front. Protogastric region clearly subdivided into 3 isolated, flat-topped lobes. Epigastric regions elongated, joining central protogastric ridge. Urogastric region V-shaped, with lateral portions extending obliquely forwards. Hepatic region with 2 notable small protuberances; anterior one conical, below orbital margin, posterior one larger, slightly elongated. Cervical groove well-defined, deeper at axial portion, interrupted by axial carina. Epibranchial region divided into 3 strap-like lobes; anterior portion subtriangular, median portion near straight, directed obliquely towards lateral margins, fairly well separated from urogastric lobe, posterior portion arched. Cardiac region relatively narrow, elongated, anterior portion laterally bounded by deep branchiocardiac grooves. Continuous axial carina along carapace fairly salient, rounded. Posterior half of carapace, strap-like lobes covered by fungiform granules, markedly enlarged on axial carina; grooves, furrows in anterior half of carapace densely covered by minute setal pits.

Remarks. The new species is differentiated from all congeners in having an uninterrupted axial carina over the complete dorsal surface. In *E. ligulatus*, the only other species that shows a distinct axial carina on the posterior carapace (Wright & Collins 1972: pl. 16, fig. 4), the carina is interrupted at both sides of the urogastric region. In addition, *E. ligulatus* bears additional branchial strap-like lobes, which are absent in *E. navarrensis* **n. sp.** Apart from the nature of the axial carina, the new species can be distinguished from *E. carteri* and *E. iserbyti* **n. sp.** by the different nature and organisation of dorsal grooves and strap-like ridges. In *E. navarrensis* **n. sp.** the grooves are broader and more numerous, which lead to narrower, more acute lobes; in *E. iserbyti* **n. sp.** the lobes are rounded, rather than flat-topped. *Eucorystes eichhorni*, a much younger (late Campanian) species from Montana (U.S.A.), also has profuse dorsal regional ornament, presents distinct, long grooves bounding the anterior mesogastric process, as well as a different distribution of strap-like lobes. *Eucorystes exiguus*, from the lower Cenomanian of Bathurst Island (Australia), and *E. oxtedensis* exhibit less clearly subdivided anterior regions and deeper branchiocardiac grooves. *Eucorystes intermedius* shows a much weaker dorsal ornament, whereas *E. mangyshlakensis* exhibits deeper branchiocardiac grooves and merged, rather than isolated protogastric strap-like lobes, which have a more forwardly directed course.

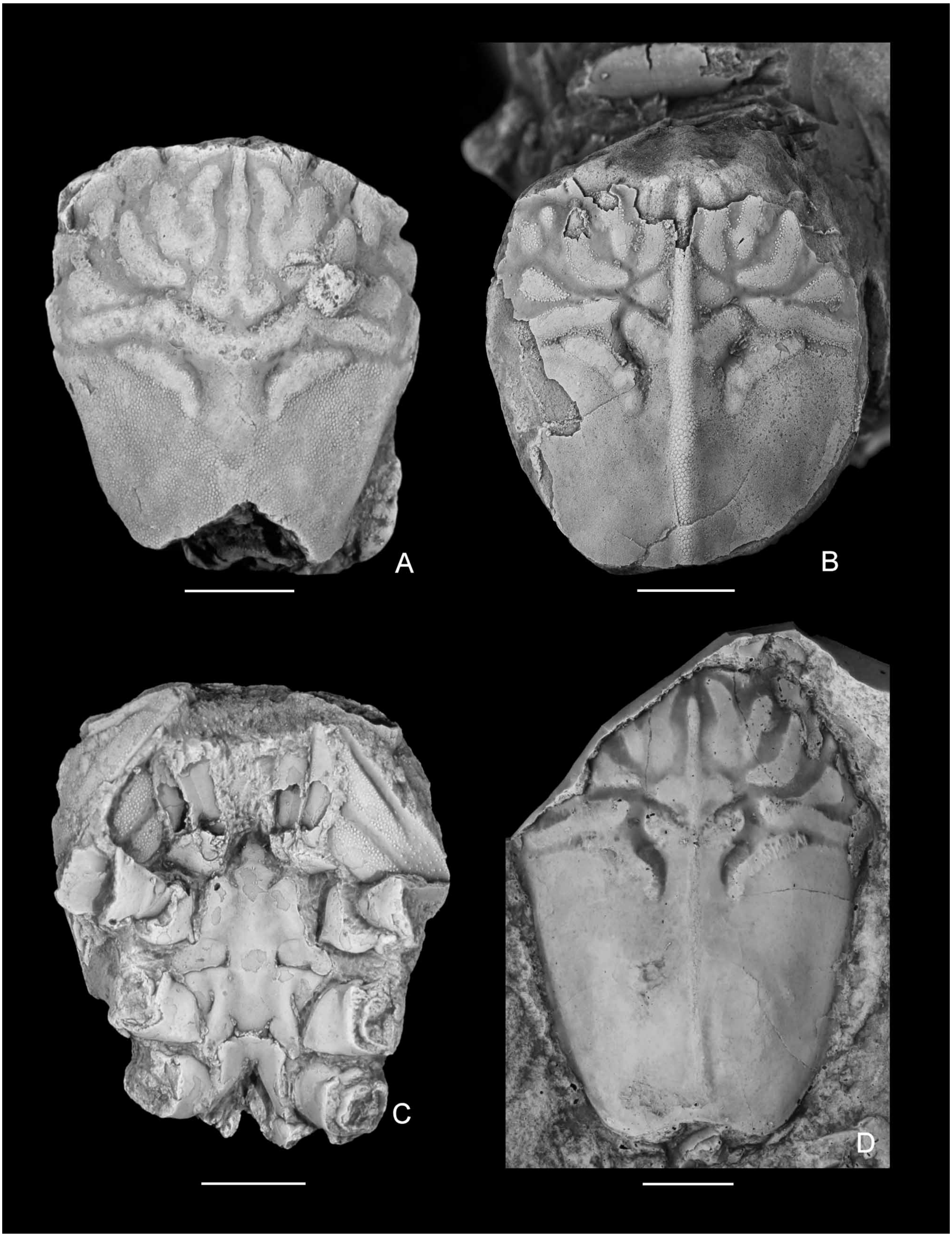


FIGURE 6. A, C, *Eucorystes carteri* (McCoy, 1854) (Palaeocorystidae), IRScNB unregistered [Van Straelen Collection; female], upper Albian Cambridge Greensand, Cambridge (southern England), dorsal view of carapace, and ventral view showing thoracic sternum and appendages; B, *Eucorystes navarrensis* **n. sp.**, MGSB75291 (**holotype**), Albian, Alloz (Navarra, northern Spain), dorsal view of carapace; D, *Eucorystes navarrensis* **n. sp.**, MGSB75292a (**paratype**), silicone rubber cast of natural mould showing dorsal carapace, without cuticle. Scale bars: 5mm.

Genus *Ferroranina* n. gen.

Type species. *Notopocorystes dichrous* Stenzel, 1945, by present designation.

Diagnosis. Carapace of medium to large size, subhexagonal in outline, widest at epibranchial spine, situated approximately one-third of total carapace length from front; dorsal surface convex in transverse cross section, moderately convex from front to posterior margin; axial carina weak; orbitofrontal margin distinctly wide; orbits large, with 2 closed supramarginal fissures, supramarginal teeth, outer orbital teeth strongly developed, with long, conical spines; front markedly narrow, with lateral margins weakly concave, distally with pair of distal, subdistal divergent spines, axial portion of front with short, narrow ridge, deep furrows, which shortly extend onto dorsal surface; anterolateral margins nearly straight, with strong spiniform teeth; posterolateral margin straight, rimmed, anteriorly with small spine; posterior margin concave; dorsal regions indistinct; cervical groove only medially defined, V-shaped, interrupted between gastric pits; post-frontal terrace created by 3 transversely placed subtriangular lobes; hepatic region depressed, with small tubercle; cardiac region rather narrow, bounded by clear branchiocardiac grooves; dorsal surface covered by fungiform nodes, hepatic, orbital regions granular. Pterygostome large, with blunt crests, buccal margin concave, with broad buccal collar. Thoracic sternum narrow, elongated, no junction with pterygostome; sternites 1, 2 narrow, subglobose, sternite 3 crown shaped, incision separating sternites 3, 4, sternite 4 subtrapezoidal, lateral margins weakly concave, anteriorly much wider than sternite 3, episternite 4 wide; sternite 5 laterally depressed, episternite 5 elongated, directed backwards; abdomen narrow, covering thoracic sternum in width in both sexes, all somites free, somites 1–6 with medial portion raised; somite 4 with central tubercle; mxp3 elongated, coxae large, flabelliform, basis short, with a clear suture; ischium, merus long, grooved axially; P1 chela homochelous, homodontous, tuberculate, upper, lower margins spinose, merus with distal crest; P2–P4 long, flattened merus, propodus, dactylus; P5 reduced, subdorsal.

Derivation of name. From Latin *ferro*, meaning ‘iron’, in reference to the rusty colour of numerous specimens of the new species.

Species included. *Ferroranina australis* (Secretan, 1964) [as *Notopocorystes*], *F. dichrous* (Stenzel, 1945) [as *Notopocorystes*] and *F. tamilnadu* **n. sp.**

Material examined. *Ferroranina australis*: holotype, MNHN F.R03874, a well-preserved carapace, lower Campanian, Berere, Menabe region, Madagascar; paratype, MNHN F.R03903, incomplete carapace, lower Campanian, Ampolipoly-Antsirasira, Madagascar (see Fig. 10G, H; Charbonnier *et al*. in press). *F. dichrous*: MAB k. 2876, large female specimen with mxp3, sternum and abdomen; MGSB unregistered (indeterminate sex), carapace with chelipeds and P2, Britton Formation, Eagle Ford Group, Cenomanian-Turonian, Dallas County, Texas; MAB k. 2878, female, partial carapace with sternum and well-preserved frontal area, Little Elm, Texas; building site named ‘Sunset Pointe addition’, just west of FM Road 423; MAB k. 2877 (indeterminate sex), carapace with well-preserved cuticle and chelipeds, MAB k. 2983 and k. 2984 (indeterminate sex), carapaces with extremely well-preserved cuticle, Elm Fork Shale, Eagle Ford Group, Cenomanian-Turonian, California Crossing on Elm Fork of Trinity River, Dallas County, Texas. *F. tamilnadu* **n. sp.**: type series, see below.

Remarks. *Ferroranina* **n. gen.** contains species that until recently were assigned to *Cretacoranina* or to *Notopocorystes*. The new genus exhibits a unique set of characters: front with short, narrow axial ridge, bounded by deep furrows that shortly extend onto the dorsal surface; post-frontal terrace present with three obliquely arranged, subtriangular lobes; cervical groove only medially defined and V-shaped; axial carina weak or obsolete; cuticle microstructure with fungiform nodes; sternite 4 anteriorly much wider than sternite 3.

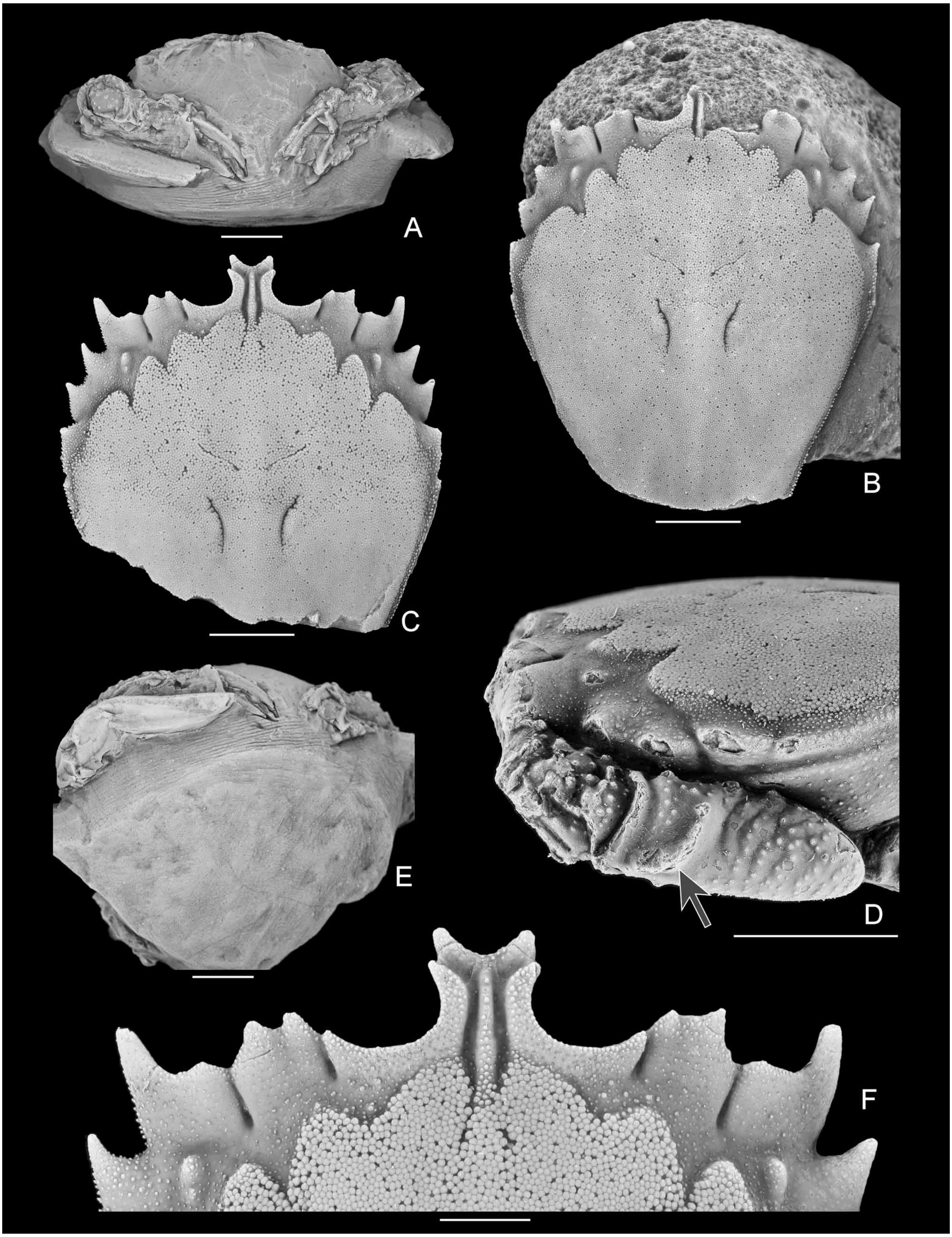


FIGURE 7. *Ferroranina dichrous* (Stenzel, 1945) **n. comb.** (Palaeocorystidae), Cenomanian, Dallas County, Texas (U.S.A); A, E, MGSB unregistered (indeterminate sex), frontal view showing chelipeds, and ventral view showing propodus and dactylus of right P2; B, MAB k. 2983 (indeterminate sex), dorsal view of carapace; C, F, MAB k. 2984 (indeterminate sex), dorsal view of anterior portion of carapace, and detail of orbitofrontal margin; D, MAB k. 2877 (male), left lateral view showing merus of cheliped, arrow indicating a distal crest. Scale bars: A-E: 5mm; F: 2mm.

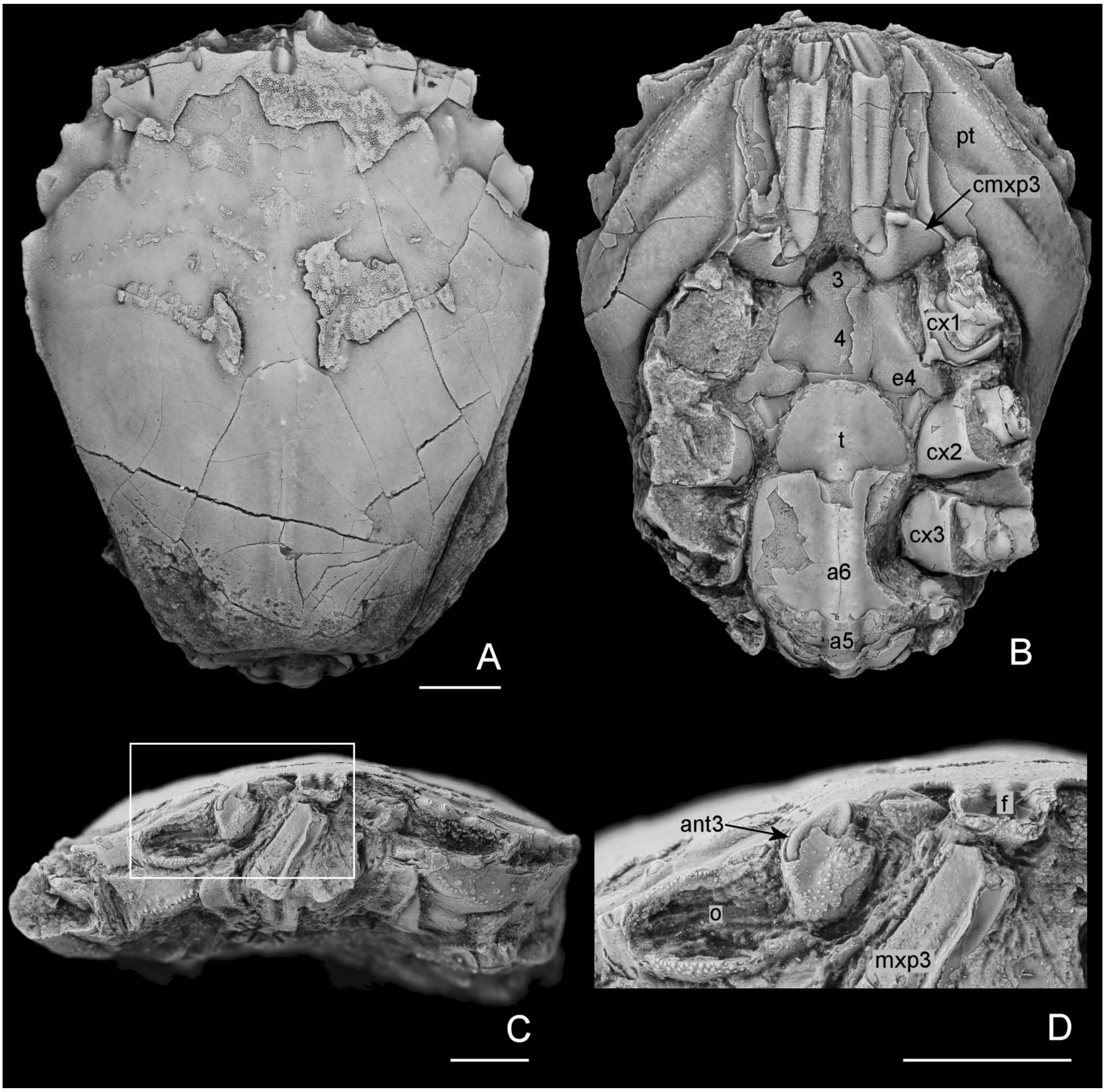


FIGURE 8. *Ferroranina dichrous* (Stenzel, 1945) **n. comb.** (Palaeocorystidae), Cenomanian-Turonian, Little Elm, Dallas County, Texas (U.S.A); A, B, MAB k. 2876 (female), dorsal view of carapace, and ventral view showing abdomen, anterior portion of thoracic sternum and appendages; C, D, MAB k. 2878 (female), frontal view, and detail of right frontal region showing orbit and antenna. **3, 4,** thoracic sternites 3, 4; **a5, a6,** abdominal somites 5, 6; **ant3,** article 3 of antenna; **cmxp3,** coxa of mxp3; **cx1, cx2, cx3,** P1, P2, P3 coxae; **e4,** episternite 4; **f,** front; **mxp3,** third maxillipeds; **o,** orbit; **pt,** pterygostome; **t,** telson. Scale bars: 5mm.

Ferroranina **n. gen.** is considered closely related to both *Cretacoranina* **emend.** and *Joeranina* **n. gen.** Characters that distinguish *Ferroranina* **n. gen.** from members of *Cretacoranina* **emend.** are: presence of a cervical groove (absent in *Cretacoranina* **emend.**), frontal furrows that are longer and extended onto the carapace (short, only on rostrum, in *Cretacoranina* **emend.**) and presence of a post-frontal terrace with three lobes (absent in *Cretacoranina* **emend.**). The new genus appears closely related to *Joeranina* **n. gen.**, but substantially differs in that frontal furrows are not as long, the cervical groove is only medially defined (cervical groove complete in *Joeranina* **n. gen.**), the medial portion of the cervical groove is V-shaped (U-shaped in *Joeranina* **n. gen.**), the axial carina weak or obsolete (well developed in *Joeranina* **n. gen.**), the dorsal carapace surface has fungiform nodes (granules and pits in *Joeranina* **n. gen.**) and sternite 4 is much wider anteriorly (only slightly wider than sternite 3 in *Joeranina* **n. gen.**).

Ferroranina **n. gen.** is easily differentiated from *Notopocorystes* by the presence of frontal furrows, the lack of tubercles on regions and an axial tuberculate carina, by the different shape and definition of the cervical groove and a better-developed anterior portion of sternite 4.

The lack of cuticle has usually been taken into account when describing fossil crabs. On some occasions, the internal mould presents features that are indistinct when the cuticle is present and well-preserved. In *Ferroranina* **n. gen.** the cuticle tends to efface the cervical groove that normally has a constant appearance in different genera. The cervical groove can be traced in some decorticated specimens of *F. dichrous*, contrary to specimens that retain the cuticle; it presents a continuous transverse, thin line from side to side of the carapace.

After re-examination of Secretan's 1964 type material (Fig. 10A, B), it has become apparent that one of the paratypes of *Notopocorystes australis* (MNHN F.R03878; Secretan 1964: pl. 18, fig. 3), should be referred to *Cretacoranina denisae* on account of the lack of the post-frontal terrace and a different orbitofrontal margin configuration.

The morphology of *Raninella*(?) *armata* Rathbun, 1935b, from the upper Albian of Texas (Rathbun 1935b: 50, pl. 11, figs. 32, 33), is typical of *Ferroranina* **n. gen**., and it may well represent the male abdomen of *Ferroranina dichrous* **n. comb.** (Figs. 7A–F; 8A–D).

Ferroranina **n. gen.** ranges from the upper Cenomanian to the upper Campanian, with records from India, Madagascar, Mexico and Texas (U.S.A.).

Ferroranina tamilnadu n. sp.

(Fig. 9A–J)

Cretacoranina cf. *dichrous* (Stenzel, 1945); Guinot *et al*. 2008: 705, 712, fig. 9C.

Diagnosis. Carapace large, elongated, greatest width anterior of mid-line, weakly convex longitudinally, more so transversely; front produced; medial keel over nearly entire length of carapace, fronto-orbital margin wide, thin; supraorbital margin with 2 fissures; anterolateral margin convex, with 5 short spines directed anteriorly, including epibranchial, even smaller mesobranchial teeth; posterolateral margin nearly straight, narrowly rimmed; short, concave posterior margin; dorsal surface with conspicuous division of anterior carapace portion along jagged line; small tubercles on hepatic region; carapace regions poorly defined; cardiac grooves short, curved; coxa of mxp3 large, placed between thoracic sternum, pterygostome; sternite 2 short, crown shaped, sternite 3 individualised, diamond shaped; sternite 4 large, clearly wider than sternite 3, with lateral expansions; episternite 4 wide, clearly separated from sternite 4; chelipeds robust, tuberculate, of comparable size.

Derivation of name. After the type locality, the Cauvery Basin in Tamil Nadu, southeastern India; noun used in apposition.

Material examined. Holotype, and only specimen so far known (OUM KY.2861; leg. A.S. Gale, 1999) from between the villages of Kunnam and Odiyam, 60 km northeast of Tiruchirapalli, section G–H (A.S. Gale 1999, field notes), Cauvery Basin (Tamil Nadu, southeastern India), Uttatur Group, Karai Formation, 209 m level, middle Cenomanian, *Acanthoceras rhotomagense* Zone (Gale *et al*. 2002).

Description. Carapace large (total length, exclusive of broken-off rostrum, 59 mm), elongated, width *c*. 80 % total length; greatest width anterior of mid-line, at level of epibranchial teeth (about one-third of carapace length); carapace weakly convex longitudinally, more so transversely, medial keel highest point; front produced, rostrum apparently extended well beyond orbits, but broken off, only thin central ridge, curved grooves on either side remaining; medial keel over nearly entire length of carapace, widest antero-centrally, effacing before reaching posterior margin; fronto-orbital margin wide, 32.5 mm (*c*. 69 % carapace width; *c*. 55 % carapace length), thin; supraorbital margin with 2 fissures, only one of which partially preserved on either side, slightly curved, widest posteriorly, slightly constricted medially; element adjoining rostrum not preserved, but assumed to have been broadly concave in dorsal view; spine at inner fissure not preserved; second element wide, quadrate but only fragmentarily preserved, lacking anterior margin; third element comparable to second, wide, with convex outer margin, no spine preserved; orbits slanting, but details not observable. Anterolateral margin convex, with 5 short, anteriorly directed spines, including epibranchial spines, even smaller mesobranchial teeth; posterolateral margin nearly straight, narrowly rimmed, tapering rather abruptly to short, concave posterior margin, 19 mm (*c*. 40 % carapace width), narrowly rimmed. Dorsal surface with conspicuous division of anterior carapace portion along jagged line, delineating a lower-lying anterior portion, extending from root of rostrum to close to epibranchial tooth; anteriorly carapace with larger, well-spaced granules of variable sizes; otherwise decorticated carapace surface apparently smooth with close-set granules; jagged line comprising 4 anteriorly directed, narrowly rounded lobes on each side, 3 posteriorly directed, pointed recesses; small tubercle on hepatic region; cervical groove only partially visible; carapace regions poorly defined; cardiac grooves short, curved. Ventral surface with subhepatic lobe divided by longitudinal furrow into 2 tuberculate crests; mxp3 endopodite ischium long, flat, grooved centrally, mxp3 exopodite thin, flat; mxp3 coxa large, placed between thoracic sternum, pterygostome; sternite 2 short, crown shaped, sternite 3 individualised, diamond shaped; sternite 4 large, clearly wider than sternite 3, with lateral expansions; central portion of sternite 4 flat, sides tilted; episternite 4 wide, clearly separated from sternite 4; suture 4/5 deep; sternite 5 partially preserved as is part of abdominal somite 6; P1 coxa flat; P2, P3 block like, sturdy; P1–P3 coxae well developed.

Chelipeds robust, tuberculate, of comparable size; propodus compressed, outer surface nearly flat, with rows of small tubercles, lower edge tuberculate, rounded at proximal end, fixed finger only partially preserved; carpus short, curved, with scattered tubercles of variable sizes, narrow ridge parallel to propodus/carpus joint; merus rounded rectangular, except for flat inner surface, covered in tubercles, with sharp, oblique ridge near proximal end; ischium short, triangular, with stout spine near merus/ischium joint.

Remarks. The closest relative of *Ferroranina tamilnadu* **n. sp.** is *F. dichrous* from the upper Cenomanian of Texas (Figs. 7A–F; 8A–D). Stenzel (1945: 408, 440) indicated the locality and stratigraphic level of *F. dichrous* to be California Crossing, about 10 miles northwest of Dallas, in Dallas County (Texas, U.S.A.), from the Britton Formation (Eagle Ford Group, Gulf Series) or ‘lower Turonian’. However, his list of associated macrofaunal taxa, in particular ammonites, and recent papers by Kennedy (1988; see also Bishop *et al*. 1992; Jacobs *et al*. 2005) document a late Cenomanian age for the Britton Fomation, equivalent to the European *Metoicoceras geslinianum* Zone. *Ferroranina dichrous* is a smaller-sized species than *F. tamilnadu* **n. sp.**; Stenzel (1945: 440) noted lengths and widths of 34.3 and 27 mm, respectively. In addition, *F. dichrous* is less elongated, with a flatter carapace, has longer and more laterally directed spines on the anterolateral margin, typically shows two small, subrounded pits just behind the grooves of the rostrum (not seen in *F. tamilnadu* **n. sp.**), a less clearly separated episternite 4 and sternite 4 and a less-developed medial keel. In other features (carapace ornament, structure and ornament of chelipeds), both species appear closely related, *F. tamilnadu* **n. sp.** predating the Texas species by about two ammonite zones (Gale *et al*. 2002).

Ferroranina australis (Secretan 1964: 158, text-figs. 90, 91, 92 (right), 97 (left), pl. 18, figs. 1–3, as *Notopocorystes*; Fig. 10G, H herein), from the upper Santonian–lower Campanian of Madagascar, is close to *F. dichrous* in size (the holotype measuring 32 and 24 mm in length and width, respectively), proportions, carapace ornament and structure of fronto-orbital margin. However, there are subtle differences in rostrum structure (Secretan 1964: text-fig. 92) and in the number of spines on the anterolateral margin. None of the specimens available to Secretan (1964) preserves the abdomen. In comparison to *F. tamilnadu* **n. sp.**, *F. australis* is smaller, has a less well-developed medial keel, a different course of the jagged line that delineates the anterior, deeper-lying carapace portion (Secretan 1964, text-fig. 97 left) and much more intricate fronto-orbital and anterolateral margins, with better-developed spines and deep recesses separating these (Secretan 1964: text-fig. 91).

Cretacoranina sp. cf. *C. dichrous* of Vega *et al*. (2007a: 418, figs. 9.6–9.8), from the lower-middle Turonian (Eagle Ford Group) of Coahuila, northeastern Mexico, appears close to *F. dichrous*, but preservation is such that a definitive assignment cannot be made, although carapace ornament is similar in consisting of fine granules (see also Haj & Feldmann 2002: fig. 10.4).

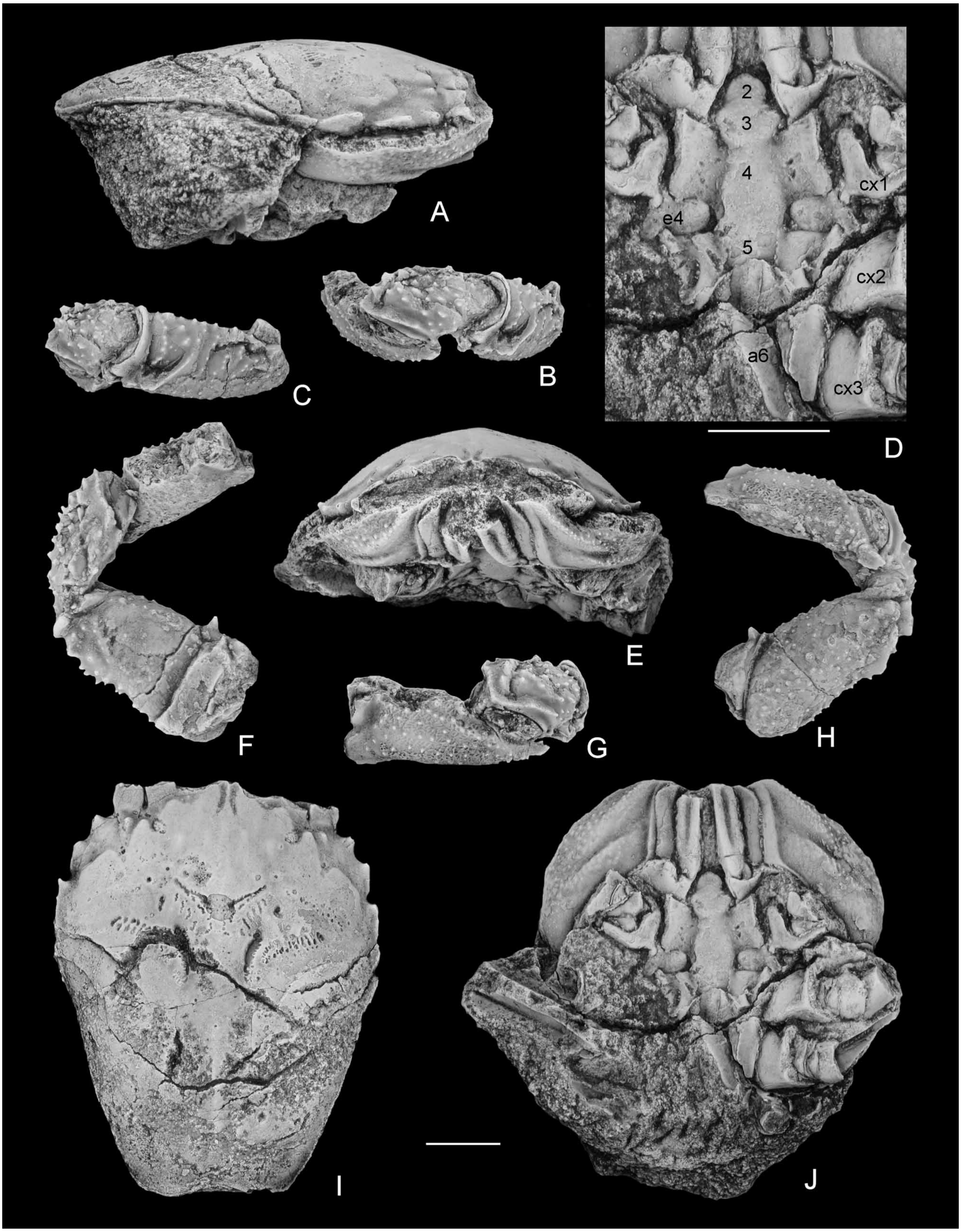


FIGURE 9. *Ferroranina tamilnadu* **n. gen., n. sp.** (Palaeocorystidae), OUM KY.2861 (**holotype**), middle Cenomanian, Tamil Nadu (southeastern India); A, right lateral view of carapace, showing displaced pterygostome; B, carpus of left cheliped; C, merus of left cheliped; D, detail of thoracic sternum with appendages; E, frontal view of carapace; F, dorsal view of left cheliped; G, propodus of left cheliped; H, ventral view of left cheliped; I, dorsal view of carapace; J, ventral view showing thoracic sternum and appendages. **2, 3, 4, 5,** thoracic sternites 2, 3, 4, 5; **a6,** abdominal somite 6; **cx1, cx2, cx3,** P1, P2, P3 coxae; **e4,** episternite 4. Scale bars: 10mm.

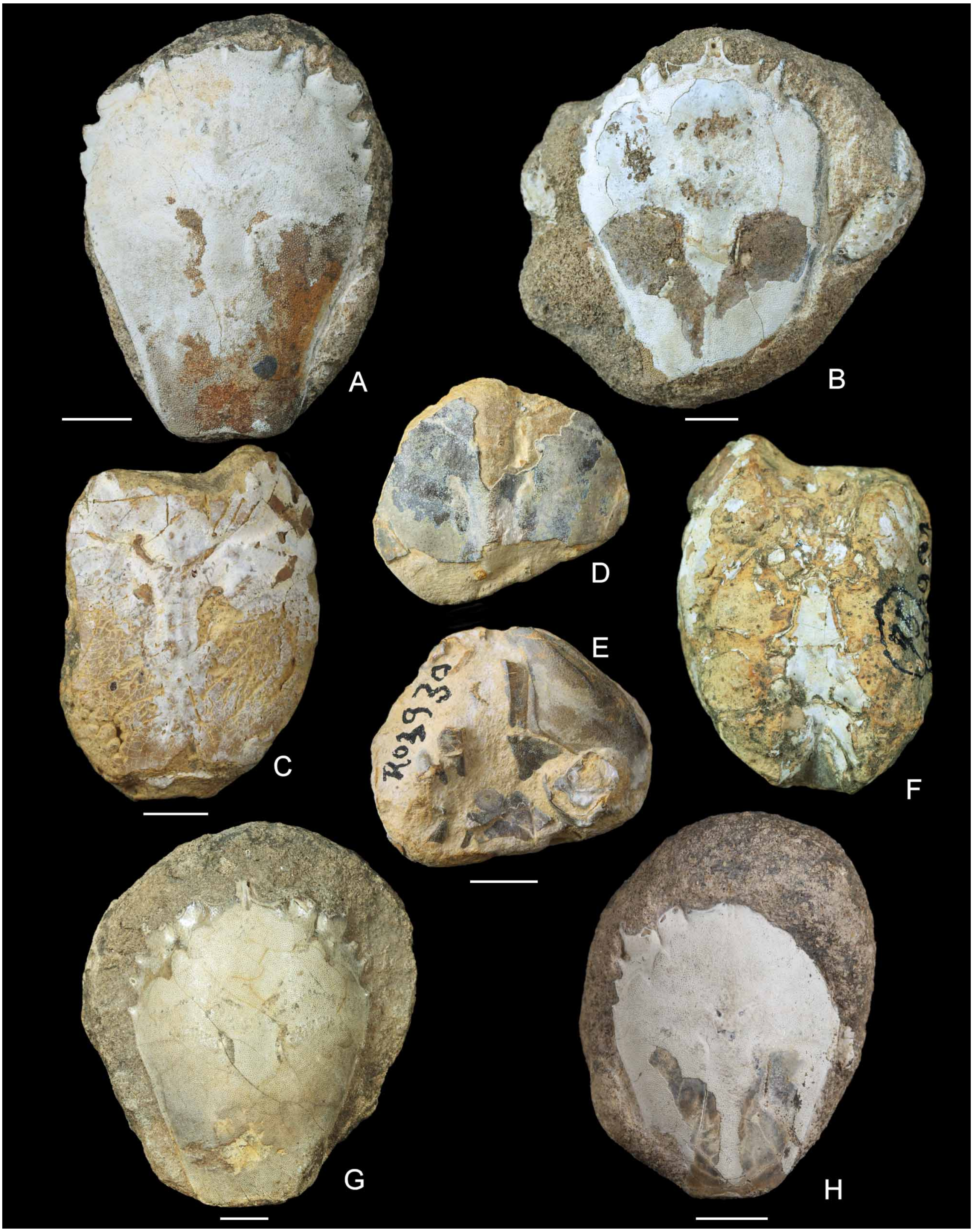


FIGURE 10. Palaeocorystids from Madagascar; A, B, *Cretacoranina denisae* (Secretan, 1964), lower Campanian, Ampolipoly-Antsirasira region; (A; **paratype**, labelled *Notopocorystes australis* Secretan, 1964; MNHN R03878) and MNHN R03875 (B; **holotype**); C, F, *Notopocorystes bituberculatus* Secretan, 1964, MNHN R03951 (**holotype**), Albian, Malandriandro, dorsal view of carapace, and ventral view showing thoracic sternum; D, E, *Joeranina* sp., MNHN R03930 (indeterminate sex), Cenomanian, Antsirane, dorsal view of fragmentary carapace and ventral view; G, H, *Ferroranina australis* (Secretan, 1964) **n. comb.**, MNHN R03874 (G; **holotype**), lower Campanian, Berere, dorsal view of carapace, and MNHN R03903 (H; **paratype**), lower Campanian, Ampolipoly-Antsirasira, dorsal view of carapace. Scale bars: 5mm.

Genus *Joeranina* n. gen.

Type species. *Corystes broderipii* Mantell, 1844, by present designation.

Diagnosis. Carapace small, subhexagonally elongated in outline, dorsal surface fairly convex in cross section, nearly flat longitudinally; maximum width at level of base of epibranchial spine; weak axial carina may be discerned; orbits large, front relatively narrow, bifid, with 2 distal, 2 subdistal spines; frontal process of mesobranchial region bounded by deep furrows, usually diverging backwards; anterolateral margins short, arched, with single (*Joeranina broderipii* **n. comb.**, *J. platys* **n. comb.**) or 2 spines (*J. gaspari* **n. sp.**, *J. syriaca* **n. comb.**) at level of hepatic region, in addition to single epibranchial spine; posterolateral margins long, with small spine behind subtle branchial notch, rimmed, may be finely denticulate; dorsal regions moderately well-defined by shallow grooves; cervical groove well defined, markedly thin, continuous, relatively deep; protogastric region defined by admedial, triangular protuberance directed forwards; hepatic lobe elongated, inclined, with small, acute suborbital protuberance directed forwards; deep frontal furrows mark the anterior mesogastric process, slightly constricted at level of epigastric regions,, extend onto rostrum; posterior half of carapace usually non-areolated. Pterygostome large, with blunt crests, buccal margin concave, with broad buccal collar. Mxp3 markedly elongated, in oxystomian condition, coxae large, flabelliform, basis-ischium long, narrow, smooth, clearly separated by fissures. Abdomen narrow, entirely covering sternal space laterally in both sexes, reaching sternite 4; all somites free, somites 1, 2 restricted for P5 coxae, somites 1, 2 medially raised, somites 3, 4 with medial tubercle, somites 5, 6 medially raised, telson rounded triangular (*J. broderipii*). Thoracic sternum narrow; sternites 1, 2 narrow, pointed; sternite 3 inverted trapezoidal; deep lateral incision separating sternites 3, 4; sternite 4 trapezoidal, anterior corners sharp; distal portion of episternite extending laterally; sternite 5 with short, arched, lateral depressions; episternite 5 triangular, with distinct double peg for abdominal holding; sternite 6 with deep lateral depressions; sternites 7, 8 oblique, spermathecal aperture elongated. P1 homochelous, margins spinose; P2–P4 with merus, propodus, dactylus flattened; P5 reduced, subdorsal. Dorsal surface with pits and/or fine granules, mostly on axial keel and laterally.

Derivation of name. In honour of J.S.H. Collins (London), a prolific author, for his contributions to our knowledge of the Palaeocorystidae.

Species included. *Joeranina broderipii* (Mantell, 1844) [as *Corystes*], *J. gaspari* **n. sp.**, *J. harveyi* (Woodward, 1896) [as *Palaeocorystes*], *J. japonica* (Jimbô, 1894) [as *Eucorystes japonicus*], *J. paututensis* (Collins & Wienberg Rasmussen, 1992) [as *Notopocorystes* (*Cretacoranina*)], *J. platys* (Schweitzer & Feldmann, 2002b) [as *Eucorystes*] and *J. syriaca* (Withers, 1928) [as *Notopocorystes syriacus*].

Material examined. *Joeranina broderipii*: MAB k. 2892 (female), carapace with thoracic sternum and pereiopods, MAB k. 2894 (indeterminate sex), dorsal carapace, MAB k. 2913 (female), carapace with thoracic sternum showing spermathecal aperture, MAB k. 2915 (female), carapace with thoracic sternum and appendages, Albian, Escalles (Calais, northern France); MAB k. 2896 (indeterminate sex), carapace with thoracic sternum and bases of pereiopods, MAB k. 2879 (ex B. Fraaije Collection, female), carapace with thoracic sternum and bases of pereiopods, NHM In. 31313 (indeterminate sex), carapace with well-preserved sternum, pterygostomes and abdomen, MNHN-B.14177, 2 specimens, NHM In. 21331 (indeterminate sex), carapace with sternum and pterygostomes, NHM In. 59796 (indeterminate sex), well-preserved carapace with legs and chelipeds, NHM In. 31312 (indeterminate sex), well-preserved carapace with partial appendages, Albian, Folkestone (Kent, southern England); NHM In. 61147 (lectotype, male), carapace with well-preserved sternum and abdomen, NHM In. 29810-11 (indeterminate sex), partial carapace with well-preserved frontal area, NHM In. 61148-49 (paralectotypes, indeterminate sex), carapace with partial sternum, middle or upper Albian, Ringmer, Sussex, southern England. *J. gaspari* **n. sp.**: type series, see below. *J. syriaca* (Withers, 1928): holotype, NHM I.8407, Upper Cretaceous, ?Cenomanian, Mt. Lebanon, Syria. *Joeranina* sp.: MNHN F.R03930, fragmentary carapace with associated remains of sternum, pterygostome and mxp3, Cenomanian, Antsirane, Madagascar (illustrated by Van Straelen 1931: 56, pl. 2, fig. 39).

Remarks. *Joeranina* **n. gen.** comprises species that had previously been assigned to either *Cretacoranina*, *Eucorystes* or *Notopocorystes*. The new genus is unique in the following features: anterior mesogastric process marked by deep, long frontal furrows, usually constricted between undefined epigastric regions; post-frontal terrace absent, only small hepatic and admedial protogastric protuberances; cervical groove complete, well-defined, also laterally, medial portion U-shaped; entire axial carina present, may be subtle to rather well-defined, raised; cuticle microstructure with granules and pits.

Cretacoranina **emend.** differs from other genera of Palaeocorystidae in having a smooth dorsal surface, without (gastric and hepatic) protuberances; in having much shorter frontal furrows, which are limited to the rostrum;

absence of a cervical groove and a longitudinal dorsal carina; dorsal carapace with fungiform nodes as cuticle microstructure, rather than pits and granules; and thoracic sternite 4 is anteriorly much wider. Members of *Cretacoranina* **emend.** attain much larger sizes.

Eucorystes **emend.** differs from other palaeocorystid genera in having raised dorsal strap-like lobes, by undulation of the cuticle; the anterior mesogastric process bounded by parallel, shallow furrows, the dorsal surface covered by denser, larger granules, or fungiform nodes. Species of *Joeranina* **n. gen.** were sometimes assigned to *Eucorystes* depending on the interpretation of the dorsal strap-like ornament; however, this is not homologous to the raised structures in *Eucorystes* **emend.** (see also remarks under *Eucorystes*).

Notopocorystes differs in having a much more convex dorsal carapace, a smaller orbitofrontal width, regions vaulted and tuberculate, the axial carina denticulate, thoracic sternites 1 and 2 on a lower level than sternite 3, and episternite 4 much less well developed. The cervical groove in *Notopocorystes* is similar in shape, but relatively less marked.

Ferroranina **n. gen.** is considered most closely related to *Joeranina* **n. gen.**; differences are discussed above. As noted by Wright & Collins (1972: 83), relationships amongst the different genera of palaeocorystids are so close that several dorsal elements are shared in the same location but with a distinct appearance in each genus (see *Relationships of palaeocorystid genera* below). The newly available material examined has permitted distinguishing details of the characters mentioned above.

Joeranina broderipii **n. comb.** (Fig. 11A, B, D) was considered a member of *Cretacoranina* by Collins (1997: 81) and Tucker (1998: 334). The species is included here in *Joeranina* **n. gen.** on the basis of having a short frontal ridge bounded by deep, divergent grooves; inclined hepatic and protogastric tubercles; thin, deep, complete cervical groove and on features of cuticle microstructure. Waugh *et al.* (2009: 32) confirmed, on cuticular structure (dorsal surface covered by pits and fine granules), that *J. broderipii* and *J. syriaca* should be excluded from *Cretacoranina* **emend.** *Joeranina* **n. gen.**, *Ferroranina* **n. gen.** and *Cretacoranina* Mertin, 1941, are differentiated in Table 3.

Joeranina japonica **n. comb.** was included in *Notopocorystes* by Collins *et al.* (1993: 300), Tucker (1998: table 3) and Yazdi *et al.* (2009: 74). However, it lacks tubercular regions, a tubercular axial carina and is not as tumid as *Notopocorystes* spp. It is here assigned to *Joeranina* **n. gen.** on the basis of the characteristic forwardly directed hepatic and admedial protogastric protuberances, thin, continuous and rather deep cervical groove, and deep and thin frontal furrows diverging backwards.

Joeranina platys **n. comb.** was included in *Eucorystes* (Schweitzer & Feldmann 2002b), based on a single, moderately preserved carapace. Better-preserved material (Schweitzer *et al*. 2009b: figs. 7, 8) confirms the absence of raised, strap-like lobes; the presence of clear hepatic and admedial protogastric tubercles; clear frontal furrows and a distinct, deep cervical groove. The oblique medial depression on the epibranchial region, also present in *Eucorystes* as a noticeable strap-like lobe, could cause confusion (see also remarks for *Eucorystes*).

Joeranina paututensis **n. comb.** is considered closely related to *J. broderipii*, *J. harveyi* and *J. syriacus* (Collins & Wienberg Rasmussen 1992: 31). The thin and deep cervical groove, the divergent frontal furrows, the triangular and forwardly directed admedial protogastric protuberance, together with the oblique epibranchial grooves, permits placement in the new genus. The species is characterised by the exceptionally narrow rostrum and the well-defined gastric regions.

The only known specimen of *Notopocorystes syriacus* is fragmentary and lacks the orbitofrontal margin and posterior carapace portion. Tucker (1998: table 4) included *N. syriacus* in *Cretacoranina*, but Waugh *et al.* (2009: 32) stated that, based on cuticle microstructures, the species could not be accommodated in that genus. It is assigned here to *Joeranina* **n. gen.** Another fragmentary specimen (Van Straelen 1931: pl. 2, fig. 39, as *Notopocorystes* sp.) (see Fig. 10D, E), can be tentatively included in *Joeranina* **n. gen.** on the basis of the smooth carapace surface, with distinct, rounded, granular axial carina. Some ventral characters are preserved in Van Straelen's specimen: mxp3 coxa large, granular; basis-ischium long, flattened, smooth, without axial depression.

The assignment of the above-listed species to a new genus leads to a more stable subdivision of Palaeocorystidae and makes typical features of the various genera to be more constant. The new genus is considered here more derived than either *Eucorystes* or *Notopocorystes* by showing a less areolated carapace, with a tendency to develop a smoother dorsal surface, a loss of dorsal convexity and the presence of a wider orbitofrontal margin.

Joeranina **n. gen.** ranges from the lower Albian to the lower Campanian, being widely distributed with records from Europe (England, France, Spain, Switzerland) to North America (U.S.A., Canada), Greenland, Syria, Japan and Madagascar. It is commonly found in association with *Notopocorystes* spp.

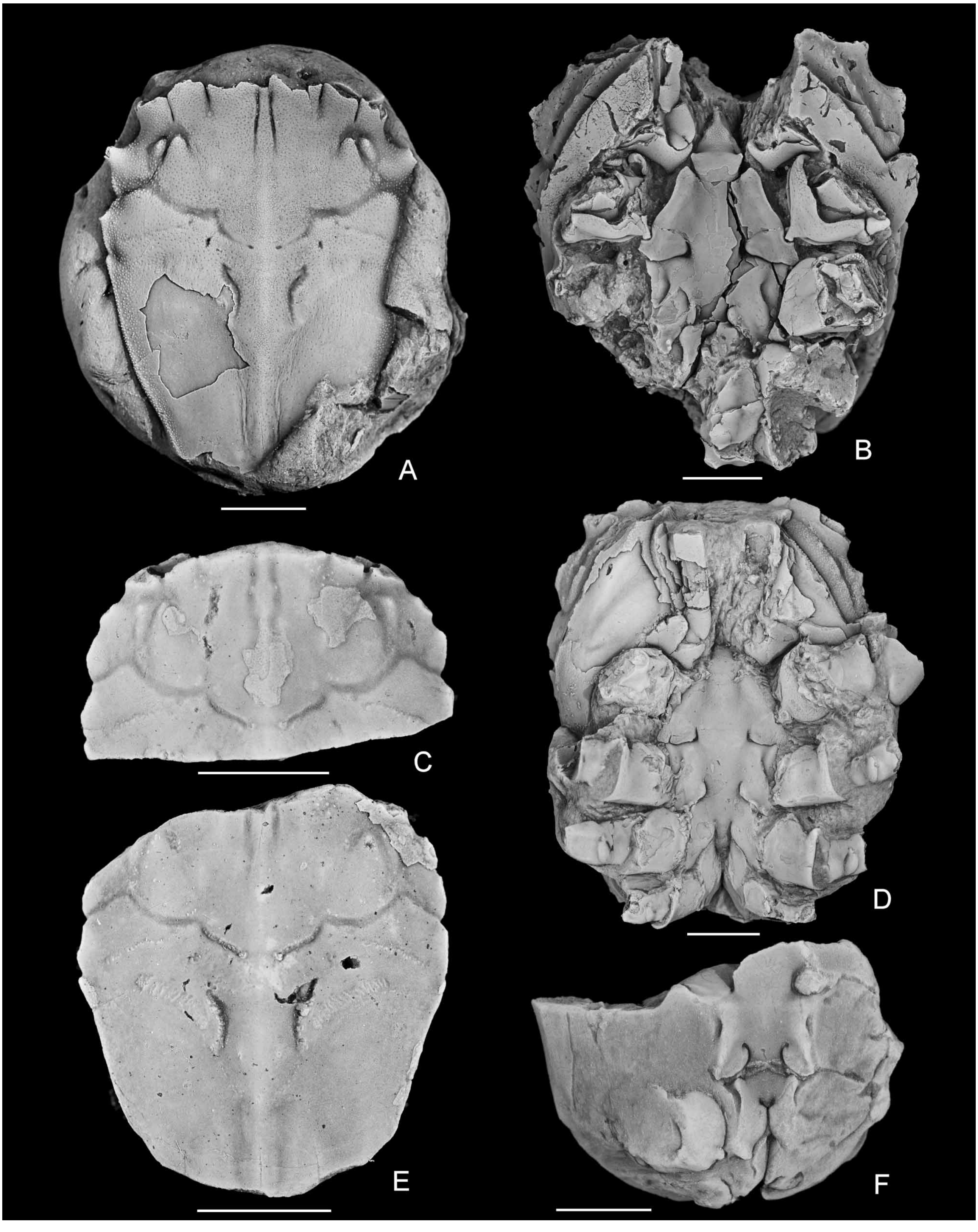


FIGURE 11. A, B, D, *Joeranina broderipii* (Mantell, 1844) **n. comb.** (Palaeocorystidae); A, MAB k. 2894 (indeterminate sex), Albian, Escalles (Calais, northern France), dorsal view of carapace; B, MAB k. 2879 (female), Albian, Folkestone (Kent, southern England), ventral view showing thoracic sternum and bases of pereiopods; D, MAB k. 2915 (female), Albian, Escalles (Calais, northern France), ventral view showing thoracic sternum and appendages; C, E, F, *Joeranina gaspari* **n. sp.**, Albian, Irurtzun (Navarra, northern Spain), MGSB75296b (C; **paratype**), dorsal view of anterior portion of carapace; MGSB75296a (E; **paratype**), dorsal view of carapace, and MGSB75296c (F; **paratype**), ventral view showing posterior portion of thoracic sternum. Scale bars: 5mm.

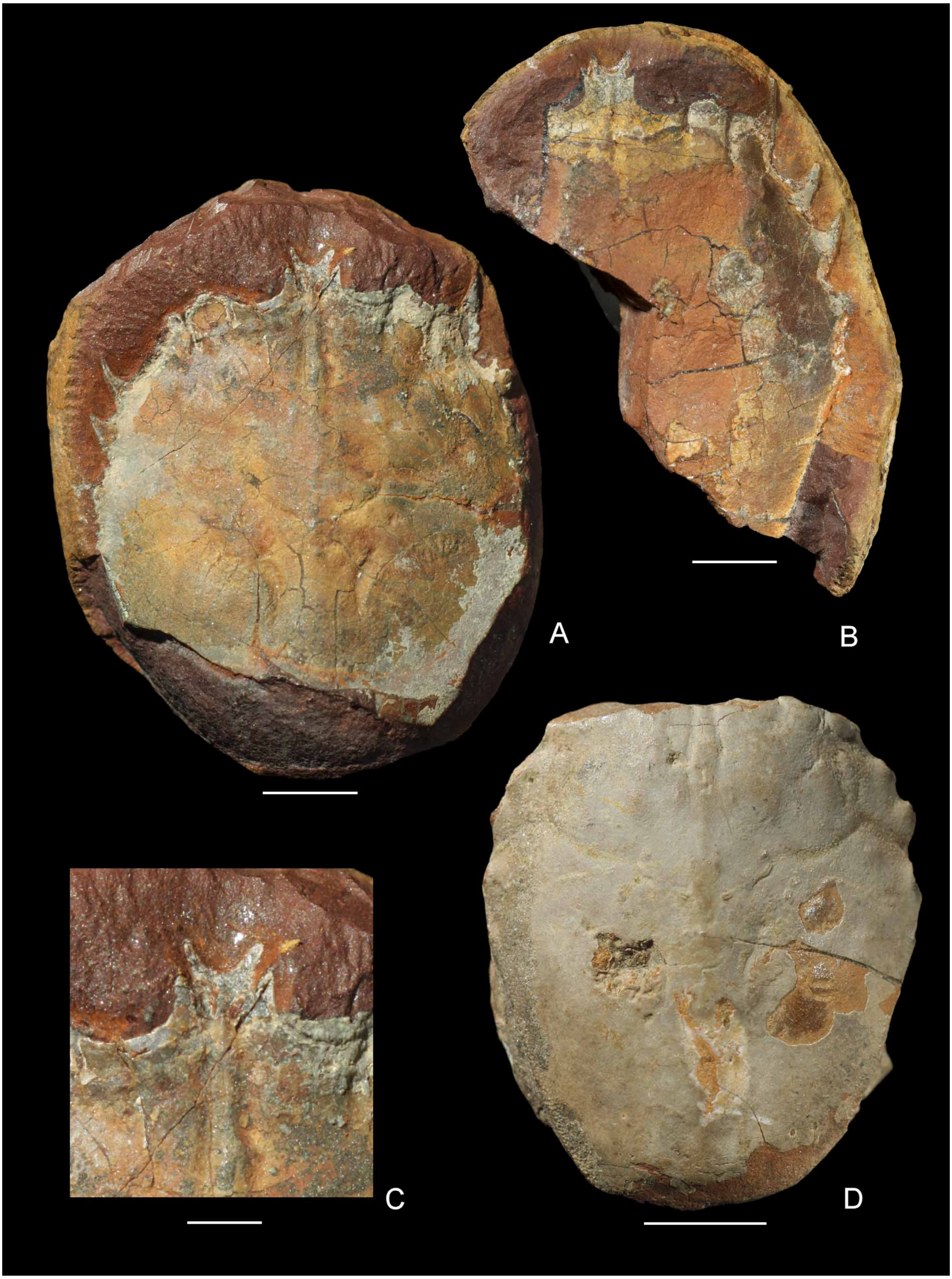


FIGURE 12. *Joeranina gaspari* **n. sp.** (Palaeocorystidae), Albian, Egiarreta (Navarra, northern Spain); A, C, MGSB75294 (**holotype**), dorsal view of carapace, and detail of rostrum; B, MGSB75295b (**paratype**), right portion of carapace, dorsal view; D, MGSB75295a (**paratype**), dorsal view of carapace. Scale bars: A, B, D: 5mm; C: 2mm.

Joeranina gaspari n. sp.

(Figs. 11C, E–F; 12A–D)

Diagnosis. Carapace small, subhexagonally elongated, widest at level of epibranchial spine; axial carina weak; front with 4 divergent spines at distal portion; orbital margin broad, with 2 deep supramarginal fissures, bounding robust central tooth with triangular upper margin; lateral margins weakly arched, with 2 long spines at level of hepatic region; cervical groove well-defined; dorsal regions scarcely defined, subtle elongated swellings in hepatic region, admedial triangular swelling in protogastric region, intestinal region elongated, somewhat inflated, bounded by shallow grooves; dorsal surface with fine granules, branchial regions pitted.

Derivation of name. In honour of Gustavo Gaspar (Navarra, Spain), who provided the first specimens to one of the authors (PA).

Material examined. Holotype, a near-complete carapace (MGSB75294), partially decorticated; paratypes, a carapace, lacking the front, cuticle fairly complete (MGSB75295a); a fragmentary carapace with well-preserved right portion (MGSB75295b), all from 1 km north of Egiarreta (Navarra), from red-coloured Albian beds (Instituto Geológico de España 1987). Additional paratypes are a near-complete carapace, lacking the front (MGSB75296a); an anterior half of a carapace (MGSB75296b); a partial ventral side (MGSB75296c), all with only few fragments of cuticle preserved, from approximately 1.5 km north of the village of Irurtzun (Navarra), from Albian limestones (Instituto Geológico de España 1978).

Description. Carapace small, subexagonally elongated, weakly convex in both directions; maximum width at level of epibranchial spine; orbitofrontal margin broad, about three-quarters of maximum width; axial carina weakly marked; orbits large, supraorbital margin with 2 deep, rather open fissures, supraorbital tooth broadly triangular, extraorbital tooth robust, with long, acute, conical extraorbital spine; front projected, narrow, with 4 divergent spines at distal portion, the posterior ones fairly long; lateral margins of carapace gently arched, anterolateral margin short, with 2 long, conical, forwardly directed spines at level of hepatic region, and 1 spine at level of epibranchial region; posterolateral margins longer, anteriorly with small, forwardly directed spine, nearly straight, diverging, sharp with subtle rim; posterior margin shorter than orbitofrontal width, slightly concave; dorsal regions poorly defined; cervical groove well-defined, complete, medially broadly U-shaped, laterally as an inverted V-shape, clearly notching carapace margin; subtriangular admedial lobe of protogastric region weakly salient, joining small hepatic protuberance; epibranchial region with subtle interbranchial scar; cardiac region relatively narrow, bounded by subtly arched branchiocardiac grooves; dorsal surface densely and finely granular over entire carapace, with some pits on branchial regions.

Remarks. *Joeranina gaspari* **n. sp.** can be easily distinguished from all congeners on the basis of the weak axial carina, the conspicuously long lateral and frontal spines, the triangular central tooth of the supraorbital margin, and the urn-shaped frontal furrows. The dorsal surface of *J. gaspari* **n. sp.** presents an arrangement of very fine granules that is denser than in other species. *Joeranina Syriacus* **n. comb.**, which is based on a single, rather incomplete specimen, also has a stronger base of the lateral spines; *J. platys* presents a wider anterior carapace; *J. paututensis* is distinguished by having more marked carapace grooves and *J. broderipii* presents more pronounced hepatic and protogastric protuberances.

The density of granulation and definition of regions of the dorsal carapace varies between specimens from Egiarreta and Irurtzun. Discovery of better-preserved material might lead to the conclusion that two species are present.

Genus *Notopocorystes* McCoy, 1849

Notopocorystes McCoy, 1849: 169.
Palaeocorystes Bell, 1863: 11.

Type species. *Corystes stokesii* Mantell, 1844, by subsequent designation of Withers (1928) (= *Notopocorystes mantelli* McCoy, 1849).

Diagnosis. Small-sized carapace, subhexagonally elongated in outline, maximum width at epibranchial spine, dorsal surface fairly convex in both directions; cervical groove marking two different slopes; axial ridge present along complete carapace, with row of single or double (*N. bituberculatus*) tubercles; orbits rather narrow for the family, with 2 supramarginal fissures; front narrow, trapezoidal, bifid, with 2 distal, 2 subdistal spines, the posterior ones strongly reduced; anterolateral margins short, arched, with 3 conical spines well separated by cervical notch: 2 anterior at level of hepatic region, one posterior at level of epibranchial region; posterolateral margins longer, with small mesobranchial spine behind discrete branchial notch, first portion sharp, usually with denticles, posterior portion rounded; posterior margin fairly concave, shorter than orbitofrontal margin; dorsal regions well defined by swellings, grooves, lobes of regions with tubercles; hepatic region with single, relatively small tubercle; protogastric lobe usually with admedial arched row of tubercles; cervical groove well-defined as thin line, complete, sinuous, medially U-shaped, gastric pits present in axial portion; branchial groove well-defined, lateral, fairly long. Dorsal surface covered by fine, dense granules (upright nodes), may be more widely spaced and larger posteriorly (*N. normani*). Pterygostome large, with blunt crests, buccal margin fairly concave, with broad buccal collar; thoracic sternum narrow, elongated, narrowing backwards, never connected to pterygostome; sternites 1 and 2 fairly narrow, situated at lower level; sternite 3 subpentagonal, with rather deep incision at base of lateral margins; sternite 4 subtrapezoidal with lateral margins long, oblique, somewhat concave, episternites suboval, posteriorly bounded by crescent-shaped suture 4/5; sternite 5 with short, arched grooves, episternites 5 long, directed obliquely, with distally a notable double peg for abdominal holding, suture 5/6 arched; sternite 6 narrow, episternites elongated, directed backwards, with arched suture 6/7; sternites 7, 8 reduced, tilted; spermathecal apertures elongated, at extremity of suture 7/8; all sternal sutures opened, directed forwards; abdomen narrow, completely filling the sterno-abdominal depression in both sexes, all abdominal somites free, somites 1–6 with raised axial portion, somites 1, 2 restricted for P5 coxae, somites 3–5 with central tubercle, somite 6 long; telson reaching sternite 4; mxp3 elongated, in oxystomian condition: coxae large, flabelliform, basis-ischium fused, long, smooth, exopod slender, long, endopod with shallow longitudinal groove; P1 with chelae homochelous, homodontous, tuberculate, upper, lower margins spinose, outer surface of merus with sharp distal crest; P2–P4 long, flattened, upper and lower margins granulate; P5 much reduced, subdorsal. Ventral regions, anterior portion of thoracic sternum densely granular.

Species included. *Notopocorystes bituberculatus* Secretan, 1964, *N. normani* (Bell, 1863) [as *Palaeocorystes*], *N. praecox* Wright & Collins, 1972 [as *Notopocorystes* (*Notopocorystes*) *stokesii praecox*], *N. serotinus* Wright & Collins, 1972 [as *Notopocorystes* (*Notopocorystes*) *stokesii serotinus*], *N. stokesii* (Mantell, 1844) [as *Corystes*] and *N. xizangensis* Wang, 1981.

Material examined. *Notopocorystes bituberculatus*: MNHN F.R03951 (holotype), incomplete carapace with associated sternum, lower Albian, Malandriandro, Sitampiky region, Mahajanga Basin, Madagascar (see Fig. 10C, F; Charbonnier *et al*. in press). *N. serotinus*: MAB k. 2872, dorsal carapace (indeterminate sex; plaster cast of specimen in L. de Putter Collection), Albian, Escalles (Calais, northern France). IRScNB unregistered, Van Straelen Collection, drawer 218, approximately 80 well-preserved specimens with preservation of ventral characters, upper Albian, Cambridge Greensand, Cambridge (southern England). *N. normani*: NHM In. 44346, carapace with cheliped, Lower Chalk, Cenomanian, Dover (Kent, southern England). *N. stokesii*: MAB k. 2870, carapace with ventral surface without abdomen (indeterminate sex); MAB k. 2873, carapace with thoracic sternum with spermathecae and ‘double peg’ for abdominal locking mechanism (female); MAB k. 2874, carapace, thoracic sternum, mxp3, with gonopore on P3 coxa (female); MAB k. 2889, carapace with thoracic sternum, mxp3 and pereiopods (juvenile female); MAB k. 2900, carapace infested on both sides by parasitic isopod (plaster cast of specimen in L. de Putter Collection; indeterminate sex); MAB k. 2906, carapace with mxp3 (indeterminate sex); MAB k. 2907, carapace with thoracic sternum, mxp3 and bases of pereiopods (female); Albian, Escalles (Calais, northern France). MNHN-B.14179, 2 specimens with ventral characters preserved; MNHN-B.14186, specimen *in situ* with chelipeds preserved; MNHN-B.14186, 7 specimens with ventral characters preserved, 1 specimen *in situ* with chelipeds preserved (A. Milne-Edwards Collection); MNHN-R.03311, carapace; MAB k. 2901: partial carapace and thoracic sternum (leg. B. Fraaije; indeterminate sex); Albian, Folkestone (Kent, southern England). IRScNB unregistered, Van Straelen Collection, drawer 218, approximately 200 specimens, most with remains of abdomen, thoracic sternum and pereiopods; MNHN-B.17958, 8 specimens with ventral characters preserved; Cambridge Greensand, upper Albian, Cambridge (southern England). MAB k. 2890, partial carapace with thoracic sternum and telson (indeterminate sex); MAB k. 2897, partial carapace and thoracic sternum showing double peg (indeterminate sex), middle Albian, Pargny (northern France). MAB k. 2924, carapace with well-preserved thoracic sternum showing spermathecae, pterygostome and bases of appendages (*ex* G. Van den Eeckhaut Collection; female); middle Albian, Lac du Der (northern France). MNHN-B.14633, carapace (indeterminate sex); Albian, St. Dizier, Haute-Marne, northern France.

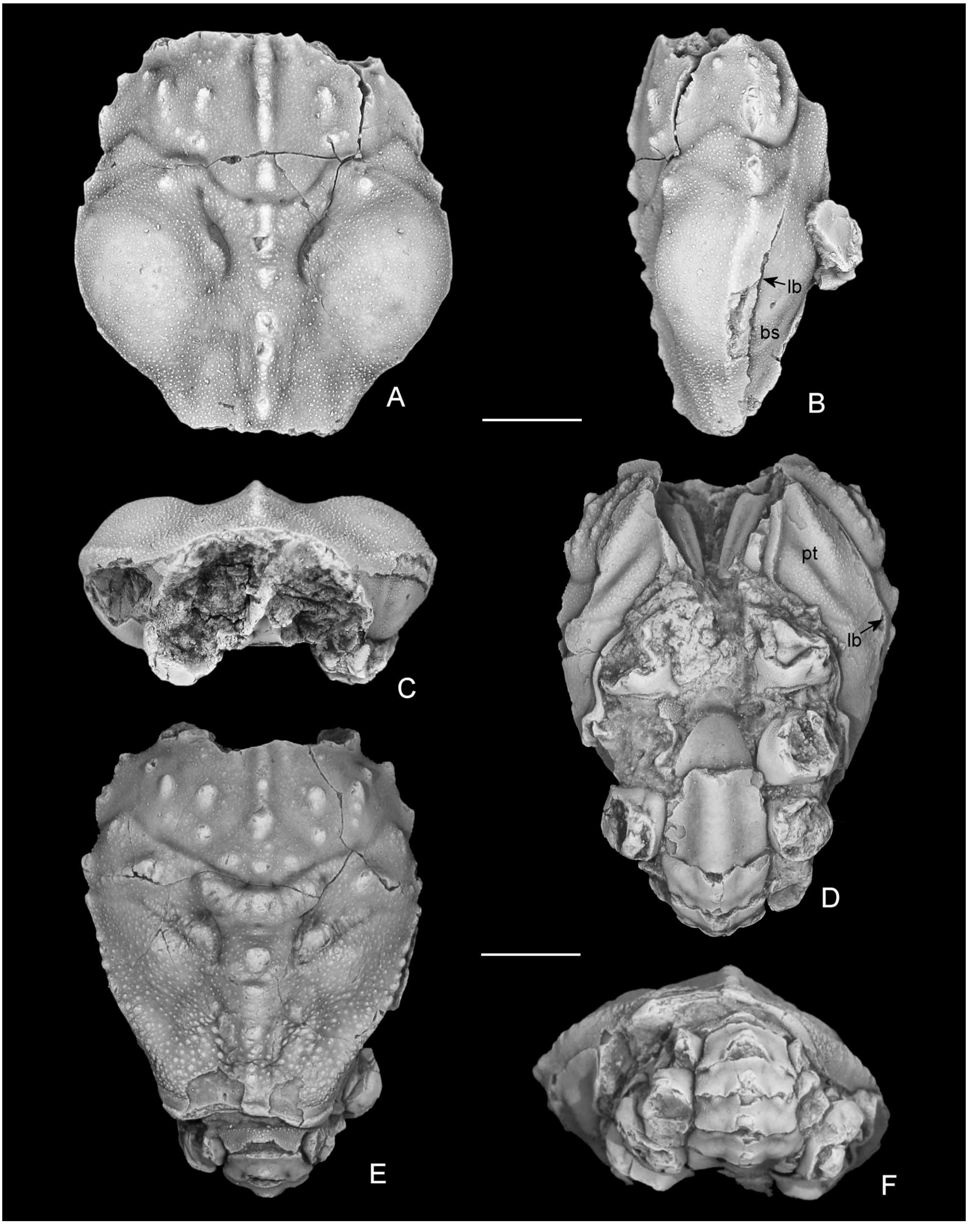


FIGURE 13. A–C, *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), MAB k. 2900 (indeterminate sex; plaster cast of specimen in Louis de Putter Collection), Albian, Escalles (Calais, northern France), infested on both sides by parasitic isopod (bopyrid); dorsal; right lateral, and posterior views; D–F, *Notopocorystes serotinus* Wright & Collins, 1972, IRScNB unregistered [Van Straelen Collection; female], upper Albian Cambridge Greensand, Cambridge (southern England), ventral view showing abdomen; dorsal view of carapace, and posterior view showing abdomen. **bs,** branchiostegite; **lb,** linea brachyura; **pt,** pterygostome. Scale bars: 5mm.

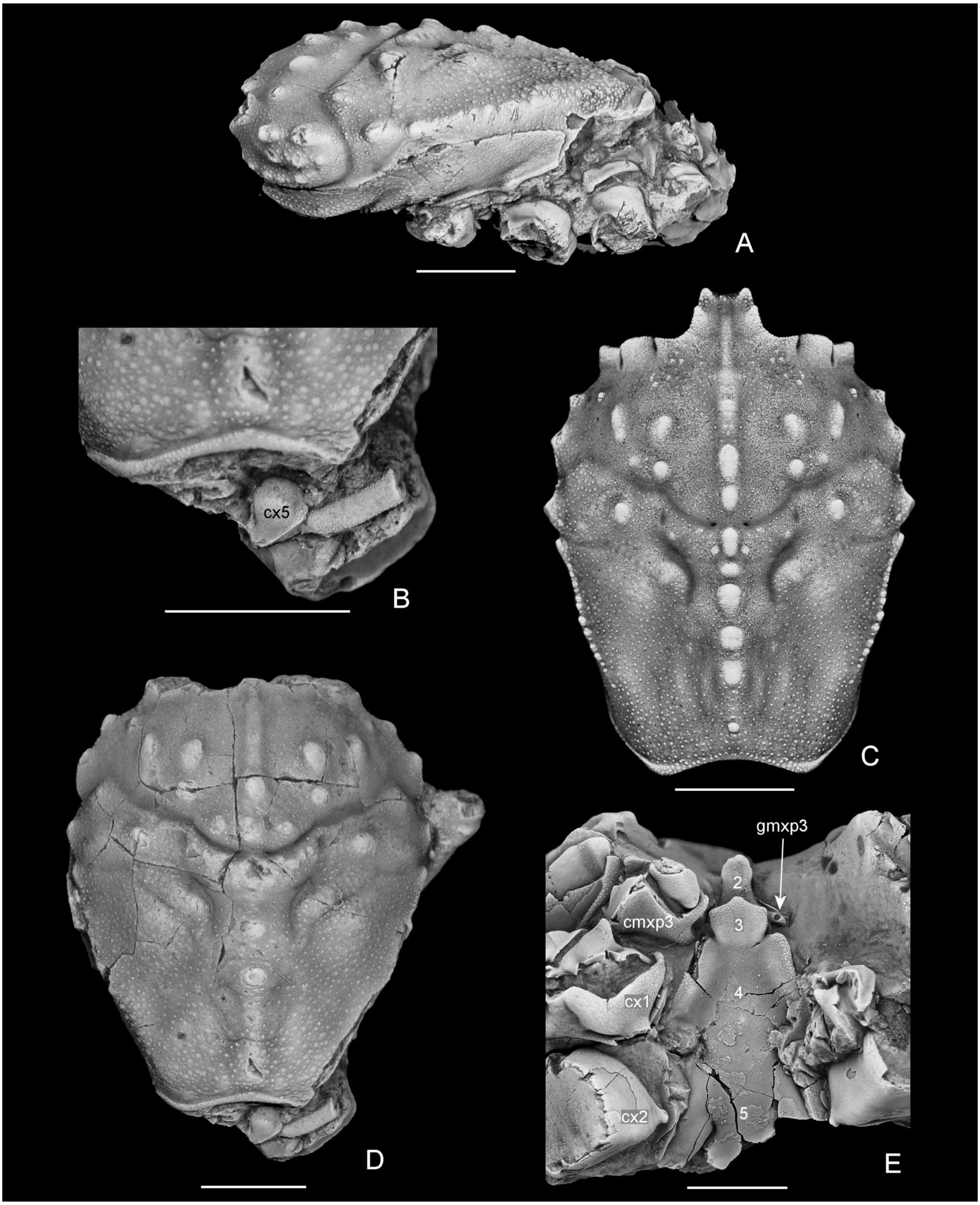


FIGURE 14. A, *Notopocorystes serotinus* Wright & Collins, 1972 (Palaeocorystidae), IRScNB unregistered [Van Straelen Collection; female], upper Albian Cambridge Greensand, Cambridge (southern England), left lateral view; B, D, *Notopocorystes serotinus*, IRScNB unregistered [Van Straelen Collection; indeterminate sex], upper Albian Cambridge Greensand, Cambridge (southern England), detail of posterior margin of carapace and P5, and dorsal view of carapace; C, MAB k. 2872 (indeterminate sex; plaster cast of specimen in Louis de Putter Collection), Albian, Escalles (Calais, northern France), dorsal view of carapace, composite photograph; E, *Notopocorystes stokesii* (Mantell, 1844), MAB k. 2901 (leg. B. Fraaije; indeterminate sex), Albian, Folkestone (Kent, southern England), ventral view showing anterior thoracic sternum. **2, 3, 4, 5,** thoracic sternites 2, 3, 4, 5; **cmxp3,** coxa of mxp3; **cx1, cx2, cx5,** P1, P2, P5 coxae; **gmxp3,** gynglyme for mxp3 coxa. Scale bars: 5mm.

Notopocorystes is distinguished from all other palaeocorystid genera in having a more convex carapace, with relatively narrow orbitofrontal margin; a wider front; tuberculate, vaulted regions; and a distinct, tuberculate carina. All species assigned here to *Notopocorystes* share constant dorsal and (when preserved) ventral features as diagnosed here. Differences among these species mainly involve the number and placement of the tubercles on the dorsal surface, orbitofrontal width and the development of the longitudinal crest (see Wright & Collins 1972; Collins 1997). Of the seven species of *Notopocorystes* listed by Tucker (1998: 333), *N. japonicus*, from the Cenomanian to Santonian of Japan, is excluded and transferred to *Joeranina* **n. gen.** on account of its less convex carapace, absence of tubercles on the dorsal surface, possession of characteristic hepatic and protogastric lobes, and typical frontal furrows. *Notopocorystes xizangensis* was established on the basis of a single, incomplete and badly weathered carapace. Material recently described from Aptian-Albian strata in Iran (Yazdi *et al*. 2009) and assigned to this species appears to be more elongated. New and better-preserved material might reveal that two distinct taxa are involved.

Genera of the Palaeocorystidae

Treated as subgenera by Wright & Collins (1972), *Cretacoranina*, *Eucorystes* and *Notopocorystes*, the last-named being the nominate genus, were given generic rank by Tucker (1998), who at the same time raised the different subspecies to species rank. The diversity of species, the abundance of material and the extended geographical distribution explain why these crabs have featured prominently in the literature for the past two hundred years (see Wright & Collins 1972, Collins 1997). A new genus, *Cenocorystes*, was recently added by Collins & Breton (2009). Here considered are six different genera within the family that can be distinguished on characters of the dorsal carapace, in combination with features of the thoracic sternum. New and well-preserved material from France and Spain, coupled with an examination of type material, has allowed recognising and diagnosing palaeocorystid genera.

The nature of the dorsal carapace is fairly constant in Palaeocorystidae. Shared characters are the subhexagonally elongated outline; a comparable orbitofrontal construction, dentate or spinose orbital margin divided by two deep fissures, large orbits, and multiple (mostly four) lateral spines.

The orbitofrontal margin of the carapace is relatively narrow in *Notopocorystes*, whereas it is distinctly wide in all other genera; in *Cretacoranina* **emend.** the anterior carapace and orbitofrontal margin are particularly wide. The cervical groove is dissimilar in the different genera, varying from deep, complete and prominent to obsolete. The cervical groove is complete, continuous, laterally marked by an inverted V-shape, medially U-shaped (‘The cervical furrow at first runs forwards from the margin, then backwards, forming three forwardly concave arcs’; Wright & Collins 1972: 73) in *Notopocorystes*, *Eucorystes* and *Joeranina* **n. gen.** By contrast, it is only medially defined and V-shaped in *Cenocorystes* and *Ferroranina* **n. gen.**; or completely absent in *Cretacoranina* **emend.** Gastric pits are usually present axially. Specific protuberances are retained in most genera in the same location, but appearance and definition differ. The hepatic region bears a small tubercle in *Notopocorystes* spp., *Eucorystes* spp., *Joeranina* **n. gen.** and *Ferroranina* **n. gen.**, but appears to be missing in species of *Cenocorystes* and *Cretacoranina* **emend.**, but low tubercles may be seen in *Cr. testacea*. The branchiocardiac groove is observed in all genera, but weakly developed in *Cenocorystes* and *Cretacoranina* **emend.** The axial carina is strong and tuberculate in *Notopocorystes*; present as a flattened strap or a low ridge in *Eucorystes*; as a gently rounded crest in *Joeranina* **n. gen.**, barely visible in *Ferroranina* **n. gen.** and absent in *Cenocorystes* and *Cretacoranina* **emend.**

A post-frontal terrace is unique for *Ferroranina* **n. gen.** It is formed by three lobes; one each epigastric, protogastric and epibranchial. A similar pattern may be recognised in *Notopocorystes,* in which the epigastric region is weakly vaulted, the protogastric region with an admedial tubercle that joins a small hepatic tubercle, and an epibranchial process being marked by the acute cervical groove. The strap-like lobes in *Eucorystes* show about the same shape; in *Joeranina* **n. gen.** the admedial protogastric protuberance and the hepatic tubercle are joined and prominent, similar to the medial lobe in *Ferroranina* **n. gen.**

The epibranchial region, which is important in attempts to trace the main dorsal grooves when these are weakly defined, is invariably subdivided. The anterior portion is bounded anteriorly by the cervical groove, and posteriorly by an interbranchial groove. This portion is subtriangular in outline, and discernible in all palaeocorystid genera, except for *Cretacoranina* **emend.** This region is observed only in decorticated specimens of *Ferroranina* **n. gen.** Posterior to the interbranchial groove, the epibranchial region is oblique and extends up to the lateral margins; it is tumid in *Notopocorystes* and *Eucorystes*, flat in *Cenocorystes* and *Joeranina* **n. gen.**, and clearly seen only in decorticated specimens of *Ferroranina* **n. gen.** A third, posterior portion of the epibranchial region may be visible in *Eucorystes*, *Joeranina* **n. gen.** and *Notopocorystes*; it is arched and bounded by branchial and branchiocardiac grooves.

The dorsal areolation and ornament of regions varies in palaeocorystid genera. Regions are strongly marked in *Notopocorystes* (regions notably swollen, divided, tuberculate), more discrete in *Eucorystes* (regions with raised, strap-like lobes), weakened in *Joeranina* **n. gen.** (regions flatter, less evidently subdivided), to weakly defined in *Cenocorystes*, *Cretacoranina* **emend.** and *Ferroranina* **n. gen.**

The ventral surface is remarkably constant in Palaeocorystidae, revealing the various synapomorphies of the family. Fortunately, numerous specimens with well-preserved ventral morphology were available for detailed study. Sternites 1 and 2 are small, narrow, pointed; they are in a lower level than sternites 3 and 4 (*Notopocorystes*, *Cenocorystes*) or in the same level (remainder of genera). Sternite 3 normally is crown shaped (Fig. 2C, *Cenocorystes*; Fig. 3C, *Cretacoranina* **emend.**; Fig. 5E, *Eucorystes*; Fig. 8B, *Ferroranina* **n. gen.**; Fig. 14E, *Notopocorystes*), may be with sharp anterior corners (*Joeranina* **n. gen.**, Fig. 41A). Sternite 4 is narrow in *Notopocorystes*, wider in *Joeranina* **n. gen.** and *Ferroranina* **n. gen.**, and distinctly wide in *Cretacoranina* **emend.** The position of the double peg is constant: it is positioned on the lower margin of epistenite 5, just below the gynglyme for P2 (Fig. 41). Sternites 5–8 decrease in width and become more excavated; the sides of sternite 8 may join and form a medial line (Fig. 57D). Sternites 5 and 6 exhibit a ridge laterally, as a special kind of ‘sterno-coxal depression’; this feature is present in all genera except *Cenocorystes*.

The cheliped fingers of *Cretacoranina* **emend.**, *Ferroranina* **n. gen.**, *Joeranina* **n. gen.**, and *Notopocorystes* are conspicuously similar to those of *Cenomanocarcinus* (Guinot *et al*. 2008: figs. 5E, 6A; Vega *et al*. 2010: figs. 7.18, 7.19). For additional descriptions of ventral surface and appendages, and considerations on palaeocorystid morphology, see *Morphology of the Raninoidia* below.

Notopocorystes has consistently been viewed as the oldest raninid (e.g., Glaessner 1960; Förster 1970; Collins 1997). A common ancestor during the Early Cretaceous, or even during the Jurassic, was suggested by Glaessner (1960: 46), who believed *Notopocorystes* to be closer to *Necrocarcinus* than to its known descendants (see also Collins 1997: 75). Förster (1968: 189) also discussed the affinities between *Necrocarcinus* and *Notopocorystes* at length. Wright & Collins (1972) used not only morphology but also stratigraphic occurrence, in describing a series of species and subspecies to document rapid evolution. In accordance with this view, the lineage *Notopocorystes*–*Eucorystes*–*Joeranina* **n. gen.**–*Ferroranina* **n. gen.**–*Cretacoranina* is suggested. The morphological differences within Palaeocorystidae are here interpreted to illustrate an evolutionary lineage from inflated, areolated and armoured carapaces to smoother, flatter dorsal surfaces. Based on carapace convexity, more salient dorsal lobes, more pronounced axial ridge and lesser orbitofrontal width, *Notopocorystes* is here seen as the most primitive form within the family, whereas *Cretacoranina* **emend.** is the most derived, with both carapace and thoracic sternum having evolved towards a raninoid bauplan.

Family Camarocarcinidae Feldmann, Li & Schweitzer, 2008 emend.

Camarocarcinidae Feldmann, Li & Schweitzer, 2008: 1742.

Type genus. *Camarocarcinus* Holland & Cvancara, 1958.

Remarks. *Cretacocarcinus* Feldmann, Li & Schweitzer, 2008, is transferred to Necrocarcinidae (see below).

Emended diagnosis. Carapace outlined hexagonally rounded to subcircular, widest at one-third from front; strongly convex in all directions; anterolateral margin short, slightly convex, bluntly rounded in cross section, with single spine. Epibranchial spine moderately strong (*Camarocarcinus obtusus*), strong (*C. quinquetuberculatus*) to conspicuously strong (*C. arnesoni*). Posterolateral margin long, arched, blunt in cross section, with 4 spines. Posterior margin clearly concave, as wide as (*C. arnesoni*) or slightly narrower (*C. quinquetuberculatus*) than orbitofrontal margin. Rostrum short, broadly triangular, sulcate, with downturned projection, bifid, with 2 distal, 2 subdistal teeth; shallow post-rostral slits may be present (*C. arnesoni*). Orbital margins raised, orbits small, deep, close set, obliquely arranged. Outer orbital corner prominent, supraorbital margin with 2 long fissures. Branchiocardiac grooves shallow, broad; branchial groove defined by scars, cervical groove indistinct to obsolete. Carapace surface with numerous pits on anterior regions (*C. arnesoni*, *C. obtusus*) or regions with indistinct tubercles (*C. quinquetuberculatus*). Dorsal carapace surface perforated, endocuticle with upright nodes.

Pterygostome grooved, with long blunt crest. Branchiostegite with strong rim along coxae (*C. arnesoni*, *C. quinquetuberculatus*), joining coxae of pereiopods, thus no exposure of pleurites. Mxp3 in oxystomian condition, endopodite strongly elongated, merus longer than ischium. Exopodite relatively wide, longer than endopodite ischium. Mxp3 coxae not observed, but presumably not close to each other.

Chelae homochelous, lower margin spinose, palm surface with few tubercles (*C. arnesoni*, *C. quinquetuberculatus*). P2 and P3 articles oval in cross-section (*C. arnesoni*). P5 not preserved, supposedly (sub)dorsal, reduced.
Thoracic sternum strongly concave over complete length, sternum narrowing towards posterior, sterno-abdominal depression deep (*C. quinquetuberculatus*). Sutures short, lateral. Suture 4/5 crescent shaped: lateral part roughly horizontal, longitudinal part deep. Sutures 5/6, 6/7 arched, clearly divergent (*C. quinquetuberculatus*). Medial line not present at sternites 1–7; sternite 8, spermathecal aperture unknown. Arthrodial cavities evenly spaced, ventrolaterally directed.

Male abdomen unknown; abdomen wide in females, occupying complete width of sterno-abdominal depression, thus in contact with coxae of pereiopods. Abdominal somite 6 long in females; medial part of abdomen raised; female telson ending between P1 and P2 coxae (*C. arnesoni*).

Remains of abdominal holding system observed on episternite 5 (*C. quinquetuberculatus*), insufficiently preserved to be described in detail.

Remarks. The Camarocarcinidae is the smallest family in terms of number of genera within Palaeocorystoidea, comprising but a single genus, *Camarocarcinus*, to which three species from Denmark, Greenland and North Dakota, all of Paleocene age, have been assigned. *Camarocarcinus* was initially placed in Raninidae (Holland & Cvancara 1958: 499), subsequently transferred to Calappidae (Glaessner 1969: R494; Collins & Wienberg Rasmussen 1992: 33; Schweitzer & Feldmann 2000: 241; Fraaije 2002: 914), to Leucosiidae (Schweitzer *et al*. 2003a: 34), included in the ‘assemblage Palaeocorystidae-Necrocarcinidae-Cenomanocarcinidae-Orithopsidae’ (Guinot *et al*. 2008: 37) and, finally, designated as type genus of a distinct family by Feldmann *et al*. (2008: 1742, 1743).

The carapace of camarocarcinids is of moderate size, yet strongly tumid both longitudinally and transversely. Camarocarcinids closely resemble necrocarcinids in size, carapace curvature and appearance. They can be, however, distinguished by having the carapace with regions non-areolated, lacking a distinct tubercle in Camarocarcinidae (areolated, clearly tuberculate in Necrocarcinidae), in having an indistinct groove system in Camarocarcinidae (distinct in Necrocarcinidae), and the anterolateral margin with one or two spines in Camarocarcinidae (four or five teeth in Necrocarcinidae). Feldmann *et al*. (2008: 1743) remarked that the orbits were elevated and more upwardly directed in Camarocarcinidae, which resulted in a more projected orbitofrontal region than in Necrocarcinidae. Based on each of these differences described above, *Cretacocarcinus* Feldmann, Li & Schweitzer, 2008, is here removed from Camarocarcinidae and transferred to Necrocarcinidae (see below, under *Cretacocarcinus*).

The pterygostome of *Camarocarcinus arnesoni* is strongly sculpted, the innermost crest being acute, sharp and extending along the branchiostegite (Holland & Cvancara 1958: pl. 74, fig. 13; Feldmann *et al*. 2008: 1746, fig. 5.1). This crest is found to be a plesiomorphic character, which also occurs, although less prominently, in Necrocarcinidae. This ‘pterygostomian rim’ (Holland and Cvancara 1958: 501) is hypothesised to have functioned as an endostegal channel in the respiratory system (see *Respiration in the Palaeocorystoidea* below). A prominent subantennary lobe of the pterygostome cannot be verified, but is assumed to be present (probably broken off in *C. quinquetuberculatus*; Collins & Wienberg Rasmussen 1992: 34, fig. 19C).

Remarks. The subgenus *Notopocorystes* (see Wright & Collins 1972: 73) was given generic rank by Tucker (1998), who also accorded specific rank to the three subspecies of *N. stokesii*. Records from England, France, Germany, Switzerland, Iran, Kazakhstan, China and Madagascar document a stratigraphic range from the lower Albian to the Cenomanian.

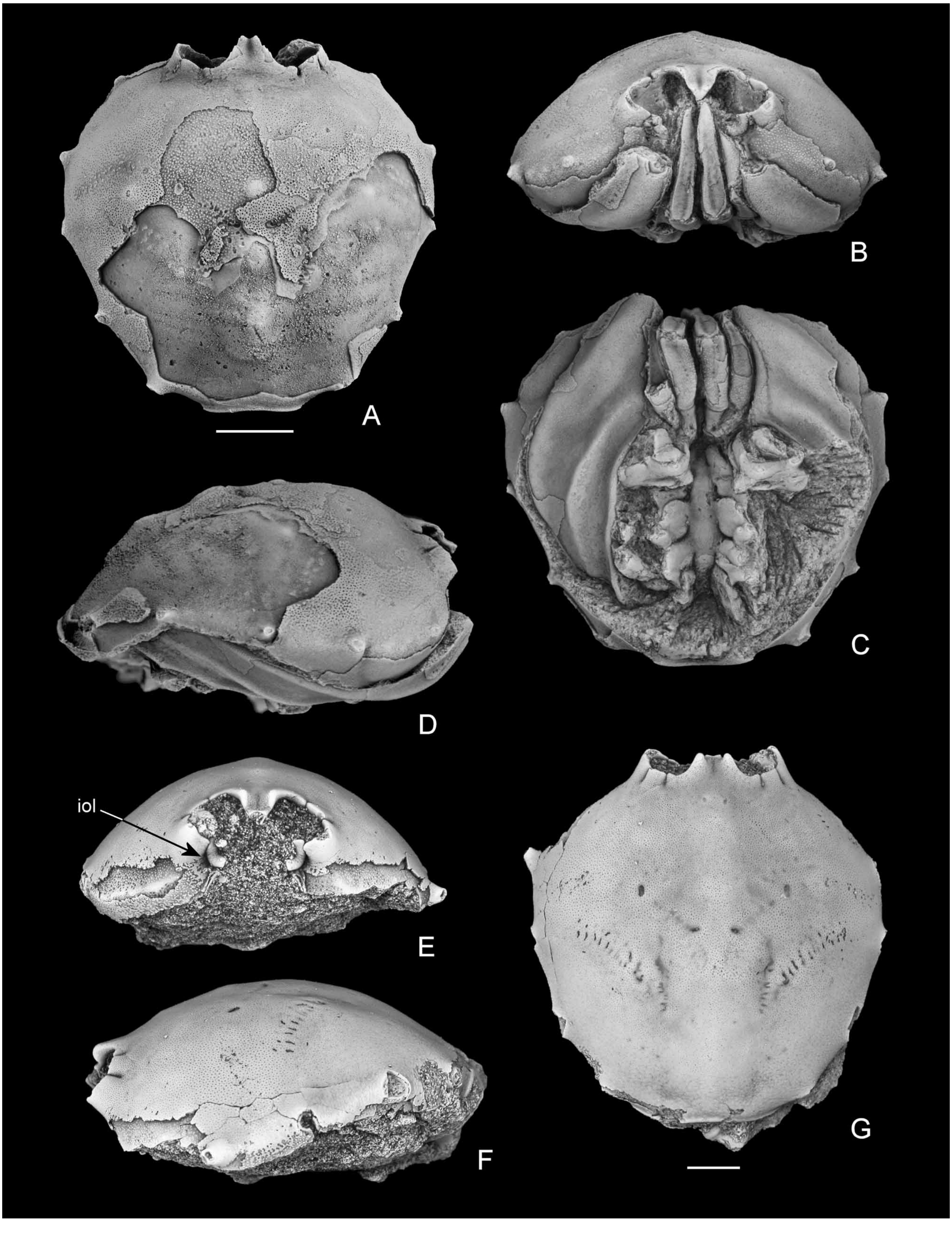


FIGURE 15. A–D, *Camarocarcinus quinquetuberculatus* Collins & Wienberg Rasmussen, 1992 (Camarocarcinidae), MGUH 21.609 (**holotype**), middle Paleocene, central Nûgssuaq, western Greenland; dorsal view of carapace; frontal view showing elongate mxp3; ventral view showing thoracic sternum, P1 coxae and mxp3, and right lateral view; E–G, *Camarocarcinus arnesoni* Holland & Cvancara, 1958, MGSB unregistered, Paleocene, North Dakota; frontal; left lateral, and dorsal views of carapace. **iol,** infraorbital lobe. Scale bars: 5mm.

Ventral features are preserved in *Camarocarcinus arnesoni* and *C. quinquetuberculatus*. The proepistome, epistome, antennae or antennules are not retained in any of the specimens examined. The thoracic sternum is well preserved in the holotype of *C. quinquetuberculatus*, the description of which was completed by Guinot *et al*. (2008: 30). Neither the pereiopods nor the posterior sternites are preserved in any of the material examined; hence no conclusion can be drawn regarding the nature of the last pair(s) of pereiopods. Feldmann *et al*. (2008: 1743) suggested that the morphology of the sternum, coupled with characters of the dorsal carapace of *Necrocarcinus* spp., differed to such an extent from those of *Camarocarcinus* and *Cretacocarcinus* that they concluded the latter two are 'demonstrably unrelated' to Necrocarcinidae. The morphology of the thoracic sternum of *Camarocarcinus quinquetuberculatus* and *Cretacocarcinus smithi* would document a morphology that is different from any known brachyuran group, according to Feldmann *et al*. (2008: 1743): 'The general sternal architecture within these two species is one of a flat-floored axial element with nearly vertical lateral elements'. According to Feldmann *et al*., this 'deep cavity' would receive a narrow abdomen. The thoracic sternum of *C. quinquetuberculatus* is deeply excavated, which corresponds to a sterno-abdominal depression, rather than to a sterno-abdominal cavity. Feldmann *et al*. (2008: 1743) compared the thoracic sternum of *Camarocarcinus* and *Cretacocarcinus* with Necrocarcinidae by way of '*Necrocarcinus siouxensis'*, of which they remarked that the species had recently been reassigned to *Cenomanocarcinus*; '*Necrocarcinus siouxensis'* is here referred, with a query, to *Orithopsis* (see below). Furthermore, they compared a single specimen of *Necrocarcinus labeschii* (SM B23180), which has also been examined for the present study (see below). The thoracic sterna of *C. quinquetuberculatus* and *N. labeschii* are, as far as material is available and preservation enables this to be compared, closely similar. The description of the thoracic sternum of *N. labeschii* by Feldmann *et al*. (2008: 1743), who stated that 'the margins of sternites 4–6 are parallel', is incorrect. In both *C. quinquetuberculatus* and *N. labeschii,* sternite 4 is subtrapezoidal with concave sides, the surface being rather strongly excavated medially, episternites 4 being the widest in the sternum; sternites 5–7 slightly decreasing in width posteriorly; the episternites are obliquely arranged, and elevated from a flat, undivided medial portion of the sternum, the sutures being only lateral (see Karasawa *et al*. 2011: fig. 10B, C). Only the anterior sternites (3 and 4, including episternite 4) of *Cretacocarcinus smithi* are preserved: sternite 4 is strongly excavated, the sides are concave and episternites 4 are distinctly elevated. This profile is stronger than, but not different from either that of *C. quinquetuberculatus* or *N. labeschii.* In addition, Guinot *et al*. (2008: 30) remarked that the thoracic sternum of '*Necrocarcinus*' *wrighti* (Feldmann *et al*. 1993: figs. 29.4, 29.5) was not substantially different from that of *Camarocarcinus*. It may be concluded, with reservation, that the thoracic sternum of Camarocarcinidae strongly resembles the sternum of Necrocarcinidae. Obviously, better-preserved material is needed to complete the diagnoses of both families.

Karasawa *et al*. (2011: 550, 551) complicated matters by stating that, 'Camarocarcinidae is the sister to the remainder of the raninoids; Necrocarcinidae and Cenomanocarcinidae are sister to Palaeocorystidae, ...' , '... separate Camarocarcinidae from its most similar taxon, Necrocarcinidae' and 'Necrocarcinidae and Camarocarcinidae appear as sister taxa'. *Camarocarcinus* and *Necrocarcinus* have a similar thoracic sternum, with a flat axial depression and lateral episternites strongly raised. The angle of the raised episternites is not substantially different in the two families, as stated by Feldmann *et al*. (2008: 1743, 1744) and Karasawa *et al*. (2011: 550). While Fraaye (1994) suggested that *Camarocarcinus* was derived from the *Necrocarcinus* stock, Feldmann *et al*. (2008: 1741) stated that, 'details of the morphology […] falsify the contention that *Camarocarcinus* was derived from a necrocarcinid ancestor'. Karasawa *et al*. (2011: 533) remarked that, 'Guinot *et al*. (2008) thought that *Camarocarcinus* belonged to Palaeocorystidae', but, in fact, Guinot *et al*. (2008: 706) assigned *Camarocarcinus* to the Raninoidea, close to the Palaeocorystidae.

Feldmann *et al*. (2008: 1743) were of the opinion that the carapace ornament of *Cretacocarcinus* differed from that of Necrocarcinidae, in that the 'nodes' [tubercles] on the dorsal surface of *Cretacocarcinus smithi* were not aligned in rows. An axial row of tubercles (one cardiac, one urogastric and two mesogastric), a tubercle on each branchial portion and two tubercles transversely arranged on the protogastric region in *C. smithi* perfectly match the arrangement in the type of *Necrocarcinus*, *N. labeschii*. Tuberculation of regions is absent or indistinct in the species of *Camarocarcinus*; in *C. quinquetuberculatus* it is only axially defined (Fig. 15A–D). Feldmann *et al*. (2008: 1743) noted that pillars of the endocuticle 'extend up to or through the exocuticle surface'. Waugh *et al*. (2009: 35) found that '*Camarocarcinus arnesoni* has cuticle that is most similar to that of *Symethis* and *Cretacoranina* because the nodes on its surface are somewhat enlarged or bulbous at their tops', whereas Feldmann *et al*. (2008: 1743, fig. 5.5) had earlier described the outer surface as 'smooth to granular'. The examined cuticles of *C.*

arnesoni and *C. quinquetuberculatus* (Fig. 15A–G) show the endocuticle to have upright nodes, overlapped by one or two layers of cuticle with numerous fine perforations. The preserved cuticular surface near the orbitofrontal region and near the posterior margin comprises fine granules with sparse perforations. These perforations most likely contained setae during life (Waugh *et al*. 2009: 16).

The Camarocarcinidae appears to be closely related to Necrocarcinidae, their differentiation currently being weak. Until additional ventral characters can be compared, features of the dorsal carapace seem to be the most reliable for distinguishing both families.

Genus *Camarocarcinus* Holland & Cvancara, 1958

Camarocarcinus Holland & Cvancara, 1958: 499.

Type species. *Camarocarcinus arnesoni* Holland & Cvancara, 1958, by original designation.

Species included. *Camarocarcinus arnesoni* Holland & Cvancara, 1958, *C. obtusus* Jakobsen & Collins, 1979, and *C. quinquetuberculatus* Collins & Wienberg Rasmussen, 1992.

Material examined. *Camarocarcinus arnesoni*: well-preserved carapace, Paleocene, Cannonball Formation, Burleigh County, North Dakota (U.S.A.) (MGSB unregistered; Fig. 15E–G); *C. quinquetuberculatus*: holotype, carapace with thoracic sternum and mxp3, Paleocene, Turritellakløft Member, Agatdal Formation, central Nûgssuaq, West Greenland (MGUH 21.609; Fig. 15A–D).

Family Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008

Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008: 684.

Type genus. *Cenomanocarcinus* Van Straelen, 1936: 37, by original designation (emend. Stenzel 1945: 447).

Genera included. *Cenomanocarcinus* Van Straelen, 1936, *Campylostoma* Bell, 1858, and *Hasaracancer* Jux, 1971.

Diagnosis (modified after Guinot, Vega & Van Bakel 2008: 684).

Carapace medium to large size (estimated maximum carapace length of 160 mm in *Cenomanocarcinus* aff. *vanstraeleni*); females probably larger than males. Carapace subhexagonal to subcircular, widest about mid-length, weakly arched in all directions, orbits raised (distinct in *Cenomanocarcinus*, *Hasaracancer*, weak in *Campylostoma*). Anterolateral margin convex, long, with 4–7 teeth, last epibranchial sometimes conspicuously strong, produced. Posterolateral margins markedly convergent posteriorly, tubercular or with 1 or 2 teeth, subdistal (at the extremity of the lateral ridge) may be marked, spiniform. Posterior margin clearly concave, as wide as or wider than orbitofrontal margin, may be convex in dorsal view. Orbitofrontal margin narrow (*Cenomanocarcinus*) or wider (*Campylostoma*, *Hasaracancer*). Front narrow, trilobate (orbital corners excluded). Orbits rounded, small (*Cenomanocarcinus*); supraorbital margin with 2 fissures. Cervical groove shallow to acute, branchiocardiac grooves shallow. Three prominent longitudinal carinae may bear strong tubercles: 1 axial (axial carina), 2 branchial (branchial carinae) that are convex or straight, may generally form characteristic ‘H’ with imaginary horizontal line crossing cardiac region; oblique carina (epibranchial carina) may be present, ending in epibranchial tooth. Transverse ridges may be present, nearly in line, one on protogastric regions, less marked one on hepatic regions. Dorsal carapace surface with upright nodes.

Pterygostome deeply grooved, with distinct, blunt crest that extends anteriorly into prominent subantennary lobe. Branchiostegite joining coxae of pereiopods, exposure of pleurites absent. Mxp3 strongly elongated (reaching half carapace length), in oxystomian condition, with coxae large, not close to each other; endopodite ischium long, developed, subrectangular longitudinally; merus ovate, approximately half ischium length (*Cenomanocarcinus*), or slender, as long as ischium (*Campylostoma*); exopodite broad, longer than endopodite ischium (*Cenomanocarcinus*), or shorter than endopodite ischium (*Campylostoma*).

Chelipeds robust, long, homochelous, homodontous; fingers elongated, gaping in adult males; upper, lower margin of chelae spinose, outer surface tuberculate (*Cenomanocarcinus*, unknown in others). Smaller, more slender in females than in males, spinose chelipeds, with propodus much longer than in males, prehensile margins of fingers appressed. P2–P4 rather long, markedly asymmetrical in both sexes. P2 slender, long; propodus moderately enlarged, flattened. P3 propodus more developed, flattened, with styliform dactylus. P4 more robust than P3; merus shorter, thick; propodus wide, ovate, flattened; dactylus semi-ovoid. P5 dissimilar in position, size, shape, markedly reduced, relatively long, thin, subdorsal, carried horizontally; merus subrectangular, length one-third of P4 merus; carpus rectangular, length two-thirds of merus; propodus subtriangular; dactylus nearly as long as propodus, simply curved, without terminal prehensile apparatus. Basis, ischium of pereiopods separated (*Cenomanocarcinus vanstraeleni*, *Campylostoma matutiforme*).

Thoracic sternum relatively narrow, entirely covered laterally by male abdomen, therefore in contact with coxae of pereiopods, leaving most of anterior sternum exposed between telson, base of mxp3. Sternal plate weakly concave anteriorly, slightly more posteriorly, flatter in females. Sternite 1 elongated between proximal portions of mxp3, sternites 2, 3 showing as small, narrow plate (may be crown shaped) intercalated between mxp3 coxae; sternite 4 long, well developed, with concave borders, its anterior side slightly wider than sternite 3 (*Campylostoma matutiforme*, *Cenomanocarcinus vanstraeleni*); sternites 5, 6 wider, showing fairly expanded lateral flanges. Sternites 7, 8 weakly tilted, sternite 8 elongated, weakly curved, not much narrower than preceding sternites (*Cenomanocarcinus beardi*). Sternal sutures 4/5–6/7 short, lateral, crescent-shaped. Spermathecal apertures at extremity of suture 7/8, rather small, oval, margins weakly raised (*Cenomanocarcinus beardi*). Thoracic sternum weakly narrowing posteriorly, an undivided portion medially, without medial line (*Cenomanocarcinus beardi*, *C. vanstraeleni*). Arthrodial cavities evenly spaced, ventro-laterally directed.

Abdomen with all somites free in both sexes, first somites dorsal, somite 6 much longer, sexual dimorphism indistinct. Male abdomen fairly long, broad, completely filling laterally sterno-abdominal depression. Surface of somites may bear several small tuberculate transverse ridges in both sexes. Male telson reaching sternite 4, at same vertical level as gynglymes for P1 (*C. vanstraeleni*); in females, abdomen slightly longer, reaching almost sternite 3, well beyond level of P1 gynglymes (*C. vanstraeleni*).

Double locking teeth on episternite 5 forming abdominal holding system (*C. vanstraeleni*, *C.* aff. *vanstraeleni*). No holding structures on coxae of pereiopods.

Remarks. The family Cenomanocarcinidae was erected by Guinot *et al*. (2008), who discussed the possible relationships with other raninoidean families. The Cenomanocarcinidae is a long-existing family, first appearing during the Albian and becoming extinct in the early Eocene (55.8–46.5 Ma). Only one Mesozoic and one Paleogene (Eocene) genus are so far included. *Campylostoma* was assigned, albeit with a query, to Cenomanocarcinidae by Guinot *et al*. (2008); newly examined, better-preserved material confirms this taxonomic placement.

Many characters of the thoracic sternum and appendages of Cenomanocarcinidae are now known (Guinot *et al*. 2008); new material illustrated herein substantiates the presence of a prominent, double structure for abdominal holding (Fig. 40C–F) and a distinct oxystomian configuration of mxp3 and endostome (Fig. 50F). The spermathecal aperture described by Guinot *et al*. (2008: 38), is also illustrated here (Fig. 58A, B); the female gonopore has yet to be observed. Karasawa *et al*. (2011: 550) diagnosed Cenomanocarcinidae as having a complete sternal suture 6/7; this likely was a weakly calcified transverse line, as seen in many podotremes, or a preservational artefact.

In the nature of the anterolateral margin, the narrow orbits and the areolated, tuberculate carapace surface, the family appears closely related to Necrocarcinidae. Necrocarcinids, however, have a very strong sterno-abdominal depression, with the episternites markedly raised, whereas the sterno-abdominal depression of Cenomanocarcinidae is rather flat. The tricarinate carapace is a feature in common with orithopsids, which, however, have concave branchial carinae, rather than the convex branchial carinae seen in cenomanocarcinids. Several sternal differences confirm separation of the two families; sternite 3 is crown shaped in Cenomanocarcinidae, diamond shaped in Orithopsidae; sternite 4 is relatively flat, gently concave in Cenomanocarcinidae, whereas it is medially strongly excavated, with a deep gutter, in Orithopsidae, and the posterior sternites are of normal shape (plesiomorphic condition) in Cenomanocarcinidae, whereas the configuration in Orithopsidae is different (see below, under *Silvacarcinus laurae*).

Cuticle ornament and microstructure in Cenomanocarcinidae is straightforward, with the anterior regions and the branchial crests (not present in *Campylostoma*) tubercular, the complete carapace surface being finely granular with upright nodes.

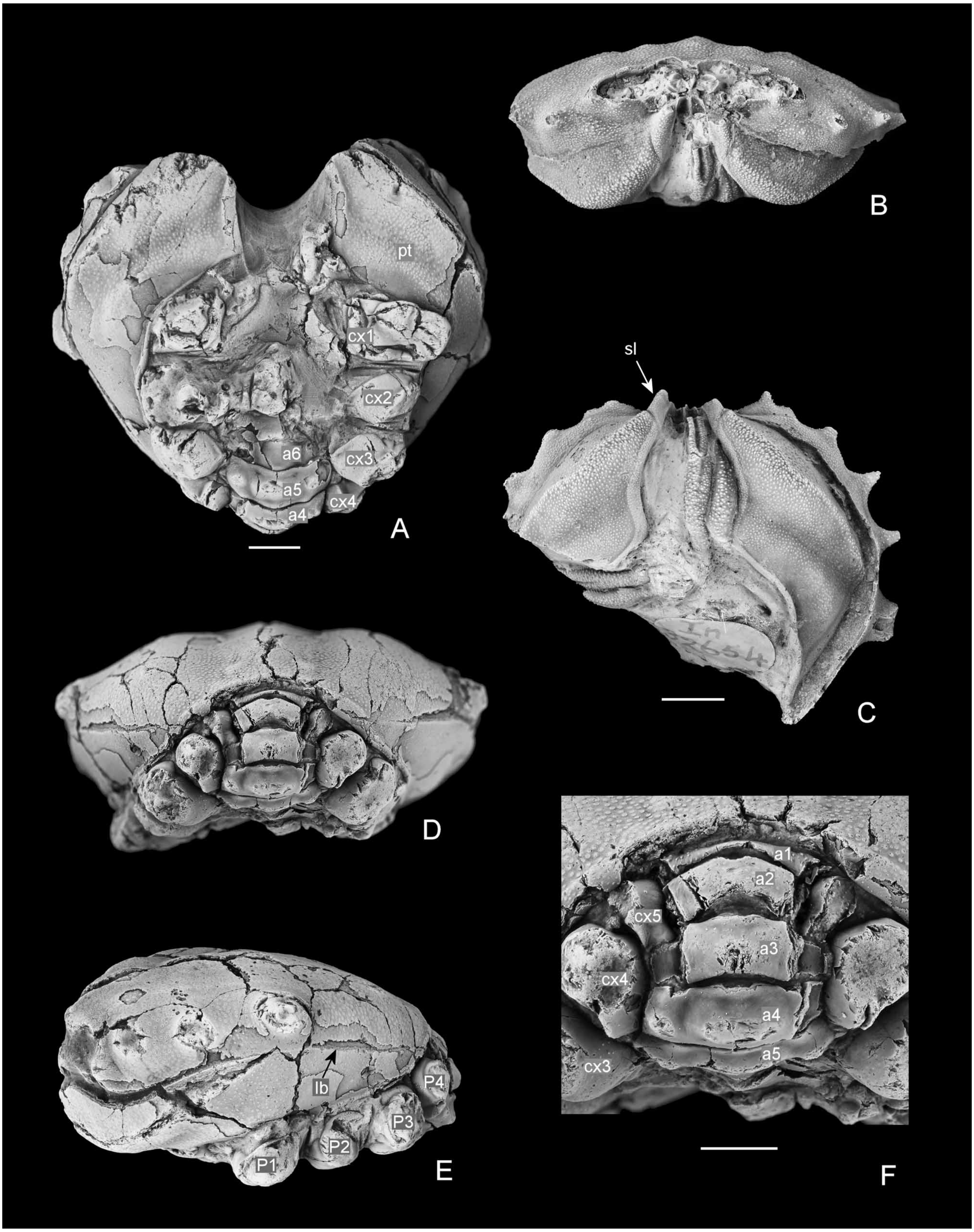


FIGURE 16. *Campylostoma matutiforme* Bell, 1858 (Cenomanocarcinidae); A, D–F, NHM In. 35231 (male), lower Eocene (Ypresian), Sheppey (Kent, southern England); ventral, posterior, left lateral, and abdominal views; B, C, NHM In. 32654/ 32655 (indeterminate sex), lower Eocene (Ypresian), Herne Bay (Kent, southern England); frontal and ventral views latter showing pterygostomes and mxp3. **a1, a2, a3, a4, a5, a6,** abdominal somites 1, 2, 3, 4, 5, 6; **cx1, cx2, cx3, cx4, cx5,** P1, P2, P3, P4, P5 coxas; **lb,** linea brachyura; **P1, P2, P3, P4,** pereiopods 1, 2, 3, 4; **pt,** pterygostome; **sl,** subantennary lobe of pterygostome. Scale bars: A-E: 5mm; F: 2mm.

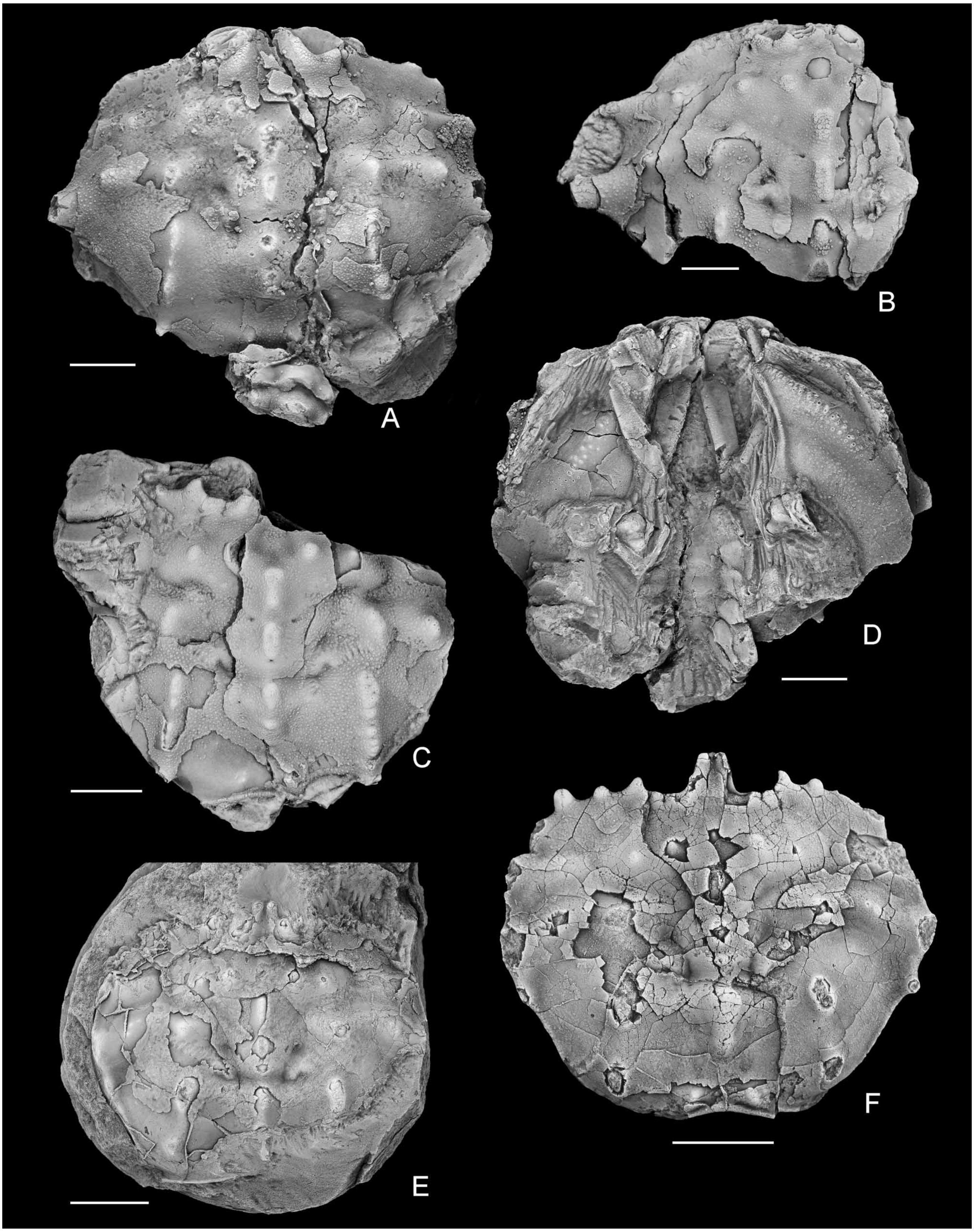


FIGURE 17. A–D, *Cenomanocarcinus beardi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a (Cenomanocarcinidae); A, D, MAB k. 2544 (female), Cenomanian (Woodbine Formation), Wagner Park, Texas (U.S.A), dorsal view of carapace, and ventral view showing thoracic sternum and mxp3; B, C, MAB k. 2916 and k. 2917 (both indeterminate sex), partial carapaces, same locality and provenance; E, F, *Cenomanocarcinus cantabricus* **n. sp.**, Albian, Cabo de Ajo (Cantabria, Spain); E, MGSB75431 (**holotype**; *ex* Manuel Díaz Collection), dorsal view of carapace; F, MGSB75423 (**paratype**; *ex* Pedro Artal Collection), dorsal view of carapace. Scale bars: A-D: 5mm; E, F: 10mm.

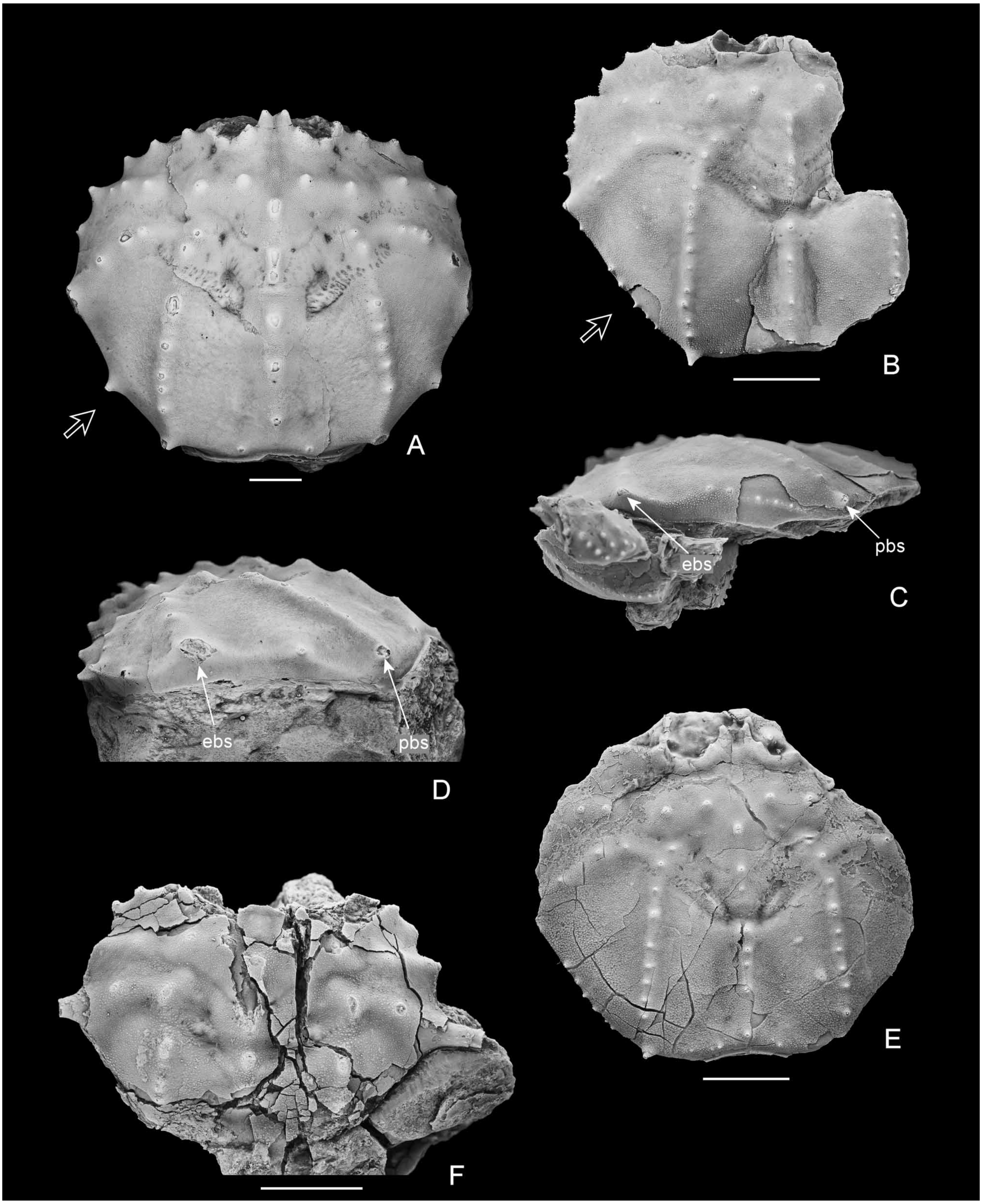


FIGURE 18. A, D. *Cenomanocarcinus inflatus* Van Straelen, 1936 (Cenomanocarcinidae), MNHN J08587 (**lectotype**), photograph of MAB k. 2968 (cast), upper Cenomanian, Butte de Gazonfier, Le Mans (northwestern France); dorsal and left lateral views (direction of photography in D indicated by arrow in A); B, C, E, *Cenomanocarcinus vanstraeleni* Stenzel, 1945, MAB k. 2909 (B, C; indeterminate sex), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County, Texas (U.S.A); dorsal and left lateral views (direction of photography in C indicated by arrow in B); MAB k. 2885 (E; indeterminate sex), dorsal view of carapace; F, *Cenomanocarcinus beardi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a, MAB k. 2880 (indeterminate sex), Cenomanian (Woodbine Formation), Wagner Park, Texas (U.S.A), dorsal view of carapace**. ebs,** epibranchial spine; **pbs,** posterobranchial spine. Scale bars: 10mm.

Genus *Cenomanocarcinus* Van Straelen, 1936

Cenomanocarcinus Van Straelen, 1936: 37.

Type species. *Cenomanocarcinus inflatus* Van Straelen, 1936, by subsequent designation of Stenzel (1945: 447).

Species included. *Cenomanocarcinus beardi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003, *C. cantabricus* **n. sp.**, *C. dissimilis* Collins, 2010, *C. inflatus* Van Straelen, 1936, *C. multituberculatus* (Joleaud & Hsu, 1935), *C. oklahomensis* (Rathbun, 1935), *C. pierrensis* (Rathbun, 1917), *C. tenuicarinatus* Collins, 2010, and *C. vanstraeleni* Stenzel, 1945.

Remarks. The genus was recently treated in detail by Vega *et al*. (2007a) and Guinot *et al*. (2008). However, those authors were unable to directly compare the closely related species, *Cenomanocarcinus beardi*, *C. inflatus* and *C. vanstraeleni*. We concur with Schweitzer *et al*. (2009: 146) in synonymising *Sagittiformosus* Bishop, 1988 (type: *S. carabus* Bishop, 1988) with *Cenomanocarcinus*. *Hasaracancer* Jux, 1971, considered synonymous with *Cenomanocarcinus* by Guinot *et al*. (2008), is here interpreted as a separate genus (see below).

Cenomanocarcinus beardi Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

(Figs. 17A–D; 18F)

Material examined. MAB k. 2969: cast of paratype (GSC 124821), provided by C.E. Schweitzer, March 2007 (see Schweitzer *et al.* 2003a: 35, fig. 12.1); MAB k. 2544, k. 2880, k. 2916, k. 2917, Woodbine Formation, Cenomanian, Creek in Wagner Park, southwest Freud Prairie, Texas (U.S.A.).

Emended description. Pterygostome large, with blunt, granular crest, buccal margin concave, rimmed. Mxp3: exopod long, slender, lateral margin gently arched; endopod ischium slightly longer than exopod, medially weakly excavated. Thoracic sternum narrow, elongated, with medial sterno-abdominal depression; sternite 3 small, crown shaped, sternite 4 trapezoidal, rather short; episternites 4 wide, large, subtriangular, anteriorly with distinct gynglyme for P1; sternites 5–8 equal in width, with flat, undivided medial surface, raised, posterolaterally directed episternites; sutures 4/5–6/7 sinuous, directed forwards; suture 7/8 long, straight, terminating in oval spermathecal aperture.

Remarks. Discovery of a specimen with preserved ventral characters necessitates an amendment of the description; dorsal carapace was described by Schweitzer *et al*. (2003a: 38). Guinot *et al*. (2008: 38) described the morphology of a specimen (MAB k. 2544) referred to as *Cenomanocarcinus* aff. *beardi*. It has spermathecae (aperture preserved at one side), hence confirming the podotreme status of Cenomanocarcinidae. This particular specimen is here assigned beyond doubt to *C. beardi*. All features of the dorsal carapace of the examined Texas material compared well with the type series. The lack of a lateral tooth between the fourth anterolateral tooth and the epibranchial spine, the strongly produced epibranchial spine, the rounded cross section of the posterolateral margin, which is devoid of spinules or teeth (except near the posterior corner), and the tuberculation of the branchial crests distinguish specimens of the new species from both *C. inflatus* and *C. vanstraeleni*. The record of *C. beardi* from the Cenomanian of Texas marks the oldest occurrence of the species and a southerly range extension. Ventral features are described for the first time for this species, which thus far represents the only example of a spermatheca in Cenomanocarcinidae.

Cenomanocarcinus cantabricus n. sp.

(Fig. 17E, F)

Diagnosis. Carapace of medium size for genus, dorsal surface weakly convex in both directions; anterolateral margins arched, with 4 teeth of similar size, additional larger tooth corresponding to epibranchial region; posterolateral margins with 2 teeth, anteriormost close to epibranchial tooth; dorsal grooves weakly marked; dorsal regions with few, coarse, blunt tubercles; hepatic region without clear tubercles.

Derivation of name. In reference to Cantabria, the region in northern Spain from where specimens of the new species were collected.

Material examined. Holotype, a complete carapace with the majority of cuticle preserved (MGSB75431) (*ex* Manuel Díaz Collection); paratype (MGSB75423) (*ex* Pedro Artal Collection), a carapace with fragments of cuticle preserved, both from the Cabo de Ajo sea cliff, within the township of Bareyo (Cantabria) from levels considered to be of Albian age (Baron-Szabo & Fernández-Mendiola 1997).

Description. Carapace medium sized for genus, subcircular in outline, wider than long; maximum width at epibranchial spine; front advanced, trilobate, with 2 additional blunt teeth at inner orbital corner; orbits small, directed forwards, with 2 short fissures in supraorbital margin, outer orbital node robust, fairly salient; anterolateral margin long, arched, with 5 teeth (excluding outer orbital node, including epibranchial spine), anterior 4 stout, fairly salient, of similar size; epibranchial tooth not completely preserved, appears to have been strong; posterolateral margin longer, converging backwards, sharp edged, with 2 small teeth, anterior one close to epibranchial node, second near posterior corner; posterior margin axially concave, defined by fine rim behind a narrow groove, slightly wider than orbitofrontal margin; dorsal carapace regions weakly vaulted, defined by shallow grooves, with coarse, blunt tubercles; protogastric region with 2 small tubercles; hepatic region barely defined with indistinct inflations, no evident tubercles present; mesogastric region with 2 elongated tubercles; epibranchial region with faint ridge, with large medial tubercle, additional barely inflated lateral tubercle; postbranchial regions with 2 longitudinally positioned tubercles, anterior one larger, rounded, weakly raised, posterior one close to end of lateral margin; cardiac region relatively broad, defined by elongated tubercle, bounded by shallow lateral grooves; intestinal region small, somewhat depressed, bounded by 2 small tubercles; cervical groove weakly marked, even axially, but clearly notching anterolateral margin; branchiocardiac groove well defined at inner portion of epibranchial region. Ventral parts or appendages not preserved. Dorsal carapace surface with dense, small granules.

Remarks. The new species is assigned to *Cenomanocarcinus* on the basis of the curvature and armature of the anterolateral margin, the strong epibranchial spine, the narrow orbitofrontal margin, triangular five-spined rostrum, division of coarse tubercles on the dorsal carapace, and possession of three ridges on the posterior carapace. The new species can be clearly distinguished from congeners on account of the shallow, weakly defined dorsal grooves; the longitudinal and transverse ridges being only weakly salient; the dorsal surface with few dorsal tubercles; the lack of tubercles in the hepatic region; the posterior half of the carapace with large, blunt tubercles; and the anterior tooth of the posterolateral margin being positioned close to the epibranchial spine.

The only other European species, *C. inflatus*, shows more marked transverse and longitudinal ridges with more numerous, evenly spaced tubercles and more convex branchial ridges. There is also a strong posterolateral tooth at mid-length, instead of being closer to the epibranchial tooth; there is an additional anterolateral tooth and the hepatic region bears several clear tubercles.

Of the American species, *C. beardi* exhibits a more subhexagonal carapace, with more divergent posterolateral margins, more salient longitudinal and transverse ridges, stronger dorsal tubercles, a longer epibranchial and posterior anterolateral spine and more distinct H-shaped grooves in the cardiac region. *Cenomanocarcinus vanstraeleni* exhibits a more subhexagonal carapace; more salient transverse and longitudinal ridges, with more numerous tubercles; the antero- and posterolateral margins with numerous small denticles. *Cenomanocarcinus oklahomensis* is characterised by stronger longitudinal and transverse ridges, the H-shaped groove pattern in the cardiac region being strongly marked; *C. pierrensis* exhibits a more distinct, continuous cervical groove; the dorsal tubercles are more raised and conical; the branchial ridges are more salient; the tubercles in the posterior branchial region are not lined up. *Cenomanocarcinus pierrensis* exhibits a mixed set of characters, which make it difficult to ascribe this species with certainty to *Cenomanocarcinus* or *Necrocarcinus*. More completely preserved material is needed to decide in this matter; for the time being, it is retained in the former genus.

Two species from Nigeria were recently described by Collins (2010). *Cenomanocarcinus tenuicarinatus*, of early Turonian age, has a more elongated carapace; posterolateral margins lack strong teeth and clearly tuberculate hepatic ridges; the axial carina is more salient and continuous, less tuberculate, whereas *C. dissimilis*, from the lower Cenomanian, exhibits a wider carapace with more distinct longitudinal ridges, clear hepatic tubercles and a narrower cardiac region.

Cenomanocarcinus inflatus **Van Straelen, 1936**
(Fig. 18A, D)

Material examined. Dorsal carapace, upper Cenomanian, Butte de Gazonfier, Le Mans, France (MNHN J08587 [see Van Straelen 1936: pl. 4, fig. 8]; MAB k. 2968 represents a cast); dorsal carapace, same provenance (MNHN R05504, the original of A. Milne-Edwards *in* Guillier 1886: 244); dorsal carapaces, same provenance (MHN LM 3804, MHN LM 3806).

Remarks. Specimen MNHN J08587 (Fig. 18A, D) was illustrated by Van Straelen (1936: pl. 4, fig. 8) as 'topotype'. The name proposed by A. Milne-Edwards in Guillier (1886), was a *nomen nudum* because a diagnosis was not given. Van Straelen (1936: 37, 38) stated that the type (A. Milne-Edwards' original) was probably in the MNHN palaeontological collections. This specimen was designated lectotype by Breton & Collins (2007: 18). MNHN J08587 is, however, a carapace from the Hébert Collection (Collections de la Sorbonne), whereas the original of A. Milne-Edwards bears registration number MNHN R05504. The latter is considered here the holotype, of *C. inflatus* (see ICZN 1999, Art. 73.1.1), and Van Straelen (1936) as the author of the taxon, because he was the first to present a diagnosis, retaining the name suggested earlier by A. Milne-Edwards in Guillier (1886). The lectotype designation by Breton & Collins (2007) is therefore invalid.

Cenomanocarcinus vanstraeleni **Stenzel, 1945**
(Fig. 18B, C, E)

Material examined. MAB k. 2885 (indeterminate sex), carapace, MAB k. 2895 (female), partial carapace with remains of abdomen, thoracic sternum and base of mxp3, MAB k. 2909, (indeterminate sex), partial carapace with remains of P1 and thoracic sternum; all from the upper Albian–lower Cenomanian (Pawpaw Formation), Tarrant County (Texas, U.S.A).

Remarks. The morphology of this species has been described by Stenzel (1945: 447), Vega *et al*. (2007a: 414) and Guinot *et al*. (2008: 14). A large specimen of *C.* aff. *vanstraeleni* was described (Guinot *et al*. 2008: 18) with episternite 5 showing 'a pair of prominences that is blunt, weathered, but well-preserved and recognisable on left side (crab seen by ventral view). This pair of prominences is assumed to be a part of the abdominal holding system'. Two new specimens, smaller in size but with well-preserved but partial thoracic sterna, retain such prominences and allow a more detailed description.

One specimen (MAB k. 2909; Fig. 40C, E) is an incomplete carapace with well-preserved proximal portion of mxp3, thoracic sternites 3–5, P1 and P2 bases, abdominal somite 6 and telson. The relatively wide, flat thoracic sternum and wide abdomen suggest a female. Abdominal somite 6 and the telson are disarticulated and posteriorly displaced, exposing episternites 5. On either side, near the P2 gynglyme, a prominent double peg is present. The structure is raised, the distal (posterior) peg being slightly larger and slightly more admedially positioned than the subdistal (anterior) one. The anterior corners of abdominal somite 6 are rounded and swollen, which suggests a socket was present ventrally.

The second specimen (MAB k. 2895; Fig. 40D, F), a left side of a well-preserved carapace, retaining elements of P1 and P2 and a small portion of the thoracic sternum. Sternites 4 and 5 are partially preserved, episternites 4 and 5 complete. Episternite 5 shows well the P2 gynglyme in ventral view. A well-preserved double peg, separated by a weak depression is present, the distal peg being larger, more posterolaterally placed than the subdistal one.

In another, rather small, specimen (MAB k. 2922), it is seen that the blunt crest on the pterygostome becomes more acute anteriorly, terminating below the orbits in a prominent, pointed subantennary lobe of the pterygostome.

A comparison of the available material permits better differentiation of *C. beardi, C. inflatus and C. vanstraeleni*. *Cenomanocarcinus inflatus* and *C. vanstraeleni* are closely similar, but both species are highly variable with regard to tuberculation and granulation. Both possess an anterolateral margin with five or six teeth anterior to the epibranchial spine. The cervical groove notches the anterolateral margin more strongly and acutely in *C. vanstraeleni* than in *C. inflatus*. The nature of the epibranchial spine differs between the two species, being strongly developed in *C. inflatus*, but similar to or only marginally better developed than the anterolateral teeth in *C. vanstraeleni*. There are also differences in the posterolateral margins: a conspicuously strong spiniform tooth halfway the otherwise smooth and rounded posterolateral margin in *C. inflatus*, whereas *C. vanstraeleni* has a posterolateral margin which is sharper in cross section and bears many small spinules, of which one may be slightly larger, but by no means similar to the spine of *C. inflatus*. The most obvious difference between the two species is the width of the cardiac region, which is much greater in *C. inflatus* (Fig. 18A, B).

Cenomanocarcinus beardi is distinguished from its congeners by the lack of a tooth between the strong fourth anterolateral tooth and the epibranchial spine. It therefore has five, instead of six or seven, anterolateral teeth (epibranchial included, outer orbital excluded). The epibranchial spine is strongly developed, and the posterolateral margin is smooth and rounded; these characters are similar to *C. inflatus* and thus differentiate *C. beardi* from *C. vanstraeleni*. The strong spiniform tooth halfway the posterolateral margin, characteristic of *C. inflatus*, is nevertheless absent in *C. beardi*. In addition, the posterior spine at the base of the branchial crest is stronger. The three crests have fewer but stronger tubercles and the transversely vaulted connection (referred to as 'H'-shape by Schweitzer *et al*. 2003a: 36) is clearly seen, whereas it is indistinct or obsolete in *C. inflatus* and *C. vanstraeleni*. Characters are summarised in Table 5.

TABLE 5. Characters of *Cenomanocarcinus beardi*, *C. inflatus* and *C. vanstraeleni*.

Species	Tooth between fourth anterolateral tooth and epibranchial spine	Epibranchial spine	Posterolateral margin	Armature of posterolateral margin	Cardiac region
Cenomanocarcinus beardi	No	Strong	Rounded	Only the spine posterior to the branchial crest	Wide
Cenomanocarcinus inflatus	Yes	Strong	Rounded	Smooth, with strong medial spine	Wide
Cenomanocarcinus vanstraeleni	Yes	Normal	Sharp	With spinules, absence of strong medial spine	Narrow

Genus *Campylostoma* Bell, 1858

Campylostoma Bell, 1858: 23.

Type species. *Campylostoma matutiforme* Bell, 1858, by monotypy.

Remarks. The genus was tentatively included in Cenomanocarcinidae by Guinot *et al*. (2008: 20). Material examined here corroborates this assignment; *Campylostoma* represents the youngest (Paleogene, Cenozoic) member of the family.

Campylostoma matutiforme Bell, 1858
(Fig. 16A–F)

Material examined. Partial carapace with mxp3, London Clay, Ypresian, lower Eocene, Herne Bay, Kent, England (NHM In. 32654/32655); syntype, carapace with sternite 4, P1 coxae and mxp3, London Clay, Ypresian, lower Eocene, Isle of Sheppey, England (NHM In. 7314); partial carapace with sternite 4, abdomen and bases of pereiopods, same provenance (NHM In. 35231); 2 carapaces, same provenance (NHM In. 39424, In. 59083).

Emended description. Pleural suture distinct, running just below anterolateral, posterolateral margins. Pterygostome large, anteriorly tumid, with blunt granular crest, extended anteriorly into prominent subantennary lobe; buccal cavity narrow, margins weakly concave, rimmed. Mxp3: coxae large, flabelliform, inserted in front of P1; exopod relatively short, wedge shaped with narrow distal end; endopod elongated, slender, basis-ischium, merus equally long, merus strongly grooved. Sternites 3–6 preserved; sternite 3 small, incompletely preserved, separated from sternite 4 by oblique lateral grooves; sternite 4 trapezoidal, lateral sides weakly raised, lateral margins slightly concave, nearly vertical groove at level of P1 gynglyme separating large raised episternite 4; episternite 5 raised, oblique, at least one prominence present for abdominal holding; sutures 4/5, 5/6 similarly shaped, only lateral, crescent shaped, medial part vertical, demarcating flat, undivided medial floor of sternum. Abdomen curvature in prolongation with carapace, all somites free, somite 1 short, wide, somite 3 narrowest, somites 3–5 with raised medial ridge, which is strong, acute in somite 4, somite 6 longer, telson unknown. P1–P3 in the same level, P4 weakly tilted, slightly reduced, P5 subdorsal, strongly reduced.

Remarks. Study of the material examined necessitates an amendment of the description; the carapace was described by Bell (1858: 23) and Carter (1898: 30). *Campylostoma matutiforme* (see Bell 1858: 23, pl. 3, figs. 8–10) was deemed a podotreme crab, possibly a cenomanocarcinid, by Guinot *et al*. (2008: 21). The re-examination of several specimens in the NHM collections (Fig. 16A–F) confirm this placement. The much elongated mxp3 with large, flabelliform coxae, sculpture of the pterygostome with pronounced, pointed subantennary lobes, crown-shaped sternite 3, subtrapezoidal sternite 4, match the cenomanocarcinid configuration. The carapace does not show the strong branchial crests that are typical of *Cenomanocarcinus* spp., and the orbits are much wider. The presence of an abdominal holding system on episternite 5 is confirmed in one specimen, where a single, sharp tubercle is visible; because of poor preservation, it is unclear if a more posteriorly situated peg was present.

Genus *Hasaracancer* Jux, 1971

Hasaracancer Jux, 1971: 157.

Type species. *Hasaracancer cristatus* Jux, 1971, by monotypy.

Species included. *Hasaracancer cristatus* Jux, 1971, *H. renfroae* (Stenzel, 1945) and *H. merijaensis* Ossó-Morales, Artal & Vega, 2011.

Material examined. Holotype, GIK 538 [GIK 536 in Jux 1971]; a transversely compressed and deformed carapace (female) with loose abdomen, upper Campanian, Afghanistan.

Remarks. *Hasaracancer* was considered synonymous with *Cenomanocarcinus* by Guinot *et al*. (2008: 20), based on an examination of the holotype and only specimen, of *H. cristatus* in GIK. This conclusion was not adopted by De Grave *et al*. (2009: 23) and Schweitzer *et al*. (2010: 44), who assigned *Hasaracancer* to the polychelidan family Coleiidae Van Straelen, 1925. Schweitzer *et al*. (2010: 146) stated that, after examination of a cast (BSP 1988III147) of the holotype, *Hasaracancer* 'clearly is a member of the Coleidae [*sic*]'. We disagree and follow Guinot *et al*. (2008) in interpreting *Hasaracancer* as a palaeocorystoid (Guinot *et al*. 2008: fig. 7). The only specimen of *H. cristatus* undoubtedly represents a brachyuran: the telson is absent but abdominal somite 6 is completely preserved and does not show uropods. Furthermore, the linea brachyura (pleural line) is seen on both sides of the carapace (Guinot *et al*. 2008: fig. 7a); it is complete and extends from below the posterior carapace margin to halfway the suborbital margin. The branchiostegite is posteriorly reduced. The anterior process of the pterygostome is pronounced, the oxystomian condition and orbits are well developed. All features of the carapace, pterygostome and abdomen fit favourably in Cenomanocarcinidae. Newly discovered, well-preserved material from Morocco (Ossó-Morales *et al.* 2011) shows carapace features that validate the separation of this genus from *Cenomanocarcinus*.

Necrocarcinus renfroae Stenzel, 1945, from the upper Albian of Texas (Stenzel 1945: 443, text-fig. 15; pl. 41, fig. 13) and Colombia (Vega *et al*. 2010: 272, figs. 8.6–8.12) is herein transferred to *Hasaracancer.*

Family Necrocarcinidae Förster, 1968 emend.

Necrocarcininae Förster, 1968: 169.

Type genus. *Necrocarcinus* Bell, 1863, by original designation.

Included subfamilies. Necrocarcininae Förster, 1968, and Paranecrocarcininae Fraaije, Van Bakel, Jagt & Artal, 2008.

Genera included. *Cretacocarcinus* Feldmann, Li & Schweitzer, 2008, *Glyptodynomene* Van Straelen, 1944, *Necrocarcinus* Bell, 1863, *Paranecrocarcinus* Van Straelen, 1936, *Protonecrocarcinus* Förster, 1968, and *Shazella* Collins & Williams, 2005.

Diagnosis. Carapace outline hexagonally or pentagonally rounded to subcircular, widest at mid-length or slightly anterior to mid-length. Carapace convex in all directions (Necrocarcininae), or arched (Paranecrocarcininae), with hepatic regions inflated. Anterolateral margin blunt, relatively long, convex, with conical teeth (Necrocarcininae) or sharp, with granular teeth (Paranecrocarcininae). Epibranchial corner with normal to moderately strong conical tooth (Necrocarcininae) or without prominent epibranchial tooth (Paranecrocarcininae). Posterolateral margin arched, with posterior (subdistal), and possibly medial tooth (Necrocarcininae); or smooth to granular (Paranecrocarcininae). Posterior margin concave, as wide as or narrower than orbitofrontal margin. Rostrum triangular, sulcate, tip sharp, with 1 or 2 pairs of subdistal teeth (Necrocarcininae); or rostrum trapezoidal, bifid, with pair of subdistal teeth (Paranecrocarcininae). Post-rostral slits absent (Necrocarcininae) or distinct (Paranecrocarcininae). Orbitofrontal margin about half carapace width, orbits elevated, small, subcircular, closely spaced, arranged obliquely; supraorbital margin simple, with 2 fissures, inner ones well closed. Branchiocardiac grooves distinct, straight to divergent; branchial groove defined by scars; cervical groove distinct, sinuous with 2 rounded deflections (Necrocarcininae), or branchial, cervical grooves indistinct (Paranecrocarcininae). Carapace surface areolated, with strong tubercles often in 3 rows (Necrocarcininae), surface may be granular to smooth, less areolated (Paranecrocarcininae). Endostome relatively narrow, anteriorly elongated with margins raised, laterally shaped into well-developed exhalant channels. Dorsal surface with upright nodes, cuticle with endocuticular pillars extending up to or through exocuticle surface.

Pterygostome deeply grooved, with blunt (*Necrocarcinus*) or tubercular (*Cretacocarcinus*) crest. Prominent subantennary lobe of pterygostome sharp, slightly elongated (*Necrocarcinus labeschii*, *Cretacocarcinus smithi*). Branchiostegite joining coxae of pereiopods, no exposure of pleurites; surface with moderate rim along coxae (*Cretacocarcinus smithi*), which may be weak (*N. labeschii*) or absent (*N. wrighti*). Mxp3 in oxystomian condition (*N. wrighti*, *Cretacocarcinus smithi*). Mxp3 coxae large, flabelliform, not close to each other (*N. wrighti*). Exopodite wide, shorter than endopodite ischium (*Cretacocarcinus smithi*).

Chelae in Necrocarcininae with several strong tubercles on outer surface; upper margin tilted, with flattened teeth; lower margin tubercular. Fingers slender, gaping (*N. labeschii*). Chelae in Paranecrocarcininae: upper margin with flattened triangular teeth, lower margin granular. Outer surface tumid, tubercular or granular, inner surface flat, smooth; fingers closing, with few rounded teeth (*Paranecrocarcinus quadriscissus*, *P. vanbirgeleni*). Pereiopod articles oval to subcircular in cross section (*Necrocarcinus wrighti*). P5 unknown, supposedly reduced, (sub)dorsal (see below).

Thoracic sternum strongly concave over complete length, sternite 4 medially strongly excavated, lateral sides of sternites 4–8 (with gynglymes) raised (*Necrocarcinus labeschii*, *N. wrighti*, *Cretacocarcinus smithi*). Sternal plate weakly narrowing towards posterior (*Necrocarcinus labeschii*). Sternites 1 and 2 at distinctly lower level than sternite 3. Distinct notch for insertion of mxp3 coxa, followed by short, yet deep groove on sternal plate (*N. labeschii*). Anterior side of sternite 4 wider than sternite 3 (*N. wrighti*). Sternite 8 strongly tilted, same size as sternite 7 (*N. labeschii*). Sternal sutures 4/5, 6/7 short, lateral, suture 4/5 crescent shaped: lateral part roughly horizontal, longitudinal part deep (*N. labeschii*). Suture 7/8 long, straight (*N. labeschii*). Spermathecal apertures not observed. Arthrodial cavities evenly spaced, ventro-laterally directed. Medial line not present, at least for sternites 1–6 (*N. labeschii*, *N. wrighti*).

Abdomen sexually dimorphic (after Carter 1898: 27, pl. 1, fig. 9; ‘abdomen of the female is half as wide again as that of the male’), all somites free, somites 1–5 with, ‘mesonotum raised into a sharp transverse rib’, somite 6 longer than preceding ones; telson rather long, triangular.

Abdominal holding system unknown.

Remarks. Necrocarcinids are generally small in size. The family is the oldest of the palaeocorystoid groups known, with the first representatives appearing in the Hauterivian (Lower Cretaceous, 136–130 Ma; *Paranecrocarcinus hexagonalis* Van Straelen, 1936). Our knowledge of necrocarcinid ventral features is unfortunately scant, a fact already stressed by Feldmann *et al*. (2008: 1743) and Guinot *et al*. (2008: 24). The only thoracic sternum of *Necrocarcinus labeschii* examined here is only of mediocre preservation; no locking structure could be detected. The presence of such structures is to be expected, however. Only one other thoracic sternum of a necrocarcinid has ever been illustrated and described, namely that of *N. wrighti* (Guinot *et al*. 2008: 28). No necrocarcinid abdomen was available for the present study; the specimens on which Wright & Collins (1972: 64) may have based their observations could not be traced. The description of the abdomen in our diagnosis therfore relies on Carter (1898: 27). His illustration shows an abdomen that matches the palaeocorystoid pattern well and likely represents a female. Sternite 8 in *N. labeschii* is strongly tilted, indicating a (sub)dorsal placement of the P5.

Based on carapace, thoracic sternum and epistome, Necrocarcinidae is here considered to represent the most basal condition within Palaeocorystoidea. Modifications for respiration whilst buried under the sediment are present, but are comparatively primitive.

Karasawa *et al*. (2011: 551) stated that necrocarcinids appeared to have a complete sternal suture 6/7. However, we consider this to be a preservational artefact, the suture in fact being only lateral. Those authors also opined that Necrocarcinidae and Cenomanocarcinidae differed from other families of Raninoidea by possessing spines on the posterolateral margin; however, cenomanocarcinids may also have a strong posterolateral spine and, additionally, a subdistal tooth.

Subfamily Paranecrocarcininae Fraaije, Van Bakel, Jagt & Artal, 2008

Paranecrocarcininae Fraaije, Van Bakel, Jagt & Artal, 2008: 201.

Genus *Paranecrocarcinus* Van Straelen, 1936

Paranecrocarcinus Van Straelen, 1936: 36.
Pseudonecrocarcinus Förster, 1968: 180.

Type species. *Paranecrocarcinus hexagonalis* Van Straelen, 1936, by monotypy. The type species of *Pseudonecrocarcinus* is *Necrocarcinus quadriscissus* Noetling, 1881, by original designation.

Remarks. The postfrontal slits, held to be diagnostic for the subfamily Paranecrocarcininae by Fraaije *et al.* (2008b: 201), may be present, albeit weak, in some other palaeocorystoids (*Camarocarcinus, Cenomanocarcinus, Ferroranina* **n. gen.**). These enigmatic slits may be interpreted as muscle scars for the ocular system. Additional observations are needed to determine their exact origin and taxonomic significance.

Paranecrocarcinus balla n. sp.

(Fig. 19A, C, E, G)

Necrocarcinus minutus Milne-Edwards *in* Guillier 1886: 244 [*nomen nudum*].
Necrocarcinus minutus A. Milne-Edwards, *nomen nudum*, *in* Guillier (1886: 244) — Guinot & Breton 2006: 610.
Necrocarcinus labeschii — Breton & Collins 2007: 18, fig. 6. — Breton 2008: 53, pl. 1, figs. 1–3.

Diagnosis. Carapace small, rounded subhexagonal, weakly convex both longitudinally, transversely; orbitofrontal width less than posterior margin; rather short, downturned rostrum, broadly sulcate; orbits close together, deep, upturned; supraorbital margin with 2 fissures; anterolateral margin slightly convex, with at least 6 spines of varying sizes; posterolateral margin straight; posterior margin broadly concave, thin; cervical groove indistinct; 2 pairs of post-rostral slits; small to large rounded tubercles on mesogastric, protogastric, epigastric, cardiac lobes; distinct epibranchial spine; test finely pitted, otherwise smooth.

Derivation of name. After the Old High German *balla* (ball, balloon), in allusion to the Marnes de Ballon Formation; noun used in apposition.

Material examined. Holotype is MNH LM 3807 [*ex* Guéranger Collection]; paratype is MNH LM 3808 [*ex* Guéranger Collection]. The holotype was in sample B16563, together with an isolated major cheliped of a necrocarcinid crab, probably *Necrocarcinus labeschii*, with a label reading, '*Necrocarcinus minutus* M. Edw., Cénomanien de la Sarthe, 1902-3', from Ballon, Sarthe (France). The holotype is from the Marnes de Ballon Formation (lower Cenomanian, *carcitanense* and basal *saxbii* zones), whereas the paratype comes from the Sables du Perche Formation at Le Mans (middle–upper Cenomanian, *jukesbrownei* to *guerangeri* zones) (for details see Collins & Breton 2009).

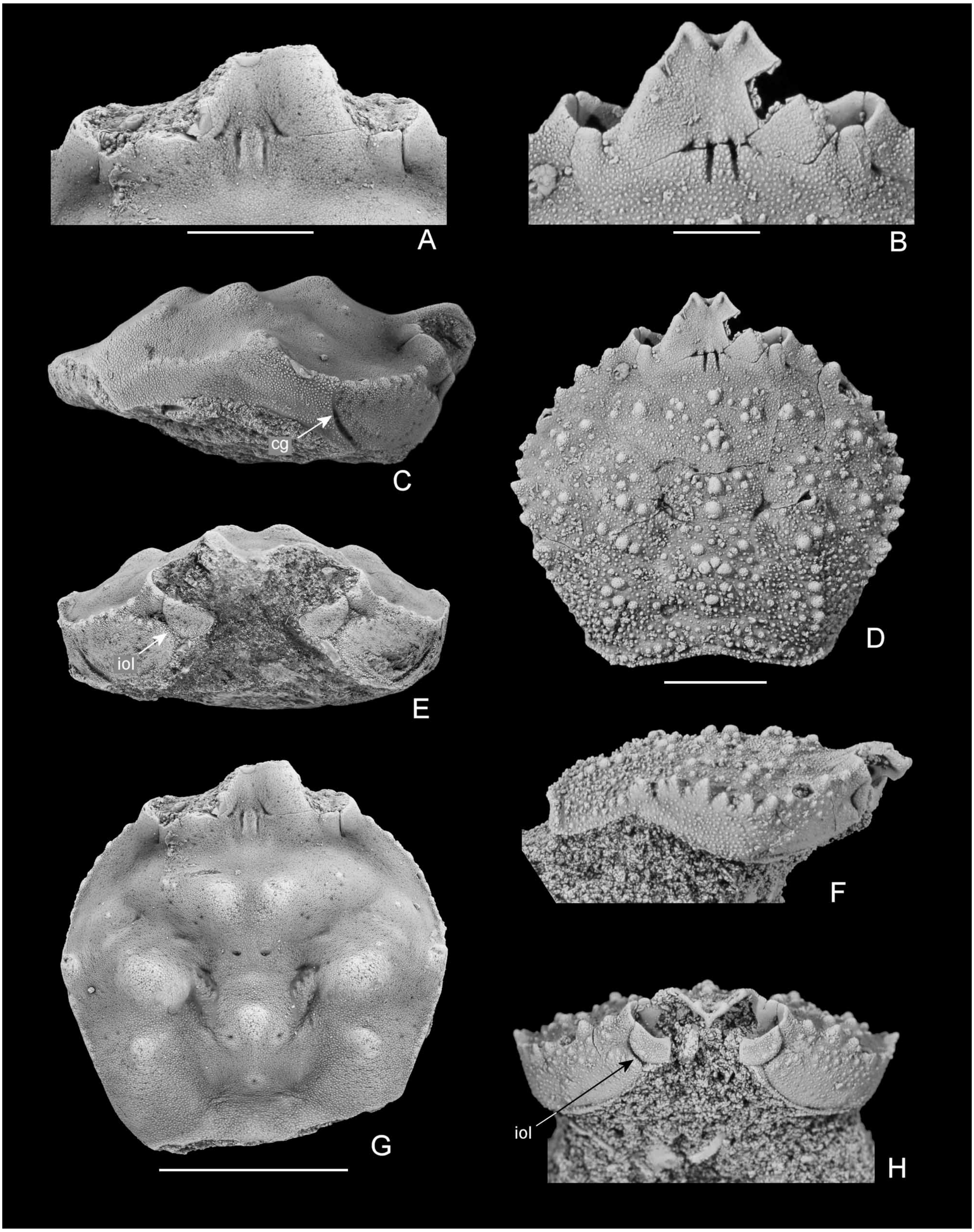


FIGURE 19. A, C, E, G, *Paranecrocarcinus balla* **n. sp.** (Necrocarcinidae, Paranecrocarcininae), MNH LM 3807 (**holotype**; *ex* Guéranger Collection), Cenomanian, Ballon (Sarthe, northwestern France); detail of orbitofrontal region showing frontal slits; right lateral view; frontal view, and dorsal view of carapace; B, D, F, H, *Paranecrocarcinus quadriscissus* (Noetling, 1881), MAB k. 2913 (indeterminate sex), upper Maastrichtian, Maastricht, the Netherlands; detail of orbitofrontal region showing frontal slits; dorsal view of carapace; right lateral and frontal views. **cg,** cervical groove; **iol,** infraorbital lobe. Scale bars: A, B: 2mm; C-H: 5mm.

Description. Carapace small (see Table 6), rounded subhexagonal in outline, carapace width exceeding length, weakly convex both longitudinally, transversely; orbitofrontal width (5.8 mm) smaller than posterior margin (7.6 mm); front produced as a rather short, downturned rostrum, broadly sulcate with sides upturned, widely rimmed; only partially preserved, thus no spines visible; orbits close together, deep, upturned, with thin margins, lacking spines; supraorbital margin with 2 fissures, relatively short, the upper slightly longer; anterolateral margin slightly convex, with at least 6 spines of varying sizes; posterolateral margin straight, with a slightly tuberculate, undulating ridge running from the epibranchial tubercles to just in front of posterior margin; posterior margin broadly concave, thin; no rim. Cervical groove indistinct, but two small longitudinal pits visible on either side of a wide medial gap; level with supraorbital rim with 2 pairs of slits, the anterior short, curved, positioned obliquely left, right of the posterior pair; posterior pair straight, elongated, close together, on either side of carapace mid-line, followed by a pair of small tubercles on the mesogastric lobe; single, small tubercle on each protogastric lobe; cardiac lobe with single, large, low, rounded tubercle, 3 small elevations in triangle behind it; distinct epibranchial spine, single, large tubercles on epigastric lobes; test finely pitted between tubercles, otherwise smooth; hepatic region depressed in lateral view, with a single small tubercle, the subhepatic relatively small, only slightly inflated.

Remarks. Breton & Collins (2007: 18, fig. 6) considered this specimen to represent a young individual of *N. labeschii*, a taxon recorded from the upper Aptian to Cenomanian in southern England, northern France (Wright & Collins 1972) and the upper Albian of southwestern Crimea (= *N. bodrakensis* Levitskyi, 1974; Ilyin 2005: 199). *N. labeschii* lacks the characteristic postfrontal fissures, however, and the carapace regions and ornament are clearly different.

Wright & Collins (1972: 71, text-fig. 10b; pl. 22, fig. 6) recorded only a single paranecrocarcinine, *Paranecrocarcinus biscissus*, based on a single specimen with two slits from correlative strata (lower Cenomanian, *mantelli* Zone) at Wilmington, Devon (southwestern England), (holotype, NHM In. 61166, *ex* Collins Collection). This species differs from the co-occurring *P. digitatus* (see below) in having a flatter carapace, with straighter margins, more numerous tubercles on the dorsal surface and two post-rostral slits. *Paranecrocarcinus digitatus* Wright & Collins, 1972 (1972: 69, text-fig. 10a; pl. 12, fig. 7a–c) from the lower Cenomanian (*mantelli* Zone) of Wilmington is easily differentiated from congeners by its elongated radiating ridges or bosses on the protogastric lobe (Wright & Collins 1972: 70, text-fig. 10a). *Paranecrocarcinus foersteri* Wright & Collins, 1972 (1972: 70, pl. 22, fig. 5a–c), from the lower-middle Cenomanian (*mantelli* and *rhotomagense* zones), is distinguished from other species of *Paranecrocarcinus* by having long and straight granular posterolateral margins and a longitudinally ridged dorsal surface. Three fragmentary specimens (MNHN A29412a–c [*ex* Pépin Collection; labelled *Paranecrocarcinus* (*hexagonalis*?) V. Straelen 1936]), all from the Craie Glauconieuse Formation (lower Cenomanian, *carcitanense* and *saxbii* zones) from Le Billot, are probably conspecific with *P. foersteri*.

Paranecrocarcinus hexagonalis Van Straelen, 1936 (1936: 36, pl. 4, figs. 6–7), from the Neocomian (lower Cretaceous, Hauterivian) of Migraine, near Auxerre (Yonne, France), appears to be closely related to *P. balla* **n. sp.** in size, the width of the orbitofrontal margin, carapace outline and ornament, but has a better-developed epibranchial spine as well as transversely elongated tubercles (rather than rounded ones) on the mesogastric and epigastric lobes. Only one pair of post-rostral slits is preserved in the type specimen (Van Straelen, 1936: pl. 4, fig. 7), but the rostral region is damaged, precluding observation of a second pair, if at all present.

Paranecrocarcinus milbournei Collins, 2010 (2010: 16, figs. 1.5–1.8), from the Cenomanian (Odukpani Formation) of Nigeria, has a subpentagonal carapace outline, with a narrow orbito-frontal margin and only one pair of post-rostral slits, as well as tumid protogastric, epibranchial, mesobranchial and cardiac lobes and a longitudinal ridge on the metabranchial lobes.

Paranecrocarcinus balla **n. sp.** differs from congeners by its rounded subhexagonal outline, apparently simple rostrum, paucity of tubercles on the dorsal surface and a finely tuberculate ridge on the posterior carapace half; from species which lack these, it is easily distinguished by the presence of two pairs of post-rostral slits. *Paranecrocarcinus quadriscissus*, from the upper Maastrichtian of northeastern Belgium and southeastern Netherlands (Fig. 19B, D, F, H), also has four slits, but the anterior pair are short and straight and the carapace ornamentation (tubercules, granules) is clearly different from the pitted ornament of *P. balla* **n. sp.** (Fraaije 2002; Jagt *et al.* 2010).

TABLE 6. Measurements (in mm) of the type material of *Paranecrocarcinus balla* **n. sp.** (MHN LM 3707–3708) and specimens questionably assigned to *P. foersteri* Wright & Collins, 1972 (MNHN A 29412a–c) (L, carapace length; W, carapace width; OF, orbitofrontal width; P, posterior width; LS, length of posterior pair of post-rostral slits. *measurements taken from Breton & Collins (2007: 18)).

Registration number	L	W	OF	P	LS
MNH LM 3807	10.5	10.9	5.8	7.6	0.8
MNH LM 3808*	19	24	-	-	-
P. foersteri					
MNHN A 29412a	>12.3	-	6.4	10.4	0.8
MNHN A 29412b	-	9.7	-	-	c. 0.5
MNHN A 29412c	>8.7	c.10.1	-	4.7	-

Family Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 emend.

Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a: 39.

Type genus. *Orithopsis* Carter, 1872 (type species: *O. bonneyi* Carter, 1872, by monotypy [Glaessner 1969: R492, R627]. Since *Necrocarcinus tricarinatus* Bell, 1863, is a senior synonym of *O. bonneyi*, the correct combination for the type species is *Orithopsis tricarinata* (Bell, 1863).

Genera included. *Cherpiocarcinus* Marangon & De Angeli, 1997, *Marycarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003, *Orithopsis* Carter, 1872, *Paradoxicarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003, and *Silvacarcinus* Collins & Smith, 1993.

Diagnosis. Carapace subhexagonal in outline, widest about or just anterior of mid-length; surface weakly arched in all directions. Anterolateral margin relatively long, gently rounded (*Cherpiocarcinus*, *Paradoxicarcinus*) or moderately convex (*Orithopsis*, *Silvacarcinus*); with 3 or 4 teeth, long, triangular (*Cherpiocarcinus*, *Silvacarcinus*) or spiniform (*Orithopsis*, *Paradoxicarcinus*); epibranchial tooth strong (*P. nimonoides*). Posterolateral margins straight, blunt in cross section, without teeth or tubercles. Posterior margin wide, concave. Rostrum triangular; short, not extended beyond outer orbital teeth (*Cherpiocarcinus*, *Paradoxicarcinus*, *Silvacarcinus*), or long, well extended beyond outer orbital teeth (*Orithopsis*), tip as single apex, may have 1 or 2 subdistal teeth (*Orithopsis*); post-rostral slits absent. Orbitofrontal margin distinctly wide, orbital margin barely elevated, weakly concave (*Cherpiocarcinus*, *Paradoxicarcinus*) to concave (*Orithopsis*, *Silvacarcinus*). Orbits large, horizontally arranged with large plain outer orbital sockets; supraorbital margin with long flattened spines, wide open fissures. Cervical groove acute, sinuous with sharp deflections, medially interrupted by distinct gastric pits. Branchiocardiac grooves deep, diverging. Carapace surface with granular ridges (carinae); branchial ridges concave, with transverse ridge over cardiac region, or H-shaped (*C.* rostratus, *O. tricarinata*, *O. angelica*, *Paradoxicarcinus*, *S. laurae*). Antennar fossae closer to each other than antennular fossae, both situated posterior of orbits. Dorsal carapace surface with upright nodes.

Pterygostome grooved, with low blunt crest. Branchiostegite not areolated (*S. laurae*), joining coxae of pereiopods, no exposure of pleurites. Mxp3 unknown, only coxae partially preserved (*S. laurae*); wide, flabelliform, not close to each other.

Upper, lower margin of palm with anteriorly directed spiniform teeth (*C. rostratus*). P2, P3 articles oval in cross section (*O. tricarinata*). P5 reduced in size, (sub)dorsal.

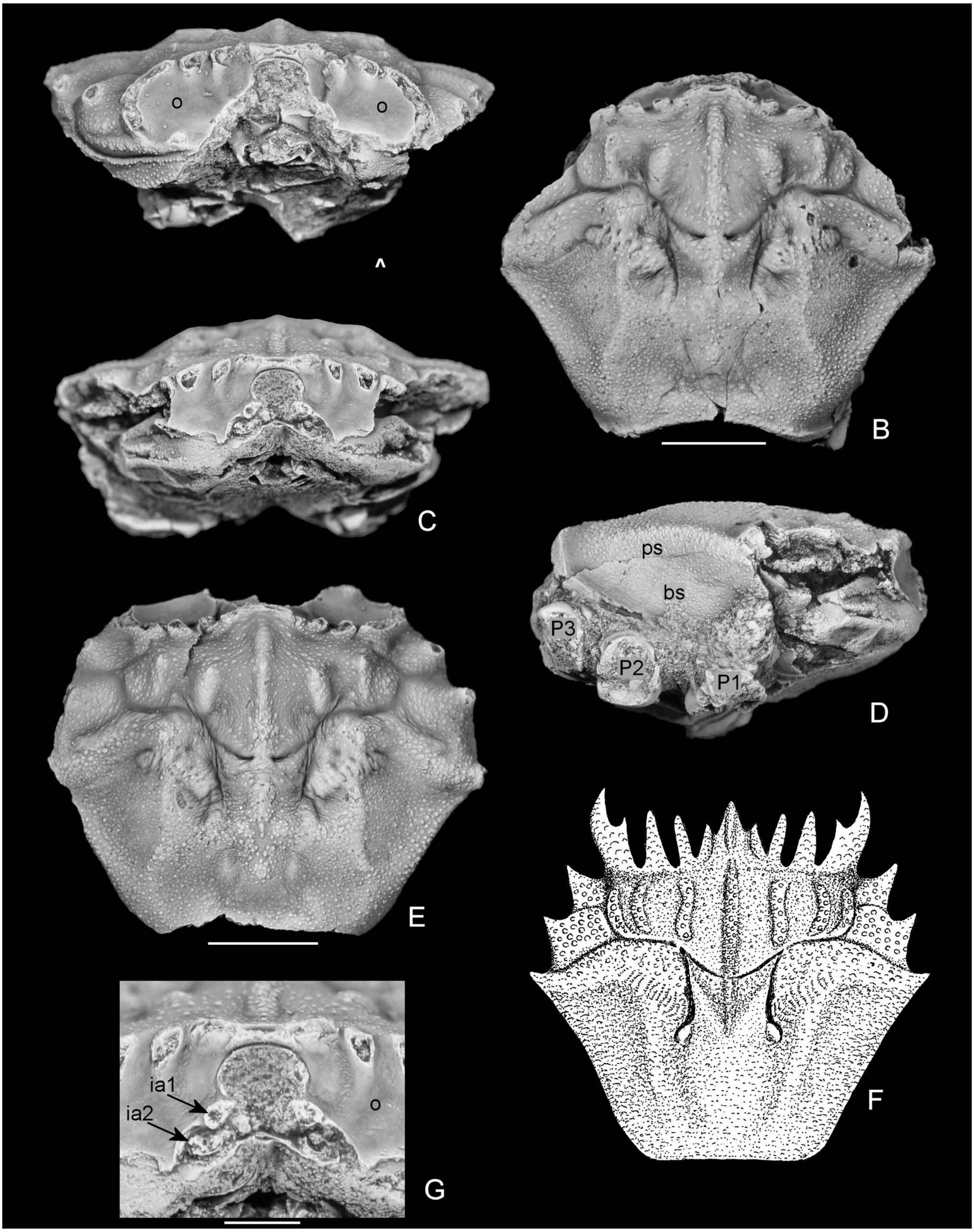


FIGURE 20. A, E, *Silvacarcinus laurae* Collins & Smith, 1993 (Orithopsidae), IRScNB TCCI 6119 (**paratype**; indeterminate sex), lower Eocene (Ypresian), Brussels (Belgium); frontal view showing huge orbits, and dorsal view of carapace; B–D, G, *Silvacarcinus laurae* Collins & Smith, 1993, IRScNB TCCI6115 (**holotype**; indeterminate sex); dorsal view of carapace; frontal view; left lateral view, and detail of frontal region; F, *Cherpiocarcinus rostratus* Marangon & De Angeli, 1997 (Orithopsidae), middle Oligocene, northern Italy; reconstruction of carapace after type material (drawing by A. De Angeli). **bs,** branchiostegite; **ia1,** insertion of antennule; **ia2,** insertion of antenna; **o,** orbit; **P1, P2, P3,** pereiopods 1, 2, 3; **ps,** pterygostome. Scale bars: A-F: 5mm; G: 2mm.

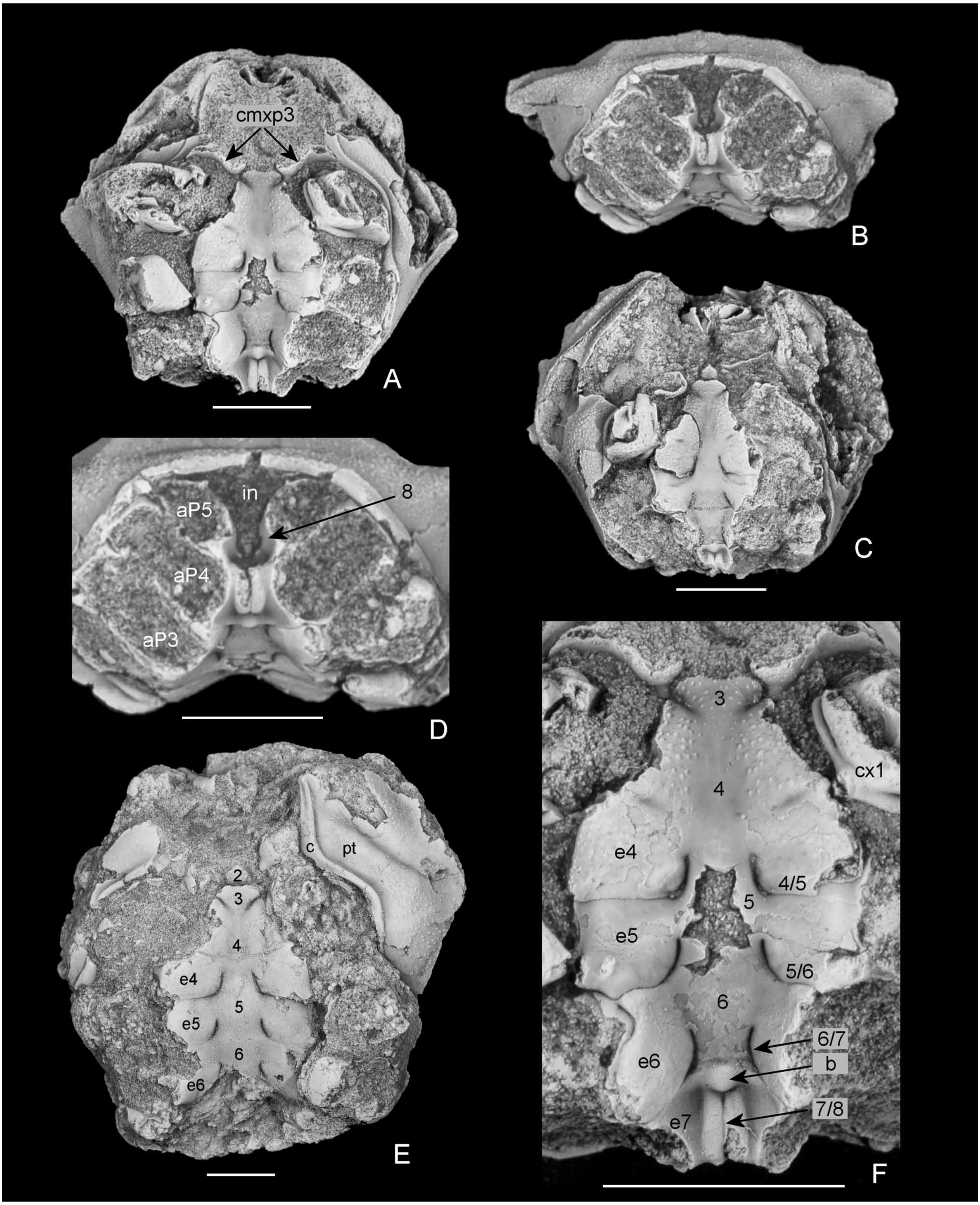


FIGURE 21. *Silvacarcinus laurae* Collins & Smith, 1993 (Orithopsidae), lower Eocene (Ypresian), Brussels (Belgium). A, B, D, F, IRScNB TCCI 6115 (**holotype**; indeterminate sex); ventral view showing thoracic sternum; posterior view; detail of posterior view, and detail of thoracic sternum; C, IRScNB TCCI 6119 (**paratype**; indeterminate sex); ventral view showing thoracic sternum; E, MAB k. 2881 (*ex* Tak Collection; indeterminate sex), lower Eocene (Ypresian), Egem, northwestern Belgium; ventral view showing thoracic sternum. **2, 3, 4, 5, 6, 8,** thoracic sternites 2, 3, 4, 5, 6, 7, 8; **4/5, 5/6, 6/7, 7/8,** thoracic sternal sutures 4/5, 5/6, 6/7, 7/8; **aP3, aP4, aP5,** arthrodial cavities of P3, P4, P5; **b,** bulge; **c,** buccal collar of pterygostome; **cmxp3,** coxa of mxp3; **cx1,** P1 coxa; **e4, e5, e6, e7,** episternites 4, 5, 6, 7; **in,** intestinal canal; **pt,** pterygostome. Scale bars: 5mm.

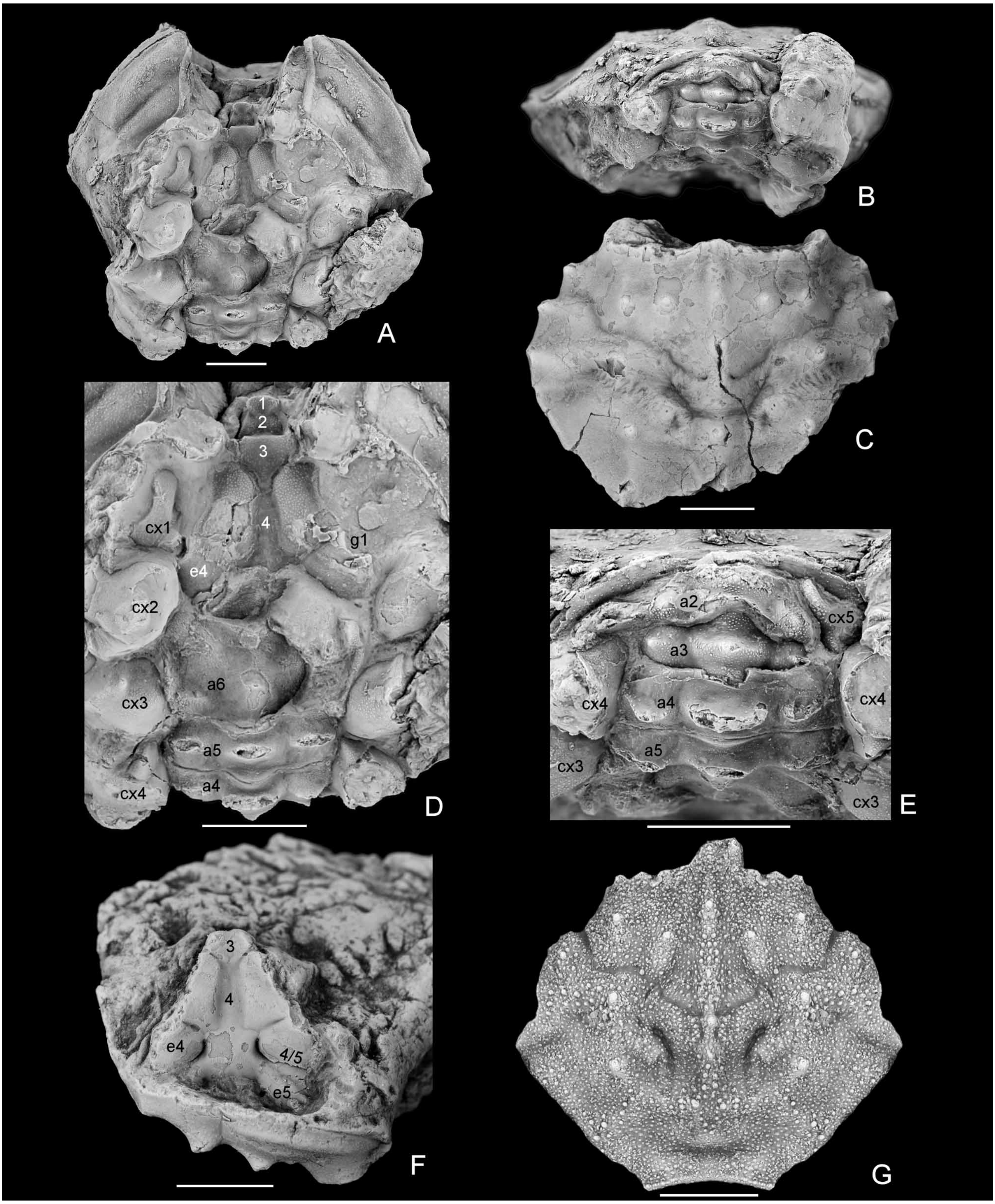


FIGURE 22. A, B, D, E, *Orithopsis tricarinata* (Bell, 1863) (Orithopsidae), NHM In.30297 (female), Albian, Folkestone (southern England); ventral view; posterior view showing abdomen; detail of abdomen, anterior portion of thoracic sternum and bases of pereiopods, and detail of abdomen and pereiopods in posterior view; C, F, *Orithopsis tricarinata* (Bell, 1863), IRScNB unnumbered [Van Straelen Collection; indeterminate sex], upper Albian Cambridge Greensand, Cambridge (southern England); dorsal view of carapace, and ventral view showing anterior part of thoracic sternum; G, *Orithopsis angelicus* (Fraaije, 2002), MAB k. 2548 (**holotype**; indeterminate sex), upper Maastrichtian, Maastricht, the Netherlands; dorsal view of carapace (composite photograph). **1, 2, 3, 4,** thoracic sternites 1, 2, 3, 4; **4/5,** thoracic sternal suture 4/5; **a2, a3, a4, a5, a6;** abdominal somites 1, 2, 3, 4, 5, 6; **cx1, cx2, cx3, cx4, cx5,** P1-P5 coxae; **e4, e5,** episternites 4, 5; **g1,** gynglyme for P1 coxa. Scale bars: 5mm.

Thoracic sternum rather long, deep sterno-abdominal cavity over complete length (*S. laurae*). Sternites 1, 2 well separated, at lower level than sternite 3 (*S. laurae*). Sternite 3 as small plate, separated by distinct groove from sternite 4, anterior side of sternite 4 as broad as sternite 3 (*O. tricarinata*, *S laurae*). Sternite 4 medially excavated (*O. tricarinata*, *S. laurae*); sternites 4–6 equal in width; sternites 7, 8 distinctly narrower (*S. laurae*). Sternite 7 with axial part as a narrow, vertical lobe, anteriorly demarcated by a central dome (*S. laurae*), forming rather complex axial construction in same level as remainder sternites. Sternite 8 strongly tilted, perpendicular to preceding sternites, strongly reduced; medially opened forming sunken pit. Sutures 4/5–6/7 relatively long, lateral, declining in angle posteriorly; 4/5 crescent shaped: lateral part long, medial part vertical, deep (*O. tricarinata*, *S. laurae*); suture 5/6 with shorter lateral part, less abruptly flexed; suture 6/7 arched, anterior half deep (*S. laurae*); suture 7/8 vertical, forming long medial line (*S. laurae*). Spermathecal apertures unknown. Arthrodial cavities evenly spaced, ventro-laterally directed.

Male abdomen unknown; female abdomen completely filling laterally sterno-abdominal depression, with all abdominal somites free, first somites dorsal, somite 6 long; somites trituberculate, tubercles strong, transversely broadened, telson reaching sternite 4 (*O. tricarinata*).

Abdominal holding system present at episternite 5, assumed to have been double (see remarks for *S. laurae*). Coxal structures not present, at least not on P1, P2.

Remarks. The Orithopsidae is a rather small group (10 species so far described), but with a long stratigraphic range (upper Aptian to middle Oligocene, 115–29 Ma). *Cherpiocarcinus rostratus*, from the middle Oligocene of northern Italy (Fig. 20F), is the youngest known member of the family and of the superfamily Palaeocorystoidea. The observation by Schweitzer *et al*. (2009a: 4) that the Orithopsidae ‘were at their peak’ during the Eocene was based on the assumption that *Goniochele* belonged to this family (see below).

Members of Orithopsidae have traditionally been included in Calappidae De Haan, 1833 (Förster 1968; Wright & Collins 1972; Schweitzer & Feldmann 2000; Fraaije 2002). When the family Orithopsidae was erected, it was placed, together with Necrocarcinidae, in Dorippoidea MacLeay, 1838. This taxonomic assignment was adopted by De Grave *et al*. (2009: 31) and Schweitzer *et al*. (2010: 80, 82). The carapace has multiple anterolateral spines, narrow anterior sternites, and only the P5 is reduced; features which exclude *Orithopsis*, and hence Orithopsidae, from Dorippoidea.

The morphology of ventral parts in the type series of *S. laurae* and in a well-preserved specimen of *O. tricarinata* have been studied. The abdomen filling the sterno-abdominal cavity over the entire width clearly indicates that orithopsids are podotreme crabs. The tumid, bluntly crested pterygostome, the shape of sternites 3 and 4, a longer abdominal somite 6 and the absence of dorsal uropods, all match Palaeocorystoidea. The abdomen of *Orithopsis*, tricarinate and tuberculate, closely resembles that of cenomanocarcinids. Differences with Cenomanocarcinidae are: sternites 1 and 2 are much shorter, sternite 3 is diamond shaped, rather than crown shaped, and sternite 4 has a deep medial gutter; the size of the orbits (much larger in Orithopsidae) and shape of branchial crests (concave in Orithopsidae, convex in Cenomanocarcinidae).

The Orithopsidae carapace is easily recognized: moderate to large size, dorsal surface only weakly vaulted, tricarinate with concave branchial carinae; anterolateral margins rather short, spinose; orbits conspicuously large, orbitofrontal margin with strong spines. Such characters may be used to revise the taxonomic placement of genera or species (see below under *O. siouxensis*). Ventral characters of Orithopsidae have so far been rarely found exposed and have not been well illustrated. The discovery of a specimen of *O. tricarinata* preserving ventral details confirms the similarity to *S. laurae* and their placement in Palaeocorystoidea. Both species show a normal-sized, a subdorsal P4 and a reduced, dorsally placed P5. The abdomen is trituberculate in Orithopsidae, with strong, thorn-like tubercles (Fig. 22D, E); this character is shared by Cenomanocarcinidae and Orithopsidae. Abdominal somite 6 is longer than preceding somites and shows a strong central spine, the anterior corners are bulbous, corresponding to sockets ventrally. The sternal abdominal holding structure is known only in a single specimen of *S. laurae* (Fig. 21F) in which the structure is worn; its location is similar to that in Camarocarcinidae and Cenomanocarcinidae. Better preserved material is needed to examine the abdominal holding structures in detail and verify whether or not it consists of a double structure. Sternite 4 shows a deep axial gutter in *Orithopsis,* which is present, though less distinct, in *Silvacarcinus*.

Through similarities of their orbital construction, carapace outline, nature of anterolateral teeth and anterior carapace areolation, Orithopsidae is considered here to be most closely related to Palaeocorystidae.

Schweitzer *et al.* (2003a: 39) included *Goniochele* Bell, 1858 in the Orithopsidae. Larghi (2004: 530) stated that *Goniochele* was perhaps related to *Cherpiocarcinus*, which he placed in Necrocarcinidae. Schweitzer & Feldmann (2011: 5) erected Goniochelidae as a new dorippoid family to contain *Goniochele*.

Genus *Orithopsis* Carter, 1872

Orithopsis Carter, 1872: 530.

Type species. *Necrocarcinus tricarinatus* Bell, 1863, by monotypy (= *Orithopsis bonneyi* Carter, 1872).

Species included. *Orithopsis angelica* (Fraaije, 2002) (Fig. 22G), *O. carinata* (Feldmann, Tshudy & Thomson, 1993), *O.*? *iserica* (Fritsch *in* Fritsch & Kafka, 1887), *O.*? *youngi* (Bishop, 1983c), *O. siouxensis* (Feldmann, Awotua & Welshenbaugh, 1976), *O.*? *transiens* (Fritsch *in* Fritsch & Kafka, 1887), and *O. tricarinata* (Bell, 1863).

Remarks. Schweitzer *et al*. (2010: 82) listed only *O. bonneyi* and *O. tricarinatus* [*sic*] for *Orithopsis*. The synonymy of these two taxa had previously been, however, discussed at length by Wright & Collins (1972), Collins (2003) and Guinot *et al*. (2008); our examination of the types of both taxa substantiates that view. Larghi (2004: 530) stated that *Orithopsis* was one of the genera most similar to *Corazzatocarcinus* and separated them by the 'marked hexagonal outline and distinct epibranchial lobes' of *Orithopsis*. Reduction of both P4 and P5 in *Corazzatocarcinus* sets it apart from *Orithopsis* and excludes it from Orithopsidae.

Orithopsis siouxensis (Feldmann, Awotua & Welshenbaugh, 1976)

'Necrocarcinus' siouxensis Feldmann, Awotua & Welshenbaugh, 1976: 986.

Remarks. *Necrocarcinus siouxensis* (see Feldmann *et al*. 1976: 986, pl. 1, figs. 1–5), from the Maastrichtian of North Dakota (U.S.A.), was considered either to be of uncertain position (Fraaye 1994: 264, fig. 1; Guinot *et al*. 2008: 698), or a member of *Cenomanocarcinus* (Bishop & Williams 1991: 452; Schweitzer *et al*. 2003a: 36; Crawford *et al*. 2006: 5; Schweitzer *et al*. 2010: 71). Feldmann *et al*. (2008: 1743) retained the species in *Necrocarcinus* and used it as reference for Necrocarcinidae in their comparison with *Cretacocarcinus*, which they assigned to Camarocarcinidae. Based on ventral characters, they stated (Feldmann *et al*. 2008: 1744) that, '*N. siouxensis* and *N. labeschii*… are more similar to one another than they are to *Cretacocarcinus smithi*.'

The ventral surface of '*Necrocarcinus*' *siouxensis* was interpreted as 'to be a composite' by Guinot *et al*. (2008: 698), comprising portions of the abdomen and thoracic sternum. In addition, it must be noted that female palaeocorystoids may have a sternum that is flatter than in males; this may cause misinterpretation in cases where only few specimens are examined. In a photograph of '*N.*' *siouxensis* (Feldmann *et al*. 2008: fig. 4.2), sternite 4 is partially overlapped by what appears to be the telson and partially by sediment particles; it is unclear if a deep axial gutter, which *O. tricarinata* and *S. laurae* reveal, is present. Additional preparation of the holotype of '*N.*' *siouxensis* is necessary to illustrate the ventral details more precisely.

The ventral surface of '*N.*' *siouxensis* does not appear very useful, having suffered from taphonomic bias, and in view of the numerous plesiomorphic features displayed by palaeocorystoid ventral surfaces. The carapace may effectively be used in this case, however. This species has a carapace in which the anterolateral margin has three teeth, which rules out both Paranecrocarcininae (with a tubercular anterolateral margin) and Camarocarcinidae (with the anterolateral margin with a single strong spine). Necrocarcinines have convex carapaces, the carapace of '*N.*' *siouxensis* being rather flat (Feldmann *et al.* 1976: fig. 3). In addition to the rather low-vaulted carapace, the tricarinate dorsal surface is not seen in any necrocarcinids but is characteristic of Cenomanocarcinidae and Orithopsidae. The branchial carinae in '*N.*' *siouxensis* are concave (Feldmann *et al.* 1976: figs. 1, 4) and the orbital cavities are distinctly large (Feldmann *et al.* 1976: fig. 3): this makes it an orithopsid rather than a cenomanocarcinid, which have convex to straight branchial carinae and small, narrow orbits (see also Guinot *et al*. 2008). The orbitofrontal margin is poorly preserved in the holotype. Until better-preserved material is available all characters of '*N.*'*siouxensis* match those of *Orithopsis*.

Orithopsis tricarinata (Bell, 1863)

(Fig. 22A–F)

Necrocarcinus tricarinatus Bell, 1863: 21.
Orithopsis bonneyi Carter, 1872: 530.

Material examined. Holotype of *Orithopsis bonneyi* Carter, 1872, upper Albian (upper Greensand), Lyme Regis, Dorset, UK (SM B58557); female, carapace and abdomen, Cambridge Greensand, Cambridge, UK (SM B58557); upper Albian, Cambridge Greensand, Cambridge, England, partial carapace with partial thoracic sternum (IRScNB unnumbered (Van Straelen Collection, see also Guinot *et al.* 2008: fig. 9f); carapace, upper Albian, 'Gault', Folkestone, England (NHM BM 59808); lectotype, designated by Wright & Collins (1972: 67), carapace, upper Greensand (probably uppermost Albian according to Wright & Collins 1972: 67), Wiltshire, England (NHM BM 59519); female, carapace with sternum, abdomen and bases of pereiopods, Albian, 'Gault', Folkestone, England (NHM In. 30297).

Emended description. Subhepatic region narrow, with single, blunt, granular crest. Pleural line distinct, raised, granular. Pterygostome tumid, with blunt crest parallel to subhepatic crest, becoming more acute anteriorly; second blunt crest less well-defined, parallel to margin of P1 coxa. Buccal cavity wide, buccal margin weakly concave, with broad, smooth buccal collar; posterior corner of pterygostome simple. Branchiostegite developed, tumid. Sternites 1–4 exposed: sternites 1, 2 on lower level; sternite 1 small, oval; sternite 2 trapezoidal; sternite 3 diamond shaped with apex pointing downwards; separated from sternite 4 by deep lateral grooves; sternite 4 large, trapezoidal, anterior margin slightly wider than sternite 3, lateral sides concave, surface with deep axial gutter; episternite 4 large, wide, gynglyme for P1 large, visible in dorsal view. P1–P4 coxae large, on same level, slightly decreasing in size posteriorly; P5 (sub)dorsal, reduced. Female abdomen with all somites free, covering thoracic sternum in width, thus in contact with coxae of pereiopods. Abdominal somite 1 not preserved; somites 2–5 progressively increasing in width, tricarinate, with strong, widened, thorn-like tubercles, strongest on somite 4; somite 6 long, widening towards telson, surface with central spine, anterior corners swollen. Telson incompletely preserved, granular.

Remarks. Discovery of a specimen with well-preserved ventral characters (NHM In. 30297) necessitates an amendment of the description; the dorsal carapace was described by Wright & Collins (1972: 67). *Orithopsis tricarinata* (see Bell 1863: 21, pl. 4, figs. 9–11), from the upper Aptian-lower Cenomanian of southern England, northern Spain, plus the lower Cenomanian of Mangyshlak, Kazakhstan (Ilyin 2005, as *Necrocarcinus tricarinatus*) and ?upper Albian of Angola, of which *O. bonneyi* Carter, 1872 (upper Aptian-lower Cenomanian, southern England) is a junior synonym, was previously known mainly from the dorsal carapace. Guinot *et al.* (2008: 32) stated that, '*Orithopsis tricarinata* has remained an insufficiently known species and, moreover, lacks preserved ventral structures, except for the trituberculate (?male) abdominal segments described by Wright & Collins (1972: 68)'. Specimen NHM In. 30297 shows well-preserved features of the thoracic sternum and abdomen for the first time.

Genus *Silvacarcinus* Collins & Smith, 1993

Silvacarcinus Collins & Smith, 1993: 263.

Type species. *Silvacarcinus laurae* Collins & Smith, 1993, by original designation.

Silvacarcinus laurae Collins & Smith, 1993

(Figs. 20A–E, G; 21A–F)

Material examined. Holotype and three paratypes, all from the Ypresian, lower Eocene, Forest, Brussels, Belgium (IRScNB TCCI 6115, 6117–6119). One additional specimen with preserved thoracic sternum (MAB k. 2881, *ex* Tak Collection; indeterminate sex), lower Eocene (Ypresian), Egem, northwestern Belgium.

Emended description. Mxp3 coxae partially preserved; well separated by sternites 1–3, large, flabelliform. Subhepatic region elongated, narrow, with granular crest; pleural suture raised, granular. Pterygostome tumid, with low, blunt crest; buccal frame wide, buccal margin concave, with smooth buccal collar; branchiostegite developed. Thoracic sternum elongated, suboval, with undivided, plain medial part, raised lateral portion of sternite 4, episternites 4–6. Sternites 1, 2, or only 2, small, crown shaped, at lower level than other sternites; sternite 3 diamond shaped, distinguished from sternite 4 by lateral grooves; sternite 4 subtrapezoidal, anterior corners slightly wider than sternite 3, lateral margins weakly concave, sternite medially with clear depression, episternite 4 large, distinguished from sternite 4 by oblique, shallow groove, P1 gynglyme just posterior to groove; suture 4/5 only lateral, crescent shaped; episternite 5 nearly square, posteriorly with abdominal holding structure near P2 gynglyme; suture 5/6 sinuous, crescent shaped; sternite 6 elongated, laterally with acute groove marking low lateral depression; sternite 7 smaller than preceding sternites, anteriorly ridged, anteromedially with pitted, spherical bulge, medially with 2 tumid, vertical elevations, separated by medial line; sternite 8 small, strongly tilted, perpendicular to preceding sternites, sides separated creating medial pit. P1–P3 gynglymes on the same level; P1 coxa large; arthrodial cavity of P4 of normal size, weakly tilted, arthrodial cavity of P5 markedly reduced, subdorsal.

Remarks. Examination of the type series and an additional specimen with ventral characters preserved necessitates an amendment of the description; the dorsal carapace was described by Collins & Smith (1993: 264). The original description of *S. laurae* by Collins & Smith (1993: 263, text-fig. 2 (not 3a, b); pl. 2, figs. 1, 2, 4–6 (not 3), from the lower Eocene of Brussels (Belgium), was based on five specimens**.** As pointed out by Guinot *et al.* (2008: 32), re-examination of the thoracic sternum (IRScNB TCCI 611) (Collins & Smith, 1993: text-fig. 3a, b; pl. 2, fig. 3) showed it was erroneously assigned to *S. laurae*, and used for the type description. The thoracic sternum is completely different from the sterna associated with the carapaces of *S. laurae*, and cannot be included in Raninoidia. To avoid further confusion, the type series has been re-examined and a new description of the ventral characters is given herein.

Some ventral characters present in the *S. laurae* material are useful to determine its taxonomic placement. Sternite 4 is subtrapezoidal; sutures 4/5 and 5/6 are lateral and crescent shaped, the medial portion pointing anteriorly. The P4 was not preserved; however, the arthrodial cavity is of normal size, indicating P4 was not reduced and in a normal position. The P5 arthrodial cavity is much reduced and tilted, which indicates the P5 was reduced and carried subdorsally, typical for Palaeocorystoidea. Sternite 3 is diamond shaped, sternite 4 shows a medial gutter, features that recall those in *Orithopsis tricarinata*. The carapace shows an acute, sinuous cervical groove and branchial crests which are concave and connected over the cardiac region (H-shaped elevation). The orbits are distinctly large, the supraorbital margin shows the broken bases of, presumably, long spines which protected the eye. All these features place *Silvacarcinus* in Orithopsidae.

The arrangement of the posterior sternites 7 and 8 is complex and cryptic, the sex of the examined material being difficult to determine. A sunken pit appears to be present between sternite 7 and the strongly tilted sternite 8 (Fig. 21D); no paired suture 7/8 is discernible but there is a medial line on sternite 7 (Fig. 21F). The apertures of the spermathecal apertures may be recessed and hidden in the sunken pit if the specimen is a female. More material is needed to verify the exact morphology, but it is apparent that the posterior sternites of *Silvacarcinus* and Orithopsidae are different from those of Cenomanocarcinidae and Palaeocorystidae.

Superfamily Raninoidea De Haan, 1839

Raninoidea De Haan, 1839: 102.

Type family. Raninidae De Haan, 1839 **emend.**

Families included. Lyreididae Guinot, 1993 **new status,** and Raninidae De Haan, 1839 **emend.**

Diagnosis. Carapace longer than wide, narrow to moderately broad, elongated, urn shaped, fusifom (lyreidinae) or ovate, anteriorly broadened or tapering, greatest width varying; moderately convex to roof shaped, may have medial carina (Notopodinae). Dorsal surface smooth or variously ornamented, may be scabrous, terraced, eroded, or with particular microstructure; cervical groove generally indistinct or lacking; branchiocardiac grooves usually marked. Anterolateral margins usually with 1–3 teeth, rarely teeth absent; teeth may be broad, developed, bifurcated or spiniform. Front narrow, generally triangular or subtrapezoidal, may be trifid or replaced by emargination (Notopodinae). Orbitofrontal margin varying from narrow to wide; supraorbital margin with 1 or 2 closed or open fissures, may be smooth, lined with granules, spinules or armed with teeth, external tooth usually produced. Orbits well defined, anteriorly or anterolaterally directed; eyestalk short to long, with 1–3 articles, folding when retracted.

Antennules, antennae not located in fossae, positioned behind eyestalks, usually considerably modified. Antennules not folded; antennae usually large, generally with 5 articles, short or long flagellum. Proepistome concealed or well developed; epistome triangular, prominent; endostome large, elongated, strongly excavated, in oxystomian condition. Buccal frame elongated with smooth collar. Mxp3 strongly elongated, narrow, operculiform; endopodite: basis-ischium, merus usually subequal in length; palp small, partially or completely concealed; exopodite weakly extending beyond ischium/merus articulation of endopodite, without flagellum. Mxp1 with exopodite and endopodite expanded, modified, forming exhalant channel; exopodite without flagellum. Pterygostome tumid, with prominent subantennary lobe.

Thoracic sternum narrow posterior to sternite 4, strongly deflected at different levels. Sternite 1 concealed; sternite 2 may be dorsally visible, inclined; sternite 3 usually crown shaped (compressed, ridged in Cyrtorhininae); sternite 4 usually wide (narrow in Cyrtorhininae), flat; suture 4/5 variously crescent shaped; sternite 5 laterally expanded; posterior sternites narrow, occasionally linear, may be keeled; sternite 8 variously reduced. Medial line present along posterior sternites, extending to sternite 5 or 6. Sternum/pterygostome junction present, narrow (Cyrtorhininae, Symethinae) to wide, rarely absent (Marylyreidinae **n. subfam.**). Sternum/exposed pleurites connection variously developed between P1, P2; usually present between P2, P3, may be absent between P2, P3 (Raninidae, Notopodinae; Marylyreidinae **n. subfam.**). Posterior part of branchiostegite markedly reduced in height; pleurites 5–7 partially exposed, calcified (gymnopleurity); exposed pleurites flat or variously excavated, with several protruding outgrowths to attach to branchiostegite. Spermathecal apertures opening anteriorly enclosed by sternite 7; generally close to each other, separated by medial line, recessed in medial depression ('sunken pit') (superficial, hooded in Symethinae). Female gonopores on P3 coxae, male gonopores on P5 coxae.

Sterno-abdominal depression weak; may be incompletely formed, narrow (Lyreididae). Abdomen with 6 free somites plus telson; short (Raninidae) or long (Lyreididae); first somites dorsal, in continuity with carapace; sexual dimorphism not strongly marked. Uropods absent, sockets present (Lyreididae) or absent (Raninidae). Locking mechanism absent in Raninidae; present in Lyreididae as pair of hook-like, short, stout or elongated projections arising from episternite 5, distally with double peg, which firmly fits into deep sockets in latero-posterior extended corners of abdominal somite 6.

Chelipeds generally robust, variously modified, homochelous, homodontous; arthrodial cavities large, placed laterally or ventrolaterally; basis-ischium short, fused with merus; propodus varying from short, inflated, flattened, armed with long, sharp spines on upper, lower margins to elongated, narrow, unarmed; fingers usually with teeth of prehensile borders joining alternately, or with several long spines (Cyrtorhininae); fixed finger diminutive to long, often deflected. P2–P4 robust or slender, rather long, at least propodus, dactylus markedly modified; dactylus paddle shaped, lanceolated, or falciform; P4 slightly subdorsal, P5 dorsal, slightly to strongly reduced (may be filiform in Lyreididae), generally matching carapace margins.

Pleopod 1 absent in females. G1, G2 variously shaped. Gills: 8 pairs, rarely 7 (Symethinae).

Respiratory mechanism strongly specialised. Absence of Milne-Edwards openings, except possibly in Marylyreidinae **n. subfam.** Respiratory inhalant, exhalant currents through strongly, variously modified frontal region, posterior branchial orifices; water flows along flanks of carapace.

Remarks. Table 7 lists the genera included herein in Raninoidea. Although variously shaped, the raninoid thoracic sternum (except Cyrtorhininae) shows a small, lanceolated anterior element, followed by a rather large shield formed by the well-developed sternite 4. The crown-shaped element only comprises sternite 3, sternites 2 and 1 being anteriorly, not visible dorsally and not participating in the formation of the sternal plastron. The crown-shaped anterior sternites in extant raninoids resemble to some extent those found in extant dynomenids, but the crown does not include sternite 3 in the latter (Guinot 2008). The posterior sternites are extremely narrow in all raninoid families, and as a result, the P2, P3 and P4 arthrodial cavities are closely contiguous. The P1 coxae also are close to each other in Cyrtorhininae.

The spermathecae of Raninoidea appear to open anteriorly on sternite 7 rather than at the extremities of sternal suture 7/8, as in other Podotremata. The spermathecal chamber, however, is still formed by the separation of the two laminae which compose endosternite 7/8, which is not a major departure from the typical podotreme configuration (Tavares & Secretan 1993), as explained by Hartnoll (1979). The spermathecal apertures are located in proximity to the female gonopore on the P3 coxae. The spermathecal apertures are close to each other and recessed in a medial pit in all raninoids, but more superficial and hooded in the Symethinae.

Pleopod 1, which is present in the basal Podotremata (Dromioidia, Homoloidia), is absent in raninoid females, as in Cyclodorippoidia and Eubrachyura.

The variously shaped male sexual gonopods indicate a strong diversity. In all Raninoidea, the G1 is partially open, it does not form a complete tube, and is foliaceous in Notopodinae; the G2 is long or short. The two G1 are close to each other and act together. Their apices, which are not in contact medially, may nevertheless inseminate the two closely placed spermathecal apertures. The sperm, ejaculated from the penis to the base of the G1 and picked up by the spoon-like G2 to be placed in the distal part of the G1, is transferred through the G1 ejaculatory channel into the spermathecae.

TABLE 7. Genera included in the Raninoidea De Haan, 1839 (extinct taxa indicated by †; extant taxa by #).

Antonioranina **n. gen.** (†)
Bicornisranina Nyborg & Fam, 2008 (†)
Bournelyreidus **n. gen.** (†)
Cosmonotus Adams & White *in* White, 1848 (†, #)
Cristafrons Feldmann, Tshudy & Thomson, 1993 (†)
Cyrtorhina Monod, 1956 (#)
Eosymethis **n. gen.** (†)
Eumorphocorystes van Binkhorst, 1857 (†)
Heus Bishop & Williams, 2000 (†)
Lianira Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991 (†)
Lophoranina Fabiani, 1910a (†)
Lophoraninella Glaessner, 1945 (†)
Lovarina Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991 (†)
Lyreidina Fraaye & Van Bakel, 1998 (†)
Lyreidus De Haan, 1841 (†, #)
Lysirude Goeke, 1986 (†, #)
Macroacaena Tucker, 1998 (†)
Marylyreidus **n. gen.** (†)
Neoraninella Hu & Tao, 1996 (*incertae sedis*) (†)
Notopella Lőrenthey *in* Lőrenthey & Beurlen, 1929 (†)
Notopoides Henderson, 1888 (†, #)
Notopus De Haan, 1841 (†, #)
Notosceles Bourne, 1922b (†, #)
Ponotus Karasawa & Ohara, 2009 (†)
Pseudorogueus Fraaye, 1995 (†)
Quasilaeviranina Tucker, 1998 (†)
Ranidina Bittner, 1893 (†)
Ranilia H. Milne Edwards, 1837 († , #)
Raniliformis Jagt, Collins & Fraaye, 1993 (†)
Ranina Lamarck, 1801 (†, #)
Raninella A. Milne Edwards, 1862 (†)
Raninoides H. Milne Edwards, 1837 (†, #)
Remyranina Schweitzer & Feldmann, 2010a (†)
Rogueus Berglund & Feldmann, 1989 (†)
Symethis Weber, 1795 (#)
Symethoides **n. gen.** (†)
Sabahranina Collins *in* Collins, Lee & Noad, 2003 (*incertae sedis*) (†)
Tribolocephalus Ristori, 1886 (†)
Umalia Guinot, 1993b (†, #)
Vegaranina **n. gen.** (†)

There are eight pairs of gills in Raninoidea, all arranged in a vertical position the anteriormost two pairs reduced in size but large enough to be observed and be functional (Bourne 1922b: 56; Goeke 1981: 978). There are only seven pairs in Symethinae, with the anteriormost two pairs greatly reduced.

Sexual dimorphism is relatively indistinct in the abdomen, which is not much widened in females. The chelae are homeomorphic in males and females. At least in males of *Ranina*, which are larger than females, the anterolateral carapace teeth are more developed, the chelae are larger and setae on the P1 propodus and dactylus different (Fielding & Haley 1976: fig. 4). In *Ranina ranina* (Linnaeus, 1758) sexual dimorphism is observed from the instar I pleopods, on abdomens of individuals over 34 mm in length and in chelipeds of individuals longer than 70 mm. Uropods of males degenerate and disappear by instar III. The puberty moult is estimated to be linked to a carapace length of 40–45 mm (Minagawa 1993a).

Ontogenetic changes may be present in raninoideans. Sakai (1937: fig. 45a–c) illustrated size changes in the anterior teeth of the carapace of *Ranina ranina*: small and simple in juvenile females, well developed and divided into three equal teeth in adult females, much stronger and wider in adult males. *Ranina ranina*, which is widely spreaded, might comprise several distinct species so information on this intraspecific variation may be misleading. Ontogenetic changes in functional morphology may be apparent in cuticle microstructures, and Savazzi (1981) documented allometric changes in a number of terraces during growth in *Lophoranina* spp. from Eocene strata in northern Italy.

The close resemblance between Raninoidea and the ‘mole crabs’ or ‘sand crabs’ (Anomura, Hippoidea) is due to parallel evolution and convergence, with similar high specialisation for burying/back-burrowing activities into sand, tail first (elongated body adapted to backing into soft sediment and modified legs). Hippoids markedly differ from raninoids in having uropods and a combination of leg movements with simultaneous tail flipping and uropod beating for swimming and digging (Faulkes & Paul 1997a, b, 1998).

Date of publication of the Raninoidea De Haan. The year of publication of Raninoidea De Haan has been cited either as 1839 (e.g., Manning & Holthuis 1981; Martin & Davis 2001; Guinot *et al*. 2008; Ng *et al*. 2008; De Grave *et al*. 2009; Schweitzer *et al.* 2010) or as 1841 (e.g., Wright & Collins 1972; Guinot 1993b; Tucker 1998; Feldmann *et al*. 2008). Crustaceans in *Fauna Japonica* by De Haan have been published in several issues (‘livraisons’) between 1833 and 1850 (Holthuis & Sakai 1970). The diagnosis of the taxon ‘Raninoidea’ can be found on p. 136, thus dated as 1841, but the name first appeared on p. 102 (i.e., in 1839) in a rather extensive comparison with ‘Dromiacea’. This earlier indication suffices as a valid use, being in accordance with the provisions of the International Code of Zoological Nomenclature (ICZN 1999), and thus the correct date should be 1839.

Historical account of extant Raninoidea. Early illustrations of raninoid crabs are those of Rumphius (1705), who depicted *Ranina ranina* (Linnaeus, 1758) [as Cancer Raniformis [*sic*]; see Rumphius 1705: 13, pl. 7, figs. T, V] and *Notopus dorsipes* (Linnaeus, 1758) [as Pediculus marinus [*sic*]; Rumphius 1705: 29, pl. 10, fig. 3) (Holthuis 1959: 107, 108, photo 8, figs. 8, 9). When erecting the *Cancer raninus*, Linnaeus (1758: 625), followed later by Lamarck (1801: 156; 1818: 224), who established *Ranina*, also alluded to the frog-like shape of these strange animals, which were initially placed within the Insecta Aptera. Some unusual characters of Raninoidea (e.g., body shape, cuticle ornament, short and unfolded abdomen, keel-like posterior sternites, cryptic spermathecal apertures, respiratory structures) are extensive modifications connected with a highly specialised burying/back-burrowing behaviour (see *Morphology of the Raninoidia* below). This partially explains why their taxonomic status has been problematic and varied over time. Even to this day, the raninoid lineage is subject of ongoing debate.

The raninids were considered either as ‘Crustacés Pédiocles’, a group which also comprised *Albunea* Weber, 1795, *Hippa* Fabricius, 1787, *Scyllarus* Fabricius, 1775, *Palaemon* Weber, 1795, and *Squilla* Fabricius, 1787 (Lamarck 1801), or as ‘Brachyuri among the Oxyrynchi’, which included *Corystes* Bosc, 1802, *Dorippe* Weber, 1795, *Maja* Lamarck, 1801 (as *Maia*) and *Orithyia* Fabricius, 1798 (Latreille 1802: 28; 1806: 43; 1810: 98). Others (Latreille 1825: 273; Berthold 1827: 259) ranked them in the brachyuran tribe Notopoda Latreille, 1817 (pp. xiii, 24, 25), which comprised various crabs with dorsal last pereiopod(s) such as *Dorippe*, *Dromia* Weber, 1795, and *Homola* Leach, 1815, but Guérin (1832: 285) subsequently excluded *Ranina* Lamarck, 1801, from this tribe. Alternatively, they were assigned to ‘Astacoïdes’ within the family ‘Oxyrhynques’, together with *Dorippe*, *Leucosia* Weber, 1795, *Maja* and *Orithyia* (Duméril 1806), considered as ‘Macroures’ among the ‘Paguriens’ (Lamarck 1818: 197, 224), or interpreted as a special tribe within the Macrouri [*sic*] (Latreille 1831: 368; see below). Desmarest (1825: 138) regarded *Ranina* as a brachyuran.

Conversely, H. Milne Edwards (1837: 167, 190) attributed the tribe ‘Raniniens’ (together with two other podotreme tribes, ‘Dromiens’ and ‘Homoliens’) to the ‘Décapodes Anomoures’ within the family ‘Aptérures’ (i.e., without tail fan), as opposed to the ‘Ptérygures’ (i.e., with biramous uropods and a tail fan) comprising ‘Paguriens’, ‘Hippiens’ and ‘Porcellaniens’. Dana (1852: 54, 402, 403, under the name of Raninidea) and Henderson (1888: ix, 26) also referred all podotreme crabs, including Raninidae, to Anomura.

Another interpretation was to view raninids as true crabs (i.e., Brachyura), and for a considerable period of time they were attributed to Oxystomata De Haan. The first author to do so was De Haan (1839: 102; 1841: 119, 136–140; 1850: xvii), who established the taxon Raninoidea. He was followed by several carcinologists (Ortmann 1892: 557, 559, 574; Alcock 1896: 135, 136, 288; Ihle 1918: 1, 294; Sakai 1937: 165, 168; Balss 1957: 1608, 1616).

Alphonse Milne-Edwards & Bouvier (1902: 7), however, excluded Raninoidea from Oxystomata, thus confirming the doubt already expressed by Boas (1880: 2002). As an outcome of his remarkable study, Bourne (1922b: 55) ranked Raninidae with the Brachyura as a special tribe, Gymnopleura, ‘equivalent to the Dromiacea, Brachygnatha and the rest of the Oxystomata.’ The separation of the raninoid crabs in a tribe next to other Brachyura was followed by several authors, including Rathbun (1937a), Gurney (1942), Garth (1946), Richardson & Krefft (1949), Barnard (1950), Gordon (1963, 1966), Monod (1956), Waterman & Chace (1960), Tyndale-Biscoe & George (1962), Bennett (1964), Sakai (1965, 1976), Pichod-Viale (1966), Forest & Guinot (1966), Takeda & Miyake (1970), Serène & Umali (1972), Fielding & Haley (1976), Hartnoll (1968, 1975, 1979), Goeke (1980, 1981), Dai & Xu (1991), Dai & Yang (1991), Chen & Xu (1991) and Watabe (2007).

For Števčić (1973: 631) ‘the raninids started their evolution from highly developed crabs’, and ‘their subsequent evolutionary pathway was regressive in both a morphological and ecological sense’, but later Števčić (2005: 33) placed Raninoidea ‘at the end of the dromiacean hierarchical system’. Similarly, Hartnoll (1979: 75) regarded the raninoids as, ‘the most advanced of the primitive Brachyura.’A reinterpretation of raninoid crabs became possible only after the discovery of an internalised spermatheca (Gordon 1963: 53, figs. 12, 13; 1966: 343, figs. 1–3; Hartnoll 1975, 1979), a primitive axial skeleton (Drach 1950: 2; Gordon 1966: 350), a special cephalic (ocular) configuration close to that of *Dromia* (Pichod-Viale 1966: 1266), the frequent incomplete tubulation of G1 and the relative length of G2 (Gordon 1966: 348; Serène & Umali 1972: figs. 5, 6; Guinot 1979: 232, fig. 62E–H).

The presence of coxal female sexual openings, plus the presence of a paired spermatheca, added to the abovementioned primitive features that all indicate a podotreme condition, led to the inclusion of Raninoidea in Podotremata, next to Dromiacea, Homoloidea and Cyclodorippoidea (Guinot 1977: 1050; 1978: 237; 1993b: 1324; Guinot & Bouchard 1998: 639; Guinot & Tavares 2001: 524, table 16; Guinot & Quenette 2005: 312).

Another turning point in classification was the abandonment of the concept of the Podotremata, based, for the most part, on molecular results. Spears & Abele (1988: 2A) removed Dromiidae from Brachyura, arguing that dromiids ‘branch very early, prior to the Anomura.’ Concluding that ‘there is no molecular support [...] for the division Podotremata (*sensu* Guinot), which groups raninids and dromiids together on the basis of a similar gonopore location’, Spears *et al.* (1993: 456) proposed to abandon the taxon Podotremata and set Raninidae at the lower limit within Brachyura. This interpretation of the molecular data was based on the study of only four species of Podotremata, without considering any dynomenid, homolodromiid, homolid, latreilliid, cymonomid or cyclodorippid taxa. Additional investigations led Spears & Abele (oral statement in 2nd European Crustacean Conference, Liège 1996; 1996: 14bis) to another major change by considering Dromiacea as true brachyurans to become the sister group of the Homoloidea and concluding Podotremata to be polyphyletic. Thus, Raninoidea (together with Cyclodorippoidea) became basal members of Eubrachyura, in which they formed a special subsection, Raninoida, consisting of only two families, Raninidae and Symethidae (Martin & Davis 2001: 49, 74). Results of Ahyong *et al.* (2007) showed that the ‘*Hypoconcha*’ sequence of Spears *et al.* (1993) represented a diogenid hermit crab rather than a brachyuran, so the *Hypoconcha*-Anomuran hypothesis should be abandoned (Ahyong *et al.* 2007: 582).

The classification of Martin & Davis (2001) has been followed by a number of palaeontologists (De Angeli & Beschin 2001; Feldmann 2003; Collins *et al.* 2003; Collins & Jakobsen 2004; De Angeli & Garassino 2006b; Schweitzer *et al.* 2010), who treated raninoids as eubrachyuran crabs. This placement of Raninoidea (and Cyclodorippoidea) within Eubrachyura was in contradiction with De Grave *et al.* (2009), who excluded section Raninoida (as well as section Cyclodorippoida) from Eubrachyura and placed them more basally, next to section Dromiacea. It is obvious that such a major change, all within a year, reflects the disagreement with how these crabs should be classified as well as the failure of the non-recognition of the Podotremata.

A molecular study by Ahyong *et al.* (2007), based on a larger sample of species and genes, suggested a paraphyletic Podotremata; and three podotreme sections, Dromiacea, Raninoida and Cyclodorippoida were proposed (Ahyong *et al.* 2009; Ng *et al.* 2009: fig. 4). In consideration of the level of generality of the characters, however, these ‘sections’ are not equivalent to the ‘section’ Eubrachyura (see *Phylogeny of the Raninoidia* below).

The study of well-preserved fossils, for which the family Cenomanocarcinidae (Guinot *et al*. 2008: 682, 712) was erected, and a brief discussion of the status of Raninoidea, formed the first step of the present revision. Neontologists and, even less so, molecular scientists would be unable to appreciate the extreme diversity and complexity of an ancestral group, especially when fossils are added, as in the case of raninoids. The practical necessity to consider new ranks therefore becomes clear so that a resolved phylogeny accommodates ancestral taxa in classifications. We therefore continue to recognise two sections in Brachyura, namely Podotremata and Eubrachyura. The former comprises four subsections, covered by earlier diagnoses: Dromioidia De Haan, 1833 (= Dromiacea De Haan, 1833, **emend.**), Homoloidia De Haan, 1839, Cyclodorippoidia Ortmann, 1892, and Raninoidia De Haan, 1839 (Guinot *et al*. in press). The section Eubrachyura de Saint Laurent, 1980, its sister group, comprises two subsections, Heterotremata Guinot, 1977, and Thoracotremata Guinot, 1977. The Raninoidia contains two superfamilies, Palaeocorystoidea (extinct only) and Raninoidea (both fossil and extant; Table 1).

The name Notopterygia Latreille, 1831. In his *Cours d'entomologie*, Latreille (1831: 368) established, within the Macrouri, the tribe Notopterygia, providing a description and type designation, viz. 'albunea scabra *de Fabricius, ou le* cancer raninus *de Linné*'. The name of his new tribe was based on the shape of all the legs, at the same time ending in 'fins' and arranged in two rows, the posterior being dorsal ('*tous les pieds … à la fois terminés en nageoire et disposés sur deux rangs, les deux ou quatre postérieurs étant dorsaux*'). Latreille (1831: 328, 369) clearly distinguished the Notopterygia from the other Macruri on the lack of uropods (forming the tail fan characteristic of Decapoda other than Brachyura) and, in particular, delimited it well from a second tribe, the 'Hippides'. Latreille (1831: 369) included in Notopterygia the fossil species *Lophoranina aldrovandii* (Ranzani, 1818). The definition was subsequently cited by Jourdan (1834: 147) and the same classification was followed by Lucas (1840: 154, 155). The taxon Notopterygia was quoted only by Bate (1888: 4) in a table showing previous classifications. In a report to the Linnean Society (December 1921), the name Gymnopleura was proposed by Bourne (1922: 55); Stebbing (1922: 108) remarked that Gymnopleura was preoccupied by the name Notopterygia (quoted previously by Stebbing 1908: 17). Bourne (1922a: 108), in a letter to the editor of *Nature*, wrote that, 'it seems that my proper course will be to withdraw the name 'Gymnopleura' and substituted that of 'Notopterygia, Latreille' in an addendum of the printer paper'. Finally, in a footnote, Bourne (1922b: 55) decided not to use Latreille's name so as to avoid confusion. The correct name Gymnopleura Bourne, 1922, to accommodate a separate tribe of crabs with exposed pleurites, was published just as it was. The name Gymnopleura was used by several authors, even fairly modern ones (see synonymy), but later was abandoned as a junior synonym of Raninoidea De Haan, 1839.

As far as we are aware, the case of the nomen 'Notopterygia Latreille, 1831' has never been discussed. The nomen Notopterygia is not formed from the stem of an available generic name. Thus, following ICZN Article 11.7.1.1, it could only be considered available if taken above superfamily rank, thus outside the family group. The Code does not cover names of ranks above the level of superfamily, and the question is in study (Guinot *et al.* unpublished).

Family Lyreididae Guinot, 1993 new status

Lyreidinae Guinot, 1993b: 1326.

Included subfamilies. Lyreidinae Guinot, 1993b and Marylyreidinae **n. subfam.**

Diagnosis. Carapace longer than wide, variously elongated; generally pyriform or fusiform, narrowing anteriorly, corresponding to elongation of pre-oral carapace region (wider anteriorly in *Marylyreidus* **n. gen.**, *Rogueus*). Dorsal surface smooth, grooves indistinct except for short branchiocardiac grooves. Cuticle microstructure with diverse pits, upright nodes (Lyreidinae) or with fungiform nodes (Marylyreidinae **n. subfam.**). Anterolateral margin lacking spines, or armed with 1, 2 small spines, or strong, outwardly directed spine that may be bifurcated. Front broadly triangular or subtrapezoidal. Orbitofrontal margin generally narrow, a third to half of maximum carapace width (broad in *Marylyreidus* **n. gen.**, *Rogueus*). Supraorbital margin generally unarmed, with single fissure or few teeth (*Macroacaena*). Orbits directed anteriorly; eyestalk composed of one article. Antennules, antennae about same size, general shape; long, slender; both modified in relation with respiratory physiology. Antennule not folded, basal article expanded, somewhat concave internally so that, when apposed, both antennules form conduit for respiration current. Proepistome concealed, epistome narrow. Endostome strongly elongated, forwardly produced between basal articles of antennules; strongly excavated. Mxp3 long, narrow, slender, operculiform; merus longer than ischium. Pterygostome tumid, subantennary lobe developed, produced far in front of mandibles, united over long distance with edges of endostome.

Thoracic sternum long, strongly deflected behind sternite 7; anterior sternites variously developed, produced; sternite 3 crown shaped; sternite 4 slightly expanded, flat; suture 4/5 crescent shaped; sternite 5 wide; sternite 6 narrower; sternites 5, 6 with ridge (Marylyreidinae **n. subfam.**); sternite 7 narrowing posteriorly; sternite 8 elongated, perpendicular to preceding ones. Medial line along sternites 7, 8. Sternum/pterygostome junction moderately developed (Lyreidinae) or absent (Marylyreidinae **n. subfam.**). Sternum/exposed pleurites connections well-developed between P1, P2 (sternite 5 to pleurite 5); less developed between P2, P3 (sternite 6 to pleurite 6) (Lyreidinae) or absent between P2, P3 (Marylyreidinae **n. subfam.**). Pleurites 5–7 partially exposed, calcified, forming flat area, not overhung by branchiostegite edge. Small spermathecal apertures facing each other on opposite sides of depression ('sunken pit') of sternite 7, separated by medial line.

Sterno-abdominal depression present posteriorly, entirely covered by male abdomen. Abdomen freely articulated (6 somites, plus small telson), conspicuously narrow; sexual dimorphism indistinct: female abdomen only marginally wider; somites 1–3 dorsal, in prolongation with carapace, remainder completely folded; sharp flexure at level of somite 4; somites 3–5 may bear long, recurved spine; somite 6 long, with long ventral sockets, medially limited by thickening for locking mechanism. Locking mechanism as pair of hook-like projections arising from episternite 5, projections short, stout (Marylyreidinae **n. subfam.**) or elongated, distally recurved (Lyreidinae); projections distally with double peg, which firmly fit into the pair of deep sockets in the latero-posterior extended corners of abdominal somite 6; locking may be effective in ovigerous females, even with large egg masses, but vestigial in large females.

Chelipeds homochelous, homodontous, may be long; basis-ischium immoveably fused with long merus; propodus short, flattened, upper margin unarmed or with single spine, lower margin with few sharp spines; dactylus long, smooth on dorsal border, bent at right angle against anterior border of palm; fixed finger conspicuously inflated; prehensile borders of both fingers with alternate, low teeth. P2–P4 arthrodial cavities lateroventral; those of P5 subdorsal. P2–P4 slender; merus long, slender; propodus, dactylus flattened, compressed. P2 propodus short, broad, dactylus slightly spatulate. P3 propodus longer, dactylus elongated, styliform, externally ridged. P4 carpus, propodus, dactylus variously lobate. P4 coxa subdorsally located; P5 more dorsal, strongly reduced, filiform, ending in small, flattened, elliptical dactylus.

Respiratory mechanism highly specialised, both inhalant, exhalant respiratory current through modified frontal area; absence of Milne-Edwards openings (except possibly Marylyreidinae **n. subfam.**); presence of posterior branchial orifices and water conduits on the flanks of carapace.

Remarks. The subfamily Lyreidinae is here elevated to the family rank, as opposed to all other Raninoidea, which are referred to the family Raninidae (Table 1). Larval characters confirm separation of Lyreididae from other Raninoidea (Rice 1980, 1981), as do sperm characteristics (Jamieson *et al*. 1994, 1995) and cuticle structure (Waugh *et al*. 2009). Furthermore, Lyreididae is the only Raninoidea that lock its abdomen, as opposed to a shortened, unlocked, abdomen in Raninidae. The respiratory morphology of Lyreididae differs from that of all other Raninoidea. Two subfamilies are recognised within Lyreididae: the extinct (late Albian–early Cenomanian, *c*. 105–98 Ma) Marylyreidinae **n. subfam.** showing several primitive characters, and Lyreidinae, which first appears during the early Turonian (*c*. 92 Ma).

Cuticle microstructure appears to be a reliable taxonomic tool in the study of raninid crabs. None of the Lyreididae examined here exhibit any inclined nodes, typical of Raninoidea (see Waugh *et al*. 2009: table 2; however, note that *Raninella* is now assigned to Ranininae). The cuticle microstructure of lyreidines comprises various types of pits and small granules (i.e., upright nodes), whereas that of marylyreidines shows fungiform nodes. Both cuticle microstructural types are characteristically found in Palaeocorystoidea.

Lyreidus is probably a more exclusive back-burrower than other raninoids. It buries itself leaving the tip of its narrow, elongated anterior portion of the carapace just breaking the surface of the sand (Bourne 1922b: 70). The long, recurved spines in the centre of abdominal somites 3–5 may be used to penetrate the sand and assure a fixed position to the crab when buried. Having no posterior branchial orifices and no Milne-Edwards openings, a lyreidid is dependent on an inhalant current in the anterior portion of the carapace (see *Respiration in the Brachyura* below). The exposed pleurites 5–7 form a flat plate, practically in continuity with the branchiostegite (Figs. 46A; 51B), and there is no excavated area overhung by the branchiostegal edge and by the P5 as in other raninoids. Griffin (1970: fig. 6O–R) illustrated the variously produced lyreidid crown-shaped sternite 3 and the shape of sternite 4.

The lyreidid spermathecal apertures face each other on opposite sides of a depression of trough-like, although less narrow, sternite 7 in contrast to other Raninoidea such as *Ranina* (Hartnoll 1979: 76, 80, figs. 1–3; Guinot 1993b: fig. 4; Guinot & Quenette 2005: 314).

While extant members of Lyreididae typically have a narrow or tapering front, their fossil representatives, assigned to a handful of genera, may show a different carapace outline as several early members (e.g., *Bournelyreidus* **n. gen.**, *Marylyreidus* **n. gen.** and *Rogueus* Berglund & Feldmann, 1989) that have a much wider front than extant lyreidids. Extinct lyreidid genera recognised here are *Bournelyreidus* **n. gen.**, *Macroacaena* Tucker, 1998, *Marylyreidus* **n. gen.** and *Rogueus*. *Lyreidus* De Haan, 1841, and *Lysirude* Goeke, 1986, both known from the Eocene onwards (see Appendix), are the only lyreidids to survive to the present day. Here 35 fossil and 6 extant species within Lyreididae are listed. Of the latter group, one species, *Lyreidus tridentatus* De Haan, 1841, is also known from the fossil record.

Subfamily Lyreidinae Guinot, 1993

Lyreidinae Guinot, 1993b: 1326.

Type genus. *Lyreidus* De Haan, 1841.

Genera included. *Bournelyreidus* **n. gen.**, *Heus* Bishop & Williams, 2000, *Lyreidus* De Haan, 1841, *Lysirude* Goeke, 1986, *Macroacaena* Tucker, 1998, and *Rogueus* Berglund & Feldmann, 1989.

Diagnosis. Carapace longer than wide, elongated, generally narrow, pyriform or fusiform, with long, narrow anterior portion, or with wide, sinuous anterior margin. Anterolateral margin lacking tooth or with 1 or 2 teeth, with long spine (*Lysirude*, *Macroacaena*) or single, strong bifurcated spine (*Rogueus*). Posterolateral margin long, generally rimmed. Posterior margin short, concave. Cervical groove absent; branchiocardiac groove short. Carapace smooth, regions indistinct; cuticle microstructure with pits and upright nodes. Rostrum broadly triangular or subtrapezoidal. Orbitofrontal margin from narrow, less than one-third of maximum carapace width, to wide, three-quarters of maximum carapace width. Supraorbital margin generally unarmed, with single fissure, or with few teeth (*Macroacaena*). Antennules, antennae about same size and general shape; long, slender, modified in connection with respiratory currents. Antennule not folded, basal article expanded, somewhat concave internally so that when apposed both antennules form conduit for the exhalant current. Proepistome narrow. Epistome anteriorly produced between basal articles of antennules. Subantennary lobe of pterygostome developed, produced far in front of mandibles, fused over a long stretch with epistome edges. Mxp3 long, narrow, slender, oxystomian condition; merus longer than ischium. Milne-Edwards openings absent. Pterygostome elongated, non-areolated, tumid. Pleurites 5–7 partially exposed, not excavated, forming flat area, not overhung by edge of branchiostegite. Sternum/pterygostome junction moderately developed; junction sternum/pleurites well developed between P1, P2, less so between P2, P3. Thoracic sternum long, narrow, strongly deflected behind sternite 7; sternite 3 variously crown shaped; sternite 4 not much expanded, flat; sutures 4/5 reduced, crescent shaped; sternite 5 relatively wide; sternite 6 only slightly narrower; sternite 7 narrowing posteriorly; sternite 8 narrow, elongated, perpendicular to preceding ones. Medial line along sternites 7, 8.

Pair of strong, elongated, hook-like projections arise from episternite 5, recurved at tip, distally with double peg that firmly fits into pair of deep sockets in latero-posterior extended corners of abdominal somite 6; locking may be effective in ovigerous females, even with large egg mass, but becoming obsolete in larger females. Socket on abdominal somite 6 long, limited by thickening.

Two small spermathecal apertures face each other on opposite sides of depression (sunken pit) on sternite 7, separated by vertical medial wall, marked externally by medial line.

Chelipeds homochelous, homodontous. Basis-ischium immoveably fused with long merus. Propodus of variable length, flattened; its upper margin unarmed or with single spine; lower margin armed with few sharp spines; dactylus long, smooth on dorsal border, bent against anterior border of palm; fixed finger much inflated; prehensile borders of both fingers with staggered, low teeth.

P2–P4 rather slender. Merus rather long, slender. Propodus, dactylus flattened, compressed. P2 propodus short, broad, dactylus slightly spatulate. P3 propodus longer, dactylus elongated, styliform, externally ridged. P4 carpus, propodus, dactylus variously lobate. P4 coxae subdorsally located. P5 more dorsal, much reduced, filiform, ending in small, flattened, elliptical dactylus.

Sterno-abdominal depression present posteriorly, entirely covered by male abdomen. Abdomen freely articulated (6 articles plus small telson), narrow, fixed; somites 1–3 dorsal, in straight line with carapace, rest completely folded; sharp flexure at level of somite 4 which bears a strong spine; somite 5 may also bear single spine; somite 6 longer, ventrally with developed sockets fitting double peg of the hook-like projections of thoracic sternite 5 for abdominal locking mechanism. Sexual dimorphism indistinct. Posterior branchial orifices or water conduits on the flanks of carapace absent; instead, with post-frontal modifications for respiratory current.

Genus *Bournelyreidus* n. gen.

Type species. *Hemioon eysunesensis* Collins & Wienberg Rasmussen, 1992, by present designation.

Diagnosis. Carapace oval, elongated, widest at one-third of total carapace length from front, nearly flat in longitudinal, convex in transverse cross section. Posterolateral margin with divergent posterior portion, vertical anterior portion; anterolateral margin shorter, with 2 curved, spiniform teeth. Orbitofrontal margin straight, occupying more than half of maximum carapace width. Outer orbital corners prominent, supraorbital borders with 2 orbital notches. Rostrum trapezoidal, bifid or triangular, with single apex, excavated. Branchiocardiac grooves shallow, well-defined, cervical groove absent. Carapace surface with minute pits, granules (upright nodes). Pterygostome tumid, with a granular blunt ridge, posterior corner recessed for relatively large mxp3 coxa. Mxp3 strongly elongated, oxystomian condition; exopod narrow, slightly shorter than equal-sized endopod ischium, merus. Branchiostegite reduced, pleurites exposed. Sternite 3 crown shaped; sternite 4 long, wide anteriorly, forming junction with pterygostome, lateral sides strongly concave. Episternite 4 rather small. Sternite 5 large, broadly extended between P1, P2, reaching pleurites. No medial line, at least on sternites 1–6. Holding mechanism present (see note under *B. tridens* **n. comb.**). Chelipeds flattened, fixed finger not downturned (*B. carlilensis* **n. comb.**; Feldmann & Maxey 1980: 859, text-fig. 1E), closing, with sharp teeth; lower margin of chelipeds smooth to spinose. P2–P4 with paddle-shaped propodus, dactylus; P5 reduced, subdorsal. Abdomen flexed under carapace, abdominal somite 3 with medial elevation, somite 4 with prominent tubercle, somite 6 long (Collins & Wienberg Rasmussen 1992: 21).

Derivation of name. In honour of the late G.C. Bourne, in recognition of his admirable contribution (Bourne 1922b) to the knowledge of raninoid crabs.

Species included. *Raninella carlilensis* Feldmann & Maxey, 1980, *Hemioon eysunesensis* Collins & Wienberg Rasmussen, 1992, *Palaeocorystes laevis* Schlüter *in* von der Marck & Schlüter, 1868, *Raninella manningi* Bishop & Williams, 2000, ?*Raninella oaheensis* Bishop, 1978, *B. teodorii* **n. sp.,** and *Raninella tridens* Roberts, 1962. Also assigned here is *Lyreidus* sp. *sensu* Collins & Jakobsen (1995).

Remarks. Members of *Bournelyreidus* **n. gen.** were previously placed either in *Raninella* A. Milne Edwards, 1862, or *Hemioon* A. Milne Edwards, 1862, two genera considered here synonymous (see below).

Several characters distinguish *Bournelyreidus* **n. gen.** from *Raninella*. The carapace of the former has the posterolateral margin subdivided into a divergent and a vertical portion (entire posterolateral margin smoothly convex in *Raninella*); moreover, the anterolateral teeth are spiniform in the new genus (flattened and strong in *Raninella*) and all its members exhibit a straight, horizontal orbital margin (a concave orbital margin in *Raninella*). In *Bournelyreidus* **n. gen.** (e.g., *B. carlilensis*; Feldmann & Maxey 1980: 859, text-fig. 1E; *B. eysunesensis*; Collins & Wienberg Rasmussen 1992: 20, fig. 10A), the cheliped merus lacks the subdistal granular crest (present in *Raninella*, see below), and the cuticle of the new genus comprises diminutive granules (upright nodes) and pits (larger, anteriorly directed granules (inclined nodes) in *Raninella*) (see also Waugh *et al*. 2009: table 2). The most important difference between the two genera seems to be sternal, sternite 5 in *Bournelyreidus* **n. gen.** being devoid of a medial line, which is typically present in *Raninella*. An abdominal holding structure, i.e. projections on sternite 5, is also present in *Bournelyreidus* **n. gen.** (see remarks for *B. tridens*), whereas in the species of *Raninella* no such structure has been observed.

Bournelyreidus **n. gen.** superficially resembles the monotypic genus, *Heus*. These genera can nevertheless be distinguished as follows: by *Bournelyreidus* **n. gen.** having a narrow carapace (wide in *Heus*); anterolateral margins with two spines (one spine in *Heus*); a wide, bifid front (narrow, strongly sulcate rostrum in *Heus*); axial keel absent (axial keel extends onto the dorsal carapace in *Heus*); closed orbital fissures (open orbital fissures in *Heus*); and dorsal surface non-areolated (two epigastric and four protogastric swellings in *Heus*).

Bournelyreidus **n. gen.** has exposed pleurites 5–7, hence its placement in Raninoidea. Assignment to Lyreididae is based on the following features: carapace fusiform, with lateral margins vertical in the medial portion; cuticle smooth or pitted (see Waugh *et al*. 2009); no medial line on anterior sternites (excluding it from Ranininae, Raninoidinae, Symethinae, Notopodinae *pro parte* and Cyrtorhininae); presence of projections for abdominal holding on sternite 5.

Bournelyreidus **n. gen.** comprises small crabs that have been recorded from the Upper Cretaceous of North America, Greenland and Germany. The youngest representative is known from the lower Paleocene (Danian) of Denmark (Collins & Jakobsen 1995: 39, pl. 10, fig. 10).

Bournelyreidus carlilensis (Feldmann & Maxey, 1980) n. comb.

Raninella carlilensis Feldmann & Maxey, 1980: 858.

Remarks. *Raninella carlilensis* (see Feldmann & Maxey 1980: 858, text-figs. 1–3), as based on four specimens from the middle Turonian of Kansas (U.S.A.), is here reassigned to *Bournelyreidus* **n. gen.** The ventral sides of all specimens is poorly preserved, but the large mxp3 coxae, intercalated between the thoracic sternum and pterygostome, are well visible (Feldmann & Maxey 1980: 859, text-fig. 1A). There is a narrow junction between sternite 4 and the pterygostome, despite the fact that this is not sufficiently well-preserved in the type series. The rostrum is excavated; its tip and the outer orbital corners may be incompletely preserved in the type series. The pterygostome is tumid, 'possessing two fairly deep sulci' (Feldmann & Maxey 1980: 859; see also their text-fig. 1C), and the carapace bears two slender anterolateral spines. *Raninella carlilensis*, *R. tridens* and *R. oaheensis* appear to have a similar rostral region (Feldmann & Maxey 1980: 860, 861).

Bournelyreidus eysunesensis (Collins & Wienberg Rasmussen, 1992) n. comb.

Hemioon eysunesensis Collins & Wienberg Rasmussen, 1992: 19.

Remarks. *Hemioon eysunesensis* (see Collins & Wienberg Rasmussen 1992: 19, fig. 10a–c), based on 82 specimens from the upper Campanian of Nûgssuaq (West Greenland) and originally referred to Raninidae, should be reassigned to Lyreididae and a new genus, *Bournelyreidus* **n. gen.**, for which it becomes the type species.

The anterolateral margin bears two spiniform teeth and the rostrum is excavated and bifid. The pterygostome is strongly tumid, with 'a ridge running parallel to the pleural suture' (Collins & Wienberg Rasmussen 1992: 21). The anterior sternites, at least sternite 3, forms a distinct crown. The anterior part of sternite 4 is expanded laterally, where it incises the rather large mxp3 coxa; the posterior corner of the pterygostome is recessed for the rounded distal margin of the mxp3 coxa (Collins & Wienberg Rasmussen 1992: 20, fig. 10c). Sternite 5 is laterally extended to join the exposed pleurites. The fourth abdominal somite bears a prominent tubercle, and the sixth abdominal somite is long (Collins & Wienberg Rasmussen 1992: 21), both characters typical of Lyreididae. Projections arising from sternite 5 have not been illustrated nor noted in the original description.

The P5 are 'more dorsally placed, smaller, less flattened and have only a small paddle-like dactylus' (Collins & Wienberg Rasmussen 1992: 22). Such fragile details are rarely seen in the fossil record, and because the type series is exceptionally well-preserved and there are many specimens '…preserving details of the ventral surface and limbs' (Collins & Wienberg Rasmussen 1992: 21), the type series of *B. eysunesensis* should be re-examined in order to document as many data as possible.

Remarks. *Palaeocorystes laevis* (see Schlüter *in* von der Marck & Schlüter 1868: 298, pl. 44, fig. 2), from the upper Turonian to upper Santonian of northern Germany, was referred to *Hemioon* by Collins (1997: table 1). An additional specimen, recently recognised in the RME collections, allows this poorly illustrated species to be reassessed. It shows the following characters which are typical of *Bournelyreidus* **n. gen.**: posterolateral margin with divergent and vertical portion; rostrum excavated and bifid; outer orbital tooth developed; orbital margin horizontal; cuticle with scattered pits, small granules (upright nodes) near the lateral margin. The posterior lateral spine is rather well developed for the genus and the branchiocardiac grooves are obsolete. *Bournelyreidus laevis* closely resembles *B. eysunesensis*.

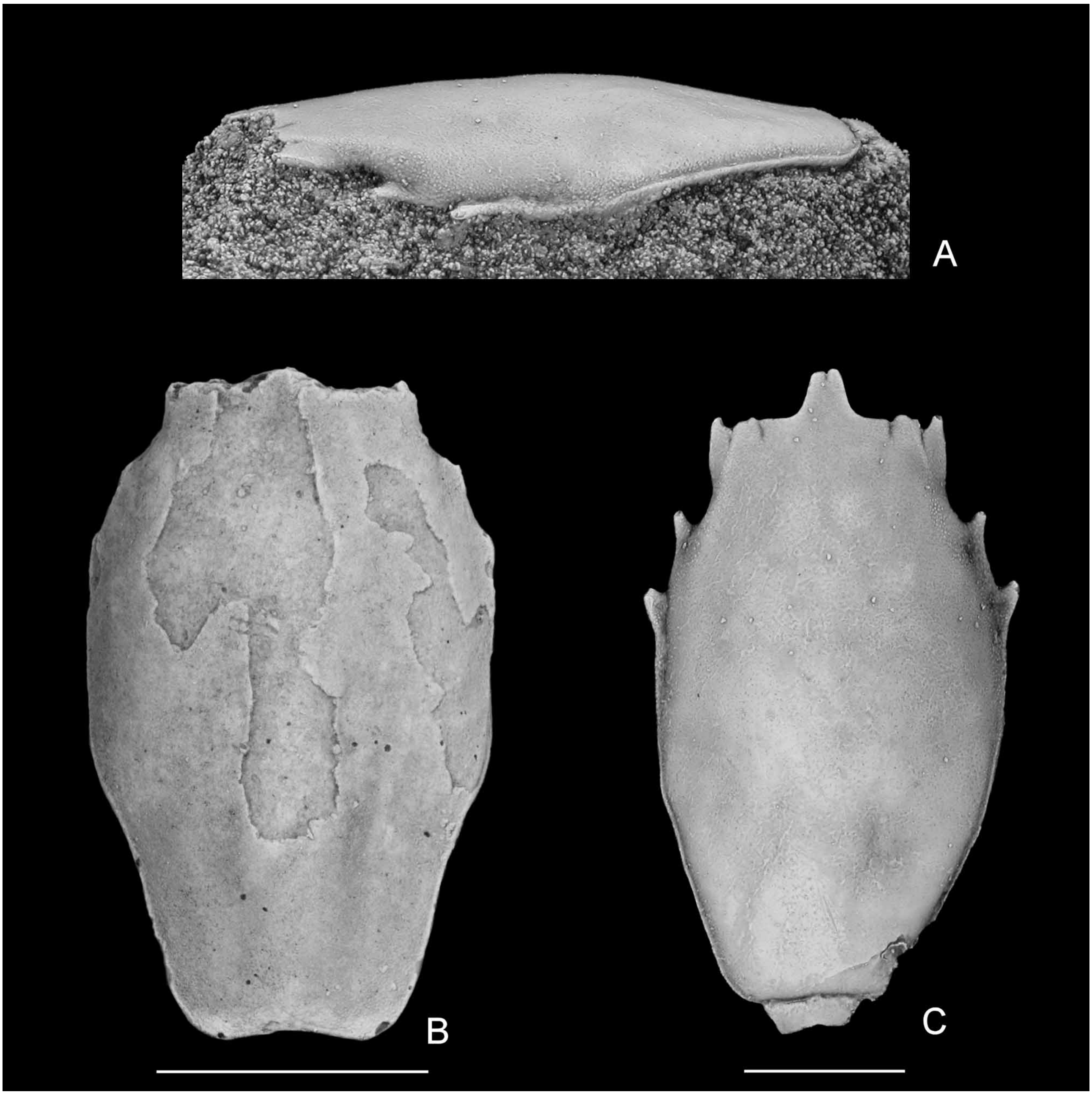


FIGURE 23. A, C, *Bournelyreidus laevis* (Schlüter *in* von der Marck & Schlüter, 1868) **n. comb.** (Lyreididae, Lyreidinae), MAB k. 2882 (cast of RME 551.763.333; indeterminate sex), upper Santonian, Erkenschwick (Münsterland, northwestern Germany); left lateral view, and dorsal view of carapace; B, *Bournelyreidus tridens* (Roberts, 1962) **n. comb.**, MAB k. 0214 (cast of GAB 37–833; indeterminate sex), lower Maastrichtian, Mississippi (U.S.A); dorsal view of carapace. Scale bars: 5mm.

Bournelyreidus laevis (Schlüter *in* von der Marck & Schlüter, 1868) n. comb.

Palaeocorystes laevis Schlüter *in* von der Marck & Schlüter, 1868: 298
(Fig. 23A, C)

Material examined. Carapace and first abdominal somite (RME 551.763.333; *ex* K.-H. Hilpert Collection, A5955 07155, as *Oncopareia* sp.), 'Recklinghäuser Sandmergel', upper Santonian, Erkenschwick, northern Germany. (MAB k. 2882 is a cast of this specimen).

***Bournelyreidus*? *oaheensis* (Bishop, 1978) n. comb.**

Raninella oaheensis Bishop, 1978: 615.

Material examined. A cast of the holotype (GAB 36-101; Bishop 1985: fig. 3), is housed in MAB (MAB k. 0217).

Remarks. *Raninella oaheensis* (see Bishop 1978: 615, pl. 1, figs. 7–11, pl. 2, figs. 1–20) was originally recorded from the Pierre Shale (upper Campanian-lower Maastrichtian) of South Dakota and Montana, U.S.A. (Bishop 1978: 615), but was subsequently recognised in North Dakota (Tucker *et al*. 1987: 278, table 1), as well as in the Fox Hills Formation (Maastrichtian) of South Dakota (Crawford *et al*. 2006). This species is here reassigned to *Bournelyreidus* **n. gen.** based on features of the carapace and thoracic sternum of which the anterior sternites are preserved in the type lot (Bishop 1978: pl. 1, fig. 7; pl. 2, fig. 3).

The posterolateral margin is not well-preserved in the type series. It was shown as more or less straight in the line drawing by Bishop (1978: 611, text-fig. 5). Better-preserved specimens (Tucker *et al*. 1987: fig. 6) clearly show the medial third of the carapace with vertical margins. The branchiocardiac grooves are well developed.

Of the thoracic sternum, only the anterior sternites are known (Bishop 1978: pl. 1, fig. 7; pl. 2, fig. 3). Sternite 4 is wide anteriorly, long, lateral margins are concave and raised, episternite 4 is rather small. Only a small central portion of sternite 5 is preserved (Bishop 1978: pl. 1, fig. 7); no medial line is present, which precludes assignment of the species to *Raninella*.

Several carapace characters distinguish *B*.? *oaheensis* from other members of the genus: the rostrum is narrower, non-bifid, with a subtle keel extending onto the carapace; the orbital margins are slightly directed outwards, rather than horizontal, with the fissures open rather than closed. The outer orbital corners, which normally are prominent in *Bournelyreidus* **n. gen.**, appear to be weakly developed in the present species; however, this needs to be verified in the type series. *Bournelyreidus*? *oaheensis* appears to have some characters in common with *Heus*, namely a narrow, sulcate and keeled rostum, and open orbital fissures. The narrow carapace with two anterolateral spines, absence of a cervical groove and of swellings on the anterior carapace, favour assignment of the present species for the time being to *Bournelyreidus* **n.gen.**.

***Bournelyreidus teodorii* n. sp.**

(Fig. 24A)

Diagnosis. Carapace large, oval, elongated, widest at one-third of total carapace length from front. Posterolateral margin with divergent posterior portion; anterolateral margin shorter, with 2 small teeth. Orbitofrontal margin tridentate, occupying about half of maximum carapace width. Outer orbital corners prominent, supraorbital borders with 2 orbital notches. Rostrum triangular, bifid, excavated. Carapace surface with minute pits and granules.

Derivation of name. Named in honour of Mr Dominique Téodori (Pechbonnieu, France), who collected and donated the specimen.

Material examined. Holotype (MNHN.F A38533) collected at working quarry southeast of the village of Saint-Loup-en-Comminges (Haute-Garonne, Midi-Pyrénées, southwest France; September 2009), from a blue-grey marly limestone bed at the base of a series assigned to the ‘Marnes bleues de Saint-Loup’. A second specimen in the private collection of D. Teodori has also been examined; this retains a better-preserved anterolateral and frontal margin, so that features of the holotype could be checked and confirmed. Co-occurring macrofaunal assemblages are rich in holasteroid echinoids, ostreid bivalves, fishes, cephalopods (e.g., the scaphitid ammonite *Hoploscaphites constrictus* (Sowerby, 1817) and other unidentified crustaceans. The thickness of such limestone levels varies between 0.1 and 0.3 m; they alternate with softer marls. As noted by Kennedy *et al*. (1986: 1004, 1005, fig. 2) and Peybernès *et al*. (1998), the ‘Marnes bleues de St. Loup’ in the Blajan-Bazordan anticline are of late Maastrichtian age.

Description. Carapace large (maximum length 66 mm, width 40 mm), oval, elongated, widest behind the lateral spines at about at one-third of total carapace length from front. Orbitofrontal margin tridentate, occupying about half of maximum carapace width. Base of rostrum about one-third of orbitofrontal region. Rostrum triangular, bifid, excavated. Large subcircular orbits with prominent outer orbital spines. Supraorbital borders with 2 relatively deep orbital fissures. Posterolateral margin with diverging posterior portion; anterolateral margin shorter, with 2 rather small, forwardly directed spines. Branchiocardiac grooves, impressions of epimeral adductor muscle scars faint. Carapace surface with minute pits, granules. Granules significantly coarser along lateral margins. Both chelipeds similar in size, form; merus, carpus, propodus of comparable length, width, covered with granules; propodus distinctly more flattened.

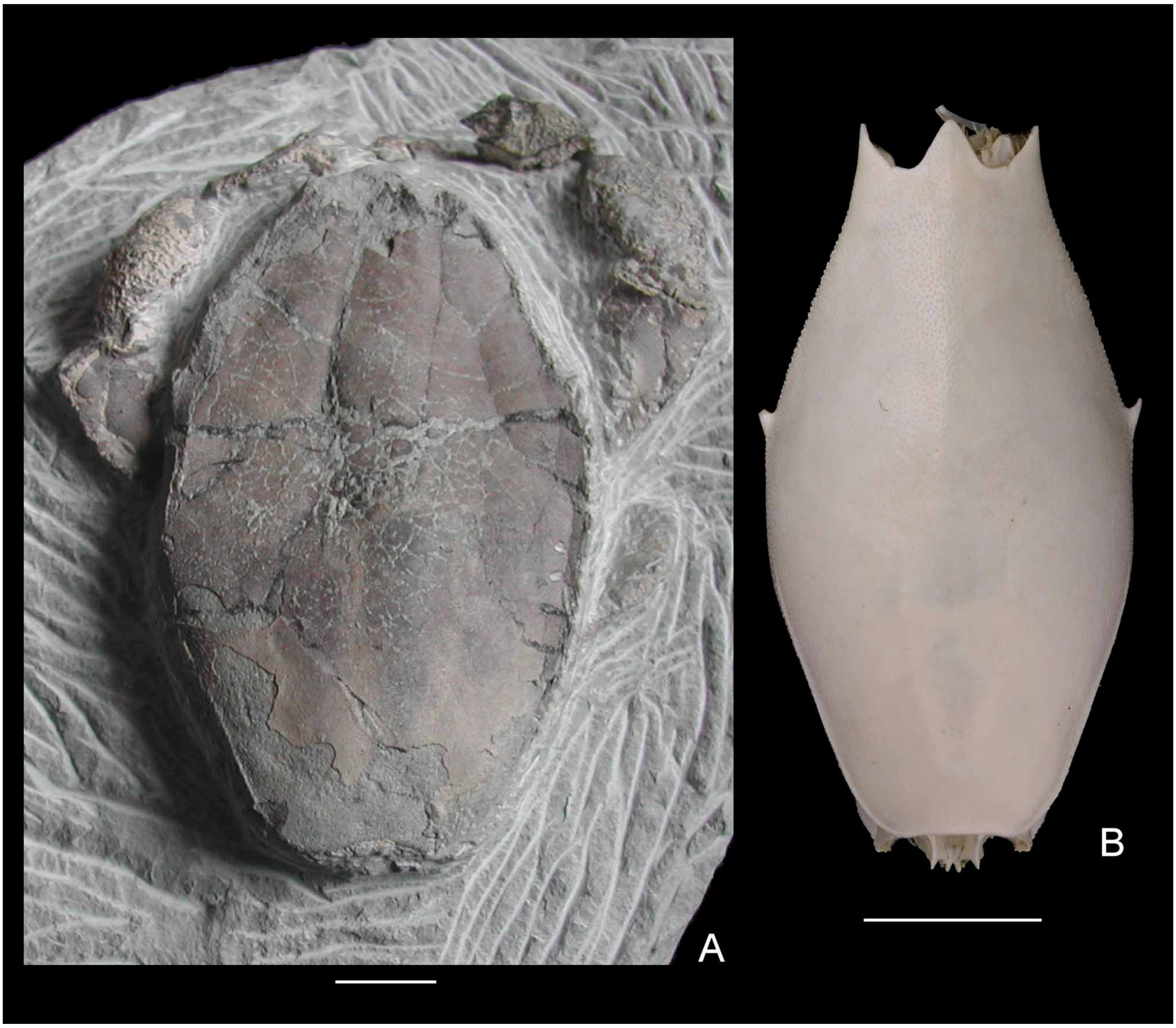


FIGURE 24. A, *Bournelyreidus teodorii* **n. sp.** (Lyreididae, Lyreidinae), MNHN.F A38533 (**holotype**; *ex* D. Téodori Collection); middle/upper Maastrichtian, Saint-Loup-en-Comminges (Haute-Garonne, southern France); dorsal view of carapace and chelipeds; B, *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), MAB k. 2883 (male), Recent, Philippines; dorsal view of carapace. Scale bars: A: 10mm; B: 5mm.

Remarks. Despite the fact that the carapace has suffered from sediment compaction, the morphology of the orbitofrontal and anterolateral margins allows assignment of this form to *Bournelyreidus* **n. gen**. It is distinguished from *B. carlilensis* **n. comb.** and *B.*? *oaheensis* **n. comb.** in attaining a markedly larger size and in having a less broad orbitofrontal region and a much larger carpus. *Bournelyreidus tridens* **n. comb.** has a much shorter anterolateral margin, and a more projected orbitofrontal region; its posterolateral margins are more concave and less divergent than the new species. *Bourneylyreidus manningi* **n. comb.** has much coarser ornamentation and a more clearly areolated carapace. The new species differs from *B. laevis* **n. comb.** in having a broader base to the rostrum and subcircular orbits rather than near-rectangular ones; it can also be distinguished from *B. eysunesensis* **n. comb.** by its less concave anterolateral margin between the outer orbital and first anterolateral spine.

Bournelyreidus tridens (Roberts, 1962) n. comb.

Raninella tridens Roberts, 1962: 187.
(Fig. 23B)

Material examined. Casts of GAB 37-832 (ventral) and GAB 37-833 (dorsal) (Bishop 1983b: fig. 3l; table 1) (MAB k.0214).

Remarks. *Raninella tridens* (see Roberts 1962: 187, pl. 88, figs. 5, 6), from the Campanian of New Jersey and Delaware, U.S.A. and the lower Maastrichtian of Mississippi (Bishop 1983b), is here transferred to *Bournelyreidus* **n. gen.** The carapace is small, elongated, and the cuticle shows fine granules (upright nodes). The orbital margin is horizontal, branchiocardiac grooves are weak, the median third of the carapace has vertical margins, the posterior portions of the posterolateral margin being divergent and slightly concave. Sternite 3 is crown shaped, sternite 4 is long, with strongly concave lateral margins and it joins the pterygostome anteriorly. The posterior corner of the pterygostome is recessed for the rather small mxp3 coxa. Episternites 4 small, separated by distinct, crescent-shaped sutures. Sternite 5 is comparatively large, widened anteriorly and with two small depressions posteriorly; the episternites show rather short, curved projections. No pegs are discernible, which may be the result of incomplete preservation, or the specimen represents a mature female in which the holding was lost. The projections are curved outwards, and seem to 'rest' on the surface of sternite 6; such configuration suggests the specimen to be a mature female. Only the anterior portion of sternite 6 is preserved; it is strongly excavated. In Lyreidinae the surface in between these projections and the anterior portion of sternite 6 is typically excavated as a kind of sterno-abdominal depression. No medial line is present on sternites 1–6, a characteristic of the genus. Exposed pleurites 5 and 6 are preserved; they are rather low, and notably granular.

Genus *Heus* Bishop & Williams, 2000

Heus Bishop & Williams, 2000: 290.

Type species. *Heus foersteri* Bishop & Williams, 2000.

Remarks. Only the carapace of *Heus foersteri* (see Bishop & Williams 2000: 290, fig. 4), from the upper Campanian of South Dakota and Colorado, U.S.A., is preserved. This reveals a unique set of characters: rostrum broad and narrow, strongly sulcate, with a keel that extending onto the carapace; oval swellings on epigastric and protogastric regions; cervical groove discernible; lateral margins with but a single, diminutive spine. These characters distinguish it easily from *Bournelyreidus* **n. gen.** Re-examination of the type series of *B.*? *oaheensis* (see above) is needed to decide if it might also be better accommodated in *Heus*.

The wide carapace, with clearly concave posterior (divergent) portions of the posterolateral margins, weakly armoured anterolateral margin, and swellings on the anterior carapace surface are somewhat similar to the configuration in *Symethis* Weber, 1795 (see below). The orbitofrontal construction, however, makes its placement in the Lyreidinae more likely.

Genus *Lyreidus* De Haan, 1841

Lyreidus De Haan, 1841: 137.

Type species. *Lyreidus tridentatus* De Haan, 1841, by monotypy.

Species included. *Lyreidus antarcticus* Feldmann & Zinsmeister, 1984, *L. bennetti* Feldmann & Maxwell, 1990, *L. brevifrons* Sakai, 1937, *L. elegans* Glaessner, 1960, *L. fastigatus* Rathbun, 1919, *L. hungaricus* Beurlen, 1939, *L. lebuensis* Feldmann & Chirono-Gálvez *in* Feldmann, 1992, *L. stenops* Wood-Mason, 1887, *L. tridentatus* De Haan, 1841, *L. waitakiensis* Glaessner, 1980, and *L.* sp. (*sensu* Karasawa 1993).

Genus *Lysirude* Goeke, 1986

Lysirude Goeke, 1986: 214.

Type species. *Lysirude nitidus* (A. Milne-Edwards, 1880), by original designation.

Species included. *Lysirude channeri* (Wood-Mason, 1885) (= *Lyreidus gracilis* Wood-Mason, 1888: 376), *L. griffini* Goeke, 1986, *L. hookeri* Feldmann, 1992, *L. nitidus* (A. Milne-Edwards, 1880), and *L. paronae* (Crema, 1895).

Remarks. Ever since its original description, *Lysirude* has been regarded as a synonym of *Lyreidus* (e.g., Feldmann 1989; Collins & Wienberg Rasmussen 1992; Waugh *et al*. 2009; Schweitzer *et al.* 2010), or as a subgenus (Feldmann 1992). Other authors have given it full generic status (e.g., Guinot 1993b; Tucker 1998; Bouchard 2000; Ng *et al*. 2008; De Grave *et al*. 2009).

Based on the hypertrophied lateral spines, the anterolateral margin typically with a blunt tooth, and on abdominal holding structures (Bouchard 2000: 175), the treatment of *Lysirude* as a distinct genus is favoured here.

Genus *Macroacaena* Tucker, 1998

Macroacaena Tucker, 1998: 325.
Carinaranina Tucker, 1998: 334.

Type species. *Lyreidus succedanus* Collins & Wienberg Rasmussen, 1992, by original designation. Type species, by original designation, of *Carinaranina* is *Eumorphocorystes naselensis* Rathbun, 1926a.

Species included. *Macroacaena alseana* (Rathbun, 1932), *M. bispinulata* (Collins & Wienberg Rasmussen, 1992), *M. chica* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003, *M. franconica* Schweigert, Feldmann & Wulf, 2004, *M. fudoujii* (Karasawa, 2000), *M. johnsoni* (Rathbun, 1935), *M. leucosiae* (Rathbun, 1932), *M. marionae* (Tucker, 1998), *M. naselensis* (Rathbun, 1926), *M. rosenkrantzi* (Collins & Wienberg Rasmussen, 1992), *M. schencki* (Rathbun, 1932), *M. succedana* (Collins & Wienberg Rasmussen, 1992), and *M. venturai* Vega, Nyborg, Fraaye & Espinosa, 2007.

Remarks. In Tucker's PhD thesis (1995), which was distributed in printed form, the new genus *Macracaena* (1995: 113) was attributed to the Lyreididae. This name, however, is preoccupied by *Macracaena* Common, 1958, a genus of moth in the family Gelechiidae Stainton, 1854. The generic name of the crab was formally introduced as *Macroacaena* by Tucker (1998). Schweitzer *et al*. (2003a: 29) synonymised *Carinaranina* and *Macroacaena* on the basis of similarities of the dorsal carapace (see also Schweitzer *et al*. 2010: 71). The type species of both genera retain ventral details and a re-examination is called for in order to verify the synonymy.

Tucker (1998: 325) noted that *Macroacaena* 'possibly' had the 'processes to lock the abdomen in the sternum' and attributed the genus to Lyreidinae. Material of the various species of *Macroacaena* needs to be re-evaluated to document the presence of hook-like projections.

Genus *Rogueus* Berglund & Feldmann, 1989

Rogueus Berglund & Feldmann, 1989: 70.

Type species. *Rogueus orri* Berglund & Feldmann, 1989, by monotypy.

Species included. *Rogueus orri*, and *Rogueus robustus* Collins & Jakobsen, 1996.

Remarks. The genus has so far been recorded from the Paleocene of Denmark and the lower middle Eocene of Vancouver Island, British Columbia, Canada. *Rogueus* sp. (*sensu* Ludvigsen & Beard 1998: 125; Trent River Formation, Upper Cretaceous, Vancouver Island, Canada), has subsequently been described as a new genus and species, *Bicornisranina bocki*, by Nyborg & Fam (2008: 689, figs. 3, 4t, 5, 6). *Bicornisranina* should be placed in the subfamily Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929 (see below), while *Rogueus* is retained in Lyreididae.

Rogueus orri Berglund & Feldmann, 1989

Rogueus orri Berglund & Feldmann, 1989: 70.

Remarks. *Rogueus orri*, described on the basis of 19 specimens from the middle Eocene of Oregon, U.S.A., comprising carapaces, chelipeds and the thoracic sternum (Berglund & Feldmann 1989: 71, figs. 2.1–2.6) and originally referred to the family Raninidae, should be placed in Lyreididae. Bouchard (2000: 126, fig. 32a) was the first to recognised hook-like projections on episternite 5 in the paratype (USNM 430034) of *Rogueus orri*. The thoracic sternum clearly shows the projections of episternite 5, which are fairly long and slightly outwardly curved. No distal locking teeth (double peg) are discernible which is either a taphonomic feature or can be ascribed to the fact that the specimen illustrated was an adult female. Sternite 5 is broad, with lateral prolongations between P1 and P2, the coxae of which are widely separated (Berglund & Feldmann 1989: 72, figs. 2.5, 2.6), these lateral extensions erroneously referred to as ‘episternum’ by these authors. Episternite 4 is diminutive, bounded by a distinct C-shaped suture; sternite 4 is tall, anteriorly widened and coupled to the recessed corner of the pterygostome. The mxp3 coxae are not preserved, but there is only little room for them because they were small. A crown is visible anterior to sternite 4. It is not clear if this represents only sternite 3, or fused anterior sternites. The orbitofrontal margin, which is wide as lyreidids go, is similar to that of *Marylyreidus* **n. gen.**, notably with a single orbital fissure. The bifid triangular front resembles that of *Bournelyreidus* **n. gen.**

Berglund & Feldmann (1989: 72) claimed that the closest relative of *Rogueus orri* may have been *Notopocorystes* (*Cretacoranina*) *fritschi* (Glaessner, 1929a) (here *Cretacoranina fritschi*, see above) as ‘based upon the strong similarity of the anterior margins and configuration of the sternal plastron’. The ventral characters of *C. fritschi* have never been described, nor illustrated, by Frič (1893: 105) or Glaessner (1929a: 155); we are not aware of any additional material described and illustrated since.

Subfamily Marylyreidinae n. subfam.

Type genus. *Marylyreidus* **n. gen.**

Diagnosis. Carapace elongated, widest anterior to mid-length, weakly arched in longitudinal cross section, convex in transverse cross section. Anterolateral margin short, with a single small spine. Posterolateral margin gently sinuous, with vertical anterior portion, divergent posterior portion; margins rounded in cross section. Posterior margin concave. Orbitofrontal margins straight, convergent, conspicuously wide (~80 % maximum carapace width), with 2 distinct orbital notches. Rostrum subtrapezoidal, bifid, with 2 small subdistal teeth. Branchiocardiac grooves short, cervical groove medially present, interrupted between gastric pits. Carapace surface covered with flattened hexagonal caps (constructed by fungiform nodes; Waugh *et al*. 2009). Pterygostome elongated, moderately vaulted, with low, blunt ridge, posterior corner without distinct recess. Exhalant channels well developed. Mxp3 elongated, oxystomian condition; coxae rather large, intercalated between thoracic sternum, pterygostome; exopod, endopod ischium, endopod merus of equal length. Branchiostegite reduced; pleurites 5–7 exposed. Sternite 3 crown shaped; sternite 4 slightly wider, squarish, not connected to pterygostome; episternite 4 large, widened; sternite 5 proportionally broad, extended between P1, P2, connected to exposed pleurites, episternite 5 with short, hook-like projections, distally with double peg; sternites 5, 6 with lateral ridge; sternite 6 narrow, no connection sternum/exposed pleurites between P2, P3; absence of medial line at sternites 1–6. Distal articles of pereiopods flattened. Abdomen narrow, somites 2, 6 long, somite 3 with blunt node.

Remarks. The Marylyreidinae **n. subfam.** is referred to Raninoidea based on the presence of exposed pleurites 5–7 (gymnopleurity). The distinctly widened sternite 5, which is connected to the exposed pleurites, and the anterolateral margin with but a single tooth, excludes it from Palaeocorystoidea. Placement in Lyreididae is based on the presence of an abdominal holding system, hence having the abdomen held against the body. The abdominal-holding system of Marylyreidinae **n. subfam.** consists of hook-like projection arising from episternite 5, distally with a double peg, here considered homologous to the long hook ending in two curved teeth of Lyreidinae. Presence of an abdominal-holding system is the most notable feature of Lyreididae; it is lost in all other Raninoidea. It consists of a double peg, similar to that seen in Palaeocorystoidea, but placed on a stout (Marylyreidinae **n. subfam.**) or elongated (Lyreidinae) hook-like projection, a feature unique amongst brachyurans. All other raninoids lack an abdominal holding system (assumed to have been lost), and keep their (shortened) abdomen behind the carapace.

Several characters distinguish Marylyreidinae **n. subfam.** from Lyreidinae. In Marylyreidinae **n. subfam.** sternite 4 is not expanded anteriorly; there is a sternum/pterygostome junction, the mxp3 coxae being intercalated between the thoracic sternum and the pterygostome. Sternite 6 is not widened; there is no junction with the exposed pleurites between P2 and P3, which is present in Lyreidinae. Sternites 5 and 6 have a lateral ridge, which is absent in Lyreidinae. The hook-like projection arising from episternite 5 are short, stout, but long, curved projection in Lyreidinae. The carapace of Marylyreidinae **n. subfam.** also shows characters that are unusual for Lyreididae. The orbital margin is conspicuously wide, its relative size being more similar to that of Palaeocorystidae than that of extant lyreidids. Of fossil representatives, only the Eocene lyreidine *Rogueus* shows an equally wide orbitofrontal margin. The cuticle microstructure of Marylyreidinae **n. subfam.** is remarkable, consisting of fungiform nodes (Haj & Feldmann 2002; Waugh *et al*. 2009), in contrast to the cuticular microstructure of Lyreidinae which comprises upright nodes and setal pits. Several palaeocorystid genera (e.g., *Cretacoranina*, *Ferroranina* **n. gen.** and *Eucorystes*) exhibit similar cuticle structures, as does one raninoid genus, *Symethis*.

Some characters of Marylyreidinae **n. subfam.** may be regarded as intermediate between those of Palaeocorystidae and Lyreididae. There is no connection joining the thoracic sternum to the pterygostome, a feature that is typical of Lyreidinae and all other Raninoidea, whereas the condition is 'normal' in Palaeocorystidae. In Marylyreidinae **n. subfam.** the mxp3 coxae are intercalated between the thoracic sternum and pterygostome, thus the presence of Milne-Edwards openings and a 'normal' repiratory system as in Palaeocorystidae. Sternite 4 is neither very narrow anteriorly (as in Palaeocorystidae), nor distinctly widened (as in Lyreididae). This is the more primitive condition found in Raninoidea, similar to that of Palaeocorystoidea. However, the presence of exposed pleurites (gymnopleure condition, synapomorphy of Raninoidea) in Marylyreidinae **n. subfam.** justifies its inclusion in Raninoidea. The character state shown by Marylyreidinae **n. subfam.** is part of a series of changes in the evolutionary modification of the respiratory system. Sternite 4 is not widened anteriorly, episternite 4 is remarkably large, together with the widened sternite 5. No medial line is present, at least on sternites 1–6. Projections of episternite 5 are present (absent in Palaeocorystidae); however, they are short, which contrasts to the long projections in Lyreidinae. We hypothesise that this condition is intermediate in an evolutionary line of shortening and posterior migration of the abdomen (see *Abdominal holding* below).

Genus *Marylyreidus* n. gen.

Type species. *Notopocorystes punctatus* Rathbun, 1935b.

Diagnosis. As for subfamily.

Derivation of name. In honour of the late Mary J. Rathbun, in recognition of her highly valuable work on fossil and extant crabs. Gender masculine.

Remarks. *Notopocorystes punctatus* (see Rathbun 1935b: 8, pl. 12, figs. 14–16; Haj & Feldmann 2002: 473, figs. 3, 4.1–4.6), which is a senior synonym of both *Notopocorystes parvus* (see Rathbun 1935b: 48, pl. 12, figs. 11–13) and *Raninella mucronata* (see Rathbun 1935b: 50, pl. 14, figs. 32, 33), from the upper Albian–lower Cenomanian of Texas, was originally referred to Raninidae. It has typically been attributed to *Cretacoranina* (e.g., Haj & Feldmann 2002; Waugh *et al*. 2009) or *Raninella* (e.g., Rathbun 1935b; Feldmann & Maxey 1980; Tucker 1995; Bishop & Williams 2000). Haj & Feldmann (2002: 478) mentioned that the species was distinguished from other members of *Cretacoranina* by the fainter carapace areolation and weaker lateral and frontal spines. Waugh *et al*. (2009: 33) noted that the thoracic sternum and frontal arrangement of the present species did not conform to that of *Cretacoranina*, but that the cuticle microstructure (fungiform nodes) was remarkably similar. *Marylyreidus* **n. gen.** is erected herein to accommodate *Notopocorystes punctatus*, and placed in Lyreididae, as the only member of Marylyreidinae **n. subfam.** The new genus can easily be distinguished from *Cretacoranina* by those characters that exclude it from Palaeocorystoidea (see above).

Characters distinguishing *Marylyreidus punctatus* **n. comb.** from members of *Raninella* are a carapace that is much less wide, anterolateral margin with one small spine (two strong, flattened spines in *Raninella*), posterolateral margin rounded (sharp, with distinct rim in *Raninella*), cuticle with fungiform nodes (inclined nodes in *Raninella*); pterygostome areolated (evenly swollen in *Raninella*), sternite 4 narrow, not connected to pterygostome (clearly widened anteriorly, junction sternum-pterygostome in *Raninella*), and sternite 5 devoid of medial line (medial line present in *Raninella*).

The presence of a single anterolateral spine, the rounded nature of the posterolateral margin and cuticle microstructure serve to distinguish the carapace of *Marylyreidus* **n. gen.** from *Bournelyreidus* **n. gen.** The condition of the pterygostome is remarkably similar in these genera. The unique condition in *Marylyreidus* **n. gen.** of sternite 4 (i.e., not widened anteriorly, no junction sternum-pterygostome) and sternite 5 (extremely wide between P1 and P2), however, is absent in *Bournelyreidus* **n. gen.**

Marylyreidus punctatus (Rathbun, 1935) n. comb.

Notopocorystes punctatus Rathbun, 1935b: 8.
Notopocorystes parvus Rathbun, 1935b: 48.
Raninella mucronata Rathbun, 1935b: 50.
(Fig. 25A–E)

Material examined. One incomplete carapace, MAB k. 2884 (male), with well-preserved pleurites, thoracic sternum and remains of appendages, one fragmentary carapace (MAB k. 2891), plus one carapace with well-preserved pleurites and thoracic sternum (MGSB75297, *ex* Àlex Ossó-Morales Collection). All from the upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County, Texas, U.S.A.

Emended description. Sternite 3 large, onion shaped, well separated from anterior sternites, narrower than sternite 4, from which it is separated by distinct indentations/notches at both sides, but not by groove on sternal plate. Sternite 4 of constant width, slightly longer than wide, its anterior part not extended laterally or connected to posterior corner of pterygostome. Gynglyme receiving P1 condyle distinctly visible in dorsal view; episternite 4 broadening posteriorly to twice sternite 4 width, forming 2 triangular plates. Sternite 5 distinctly wide, anterior part markedly extended between P1, P2, thus effectuating distinct separation of 2 anterior pereiopods; this lateral extension connected to anterior thoracic pleurite. Posterior part of sternite 5 much narrower, equalling sternite 4 width. Posterior margin of lateral projection of sternite 5 concave, corresponding to P2 coxa. Episternite 5 slightly raised, separated from anterolateral sternite 5 by deep gutter; P2 gynglyme visible in dorsal view. Sternite 5 medially forms weak cavity between raised episternites 5. Mxp3 long; coxa moderate in size, not well extended anterior to P1 coxa, intercalated between anterior portion of sternite 4, pterygostome, with sharp extension intercalated between sternites 3, 4; surface flabelliform, posterolaterally curved inwards to branchial chamber. Mxp3 basis with rounded proximal side; ischium long, widening distally with sinuous lateral side matching curvature of exopod; merus long, with weak medial depression. Mxp3 exopod long, slender, sinuous, tip slightly beyond ischium of endopod. Pterygostome tumid, with blunt crest and groove.

Remarks. Discovery of two specimens with preserved ventral characters necessitates an amendment of the description. The dorsal carapace was described by Rathbun (1935b: 48) and Haj & Feldmann (2002: 474).

Family Raninidae De Haan, 1839 emend.

Raninidae De Haan, 1839: 102.

Included subfamilies. Cyrtorhininae Guinot, 1993b (see below), Notopodinae Serène & Umali, 1972, Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929, Ranininae De Haan, 1839, and Symethinae Goeke, 1981 (see below).

Type genus. *Ranina* Linnaeus, 1758.

Diagnosis. Carapace elongated to oval, rounded, widened anteriorly; convex in transverse direction; may be roof shaped, with medial carina. Dorsal surface smooth, pitted, granular, inclined or fungiform nodes, eroded, scabrous or terraced; cervical groove generally indistinct, branchiocardiac grooves present. Anterolateral margin armed with 1–3 teeth, which may be broad, or long, bifurcate, spinose, or small, blunt. Posterolateral margin long, often rimmed. Front generally triangular or subtrapezoidal, pointed, may be trifid, or replaced by V-shaped emargination. Orbitofrontal margin narrow to conspicuously wide. Supraorbital margin with 1 or 2 closed or open fissures, lined with granules, spinules or armed with teeth; extraorbital tooth generally produced, may be broad, bilobate. Orbits directed anteriorly or anterolaterally, narrow to wide. Eyestalks short to long, composed of 1–3 calcified articles, bent at angle to one another when retracted into orbit.

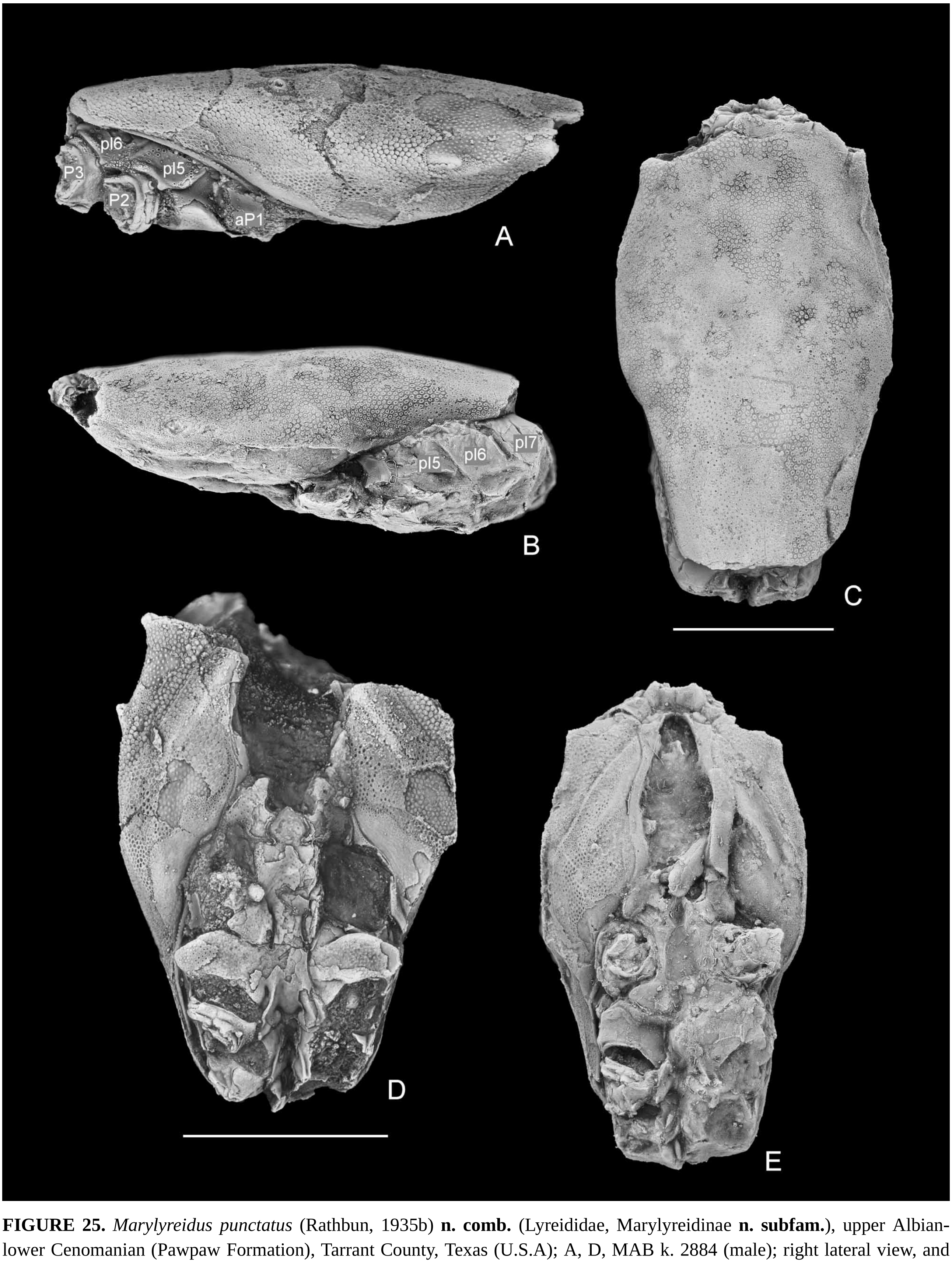


FIGURE 25. *Marylyreidus punctatus* (Rathbun, 1935b) **n. comb.** (Lyreididae, Marylyreidinae **n. subfam.**), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County, Texas (U.S.A); A, D, MAB k. 2884 (male); right lateral view, and ventral view showing thoracic sternum and bases of appendages; B, C, E, MGSB75297 (*ex* Àlex Ossó-Morales Collection; indeterminate sex); left lateral view showing exposed pleurites (thoracic sternum slightly displaced); dorsal view of carapace, and ventral view showing thoracic sternum and bases of appendages**. aP1,** arthrodial cavity of P1; **P2, P3,** pereiopods 2, 3; **pl5, pl6, pl7,** exposed pleurites 5, 6, 7. Scale bars: 5mm.

Antennules, antennae rather stout; antenna not folded, inserted somewhat below antennule; antennules, antennae modified in connection with respiratory currents. Proepistome concealed; epistome short; endostome large, produced; strongly excavated. Pterygostome large, tumid, subantennary lobe well defined. Buccal frame large, with broad collar. Mxp3 strongly elongated, operculiform, endopod often grooved.

Thoracic sternum wider anteriorly, conspicuously narrow posteriorly, strongly deflected at different levels. Sternite 3 crown shaped (compressed in Cyrtorhininae); sternite 4 usually wide, flat (narrow in Cyrtorhininae); suture 4/5 crescent shaped; sternite 5 expanded laterally; sternite 6 smaller, wide anteriorly, restricted between P3 coxae; sternites 6–8 conspicuously narrow. Medial line present along posterior sternites, running up to sternite 5 or 6. Sternum/pterygostome junction present, narrow to large. Junction sternum/exposed pleurites present between P1, P2 and between P2, P3, or only between P1, P2 (Notopodinae). Pleurites 5–7 partially exposed (gymnopleurity), calcified, forming polished surface, generally excavated, concave. Spermathecal apertures various: opening anteriorly, within sternite 7; generally close to each other, recessed in medial depression (more superficial, wider, hooded in Symethinae).

Absence of sterno-abdominal cavity. Abdomen short, incompletely folded, 6 freely articulated somites plus small telson; somites smooth; first somites dorsal, in prolongation with carapace, relatively wide in male, not much enlarged in female, thus sexual dimorphism relatively indistinct. Uropods or sockets absent; absence of abdominal-holding structures.

Chelipeds homochelous, homodontous; arthrodial cavities large, placed laterally. Basis-ischium short, immoveably fused with long merus; propodus short, inflated, flattened, armed with long, sharp spines on upper and lower margins, or elongated, narrow, unarmed; fingers usually with teeth of prehensile borders joining alternatively, unarmed (several long, sharp spines in Cyrtorhininae); fixed finger short to long, may be strongly deflected. Arthrodial cavities of P2–P4 almost ventral; those of P5 only, or both P4, P5 subdorsal. Carpus, propodus, dactylus flattened; dactylus variously modified: flattened, paddle shaped, lanceolated, or falciform. P5 weakly to strongly reduced, dorsal or subdorsal in position, usually fitting posterolateral border of carapace.

Respiratory mechanism highly specialised. Absence of Milne-Edwards openings; strongly modified frontal region, antennules, antennae modified for inhalant current; posterior branchial orifices generally present, or absent (Notopodinae).

Remarks. Included in Raninidae are those raninoidean crabs that are markedly modified by their burying behaviour, thus with peculiar respiratory properties and having lost abdominal holding, in contrast to Lyreididae. The Cyrtorhininae and Symethinae are here tentatively placed in Raninidae awaiting the revision of the Raninoidea by M. Tavares.

Subfamily Ranininae De Haan, 1839

Ranininae De Haan, 1839: 102.
Raninellidae Beurlen, 1930: 363.
Ranininae—Serène & Umali 1972: 34.

Type genus. *Ranina* Lamarck, 1801.

Genera included. *Lophoranina* Fabiani, 1910, *Lophoraninella* Glaessner, 1945, *Ranina* Lamarck, 1801, *Raninella* A. Milne Edwards, 1862, *Remyranina* Schweitzer & Feldmann, 2010a and *Vegaranina* **n. gen.**

Diagnosis. Carapace large, wide, broadened anteriorly with wide teeth. Dorsal surface granular, with flattened inclined nodes, scabrous or terraced; branchiocardiac grooves present. Rostrum triangular, pointed, subtrapezoidal or trifid. Anterolateral margin armed immediately behind extraorbital tooth with wide teeth, single or consisting of 3 or 4 protruding processes, may be sexually dimorphic. Posterolateral margins rimmed. Orbitofrontal margin wide. Supraorbital margin with 2 deep fissures, may be armed with teeth. Orbits directed anteriorly, relatively wide. Eyestalk composed of 3 articulated, calcified articles, bent at angles to one another when retracted into orbit. Both antennules, antennae modified for respiratory currents. Antennule not folded: basal article expanded distally into flabelliform lobe, concave internally; within larger passage formed by antennae, formation of antennulary cleft or passage serving as conduit for exhalant stream of water. Proepistome well developed, ovate. Antenna inserted somewhat below antennule, inclined inwards, short, thick, with reduced flagellum; article 1 with triangular apex directed anteriorly, urinal opening placed to its dorsal side; articles 2, 3 fused but with suture still visible, lying directly in front of subantennary lobe of pterygostome; article 3 well developed, forming lobe projecting anteriorly as far as article 4, forming ventral, internal walls of orbital cavity; article 4 flabelliform, with concave internal surface; article 5 small; flagellum rudimentary. Inhalant chamber bounded laterally by concave surface of eyestalk, ventrally by mxp3 merus, dorsally by mxp1 exopod.

Subantennary lobe of pterygostome short but well defined. Mxp3 operculiform, elongated, merus shorter than ischium. Pleurites 5–7 largely exposed, forming excavated, concave plate. Sternum/pterygostome junction developed, connections between sternum, exposed pleurites normal or large between P1, P2, much narrower between P2, P3. Thoracic sternum strongly deflected at different levels. Sternite 3 crown shaped; sternite 4 distinctly wide, flat; suture 4/5 deep, short, crescent shaped; sternite 5 generally with foliaceous expansions; sternite 6 linear, especially between P3 coxae, of considerable depth; sternite 7 similarly narrow, strongly bent, deep vertically; sternite 8 deep vertically, perpendicular to sternite 7. Medial line along sternites 6–8. Anterior part of sternite 7 showing elongated, deep, medial depression; its bottom with longitudinal apertures of the spermathecae.

Chelipeds strong, homochelous, homodontous; arthrodial cavities large, placed laterally. Basis-ischium short, immoveably fused with long merus. Propodus large, flattened; upper, lower margins armed with long, sharp spines; dactylus spinose on dorsal margin, nearly at right angles against anterior border of palm; fixed finger short; prehensile borders of both fingers with teeth closely joining alternatively.

P2–P5 robust, broad. P2, P3 arthrodial cavities almost ventral; those of P4 subdorsal, P5 dorsal. Upper margin of carpus, propodus markedly carinate. Carpus flattened, propodus, dactylus extensively flattened. Dactylus leaf shaped, falciform, more enlarged on P3, P5. P5 not reduced, nearly similar in size, shape to preceding pereiopods, but dorsal in position, fitting lateral border of carapace.

Sterno-abdominal cavity absent. Abdomen short, freely articulated, 6 articles plus small telson, incompletely folded, first articles dorsal, wide in male, not much enlarged in female, thus sexual dimorphism relatively indistinct with regard to size; uropods or sockets absent.

Large posterior branchial orifices present.

Genus *Raninella* A. Milne Edwards, 1862 (= *Hemioon* Bell, 1863)

Raninella A. Milne Edwards, 1862: 492.
Hemioon Bell, 1863: 10 [as *Hemioön*].

Type species. *Raninella trigeri* A. Milne Edwards, 1862, by original designation. Type species of *Hemioon*, by monotypy, is *H. cunningtonii* Bell, 1863 (= *Raninella elongata* A. Milne Edwards, 1862).

Species included. *Raninella*? *bidentatum* (Rathbun, 1935b), *R. circumviator* (Wright & Collins, 1972), *R. elongata* A. Milne Edwards, 1862 (= *Palaeocorystes callianassarum* Fritsch *in* Fritsch & Kafka, 1887), *R. eocenica* Rathbun, 1935b, *R. libyca* Van Straelen, 1935, *R. novozelandicum* (Glaessner, 1980), *R. quadrispinosum* (Collins, Fraaye & Jagt, 1995), *R. trigeri* A. Milne Edwards, 1862, *R. yanini* (Ilyin & Alekseev, 1998) and *Raninella*? **n. sp.** (*sensu* Lehmann 2004).

Emended diagnosis. Carapace oval, elongated, widest anterior to mid-length, weakly arched in longitudinal cross section, tumid in transversal cross section. Posterolateral margin weakly arched, sharply rimmed; anterolateral margin shorter, with 2 slightly raised, strong, triangular teeth. Orbitofrontal margin concave, slightly narrower (about 45 % in *R. trigeri*) or slightly wider (about 55 % in *R. elongata*) than maximum carapace width (including lateral teeth), with distinct triangular outer orbital corner, 2 long orbital notches. Rostrum triangular, excavated, with 2 small subdistal teeth. Branchiocardiac grooves weak, cervical groove obsolete. Post-frontal region depressed, coarsely granular. Carapace surface with minute granules; in lateral, posterior regions granules directed anteriorly (inclined nodes), flattened. Suborbital margin with long notch. Pterygostome tumid, granular; posterior corner with distinct semi-circular recess for mxp3 coxa; wide, smooth buccal collar lining buccal cavity; exhalant channels deep, well developed. Mxp3 elongated, in oxystomian condition. Branchiostegite reduced; pleurites exposed, surface smooth (polished). Sternite 3 crown shaped; sternite 4 anteriorly wide, joining pterygostome;

episternite 4 small. Sternite 5 extended laterally between P1, P2, reaching exposed pleurites. Sternite 5 with medial line. Sternites 6–8 distinctly narrow. No abdominal holding mechanism. Chelipeds homochelous, merus with subdistal granulate crest, chelae flattened, fingers weakly downturned, closing, prehensile margin with sharp teeth; lower margin of chelipeds smooth or with small spines. P2 with flattened merus; other pereiopods not studied. Abdomen unknown.

Remarks. Wright & Collins (1972: 87) and Breton & Collins (2007: 18) considered that the description by A. Milne Edwards (1862) of *Raninella trigeri*, type species of the genus, was meagre, yet valid; we concur. Based upon direct comparison of nearly all key specimens, *Hemioon* is here considered to be synonymous with *Raninella*, on account of close similarities in carapace, pereiopods, thoracic sternum and mxp3 in *R. trigeri* and *R. elongata*, the latter being the type species of *Hemioon*, by synonymy with *H. cunningtoni* (see below under *R. elongata*).

Beurlen (1930: 363) erected the family Raninellidae for a wide array of fossil genera, viz. *Eumorphocorystes*, *Hemioeon* [*sic*], *Notopocorystes*, *Pseudoraninella*, *Raninella*, *Raninellopsis* and *Raninoides*. His brief diagnosis was based solely on the developed anterior sternites, a plesiomorphy which cannot be succesfully used within this group, and which is even incorrect for *Notopocorystes*. The genera he listed are now part of several (sub)families and there is no reason to retain Raninellidae.

Raninella has been used as a waste-basket genus, accommodating numerous, highly diverse species. Some species traditionally referred to *Raninella* are here transferred to either *Bournelyreidus* **n. gen.** or *Marylyreidus* **n. gen.** (see above). The higher-level taxonomy of *Raninella* has also varied, the genus being referred to Raninidae (Crawford *et al*. 2006) or Lyreidinae (see e.g., Tucker 1998; Nyborg & Fam 2008; Waugh *et al*. 2009). Waugh *et al*. (2009: 27) examined a specimen (NHM In. 63689), which is here confirmed to belong to *R. trigeri*. Based on a study of its cuticle, these authors suggested that '*Raninella* … may not fit within the Lyreidinae', and noted that 'The front and sternum [of *R. trigeri*] resemble *Ranina americana*'. Wright & Collins (1972: 87) had earlier remarked that the flattened anterior teeth of *Raninella* resembled those of *Ranina*.

Raninella shows typical traits of Raninoidea, such as the possession of exposed pleurites, junction of sternite 4 with the pterygostome, anteriorly widened sternite 5 with junction to exposed pleurites, posterior sternites conspicuously narrow and lack of an abdominal holding system. *Raninella* is here included in Ranininae on the basis of its rimmed posterolateral margin, strong anterolateral teeth, anteriorly directed granules on the carapace surface and broad sternite 4.

The carapace of *Raninella* differs from that of *Bournelyreidus* **n. gen.** in being wider, in possessing much stronger anterolateral teeth and a continuously arched posterolateral margin. Sternal differences include the presence of a medial line on sternite 5 and the absence of an abdominal holding system. A remarkable character displayed by this genus is the granular subdistal crest of the cheliped merus, which is reminiscent of that in Palaeocorystidae.

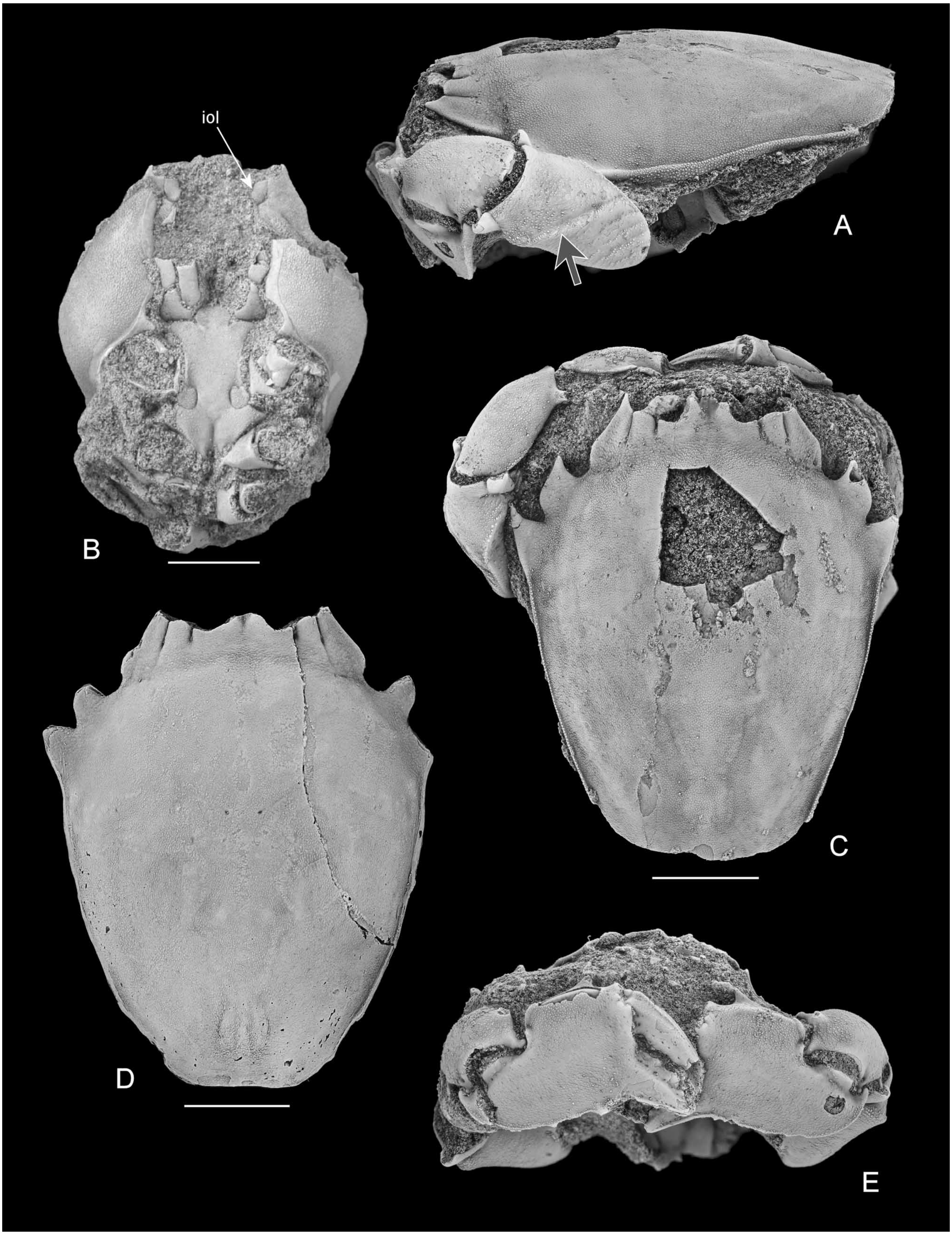


FIGURE 26. *Raninella trigeri* A. Milne Edwards, 1862 (Raninidae, Ranininae), upper Cenomanian, Butte de Gazonfier, Le Mans (northwestern France); A, C, E. NHM LM 2003-1-3787A (indeterminate sex); left lateral view of carapace and cheliped (arrow indicating crest on merus of left cheliped); dorsal view of carapace and chelipeds, and frontal view showing chelipeds; B. NHM In. 63689 (male); ventral view showing thoracic sternum and base of appendages; D. MNHN B16565 (**lectotype**; indeterminate sex); dorsal view of carapace. **iol,** infraorbital lobe. Scale bars: 10mm.

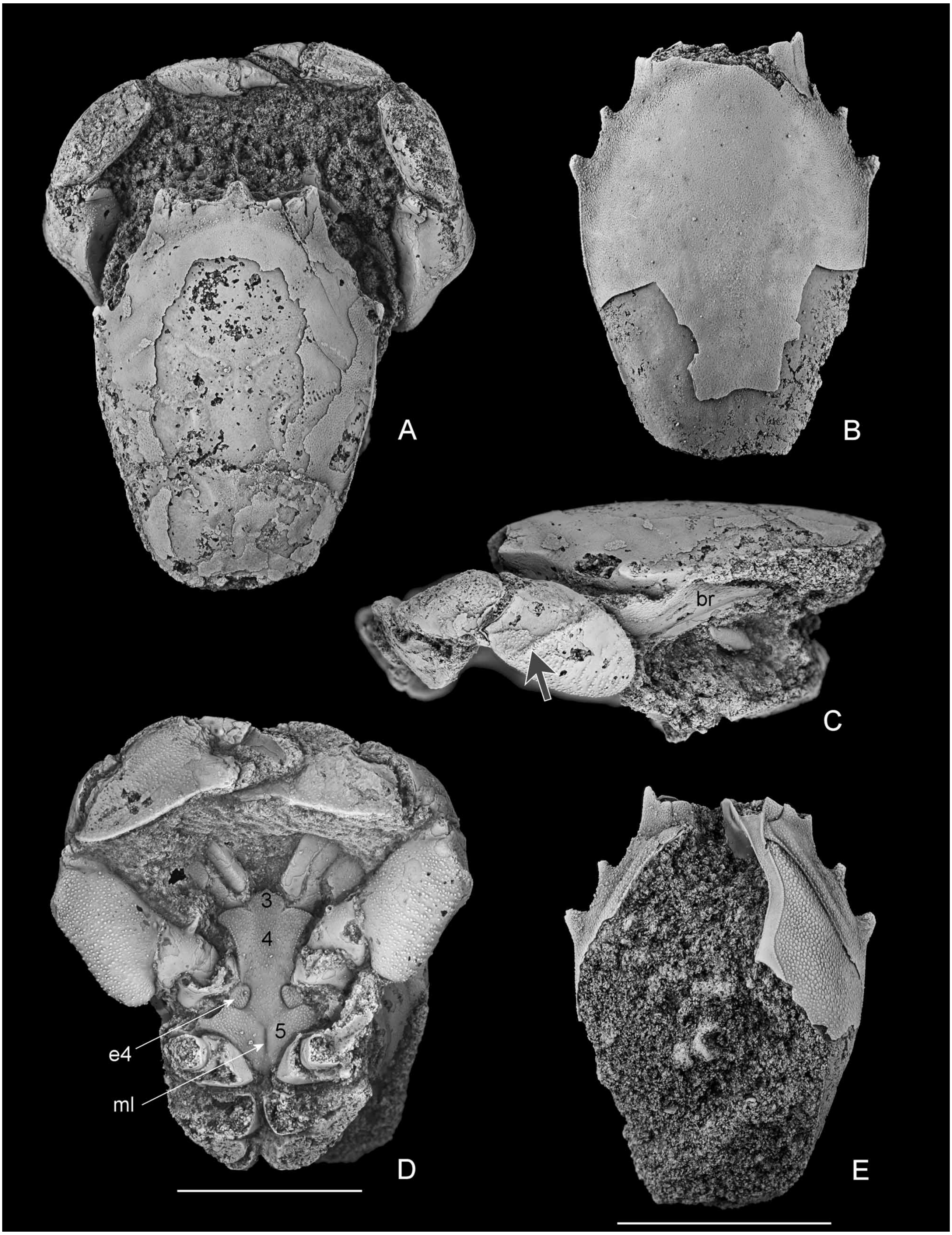


FIGURE 27. *Raninella elongata* A. Milne Edwards, 1862 (Raninidae, Ranininae), upper Cenomanian, Butte de Gazonfier, Le Mans (northwestern France); A, C, D, MNH LM3788 (indeterminate sex); dorsal view of carapace and chelipeds; left lateral view of carapace and cheliped (arrow indicating crest on merus of left cheliped), and ventral view showing thoracic sternum and chelipeds; B, E. MNHN R03934 (**paralectotype**); dorsal view of carapace, and ventral view showing pterygostome. **3, 4, 5,** thoracic sternites 3, 4, 5; **br,** branchiostegite; **e4,** episternite 4; **ml,** median line. Scale bars: 10mm.

Raninella elongata A. Milne Edwards, 1862
(Fig. 27A–E)

Raninella elongata A. Milne Edwards, 1862: 493.
Palaeocorystes callianassarum Fritsch *in* Fritsch & Kafka, 1887: 46.
Hemioon cunningtonii Bell, 1863: 10.
Raninella atava Carter, 1898: 24.

Material examined. From the upper Cenomanian of Le Mans, Butte de Gazonfier: carapace with both chelipeds preserved (LM3788); carapace and sternum, illustrated by Brocchi (1877: figs. 4, 5), designated lectotype by Breton & Collins (2007: 18) (MNHN A25922); syntypes, two carapaces (MNHN R03927); paralectotype, one of two carapaces (see also under *Raninella trigeri*) with exposed pleurites 5–7 preserved (MNHN R03934, as *Raninella trigeri*); one carapace (MNHN A29413); from the 'Upper Greensand', Isle of Wight, southern England (NHM In. 31302, indicated as 'new species' by Woodward 1874; see Wright & Collins 1972: 89).

Remarks. *Raninella elongata* (see A. Milne Edwards 1862: 493; Fritsch *in* Fritsch and Kafka, 1887: 46, text-fig. 69, pl. 10, fig. 9, as *Palaeocorystes callianassarum*; Bell, 1863: 10, pl. 2, figs. 4–7, as *Hemioon cunningtonii*; Carter, 1898: 24, pl. 1, fig. 7, as *Raninella atava*), from the upper Albian to Coniacian of southern England, Bohemia (Czech Republic), northern France and Germany, was considered a juvenile form of *Raninella trigeri* by Van Straelen (1936: 41). Later authors (e.g., Wright & Collins 1972; Tucker 1995; Breton & Collins 2007) did not subscribe to this view and considered these two species distinct. Glaessner (1969: R627) was of the opinion that *H. cunningtonii* represented juvenile specimens of *Raninella elongata* and synonymised the two genera. Most subsequent authors (e.g., Wright & Collins 1972; Collins & Wienberg Rasmussen 1992; Tucker 1995, 1998; De Grave *et al*. 2009; Schweitzer *et al.* 2010) treated the two genera as distinct, but these authors also included species that are now placed in *Bournelyreidus* **n. gen.** Breton & Collins (2007: 18) referred to *Raninella elongata*, thus relegating *Hemioon* as a junior synonym of *Raninella*. We concur.

Direct comparison of the types and additional material of both *R. elongata* and *R. trigeri* has revealed ample differences. Both species do exhibit similar carapaces: elongated but rather wide (width [between bases of widest anterolateral spine] 67 % of maximum carapace length in *R. elongata*, 75 % in *R. trigeri*), widest at approximately one-third of total carapace length from the front; posterolateral margin long, continuously arched and sharply rimmed; two anterolateral teeth: flattened, wider in *R. trigeri*, whereas in *R. elongata* the posterior tooth is strong, somewhat flattened, not as wide as in *R. trigeri*; the anterior lateral tooth being subtler; orbitofrontal margins of both species are nearly identical, only the lateral margin below the outer orbital corner is convex and widened in *R. trigeri*. The sterna of *R. elongata* and *R. trigeri* are remarkably similar in all details, the only difference being that sternite 4 is slightly wider in the latter. The position of the pereiopods, nature of pterygostome, areolation of subhepatic region and construction of the suborbital border are identical. Chelipeds are conspicuously similar, inclusive of the characteristic crest on the outer distal surface of the merus; yet, the chelae of *R. trigeri* appear to be taller than those of *R. elongata*. There are many analogues in the cuticle microstructures of the two species.

The differences between *R. elongata* and *R. trigeri* match sexual and ontogenetic differences observed in *Ranina ranina* as well. In the latter, the orbitofrontal margin and anterolateral spines are much more weakly developed in juveniles than in adults, resulting in a wider appearance of the carapace (Barnard 1950: 397, 398, fig. 75a, b). The orbital margin is nearly equally well developed in adult females as in males, but the two trifid anterolateral teeth are clearly less prominent (Sakai 1937: 179, text-fig. 45). No juvenile or specimens of intermediate size of either *R.elongata* or *R. trigeri* have so far been documented (Breton & Collins 2007: 18). *Raninella elongata* was recorded from various localities throughout Europe, whereas *R. trigeri* is known exclusively from its type locality. So long as no additional material, preferably retaining sternum or abdomen to allow determination of sex, is forthcoming, it is prefered to keep these species apart.

A similar case is known from Alabama (Paleocene, Sucarnoochee Beds, Prairie Creek, Wilcox County), from where *R. bidentata* (see Rathbun 1935b: 84, pl. 18, figs. 9–12, as *Symnista*) and *R. eocenica* (see Rathbun 1935b: 82, pl. 18, figs. 13–16) have been recorded. In the absence of additional material which preserves thoracic sternum or abdomen, these species are here considered as distinct.

Raninella trigeri A. Milne Edwards, 1862

Raninella trigeri A. Milne Edwards, 1862: 492.
(Fig. 26A–E)

Material examined. From the upper Cenomanian of Le Mans, Butte de Gazonfier, two specimens, carapace and chelipeds (MHN LM 2003-1-3787A and B; Guéranger Collection); designated lectotype by Breton & Collins (2007: 18), complete specimen preserving chelipeds, portions of thoracic sternum and pereiopods (MNHN B16565; Triger Collection); paralectotype (see Brocchi 1877: pl. 29, fig. 3), one of the two carapaces (see also under *Raninella elongata*) (MNHN R03934); carapace with thoracic sternum and chelipeds, labels reading '*Raninella trigeri*' and '*Hemioon elongatum*'(see Waugh *et al*. 2009: 27, figs. 5.3, 5.4) (NHM In. 63689 (Taylor & Hammond Collection).

Remarks. *Raninella trigeri* (see A. Milne Edwards 1862: 493; Brocchi 1877: 2), from the Cenomanian of the Le Mans region (northern France), is known from a handful of well-preserved specimens. The lectotype (MNHN B16565) is well-preserved, retains both chelipeds as well as portions of the thoracic sternum and walking legs and shows exposed pleurites.

Genus *Vegaranina* n. gen.

Type species. *Lophoranina precocious* Feldmann, Vega, Tucker, García-Barrera & Avendaño, 1996, by present designation.

Diagnosis. Carapace large, convex transversely, widest one-quarter from front; rostrum tridentate; orbital margins wide, with 2 notches; anterolateral margin short, with 3 strong spines (excluding extraorbital tooth); long, non-terraced post-frontal region; few (6–8) strong terraces, broadly V-shaped, complete from side to side, posterior to branchiocardiac grooves; lobed terraces anterior of branchiocardiac grooves; terraces finely spinulate; branchiocardiac grooves extended, strongly divergent anteriorly. Pterygostome with few short terraces. Mxp3 expod, endopod elongated, smooth. Sternite 3 crown shaped; sternite 4 wide anteriorly, with junction sternum-pterygostome, episternite 4 small; sternite 5 with large lateral expansions, leading to junction sternum-exposed pleurites; sternites 5, 6 with medial line; sternite 6 narrow. Pleurites 5–7 partially exposed (gymnopleurity), excavated.

Species included. *Vegaranina precocia* and *Vegaranina* sp.

Derivation of name. In honour of Francisco J. Vega, in recognition of his valuable work on fossil decapods from Mexico. Gender feminine.

Remarks. *Vegaranina precocia* **n. comb.** is known from the lower Maastrichtian of southeastern Mexico (Feldmann *et al.* 1996: 297, figs. 3.1–3.3, 4.1, 4.2) and from the Campanian–Maastrichtian of Cuba (Varela & Rojas-Consuegra 2009: 119, fig. 1A), whereas *V.* cf. *precocia* was recorded from the lower upper Maastrichtian of Puerto Rico (Schweitzer *et al*. 2008, p. 5, fig. 3). An unnamed species of the new genus has recently been found in the MNHN collections (Fig. 28A–C) but with an undoubtedly erroneous label so that locality and provenance remain unknown). The presence of the genus in Europe is documented by a specimen of another unnamed species from the Maastrichtian of southern France that was examined but is currently in private hands and not available for study.

Vegaranina **n. gen.** differs from *Lophoranina* in having three anterolateral spines (two in *Lophoranina*); a longer, non-ridged, post-frontal region; fewer terraces posterior to the branchiocardiac grooves (only 6–8 terraces), which are stronger, more V-shaped and complete from side to side; lobed terraces anterior of the branchiocardiac grooves, and branchiocardiac grooves that are extended and strongly divergent anteriorly, instead of being similarly arched anteriorly and posteriorly in *Lophoranina*.

Lophoraninella was included in Galatheoidea by Schweitzer *et al.* (2003b: 890) based upon an examination of the holotype (MB.A.229a, b; equivalent to k123a, b) of *Ranina cretacea* Dames, 1886. This taxonomic placement was adopted by De Grave *et al.* (2009: 24), Schweitzer *et al.* (2010: 50) and Ahyong *et al.* (2010: 59). Glaessner (1945) erected *Lophoraninella* for a specimen in the NHM collections (NHM I. 4553, Fig. 30D) after examination of Dames's holotype. The NHM specimen was re-examined, the holotype and paratypes photographed (Fig. 30A–D), and there is no doubt that this material is conspecific and represents a raninid crab, rather than a galatheoid anomuran. The preservation of the type material may cause confusion because the specimens are preserved in dorsal aspect, compacted, and parts of the carapace have collapsed, exposing remains of the ventral side. Both specimens show parts of the pterygostome and the outline of the buccal frame fairly clearly; the paratype shows the posterior part of the thoracic sternum (Fig. 30C). The NHM specimen represents a crushed carapace with frontal aspect preserved (Fig. 30D). *Lophoraninella* differs from *Vegaranina* **n. gen.** in having more terraces on the posterior carapace; terraces are finer and straighter; less divergent branchiocardiac grooves; two, rather than three, anterolateral spines (excluding the extraorbital tooth), which are much weaker; a rectangular or subtrapezoidal front, instead of a tridentate front; and a scabraous rather than smooth post-frontal region.

It appears that *Vegaranina* **n. gen.** (Campanian–Maastrichtian) links the older *Lophoraninella* (Cenomanian of Lebanon) to the widely distributed Cenozoic (Eocene–Oligocene) *Lophoranina*.

Subfamily Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929

Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929: 299.

Genera included. *Bicornisranina* Nyborg & Fam, 2008, *Cristafrons* Feldmann, Tshudy & Thomson, 1993, *Notopoides* Henderson, 1888, *Notosceles* Bourne, 1922b, *Pseudorogueus* Fraaye, 1995, *Quasilaeviranina* Tucker, 1998, and *Raninoides* H. Milne Edwards, 1837.

Diagnosis. Carapace longer than wide, oblong-ovate, urn shaped or lateral margins nearly parallel or tapering posteriorly. Dorsal surface punctate-granular or smooth, polished; post-frontal transverse demarcation may be present, diversely ornamented; grooves indistinct, cervical groove may be present (*Cristafrons*). Anterolateral margin unarmed, or with single spine, may be highly produced, bifurcate or spinose. Rostrum pointed, triangular or trilobate/tridentate, may be carinate. Orbitofrontal margin equal to or greater than half carapace width. Supraorbital margin spinose with medial tooth between 2 fissures, which may be deep, long.

Ocular peduncle folded longitudinally, long, exposed, composed of 2 articles, basophthalmite small, podophthalmite basally inflated, narrowing at tip. Antennules, antennae modified in relation with respiratory currents. Antennule: basal article expanded, may have distal flabelliform lobe, concave internally. Poepistome rather developed, may be medially carinate. Antenna: inserted somewhat below antennule, inclined inwards, short, thick; article 1 with triangular apex directed forwards, urinal opening placed to its dorsal side; articles 2, 3 fused but with suture still distinct; article 3 much better developed, with greatly developed lobe (‘crest’) projecting forwards as far as article 4, forming ventral, internal walls of orbital cavity; article 4 flabelliform, with concave internal surface; article 5 small; flagellum fairly well developed.

Epistome triangular, not prominently produced forwards. Subantennary lobe of pterygostome developed, widened anteriorly. Mxp3 elongated, operculiform; merus rather short, little more than half ischium length. Pleurites 5–7 largely exposed, forming excavated area, overhung by the edge of the branchiostegite, being a water-passage for inhalant respiratory current (*Notopoides*, *Notosceles*), or area not excavated, not overhung by branchiostegite (*Raninoides*).

Sternum/pterygostome junction developed; sternum/exposed pleurites connection wide between P1, P2, wider, may be distinctly developed between P2, P3. Thoracic sternum with sternites 3–6 forming long, flat shield, strongly deflected at different levels; sternite 3 variously crown shaped; sternite 4 much enlarged, flat, anterior part variously expanded laterally; sutures 4/5 variously oblique, prolonged laterally; sternite 5 with foliaceous or acute expansions; sternite 6 as 2 unequal parts: anterior in the form of widely exposed, long plate, posterior short, linear; sternite 7 slighty wider, markedly bent; sternite 8 perpendicular to sternite 7, saddle shaped. Medial line along sternites 5–8. Small spermathecal apertures located in tilted posterior part of sternal plate, lying at the bottom of deep, pit-like depression.

Chelipeds homochelous, homodontous; sometimes slender; basis-ischium immoveably fused with long merus. Propodus flattened, upper margin with double carina or only spine on dorsal border; lower margin with few or several sharp spines; both fingers long, sharp; dactylus bent against anterior border of palm, may largely exceed fixed finger length in dimorphic males, unarmed, prehensile border smooth; fixed finger broad with prehensile border armed with several developed teeth.

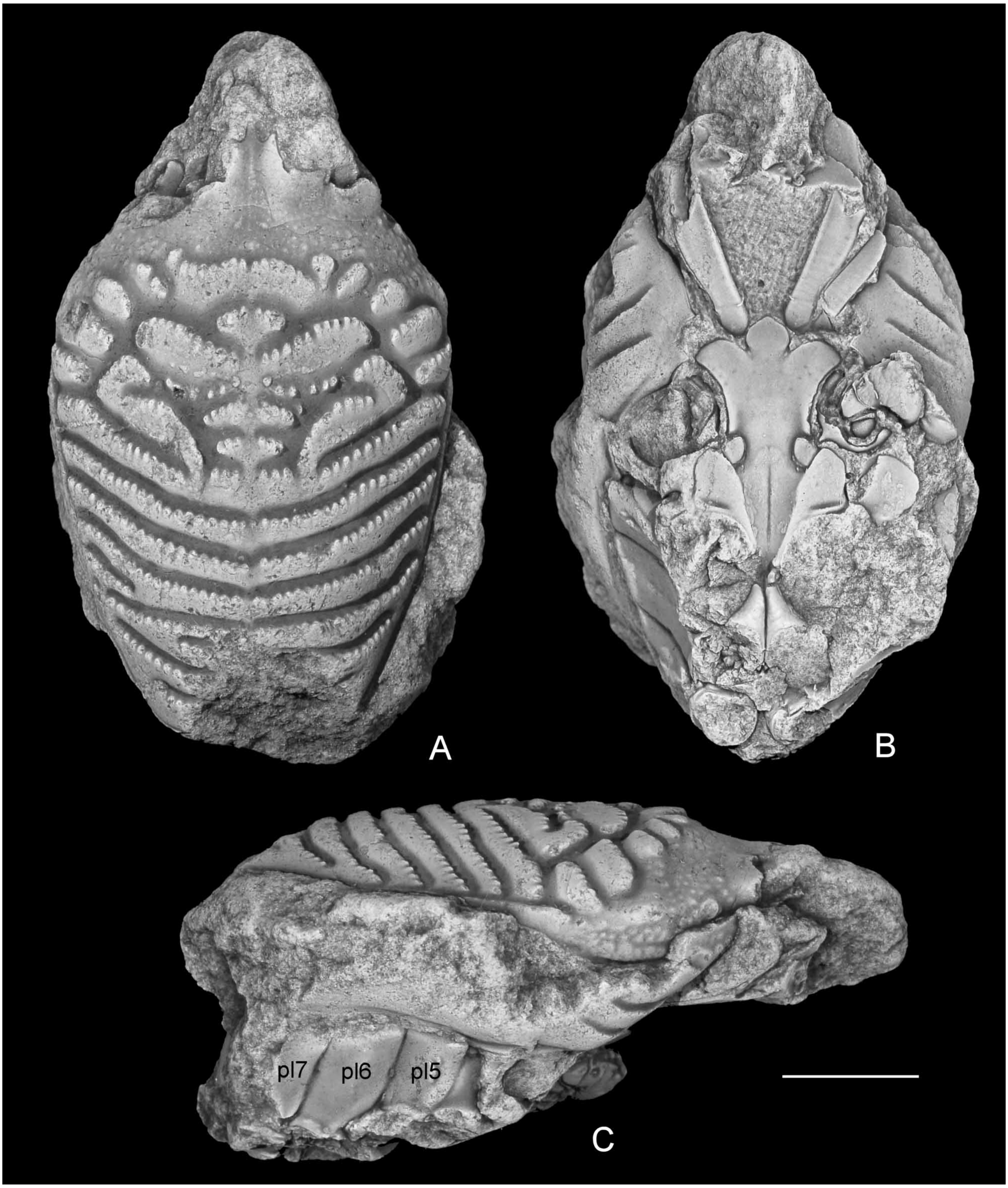


FIGURE 28. *Vegaranina* **n. gen.** (Raninidae, Ranininae), MNHN R03385 (indeterminate sex); stratigraphic age and provenance unknown; A, dorsal view of carapace; B, ventral view showing thoracic sternum; C, right lateral view showing exposed pleurites. **pl5, pl6, pl7,** exposed pleurites 5, 6, 7. Scale bars: 10mm.

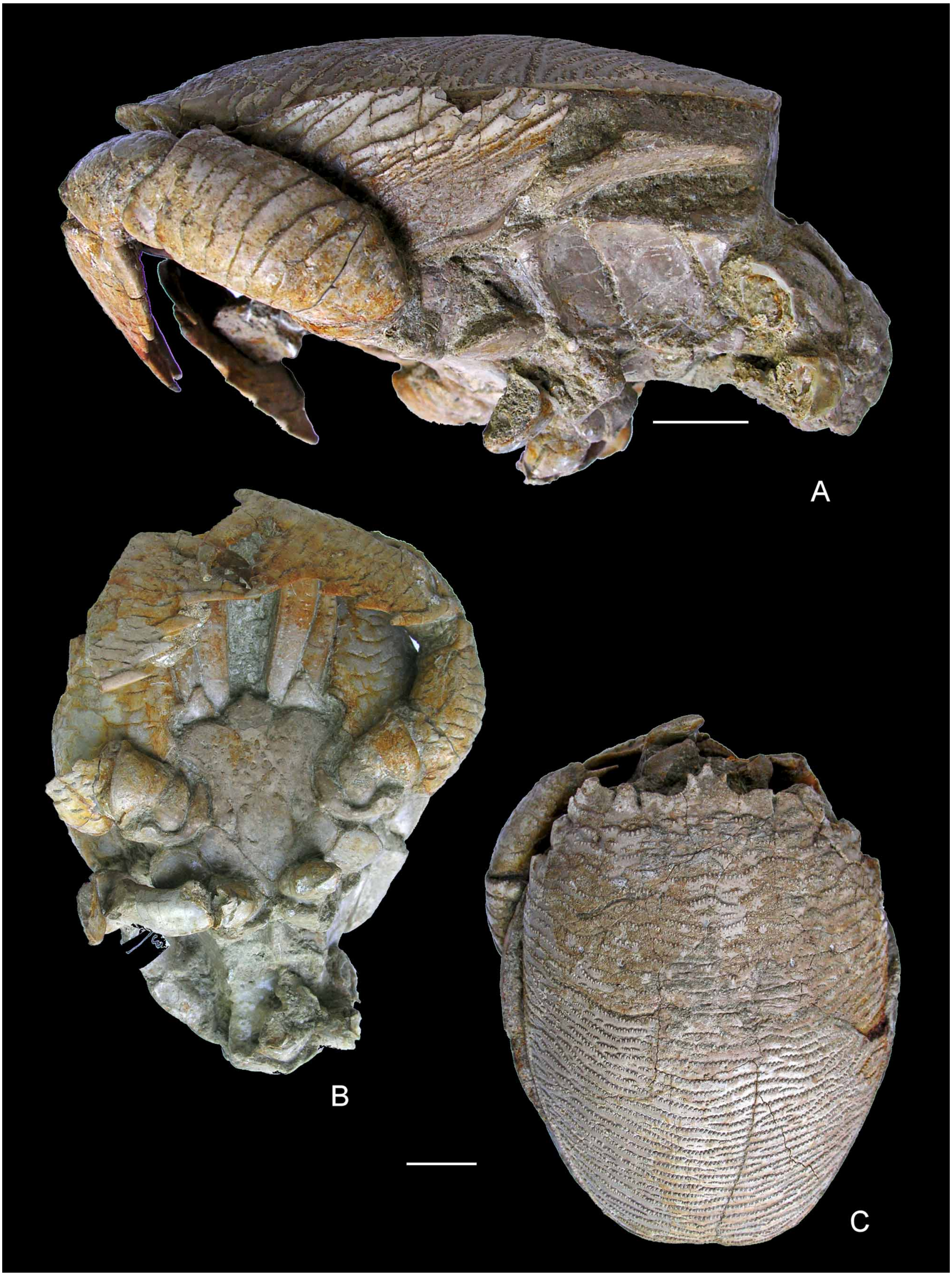


FIGURE 29. *Lophoranina maxima* Beschin, Busulini, De Angeli & Tessier, 2004 (Raninidae, Ranininae), SV 321 (indeterminate sex), middle Eocene, Arzignano (Vicenza, northern Italy); A, left lateral view showing exposed pleurites; B, ventral view showing thoracic sternum and appendages; C, dorsal view of carapace. (photographs by A. De Angeli) Scale bars: 20mm.

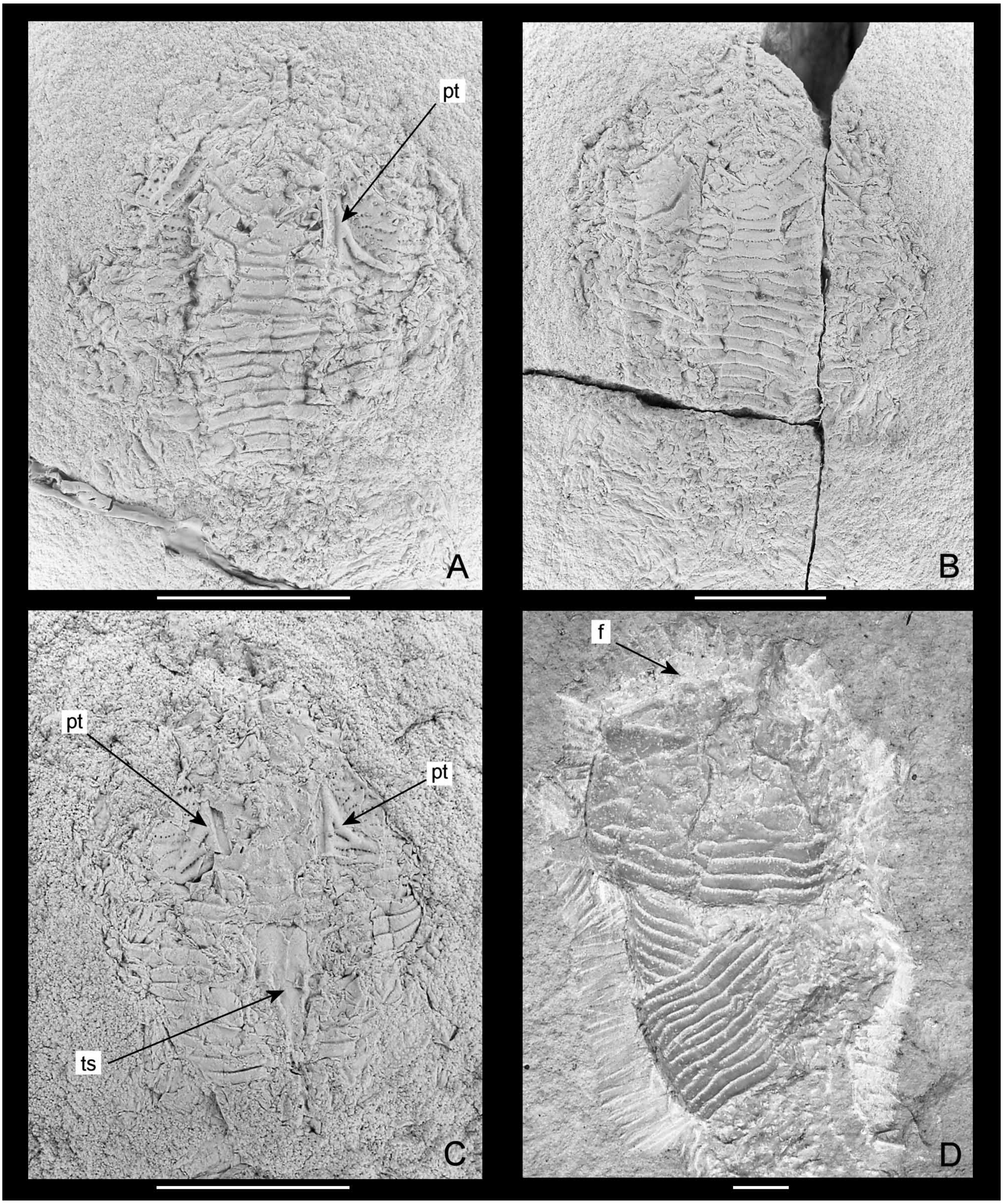


FIGURE 30. *Lophoraninella cretacea* (Dames, 1886) (Raninidae, Ranininae), Cenomanian, Hakel (Lebanon); A, B, MB.A229a, b (= k123a, b, **holotype**; indeterminate sex), dorsal view in normal aspect and counterpart; C, MB.A230a (= k124a, **paratype**; indeterminate sex) in dorsal view; D, NHM I. 4553 (indeterminate sex), crushed carapace in dorsal view (photographs A–C by C. Neumann, Museum für Naturkunde, Berlin). **f,** front; **pt,** pterygostome; **ts,** thoracic sternum. Scale bars: 5mm.

P2–P4 moderately stout. Merus long; carpus may be carinated; both propodus, dactylus flattened, compressed; propodus short, enlarged, dactylus variously modified, acute or variously sickle shaped. P4 coxa subdorsally located. P5 more dorsal, strongly or slightly reduced, thus distinct from preceding ones, always applied alongside carapace posterolateral borders; carpus, propodus about same size, small, widened; propodus rounded; dactylus rather small, flattened oval, weakly sickle shaped.

Absence of sterno-abdominal depression. Abdomen short, extremity only reaching level of P4 or P3, freely articulated, 6 articles plus telson, only distally flexed, first 4 articles dorsal; proximal articles wide, as broad as or narrower than posterior margin of carapace. Abdomen not much enlarged in female. Sexual dimorphism relatively indistinct with regard to shape, size. No abdominal locking mechanism.

Presence of posterior branchial orifices, variously developed, may be large, functioning as as inhalant passages (*Raninoides*, *Notopoides*, *Notosceles*).

Remarks. Lőrenthey *in* Lőrenthey & Beurlen (1929: 299) created Raninoidinae to accommodate *Raninoides*, *Notopella*, *Pseudoraninella*, *Ranidina*, *Raninellopsis*, *Tribolocephalus* and *Lyreidus*, as opposed to both Palaeocorystinae and Ranininae. Guinot (1993b: 1327) revived Raninoidinae. Tucker (1998: 334) erred in noting 'Raninoidinae De Haan, 1841: 136–137'. Guinot (1993b) assigned the following extant genera to the subfamily Raninoidinae: *Raninoides*, *Notosceles* and *Notopoides*; Tucker (1998, fig. 22) added the fossil taxa *Carinaranina* [= the lyreidid *Macroacaena*; see above], *Quasilaeviranina*, *Laeviranina*, and *Cristafrons*. De Grave *et al*. (2009: 29) and Schweitzer *et al*. (2010: 75) also included *Cenocorystes*, originally referred to the Palaeocorystinae by Collins & Breton (2009: 45), which is incorrect (see above, under *Cenocorystes*).

The carapace outline is long, oblong-ovate, urn shaped as in *Notopoides latus* (see Dawson & Yaldwyn 2002), or has near-parallel lateral margins, tapering posteriorly as in the 'boat-shaped' *Raninoides benedicti*. The axial skeleton shows the typical and unique arrangement of raninoids (Guinot & Quenette 2005: fig. 26B). The medial line is long, extending on to sternites 5–8 (Guinot 1993b: fig. 5; Guinot & Quenette 2005: 314, fig. 26A). For the diverse shapes of the crown-shaped anterior sternites and sternites 4–6, see Chopra (1933: fig. 1).

Genus *Cristafrons* Feldmann, Tshudy & Thomson, 1993

Cristafrons Feldmann, Tshudy & Thomson, 1993: 31.

Type species. *Cristafrons praescientis* Feldmann, Tshudy & Thomson, 1993, by monotypy.

Remarks. *Cristafrons* shows an unusual set of characters. Feldmann *et al*. (1993: 31) remarked that the general form was similar to species of *Notopocorystes*. *Cristafrons* can be readily distinguished from Palaeocorystidae by the prescence of only a single lateral spine and a narrow, non-bifurcate rostrum. The well-defined cervical groove and the hepatic and postfrontal areolations, however, are unusual for Raninoidea, whereas those features are commonly found in Palaeocorystoidea. The thoracic sternum of *Cristafrons* is 'not cleft longitudinally', i.e., the medial line is absent (sternites 1–5 are described), members of Raninoidinae typically having a medial line up to sternite 5 (Fig. 44C, D). It is unlikely that *Cristafrons* belongs to Ranininae, which has wider carapaces and two wide lateral teeth. Exposed pleurites are not described in the type series: they may be concealed by matrix or were overlooked in the original description, which states that the type specimens 'are deposited in the Natural History Museum, London' (Feldmann *et al*. 1993: 33), where only two specimens could be traced by us. The majority of the type series appears to have been forwarded to the British Antarctic Survey (BAS), under '*Cretiscalpellum praescientis*' (see also http://www.antarctica.ac.uk/bas_research/data/access/fossildatabase/filter.php?taxonKeyword=CRUSTACEA). A re-examination of the type series is called for in order to resolve the precise taxonomic placement of *Cristafrons*.

Genus *Pseudorogueus* Fraaye, 1995

Pseudorogueus Fraaye, 1995: 66.

Type species. *Pseudorogueus rangiferus* Fraaye, 1995, by original designation.

Material examined. Holotype, and only specimen so far known, a partly decorticated carapace (MAB k. 1040). Locality and stratigraphy were not included in the original description; the specimen was recovered from a roadcutting along the road Ager-Tremp on Serra del Pi, 1 km northwest of the village of La Baronia, northern Spain, from the top of the Ei2 Member of the 'Gresos deltaics', of early Eocene age (Rosell & Llompart 1988).

Remarks. *Pseudorogueus rangiferus* (see Fraaye 1995: 66, figs. 1, 2) should be included in the subfamily Raninoidinae. The frontal characters do not match those of *Rogueus* Berglund & Feldmann, 1989, or any other member of Lyreididae for that matter. According to Tucker (1998: 359) 'the specimen described by Fraaye (1995) is more closely related to the Raninoidinae clade, not the Lyreidinae which includes *Rogueus*'. *Pseudorogueus* was synonymised with *Raninoides* by Tucker (1998: 359), but considered valid by Nyborg & Fam (2008: 689), the latter decision we agree with. The wide carapace and strong anterolateral spine with multiple anteriorly directed spinules warrant generic separation of *Pseudorogueus* and *Raninoides*.

Subfamily Notopodinae Serène & Umali, 1972

Notopodinae Serène & Umali, 1972: 29.

Included tribes. Notopodini Serène & Umali, 1972 and Cosmonotini Števčić, 2005.

Genera included. *Cosmonotus* Adams &White *in* White, 1848, *Eumorphocorystes* van Binkhorst, 1857, *Lianira* Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991, *Lovarina* Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991, *Notopella* Lőrenthey *in* Lőrenthey & Beurlen, 1929, *Notopus* De Haan, 1841, *Ponotus* Karasawa & Ohara, 2009, *Ranilia* H. Milne Edwards, 1837, *Raniliformis* Jagt, Collins & Fraaye, 1993, *Ranidina* Bittner, 1893, and *Umalia* Guinot, 1993.

Diagnosis. Carapace subovate, urn shaped, widened or narrowing anteriorly, regularly convex or strongly constricted, chevron shaped or with medial keel. Dorsal surface smooth or ornamented with granules, squamiform tubercles, striae, pits, transverse rows of granules, raised granular rods, or transverse spinulate ridge between anterolateral spines; no visible carapace grooves. Anterolateral margin with single spine. Orbitofrontal margin wide; rostrum prominent, narrow, ventrally keeled, generally downturned, or absent, replaced by a V-shaped emargination. Orbits generally long or relatively short, from near-horizontal to positioned downwards, directed obliquely backwards, always deeply excavated. Supraorbital margin long or produced, flabelliform (*Lianira*), with 1, 2 fissures, with medial tooth or several spines. Eyestalk relatively short, flattened, or long to conspicuously long (longer than the half carapace length), slender; composed of 3 articles, 2 short proximal ones, distal article long, can be entirely retracted into orbit; cornea may be reduced. Antennary fossae situated behind antennulary fossae. Antennules, antennae highly specialised. Antennule not folded, hidden by antenna; basal article much developed, following articles flattened. Proepistome shield shaped, strongly keeled medially, posteriorly narrow. Antenna stout: article 1 admedial in position, short antero-posteriorly but wide ventrally, largely concealed by subantennary lobe of pterygostome, with urinal opening at inner angle; articles 2, 3 fused, but with suture still distinct, lying directly in front of subantennary lobe of the pterygostome; article 2 lying on same level as article 1, external to it, also small, partially concealed by subantennary lobe of pterygostome; article 3 large, subquadrangular, slightly concave internally, its admedial margin being prominent, curved, its external angle not projected or with a projection which embraces proximal part of article 4; articles 4, 5 fairly long, with fringes of plumose setae which interlock with setae of the antenna of the other side; flagellum long, with rows of setae which similarly interlock with setae of the other antenna. Thus, this forms a fully functional water-tube (Bourne 1922b: 61). Epistome broad triangular or V-shaped. Subantennary lobe of the pterygostome well developed. Mxp3 operculiform, moderately or distinctly elongated, tapering; ischium with transverse or oblique ridge; merus shorter or longer than ischium. Exposed pleurites 5, 6 large, 7 small, forming flat area, not overhung by edge of branchiostegite, which is not prominent. Sternum/pterygostome junction developed; sternum/exposed pleurites connections large between P1, P2, absent between P2, P3.

Thoracic sternum strongly deflected at level of sternites 7, 8; sternite 3 variously crown shaped; sternite 4 rather wide, with long anterolateral extensions; suture 4/5 crescent shaped, elongated, or indistinct; sternites 4, 5 ridged; sternites 5–7 narrow; sternite 8 saddle shaped, with long posterolateral extensions. Medial line along sternites 5–7 or 6, 7. Anterior part of sternite 7 with elongated, deep, medial depression with 2 small apertures of the spermathecae.

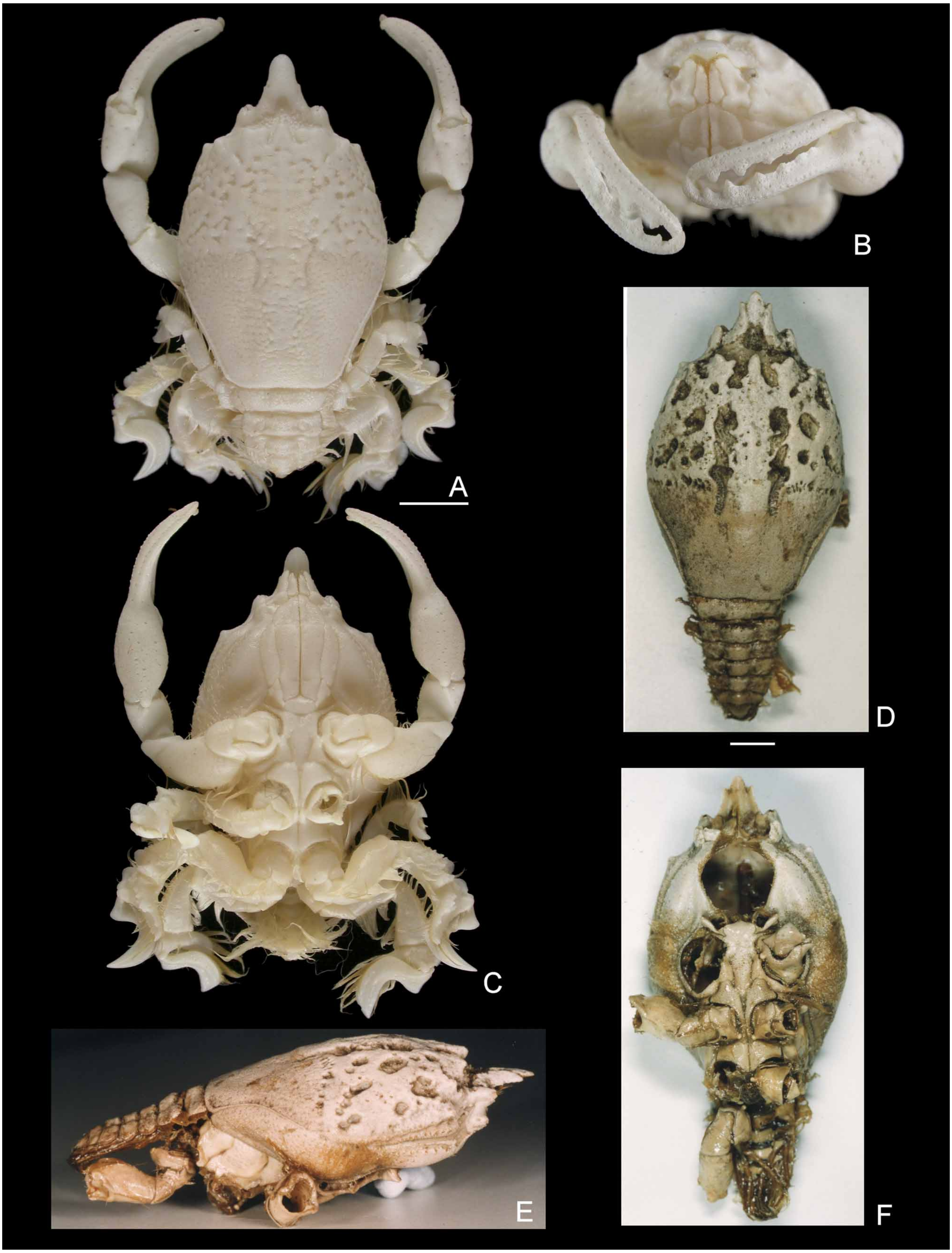


FIGURE 31. A–C. *Symethis corallica* Davie, 1989 (Raninidae, Symethinae), MNHN-B20795 (**holotype**; female), Coral Sea, Chesterfield Islands; dorsal view of carapace; frontal view showing chelipeds, and ventral view; D–F. *Symethis variolosa* (Fabricius, 1793), ZMC Cru 75 (**holotype**; female, after rehydration), Indian Ocean; dorsal view of carapace, right lateral and ventral views. Scale bars: 10mm. (photographs A-C by J.-F. Dejouannet; D-F by P.K.L. Ng).

Chelipeds homochelous, homodontous. Basis-ischium short, immoveably fused with long merus, fitting closely with the patch of dense setae on lateral pterygostomial sides. Propodus short, high, flattened; its upper, lower margins unarmed; dactylus nearly bent at right angles against anterior border of palm, prehensile border with low, blunt teeth; fixed finger diminutive. P2–P5 rather similar in size, shape, strongly compressed laterally; P4 dactylus distally tapering, acute, or blunt, truncate or foliaceous, or elongated, quadrangular. Coxa of P4 subdorsally located. P5 more dorsal, barely reduced, with remarkably large coxa; propodus short, broad, dactylus lanceolated. Sterno-abdominal cavity absent. Abdomen small, freely articulated, 6 articles plus telson, incompletely folded, first articles dorsal, wide in male, sexual dimorphism indistinct: abdomen barely enlarged in female.

Posterior branchial orifices absent; respiration only frontal.

Remarks. Posterior branchial orifices are not found in any member of the subfamily Notopodinae. Both antennules and antennae are highly specialised and serve to generate an inhalant water current. Bourne (1922b: 62) suspected that *Notopus dorsipes* made use of the posterior branchial orifices only when it was buried in the loose upper stratum of the sand, but the antennary water tube was brought into action when it had dug down into the more compact, deeper layers of sand with restricted source of water. But because of the absence of posterior branchial orifices, it is probable that *Notopus* and *Ranilia*, as well as *Cosmonotus*, always use the flagellae of the antennae as a water tube, with a possible reversion of the current.

The vaulted or roof-shaped carapace affects the positioning of the branchial chamber and the gills, which have become vertically oriented.

Subfamily Symethinae Goeke, 1981

Symethinae Goeke, 1981: 972.

Type genus. *Symethis* Weber, 1795 (= *Zanclifer* Henderson, 1888).

Genera included. *Eosymethis* **n. gen.**, *Symethis* Weber, 1795 (Fig. 31A–F) and *Symethoides* **n. gen.**

Diagnosis. Carapace tumid, elongated, suboval, narrowing anteriorly, extending as elongated rostrum. Dorsal surface may appear eroded; cuticle microstructure with fungiform nodes, upright nodes, or pits. Branchiocardiac groove distinct. Anterolateral margin uneven, with 1, 2 small, blunt teeth. Orbitofrontal margin narrow; with postfrontal depressed region, frontal axial ridge may be present. Rostrum considerably produced beyond general outline of carapace into blunt, trilobate process. Orbits small, formed by lateral projection of carapace, ventral suborbital projection, closed internally by the border of the antenna; supraorbital margin with 2 closed fissures. Eyestalk short, folded obliquely or longitudinally forwards; basal article concealed under the rostrum, following article exposed, calcified as carapace; cornea small, hardly visible when stalk retracted into orbit. Antennary fossae situated behind antennulary fossae. Antennule small, deeply located, completely hidden by antenna; basal article developed, following articles small, flattened. Proepistome hidden. Antennae massive, meeting medially; article 1 admedial, fused to carapace, urinal opening at its inner angle; articles 2, 3 fused, expanded, with extremely prominent external prolongation; other articles, flagellum small or lost. Epistome triangular, strongly raised, keeled medially. Subantennary lobe of pterygostome not delimited. One pterygostomial groove, becoming obsolete posteriorly. Mxp3 covering other buccal elements, long, moderately broad; merus much shorter than ischium. Exopod short, wide. Exposed pleurites 5–7 convex but not forming an excavated plate; branchiostegite developed, excavated, overhanging area of exposed pleurites, limited by P5 strictly apposed along branchiostegal margins. Sternum/pterygostome junction conspicuously narrow. Sternum/exposed pleurite connections between P1 and P2, P2 and P3 highly developed.

Thoracic sternum narrow, strongly deflected at level of sternite 7; sternite 3 short, relatively wide, crown shaped; sternite 4 rather narrow, with elongated, slender anterolateral extensions; suture 4/5 long, distinct, deep, with vertical portion, then prolonged laterally; sternite 5 inflated posteriorly; sternites 6, 7 narrow; sternite 8 perpendicular to sternite 7; medial line along sternites 5–8. Spermathecal apertures not situated in medial pit, nor recessed: apertures large, widely separated, horizontally located, overhung by 2 calcified hoods.

Chelipeds homochelous, homodontous. Basis-ischium conspicuously short, immoveably fused with massive merus. Propodus swollen, even bulbous, upper, lower margins smooth; fingers conspicuously long, crossing at recurved acute tips; dactylus only slightly deflected, fixed finger more deflected, prehensile border with low, blunt, interlocking teeth. P2–P4 stout, with spatulate, carinate processes. P5 dorsal, reduced but rather thick, situated along posterolateral carapace margin, strictly adapted to branchiostegal edge. P2–P5 dactyli sickle shaped.

Abdomen rather short, wide in male, freely articulated, 6 somites plus telson, incompletely folded, first 5 articles dorsal, first somite of about same width as posterior carapace margin. Abdomen only slightly enlarged in female, thus sexual dimorphism indistinct; uropods or sockets absent.

Large posterior branchial orifices present. Only 7 pairs of gills, anteriormost 2 pairs greatly reduced.

Remarks. The exposed pleurites 5–7 (7 smaller) do not form an excavated plate, but the branchiostegite overhangs the area, limited by the P5 strictly apposed along branchiostegal margins, thus a clear passage for the water current. The symethine spermathecal apertures are not situated in a medial trough and are not recessed as in other raninoids, their apertures being large, widely separated, horizontally located and overhung by two calcified, arched hoods; the decalcified portion is located below the hood (Goeke 1981: 976, fig. 2B; Davie 1989: fig. 1c).

Genus *Eosymethis* n. gen.

Type species. *Eosymethis aragonensis* **n. sp.**

Diagnosis. Small-sized carapace, elongatedly suboval, weakly convex in both directions. Orbitofrontal margin extremely narrow, well projected, orbits small, front strongly advanced. Anterolateral margins with a notable angular node at level of hepatic region. Dorsal regions weakly defined; post-frontal depression present; arched branchiocardiac grooves, oblique branchial scars. Dorsal surface densely covered by large pits. Pereiopods with short, flattened articles, dactyli falciform.

Derivation of name. Indicating an ancestral form of *Symethis*.

Eosymethis aragonensis n. sp.

(Fig. 32A–C)

Diagnosis. As for genus.

Derivation of name. From the region of Aragón, northern Spain.

Material examined. Holotype, and only specimen so far known, a near-complete carapace with remains of the pereiopods, preserved as a natural mould, from the marls of the ‘upper Ilerdian’ (lowermost Ypresian, Eocene) Roda Formation (Cuevas-Gozalo *et al*. 1985), approximately 7 km northwest of the village of Isabena (Huesca, Aragón) (MGSB75293; *ex* José Enrique Ortega Collection).

Description. Carapace small, subovally elongated in outline, longer than wide; maximum width at confluence of lateral margins, posterior of mid-length. Dorsal surface slightly concave in both directions. Orbitofrontal margin narrow, markedly advanced; orbits small, directed anteriorly; front strongly projected with triangular tip. Anterolateral margins long, with notable angular hepatic node after concave first portion; posterior portion nearly straight, diverging posteriorly. Posterolateral margins shorter, from straight to slightly concave, rimmed, convergent to the rear. Posterior margin fairly concave, much broader than orbitofrontal margin. Dorsal regions poorly defined; post-frontal depression present; gastric regions weakly defined; branchial regions with notable oblique branchial scars, lateratelly disposed; cardiac region large, elongated, bounded by marked branchiocardiac grooves, with angular node at lateral upper portion; anterior portion separated from gastric regions by subtle groove. Dorsal surface covered by large, dense pits, uniformly distributed over entire carapace; some granules in posterior portion of posterolateral margins. Pereiopods partially preserved, showing short, flattened articles with falciform dactylus.

Remarks. The species exhibits features that permit placement in Symethinae: the carapace has a narrow, projected anterior portion of the carapace and a post-frontal depression; the dorsal surface shows an isolated, lateral, acute groove; the anterolateral margin has only a diminutive node; and falciform dactyli of the pereiopods. Symethinae so far consists of a single genus, *Symethis*, with only three extant species (Ng *et al.* 2008: 43). *Eosymethis* **n. gen.** can be distinguished from *Symethis* on the basis of a smoother, less ‘eroded’ anterior carapace and in having the cuticle microstructure consisting of large perforations or setal pits rather than fungiform nodes (Waugh *et al.* 2009). *Eosymethis aragonensis* **n. sp.** originates from what appears to have been a fairly muddy-bottom habitat.

Genus *Symethoides* n. gen.

Type species. *Symethoides monmouthorum* **n. sp.**

Diagnosis. Small fusiform carapace; narrow orbitofrontal region, pronounced axial ridge on anterior third of carapace; diminutive, forwardly directed anterolateral spine; cuticle granular.

Derviation of name. As for *Symethis*.

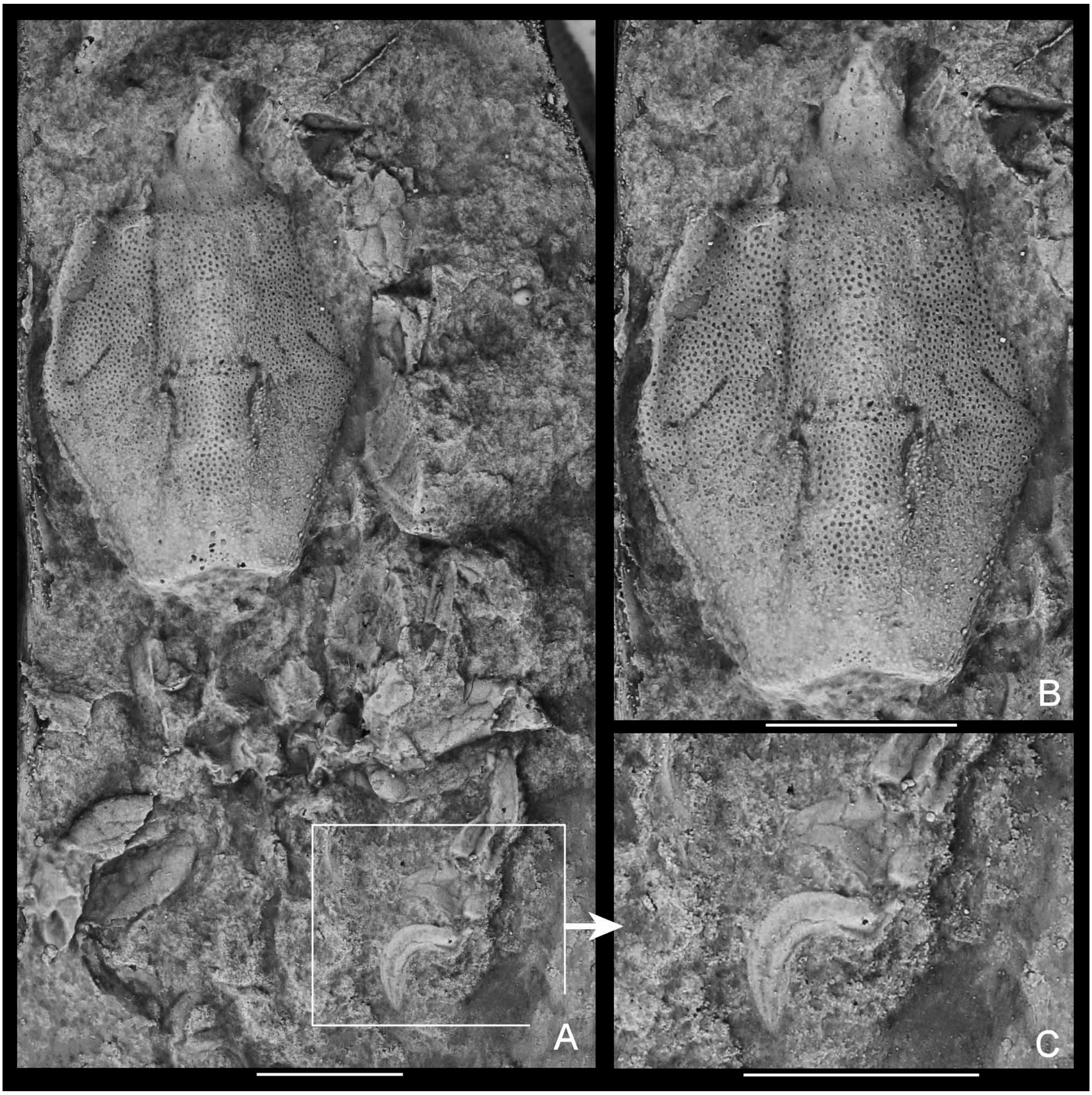


FIGURE 32. A–C. *Eosymethis aragonensis* **n. gen., n. sp.** (Raninidae, Symethinae), lower Eocene (Ypresian), Isabena (Huesca, northern Spain), MGSB75293 (**holotype**; *ex* José Enrique Ortega Collection; indeterminate sex); overview of specimen, detail showing carapace, and detail showing falciform dactylus of right P2/P3. Scale bars: 5mm.

Symethoides monmouthorum n. sp.

Notopocorystes cf. *N. tridens* — Landman *et al*. 2007, p. 29, fig. 15N, O.
(Fig. 33A–D)

Diagnosis. As for genus.

Derivation of name. In honour of the Monmouth Amateur Paleontologist's Society (New Jersey, U.S.A.), of which Ralph Johnson is a member, for bringing this specimen to our attention.

Material examined. One partly decorticated carapace from the top of the lower Danian Tinton Formation, Manasquan River Basin, Monmouth County, New Jersey, U.S.A. (AMNH 50421).

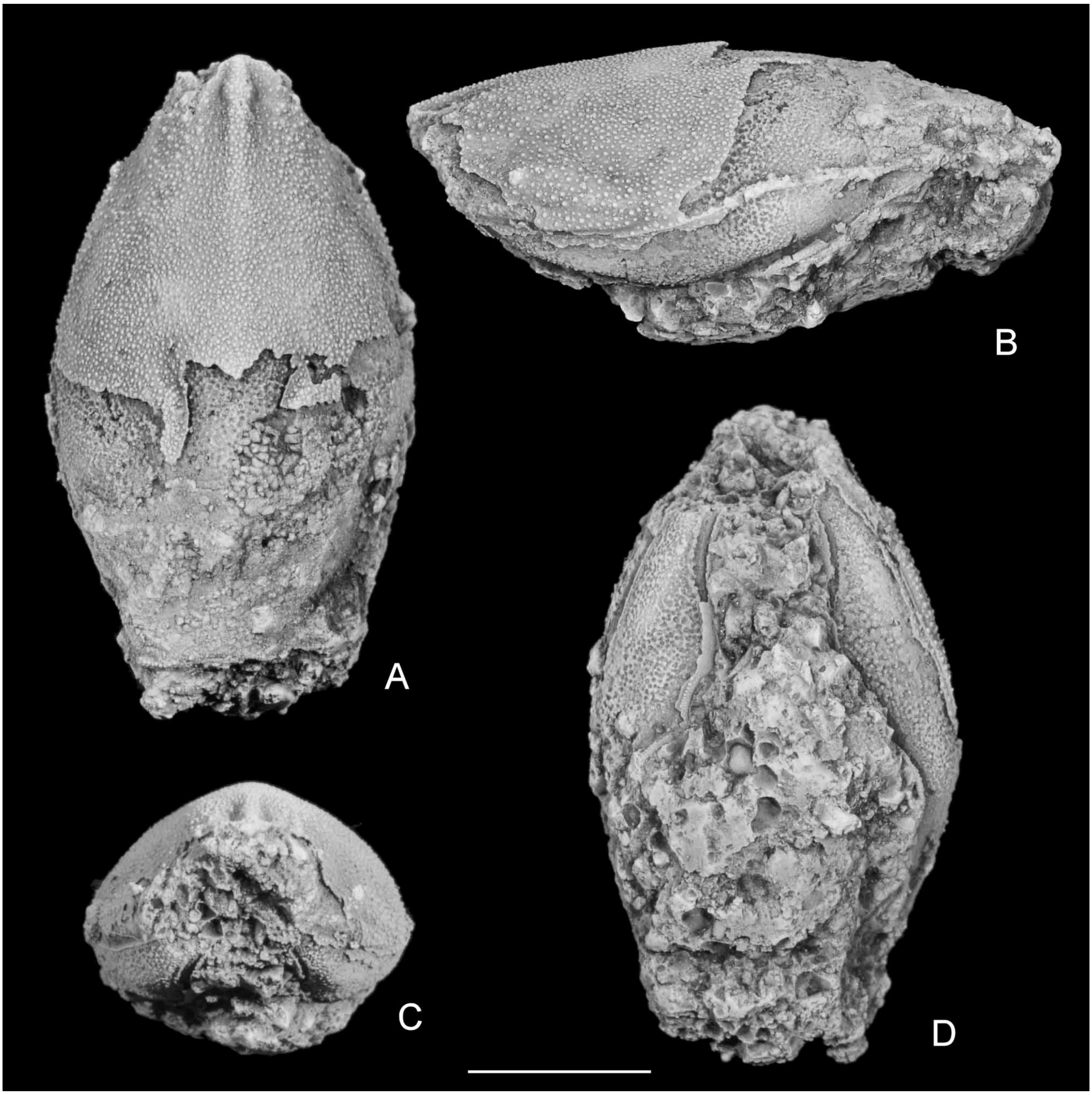


FIGURE 33. A–D. *Symethoides monmouthorum* **n. gen., n. sp.** (Raninidae, Symethinae), lower Paleocene (Danian), Monmouth County, New Jersey (U.S.A), AMNH 50421 (**holotype**); dorsal view of carapace, left lateral view, frontal view, and ventral view showing pterygostomes. Scale bar: 5mm.

Description. Carapace small, fusiform, about twice as long as broad, widest at mid-length, strongly convex in transverse cross section, slightly convex in longitudinal cross section, uniformly covered with granules, coarsest towards orbitofrontal, anterolateral regions. Orbitofrontal margin narrow. Broad base of rostrum with prominent ridge extending posteriorly about one-third of total carapace length, bounded by 2 deep grooves effacing posteriorly. Convex anterolateral margin with diminutive, anteriorly directed spine at approximately one-fifth of total carapace length from front. Subhepatic region with blunt crest.

Posterior margin slightly wider than orbitofrontal margin. Branchiocardiac grooves curved, situated slightly posterior of mid-length. Pterygostome elongated, convex, covered by evenly spaced, fine granules; buccal margins concave, with smooth rim; posterior corner of pterygostome recessed for mxp3 coxa. Branchiostegite low posteriorly, with pronounced border.

Remarks. Despite the superficial resemblance to Lyreidinae, *Symethoides* **n. gen.** differs markedly from *Lyreidus*, *Lysirude* and *Macroacaena* in having an anterior axial ridge bounded by two grooves and a completely granular carapace, and in lacking long anterolateral spines (few exceptions in *Lyreidus*). It differs also from *Macroacaena* in lacking a posterior ridge and a narrower orbitofrontal region. The latest Cretaceous *Lyreidina* Fraaye & Van Bakel, 1998, shows an anterior axial ridge, but differs by its pyriform shape, carapace areolation and ornament. From all currently known raninids, the new genus is distinguished by a unique combination of carapace outline, frontal region and ornamentation. The fusiform carapace, small, forwardly directed anterolateral spine and narrow orbitofrontal region support assignment to the subfamily Symethinae.

Subfamily Cyrtorhininae Guinot, 1993

Cyrtorhininae Guinot, 1993b: 1330.

Type genus. *Cyrtorhina* Monod, 1956.

Genera included. *Antonioranina* **n. gen.**; *Cyrtorhina* Monod, 1956.

Diagnosis. Carapace ovate, variously wide, convex in both directions. Cervical groove obsolete, branchiocardiac groove indistinct. Posterolateral margins straight, anterolateral margins rounded; margins rimmed or lined by granules. Anterolateral margin with 2, 3 teeth, subhepatic spine may be present. Cuticle microstructure diverse: upright nodes, fungiform nodes, inclined nodes, pits.

Front short, widely triangular, weakly to strongly sulcate, with sharp, anteriorly directed tooth on each side. Supraorbital margin with 2 fissures, inner fissure proportionally short, outer fissure longer, separating extraorbital teeth; outer extraorbital tooth robust, falciform. Orbits small; eyestalk short, of 3 elements: proximal article reduced, only ventrally visible; second article triangular, elongated; third dorsally exposed, calcified, strongly arched, with fungiform granules; cornea small. Antennary fossae situated posterior to antennulary fossae. Antennule deeply inserted, completely hidden by antenna, basal article notched distally, following articles much smaller; flagellum short. Proepistome distinct. Antennae massive, meeting medially, with external surface granular; articles 1, 2 fused, urinal opening at inner angle; article 3 expanded, with spatulate dorsal lobe, pointed ventral lobe; article 4 with salient anterodorsal angle; article 5 short; flagellum developed. Epistome triangular, medially raised, keeled. Subantennary lobe of pterygostome not delimited._

Mxp3 operculiform; endopod long, blunt anteriorly, merus shorter than ischium; palp short, concealed. Exopod short, wider than endopod, anteriorly pointed. Pterygostome granular, ridged, with rows of dense setae, completely setiferous posteriorly. Exposed pleurites 5–7 forming large, unexcavated plate; branchiostegite developed, high, overhanging exposed pleurites, limited by P5 apposed along branchiostegal margins. Sternum/pterygostome junction very narrow, recessed. Sternum/exposed peurite connections large between P1, P2, narrower between P2, P3. Thoracic sternum narrow all along, thus P1–P5 coxae approximated. A strong deflection at level of sternite 8. Sternite 1, 2 in a lower level, concealed; sternite 3 exposed, as small, V-shaped, horizontally extended strip; sternite 4 narrow, not laterally expanded except the slender, recessed anterolateral extensions forming sternum/pterygostome junction; sternites 4, 5 expanded laterally between P1, P2; sternites 6, 7 conspicuously narrow, linear; sternite 8 perpendicular to sternite 7. Medial line along sternites 5–8. Spermathecal apertures recessed, small, contiguous.

Chelipeds homochelous, homodontous. Basis-ischium short, immoveably fused with massive merus. Propodus longer than wide, narrow, upper, lower margins smooth, except for acute superodistal spine; fingers long, acicular, crossing at acute tips; dactylus deflected, proximally with long acute spine, prehensile border unarmed; fixed finger only slightly deflected, prehensile border with 3 acute spines proximally. P2–P4 moderately stout; carpus short, modified. P2–P4 dactylus spatulate on P2, sickle shaped on P3, P4. P5 dorsal, moderately reduced, granular, lying along posterolateral carapace margin, adapted to branchiostegal edge; dactyl narrow, elongated.

Abdomen proportionally small but rather wide in male, freely articulated, 6 articles plus telson, incompletely folded, first 4 articles dorsal, first somite as wide as posterior carapace margin. Female abdomen only slightly enlarged, thus sexual dimorphism indistinct. Uropods or sockets absent.

Large posterior branchial orifices present.

Genus *Antonioranina* n. gen.

(Figs. 34C, D; 35A–D)

Type species. *Cyrtorhina globosa* Beschin, Busulini, De Angeli & Tessier, 1988, by present designation.

Diagnosis. Carapace oval, with rounded lateral margins. Front triangular, advanced, with 2 adjacent teeth. Orbits small, extraorbital teeth falciform. Orbitofrontal region clearly delimited from dorsal surface of carapace by horizontal row of closely spaced granules. Anterolateral margins with 3 or 4 teeth. Dorsal carapace surface densely granular, posterior portion with larger, scabrous granules. Thoracic sternum narrow; sternite 2 narrow, inclined; sternite 3 V-shaped, wide; sternite 4 elongated, only slightly broadened; episternites 4 subparallel, straight, directed backwards; sternite 5 anteriorly wide, with moderate sternum/exposed pleurites connection; sternite 6 rhomboid, developed, with narrow sternum/exposed pleurites connection; medial line on sternites 5–8. Buccal frame relatively large, mxp3 narrow; endopod with slender, elongated elements; merus small; exopod wider than endopod. Chelipeds homochelous, homodontous; coxae stout; basis-ischium fused; merus long, robust, curved; carpus elongated; propodus dorsoventrally flattened; fingers long, slender. P2–P4 rather robust, propodus flattened; P5 reduced, subdorsal.

Species included. *Antonioranina fusseli* (Blow & Manning, 1996), *A. globosa* (Beschin, Busulini, De Angeli & Tessier, 1988), *A. ripacurtae* (Artal & Castillo, 2005) and, tentatively, *A. oblonga* (Beschin, Busulini, De Angeli & Tessier, 1988).

Derivation of name. In honour of Antonio De Angeli, in recognition of his numerous contributions to our knowledge of fossil decapod crustaceans from Italy.

Remarks. Carapace features of the new genus are closely similar to those of *Cyrtorhina*, a name that is here exclusively used for extant members. The two closely allied genera share a broadly ovate carapace, a characteristic orbitofrontal construction and dorsal surface ornament (Fig. 34A-D). Differences are nevertheless visible in the ventral construction. In *Antonioranina* **n. gen.** sternite 4 is much broader than in the extant genus, where this is markedly restricted between the P1 coxae and practically leaves only room for the gynglymes; episternites 4 are subparallel, nearly straight in fossils, whereas in *Cyrtorhina* episternite 4 is long and arched. In *Antonioranina* **n. gen.** sternite 5 is wider anteriorly; sternite 6 is longer, rhomboid and better developed than in the extant genus. This results in a greater interspace between the bases of P2 and P3 in the fossil form.

The middle Eocene *A. oblonga* from northern Italy (Fig. 35C, D) is tentatively assigned to the new genus. Carapace features reveal some slight differences: more slender than other species of the genus, elongated, and with the dorsal surface without distinct granules or ornament in the posterior portion. The partial thoracic sternum preserved in this species shows the wide type of sternite 4, hence favouring assignment to the new genus, but also presents a slightly better-developed episternite 4. More completely preserved material is needed to clarify its taxonomic position.

Include here is *A. fusseli* from the middle Eocene of North Carolina, U.S.A. and *A. ripacurtae* from the lower Ypresian (lower Eocene) of northeastern Spain, which have similar carapaces; however, ventral parts are still unknown in either species. The latter is the oldest member so far known, and is of much smaller size compared to the type species. More confident taxonomic placement awaits the discovery of material retaining the ventral features.

Morphology of the Raninoidia

Abdominal holding

Abdomen. The reduction of the abdomen (in length, width and thickness), with its calcification and its folding, and the concomitant loss of the tail fan and locomotory appendages, is a major event in decapod crustacean evolution towards Brachyura. This is completed by the acquisition of a holding system to fix the abdomen firmly to the ventral surface and prevent it from slipping. Amongst decapod crustaceans, this condition is unique to Brachyura and a component of the carcinisation process (McLaughlin & Lemaitre 1997; McLaughlin *et al.* 2004; Guinot, Tavares & Castro in press). The elaboration and evolution of the abdominal-holding system have been of prime importance within Brachyura.

Several traits, including the protection of the abdomen itself, protection of the pleopods, covering of the sexual openings in females (spermathecal apertures in podotremes, vulvae in eubrachyurans) as well as in males (penis), and locomotion, no longer provided by the abdomen, to a great extent depend on the ability to hold the abdomen firmly fixed and on its integration into the body. The thoracopods (P3, P5) became free from all reproductive functions in Eubrachyura (presence of sternal female gonopores or vulvae in Heterotremata and Thoracotremata, sternal male gonopores in Thoracotremata).

Holding structures. The arrangement and morphology of the holding structures is variable amongst crabs and provides a useful diagnostic character at different taxonomic levels. This criterion allows a reapparaisal of taxa, as noted previously by Guinot & Bouchard (1998: 615), and analysis of the different devices or strategies utilized by brachyuran crabs to retain or lock their abdomen sheds new light on the evolution of the group.

The structures adapted for abdomen holding are present in the male during its entire life span and up to the puberty moult in the female in both Podotremata and Eubrachyura. The female abdomen shows a marked size increase at this moulting stage and, when the egg mass is held by the large and feathery pleopods, the abdomen is in an unlocked position. In the natural posture, probably the resting position, mature males have their abomen closed and attached to the thoracic sternum; pre-puberty females similarly keep their abdomen closed. Normally, mature females have unlocked abdomens although there are some exceptions (see below). Crabs fasten and unfasten their abdomen by an axial (postero-anterior) movement (Guinot & Bouchard 1998: 675, 676); the sixth abdominal somite, just preceding the telson, is invariably involved in the immobilisation of the abdomen. The abdominal configuration, with the anus opening onto its extremity, at the tip of the telson, makes it possible to move only the telson for defecation. It thus appears that movement of the telson alone might suffice for defecation in both sexes rather than flapping the entire abdomen. Abdomen flapping in males has been recorded essentially during copulation. Abdomen extension is also probably required during the processes of recognition and courtship. The male abdomen is unfastened at the moment of the mating process, including pre- and post-copulatory periods.

Crabs lacking morphological specialisations to hold or lock the abdomen are very rare. The statement by Karasawa *et al.* (2011: 533) that the Cyclodorippoidea + Eubrachyura clade (‘with bremer support of 3’) are united by four synapomorphies, one of which is the absence of a pleonal locking system, is incorrect and confusing. Abdominal holding of the press-button type is the mechanism in which an abdominal socket fits over a structure on the thoracic sternum: a prominence on the thoracic sternum (invariably on sternite 5) and a socket invariably on the ventral surface of the sixth abdominal somite (see Guinot & Bouchard 1998). From a mechanical perspective, the press-button mechanism may be regarded as a coaptation by assemblage (Guinot & Bouchard 1998: 614). This system is the commonest amongst brachyurans. It occurs exclusively in Eubrachyura and is an apomorphy for this group (Guinot & Tavares 2001: 532, fig. 16, synapomorphy 8). Whereas other mechanisms are seen in primitive podotreme crabs (i.e. present only in a few families of Brachyura), the press-button, with a few variants, characterises numerous families of eubrachyurans.

The eubrachyuran press-button is not known in Podotremata, in which a wider range of structures to hold the abdomen is recognised. Most podotremes ‘immobilize their abdomens by means of a tubercle, knob, elongated flange, serrated ridge, projection, or spine that arises from the thoracopod coxae (mxp3 and/or pereiopods P1–P2 and even P3)’ (Guinot & Bouchard 1998: 618). These structures overhang the abdominal margin, match complementary parts of the abdomen, or sometimes act solely as a barrier so that the abdomen cannot slip out of position (coaptation by juxtaposition or engagement).

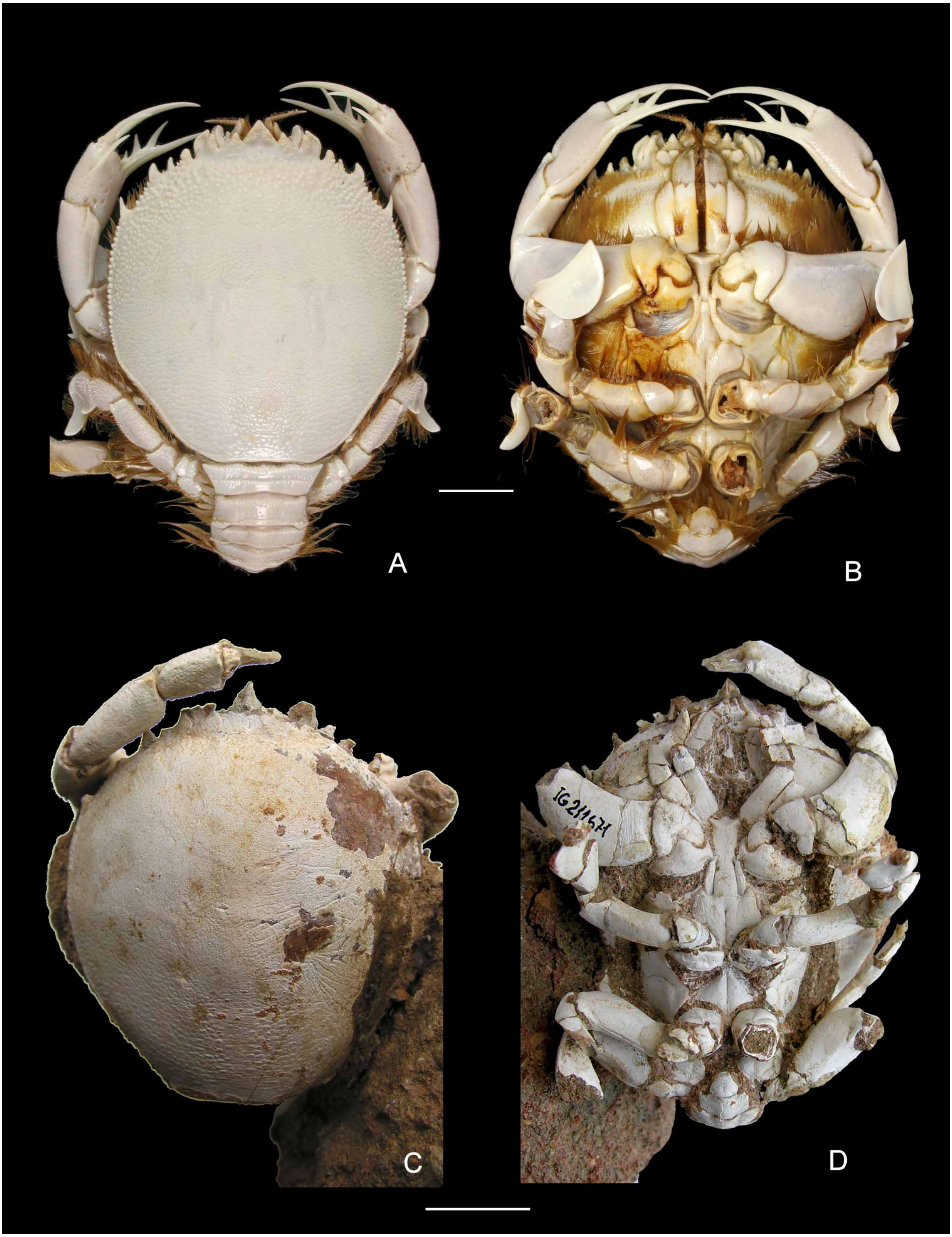


FIGURE 34. A, B, *Cyrtorhina granulosa* Monod, 1956 (Raninidae, Cyrtorhininae), MNHN-B16181 (female), Príncipe, Gulf of Guinea; dorsal and ventral views; C, D, *Antonioranina globosa* (Beschin, Busulini, De Angeli & Tessier, 1988) **n. comb.** (Raninidae, Cyrtorhininae), MCZ 1135 (**holotype**; female) [see also Fig. 35A, B], lower Eocene, Chiampo (Vicenza, northern Italy); dorsal view of carapace and left cheliped, and ventral view showing thoracic sternum and appendages (photographs A, B by J.-F. Dejouannet; C, D by A. De Angeli). Scale bars: 10mm.

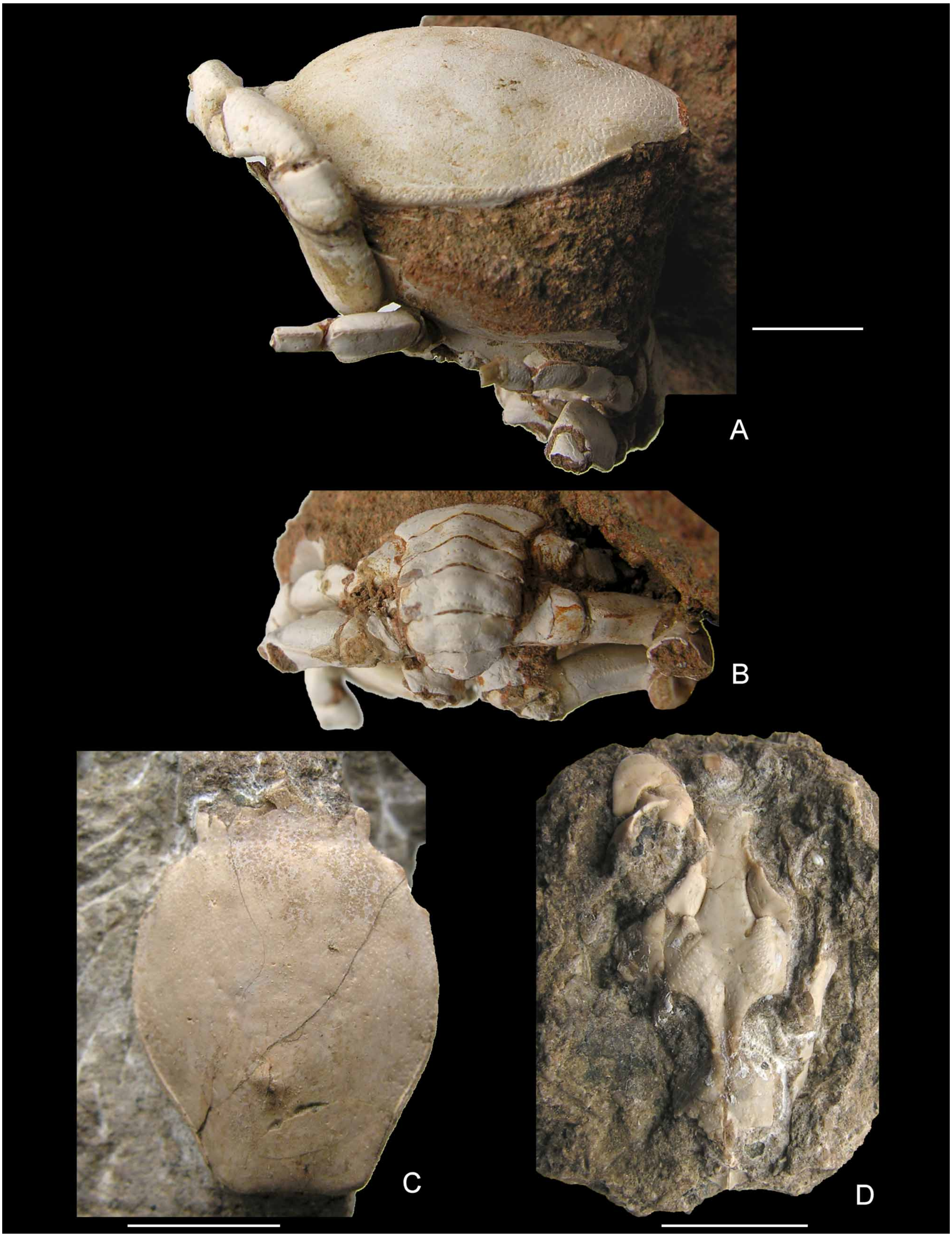


FIGURE 35. A, B, *Antonioranina globosa* (Beschin, Busulini, De Angeli & Tessier, 1988) **n. comb.** (Raninidae, Cyrtorhininae), MCZ 1135 (**holotype**; female) [see also Fig. 33C, D], lower Eocene, Chiampo (Vicenza, northern Italy); left lateral view, and posterior view showing abdomen; C, D, *Antonioranina oblonga* (Beschin, Busulini, De Angeli & Tessier, 1988) **n. comb.**, MCZ 1100 (C, **holotype**), lower Eocene, Arzignano (Vicenza, northern Italy); MCZ 1102-I.G.211641; D, indeterminate sex; ventral view showing thoracic sternum. (photographs A,B by A. De Angeli) Scale bars: 10mm.

A system comparable to the eubrachyuran press-button is found, however, in some Podotremata as in Homoloidea, with a 'homoloid press-button' (see e.g., Guinot & Richer de Forges 1995; Guinot & Bouchard 1998: 636, 637, figs. 9, 10); Lyreididae, with a 'lyreidid hook' (see e.g., Guinot 1979: 128, pl. 22, figs. 6, 7; 1993b: 1326, 1330, figs. 4, 6, 7; Guinot & Bouchard 1998: 639, fig. 11; Bouchard 2000: figs. 41a–f, 42a–c); the extinct Dakoticancroidea (see e.g., Guinot 1993a: 1231, fig. 8; Artal *et al.* 2008: 17), with a 'dakoticancroid holding' (see below). In Homolidae and Poupiniidae, the homoloid press-button (button situated on sternite 4, instead of sternite 5) adds to the holding provided by the thoracopods (mxp3, P1, P2), thus jointly appendicular and sternal holding, whereas in Latreilliidae the homoloid press-button remains the only effective locking mechanism. In all these podotreme examples, there is always a socket on the ventral surface of abdominal somite 6, as is usual in the press-button typical of Eubrachyura.

Among members of Dynomenidae Ortmann, 1892, which show different patterns of abdominal-holding involving coxal structures in the basal subfamilies (Acanthodromiinae Guinot, 2008, Metadynomeninae Guinot, 2008, and Paradynomeninae Guinot, 2008), a small sternal structure may be present (sternite 5) in the more derived subfamily Dynomeninae. This sternal structure, however, is lateral to the abdomen, does not function with a socket, and only interacts with a large, calcified dorsal uropod, although without any apparent efficiency (Guinot 1979: 125, pl. 21, figs. 8, 9; Guinot & Bouchard 1998: 631, 632, figs. 6D, 7D; McLay 1999: 456; Guinot 2008: 9, fig. 3C, D). The sternal button of Dynomeninae thus solely restricts lateral movement of the abdomen (as does the P2 coxal structure in Metadynomeninae), and is quite different from the typical eubrachyuran press-button (Guinot 2008: 11, fig. 3A).

In all cases requiring a socket for abdominal holding, the socket invariably occupies the same position in both Podotremata and Eubrachyura: ventrally, at the lateral side of abdominal somite 6 (most often in the postero-lateral corner). In the most basal clade, Dromiidae, uropods develop as calcified dorsal plates which generally participate actively in abdominal holding. Dromiid and dynomenid dorsal plates may be regarded as vestigial compared to the biramous uropods of other Decapoda, but nevertheless they represent a remarkable specialisation compared to the small ventral lobes of the Homolodromiidae, which are not functional in abdominal holding.

In the brachyuran evolutionary scheme, when these vestigial uropods (as well as dorsal plates and ventral lobes) are lost, sockets are uniformly developed at the same position, a criterion of phylogenetic position. Several arguments support the hypothesis that brachyuran sockets are homologous to the ancient biramous uropods, obviously a functional significance to the loss of tail fan and uropods, a crucial step discussed at length by Guinot & Bouchard (1998: 682). This idea had already been hinted at by Pérez (1928: 649; 1929: 1145), Hartnoll (1975: 16), Guinot (1979: 156), and Guinot & Richer de Forges (1997: 472).

Brachyurans lacking both uropods and sockets are very rare. Examples are the Raninoidea (except Lyreididae), which do not hold their short abdomen under the body, and Cyclodorippoidea, which have evolved an abdominal cavity with either a sliding system (Tavares 1994: 210; 1996: fig. 9A–C, E; 1998: 116, figs. 7A–C, 8), a blocking system (Tavares 1994: 28, 209; 1998: 116, fig. 1B), or lack any special structures (Guinot & Bouchard 1998: 640–642).

It is obvious that Podotremata have evolved several means of abdominal holding, instead of a single one, the press-button, which is present in nearly all eubrachyurans. This may suggest that the eubrachyuran press-button is the most reliable system when the crab widens its thoracic sternum during changes brought about by carcinisation and when abdominal somites become fused. The consistency in general shape, position and function indicates that the press-button is an efficient mode of abdominal holding. This uniformity within a wide range of body shapes in the Eubrachyura probably shows that it is the most efficient use of energy resources in order to achieve locomotion, reproduction and other functions. In all eubrachyurans, the pereiopods are free of abdominal holding. In Heterotremata, the P5 are involved in reproduction, but the P3 are free of reproductive purposes, whereas in Thoracotremata both P3 and P5 serve no reproductive function. Absence of a press-button in some thoracotremes as in Heloeciidae H. Milne Edwards, 1852, and Mictyridae Dana, 1851 (Guinot & Bouchard 1998: 677) may be considered the result of secondary loss. The success of the single structure, the press-button, may be correlated with the condition of the brachyuran male abdomen: calcified, reduced, usually rather narrow, flexed to the ventral plate, sheltered in a special cavity and with a tendency towards fused abdominal somites.

Abdominal holding in fossil podotremes. The abdominal holding system, rarely used as a taxonomic feature for a long time, even by neontologists, has rarely been recognised in fossils (Guinot & Bouchard 1998: 681, 682). These important structures should receive more attention, certainly during preparation of the material. An abdomen may be sacrificed to expose these structures when numerous specimens are available. A cast of the original specimen with abdomen *in situ* can ideally be produced prior to preparation.

A holding mechanism is known in several fossil podotreme groups.

Homoloidea: The extinct *Mithracites vectensis* Gould, 1859, which shows a sternal configuration typical of homoloids, possesses a 'homolid button' on sternite 4 ('*une proéminence serrulée sur le sternite 4 correspondant très probablement au bouton-pression homoloïdien*'; see Guinot & Tavares 2001: 535; Bouchard 2000: 117, fig. 27B). Family rank was suggested with reservation for *Mithracites* Gould, 1859, by these authors and subsequently, Števčić (2005: 23) erected Mithracitidae. The family, however, is in urgent need of reappraisal.

Dromioidea: Two extinct genera, *Basinotopus* McCoy, 1849, and *Dromilites* H. Milne Edwards, 1837, have uropods showing as dorsal plates, which most probably had a function in abdominal holding. These uropods (Bell 1858: pl. 5, figs. 1, 7–9) are assumed to have interacted with prominences on the coxae of the pereiopods.

Dakoticancroidea: Both Dakoticancridae and Ibericancridae exemplify a particular holding of the abdomen, which is received in a cavity. Artal *et al.* (2008: 17, fig. 3C) described and illustrated the abdominal holding structure in a male specimen of *Dakoticancer overana*. A similar structure was found in both sexes of the more basal *Ibericancer sanchoi* (Artal *et al*. 2008: 18, fig. 4A, D). The sterna in female dakoticancrids are devoid of any abdominal locking structures, as shown by two well-preserved specimens examined here. A 'salient button' was observed in a male and a female (Artal *et al*. 2008, fig. 4a [male], 4d [female]) ibericancrid, in contrast to dakoticancrids, in which a locking mechanism is present exclusively in the males. The 'salient button' in *I. sanchoi* could be not a single structure, but the preservation does not allow a detailed study. Attention must be paid in cases when only few female sterna are available because an abdominal holding system may be present in prepuberous females and lost after the puberty moult; specimen size of the fossils may not be a reliable indicator.

The locking system of Dakoticancridae was first observed by Guinot (1993a: 1231, fig. 8, enlargement), who illustrated the male thoracic sternum with three to four recurved tubercles, the abdomen covering some, but not all, teeth (indicated by a dashed line in her fig. 8). These observations were overlooked by Artal *et al.* (2008: 17) in their description of the family, which was based on a cast of *Dakoticancer overana* showing 'a small protuberance on sternite 5 at the level of the socket on the ventral surface of pleomere 6', the intact abdomen obviously covering all teeth except the most ventro-lateral one. More recent analyses of specimens confirm the presence of several (three to four) teeth partially covered by the abdomen, interpreted here as multiple locking teeth. In two male specimens, with the abdomen removed, there are at least three close-set teeth on sternite 5 in close proximity to suture 4/5 and located on the steep walls of the sterno-abdominal cavity. These teeth are anteriorly directed, not in line with the body axis, but obliquely positioned. Because of their partial observation, Artal *et al*. (2008) misinterpreted the condition of the abdominal holding system of Dakoticancroidea, erroneously assumed to be of the press-button type. The present clarification confirms the unique position of Dakoticancroidea within Podotremata. The dakoticancroid locking consists of several teeth that interact with a socket on the ventral surface of abdominal somite 6, a system referred here as 'dakoticancrid holding'. Consequently, it follows that the typical press-button remains an apomorphy for Eubrachyura. In Dakoticancroidea the locking teeth are not placed on episternite 5 on the outer lateral margin of the thoracic sternum but in the medial part of the thoracic sternum, thus a configuration different from that of Palaeocorystoidea and Lyreididae.

Etyoidea: In *Etyus martini* Mantell, 1844, the abdominal holding involves prominences of the coxae; in males sternite 4 is excavated medially, so that the telson rests in a depression. The peculiar and sexually dimorphic locking structures in *Etyxanthosia* Fraaije, Van Bakel, Jagt & Artal, 2008, and *Feldmannia* Guinot & Tavares, 2001, were described by Guinot & Tavares (2001: 511, 520, 521, 526, 527, figs. 7–9, 14, under *Xanthosia* Bell, 1863). The observation by Števčić (2005: 25) that, 'the abdomen fixed laterally by coxae of 1–2 anterior pairs of pereiopods' needs reassessment. New material currently under study confirms the sexual dimorphism of the locking system in *Etyus* Leach *in* Mantell, 1822. The etyoid thoracic sternum also bears tubercles and protuberances that may be involved in locking the abdomen (Guinot & Tavares 2001: fig. 14). The abdominal holding in Etyidae is here considered to be composite and is referred to as 'etyoid holding'.

Lyreididae: The thoracic sternum of *Rogueus orri* clearly shows the posterior extensions of sternite 5, although not noted in the original description (Berglund & Feldmann 1989: 71, fig. 2.5), as stressed by Tucker (1998: 371), Guinot & Bouchard (1998: 640) and Bouchard (2000: 128, fig. 32A) (see remarks for *R. orri*). A cast of *Bournelyreidus tridens* (MAB k. 0214; Fig. 38C, D) shows the presence of posterior extensions on episternite 5, but without locking teeth. As in this specimen the posterior sternites (with possible spermathecal apertures if the specimen was a female) and the P3 coxae (with possibly the female gonopores) are missing, sex cannot be determined; this individual might represent a mature female (see remarks for *B. tridens*). The Lyreididae is the only extant family in the superfamily Raninoidea to display double lock teeth. The locking system is considered to have been lost in the other families of Raninoidea.

The presence of several locking teeth as part of a locking mechanism is rare in podotremes, being only known in Dakoticancroidea (in medial part of sternum) and Raninoidia (outer part of sternum, episternite 5). Guinot & Bouchard (1998: 681) hypothesised that the abdominal holding was innovated more than once in Brachyura.

The lyreidid holding system and the eubrachyuran press-button can be delineated with more refinement and compared with increased accuracy by considering structures found in fossils. It is necessary to partially modify Artal *et al.* (2008: 18) statement that 'the press-button is not exclusive to the Eubrachyura since a socket (although not coupled with a typical 'button') also occurs in another podotreme group, Lyreidinae Guinot, 1993, among the Raninoidea De Haan, 1839.' The press-button system consists of a single, unpaired tooth on sternite 5 and of a socket located ventrally on the lateral side of abdominal somite 6. In our present understanding, the lyreidid holding system, which consists of a socket in the same location, works with two teeth, so it cannot be considered a typical press-button. The typical press-button therefore exclusively characterises Eubrachyura.

Terminology of the abdominal holding system in Raninoidia. The abdominal-holding system in Lyreididae, as a whole, resembles a hook. Guinot (1993b: 1326, 1330) erected Lyreidinae in recognition of the unique condition of its abdominal holding ('*Sternum thoracique … avec le sternite 6 recouvert par l'abdomen, ce dernier présentant un dispositif d'accrochage, unique chez les Raninoidea*'). The projection was called '*crochet du sternite 5*' [sternite 5 hook] (Guinot 1993b: 1326, figs. 4, 6, 7), 'strong elongate projection arising from sternite 5', or 'projection with hooks' (Guinot & Bouchard 1998: 639, 682, fig. 11). Števčić (2005: 28), in his diagnosis of Lyreidinae, referred to a 'press-button mechanism of abdomen present on sternite 5'. Athough the lyreidid socket may be homologous to the eubrachyuran socket and the mechanism could work by analogous apposition, the lyreidid structure with its two teeth is here distinguished from the eubrachyuran press-button type and referred to as 'hook-like projection'.

In Lyreididae the tip of the hook-like projection bears two close-set teeth. Bourne (1922b: 69, pl. 4, fig. 4) described the 'pterygoid processes' of sternite 5 with two small knobs. According to Guinot & Bouchard (1998: 639) 'The tip of the projection, more or less strongly recurved and distally hook shaped, bears an additional subdistal hook' and the whole structure 'acts as a safety catch'. In order to use consistent terminology in describing abdominal holding structures, we prefer to use the term **'**double peg' for the two teeth located on episternite 5. The double peg consists of a distal (posterior) and a subdistal (anterior) peg. Based on the hypothesis that the locking system of Lyreididae is homologous to that of Palaeocorystoidea in which, however, a hook-like projection is absent (Figs. 37, 39–41), the pegs are named accordingly. More than one subdistal peg has been observed in rare, abnormal cases. A mature female of *Lyreidus stenops* Wood-Mason, 1887, has two subdistal pegs, making a total of three (Guinot & Bouchard 1998: 640). A mature female of *L. tridentatus* (MAB k. 2923) showed a right-hand, hook-like projection with an additional subdistal hook, the left-hand projection revealing the normal configuration.

The double peg is opposed to the posterior corner of abdominal somite 6 when the abdomen is pressed against the body. The teeth of the double peg are anteriorly directed, and assumed to interact with an abdominal socket. According to Bourne (1922b: 69), abdominal somite 6 is 'long and narrow; its posterior angles are produced into small aliform processes which at first sight might be mistaken for vestigial uropods, but they are only processes of the tergum having on their ventral surfaces small concavities which, when the abdomen is flexed to its fullest extent, engage with small knobs on the two pterygoid processes extending backwards from the twelfth sternum'. Bourne's 'small concavity' is homologous to what is herein named the 'lyreidid socket'. The lyreidid socket is long and anteriorly undefined. The extent of differences in the shape of the lyreidid socket from the typical socket of Eubrachyura, the complementary part of the typical press-button, remains unknown.

The abdominal holding system in the Raninoidea. An abdominal holding mechanism never involves the pereiopods in Raninoidia; only a sternal structure corresponding to a coadapted abdominal structure is present in some members of the taxon.

Guinot & Bouchard (1998: 677) noted that, 'a firm locking is found in the subfamily Lyreidinae, the abdomen of which is a little longer, narrower, and better included between legs than in other raninid subfamilies'. In *Lyreidus tridentatus* abdominal somite 6 is narrow, but the posterolateral angles have small, rounded projections resembling extended corners of this somite. Each rounded projection corresponds ventrally to a deep, elongated depression, a socket, limited at the axial side by a vertical wall; this ventral depression represents the lyreidid socket (Fig. 36C, D here). The abdominal socket and the double peg practically face each other. When the abdomen is pressed against the body, slightly pulled towards its posterior side, the double peg becomes situated along the ventral wall of abdominal somite 6 and the socket grabs hold of the subdistal peg. The abdomen, thus locked against the body, cannot be moved away from the body, not even laterally, being secured for transverse movement. In all Brachyura where an abdominal socket is involved, this postero-anterior movement is similar to varying extent. In contrast, the configuration in Dromioidea involves holding structures positioned side by side, with coxal structures (or, exceptionally, sternal as in Dynomeninae) never facing the abdominal elements (e.g., uropods), and there is never an abdominal socket. The dromioidean and raninoidian types are therefore completely different.

Lyreidids (fossil and extant) are the only representatives of Raninoidea that exhibit an abdominal holding system. In extant lyreidids, episternite 5 is much extended towards the posterior side of the body, slightly curved in males or pointed outwards in adult females, forming two prominent hook-like projections (Fig. 36F, G). The distal end of the hook-like projection bears a peg, and there is an additional, larger subdistal peg. The pegs are close to each other, and there is a moderately deep depression in front of the subdistal peg. It is clearly visible in lateral view that the teeth are sharp and pointed towards the anterior side of the body. When locking, the abdominal socket catches behind the subdistal peg, firmly securing the abdomen. The hood-like posterior margin of the socket is in the depression in front of the subdistal peg. The distal peg is also received in the elongated socket, but apparently does not play any role in locking. The thoracic sternum becomes similar to a typically podotreme sterno-abdominal depression (the space between the pereiopods) in which the abdomen may be secured against the thorax. Moreover, in lyreidids the small telson rests in a hollow space formed by the raised projections of episternite 5. Because the telson is positioned in this depression, being pressed against the sternal plate, the anal opening at its extremity is protected against substrate particles when burying. The anus is protected by a special plate in several other raninoids (see *The telson protection valve* below).

Similar hook-like projections arising from episternite 5 are observed in several fossil specimens assignable to Lyreididae. As a result of preservation, however, the double peg is not always seen. The hook-like projections are clearly visible in *Rogueus orri* (see Berglund & Feldmann 1989: 71, fig. 2.5), a condition also noted by Guinot & Bouchard (1998: 640), Tucker (1998: 325) and Bouchard (2000: 128, fig. 32A), but no double peg has been observed by these authors. Roberts (1962: 187, pl. 88, figs. 5, 6; *Raninella tridens*) and Bishop (1983b: 419; *Raninella tridens*) did not pay any attention to the hook-like projections in *Bournelyreidus tridens* **n. comb.**, but casts examined here (MAB k. 0214 = GAB 37-832) do show such hook-like projections, *albeit* without pegs. The sex of this specimen is unknown due to the lack of the posterior sternites (and thus spermathecal apertures) and the P3 coxae (and thus female openings). It might represent a mature female (see remarks for *B. tridens*). Hook-like projections were noted and illustrated by Tucker (1998: 325, fig. 2.2) for *Macroacaena*, but this character was not included in her diagnosis. Guinot & Bouchard (1998: 682) observed that projections arising from sternite 5 were present in several fossil raninids, e.g. *Lyreidus succedanus*, *L. rosenkrantzi*, *L. bispinulatus* and in *Rogueus orri*, but information on structures which would allow locking with sockets on abdominal somite 6 was lacking. Accordingly, Guinot & Bouchard (1998) suggested detailed comparisons to be made with representatives of the exclusively fossil subfamily Palaeocorystinae, for example *Notopocorystes stokesii* (Fig. 37A–E).

Abdominal holding in Brachyura is normally lost in females after the puberty moult because at that moulting stage the female abdomen shows a marked size increase in order to carry and protect the egg mass. In Raninoidea, there is no such increase in size of abdominal somites, so sexual dimorphism is indistinct. The pleopods (female pleopod 1 absent) are well developed and abundantly setiferous. The eggs are carried by pleopods, which may be laterally extended on each side of the abdomen such as in *Lyreidus tridentatus* (Guinot 1993b: fig. 7) or the exopods of the pleopods are laterally disposed so that a kind of basket is formed that encloses and protects the egg mass, such as in *Raninoides louisianensis* Rathbun, 1933 (Feldmann & Schweitzer 2007: fig. 7c, d), *Notopoides* and *Notosceles*.

The two teeth of the hook become blunt, or obsolete, after the puberty moult in female lyreidids. The hook may thus still be vestigially present in adult lyreidid females (Fig. 36G), remaining even effective in ovigerous females (e.g., *Lyreidus tridentatus*; Guinot 1979: pl. 22, figs. 6, 7; 1993b: figs. 6, 7). In *Lysirude channeri* the pegs are well developed in males and obsolete in females (Guinot & Bouchard 1998: fig. 11D; Bouchard 2000: figs. 40E, F; 41A–C). This character was not used by Feldmann & Schweitzer (2007) in their review of sexual dimorphism in extinct and extant Raninidae. According to Griffin (1970: 100, fig. 8f, g), the abdominal somite 5 of lyreidids is proportionally wider and abdominal somite 6 proportionally longer in females, a dimorphic trait confirmed by Feldmann & Schweitzer (2007: 46). The microstructure of the sternal prominences which, amongst other characters, distinguishes *Lyreidus* from *Lysirude* might represent a valuable criterion at the generic level and, hypothetically, at higher levels as well (Bouchard 2000: 175).

The abdominal holding is considered lost in raninoideans other than Lyreididae in correlation with modifications linked to burying (see Modifications for a burying mode of life below). The double peg may therefore be assumed to be a synapomorphy for Raninoidia. The lyreidid hook-like projection is a secondary modification which is derived from the double peg of Palaeocorystoidea, hence the hook-like projection constitutes an apomorphy for the Lyreididae.

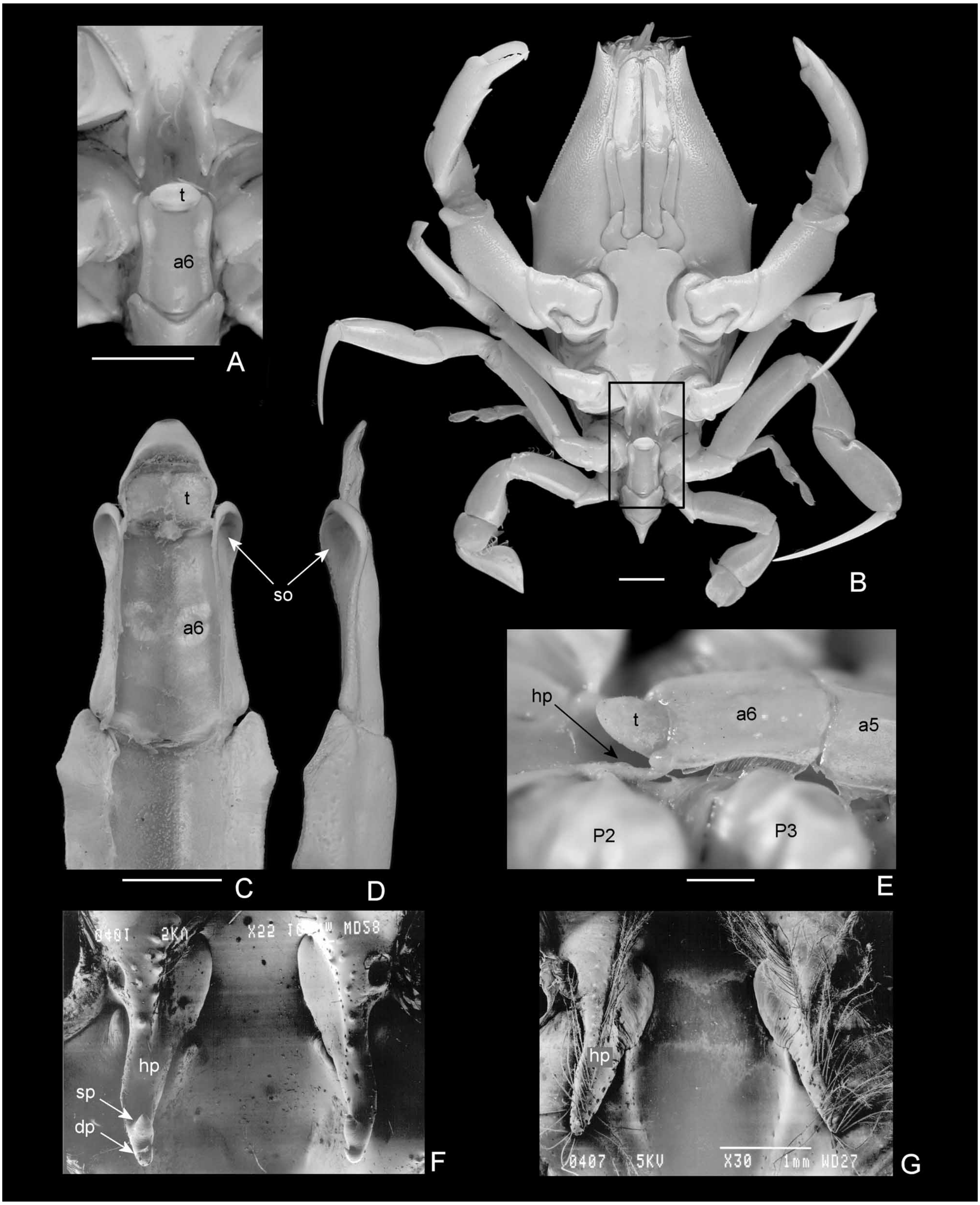


FIGURE 36. *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae); A, B, MNHN-B13364 (male, 37.1 x 20.7 mm); C, D, MAB k. 2887 (male); E, MAB k. 2888 (male); A, detail showing abdominal holding system (abdomen slightly displaced); B, ventral view, rectangle indicating detailed view in A; C, D, distal portion of abdomen and telson, interior and lateral views; E, oblique lateral view of abdomen locked by abdominal holding structure; F, G, *Lysirude channeri* (Wood-Mason, 1885) (Lyreididae, Lyreidinae), MNHN-B11562, Philippines; F, male (SEM by J.-M. Bouchard), details of hook-like projection of episternite 5 with pointed double peg; G, mature female (SEM by J.-M. Bouchard), same region; note obsolete double peg. **a5, a6,** abdominal somites 5, 6; **dp**, distal peg; **hp**, hook-like projection; **P2**, **P3**, pereiopods 2, 3; **so,** socket; **sp,** subdistal peg; **t,** telson. Scale bars: A, B: 5mm; C–E: 2mm; F, G: 1mm.

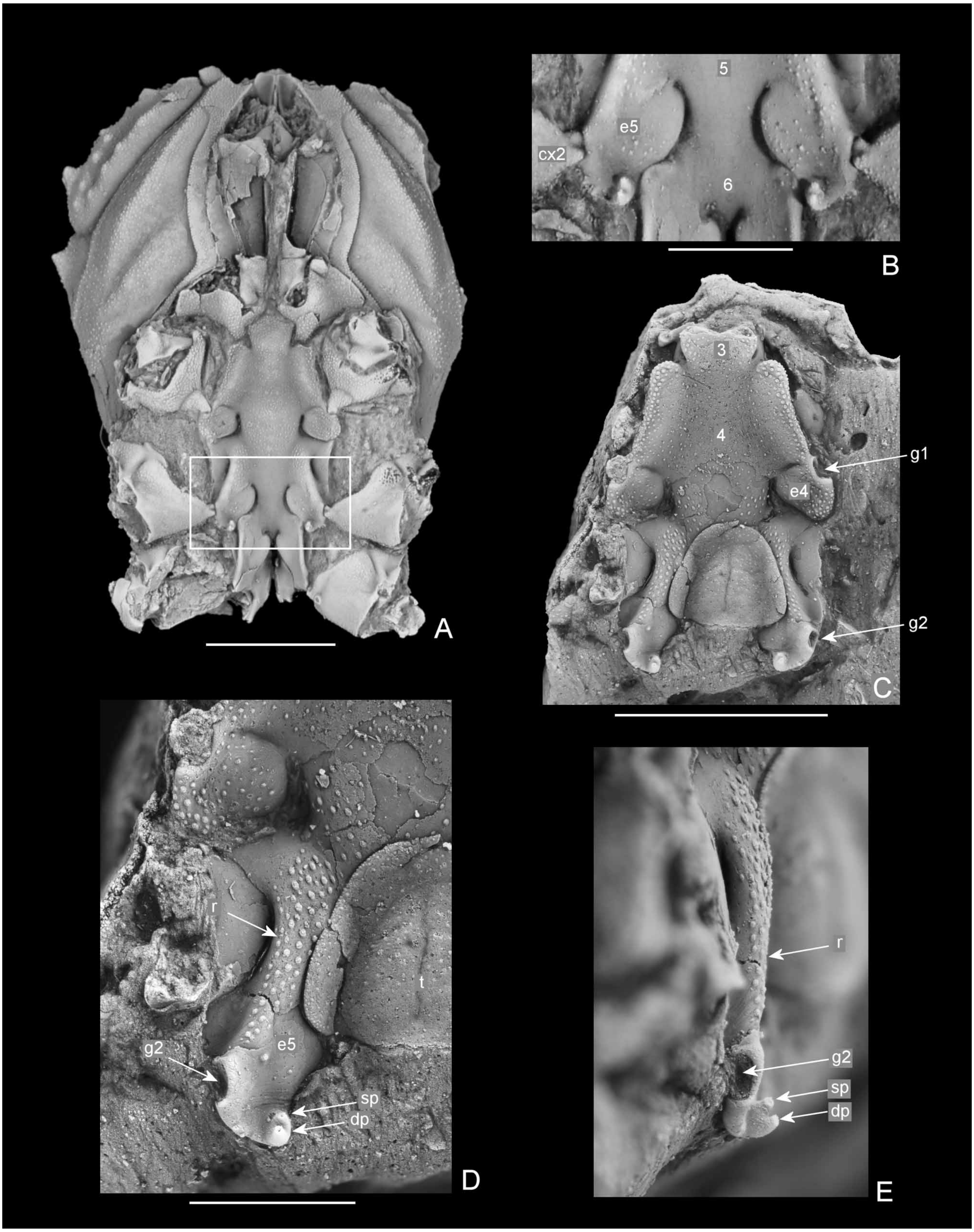


FIGURE 37. Double peg in *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae); A, B, MAB k. 2889 (juvenile female), Albian, Escalles (Calais, northern France); ventral view showing thoracic sternum, mxp3 and pereiopods, and detail of thoracic sternum; C–E, MAB k. 2890 (indeterminate sex), middle Albian, Pargny (northern France); ventral view showing thoracic sternum and telson; detail of thoracic sternum, and left lateral view showing double peg. **3, 4, 5, 6,** thoracic sternites 3, 4, 5, 6; **cx2,** P2 coxa; **dp,** distal peg; **e5,** episternite 5; **g1, g2,** gynglymes for P1 and P2 coxa; **r,** ridge; **sp,** subdistal peg; **t,** telson. Scale bars: A, C: 5mm; B, D, E: 2mm.

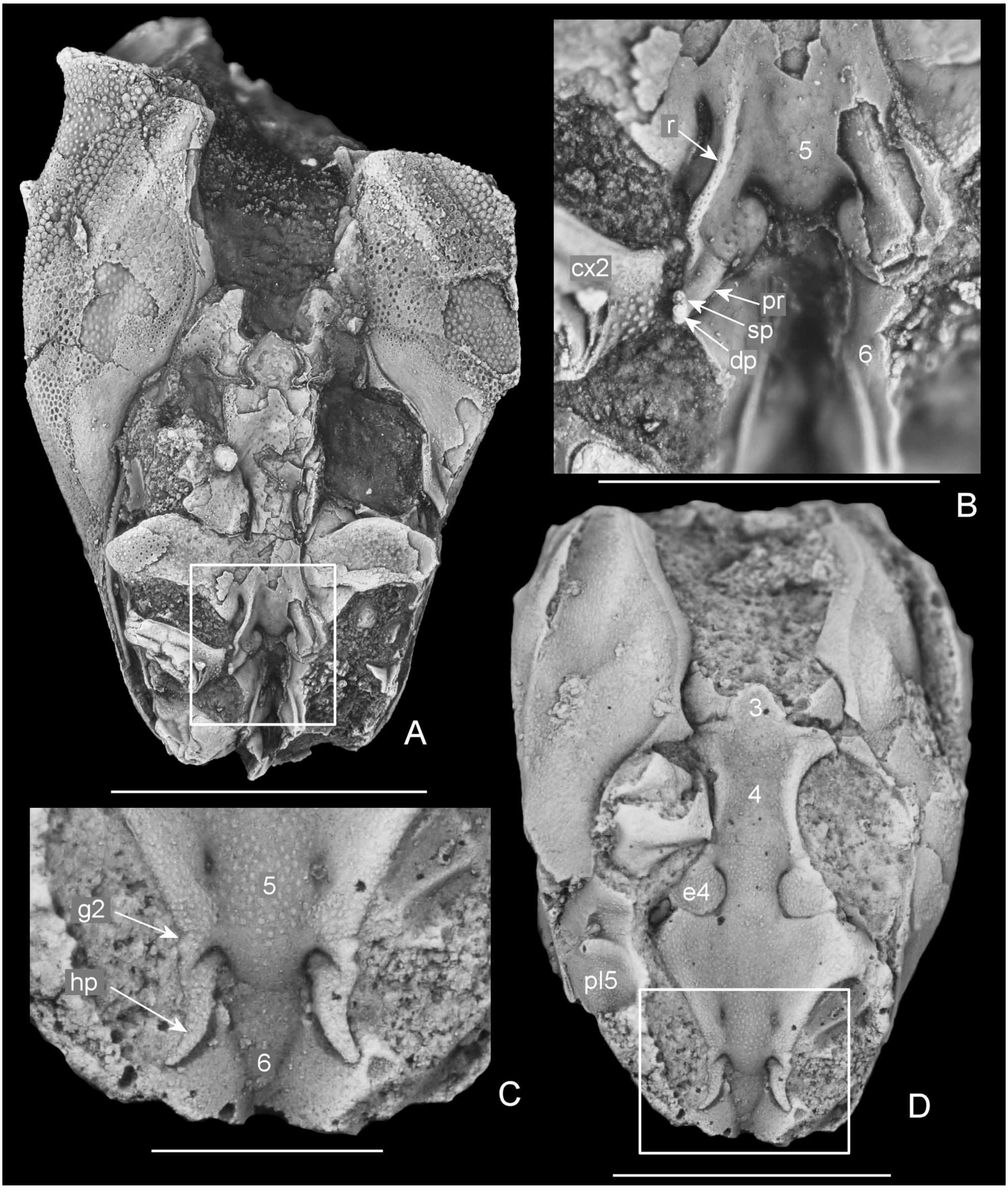


FIGURE 38. Hook-like projection in fossil lyreidids (subfamilies Lyreidinae and Marylyreidinae **n. subfam.**); A, B, *Marylyreidus punctatus* (Rathbun, 1935b) **n. comb.** (Marylyreidinae **n. subfam.)**, MAB k. 2884 (male), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County, Texas (U.S.A); ventral view showing pterygostomes, thoracic sternum and bases of pereiopods, and detail of thoracic sternum; C, D, *Bournelyreidus tridens* (Roberts, 1962) **n. comb.** (Lyreidinae), MAB k. 0214 (cast of GAB 37-832; ?adult female), lower Maastrichtian, Mississippi (U.S.A); detail of thoracic sternum, and ventral view showing thoracic sternum and exposed pleurites. **3, 4, 5, 6,** thoracic sternites 3, 4, 5, 6; **cx2,** P2 coxa; **dp,** distal peg; **e4,** episternite 4; **g2,** gynglyme for P2 coxa; **hp,** hook-like projection; **pl5,** exposed pleurite 5; **pr,** projection; **r,** ridge; **sp,** subdistal peg. Scale bars: A, D: 5mm; B, C: 2mm.

The abdominal holding system in the Palaeocorystoidea. The abdomen in palaeocorystoids is long, the first abdominal somites being in prolongation with the carapace and thus dorsal. The abdomen is nearly always found *in situ*, locked against the body in specimens preserving the abdomen.

All five families of Palaeocorystoidea have a double peg, which permits abdominal holding. The palaeocorystoid double peg is simply placed on sternite 5, consisting of two sharp, anteriorly curved teeth, the subdistal peg being slightly more medial than the distal one. The possible effect of the subdistal peg in abdominal holding remains unclear.

The abdominal holding structures have been examined in the five palaeocorystoid families.

Palaeocorystidae. The thoracic sternum is only slightly narrower and episternites 5 are relatively more widely separated than in the other palaeocorystoid families. The abdominal holding system consists of a double peg on episternite 5; hook-like projections never occur. The pegs are acute in males, blunt in large (adult) female specimens, more accute in younger individuals of both sexes. A double peg has been observed in numerous well-preserved specimens of *Eucorystes carteri*, *E. iserbyti* **n. sp.**, *Joeranina broderipii* **n. comb.**, *Notopocorystes serotinus* and *N. stokesii*. The presence of a double peg could not be confirmed in other palaeocorystid species because episternite 5 was not well-preserved. The blunt holding system in adult females is verified only in *J. broderipii* **n. comb.** and *N. stokesii*; in these females the double peg is blunt, or has eroded into a low, elongated elevation (Fig. 39A-D, 59B). Episternite 5 extends rather far backwards in *Joeranina broderipii* **n. comb.** and *Notopocorystes stokesii*, and the position of the double peg may slightly vary. The double peg is situated near the posterior border of episternite 5, just below the level of the P2 gynglymes, in *Joeranina* **n. gen.** and *Notopocorystes*. The structure is distal to the gynglyme and close to sternite 6. The double peg is much nearer the P2 gynglyme in *Eucorystes* than in *Joeranina* **n. gen.** and in *Notopocorystes*; it is raised higher and, in lateral view, clearly elevated from the sternal plate. Karasawa *et al*. (2011: 533) stated erroneously that the Palaeocorystidae shared with the Raninidae the absence of a ‘pleonal locking system’.

Camarocarcinidae. *Camarocarcinus* is the only genus here included in Camarocarcinidae; *Cretacocarcinus smithi*, originally referred to this family, is here included in Necrocarcinidae (see remarks for *Cretacocarcinus smithi*). Ventral parts are poorly known. An abdominal-holding system does exist on episternite 5 of the holotype (MGUH 21609) of *Camarocarcinus quinquetuberculatus* (Fig. 39E, F), but the cuticle is not sufficiently well-preserved to allow a precise description, and the available material does not allow verification if the system is double.

Cenomanocarcinidae. This family was diagnosed by ‘a pair of prominences’ on sternite 5, being part of the abdominal holding system (Guinot *et al*. 2008: 694). This observation was made in a large female referred to as *Cenomanocarcinus* aff. *vanstraeleni* from the Coniacian of Apulo, Colombia (NCB-RGM M902). The structure was ‘blunt, weathered, but well-preserved and recognisable’ (Guinot *et al*. 2008: 694, 710). In newly collected material, a double peg has been observed in *Cenomanocarcinus vanstraeleni* from the upper Albian–lower Cenomanian Pawpaw Formation of Tarrant County, Texas, U.S.A. In another specimen of *C. vanstraeleni* (MAB k. 2893), with a partial, well-preserved carapace and remains of mxp3 and walking legs, there is a partial thoracic sternum that is wide and rather flat, assumedly that of a fairly young female. The well-preserved sternite 5 shows a distinct double peg just below the level of the P2 gynglyme (Fig. 40C, E), with the distal peg more laterally placed and clearly larger than the proximal one. As the two pegs, both directed anteriorly and slightly outwards, are close set, only a narrow space is left between them. The area between the P2 gynglyme and the double peg is depressed. A second specimen of *C. vanstraeleni* (MAB k. 2895; Fig. 40D, F), with a well-preserved ventral side and a posteriorly displaced abdomen, shows the double peg on both sides. In contrast to the Palaeocorystidae, the abdominal holding system is not at the margin of the sternal plate, but rather central on episternite 5.

The holotype of *Hasaracancer cristata* (see Guinot *et al*. 2008: 20, fig. 7a, b) and a newly collected specimen of *Cenomanocarcinus vanstraeleni*, both retain their abdomen, and both are considered to represent moults.

Necrocarcinidae. The only thoracic sternum available for study, that of *Necrocarcinus labeschii* (SM B23180), is not well preserved, and no abdominal structure could be discovered. A double peg is expected, however.

Orithopsidae. The thoracic sternum of the holotype of *Silvacarcinus laurae* (IRScNB TCCI 6115) was examined (Fig. 40A, B), showing a slightly damaged abdominal holding structure, rather central on episternite 5, at the same level as the P2 gynglyme. Despite fragmentary preservation, the elongation of the base of this structure could be indicative of the presence of a double peg in *Silvacarcinus*.

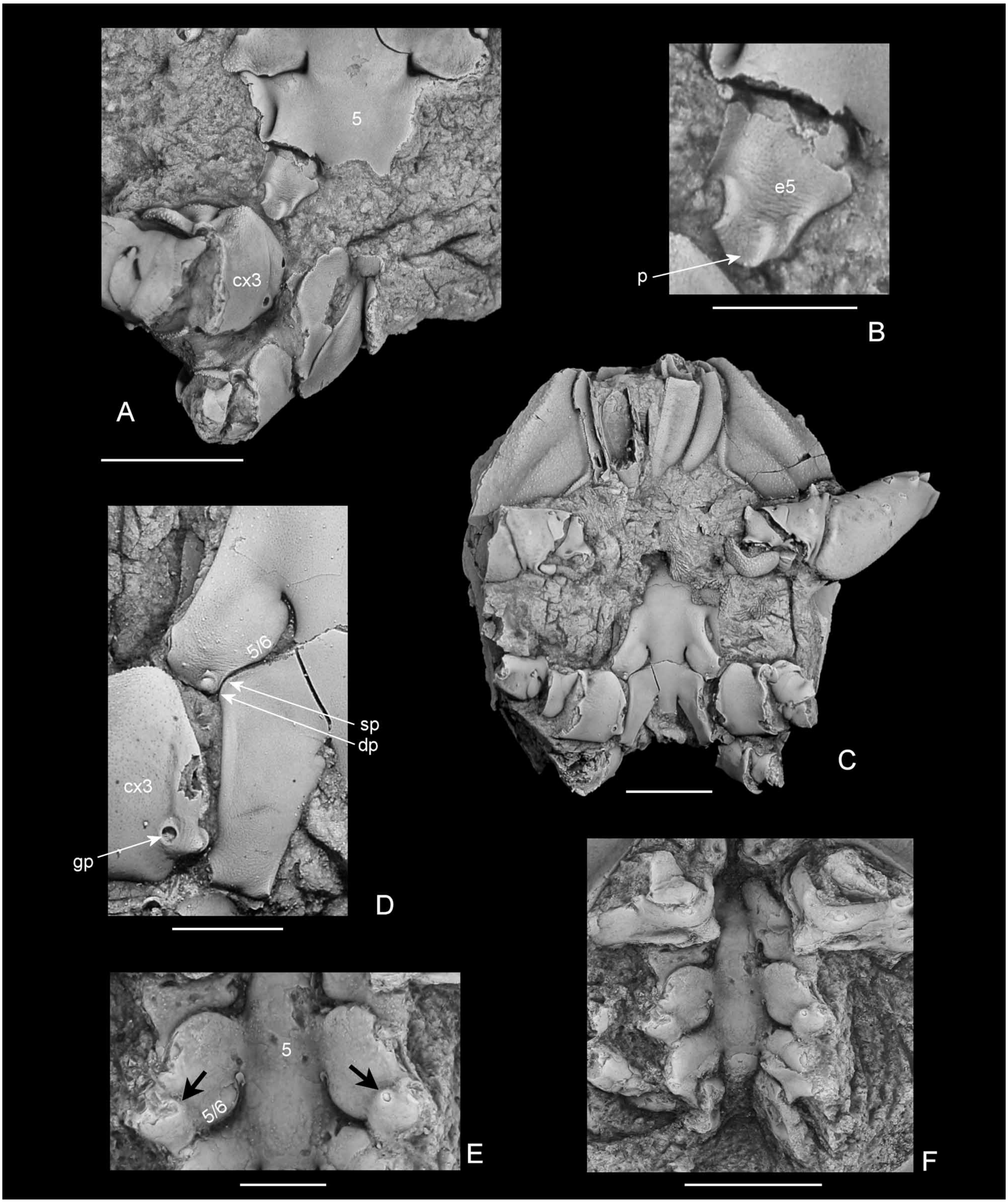


FIGURE 39. Various conditions of the double peg in Palaeocorystoidea; A, B, *Joeranina broderipii* (Mantell, 1844) **n. comb.** (Palaeocorystidae), MAB k. 2892 (female), Albian, Escalles (Calais, northern France); ventral view showing sternum and pereiopods, and detail showing worn double peg on episternite 5; C, D, *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), MAB k. 2874 (female), Albian, Escalles (Calais, northern France); ventral view showing mxp3, pterygostome, sternum and pereiopods, and detail showing weak double peg at episternite 5 and P3 coxa with gonopore; E, F, *Camarocarcinus quinquetuberculatus* Collins & Wienberg Rasmussen, 1992 (Camarocarcinidae), MGUH 21609 (**holotype**; indeterminate sex), middle Paleocene, central Nûgssuaq, western Greenland; detail of sternum, arrows indicating damaged abdominal holding system, and ventral view showing P1 coxae and sternum. **5,** thoracic sternite 5; **5/6,** thoracic sternal suture 5/6; **cx3,** P3 coxa; **dp,** distal peg; **e5,** episternite 5, **gp,** female gonopore; **p,** peg (undifferentiated); **sp,** subdistal peg. Scale bars: A, C, F: 5mm; B, D, E: 2mm.

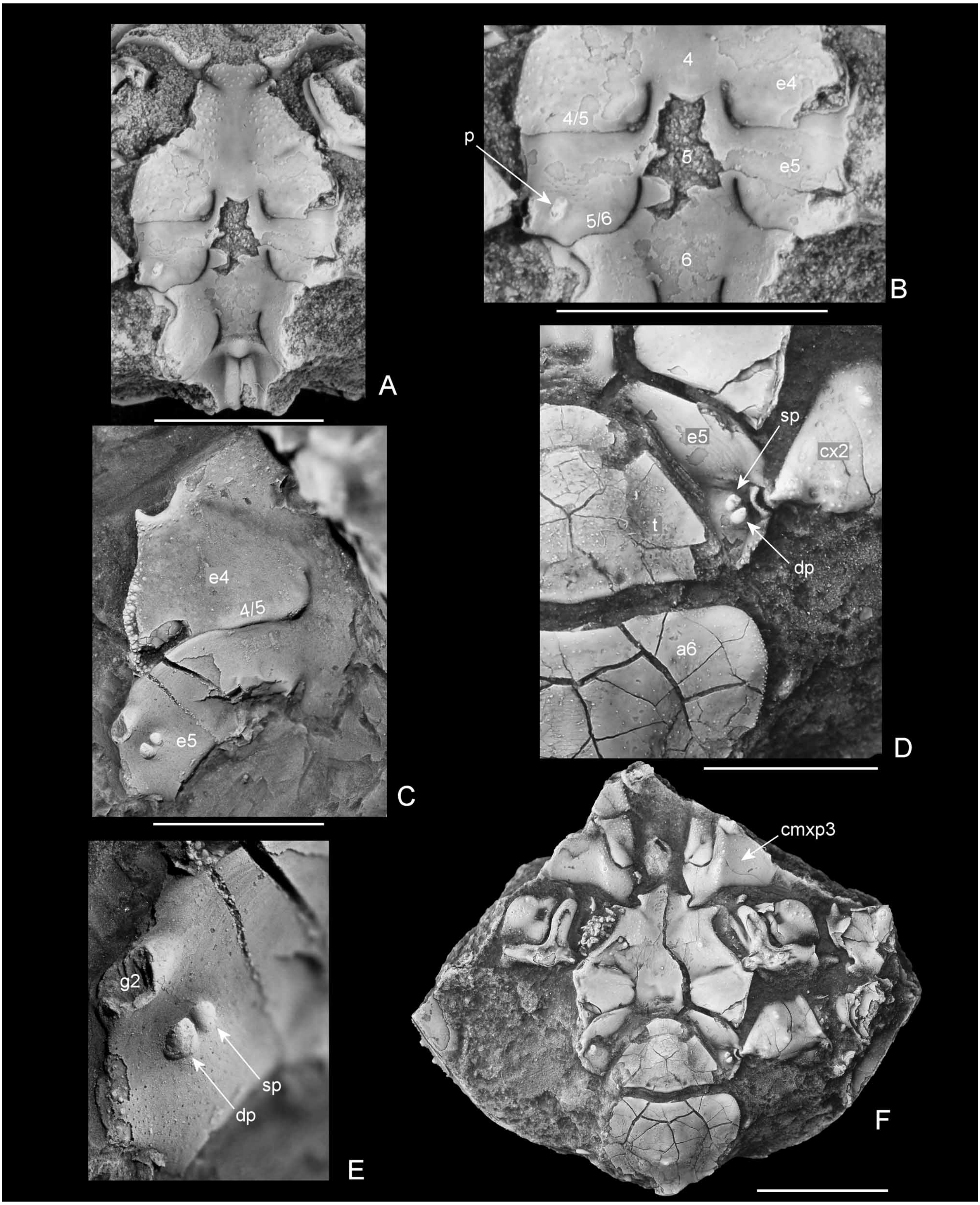


FIGURE 40. Double peg in Palaeocorystoidea; A, B, *Silvacarcinus laurae* Collins & Smith, 1993 (Orithopsidae), IRScNB TCCI 6115 (**holotype**), lower Eocene (Ypresian), Brussels (Belgium); ventral view showing thoracic sternum, and detail of thoracic sternum; C–F. *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Cenomanocarcinidae), MAB k. 2909 (C, E), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County, Texas (U.S.A); details of thoracic sternum; MAB k. 2895 (D, F); same provenance, detail of abdomen and thoracic sternum, and ventral view showing thoracic sternum, abdomen and base of mxp3. **4, 5, 6,** thoracic sternites 4, 5, 6; **4/5, 5/6,** thoracic sternal sutures 4/5, 5/6; **a6,** abdominal somite 6; **cmxp3,** coxa of mxp3; **cx2,** P2 coxa; **dp,** distal peg; **e4, e5,** episternites 4, 5; **g2,** gynglyme for P2 coxa; **p,** peg (undifferentiated); **sp,** subdistal peg; **t,** telson. Scale bars: A-E: 5mm; F: 10mm.

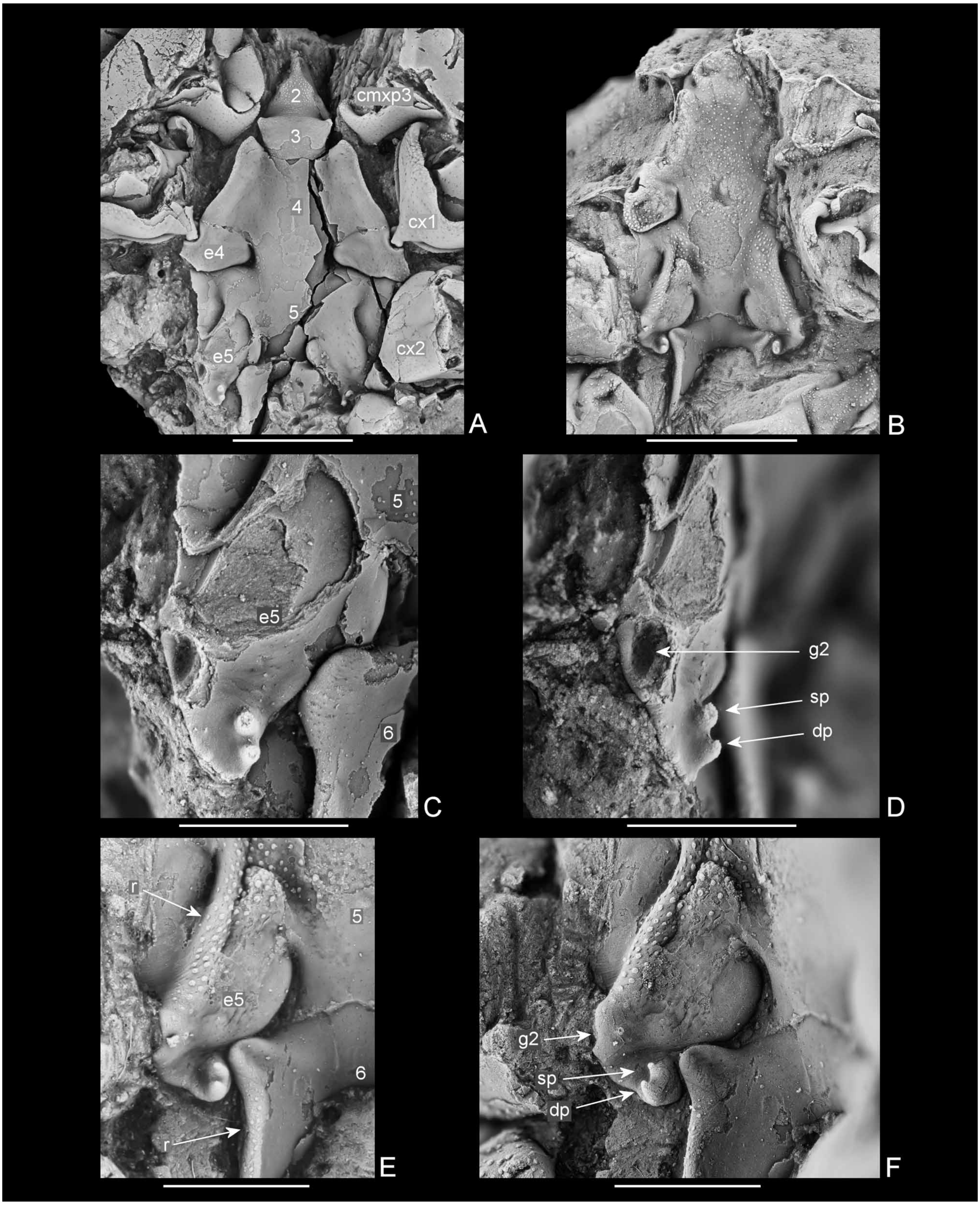


FIGURE 41. Double peg in palaeocorystids; A, C, D. *Joeranina broderipii* (Mantell, 1844) **n. comb.**, MAB k. 2896 (indeterminate sex), Albian, Folkestone (Kent, southeastern England); ventral view showing thoracic sternum and bases of pereiopods; detail of thoracic sternum, and left lateral view showing double peg; B, E, F. *Notopocorystes stokesii* (Mantell, 1844), MAB k. 2897 inndeterminate sex), middle Albian, Pargny (northern France); ventral view showing thoracic sternum; detail of thoracic sternum showing double peg, and right oblique lateral view showing double peg. **2, 3, 4, 5, 6,** thoracic sternites 2, 3, 4, 5, 6; **cmxp3,** coxa of mxp3; **cx1, cx2,** P1, P2 coxae; **dp,** distal peg; **e4, e5,** episternites 4, 5; **g2,** gynglyme for P2 coxa; **r,** ridge; **sp,** subdistal peg. Scale bars: A, B: 5mm; C–F: 2mm.

Evolution of Palaeocorystidae and Lyreididae. The acquisition of an abdominal-holding mechanism is the prime brachyuran innovation, absence of any locking mechanism being extremely rare. The lack of a holding mechanism in most Raninoidea is not regarded as primitive, but considered derived in view of the high degree of specialisation and therefore a secondary loss. We agree with Wright & Collins (1972: 72) that, 'the uncoiled abdomen of so many raninids is obviously a secondary adaptation'.

The diverse variations of the abdominal holding system that can be recognised in Raninoidia have great phylogenetic value. A sequence may be envisaged in the evolution of Raninoidea, commencing with Palaeocorystoidea. The rather long and wide male abdomen excavated on a 'normal' thoracic sternum in Palaeocorystidae is received in a sterno-abdominal depression as is the case in basal podotremes, the telson reaching sternite 4 at about the vertical level of the gynglymes for the P1 coxae. In contrast, the abdomen of Lyreididae is shorter and narrower, the telson only reaching sternite 5 and resting in a small cavity between the projections of episternite 5. The lyreidid abdomen is obviously shortened compared to that of palaeocorystoids. The abdominal somite 6 in palaeocorystids has nearly straight lateral margins, only a swollen surface at the posterolateral corners, more distinct in males than in females, but without any lateral projections. It is predicted that these inflated corners correspond to underlying sockets although it was not possible to prepare the ventral side of abdominal somite 6 in any palaeocorystoid to illustrate these.

Sternites 5–8 are wide in Palaeocorystidae, wider than in Lyreididae. In Raninoidea other than Lyreididae sternites 5–8 are distinctly narrow, even keel-like. The posterior sternites in palaeocorystoid families show a 'normal' podotreme condition, not particularly reduced in width, except for Palaeocorystidae, in which posterior sternites are only slightly narrower.

The double peg is known from several positions on episternite 5 in Palaeocorystoidea. It is placed centrolaterally on the episternite in *Cenomanocarcinus*, the two strong, sharp teeth being on a slightly vaulted part of the episternite, separated from the gynglyme for P2 by a shallow depression (Fig. 40C–F). This position roughly corresponds to that in *Silvacarcinus* (Orithopsidae; Fig. 40A, B) and *Camarocarcinus* (Camarocarcinidae; Fig. 39E, F). The pegs in *Cenomanocarcinus* are not parallel to the body axis, but lined up obliquely. In Palaeocorystidae the double peg is situated at the lower margin of the episternite 5, which extends slightly posterior of the P2 gynglyme (Figs. 39A–D; 41A–F). A short depression between the pegs and the gynglyme is most distinct in *Notopocorystes stokesii*, where it extends to the lateral ridge of sternite 6 and thus 'isolates' the posterior portion of the episternite (Fig. 41E). The depression is weaker, and the posterior portion of the episternite is more elongated in *Joeranina broderippii* **n. comb.** (Fig. 41C). The pegs are lined up parallel to the body axis in Palaeocorystidae.

Among Raninoidea, only lyreidids lock their abdomen. A holding system is known in the oldest known lyreidid, *Marylyreidus punctatus* **n. comb.** Short hook-like projections, distally with a double peg (Fig. 38A, B) are present in one specimen (MAB k. 0214). The short, triangular projections pointed slightly outwards are situated posterior the P2 gynglyme. Possession of hook-like projections with distally a double peg place *Marylyreidus* **n. gen.** in Lyreididae; because of a unique sternal configuration (condition of sternite 4, and mxp3) and a peculiar cuticle structure (fungiform nodes), it is placed in its own subfamily. The hook-like projections in *Lyreidus* and *Lysirude* are slender and long, extending far posteriorly (Fig. 36A, B, E–G), curved, and starting at the P2 gynglyme.

It is hypothesised that the holding mechanism of Palaeocorystoidea evolved from a double peg centrally on the episternite (the basal condition: Camarocarcinidae, Cenomanocarcinidae and Orithopsidae) into a more laterally placed double peg, due to migration to the border of the episternite (Palaeocorystidae). The double peg is at the border of the episternite, not placed on a hook-like projection in Palaeocorystidae. It appears that the palaeocorystid pegs are homologous to the lyreidid double peg, which is placed at the distal end of the hook-like projections. We may thus assume that the double peg is a preserved plesiomorphy in Lyreididae (lost in other Raninoidea), the hook-like projections being shared apomorphically by all lyreidids.

The abdominal-holding system in Palaeocorystidae and Lyreididae likely has the same functional effect, a similar movement to lock the abdomen. The abdomen is first moved anteriorly and then posteriorly to place the socket over the double peg. The palaeocorystid abdominal holding mechanism is formed by a wider construction and is more anterior than in Lyreididae, in which the double peg has attained a more posterior location on the hook-like projections, which corresponds to a rather broad and long abdomen in Palaeocorystidae. In a normal position (i.e., pressed against the body, thus 'locked'), the palaeocorystid telson is able to reach further, to sternite 4, in contrast with the shorter abdomen of extant and fossil Lyreididae where the telson reaches only sternite 5.

Abdominal somite 6 is narrow and the large P3 coxae have a more axial placement in lyreidids than in palaeocorystids. Abdominal somites 5 and 6 are of equal width in Palaeocorystidae. Extant lyreidids show an abdomen with completely flexed somites 4–6, which entirely cover in width the thoracic sternum, a podotreme characteristic (Guinot 1993b: 1326, 1330, fig. 4).

A strong specialisation to burying made raninoidids reduce the thoracic sternum in width which, concomitantly, led to a reduction of the abdomen in length. Within Raninoidea, lyreidids, with a longer abdomen that can be locked, is considered basal. The Marylyreidinae **n. subfam.** appear to illustrate an intermediate phase, with more basal characters than the more derived Lyreidinae, and has no equivalent amongst extant forms. Ultimately, the evolutionary pathway supposedly gave rise to the other Raninoidea. The hook-like projection with the double peg in extant Lyreididae is a certain indicator of the polarity outlined here. The holding system has disappeared in the more modified Raninoidea, where most of the thoracic sternum is narrow and the shortened abdomen not firmly held against the body.

The palaeocorystid body is elongated length-wise, allowing rapid burying; disposition of the endostome and mxp3 was oxystomian, evidence of a buried lifestyle. The specialisation in back-burrowing led the palaeocorystids to reduce the width of both thoracic sternum and abdomen, to shorten the abdomen, and, as a result of these morphological adaptations, to modify the abdominal holding mechanism. When the abdomen shortens, the posterior migration of somite 6 was accompanied by the posterior migration of the double peg. A projection of episternite 5 already existed in early lyreidids (late Albian–early Cenomanian).

The changes between the palaeocorystoid and raninoid conditions required several near-simultaneous modifications and different adjustments, which include the exposure of several thoracic pleurites, changes in the location of the spermathecal apertures, the junctions between the thoracic sternum and the pterygostome and between the thoracic sternum and the exposed pleurites, and the loss of Milne-Edwards openings and of abdominal holding. The Marylyreidinae **n. subfam.**, without a sternum/pterygostome junction but with a sternum/exposed pleurites junction, appears intermediate within this evolutionary series, and thus represents a link of great importance in the raninoidian morphocline.

Modifications for a burying mode of life

Burying and burrowing behaviour. The terms ‘burrowing’ and ‘burying’ have often been used interchangeably in the literature, even if these two types of behaviour are clearly distinguishable (Atkinson & Taylor 1988; Bellwood 2002b: 1223, 1224, fig. 2). In burrowing, a physical structure (burrow) is formed, whereas in burying the body is partially or entirely covered and is surrounded by sediment without the formation of a burrow. The behaviour in which the crab constructs a permanent burrow is described as ‘side-burrowing’ (*sensu* Warner 1977: 75). The term ‘digging’ describes the behaviour in slipper lobsters, sand crabs and some true crabs, but is applicable to raninoid crabs as well (Faulkes 2006: 144). Raninoids are typical ‘back-burrowers’ (e.g., Warner 1977: 75; Collins 1997: 75) by propelling the body backwards to descend into the substrate. Burying behaviour is primarily involved in predator avoidance (Nye 1974; Barshaw & Able 1990).

It is surprising how little is known of the biology of the living Raninoidea. Only studied is the biology of *Ranina ranina*, the large-size commercial crab, but its locomotion and process of entering the sediment were not described in detail until Faulkes (2006). In *R. ranina* all pereiopods are active for digging in a co-ordinated movement pattern, using mainly P2–P4 as shovels, P5 being less flexible. The short and stiff abdomen is also rhythmically active during digging, individuals remaining half-submerged in sand, with several movement patterns of locomotion above the sand (Faulkes 2006: 147, fig. 2, table 1; see also Tinker 1965: 80, 81; Catala 1979: fig. 45).

There are several ways to bury into substrates, but similar behaviours occur in different brachyuran families. Bellwood (2002b: fig. 2, table 1) recognised burying in ten families: Atelecyclidae Ortmann, 1893, Calappidae De Haan, 1833, Cancridae Latreille, 1802, Corystidae Samouelle, 1819, Hymenosomatidae MacLeay, 1838, Leucosiidae Samouelle, 1819, Matutidae De Haan, 1835, Orithyiidae Dana, 1852, Portunidae Rafinesque, 1815 and Raninidae, of which nine are currently included in Heterotremata (see Ng *et al.* 2008), and only one (Raninidae) in Podotremata. Conversely, strict burrowers actively excavate permanent burrows or tunnels in sand or mud by using their chelipeds and/or their legs. This different activity pattern is part of the complex behaviour encountered in some Heterotremata and most Thoracotremata, the most derived Brachyura.

Burying also occurs in Dorippoidea, a group showing some characters that, at first sight, resemble podotreme traits. Both dorippids and ethusids nevertheless have true eubrachyuran features, which place them in Heterotremata (e.g., Guinot 1978: 245; Jamieson 1994: 390). Dorippids and ethusids are known to carry a wide variety of live and dead objects (sponges, bivalve shells, starfish, both regular and scutellid echinoids, jellyfish, sea anemones, or even leaves) with their reduced, mobile and subcheliform P4 and P5 (Guinot *et al*. 1995: 387; Ng *et al*. 2008: fig. 44). Dorippids may partially bury themselves while holding objects, the posterior body rapidly entering sand or mud, thus burying backwards. Nevertheless, burying in dorippids differs markedly from that of Raninoidea.

Among podotremes, cyclodorippoids partially bury themselves, combined with camouflaging, both types of behaviour similar to those of dorippoids. Observations are scanty, except for *Deilocerus* Tavares, 1993b (Cyclodorippidae) in which carrying behaviour was observed (Garth 1946: 353; Wicksten 1982: 307; Tavares 1994: 164), but no burying behaviour has been described. *Krangalangia* sp. has been observed burying into the sediment in an aquarium onboard the RV Alis (New Caledonia) (observation by M. Tavares). According to Guinot & Tavares (2001: 529) because of their mobile and subcheliform P4 and P5, carrying behaviour in cyclodorippoids could take place in addition to a burying activity, seen the oxystomian disposition of the respiratory system. The fossil record for the Cyclodorippoidea is unfortunately extremely meagre (De Grave *et al*. 2009: 29, excluding the Torynommatidae Glaessner, 1980).

Modifications for burying are diverse and ‘there appears to be no specific morphological adaptations for burying in brachyurans, apart from those features associated with respiration whilst buried in the sediment’ (Bellwood 2002b: 1223). Several morphological adaptations for burying, including those relating to respiratory features, can be recognised in fossil specimens.

The exclusively fossil Dakoticancroidea most likely used their reduced P5 (Dakoticancridae) or P4 and P5 (Ibericancridae) to camouflage their body by carrying objects (Artal *et al*. 2008: 18). Nevertheless, the thickness of the body and the reduction of P4 and P5 indicate a different mode of life in both families (Artal *et al*. 2008: 19). Differences in their respiratory configuration support this hypothesis (see below).

All palaeocorystoids were able to bury. The Necrocarcinidae and Camarocarcinidae, the most basal and less modified, are the least well adapted for back-burrowing. The body is distinctly convex; nevertheless, distinct modifications of their maxillipeds, pterygostome, branchiostegite and chelipeds can have contributed to respiration. Burying habits are assumed on the basis of such modifications and may be compared to a large extent to those of the Calappidae (Garstang 1897b; Bellwood 1996).

Cenomanocarcinids and orithopsids may have preferred a swimming mode of life, but most likely could have also buried. The flattened articles of the P3 and P4 of *Cenomanocarcinus vanstraeleni* were modified probably for both swimming and burying (Guinot *et al*. 2008: 12). Many swimming crabs are able to bury themselves thanks to their flattened pereiopods and streamlined bodies, and are modified to breathe whilst buried (Garstang, 1897b; Bellwood 2002a, b). The same holds true for cenomanocarcinids and orithopsids, although a similar mode of life may have arisen independently in the two families.

The body shape and morphology of palaeocorystids is specialised for rapid back-burrowing. Förster (1970: 142) hypothesised that the earliest known palaeocorystid, *Notopocorystes*, was a back-burrowing specialisation of a necrocarcinid ancestor; a concept with which we agree. The Palaeocorystidae is the only of the five palaeocorystoid families that is often found *in situ*, and may occur in great numbers. Such large populations are ideal to further specialisation as a result of natural selection (Ernst & Seibertz 1977; Kier 1982). The fossil record reveals that their body and appendages were modified into a raninoid (gymnopleure) condition during a short timespan (see below).

Elongation of the body. Evolution has led to elongation and narrowing of the body, which encompasses an alternative polarity to typical carcinisation (McLaughlin & Lemaitre 1997). A streamlined body is more efficient for rapid burying than non-elongated bodies, although particular substrates are likely to require special approaches. It is evident, for instance, that the ability to bury rapidly is enhanced by the elongated body of *Corystes* (Hartnoll 1968, 1972).

Extant raninoids typically have elongated bodies, although there are a few exceptions. *Symethis* has a long body, an elongated anterior portion of the carapace, and an ‘eroded’ carapace surface; *Ranina* a wide body and a scabrous dorsal carapace (Savazzi 1981); *Notopus* a moderately wide body and a spinous suborbital ridge; *Cyrtorhina* a wide, rounded body and densely ornamented dorsal carapace. Palaeocorystoids typically have a subhexagonal carapace, which is elongated in Palaeocorystidae. The latter have particularly wide orbits that occupy most of the carapace width. A subhexagonal carapace outline can still be recognised in lyreidids, although the anterolateral margin lack the several teeth that characterise palaeocorystids, a result of different respiration mechanisms (see *Respiration in the Brachyura* below). Carapace outline may thus help in recognising family placement (see under *Bournelyreidus* **n. gen.**, *Cristafrons*).

A globular body shape does not deprive a crab of its ability to bury. Leucosiids, calappids and hepatids, all with a tumid carapace, have been reported to bury (Bellwood 2002b: 1225, 1226, fig. 1, table 1). Camarocarcinids and necrocarcinines have a distinctly tumid carapace. The early forms of *Notopocorystes* (Collins 1997: 79, pl. 22, figs. 1b, 2b, 4) are rather tumid, 'in outline *Necrocarcinus* is more 'Brachyurous' than *Notopocorystes* but the latter was the source of a flourishing stock that became increasingly specialised for burrowing' (Wright & Collins 1972: 72). Portunids have a streamlined body, which generally is wider than long, and elongated pereiopods in a modified dorso-ventral level, with flattened distal articles, at least on the P5. Primarily, these modifications allow swimming through the water column (Schäfer 1954; Hartnoll 1971), and secondarily to bury in the sediment. On the other hand, raninoids may use the burying modifications of their pereiopods to swim (Hartnoll 1971: 35), as described in detail for *Ranina ranina* (Faulkes 2006: 151).

Size of arthrodial cavities. One of the most notable features of extant Raninoidea are the large P1–P4 coxae and their similarly large arthrodial cavities. The robust digging pereiopods and rapid burial into the sediment imply powerful muscles that are housed in deep muscle cavities in the interior of the thorax. The P1–P3 are 'exceedingly strong, and are actuated by largely developed muscles enclosed in remarkably deep cavities formed by the endophragmal skeleton' (Bourne 1922b: 32). The large muscle chambers would not be possible without the elongation (and as a consequence, the exposure) of pleurites 5–7, which act as lateral walls and extend the depth of the body. Conversely, palaeocorystoids have bodies thicker than raninoids, without exposed pleurites. The large sizes of the arthrodial cavities and the P1–P4 coxae are, however, similar to those of Raninoidea.

The thoracic nerve ganglia of *Lyreidus tridentatus* and *Ranina ranina* examined by Bourne (1922b: 32, the latter as *R. dentata*) show a tendency to form two groups correlated with the development of pereiopods into digging organs. The last two arthrodial cavities (of P4 and P5) are tilted in Raninoidea, their openings pointing more posteriorly than in Palaeocorystoidea; the P5 arthrodial cavity is small and opens dorsoventrally. The P5 coxa of Raninoidea, which is partially overlapped by the first abdominal somite, bears the male gonopore and the penis, thus has a function in reproduction. In addition, the P5 forms the roof of the accessory water channel in most raninoids (see *Respiration in the Brachyura* below).

Coxae narrowing and ventral opening of arthrodial cavities. The normal condition in Brachyura is that the arthrodial cavities open laterally (Fig. 42A). Because the relative position between the sternal and pleural gynglymes determines the orientation (ventro-lateral) and angle of movement (postero-anterior) of the coxae and hence the legs, these positions are the key to the locomotory characters of the crab.

The carapace architecture of palaeocorystoids shows the 'normal' brachyuran condition: carapace rather convex in transverse cross section, *linea brachyura* located below the lateral carapace margins, and a high branchiostegite. The thoracic sternum lies clearly in a lower level than the lower margin of the branchiostegite and is never keel like. The body of palaeocorystids is slightly flattened, the branchiostegite fairly well developed (Figs. 2D, 45A–C), the thoracic sternum is slightly reduced in width, especially posteriorly. The coxae show a typical ventro-lateral orientation in Palaeocorystidae. The coxo-pleural articulation apparently displays a lower position than in other palaeocorystoid families; in *Notopocorystes* (Figs. 14A, 45B) the lower margin of the branchiostegite shows distinct convex deflections for the articulations for the P2 and P3, contrary to other palaeocorystoids. The branchiostegite is slightly reduced in height in *Ferroranina* **n. gen.** and *Joeranina* **n. gen.** (Fig. 45A, C) and deflections of its lower margin are indistinct, which suggests the gynglymes are positioned just below the lower margin of the branchiostegite. In deformed or fragmentary palaeocorystid specimens with damaged branchiostegite or displaced axial skeleton, the internal pleurites are visible but no part of them corresponds to the exposed pleurites of Raninoidea.

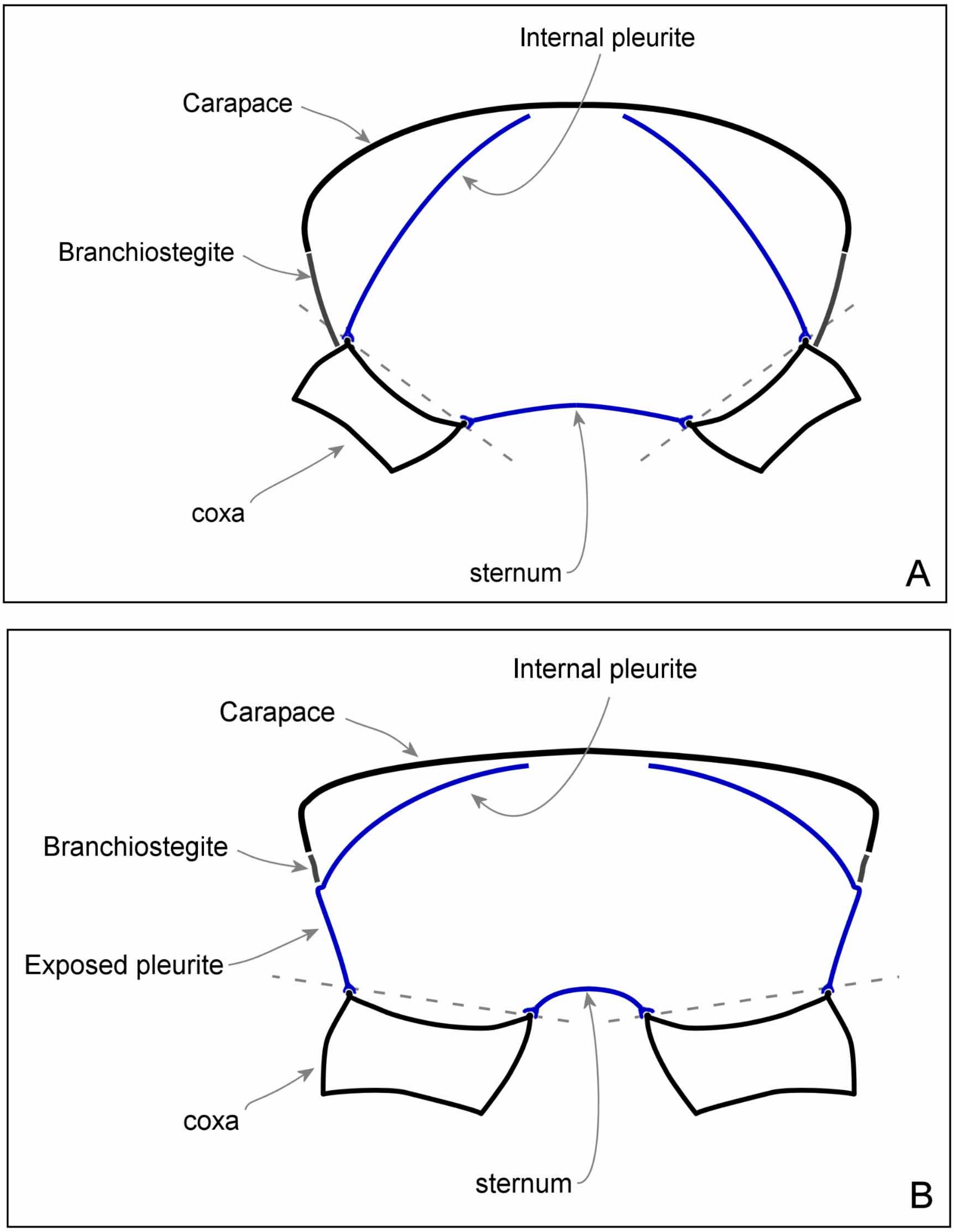


FIGURE 42. Diagrammatic cross section showing architecture of body; A, generalised brachyuran; B, generalised raninoidean with exposed pleurites (gymnopleurity).

The thoracic sternum is narrow but never keel-like in Lyreididae; sternite 5 narrows posteriorly, sternites 6–8 slightly decrease in width. Pleurites 5–7 are partially exposed, the length of each pleurite (measured along the border of the branchiostegite) is larger than the exposed height.

In most other Raninoidea sternite 5 is markedly narrowed between the P2, and sternites 6 and 8 are keel-like (Bourne 1922b: 27, 55; Guinot & Bouchard 1998: 639). The length of each pleurite is smaller than its exposed height.

It is proposed that the width of the thoracic sternum and the relative exposure of the pleurites are related in Raninoidea, and their condition dependent of the degree of back-burrowing specialisation. Palaeocorystoidea is basal, Lyreididae intermediate when considered in an evolutionary series.

By reducing the sternal width, the coxae attain a more axial (medial) placement compared to the original condition, an organisation that is also the normal one in Brachyura. The height of the exposed pleurites determines the ventro-lateral orientation of the coxae. Because the pleurites attain a great height in Raninoidea, the pleural and sternal gynglymes come in nearly the same level. The arthrodial cavities attain a near-ventral opening, and the coxae acquire a ventral orientation. The enlarged coxae accompany a narrow sternum, which is no longer a ventral plate, but only serves to receive the articulation of the pereiopods and house the spermathecal apertures in the females. With the exposed pleurites present as tall lateral walls, the wider endoskeletal chambers can now house larger muscles, whereas the carapace remains relatively flat.

This new configuration results in several biomechanical benefits for burrowing. A wide sternal plate under the body means a place where it is difficult to remove sand to the surface. The keel-like thoracic sternum of raninoids is not a primitive feature *per se*, but the result of significant narrowing for back-burrowing. The ventral orientation of the legs enhances the burrowing capabilities underneath the body; in combination with the tilted posterior sternites, the crab has its digging tools in the most efficient position.

Exposed pleurites in Raninoidea: the gymnopleure condition. A feature unique to Raninoidea, an autapomorphy, is the partial exposure of pleurites 5–7, the exposed external portions being more heavily calcified than the internal ones. In contrast, the lower edge of the branchiostegite normally fits closely to the coxae of the pereiopods in other Brachyura. According to Bourne (1922b: 37), ‘The lower moieties of the epimera [*pleurites*] of the eleventh, twelfth, and thirteenth segments [somites 5, 6 and 7] are therefore exposed on the surface, and form a somewhat excavated and roughly quadrilateral area between the coxae of the limbs and the branchiostegite.’ Hence, the establishment of the tribe Gymnopleura (with ‘exposed pleurites’, as opposed to pleurites which are completely covered and internal, as usual in other Brachyura) to include all Raninoidea (Bourne 1922b: 55).

In Palaeocorystoidea, including the back-burrowing stock Palaeocorystidae, the pleurites are in the normal brachyuran condition: internal, not exposed, being concealed under the branchiostegite and carapace, as shown by the examination of hundreds of well-preserved palaeocorystoid specimens. In contrast, in Raninoidea, thoracic pleurites 5–7 are partially exposed by a strong reduction of the branchiostegite, resulting in a narrowing of the thoracic sternum, and a more axial and ventral placement of the arthrodial cavities (Figs. 42B, 60C). Partial exposure of the thoracic pleurites, which is an apomorphic trait for Raninoidea, makes this unusual placement of the arthrodial cavities possible. The earliest known raninoid, the lyreidid (marylyreidine) *Marylyreidus punctatus*, from the upper Albian–lower Cenomanian of Texas, clearly shows this unique condition, i.e. exposed pleurites 5–7. The posterior carapace is rather flat, the branchiostegite reduced posteriorly, and exposed pleurites 5–7 forming a rather flat plate, which increases the depth of the body.

We concur with Bourne (1922b: 53) that the exposure of pleurites in Raninoidea is the result of the strong specialisation to the back-burrowing habits. Concomitant with the acquisition of exposed pleurites 5–7, the crab is adaptable to modify its respiratory system. A subsequent adaptation is the transformation of the shape of the plate formed by the exposed pleurites. This plate varies from slightly to strongly modified in Raninoidea. The branchiostegite and the plate formed by the exposed pleurites become excavated in the more derived raninoids, resulting in the formation of a water circuit alongside the body. The reduced, often long and plumose P5, are pressed along the posterolateral margins, contributing to form the roof of this lateral waterway.

The raninoid plate formed by the exposed pleurites 5–7 varies from rather low and flat (Lyreididae, Notopodinae) to large and strongly excavated (Raninidae) (Figs. 43A, B; 46A, B). The exposed pleurites 5–7 form a flat plate in lyreidids, practically in continuity with the branchiostegite and only lined by the filiform P5 (Figs. 46A, 51B). Conversely, in Raninidae (Fig. 43A), the exposed pleurites 5–7 form a deeply excavated area, overhung by the branchiostegal edge and complemented by the P5, precisely fitting the carapace margin. The plate formed by exposed pleurites 5–7 is not excavated in Symethinae (Fig. 31E), but the branchiostegite itself is excavated, and this area is overhung by the adapted P5 strictly apposed along branchiostegal margins.

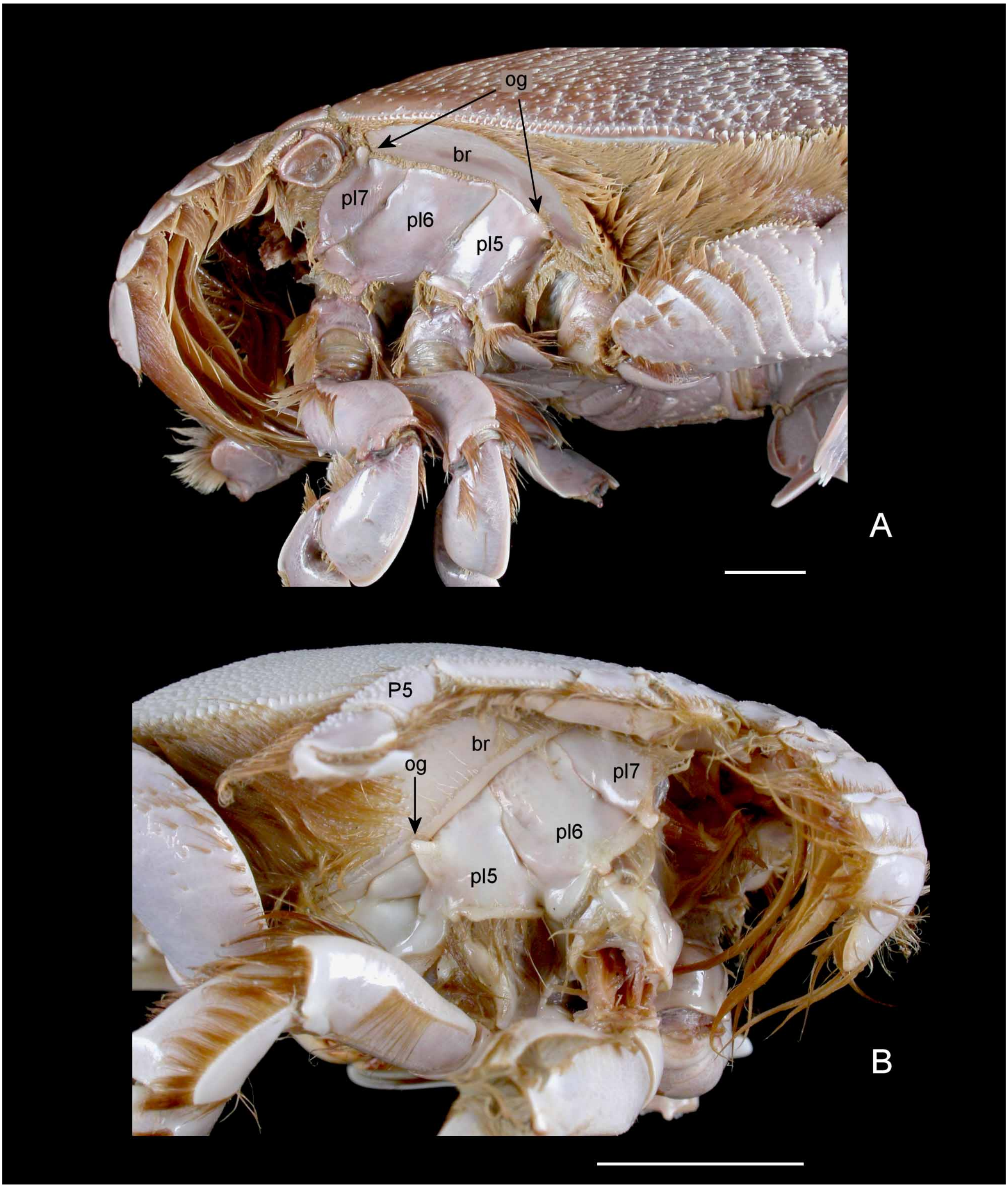


FIGURE 43. Exposed pleurites (gymnopleurity) in extant raninids; A, *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), MNHN-B31983 (female), Tulear, Madagascar; right lateral view showing exposed pleurites; B, *Cyrtorhina granulosa* Monod, 1956 (Raninidae, Cyrtorhininae), MNHN-B16181 (female), Príncipe, Gulf of Guinea; left lateral view showing exposed pleurites. **br,** branchiostegite; **og,** outgrowth on exposed pleurite; **P5,** pereiopod 5; **pl5, pl6, pl7,** exposed pleurites 5, 6, 7. (photographs by J.-F. Dejouannet) Scale bars: 10mm.

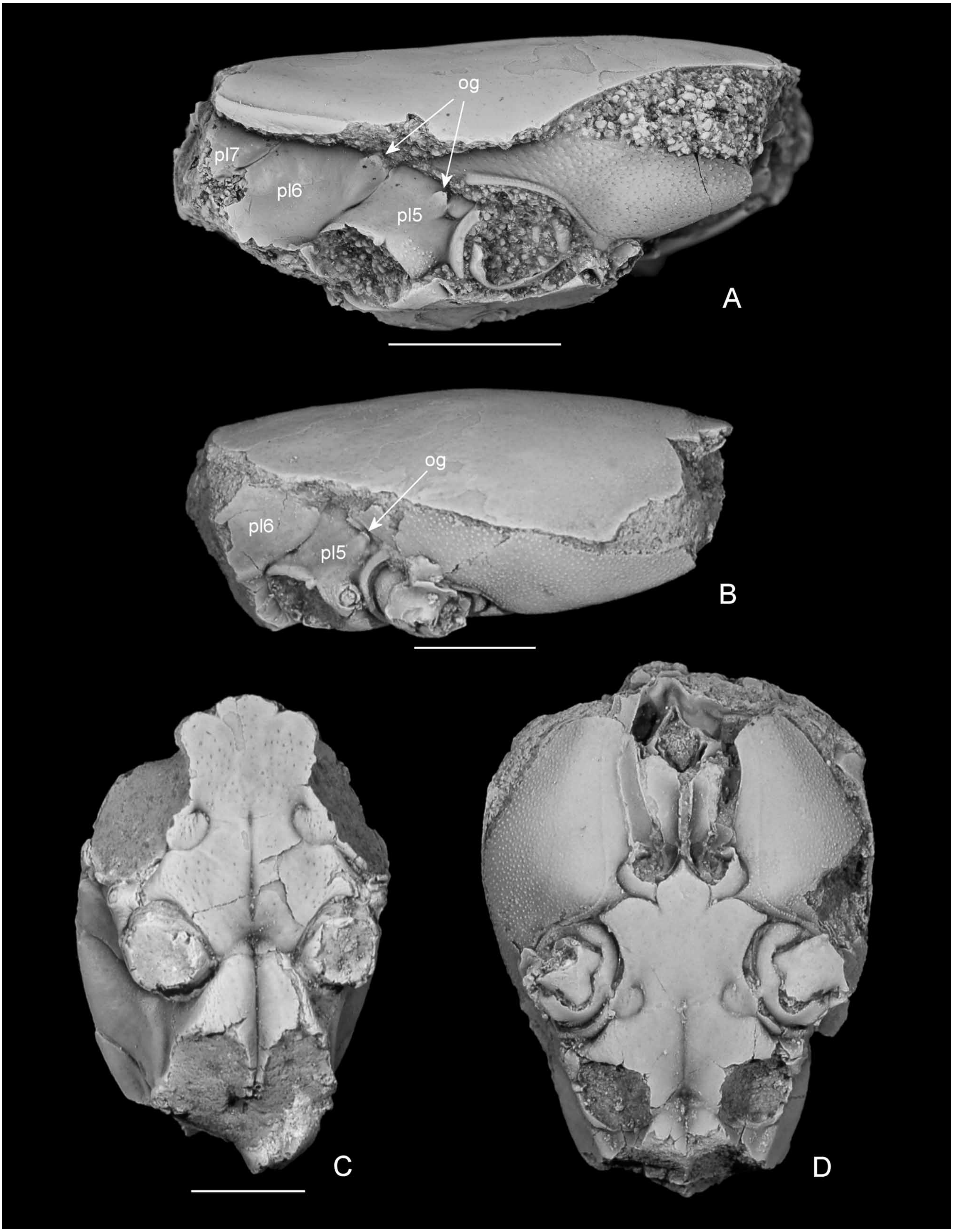


FIGURE 44. Fossil raninids; A, *Raninoides hollandica* (Collins, Fraaye, Jagt & van Knippenberg, 1997) (Raninidae, Raninoidinae), MAB k. 2004 (**holotype**; indeterminate sex), ?upper Oligocene, Winterswijk-Miste (eastern Netherlands); right lateral view showing exposed pleurites; B, D, *Raninoides glabra* (Woodward, 1871), IRScNB TCCI 6120 (indeterminate sex), lower Eocene (Ypresian), Brussels (Belgium); right lateral view showing exposed pleurites and ventral view showing thoracic sternum and appendages; C, *Raninoides glabra* (Woodward, 1871), IRScNB TCCI 6122 (indeterminate sex); ventral view showing thoracic sternites. **pl5, pl6, pl7,** exposed pleurites 5, 6, 7; **og,** outgrowth on exposed pleurite. Scale bars: 5mm.

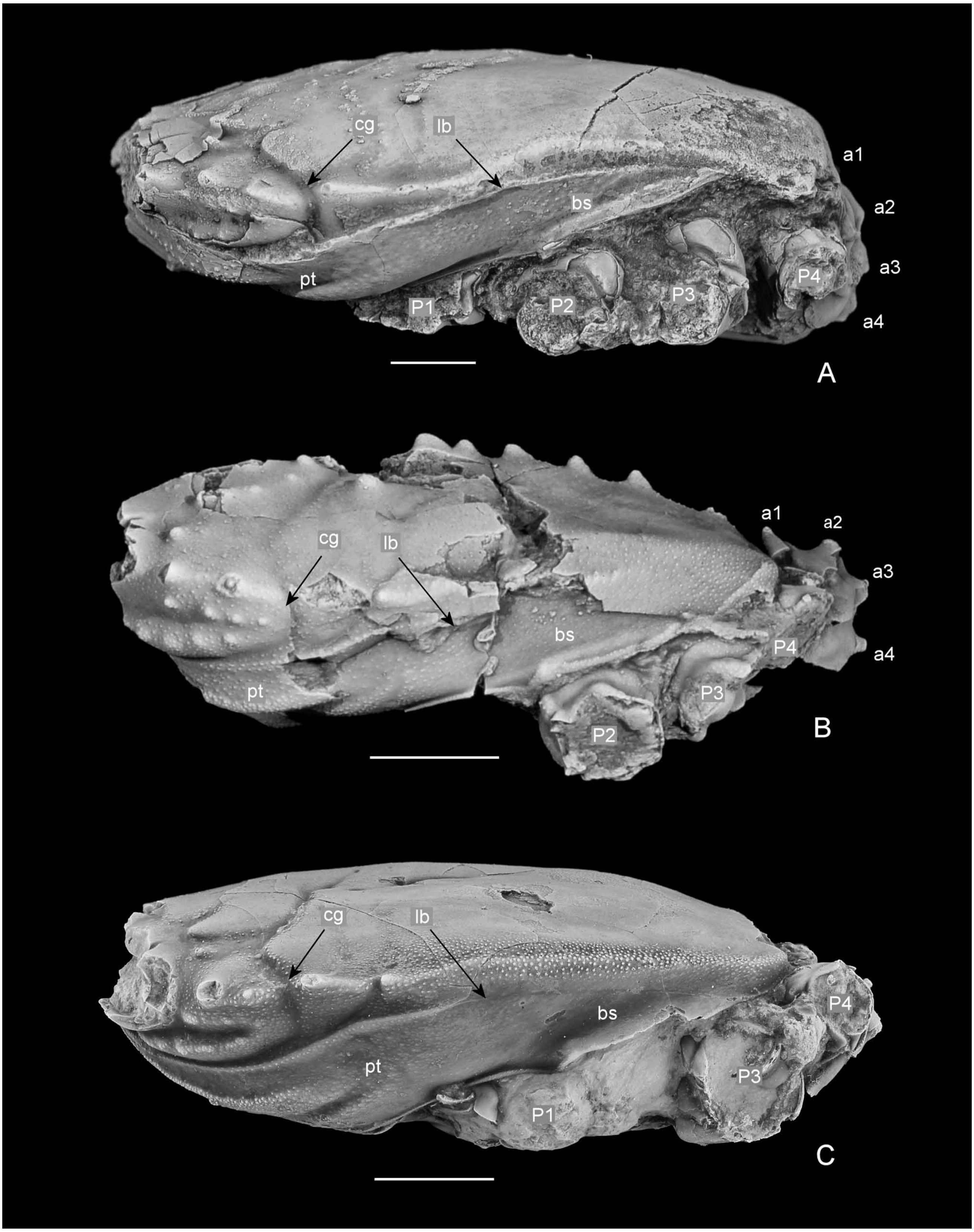


FIGURE 45. Lateral view of palaeocorystids, to illustrate that pleurites are not exposed; A, *Ferroranina dichrous* (Stenzel, 1945) **n. comb.**, MAB k. 2876 (female), Cenomanian-Turonian, Little Elm, Dallas County (Texas, U.S.A); left lateral view; B, *Notopocorystes stokesii* (Mantell, 1844), MAB k. 2873 (female), Albian, Escalles (Calais, northern France); left lateral view; C, *Joeranina broderipii* (Mantell, 1844) **n. comb.**, NHM In. 21331 (male), Albian, Folkestone (Kent, southeastern England); left lateral view. **a1, a2, a3, a4,** abdominal somites 1, 2, 3, 4; **bs,** branchiostegite; **cg,** cervical groove; **lb,** linea brachyura; **P1, P2, P3, P4,** pereiopods 1, 2, 3, 4; **pt,** pterygostome. Scale bars: 5mm.

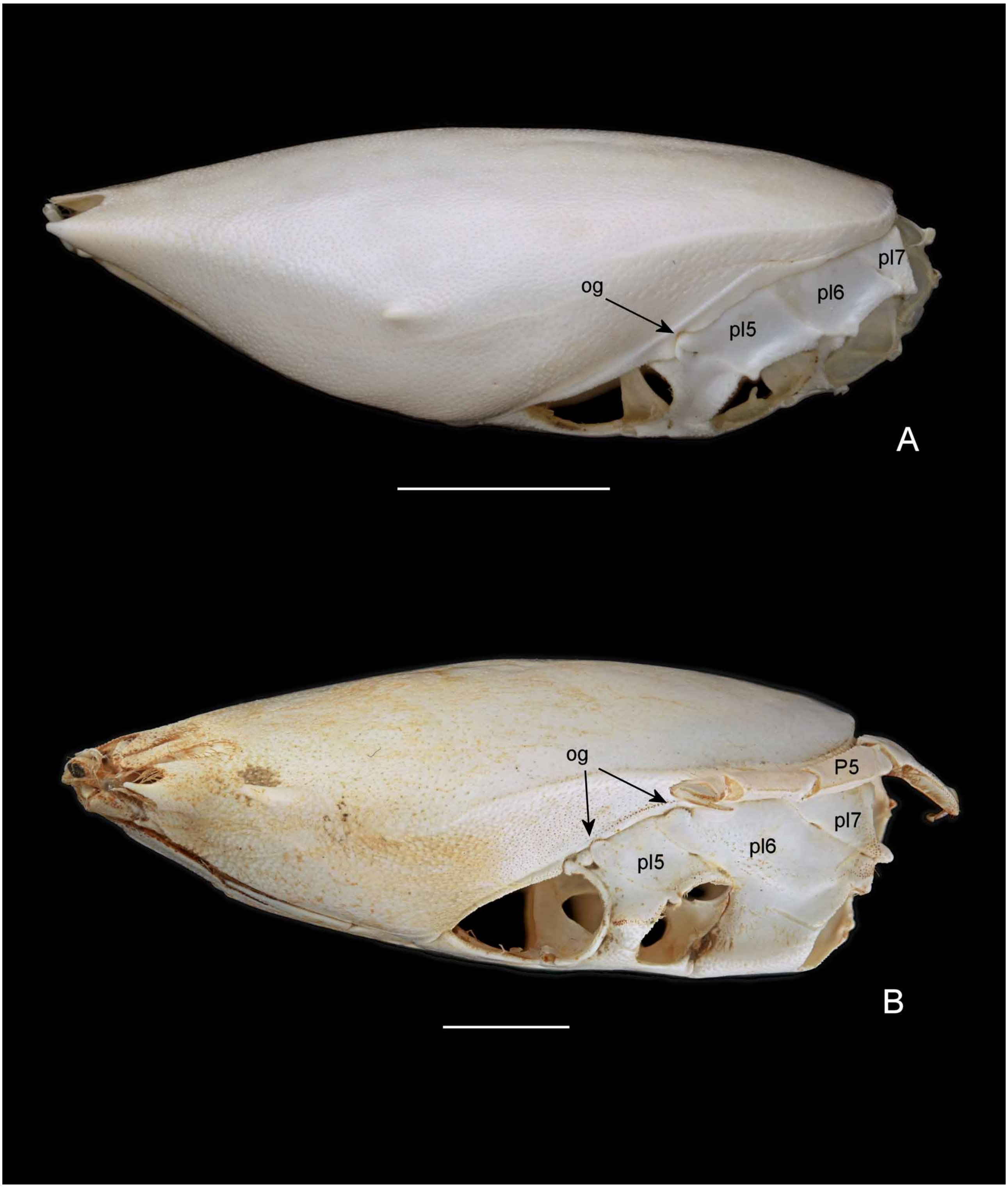


FIGURE 46. Exposed pleurites (gymnopleurity) in *Lyreidus* (Lyreididae) and *Raninoides* (Raninidae); A, *Lyreidus tridentatus* De Haan, 1841, MAB k. 2914 (male), Recent, Philippines; left lateral view; B, *Raninoides bouvieri* Capart, 1951, MAB k. 2919 (male), Recent, Philippines; left lateral view. **og,** outgrowth on exposed pleurite; **P5,** pereiopod 5; **pl5, pl6, pl7;** exposed pleurites 5, 6, 7. Scale bars: 5mm.

The edge of the branchiostegite is typically held in place by two outgrowths protruding from the outer surface of the exposed pleurites, one on the anterior edge of exposed pleurite 5 proximally, another one on the anterior edge of exposed pleurite 6 or 7 distally (Figs. 43A, B; 44A, B; 46A, B). These outgrowths mark the line between the exposed and internal pleurites. These protuberances are recognisable when the exposed pleurites are preserved *in* *situ* in fossil specimens, and were observed in *Notopus mulleri* (van Binkhorst, 1857) (Notopodinae), *Raninella trigeri* A. Milne Edwards, 1862 (Ranininae), *Raninoides glabra* (Woodward, 1871) and *Raninoides hollandica* (Collins, Fraaye, Jagt & van Knippenberg, 1997) (both Raninoidinae).

Sterno-pterygostomal junction. The mxp3 normally separate the pterygostome from the thoracic sternum, being usually the location for the anterior respiratory entrance. These main inhalant respiratory openings, the Milne-Edwards openings, are situated on each side of the mxp3 in front of the chelipeds. The mxp3 coxae, which articulate on sternite 3, are intercalated between the anterior side of sternite 4 and the pterygostome. These coxae, and their epipods, are inserted between the lower margin of the pterygostome and the P1 coxa, thus in front of the chelipeds at the entrance of the inhalant respiratory opening. Exceptions are rare, and include Dorippidae Macleay, 1838 Leucosiidae and Cyclodorippinae Ortmann, 1892 as well as all Raninoidea (except *Marylyreidus* **n. gen.**). All these forms have a modified respiratory system.

Within Dorippoidea, the Dorippidae shows a peculiar structure: the ovate, elongated Milne-Edwards openings are placed in front of the bases of chelipeds, being separated from the latter by a process of the carapace reaching down to the thoracic sternum (Fig. 47D). The thoracic sternum (in that case episternite 3) develops a junction with the pterygostome. Thus, despite the junction, there is an inhalant entry at the base of P1 in Dorippidae. The Ethusidae Guinot, 1977 shows the usual condition: no junction thoracic sternum/pterygostome and Milne-Edwards openings normally placed at the bases of chelipeds (Fig. 47C).

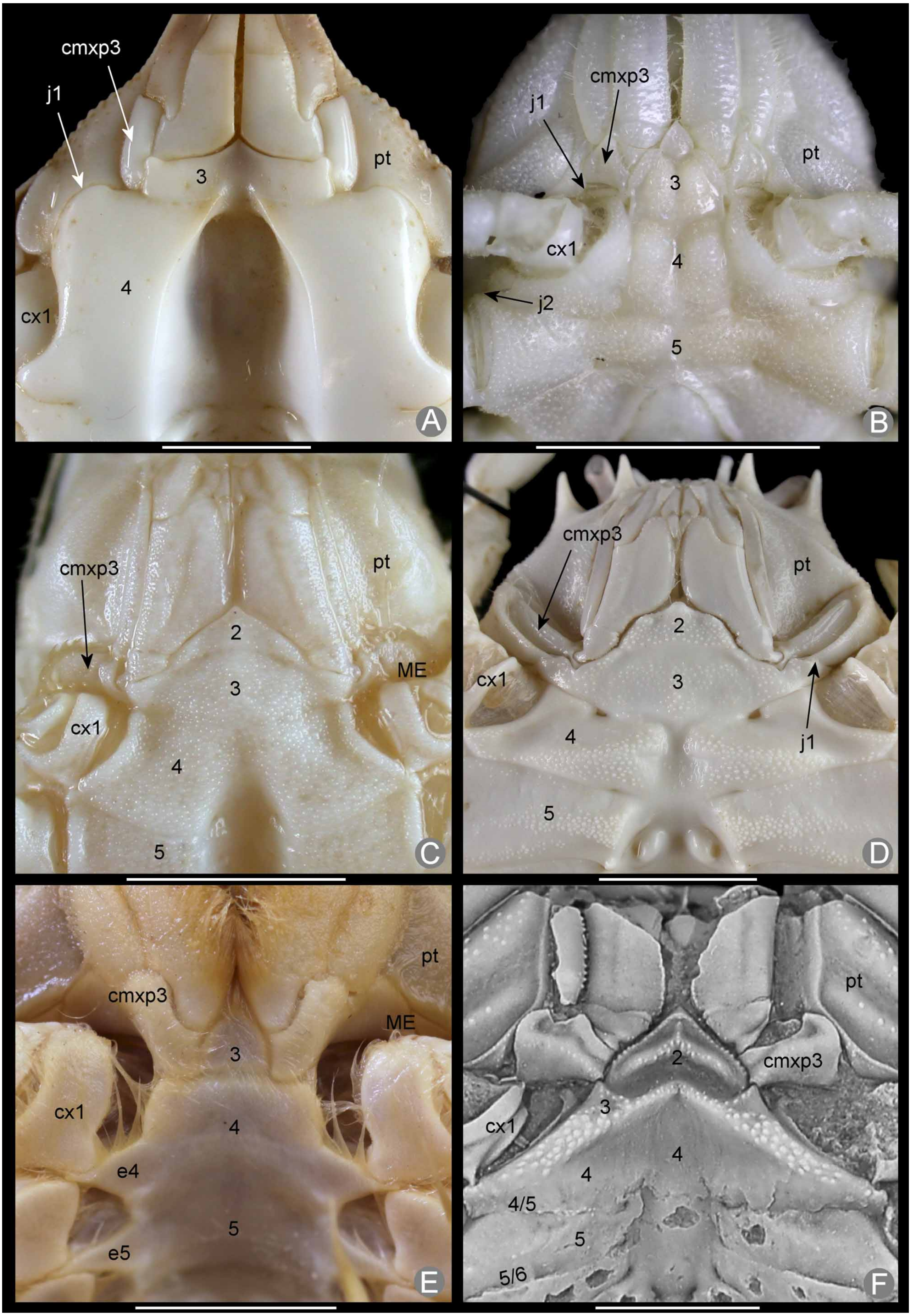
Leucosiids show a large junction of the thoracic sternum with the pterygostome (presence of a ‘sutura carapaco-sternalis’, a term used by Ihle 1915, 1918), but this junction is not present in all Leucosioidea. Bourne (1922b: 53) noted that, ‘in the Leucosiidae ... the posterior margin of the pterygostome is as intimately fused with the plastron as in the Raninidae, and with the disappearance of the pre-chelipedal branchial openings the epipodite of the third maxilliped has disappeared even more completely than in the Raninidae’. The pterygostomial gutter of Leucosiidae, which is closed by the mxp3 exopodite, is twisted posteroventrally to lead a respiratory flow under the sterno-pterygostomial junction. Thus, despite that there is no external opening in front of the chelipeds, oxygenated water enters the branchial chamber in the normal position. De Haan’s (1850: 33) suggestion that the Leucosiidae and Raninidae were related through *Lyreidus* has long been refuted (e.g. Bourne, 1922); their superficial similarities are attributed to convergence.

Among cyclodorippoids, *Tymolus* Stimpson, 1848 shows a narrow sternum/pterygostome junction (Fig. 47B). Sternite 4 is not anteriorly wide, the junction being formed by an inclined lateral extension of sternite 4. The sternum/pterygostome junction is not present in all Cyclodorippoidea, being absent in Phyllotymolinidae Tavares, 1998 (see e.g., *Genkaia keijii* Tavares, 1993a: fig. 13d) and Cymonomidae Bouvier, 1898.

The configuration in Palaeocorystoidea is similar to the one usually found in most Brachyura. In Palaeocorystoidea, however, the mxp3 coxae are remarkably large and flabelliform. A similar condition can be found in Calappidae, and Bellwood (2002a: 138) suggested that ‘this flanged condition of the 3rd maxilliped coxa is unique to the Calappidae’ (see Bellwood 1996: 176, fig. 3A; 2002b: 1226).

Sternite 4 is trapezoidal in Palaeocorystoidea, its anterior margin slightly broader than sternite 3, roughly half the width of the posterior side of sternite 4. The convergent lateral margins of sternite 4 are always slightly concave, and are variously raised. The pterygostome shows a constant pattern in Palaeocorystoidea, namely a concave buccal margin, with a broad buccal collar, and a blunt posterior corner followed by a concave posterior margin. The anterior margin of sternite 4 is clearly at a lower vertical level than the posterior corner of the pterygostome. The distal margin of the mxp3 coxa closely matches the posterior margin of the pterygostome.

In *Marylyreidus punctatus* **n. comb.** sternite 4 shows as a flat, subrectangular plate, its lateral margins being parallel to each other (Fig. 56C). The sternal plate with the anterior margin of sternite 4 located higher towards the buccal region seems to have a more derived condition than in Palaeocorystoidea. At the pterygostome, below the concave buccal margin, a large concavity is present instead of the simple blunt corner. This concavity gives room to the moderately sized mxp3 coxa, its distal margin lining the cavity. There is no junction of the thoracic sternum with the pterygostome.


cmxp3
j1
3
pt
4
cx1
A
cmxp3
j1
3
cx1
4
j2
5
pt
B
pt
cmxp3
2
ME
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cx1
4
5
C
cmxp3
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pt
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F

FIGURE 47. Configuration of sternum-pterygostome in diverse extant and fossil brachyurans; A, *Coleusia signata* (Paul'son, 1875) (Leucosioidea, Leucosiidae), MNHN-B31894 (male), Recent, Suez Canal, Egypt; B, *Tymolus brucei* Tavares, 1991 (Cyclodorippoidea, Cyclodorippidae), MAB k. 2902 (male), Recent, Palau, Micronesia; C, *Ethusa magnipalmata* Chen, 1993 (Dorippoidea, Ethusidae), MNHN-B21524 (**holotype**; male), Recent, Loyalty Islands, New Caledonia; D, *Medorippe lanata* (Linnaeus, 1767) (Dorippoidea, Dorippidae), MNHN unregistered (female), Recent, Mediterranean Sea; E, *Metadynomene tanensis* (Yokoya, 1933) (Dromioidea, Dynomenidae), MAB k. 2903 (female), Recent, south off New Caledonia; F, *Dakoticancer overana* Rathbun, 1917 (Dakoticancroidea, Dakoticancridae), MNHM B22902-2 (cast of USNM 173529-2; female), Campanian, South Dakota (U.S.A). **2, 3, 4, 5,** thoracic sternites 2, 3, 4, 5; **4/5, 5/6,** thoracic sternal sutures 4/5, 5/6; **cmxp3,** coxa of mxp3; **cx1,** P1 coxa; **e4, e5,** episternites 4, 5; **j1,** junction thoracic sternum/pterygostome; **j2,** junction thoracic sternum/exposed pleurites; **ME,** Milne-Edwards opening; **pt,** pterygostome. (photographs by J.-F. Dejouannet) Scale bars: 5mm.

In all other known Raninoidea, the posterior corner of the pterygostome forms a junction with the much expanded anterolateral parts of sternite 4. The mxp3 coxae are thus separated from the P1 coxae. The sternum/pterygostome junction varies from narrow (Lyreididae: Lyreidinae; Raninidae: Cyrtorhininae, Symethinae) to wide (Raninidae: Notopodinae, Ranininae, Raninoidinae). Anterior to this sterno-pterygostomial junction, the pterygostome shows a rather small, acute concavity in which the mxp3 coxa is placed. This concavity is clearly smaller in Raninoidea than in Palaeocorystoidea; it has been observed in numerous raninoid fossils, such as *Bournelyreidus eysunesensis* **n. comb.** (see Collins & Wienberg Rasmussen 1992: 20, fig. 10c) and *Rogueus orri* (Berglund & Feldmann 1989: 71, fig. 2.5). The sterno-pterygostomial junction is wider, more robust in more derived forms. Such is the case in Ranininae (Fig. 48B) and Raninoidinae (Fig. 44D), where the connection is broad, and the pterygostome modified.

A series with a tendency towards anterior expansion of sternite 4, resulting finally in a junction of the thoracic sternum with the pterygostome, is recognised here. Sternite 4 is trapezoidal in the basal forms (Palaeocorystoidea), subrectangular in the intermediate condition (Marylyreidinae **n. subfam.**), and widely expanded anteriorly in the most derived forms. Thus, a major difference between Palaeocorystoidea and Raninoidea is the interaction of the thoracic sternum with the pterygostome. *Marylyreidus punctatus* **n. comb.** shows an intermediate condition in this polarity.

The construction of the body becomes much stronger when the pterygostomes are interconnected. In a transverse cross section, the body outline in the Raninoidea is completely interconnected, which can be considered one of the main reasons why raninoid fossils are often found with the thoracic sternum connected, even if the specimen represents a moult rather than a corpse.

While superficially similar, the sterno-pterygostomal junctions of the Raninoidea are thus different from those in Leucosioidea. The junctions are accomplished by an anterolateral expansion of sternite 4 in Raninoidea (Fig. 48), whereas only a short projection of the pterygostome is needed to reach the wide sternite 4 in Leucosiidae (Fig. 47A). A water passage below the sterno-pterygostomal junction, as in Leucosiidae, is absent in Raninoidea. As a result, the inhalant opening in front of the chelipeds is absent in raninoids (with the exception of *Marylyreidus* **n. gen.**). This is an apomorphic trait for the superfamily Raninoidea.

Sterno-pleural junction. The implementation of a junction of the anterior part of the thoracic sternum with the pterygostome in Raninoidea improved the strength of the body. Posterior to this junction, several configurations of the thoracic sternum may be recognised in the Raninoidia.

The episternites of sternite 4 are of considerable size in Palaeocorystoidea, and form the greatest width of the sternum. Sternite 5 may be equal in width, with near-vertical lateral sides. In ventral view, the arthrodial cavities of P1–P3, as well as their sternal gynglymes, are in a near-vertical line, and close set. P4 follows this arrangement, but is slightly tilted dorsoventrally. The pereiopod coxae are large; when hinging in postero-anterior direction, they may slide along each other. The most basal member of Palaeocorystidae, *Notopocorystes*, does not show a different configuration. *Eucorystes carteri* has a rather wide episternite 4 that is joined by the wide anterior part of sternite 5. This wide process is directed between P1 and P2, but does not alter their disposition.

Sternite 4 is subrectangular in *Marylyreidus punctatus* **n. comb.** (Marylyreidinae **n. subfam.**), with the episternites as triangular plates pointing outwards, and much wider than the preceding sternite. The episternites 4 are joined posteriorly by a wide expansion of the anterior portion of sternite 5, which points outwards and slightly backwards, its ventral surface plain (Figs. 38A; 56C). These sternal expansions are much wider than the remaining sternites, and they are so wide in ventral view that they reach the margins of the branchiostegites. As the ventral carapace is rapidly reduced in height posterior to the pterygostome, the expansions of sternite 5 are in a level lower than the margin of the branchiostegite. The posterior portion of the pleurite of the cheliped somite is exposed between the branchiostegite and the expansion of sternite 5. This exposed pleurite is excavated and ventrally inclined to form a prominent junction with sternite 5. The wide expansions of sternite 5 are thus intercalated between P1 and P2, pushing them wide apart. The posterior margin of this wide expansion is concave and it opposes the upper margin of the P2 coxa. Episternite 5 is normal in width, accommodates the gynglymes for P2, and has a short hook-like projection with a double peg to lock the abdomen. Sternites 6–8 are equally narrow.

In all other extant and fossil Lyreididae, all of which having a sterno-pterygostomial junction, the episternites 4 are much smaller than in *Marylyreidus* **n. gen.** and not expanded laterally, with only the anterior part of sternite 5 expanded between P1 and P2. The chelipeds are completely isolated from the other pereiopods; anteriorly they are separated from mxp3 by a sterno-pterygostomial junction; they are posteriorly separated from P2 by a sterno-pleural junction. The ventral surface of *Rogueus orri* (see Berglund & Feldmann 1989: 71, figs. 2.5, 2.6) typically shows this lyreidid configuration, with small episternites 4 and a widely expanded anterior portion of sternite 5. The same holds true for *Macroacaena johnsoni* (see Rathbun 1935b: pl. 17, fig. 12; see also Waugh *et al*. 2009: 35, fig. 11.1).

This second junction, involving the thoracic sternum and the exposed pleurites, further enhances the strength of the body architecture. These are considered as derived modifications for burying. The configuration of the sterno-pleural junctions, complementary to the sterno-pterygostomial junctions, may aid in assigning raninoid taxa to family level.

The Symethinae shows a distinct configuration. The sterno-pterygostomial junction is conspicuously narrow, and episternite 4 is widely expanded posterior to the P1 gynglyme to form the lateral expansions between P1 and P2 joined by the anterior part of sternite 5. Symethines are here regarded as rather basal raninoids.

Episternite 4 is small in Ranininae, and the anterior portion of sternite 5 widely expanded, which forms a particular tongue, which were referred by Bourne (1922b: 59) as ‘epaulettes’. These expansions are not developed in early members of this subfamily, such as *Raninella elongata* and *R. trigeri*, but are observed in stratigraphically younger forms, such as *Vegaranina* sp. (Fig. 28B). Posterior to the widely expanded sternite 5, the thoracic sternum becomes keel like.

Fossil and extant members of Raninoidinae can be easily recognised by the particular configuration of the sternal plate, as it is the only subfamily where a second sterno-pleural junction is formed. Medially between the P2 coxae, the thoracic sternum is narrow, and a complete suture 5/6 is present. Sternite 6 is trapezoidal, wider posteriorly, where it separates P2 from P3, and forms a second junction with the exposed pleurites. The P1, P2 and P3 are equally interspaced. Raninoidines are here considered as derived raninoids.

Blocking system for P2 and P3. The thoracic sternites normally appear as rather flat, regular plates in palaeocorystoids. A particular type of ‘sterno-coxal depression’ is present on sternites 5 and 6 of the Palaecorystidae. Here a deep depression runs obliquely forwards and inwards from just above the P2 and P3 gynglymes (Figs. 5E; 37D; 59). The depression of sternite 5 ends rather abruptly in front of suture 4/5. It separates the lateral portion of sternite 5 from the main sternal plate, this lateral portion clearly lower, forming an oblique ridge. This ridge is complete on sternite 6, where it is more vertical and more acute, and anteriorly reaches episternite 5. Sternite 7 does not exhibit such a ridge.

The upper margin of the coxa eventually slides in this kind of sterno-coxal depression when the P2 or P3 make a postero-anterior movement. The movement of the leg will be restricted by the ridge on the sternal plate, acting as a blocking system for the coxa of the pereiopod. The P2 and P3 of *Ranina ranina* are the main digging appendages to shovel sand from underneath the body, whereas the P4 pushes the animal into the substrate (Faulkes 2006: 151). The presence of a blocking system only on sternites 5 and 6 for the P2 and P3 indicates that this burying approach was similar in palaeocorystids. The acquisition of a blocking system is clearly correlated with the specialisation of back-burrowing, preventing the obstruction of the appendages, which may occur during the displacement of sand.

A relatively lower, yet acute, ridge is present on sternites 5 and 6 of *Marylyreidus punctatus* **n. comb**. Because this raninoid has exposed pleurites, the coxae are directed more ventrally, and their movement is less inwardly than in palaeocorystoids. The coxa does not slide in a sterno-coxal depression and the ridge on the sternites is not applied as a blocking system. Their presence can be seen as a remnant from a recent precursor, and is one of the many features that make *Marylyreidus* **n. gen.** an intermediate form. Other lyreidids do not have a clear ridge, but a depression just above the P2 and P3 gynglymes remains.


pt
j1
3
cmxp3
4
cx1
e4
j2
5
A
pt
j1
cmxp3
3
cx1
4
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B
j1
cmxp3
pt
3
4
e4
cx1
j2
5
C
c
pt
j1
3
cmxp3
4
cx1
e4
5
j2
D
4
cx1
e4
j2
5
E
pt
cmxp3
3
4
4
j1
F

FIGURE 48. Sternum-pterygostome junction in extant raninoideans; A, *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), MNHN-B13364 (male), no locality data; B, *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), MNHN-B31983 (female), Tulear, Madagascar; C, *Symethis corallica* Davie, 1989 (Raninidae, Symethinae), MNHN-B20795 (**holotype**; female), Coral Sea, Chesterfield Islands; D, *Notopus dorsipes* (Linnaeus, 1758) (Raninidae, Notopodinae), MNHN-B7933 (male), probably Philippines; E, F, *Cyrtorhina granulosa* Monod, 1956 (Raninidae, Cyrtorhininae), MNHN-B16181 (female), Príncipe I., Gulf of Guinea. **3, 4, 5,** thoracic sternites 3, 4, 5; **c,** buccal collar of pterygostome; **cx1,** P1 coxa; **cmxp3,** coxa of mxp3; **e4,** episternite 4; **j1,** junction thoracic sternum/pterygostome; **j2**, junction thoracic sternum/exposed pleurites; **pt,** pterygostome. (photographs by J.-F. Dejouannet) Scale bars: 5mm.

A blocking system may be present in more back-burrowing or burrowing taxa. In the eubrachyuran *Corystes*, a slightly different system occurs in which the lateral episternites are involved (see e.g., Guinot & Bouchard 1998: 643, fig. 12A).

Modifications of pereiopods. Podotreme pereiopods generally have many functions and modifications: housing their sexual organs (female gonopore on P3 coxa, male gonopore on P5 coxa), reduced P5 or P4 and P5 often holding an object as camouflage, and holding the abdomen in the most basal groups. A burying mode of life, where the pereiopods are modified to enter the substrate rapidly, does not make much sense for a podotreme crab. The vast majority of burying crabs are found in Heterotremata (Bellwood 2002a: 87). Except for Raninoidia, cyclodorippoids are known to show burying behaviour, and in most the frontal region shows the oxystome condition.

The P2, P3 and P4 have been demonstrated to be the prime movers of sand in *Ranina ranina* (Faulkes 2006: 147). The P1 (chelipeds) and P5, however, are involved in diggingto a lesser degree than the remainder of the pereiopods because of their role in the respiratory system (see below). There is no reason to believe that this mechanism of back-burrowing has been modified since the origin of Palaeocorystidae, except for involvement of the abdomen (see below). The adaptation of a reduced P5 towards a pereiopod relatively normal in size in Notopodinae and Ranininae (for *Ranina ranina*; 'Pereopod 5 well developed, not markedly smaller than pereopod 4'; Ahyong *et al*. 2009: 136), and implementation of the abdomen in burying (Faulkes 2006: 149) can be seen as strong specialisation for back-burrowing. The last pereiopods are often used by eubrachyurans to loosen the substrate and to propel the body backwards when entering the substrate (Bellwood 2002a: 93).

The chelipeds of the Notopodinae and Symethinae are particularly modified, those of the former closely resembling those of albuneid sand crabs (Fig. 54C; Fraaije *et al*. 2008a: 22, pl. 1, fig. A–D).

The chelipeds of palaeocorystoids, when preserved, show complete or near-complete homochely, as in all raninoids. Heterochely seems ineffective for either back-burrowing or respiration biomechanics. Chelae typically have a tumid outer surface in Necrocarcinidae (Fig. 54B, D–E) and Camarocarcinidae (see Holland & Cvancara 1958: pl. 74, figs. 1–4, 8, 9; Feldmann *et al*. 2008: 1746, fig. 5.4), but they are clearly flattened and smooth on their inner surface (Fig. 54A; see also *Respiration in the Brachyura* below). The same holds true for the Palaeocorystidae, although the outer surface is not as tumid as in the former two families. The upper and lower margins of the palaeocorystid cheliped always bear anteriorly pointed spines (Fig. 54D, E), which 'rake' sand from underneath the body while back-burrowing (see Wright & Collins 1972: 80, text-fig. 11A). The upper margins of both propodus and dactylus are flattened as in *Necrocarcinus*, considered to be the ancestral condition. In addition, palaeocorystids typically have a distinct, sharp crest at the outer surface of the merus (Figs. 7D; 9B, C). This structure may have functioned in burying. The Cenomanocarcinidae and Orithopsidae typically exhibit flattened chelae (for *Cherpiocarcinus rostratus*; see Marangon & De Angeli 1997: 101, fig. 2.2) with long, forwardly directed spines on upper and lower margins of the propodus. Wright & Collins (1972: 68) described the claws of *Orithopsis tricarinata* as having spines along the upper and lower margins.

Sexual dimorphism is present in the pereiopods of the Palaeocorystoidea, at least in Cenomanocarcinidae. Guinot *et al.* (2008: 8) described sexual dimorphism of the chelipeds 'including in females smaller, more slender and spinose chelipeds, with carpus much longer than in males and prehensile margins of fingers appressed'. No distinct sexual dimorphism has been observed in the pereiopods of Palaeocorystidae, but specimens for which sex could be determined and which retained well-preserved chelipeds are rare. Raninoids may have weakly sexually dimorphic pereiopods, as described for e.g., *Ranina ranina* by Minagawa (1993b) and Krajangdara & Watanabe (2005; also Feldmann & Schweitzer 2007: 40, fig. 1B, D; Ahyong *et al*. 2009: 137, figs. 99, 100).

The inner surface of the propodus of *Necrocarcinus labeschii* was described as flat by Wright & Collins (1972: 64). The upper margins of the dactylus and propodus are flattened, turned inwards, the edges with flat teeth (Jagt *et al.* 2010: figs. 4B, C). Many chelipeds previously assigned to *Necrocarcinus* (see e.g., Förster 1968) appear to belong rather to dynomenids (Jagt *et al*. 2010).

Paranecrocarcinus possesses chelae that are flattened on their inner surface, with weakly incurved fingers (Fig. 54A). The lower margin of the palm is tubercular, as is the upper margin of the dactylus. The upper margin of the propodus is set with flattened, triangular teeth, similar to members of e.g. *Calappa* Weber 1795.

Only the P2–P5 of Cenomanocarcinidae and Palaeocorystidae among Palaeocorystoidea were examined here. *In situ* specimens of *Ferroranina dichrous* **n. comb.**, *Joeranina broderippii* **n. comb.,** and *Notopocorystes stokesii* showed articles of the pereiopods. *In situ* specimens of the latter were examined, and the angle of burial was noted. The P1 is always flexed in front of the body, with the claws anterior to the orbits, upright, or with the outer surface directed upwards. The P2 was in a forwardly curved position under the chelipeds. The P3 has a more lateral or slightly anterior position. The P2 and P3 were found with a remarkably long, flattened dactylus in *Ferroranina dichrous* **n. comb.** (Fig. 7E) and *Notopocorystes stokesii*. The propodus and merus are invariably flattened, with a single or a double row of spiniform tubercles along the margins, accompanied by setal pits. The P4 was found in all cases to be bent sideways or posteriorly. Wright & Collins (1972: 75) noted that in *Notopocorystes stokesii* 'the last 2 legs are much shorter than the second and third and are turned backwards in a typical raninid fashion'. The P4 was here found to be only marginally reduced in comparison to the P2 and P3, the P2 and P3 longer and (in preserved condition) directed to the anterior, whereas the P4 was directed outwardly or posteriorly. In most cases the P5 was not preserved, or only its proximal articles, especially the coxa and merus. The P5 merus was found to be oval in cross section in *Joeranina broderippii* **n. comb.** and *Notopocorystes stokesii*. No conclusions about the natural position of the P5 can be made. In Cenomanocarcinidae the P2, P3 and P4 are long, increasing in size posteriorly, with distinctly flattened propodus and dactylus. The P5 is strongly reduced and subdorsal in position (Guinot *et al.* 2008: 684, figs. 2A, B; 4A–E). The pereiopods of *Cenomanocarcinus* were obviously better adapted for swimming than for burying.

The abdomen in back-burrowing. The abdomen, not held under the body in Raninoidea, may be involved in back-burrowing (Faulkes 2006: 149, 152, for *Ranina ranina*), not as an extra pereiopod to shovel forwards, but as an aid in 'liquifying' the sand, similar to the habit described for sand crabs (Faulkes & Paul 1997a). In *Ranina ranina* (Fig. 49A, C) a remarkable obstruction system was found to prevent straining the abdomen caused by the large forces this 'liquifying' technique may bring along. The abdomen ventrally bears a central row of elongated protuberances, pointed downwards. Abdominal somites 2–4 each have such a protuberance at their posterior margin, which corresponds to an opposing protuberance on the next abdominal somite. When trying to bend the abdomen, these protuberances limit the curvature of the central part of the abdomen, turning it into a stiff plate. A similar obstruction system, although less prominent, was observed in *Notopoides latus* (Fig. 49B). Palaeocorystidae and Lyreididae likely use(d) a different 'liquifying' technique, as their abdomens are locked against the body. Members of these families typically exhibit a narrow abdomen in both sexes (Feldmann & Schweitzer 2007: fig. 4a, c). Abdominal somites 1–5 may bear a central spine, which is present on all somites in *Notopocorystes,* on abdominal somites 2–5 in *Eucorystes*, and on somites 3 and 4 in *Ferroranina* **n. gen.,** where somite 3 bears only a weak node and somite 4 a sharp spine. Through the abdominal curvature, somites 3 and 4 are the most posterior elements of the body, the first elements to be in contact with the substrate when back-burying. It appears that the abdominal spines in Palaeocorystidae and Lyreididae 'liquify' the sediment when entering the substrate to facilitate shovelling by the P2–P4. These abdominal spines are missing in all other Raninoidea.

The telson protection valve. A type of movable, hard plate, at the ventral side of the telson was observed among extant raninoids. It represents the exposed surface of the tegument of the distal intestine that has become calcified. This plate apparently protects the last portion of the rectum, the anus being close to the tip of the telson. Raninids do not have a locked abdomen, but keep it loose behind the body, even aiding in back-burrowing. The hard plate at the ventral side of the telson likely serves to protect the distal portion of the intestine while the crab enters the substrate. No mention or illustration of this feature appears to have been made in the literature, and it is herein tentatively named 'telson protection valve'. The exact function, intraspecific, sexual and ontogenetic variation (if any) and implications of the telson protection valve merit a detailed study of its own, which is beyond the scope of the present paper.

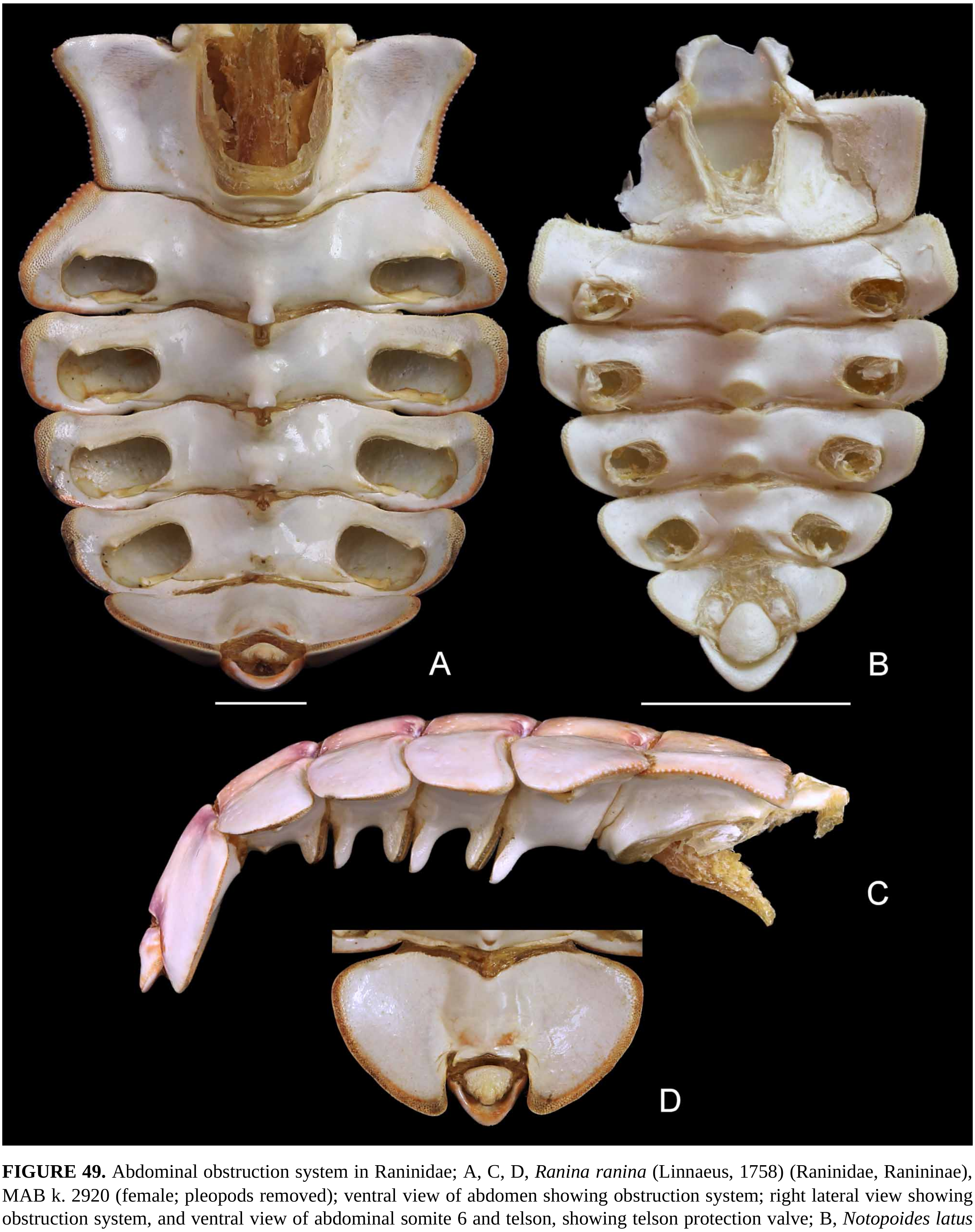

FIGURE 49. Abdominal obstruction system in Raninidae; A, C, D, *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), MAB k. 2920 (female; pleopods removed); ventral view of abdomen showing obstruction system; right lateral view showing obstruction system, and ventral view of abdominal somite 6 and telson, showing telson protection valve; B, *Notopoides latus* Henderson, 1888 (Raninidae, Raninoidinae), MAB k. 2921 (female; pleopods removed); ventral view of abdomen showing obstruction system. Scale bars: 5mm.

The females of *Ranina ranina* examined showed the telson protection valve (Fig. 49A, D) to be small, triangular and shorter than the telson; the preceding intestinal portion is strongly calcified. In Raninoidinae both sexes of *Notopoides latus* exhibit the telson protection valve in addition to a calcified intestine (Fig. 49B). *Raninoides* and

Notosceles were also examined, showing a rectangular calcified portion, which is rather hard and extending along three-quarters of the telson. Notopodinines show a different configuration: in *Notopus* and *Cosmonotus* the last portion of the intestine (which leaves a gap from the telson's tip) is not calcified, and there is no calcified distal plate. In *Cyrtorhina* (only two specimens examined) the female distal portion of the intestine leaves a large gap from the tip of the telson; there is a rather long telson protection valve that extends on to somite 6, which is also calcified. The valve clearly enters an excavation of the telson in the male, and somite 6 is not calcified. In *Symethis* (a single specimen with abdomen was studied), the protection valve seems hard but is small, extending on to the preceding abdominal somite 6, which is also ventrally calcified.

Lyreidus and *Lysirude* seem to lack a telson protection valve. The distal part of the intestine appears to have a small, short portion that is only slightly hardened in *Lyreidus*, but weaker in *Lysirude*; the intestine is generally non-calcified (Fig. 36C). The abdomen is locked against the thorax in lyreidids, the telson being placed in a cavity of the thoracic sternum (Fig. 36E), which is situated between the hook-like projections of episternite 5. There seems to be no need to protect the anus in Lyreididae because the abdomen is not involved in burying.

Respiration in the Brachyura

The normal pattern of respiratory ventilation of brachyurans is the forward-ventilatory mode. The pumping action is produced by the beating of the scaphognathites, which are situated in the pre-branchial chamber (Borradaile 1922; Cumberlidge & Uglow 1978). Water enters the branchial chamber through openings at the bases of pereiopods and flows through that chamber in a posterior-anterior direction. After extraction of oxygen by the gills, the water is expelled frontally, between the mxp3 and endostome (Garstang 1896; Bohn 1901; Bourne 1922b; Bellwood 2002a, b; McGaw 2005). No modifications for respiration are normally present in the frontal region or pereiopods in surface-dwelling crabs.

The main inhalant openings of the respiratory channel are normally situated at the base of the chelipeds, between these and the pterygostome, and are referred to as 'Milne-Edwards openings' or 'pre-chelipedal openings'. The mxp3 coxae are normally intercalated between the thoracic sternum and pterygostome.

Respiration in burying crabs. Many decapod crustaceans are able to bury in the sediment, mainly to avoid being detected by predators (Bellwood 2002b; McGaw 2005) and to conserve energy (McGaw 2005: 380). Most species are shallow buriers, either partially within the sediment or partially covered by material displaced during burying. Whilst buried, the animal must maintain a flow of oxygenated water through the branchial chamber.

In a buried crab, before water can enter the branchial chamber via the bases of the pereiopods, water must be transported there through accessory inhalant channels. These inhalant channels were divided into 'exostegal' and 'endostegal' channels by Garstang (1897b: 215). When the channels run over the pterygostome, i.e. are adjacent to the medially placed exhalant orifices, they are referred to as exostegal; they are termed endostegal when formed by the branchiostegite. Endostegal channels, with entrances at the bases of P1–P4, are regarded as the most basal disposition. Exostegal channels are created between the flexed chelipeds and the pterygostome. Water can pass through the narrow channel between the chelipeds and the carapace by entering through slit-like openings between the antero-lateral carapace margin and the upper margin of the chelipeds (e.g., Caine 1974: fig. 1B; Cumberlidge & Uglow 1978: fig. 2; McGaw 2005: fig. 1a).

The modification of the respiratory system of crabs was a key step for burying (Bourne 1922b: 56; Bellwood 2002a: 105). Sediment type and physical properties (such as thixotropy; see Savazzi 1981 and Faulkes 2006) are aspects that undoubtedly determine respiratory modes. Thus far, these properties have received little attention. Attached to burying are great risks, such as blockage of respiratory openings when buried, or pollution of the gills (Garstang 1896). Several important modifications to the respiratory system have occurred to overcome these drawbacks. Simple modifications for respiration whilst buried involve the creation and maintenance of an exostegal waterway. In such cases, the inner face of the cheliped is variously excavated, matching the subhepatic region and pterygostome, in order to create a constant and narrow space between them. The exostegal channels are normally bounded medially by a setose mxp3 and admedially by setae on the cheliped merus and pterygostome to prevent sand particles from becoming part of the water current. Additional modifications for an exostegal channel may be recognised in the lateral margins of the carapace. In forms that bury but are not extensively modified, antero-lateral spines are commonly found. Garstang (1897b: 216) noted that, when partially buried, these marginal spines broke the substrate surface and overhung the slit-like orifice between the chelipeds and antero-ventral carapace and demonstrated that these spines acted as a coarse sieve to prevent undesirable particles from entering the inhalant respiratory channel. He used the term 'sieve-forming teeth' (Garstang 1897b: 217) and concluded (Garstang 1897a: 398) that the exostegal channels in Portunidae and Atelecyclidae *sensu stricto* represented a more primitive form than the advanced exostegal channels of Leucosiidae. Absence of antero-lateral teeth, such as in calappids and leucosiids, is linked to a modified respiratory system. In such cases the exostegal position of the inhalant opening is restricted. Garstang (1897b: 217) hypothesised that, 'the peculiar respiratory adaptations of these forms have been derived from the more generalised type of adaption'.

Burying crabs which spend most of their lives under the sediment have several advanced modifications to maintain a respirative flow of water through the gills. Strong modifications of the respiratory system may have an impact on body architecture and the thoracic skeleton. Advanced modifications to the respiratory system comprise the oxystomian condition and modifications of the mxp3, modifications of the antennae and a prostomial chamber, implementation of a gutter in the pterygostome or suborbital region, posterior inhalant openings, and ventilatory reversals.

The most obvious modification is the oxystomian condition of the frontal region, where the endostome is projected forwards and tapers into a rounded tip ('oxystomian mouth'). The medial surface of the endostome is excavated and forms the anterior roof of the buccal region. The mxp3 are elongated, tightly closing the buccal frame; the exhalant openings are located at the anterior tip of the buccal region. Crabs with such a specialised condition were previously assembled in Oxystomata, which comprised Calappidae, Dorippidae, Leucosiidae and Raninidae. It is widely accepted now that the oxystomian condition reflects morphological convergence (homoplasy), having originated independently in diverse brachyuran groups, and initiated by burying. It is apparent that this condition has originated more than once and is not a derived character state.

Another advanced modification may be the condition of the mxp3. In *Calappa* the only inhalant opening used during burial is the anteriormost, thus in front of the P1. Bellwood (2002a: 137) hypothesised that this may be facilitated by the large, flanged mxp3 coxae. These flabelliform coxae could regulate the volume and direction of the water entering the branchial chambers. She suggested (Bellwood 2002a: 138) that, 'by opening fully, it may be possible to ventilate even the posteriormost gills through the M-E openings [Milne-Edwards openings] alone'.

The eubrachyuran *Orithyia* Fabricius, 1798, monotypic type genus of Orithyiidae Dana, 1852 (type species: *Orithyia sinica* (Linnaeus, 1771), is highly specialised, with an unpaired septum separating two distinct exhalant channels transformed into two tubes, looking like two short tunnels ending in two rounded orifices; the Milne-Edwards openings appear as long and narrow slits in front of the chelipeds bases (H. Milne Edwards 1837: 111; 1836-1844, atlas, pl. 8, fig. 1a; Ihle 1918: 169, fig. 88; Bellwood 1996: fig. 3C, D; Ng *et al.* 2008: fig. 94).

The antennae are modified in several taxa of burying crabs, often complemented with a reversed respiratory waterflow and a prostomial chamber. In *Corystes* Bosc, 1801, setae between the cylindrical particles of the elongated antennae interlock and form a water tube acting as a sort of straw (see Garstang 1897b: pl. 14, fig. 3a, b; Bohn 1901; Hartnoll 1972: 142, fig. 2); a similar system is observed in Phyllotymolinidae (Tavares 1998), Trichopeltariidae Tavares & Cleva 2010, and Atelecyclidae (Tavares & Cleva 2010). These modifications enable crabs to bury deep into the sediment, while still remaining in contact with the surface. Water is drawn downwards into a specialised chamber under the forwardly extended merus of the mxp3 endopod (prostomial chamber), and between widely placed basal articles of the antennae, with additional dense setation of different articles (see Hartnoll 1972: 141, fig. 1). Water in this chamber is then transported to the branchial chamber.

There may also be modifications to the antennae for the exhalant water current, such as in *Atelecyclus* Ortmann, 1893, and in some raninids, such as *Ranina* and *Notosceles*, the enlarged proximal articles of the antenna forming a funnel for the exhalant water current when the animal is buried (see Bourne 1922b: pl. 6, fig. 35; pl. 7, fig. 57).

Most leucosiids have a remarkable exostegal channel, the orifice of these inhalant channels being situated beneath the upraised orbits, adjacent to the medially placed exhalant openings. They lead backwards to gutters in the pterygostome, which are closed by the mxp3 exopods. This arrangement was well described and illustrated by H. Milne Edwards (1839: pl. 4, figs. 2, 3). In *Matuta* Weber, 1795, respiration continues while deeply buried under the sediment (Bellwood 2002a: 136). Water is drawn through the orbital cavity and reaches the exostegal channel between the cheliped and pterygostome through a deep gutter in the suborbital region (H. Milne Edwards 1839: pl. 7, fig. 1a; Bellwood, 2002a: 112, fig. 4.5b).

The oxystomian organisation in the podotreme subsection Cyclodorippoidia is diverse (Tavares 1991, 1992b, 1993a, 1997, 1999). The disposition is only described or illustrated in a few taxa. The Milne-Edwards openings are absent in the Cyclodorippidae (Fig. 47B), having been replaced by a pterygostomial channel (Bouvier 1899; A. Milne-Edwards & Bouvier 1902; Ihle 1916). The endostome, however, is not elongated in the Phyllotymolinidae and Cymonomidae, in which there is no sternum/pterygostome junction either.

Several burying brachyurans have acquired special posterior respiratory openings that are situated laterally below the posterior margin of the carapace, covered by the first abdominal somite, with the P5 coxa forming the floor. A posterior-anterior waterflow through the posterior orifices aids in irrigating the posterior gills, the P2–P5 bases may then be hermetically closed to prevent entrance of sediment particles. Posterior orifices are found in e.g. *Corystes* and *Thia* Leach, 1815, and *Cancer pagurus* (Linnaeus, 1758) (see Pearson 1908: 127; Borradaile 1922: 129). *Corystes cassivelaunus* (Pennant, 1777), with short and non-locking abdomen, has posterior branchial openings in addition to the normal Milne-Edwards openings (no sternum/pterygostome junction) and the respiratory tube formed by the apposed antennae (Hartnoll 1972; 142, figs. 1, 2). These posterior orifices would be effectively closed if the abdomen rested against the ventral surface. The posterior orifices may be regarded as strong modifications to the body resulting from a specialised mode of life.

Reversal of the ventilatory mode occurs more frequently in burying crabs than in crabs living freely on sand. Reversal of the water flow is accomplished by reverse action of the scaphognathite. Frequent reversals ventilate the gills more effectively, and cleanse the entrances from blocking sediment (Bohn 1901; Borradaile 1922; Arudpragasam & Naylor 1964; McGaw 2005).

Respiration in fossil crabs. Comments on the respiratory modifications of fossil crabs are few. One reason may be that many palaeontologists poorly understand the respiratory function of crabs. More importantly, much of the ventral morphology must be preserved and exposed for a reliable reconstruction of an animal's respiratory adaptations. Such cases are relatively rare in the fossil record.

Crawford *et al*. (2008) recorded early Miocene palaeosurfaces in southern Patagonia (Argentina), with evidence of mass mortality of two large-sized species of crab, *Chaceon peruvianus* (d'Orbigny, 1842) and *Proterocarcinus latus* (Glaessner, 1933). Most of the specimens were preserved with gaping maxillipeds. This would suggest that 'the crabs were experiencing respiratory distress when they died.' The authors hypothesised (Crawford *et al*. 2008: 283) that volcanic ash might have caused this distress.

Respiration in the Raninoidea. Extant raninoids are specialised back-burrowers that spend most of their time deeply buried in the sediment, with only the front of the carapace or the eyestalks visible. Their respiratory mechanism is highly specialised and refined.

Sternite 4 is connected to the pterygostome in all Raninoidea and the Milne-Edwards openings or pre-chelipedal branchial openings are absent. In the diagnosis of his tribu 'Raniniens' (including Anomura), H. Milne Edwards (1837: 190) noted, '*Les pates*[*sic*]*-mâchoires externes sont très alongées* [*sic*], *mais nullement pédiformes, et en arrière de leur insertion, les régions ptérygostomiennes de la carapace se réunissent au plastron sternal, sans laisser d'ouverture pour l'entrée de l'eau dans la cavité branchiale*' [the external maxillipeds are very elongated but not pediform and posteriorly to their insertion, the pterygostomial regions of the carapace join the thoracic sternum, without leaving an opening for the entrance of water in the branchial cavity] (Milne Edwards 1837: pl. 21, fig. 2). Bourne (1922b: 53) found that there was no inhalant opening in front of the cheliped and that the mxp3 epipodite was reduced to a vestigial setobranch, evidence of the functional loss of the mxp3 coxae in respiration.

Rather than Milne-Edwards openings, Raninoidea have a set of modifications to their respiratory system, which varies between members of this group. These modifications may comprise: modification of the antennules and antennae; oxystomian condition of mxp3; modification of the chelae; setation for the exostegal channel; excavation of the branchiostegite and exposed pleurites; the posterolateral margin that matches the P5; and the acquisition of posterior inhalant openings.

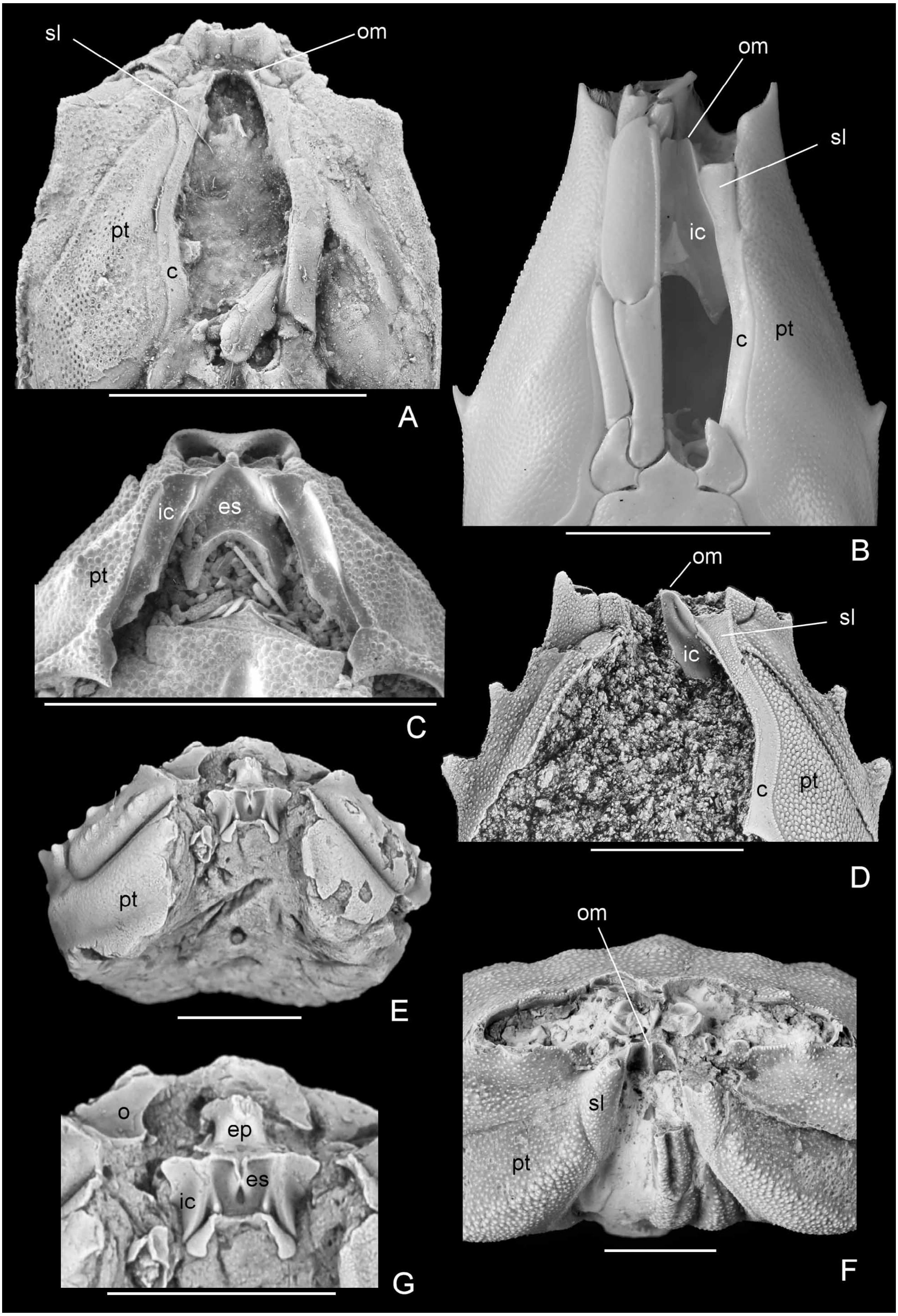
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FIGURE 50. Oxystomian condition in various fossil and extant brachyurans; A, *Marylyreidus punctatus* (Rathbun, 1935b) **n. comb.** (Lyreididae, Marylyreidinae **n. subfam.**), MGSB75297 (*ex* Àlex Ossó-Morales Collection; indeterminate sex); upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County, Texas (U.S.A); ventral view of buccal region; B, *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), MAB k. 2914 (male), Recent, Philippines; ventral view of buccal region; C, *Ebalia cranchii* Leach, 1817 (Leucosioidea, Leucosiidae) (S. Mermuijs Collection, unregistered), Pliocene, Kallo (Antwerpen, northwestern Belgium); ventral view of buccal region; D, *Raninella elongata* A. Milne Edwards, 1862 (Raninidae, Ranininae), MNHN R03934 (**paralectotype**), upper Cenomanian, Le Mans (northwestern France); ventral view of buccal region; E, G, *Necrocarcinus labeschii* (J.-A. [Eudes-]Deslongchamps, 1835) (Necrocarcinidae), MAB k. 2904, Albian, Escalles (Calais, northern France); oblique frontal view showing buccal region and detail of frontal region; F, *Campylostoma matutiforme* Bell, 1858 (Cenomanocarcinidae), NHM In 32654/32655 (indeterminate sex), lower Eocene (Ypresian), Herne Bay (Kent, southern England); detail of frontal view. **c,** buccal collar of pterygostome; **ep,** epistome; **es,** endostome; **ic,** inhalant channel; **o,** orbit; **om,** oxystomian mouth; **pt,** pterygostome; **sl,** subantennary lobe of pterygostome. Scale bars: 5mm.

In Raninoidea (with the exception of Notopodinae, see below) the basal articles of the antennules and antennae are expanded and form the floor of the orbital cavities. The shape of the antennae and antennules matches and coincides with each other; their inner (medial) surfaces are excavated and together they form a passage for the exhalant waterflow. As such they form an extension of the oxystomian mouth (see below), bridging the distance between the tip of the oxystomian mouth and the sediment surface when buried. The tip of the mxp3 may just overlap the antennae to close the circuit. In addition to acting together as a funnel, the antennae may be separated from the antennules and admedial waterways between the antennules and antennae are created. Action of the mxp2 scaphognathite creates an inhalant current through this artificial passage. Such a mechanism is seen in Lyreididae, where both exhalant and inhalant currents are regulated frontally. Lyreidids lack Milne-Edwards openings as well as posterior inhalant openings; they have no modifications to form an exostegal channel between the pterygostome and chelipeds. The Notopodinae is another group that lacks inhalant openings at the base of the chelipeds or below the posterior carapace margin. Here the articles of the flagellae of the antennae are cylindrical with many interlocking setae at the medial surfaces, together forming a straw (see Bourne 1922b: pl. 7, fig. 56). The precise performance of this modification for the inhalant current needs to be studied in more detail. The basal elements of the antennae are preserved in well-preserved specimens of *Notopus mulleri* from the Maastrichtian type area (Late Cretaceous; southeastern Netherlands, northeastern Belgium), their geometry being homologous to their extant congeners.

All raninoids show the oxystomian condition. The endostome is elongated, overlapping the epistome and proepistome, and forms the ‘oxystomian mouth’ under the front. Here, the exhalant channel is formed thanks to expansion and modification of both the exopodite and endopodite of the mxp1; the long exopodite, devoid of flagellum, is the most effective agent in forming the operculiform floor of the anterior part of the deeply excavated sides of the endostome. Laterally, the deeply excavated channels are fused to the pterygostome. The oxystomian condition has so far not been assessed in any detail in the fossil record, being often not exposed as a result of insufficient preparation. One specimen of *Raninella elongata*, from the upper Cenomanian of Le Mans (northern France) clearly shows the forwardly elongated endostome, expanded in deep exhalant channels. In another lyreidid, *Macroacaena johnsoni*, the exhalant channels are obvious in one of the paratypes (Waugh *et al*. 2009: fig. 11.1, right (ventral) view).

The contribution of the chelipeds in burying is very limited (Faulkes 2006: 147), their role in forming a respiratory channel being a reason. Bourne (1922b: 58, 59) suggested that the spines on the lower cheliped margin of *Ranina* had a raking function. In addition, it may also be possible that these spines functioned as surface extension of the exostegal channel. Notopodines notably have chelae atypical of the Raninoidea, with tall palm, smooth lower margin, and a diminutive fixed finger. This group likely buries into a different substrate, and their respiratory system is different: they do not depend on an exostegal channel. Symethines have claws that are atypical of Raninoidea, the palm being bulbous, with long, slender fingers having teeth only on prehensile margins, the complete structure resembling a pectinate claw. Such a claw is most probably modified for feeding, not for a respiratory function.

A ‘hairy patch’ can be found on the pterygostome, under the merus of the cheliped of most raninoids, extending posteriorly on the branchiostegite. The upper and lower margins of the cheliped merus may also have a line of dense setae. The exostegal waterway is laterally closed when the cheliped is pressed against the body, from the anterolateral margin up to the base of the cheliped. The inner surface of the merus is smooth and matches the opposing pterygostome, thus the cheliped may be moved while the exostegal waterway remains intact. The exostegal channel is also medially limited in *Ranina ranina*. The inner margin of the cheliped dactylus is lined with dense setae, which limits the exostegal waterway medially. This feature is found to have distinct variation within the species, and more study is called for to determine their precise function.

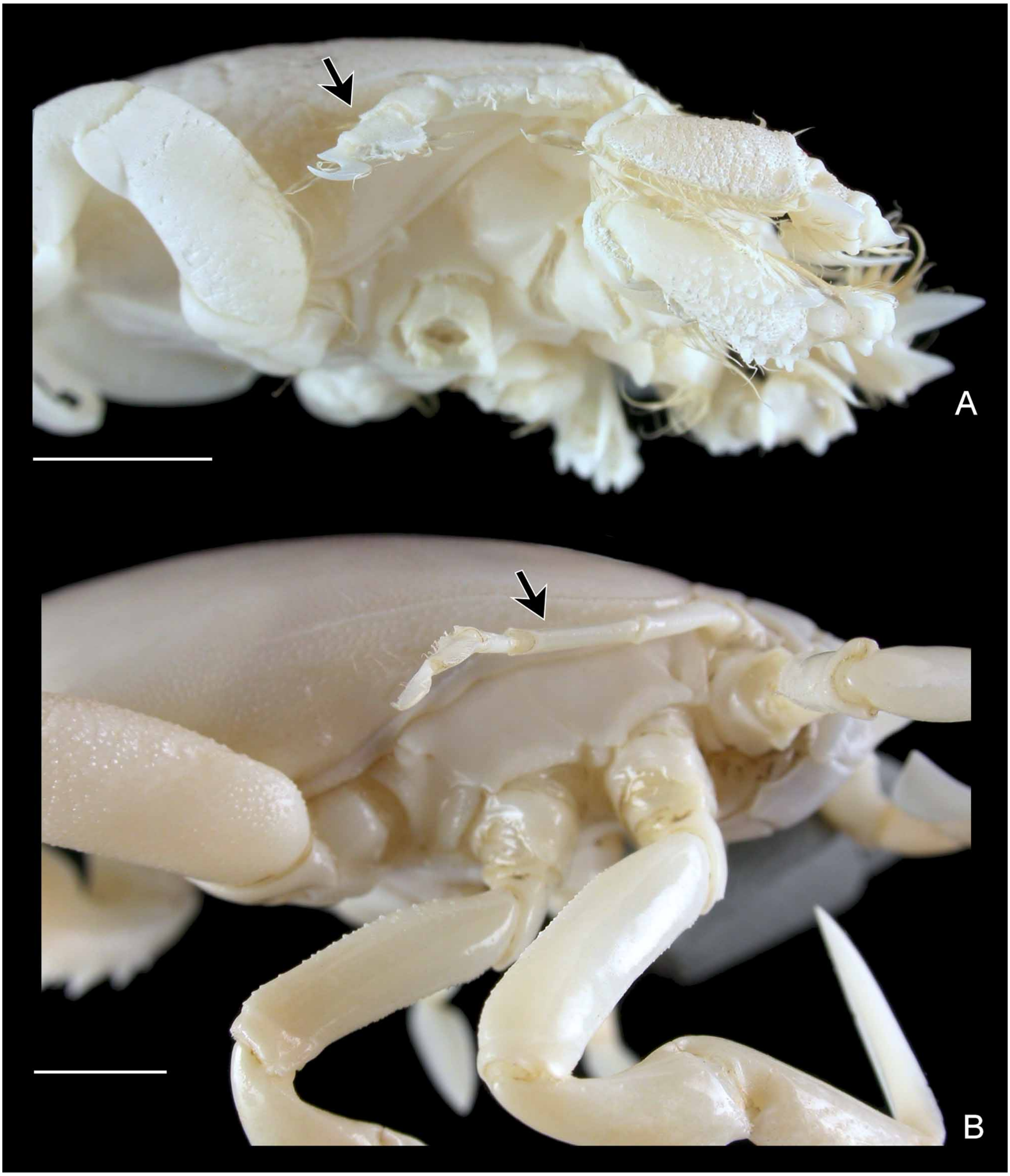

FIGURE 51. Orientation of P5 in Raninoidea; A, *Symethis corallica* Davie, 1989 (Raninidae, Symethinae), MNHN-B20795 (**holotype**, female), Coral Sea, Chesterfield Islands; B, *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), MNHN-B13364 (male). Arrows indicate filiform P5. (photographs by J.-F. Dejouannet) scale bars: 5mm.

In Lyreididae and Notopodinae, groups in which posterior respiratory openings are absent, the exposed pleurites 5–7 form a rather flat plate, not distinctly overhung by the branchiostegite. The low branchiostegite is in prolongation of the exposed pleurites. The exposed pleurites are excavated and concave in other Raninoidea. This region appears as a smooth, polished surface in all cases. The exposed pleurites are flat in Symethinae, but the low branchiostegite is not in prolongation, but rather overhangs the region. This excavated, lateral area acts together with the modified P5.

The P5 is reduced in most raninoids. Such a reduction is weak in Ranininae and Notopodinae (virtually absent in *Ranina*), the leg nearly reaching the size of other pereiopods. The P5 is rather long and strongly setose in all raninoids. The shape of the P5 articles is such that, when placed alongside the carapace, the P5 closely matches the posterolateral margin of the carapace, any gap closed by fringes of setae. The P5 thus forms the roof of the water-chamber enclosed between the preceding pereopods and the thoracic flanks formed by the excavated surface of the branchiostegite and exposed pleurites. Whereas the P2–P4 are the prime movers of sand, the P5 contributes little when burying (Faulkes 2006: 147). Their main function is apparently creating a lateral path for water to flow to the posterior respiratory openings. Implementation of this lateral water conduit is 'by no means primitive but a definite specialisation' (Bourne 1922b: 53).

Raninoids (except Lyreididae and Notopodinae) have acquired a new, posterior entrance to the branchial chamber in the form of inhalant openings situated between the tergite of the abdominal somite 1 and the P5 coxa. Števčić (2005: 26) used this feature to characterise Raninoidea: 'supplementary paired inhalant opening between coxae of last pair of legs and terga of first abdominal segment'. Lyreidids and notopodines, however, do not possess such an opening, which may be replaced or completed by arrangements in the frontal region. Henri Milne Edwards (1837: 192, 193; atlas, pl. 21, fig. 2) was the first to observe this unique mechanism, which Bourne (1922b: 57) discussed at length stating:

> '*In the Raninidae, however, the arrangements differ from those usually observed in crabs. There is, in most of them, a pair of posterior respiratory orifices situated between the tergum of the first abdominal somite and the coxa of the last pair of pereiopods. When the abdomen is extended or only slightly flexed, water can pass freely into or out of these orifices, but they are pretty effectively closed when the abdomen is closely flexed under the thorax*'.

Implementation of the posterior respiratory opening is poorly understood in raninoids. Except for its function in the respiratory system, we may suspect that it is used as a temporary event during back-burrowing and, together with a reversed respiratory current, to spout water out of the posterior orifices to aid in 'liquifying' the substratum. Such hypothesis must be tested with live animals. Water reaches the posterior orifices through the lateral water-conduit, formed by the: 1) excavated exposed pleurites, 2) filiform P5 as the roof, and 3) remaining pereiopods and their setation as the outer barrier. The formation of this lateral water-conduit is 'by no means primitive but a definite specialisation, and I have attributed it to the burrowing habits of the family' (Bourne 1922b: 53). Water can flow posteriorly over the P5 coxa and enters underneath the first abdominal somite into this posterior branchial entrance (Figs. 52B; 53A–C). This entrance is created by outgrowths of pleurite 7 (laterally) and sternite 8 (medially), which leave a narrow opening close to the carapace, and so a new channel to the branchial chamber (Fig. 52A). This feature was studied in a single fossil specimen of *Raninoides glabra* (Woodward, 1871) (Raninoidinae). In this unusually preserved specimen, the carapace was eroded away, thus exposing the pleurites and sternites in dorsal view.

Little is known about the function of the spines on the frontal margin of raninoids. Members of Ranininae and Notopodinae may have distinct spines along a wide orbitofrontal margin, which is densely setose. When these spines break the surface of the sediment, water may be filtered through the setae, and drawn through the wide, deep orbital cavities towards the oxystomian mouth. The notopodine *Lianira* Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991, represented by three species in the Eocene of northern Italy, is characterised by distinctly projected, wide, spiniform orbital margins (Beschin *et al*. 1991: figs. 4, 5; pls. 1–4; Beschin *et al*. 2007: fig. 3, pl. 1, figs. 1–4; De Angeli & Beschin 2007: figs. 2.1–2.3), which may serve for such a function. The function of the orbitofrontal margin in respiration must be tested with live animals.

Sternite 4 is connected to the pterygostome in all raninoids; the Milne-Edwards openings are absent. The only exception is Marylyreidinae **n. subfam.** (Lyreididae), in which the mxp3 coxae are intercalated between the thoracic sternum and pterygostome (Fig. 25D, E), a primitive condition. The mxp3 coxa is flabelliform, and the Milne-Edwards openings were possibly present. *Marylyreidus* **n. gen.** shows an intermediate condition of the respiratory system, resembling the disposition seen in the Palaeocorystoidea.

Respiration in the Palaeocorystoidea. All Palaeocorystoidea show a large, flabelliform mxp3 coxa, which is intercalated between the thoracic sternum and pterygostome, and inserted anterior to the P1. A Milne-Edwards opening is present, contrary to the raninoid condition where this pre-cheliped inhalant opening is absent. It may thus be concluded that the respiratory mechanism must have functioned differently.

Several modifications to the respiratory system are discernible in the Palaeocorystoidea: modification of the carapace and chelipeds, pterygostome and branchiostegite; setation on antero-ventral regions; oxystomian condition of endostome and mxp3; modification of the antennae; and flabelliform mxp3 coxae.

The anterolateral margin of palaeocorystoids typically bears multiple, mostly spiniform teeth. The Cenomanocarcinidae and Necrocarcinidae, two groups considered basal within Palaeocorystoidea, have convex anterolateral margins with spiniform teeth and a narrow, clearly upraised orbitofrontal margin. The anterolateral teeth adjacent to the orbits are pointed almost anteriorly. In contrast to Necrocarcininae, Paranecrocarcininae have granular anterolateral margins without teeth or spines.

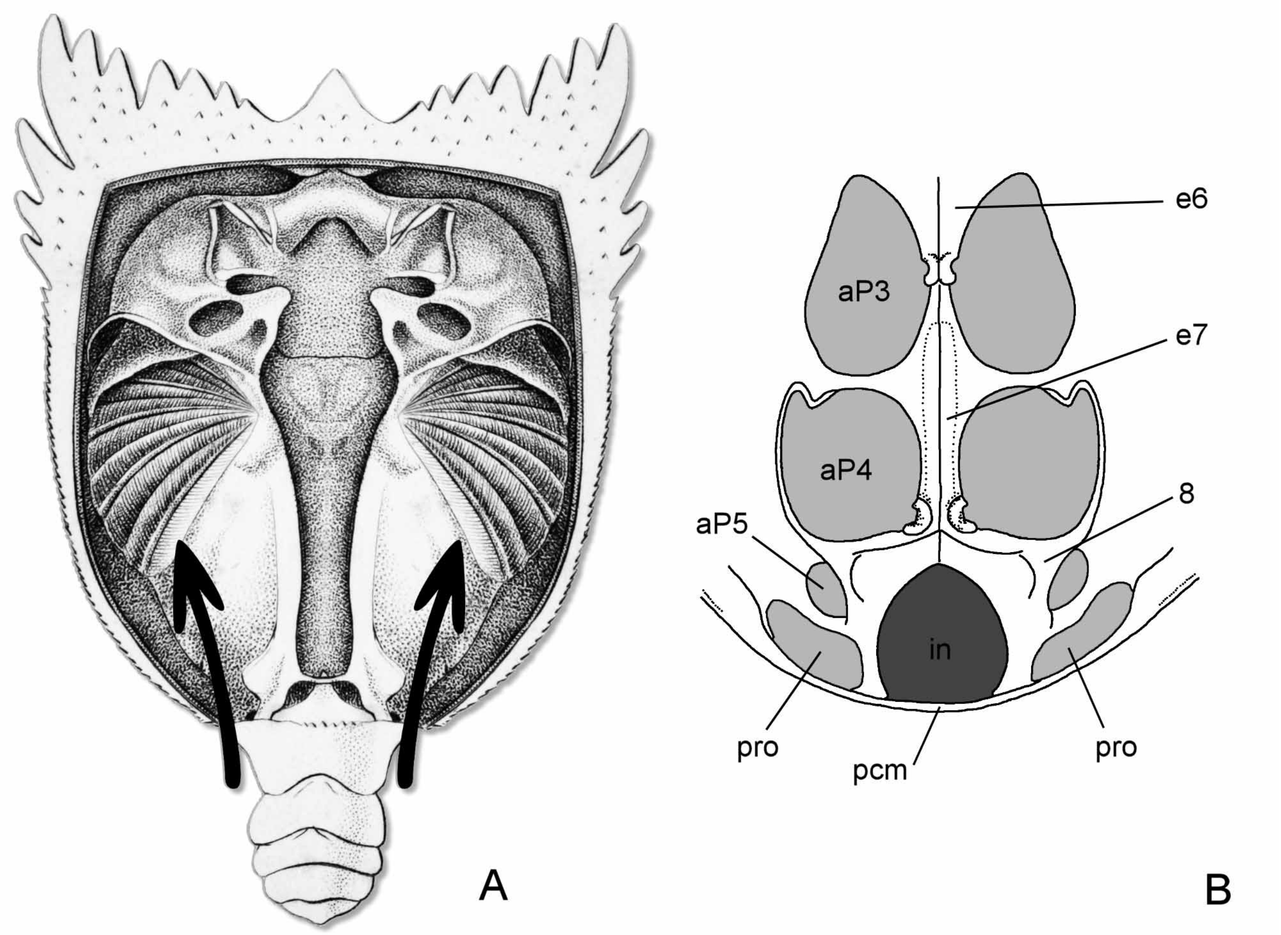

FIGURE 52. Posterior respiratory openings in selected raninids; A, *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), dorsal view, carapace partially removed to reveal branchial chambers (modified after H. Milne Edwards 1839: pl. 4, fig. 4); B, *Notopoides latus* Henderson, 1888 (Raninidae, Raninoidinae) (male), posterior thoracic sternites showing posterior respiratory opening (modified after Gordon 1966: fig. 2a). **8,** thoracic sternite 8; **aP3, aP4, aP5,** arthrodial cavities of P3, P4, P5; **e6, e7,** episternites 6, 7; **in,** intestinal canal; **pcm,** posterior carapace margin; **pro,** posterior respiratory opening.

Palaeocorystids have wide orbits, occupying the anterior margin of the carapace. The anterolateral margins are rather straight, with long, spiniform teeth. *Notopocorystes* has a slightly narrower orbitofrontal margin, here considered to be a basal character within Palaeocorystidae.

Orithopsids have a distinctly wide, straight, orbitofrontal margin, with long, flattened orbital spines, separated by deep, open notches. The lateral carapace margins are straight, the anterolateral margin being armed with long spines (see also Marangon & De Angeli 1997: fig. 2.1; Schweitzer *et al.* 2003a: figs. 14.1–14.3; Guinot *et al.* 2008: fig. 9e). The carapace structure closely resembles that of Palaeocorystidae.

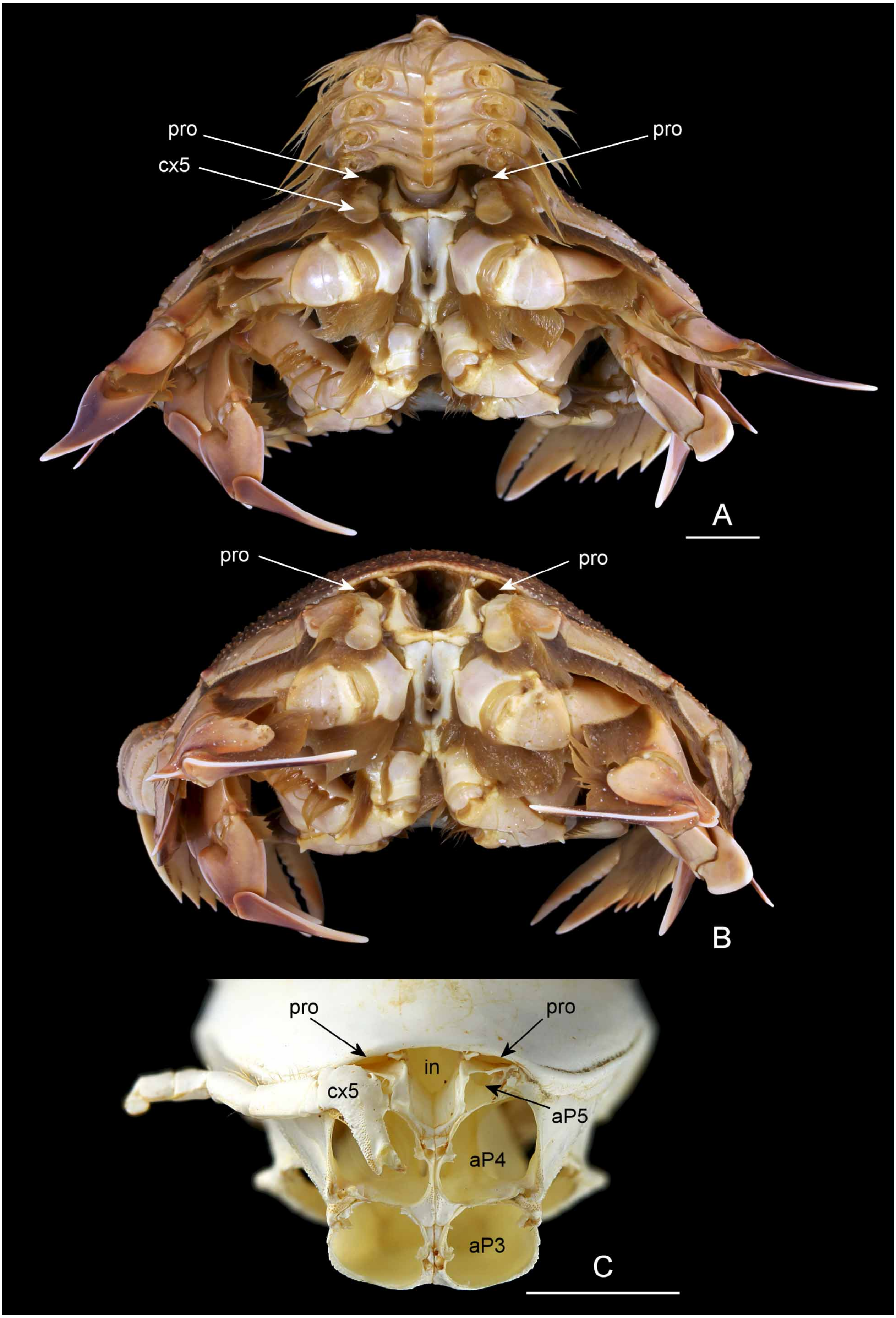
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FIGURE 53. Posterior respiratory openings in selected raninids; A, *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), NCB-RGM unregistered (female), Recent, Sulawesi, Indonesia; posterior view, abdomen pulled upwards to reveal posterior respiratory openings; B, same view, abdomen removed; C, *Raninoides bouvieri* Capart, 1951 (Raninidae, Raninoidinae), MAB k. 2919 (male), Recent, provenance unknown; posterior view showing posterior respiratory openings. **aP3, aP4,** arthrodial cavities of P3, P4; **cx5,** P5 coxa; **in,** intestinal canal; **pro,** posterior respiratory opening. Scale bars: A, B: 10mm; C: 5mm.

The Camarocarcinidae is characterised by having rather blunt lateral margins. The anterolateral carapace margin bears one spine in all members so far known (note that *Cretacocarcinus* Feldmann, Li & Schweitzer, 2008 is here transferred to Necrocarcinidae).

Different modifications of the chelae can be seen among palaeocorystoids. The upper margin of the palm of *Necrocarcinus* is strongly inclined inwards and bears four wide teeth (Jagt *et al*. 2010: fig. 4b), the lower margin being tuberculate. Paranecrocarcinines have chelipeds in which the upper margin bears triangular flattened teeth (Fig. 54A), similar to those seen in most calappids. The proximal part of the upper margin of the dactylus of *Paranecrocarcinus quadriscissus* (Noetling, 1881) bears several larger tubercles (Jagt *et al*. 2010: fig. 3e–g). All palaeocorystid claws examined (*Cretacoranina schloenbachi*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderippii* **n. comb.,** and *Notopocorystes stokesii*) have spines on both upper and lower margins of the cheliped. The upper margin of the propodus of *N. stokesii* is slightly inclined and lined with four strong, triangular teeth. The proximal part of the upper margin of the dactylus bears strong, inwardly directed spines; the lower margin of the cheliped shows slender, evenly distributed spines (Fig. 54D, E).

Spinose upper and lower margins of chelipeds also characterise Cenomanocarcinidae (*Cenomanocarcinus vanstraeleni*, *Campylostoma matutiforme*) and Orithopsidae (*Cherpiocarcinus rostratus*; see Marangon & De Angeli 1997: fig. 2.2). The spines on the upper margin of the propodus are long and thin in both families. The chelae of *Camarocarcinus arnesoni* were described as 'the upper surface of the manus bears a row of tubercles and spinules on its inner margin' (Holland & Cvancara 1958: 501, text-fig. 2). The lower cheliped margin has small spines (Holland & Cvancara 1958: pl. 74, figs. 1–5; Feldmann *et al.* 2007: fig. 5.4). In addition to the upper and lower margins, the inner surfaces of the palaeocorystoid P1 merus, carpus and propodus are modified, being smooth and flat or concave, as a whole closely fitting the pterygostome. The condition has been verified here in Cenomanocarcinidae, Necrocarcinidae and Palaeocorystidae. Holland & Cvancara (1958: 501) described the chelae with, 'all surfaces granular and pitted except inner surface which is commonly quite polished.'

Garstang (1897a, b) explained in detail the function of the brachyuran anterolateral carapace spines in collaboration with spines on the upper margin of the cheliped. The chelipeds are held in close approximation to the body when individuals are buried. The flat or concave, 'polished' inner surface of the cheliped matches the altitude of the pterygostome, between which a narrow exostegal channel is formed. Water can flow between them in order to reach the Milne-Edwards openings and enter the branchial chamber. The orifice of this channel is formed between the anterolateral margin of the carapace and the upper margin of the propodus. This narrow opening is overhung by spines or teeth of the carapace and propodus as a coarse filtering mechanism to prevent larger sediment particles from entering the respiratory flow.

In addition to filtering off larger particles, Garstang (1897a: 399, 400) hypothesised that a strong epibranchial spine might be a mechanical solution to place the cheliped in exactly the right position for a respiratory function. A strongly developed anterolateral or epibranchial spine is present in camarocarcinids, cenomanocarcinids as well as in many raninoids. It is here assumed that in the Palaeocorystoidea the anterolateral carapace spines and the upper margin of the cheliped were functional within the respiratory process. Palaeocorystoids were likely shallow buriers because their anterolateral margins would need to have been in contact with the sediment to create the exostegal waterways. The shallow depth of burial may also indicate why nearly all palaeocorystoids have areolated, tuberculate carapaces; they gathered sediment on their anterior carapace, which was buried under a weak angle in the sediment. Many palaeocorystids (i.e., *Notopocorystes*, *Eucorystes*) and orithopsids (i.e., *Cherpiocarcinus*, *Orithopsis*) have anterior areolation or ornamentation. The trend towards a carapace without tuberculation or areolation, as documented for Palaeocorystidae, is interpreted as a progressive adaptation to a more sophisticated burying.

The respiratory adaptations in Necrocarcinidae and Cenomanocarcinidae are considered basal. The wide, straight orbitofrontal margin of Orithopsidae, with flattened orbital spines and deep open notches, may be involved in the respiratory system. A possible mechanism was to draw water through the orbital notches and through the wide orbital cavities into the exostegal channel.

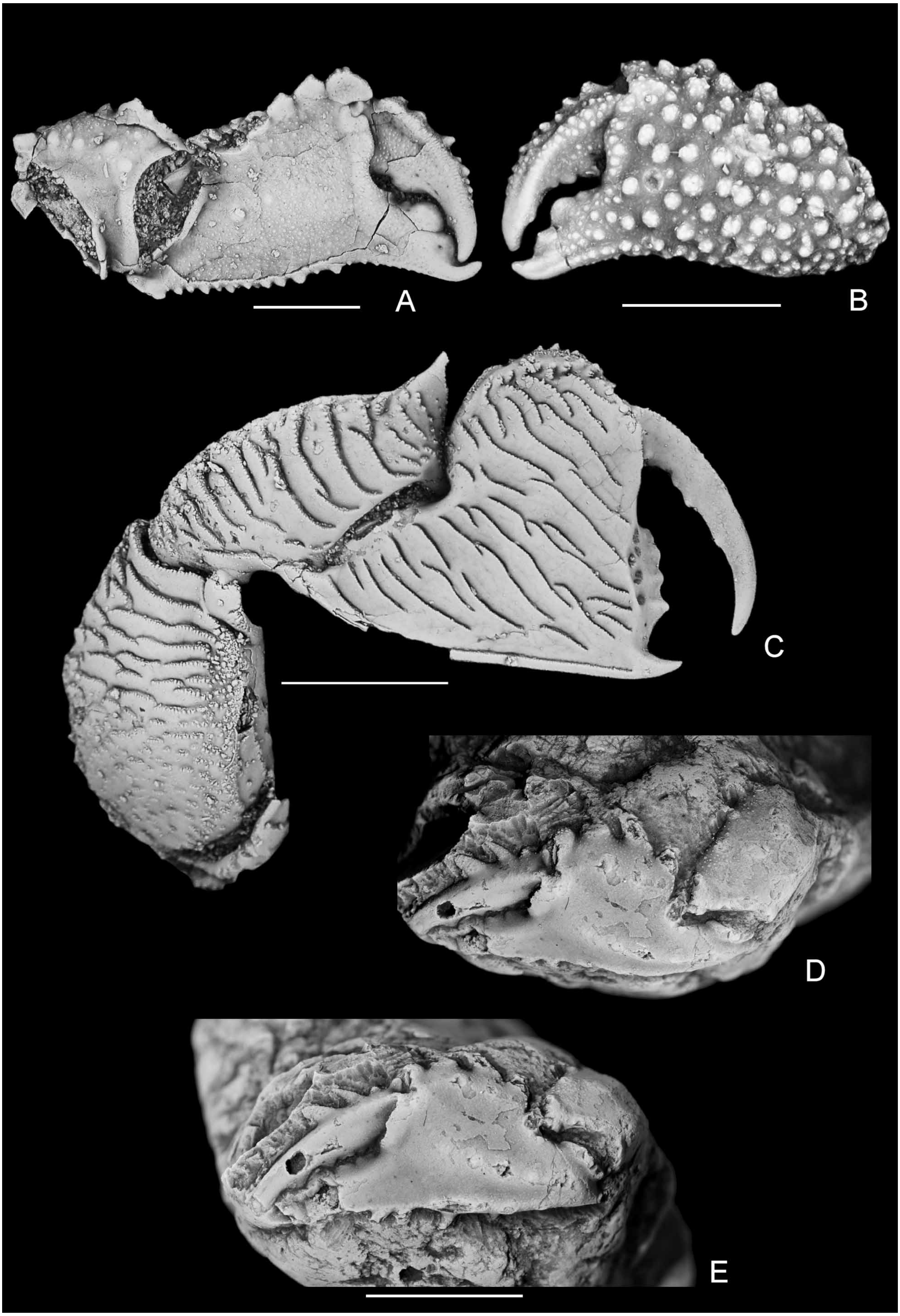
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FIGURE 54. Chelipeds of raninoidian crabs; A, B, *Paranecrocarcinus quadriscissus* (Noetling, 1881) (Necrocarcinidae, Paranecrocarcininae), upper Maastrichtian, Maastricht, the Netherlands, left chelae, NHMM JJ 6737 (A, inner view) and MAB k. 0720 (B, outer view); C, *Eumorphocorystes sculptus* van Binkhorst, 1857 (Raninidae, Notopodinae), MAB k. 2905 (right chela, outer view), upper Maastrichtian, Bemelen, the Netherlands; D, E, *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), IRScNB unregistered [Van Straelen Collection], left cheliped, upper Albian Cambridge Greensand, Cambridge (southern England), oblique dorsal view showing upper margin of propodus and dactylus and outer view showing spinose lower margin. Scale bars: 5mm.

The spinose anterolateral margin of Palaeocorystoidea, functional in respiration, contrasts with that of Raninoidea, in which one spine (rarely two) may be present, which more likely functioned in limiting cheliped flexion. The lateral carapace margin presents an obvious difference between Palaeocorystoidea and Raninoidea, which can be explained by modifications of the exostegal channel. A secondary loss of anterolateral spines thus occurred in Raninoidea as a result of a modification of the respiratory system. Nearly all raninoids also have non-areolated carapaces in order to deeply and rapidly penetrate the sediment. Surface structures are applied to prevent the animal being pulled out of the sediment (Schmalfuss 1978a, b; Savazzi 1981, 1982, 1985) rather than to gather sediment on the carapace to camouflage the shallowly buried body.

The palaeocorystoid pterygostome shows a constant condition morphology, the surface being tumid, a broad oblique groove separating two long, blunt crests, of which the outer (lateral) extends into the prominent subantennary lobe of the pterygostome. The inner blunt crest may be parallel to the outer crest, or they may diverge. The crest's surface is invariably granular, and the grooves may be smooth or having pits. It may be hypothesised that this constant arrangement is related to the exostegal waterway, thus the inhalant respiratory flow of water between the pterygostome and chelipeds. The crests on the pterygostome are parallel in Necrocarcinidae and Camarocarcinidae, the inner crest extending onto the branchiostegite. The crest becomes obsolete on the branchiostegite of *Necrocarcinus*, the surface between this crest and the pereiopods being flattened (see Wright & Collins 1972: pl. 11, fig. 8a, b), whereas the crest is more pronounced in *Cretacocarcinus*, the flat surface along the pereiopods being more obvious (see Feldmann *et al.* 2008: fig. 4.1); In *Camarocarcinus*, the inner crest is distinct and sharp, the surface between the crest and the pereiopods concave and excavated (Fig. 15C, D). This was described as a 'pterygostomian rim' by Holland & Cvancara (1958: 501) (see also under Camarocarcinidae).

This excavated surface on the branchiostegite may have facilitated the flow of water between the bases of the pereiopods and the branchiostegite in order to enter the branchial chambers through the inhalant openings at the bases of the pereiopods. Such endostegal system was regarded as 'primitive' by Garstang (1897b: 215).

Setal pits are observed on the mouthparts and pterygostome and frontal region in all palaeocorystoids, but the most distinct setation is found in Palaeocorystidae. In this family especially the mxp3 exopod, the flabelliform mxp3 coxa, along the broad buccal collar, the groove between the crests on the pterygostome and the basal elements (coxa, basis-ischium) of the P1 are covered with setal pits. The setation on the mxp3 coxa and the P1 coxa most likely served a filtering function; when these setae interlock in front of the Milne-Edwards opening they could have prevented particles from entering the branchial chamber. Such dense setation may indicate that fine particles, such as mud, must be filtered from the inhalant current (see also Garstang 1897b: 219). On the other hand, setation on the mxp3 exopod and in the depression along the broad buccal collar of the buccal frame, appears to be homologous to setation in these regions in extant raninids, serving to limit the exostegal waterway.

The endostome is preserved in several palaeocorystoids. The endostome of *Necrocarcinus* is clearly modified, being elongated, anteriorly projected and with the lateral sides forming deep channels (Fig. 50E, G). It is wide and excavated into two broad, concave surfaces in *Cenomanocarcinus vanstraeleni*. *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii* and *Eucorystes iserbyti* **n. sp.**, have strongly elongated endostomes, their tips projected and rounded (Fig. 55A, D); the lateral surfaces are deeply excavated posteriorly and extend under the pterygostome (Fig. 55B, C). Without exception, the mxp3 are distinctly elongated in Palaeocorystoidea. The mxp3 of Orithopsidae was not examined. The exopod of palaeocorystoids is typically elongated, weakly curved and acutely tipped; the endopod basis-ischium and merus are slender, axially sulcate and nearly equal in length, closing medially. In camarocarcinids and necrocarcinids, both groups having tumid bodies and pterygostomes, the endopod basis-ischium and merus are positioned in two different planes (see Feldmann *et al.* 2008: 1743). These elements are in about the same plane in the other palaeocorystoid families. Anteriorly, the pterygostome terminates in a distinct, pointed process, the subantennary lobe of the pterygostome (Fig. 50F; for *Cretacocarcinus smithi* see Feldmann *et* *al.* 2008: figs. 6.3, 7.3). These pointed processes are parallel to the elongated endostome, and in the same plane as the mxp3 endopod merus. Together these three elements (subantennary lobe of the pterygostome, elongated endostome and tips of mxp3 endopods) are projected, and they form the oxystomian mouth, whichs form the exhalant orifice (and, in case of flow reversal, the inhalant opening) in the normal respiratory mode.

Two specimens of *Ferroranina dichrous* retain the basal articles (element 3) of the antenna (Fig. 8C, D). These elements are enlarged, strongly flabelliform, and, when opposed, form a funnel. There is a remarkable similarity to the structure seen in extant raninoids, and it may be assumed they had a similar function correlated to the oxystomian condition.

All palaeocorystoids have a similar configuration of the mxp3 coxae, not being close to each other, but separated by sternite 3; they are large, flabelliform, with many setal pits and intercalated between the thoracic sternum and the pterygostome, and in front of the P1. The posterior surface of the mxp3 coxa is curved inwards, which represents the Milne-Edwards openings. The distal margin of the coxa coincides with the posterior margin of the pterygostome, in contrast to the raninoid disposition where they do so with the lateral (buccal) margin of the pterygostome. A similar shape of the mxp3 coxa was described for *Calappa* by Bellwood (2002a: 118). The densely setose coxae 'appear to have the ability to regulate, and filter, the water entering the branchial chamber'. The same function is suggested here for the palaeocorystoid mxp3 coxae.

It may be concluded that the palaeocorystoid respiratory system is more basal than the raninoid respiratory system, with *Marylyreidus* **n. gen.,** showing an intermediate condition. The reduced P5 in Palaeocorystoidea most probably had no role in the respiratory process; implementation of the P5 in the respiratory process in Raninoidea (*pro parte*) is considered a subsequent innovation associated with innovation of posterior respiratory openings.

It is hypothesised that the respiratory function in Cenomanocarcinidae, Camarocarcinidae and Necrocarcinidae illustrates the most basal condition. The primitive modifications of *Necrocarcinus* rapidly evolved into the more specialised condition of *Notopocorystes*. The spinose anterolateral margins, areolated pterygostome and large, flabelliform mxp3 coxae, all efficient in respiration, are features that distinguish Palaeocorystoidea from Raninoidea. The Palaeocorystoidea flourished during the mid-Cretaceous (Albian–early Turonian). A global change in sediment type may have subsequently triggered their replacement by raninoid crabs, with the specialised stock (Palaeocorystidae) going extinct first.

Spermathecae and spermathecal apertures

The thoracic sternum is strongly modified in suture 7/8 of females in Podotremata. The interosternites between sternite 7 and 8 are altered by having its two component sheets separated (all thoracic sternites consisting of two sheets at the level of the sutures, the interosternites, at least in sutures 4/5–7/8) on both sides of the body to form internalised sperm chambers, the spermathecae. The podotreme spermatheca is thus derived from two adjacent thoracic somites, basically a split between the two sheets of the intersegmental phragma 7/8, one derived from sternite 7, the other from sternite 8 (Gordon 1950, 1963, 1966; Hartnoll 1975, 1979; Tavares & Secretan 1993; Guinot & Quenette 2005). The apertures of these paired spermathecae are located at the distal end of the suture 7/8. The chambers may be in direct contact with the aperture, or, in several cases (see below)**,** a tube is formed to accomplish sperm transfer from the aperture to the chamber. The shape, size and location of the podotreme spermathecal apertures vary (see Guinot & Tavares (2001: fig. 10).

The process of fertilisation in podotremes still is far from clear. Eggs are released from the female gonopores on P3 coxae and must be fertilised by sperm stored in the spermathecae. It is not known how this is achieved in the different groups.

Paired spermathecae are an apomorphy of Podotremata, in contrast to the unpaired spermathecae of e.g. Nephropidae Dana, 1852, and Cambaridae Hobbs, 1942. It is not homologous to the paired vulva on thoracic sternite 6 of Eubrachyura, in which the region for the sperm storage should be referred to as seminal receptacle (Tavares & Secretan 1993; Guinot & Quenette 2005).

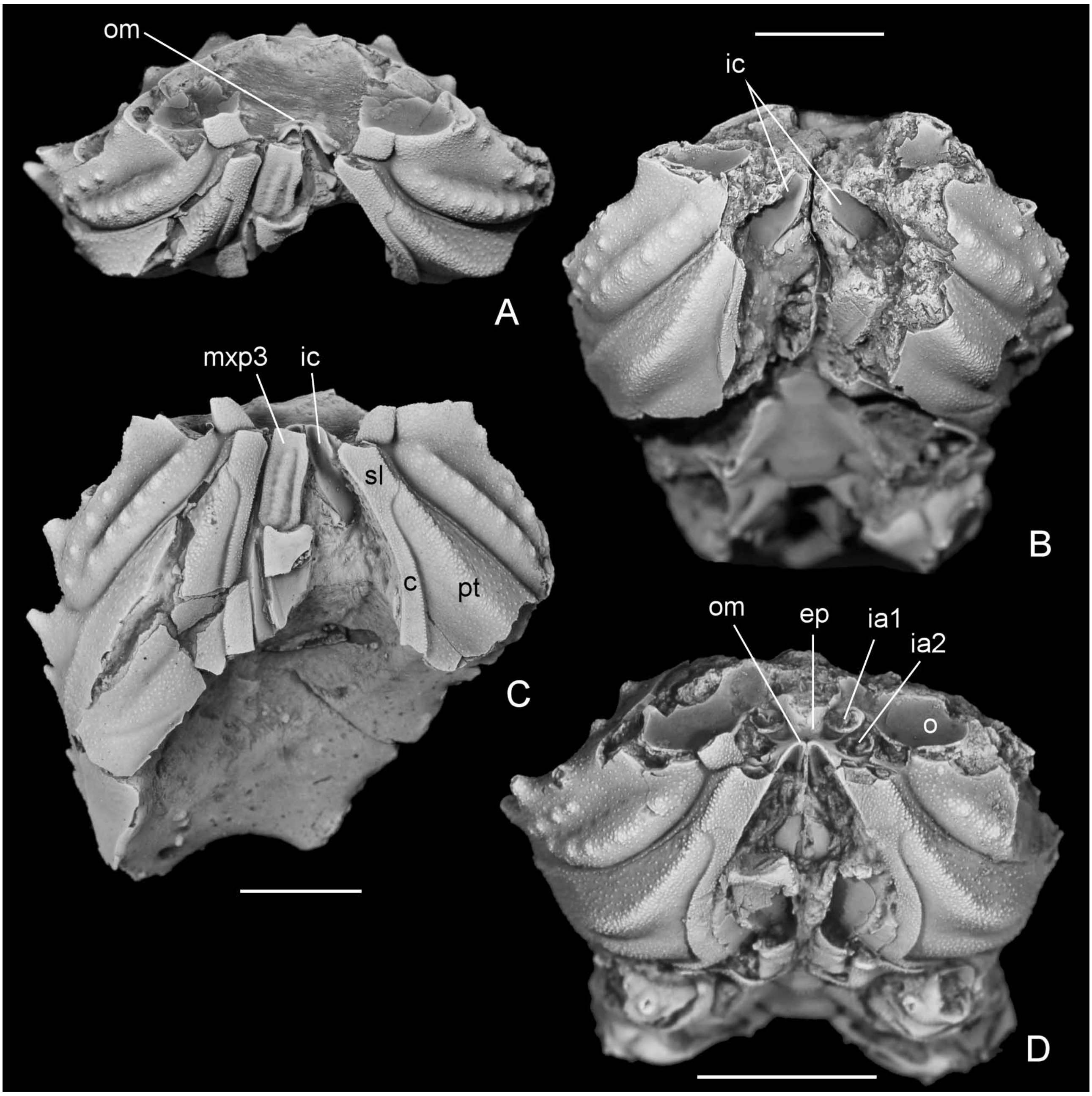

FIGURE 55. Oxystomian condition in *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), Albian, Escalles (Calais, northern France); A, C, MAB k. 2906 (indeterminate sex); frontal and ventral views; B, MAB k. 2873 (female), oblique frontal view; D, MAB k. 2907 (female), oblique frontal view. **c,** buccal collar of pterygostome; **ia1,** insertion of antennule; **ia2,** insertion of antenna; **ic,** inhalant channel; **ep,** epistome; **mxp3,** third maxilliped; **o,** orbit; **om,** oxystomian mouth; **sl,** subantennary lobe of pterygostome; **pt,** pterygostome. Scale bars: 5mm.

Gordon (1963, 1966) gave an account of the spermathecae in Raninidae. She externally examined specimens of *Ranina ranina*, and dissected individuals of *Notopoides latus*, suggesting that there was but a single, unpaired spermatheca. Hartnoll (1979) observed that there were paired apertures, and he put forward a hypothesis on the modified position of the spermathecal aperture in Raninoidea. Guinot (1993b) briefly mentioned the peculiar nature of the spermathecal aperture in raninoids and illustrated the paired apertures, which are mostly situated in a sunken pit in the different subfamilies. Guinot & Quenette (2005) studied and reviewed the spermathecae in podotremes and illustrated (Guinot & Quenette 2005: fig. 25) different patterns amongst the diverse subfamilies. Despite these accounts, and Hartnoll's (1979) well-argumented discussion in particular, the construction of the spermathecae in Raninoidea has never been well understood.

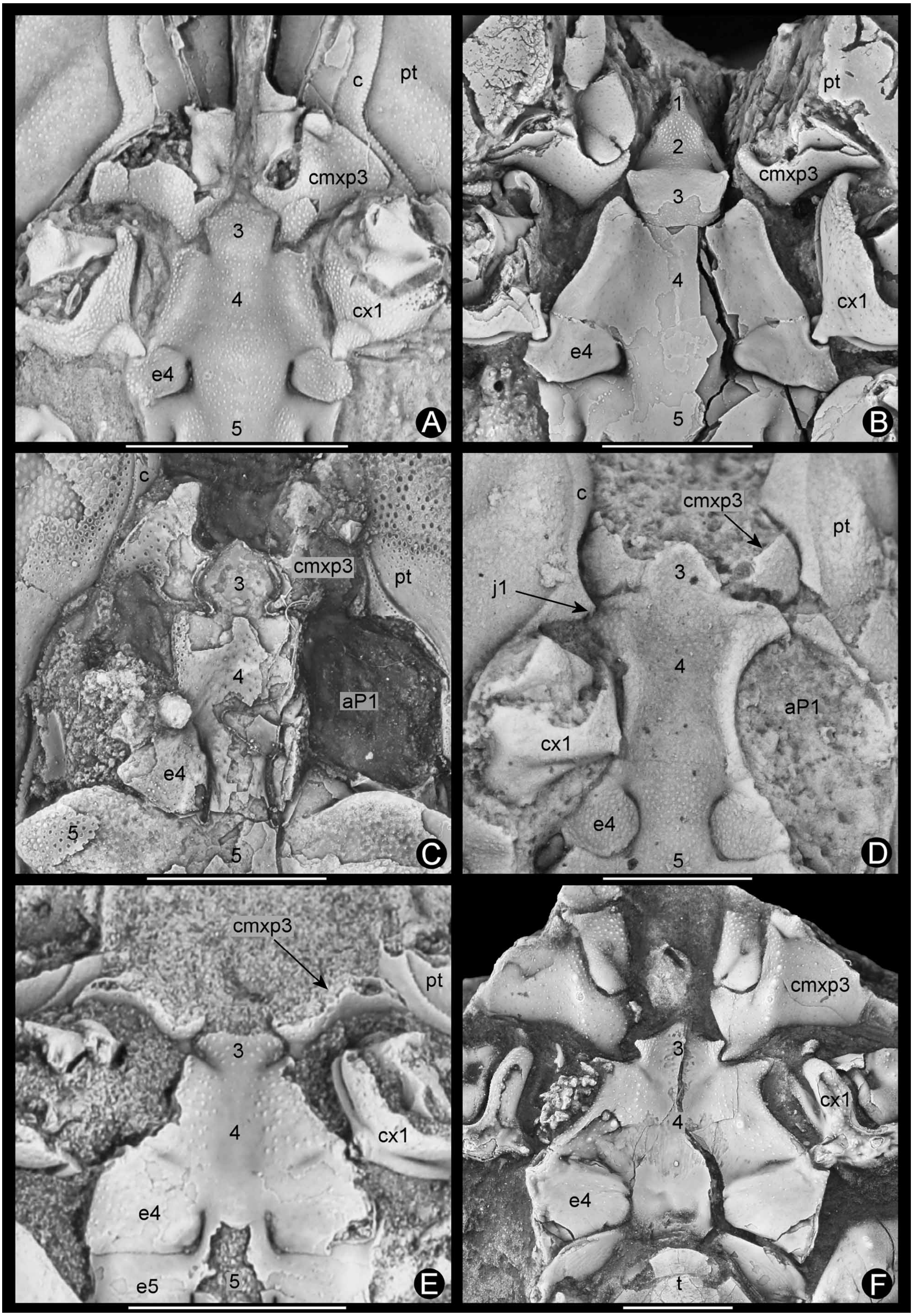
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FIGURE 56. Configuration of sternum-pterygostome and details of thoracic sternum in fossil Raninoidia; A, *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), MAB k. 2889 (female), Albian, Escalles (Calais, northern France); B, *Joeranina broderipii* (Mantell, 1844) **n. comb.** (Palaeocorystidae), MAB k. 2896 (indeterminate sex), Albian, Folkestone (Kent, southeastern England); C, *Marylyreidus punctatus* (Rathbun, 1935b) **n. comb.** (Lyreididae, Marylyreidinae **n. subfam.**), MAB k. 2884 (male), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County (Texas, U.S.A); D, *Bournelyreidus tridens* (Roberts, 1962) **n. comb.** (Lyreididae, Lyreidinae), MAB k. 0214 (cast of GAB 37-832, ?adult female), lower Maastrichtian, Mississippi (U.S.A); E, *Silvacarcinus laurae* Collins & Smith, 1993 (Orithopsidae), IRScNB TCCI 6115 (**holotype**; indeterminate sex), lower Eocene (Ypresian), Brussels (Belgium); F, *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Cenomanocarcinidae), MAB k. 2895 (female), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County (Texas, U.S.A). **1, 2, 3, 4, 5,** thoracic sternites 1, 2, 3, 4, 5; **aP1,** arthrodial cavity of P1; **c,** buccal collar of pterygostome; **cmxp3,** coxa of mxp3; **cx1,** P1 coxa; **e4, e5,** episternites 4, 5; **j1,** junction thoracic sternum/pterygostome; **pt,** pterygostome; **t,** telson. Scale bars: A-B, E-F: 5mm; C-D: 2mm.

Fossil record of spermathecae. The spermathecal apertures of fossil Podotremata have only been rarely noted. As recent examples have shown, however, dedicated research and delicate preparation has resulted in the discovery of spermathecal apertures in extinct podotremes, which invariably involve thoracic sternal suture 7/8 and which are often accompanied by a well-visible female gonopore on the P3 coxa.

Amongst Dromioidea, a spermathecal aperture was illustrated for *Dromilites simplex* Quayle and Collins, 1981 from the lower Eocene (Ypresian) of Kent, southeastern England (see Schweitzer & Feldmann 2010d: figs. 4h, 5). *Dromilites* was assigned to Sphaerodromiinae, which they considered to be of family rank. Previously, Van Bakel *et al.* (2009: 49) had observed that *Basinotopus tricornis* Collins & Jakobsen, 2004 from the middle Eocene of Jylland (northern Denmark) revealed spermathecal apertures (see Collins & Jakobsen 2004: pl. 2, fig. 1b). The specimen illustrated is a female and the gonopore on the P3 coxa is clearly seen. Sternal suture 7/8 is rather short, the small spermathecal apertures being situated at about the same level as the gonopore (see also Guinot *et al.* in press). Spermathecal apertures (sometimes well-preserved) have also been documented in Dakoticancroidea, in particular for *Dakoticancer overana* Rathbun, 1917 (see Guinot 1993a: fig. 7; Guinot & Tavares 2001: fig. 7; Artal *et al*. 2008: fig. 3D) and for *Tetracarcinus subquadratus* Roberts (1962: pl. 87, fig. 3). Spermathecal apertures of *Ibericancer sanchoi* Artal, Guinot, Van Bakel & Castillo, 2008, are fairly large, ovate and oblique.

Amongst the Etyoidea Guinot & Tavares, 2001, spermathecal apertures in *Etyus martini* Mantell, 1844, were demonstrated by Guinot & Tavares (2001: figs. 2, 3) in a specimen figured by Wright & Collins (1972: pl. 21, fig. 6a-e) from the Albian of southern England. Newly collected material of this species is currently under study.

Spermathecae in the Palaeocorystoidea. Only one example of spermathecal apertures for Cenomanocarcinidae and several instances for Palaeocorystidae exist in the material examined. As to the former family, a specimen of *Cenomanocarcinus beardi* with a partially preserved thoracic sternum reveals a spermathecal aperture on the left-hand side (Fig. 58A–D). Although the cuticle of this specimen is not particularly well-preserved, the spermathecal aperture can be clearly observed; it is elongated, slightly raised and its position at the extremity of sternal suture 7/8 is plesiomorphic for Podotremata. There is no median line on the thoracic sternum. Better-preserved material needs to be examined. Spermathecal apertures in Palaeocorystidae are documented for *Notopocorystes* and *Joeranina* **n. gen.** (Figs. 57A–D; 59A, B; 61A). The fairly large and elongated apertures have slightly raised or thickened margins and are situated at the extremities of sternal sutures 7/8. The spermathecal apertures are exposed at the surface of the thoracic sternum, thus not located in a pit or depression. There is a median line along thoracic sternite 8 in both genera. The cuticle in the great majority of specimens of *Notopocorystes* and *Joeranina* **n. gen.** is well-preserved, so that the presence and nature of the spermathecal aperture are proved unambiguously.

Spermathecae in the Raninoidea. Spermathecal apertures in Raninoidea are known only in extant material, their position being modified as they appear to open anteriorly on thoracic sternite 7 in proximity of the female gonopore on the P3 coxa. Various modes may be recognised.

Lyreididae: The small spermathecal apertures face each other on opposite sides of a depression (‘sunken pit’) of thoracic sternite 7, and are separated by a median line. Spermathecal apertures have not been recognised in the available Marylyreidinae **n. subfam.** material, but a depression is seen (Haj & Feldmann 2002: figs. 3.2, 4.2, 4.5).

Ranininae: The anterior part of thoracic sternite 7 shows a deep, elongated median depression; the apertures of the spermathecae are at the bottom of this depression (see Figs. 60C; 61B).

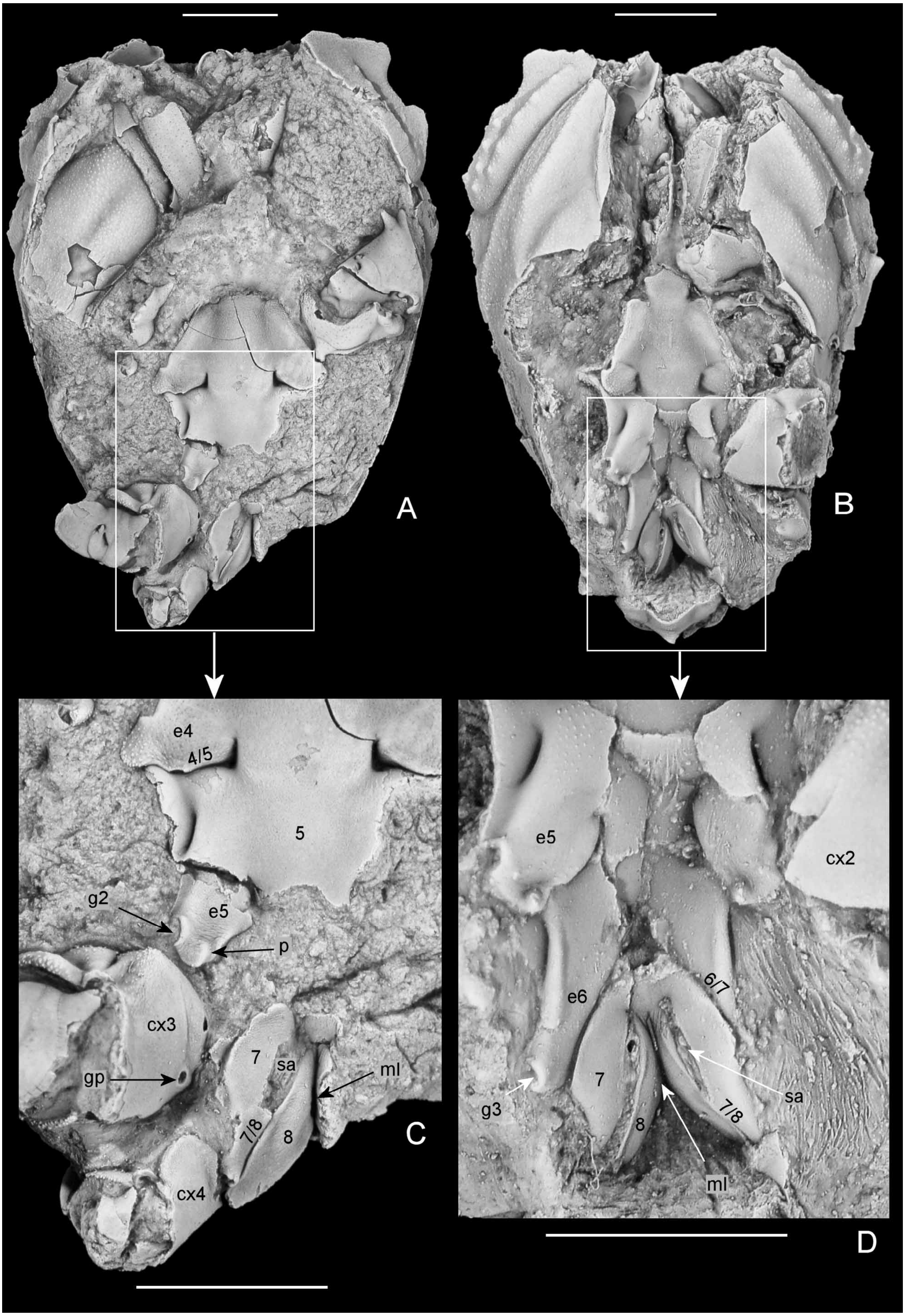
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FIGURE 57. Spermathecal aperture in palaeocorystids; A, C, *Joeranina broderipii* (Mantell, 1844) **n. comb.**, MAB k. 2913 (female), Albian, Escalles (Calais, northern France), ventral view showing thoracic sternum and detail of posterior thoracic sternum showing spermathecal aperture; B, D, *Notopocorystes stokesii* (Mantell, 1844), MAB k. 2873 (female), Albian, Escalles (Calais, northern France); ventral view showing thoracic sternum and detail of posterior thoracic sternites showing spermathecal apertures. **5, 7, 8,** thoracic sternites 5, 7, 8; **4/5, 6/7, 7/8,** thoracic sternal sutures 4/5, 6/7, 7/8; **cx2, cx3, cx4,** P2, P3, P4 coxae; **e4, e5, e6,** episternites 4, 5, 6; **g2, g3,** gynglymes for P2, P3 coxa; **gp,** female gonopore; **ml,** median line; **p,** peg (undifferentiated); **sa,** spermathecal aperture. Scale bars: 5mm.

Raninoidinae: Small spermathecal apertures situated on the tilted posterior part of the sternal plate and lying at the bottom of a deep, pit-like depression.

Notopodinae: The anterior part of sternite 7 shows a deep, elongated median depression with two small spermathecal apertures.

Symethinae: The spermathecal apertures are peculiar, neither situated in a median pit nor recessed. They are large, widely separated, horizontal in position and overhung by two calcified hoods.

Cyrtorhininae: The spermathecal apertures are small, contiguous and are recessed in a rather deep depression.

We agree with Hartnoll (1979: 80) and Goeke (1981: 975) that on the basis of spermathecal structure Lyreididae and Symethinae are the most basal, whereas Cyrtorhininae, Notopodinae, Raninoidinae and Ranininae, with more recessed spermathecal apertures, are derived.

Evolution of the raninoidian spermathecae. The plesiomorphic state of the spermathecal aperture is clearly seen in Palaeocorystoidea. The posterior thoracic sternum is relatively wide in Cenomanocarcinidae, yet narrower in Palaeocorystidae (Figs. 37A; 58A, B). Through specialisation towards burying, the raninoidian body has become extremely narrowed, inclusive of the thoracic sternum. When in an evolutionary series the thoracic sternum narrows, the sternites initially will not drastically decrease in size, but their surfaces become steeper and the coxae closer together (Fig. 61C). At first, narrowing the body will not strongly affect the width of sternite 4 (i.e., the chelipedal sternite), but does have an impact on the posterior sternites (Fig. 61A). The steep angle of the posterior sternites is clearly seen in specimens of *Notopocorystes* spp. (Figs. 11D, 57D, 59B). The steep surfaces of the sternites on both sides of the thoracic sternum abut. A median plate is initiated when the sternites on both sides of the thoracic sternum do so, a process that may be refered to as ‘infolding’ (Fig. 61C). The narrowing process starts posteriorly, hence the median line originates posteriorly, along thoracic sternite 8. If in an evolutionary polarity the sternum becomes narrower, the posterior sternites become increasingly narrower, and the median line will expand forwards. If the sternal sutures are situated laterally, their extremities will come closer to the median line.

The median line (see Pearson 1908: 35, fig. 6; pl. 3, fig. 18) forms an internal, median septum called the ‘median plate’. This is formed by the invaginated surfaces of the thoracic sternites. According to H. Milne Edwards (1851: 57, pl. 9, figs. 9, 10), the endosternites of the axial skeleton are medially connected by a ‘mesosternal plate’. Pearson (1908: 35) observed that the median plate was composed of two closely applied laminae in *Cancer pagurus* (Linnaeus, 1758). According to Drach (1939: 370, pl. 6, fig. 27; pl. 7, figs. 31, 32; in the cancrid *Cancer pagurus*), the somites were divided into two symmetrical parts by a vertical median partition (*lame*, *plaque médiane*) issued from an invagination of the sternal floor.

Various terminologies for the median line and median plate have been used: ‘deep longitudinal mid-ventral apodeme’ (Bourne 1922: 39), ‘median infolding of sternal apodeme’ (Gordon 1966: 348, 350), ‘median apodeme’ (Hartnoll 1979: 76), ‘*ligne médiane*’ and ‘*plaque médiane*’ (Guinot 1979a: 253) and ‘median line’ and ‘median plate’ (Guinot *et al.* in press).

That the median plate is situated mainly at the posterior sternites is clearly seen in the longitudinal sections of *Notopoides latus* of Gordon (1966: figs. 2b, 3b). The median plate is prominent at sternites 6 and 7, but weakly developed at sternite 5. When the sternum is so narrow that the sutures reach the median line, the internal phragmae corresponding to the sternal sutures are connected to the internal plate of the median line. This forms a very strong, grating-like structure, much stronger than the initial state; a favourable body construction for a burying crab. A similar modification is seen in other (unrelated) specialised burying species such as *Corystes cassivelaunus* (see Gordon 1966: figs. 5, 6). Burying crabs in general have a long median line (sutures 5/7–7/8 complete or only the first weakly interrupted) and a well-developed median plate. It appears that raninoids have the highest median plate amongst all brachyurans.

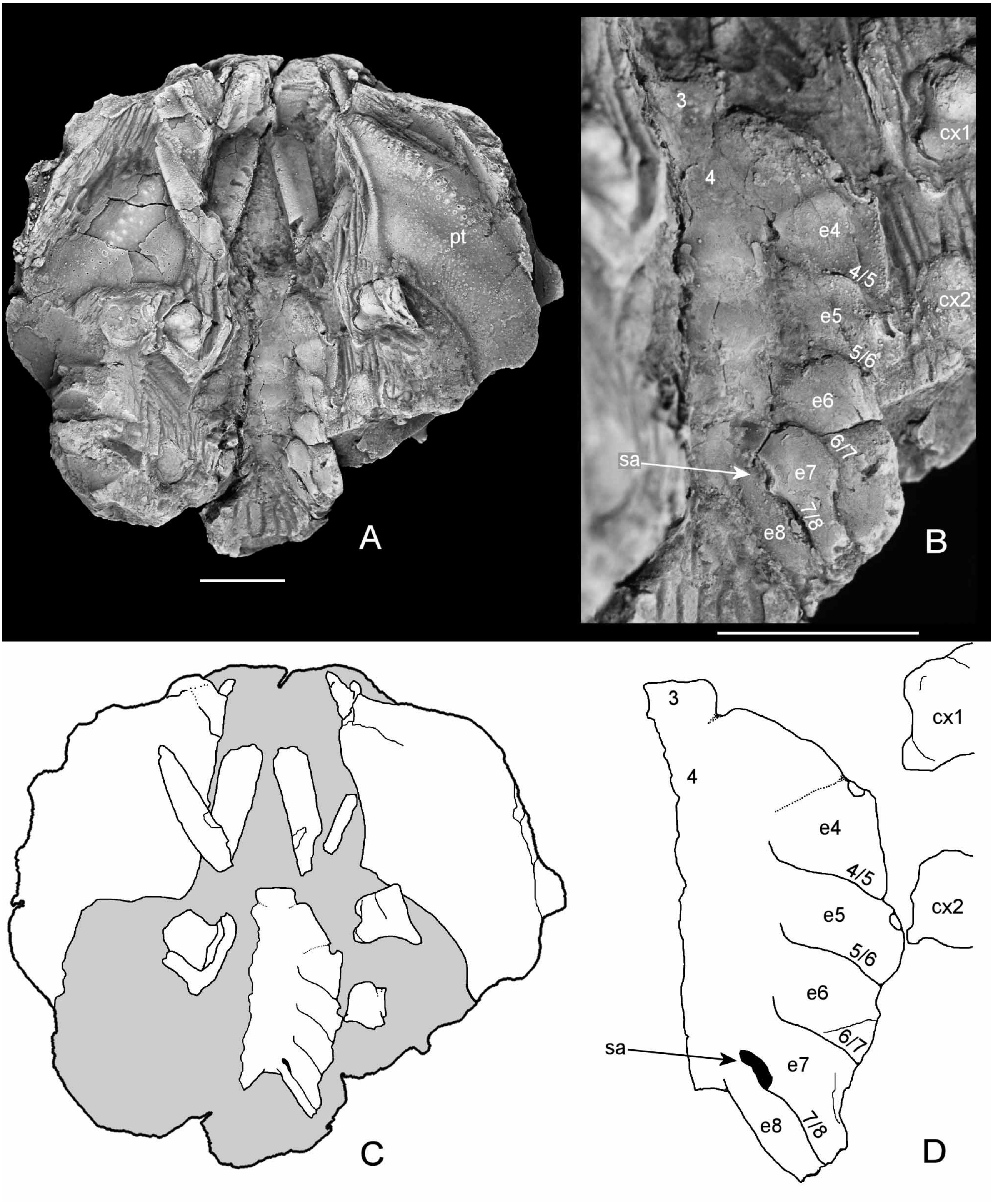

FIGURE 58. Spermathecal aperture in cenomanocarcinids; A, B, *Cenomanocarcinus beardi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a, MAB k. 2544 (female), Cenomanian (Woodbine Formation), Wagner Park, Texas (U.S.A); ventral view showing thoracic sternum, mxp3 and detail of thoracic sternum showing spermathecal aperture; C, D, Interpretative line drawings of A and B. **3, 4,** thoracic sternites 3, 4; **4/5, 5/6, 6/7, 7/8,** thoracic sternal sutures 4/5, 5/6, 6/7, 7/8; **cx1, cx2,** P1, P2 coxae; **e4, e5, e6, e7, e8,** episternites 4, 5, 6, 7, 8; **pt,** pterygostome; **sa,** spermathecal aperture. Scale bars: 5mm.

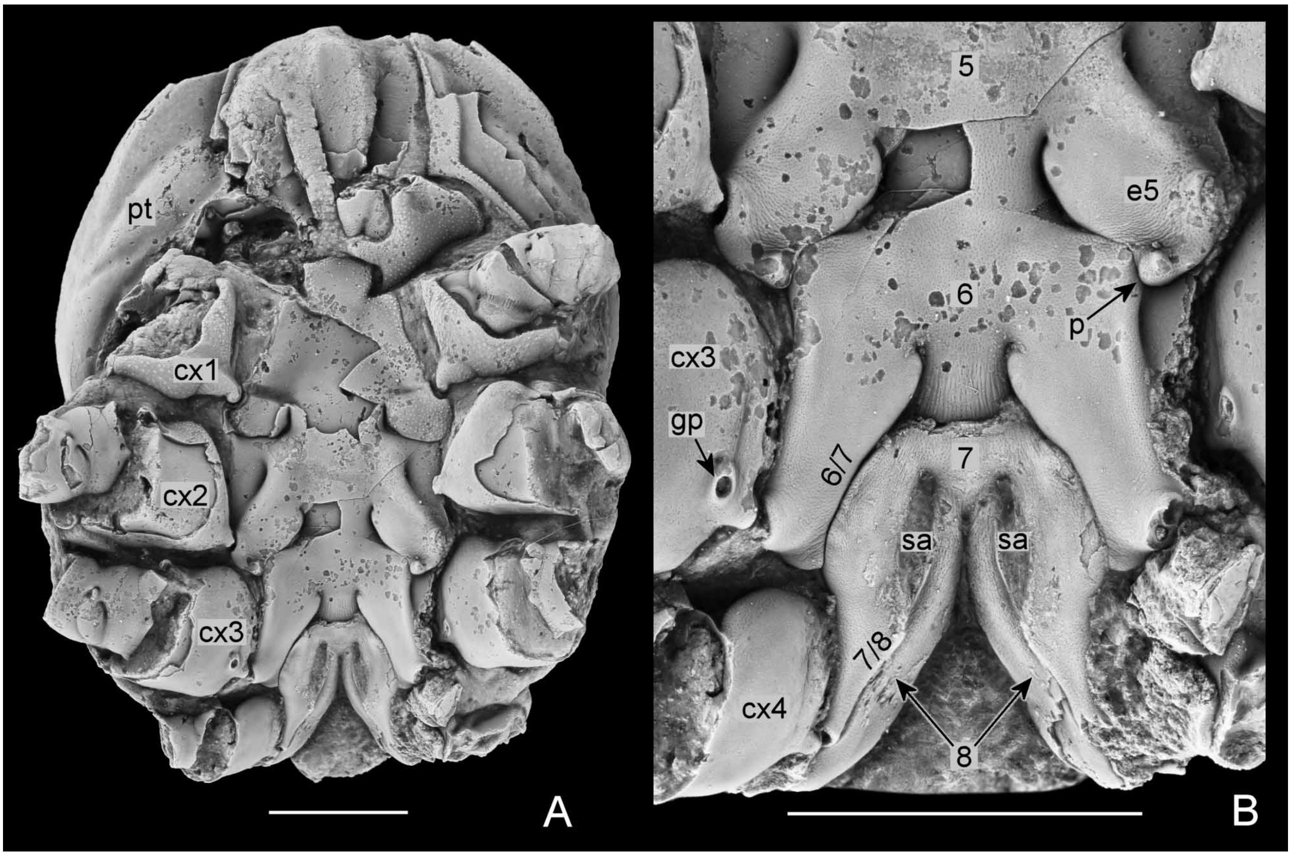

FIGURE 59. Spermathecal apertures in *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae); MAB k. 2924 (*ex* Guy van den Eeckhaut Collection; female), middle Albian, Lac du Der (northern France); A, ventral view showing well-preserved thoracic sternum, pterygostome and bases of appendages; B, detail of posterior thoracic sternites, showing spermathecal apertures. **5, 6, 7, 8,** thoracic sternites 5, 6, 7, 8; **6/7, 7/8,** thoracic sternal sutures 6/7, 7/8; **cx1, cx2, cx3, cx4,** P1, P2, P3, P4 coxae; **e5,** episternite 5; **gp,** female gonopore; **p,** peg (undifferentiated); **pt,** pterygostome; **sa,** spermathecal aperture. Scale bars: 5mm.

Extreme narrowing and infolding of the posterior thoracic sternites nevertheless leads to biomechanical difficulties. The spermathecal apertures are situated at the extremity of sternal suture 7/8 in females. In a gradual evolutionary process of infolding, the area which becomes internalised has gradually increased. The spermathecal apertures may migrate forwards (as in Dromiinae, see Tavares & Franco 2004), but this possibility is finite. Through infolding of sternite 7, the spermathecal apertures become ‘trapped’ within sternite 7. Despite the displaced position and cryptic construction, the spermathecal aperture is plesiomorphically situated at the extremity of suture 7/8, thus does not represent a secondarily acquired opening. It illustrates the normal configuration of Podotremata. This observation contrasts with Hartnoll (1979: 82, fig. 5), who discussed the possibility that ‘the present raninid spermathecal openings are not the original ones.’ The spermathecal aperture is thus still in connection with the spermathecal chamber, formed by separation of the two laminae composing endosternite 7/8. In other words, suture 7/8 has become partially internalised. Suture 7/8 is not short *per se*, but long, continuing ‘within’ the median plate (Fig. 61D), a condition verified by dissecting the thoracic sternum of a female *Ranina ranina* (Fig. 60A, B). The fact that suture 7/8 continues within the median plate demonstrates that the ‘walls’ of the infolding are actually the internalised exterior surfaces of somites 7 and 8. Through this cryptic construction, suture 7/8 is visible between the narrowly interspaced spermathecal apertures, as seen in Hartnoll (1979: fig, 1).

The potential survival value of narrowing the body must be substantial in view of the complex modification of the thoracic sternum, and it may be stated that the absolute limit of sternal narrowing has been achieved amongst raninoideans. The raninoid male gonopods are modified, coherent with the modified condition of the female spermathecal apertures (axial placement, paired but approximate) and the posterior/dorsal orientation of the abdomen. Gordon (1966: 348, 349, fig. 4a-c) described how the proximal segments of male pleopods 1 and 2 were extended backwards and the distal segments positioned at right angles to the proximal segments. The tips of the first pair of pleopods are closely apposed so they can enter the spermathecal pit.

Phylogeny of the Raninoidia

The status of subsection Raninoidia ranks amongst the most important issues in discussions on brachyuran systematics, not only as far as their early differentiation is concerned, but also from the viewpoint of understanding brachyuran macroevolutionary patterns. The inability to determine what the fundamental characters of extant Raninoidea are and how to interpret their organisation have been the major reasons behind this impediment for taxonomy. The strange, frog-like shape, plus various unusual features displayed by modern representatives have led to a number of hypotheses on their affiliation, either with anomurans, macrurans or brachyurans. The uniqueness of the Raninoidea was recognised on a number of occasions, which explains their assignment to distinct tribes: the Notopterygia within the 'Macruri' (see *The name* Notopterygia *Latreille, 1831* above), or the Notopoda and Gymnopleura within Brachyura. The last-named epithet refers to a unique raninoid characteristic, the partial exposure and calcification of several pleurites ('gymnopleure'), the gymnopleurity being a trait that has been insufficiently studied by neontologists following publication of Bourne's seminal paper (Bourne 1922b), and has even been largely ignored in palaeontological studies. The brachyuran nature of Raninoidea is presently widely accepted, but its precise placement amongst the true crabs remains controversial, with substantial debate during the last decade (Martin & Davis 2001; Ahyong *et al*. 2007, 2009; De Grave *et al.* 2009; Ng *et al.* 2009; Schweitzer *et al*. 2010). A decisive key is to determine whether or not this gymnopleurity, combined with other unique features, suffices to grant Raninoidea a distinct, high-level phylogenetic position within Brachyura. Carcinologists have recently favoured either: (1) a subsection Raninoida (containing the Raninoidea and Cyclodorippoidea) within the Eubrachyura, next to two other subsections, Heterotremata and Thoracotremata, as proposed by Martin & Davis (2001) and adopted by, for example, by Feldmann (2003), De Angeli & Garassino (2006b) and Schweitzer *et al.* (2010); (2) a separate section, Raninoida, next to two other sections, Dromiacea and Cyclodorippoida, alongside the section Eubrachyura (Ahyong *et al*. 2007, 2009; Ng *et al.* 2009; De Grave *et al.* 2009; Karasawa *et al*. 2011). This second scheme questions the monophyly of Podotremata, a status that has not been supported by most molecular studies and has been considered 'untenable' (Ahyong *et al.* 2007: 576, 581) (see below).

An alternative scheme is proposed here, the placement of Raninoidea within Podotremata together with four other main podotreme taxa, Homolodromioidea, Dromioidea, Homoloidea and Cyclodorippoidea (see Table 2), all of equivalent rank. The section Podotremata should be the sister group of the section Eubrachyura, which includes two subsections, Heterotremata and Thoracotremata (see Table 2; Guinot 1977, 1978, 1993a, b; Guinot & Tavares 2001; Guinot & Quenette 2005; Števčić 2005; Guinot *et al.* 2008; Ng *et al*. 2008; Guinot *et al*. in press).

This study of Palaeocorystoidea and Raninoidea does not support the opinion that raninoid crabs are eubrachyurans (see also Guinot *et al.* in press). The Raninoidia shows the presence of an internalised paired spermatheca formed by phragma 7/8 (synapomorphy of Podotremata) (Fig. 57A–D), and the podotreme condition of the female gonopore on the P3 coxa (Fig. 39A, D). Furthermore, despite its distinctive characters, the raninoid thoracic sternum (e.g., Figs. 31C; 34B) is not eubrachyuran in nature. Inclusion of the podotreme Raninoidea and Cyclodorippoidea in Eubrachyura conflicts with the major eubrachyuran synapomorphy; presence of sternal vulvae. Such a placement was considered 'counterproductive', rendering the 'eubrachyuran clade meaningless with respect to the degree of structural organisation of the heterotreme-thoracotreme assemblage' (Ahyong *et al.* 2007: 584).

The only alternative is to accept the podotrematous nature of Raninoidea together with that of Cyclodorippoidea. The taxonomic placement of both groups is intimately linked, even if a wide thoracic sternum characterises the latter (Fig. 47B). Brösing (2008: 277) assumed that, 'a common ancestor for Raninidae and Cymonomidae occurred in the middle of the Cretaceous'. Karasawa *et al.* (2009: 80) concluded that Podotremata consisted of 10 major subclades (but was clearly paraphyletic); this is a step in the good direction in recognising that a podotreme clade does exist, in opposition to the eubrachyuran crabs (with heterotremes and thoracotremes).

The Raninoidea, as previously noted above, exhibits unique, morphological characters. The study of well-preserved fossils which led to the establishment of Cenomanocarcinidae (Guinot *et al.* 2008) and the present results based on a range of new palaeontological data now permit a more comprehensive view of the evolutionary history of the group in a phylogenetic context. The extinct Palaeocorystoidea is here considered to be the sister group of Raninoidea, and the two superfamilies are grouped in subsection Raninoidia alongside the three other podotreme subsections, Dromioidia, Homoloidia and Cyclodorippoidia (Table 2).

Karasawa *et al*. (2011: 550) considered the assignment of Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae, Orithopsidae and Palaeocorystidae in a separate superfamily to be 'unwarranted'. Their analysis

(Karasawa *et al*. 2011: 533) rejects the opinion of Guinot *et al*. (2008) that a subsection Raninoidia could be divided into two superfamilies. However, theirs is based on a character matrix with several incorrect observations, a lack both of thorough examination of material available and understanding of extant raninoids; in consequence, there is no sound interpretation of evolutionary polarities. Karasawa *et al*. (2011: table 2) used a data matrix with several erroneous interpretations. For example, they stated that Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae and Palaeocorystidae (Orithopsidae not included in their analysis) do not have a socket ventrally at abdominal somite 6 (2011: 529, character 52; erroneously termed 'socket on sternite 6'); that Cenomanocarcinidae, Necrocarcinidae and Palaeocorystidae have a complete sternal suture 6/7 (character 33); and that Raninidae and Symethidae have the spermatheca 'united' (character 42). In addition, key characters of the raninoid clade were not studied and used in their consideration (i.e., exposure of pleurites, respiratory system, Milne-Edwards openings, junction of sternum with pterygostome). Therefore, we here consider their conclusions unsubstantiated.

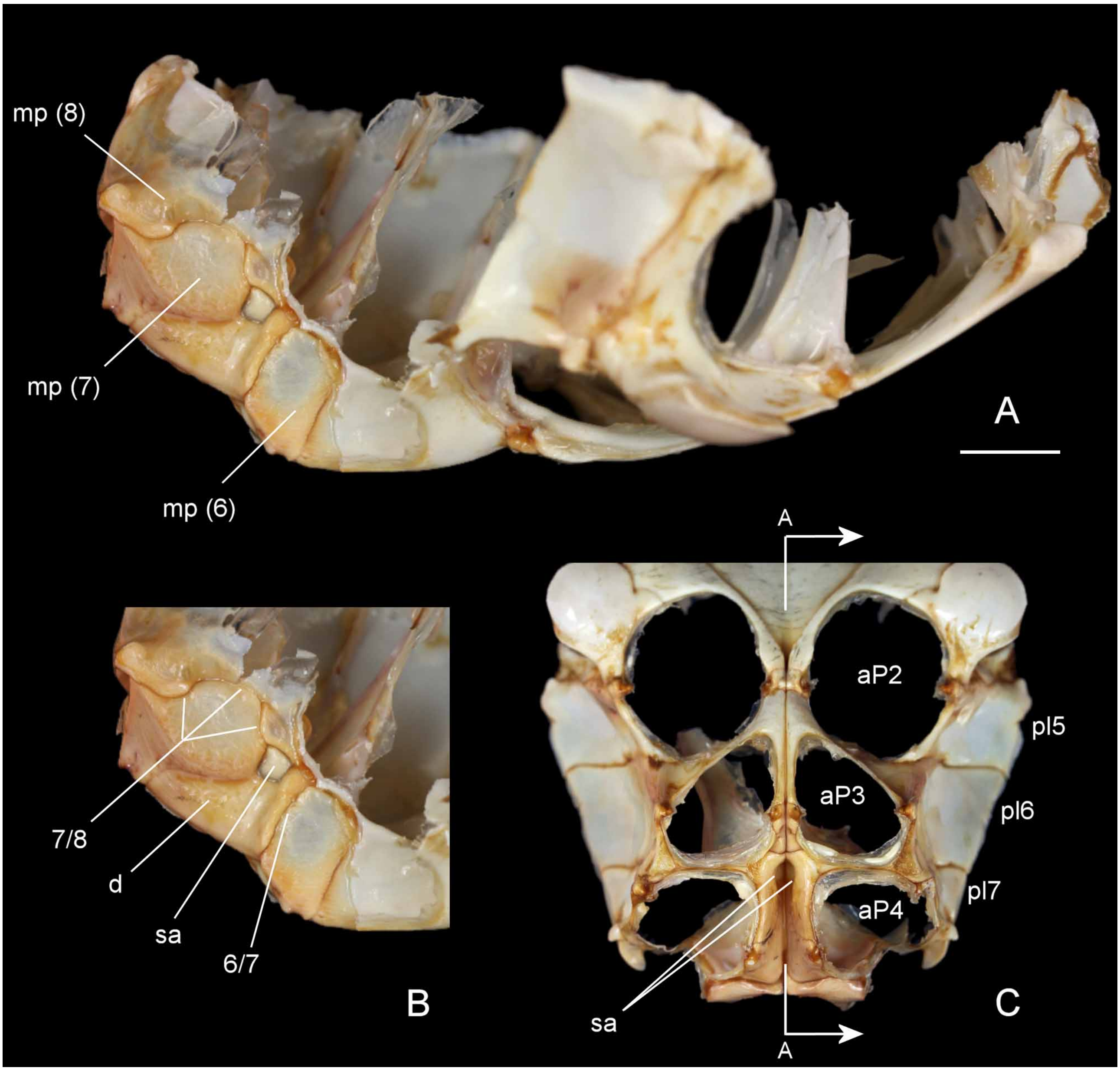

FIGURE 60. Thoracic sternum of *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae); MNHN unregistered (female), Recent, provenance unknown, prepared by S. Secretan; A, right lateral view showing partial internal view (axial section, for direction see Fig. C) of median plate; B, detail of internal view (axial section) of median plate showing long, sinuous suture 7/8 and spermathecal aperture; C, ventral view showing posterior thoracic sternites and spermathecal apertures in depression. **6/7, 7/8,** thoracic sternal sutures 6/7, 7/8; **aP2, aP3, aP4,** arthrodial cavities of P2, P3, P4; **d,** depression; **mp(6), mp(7), mp(8),** median plate (thoracic sternites 6, 7, 8); **pl5, pl6, pl7,** exposed pleurites 5, 6, 7; **sa,** spermathecal aperture. Scale bars: 5mm.

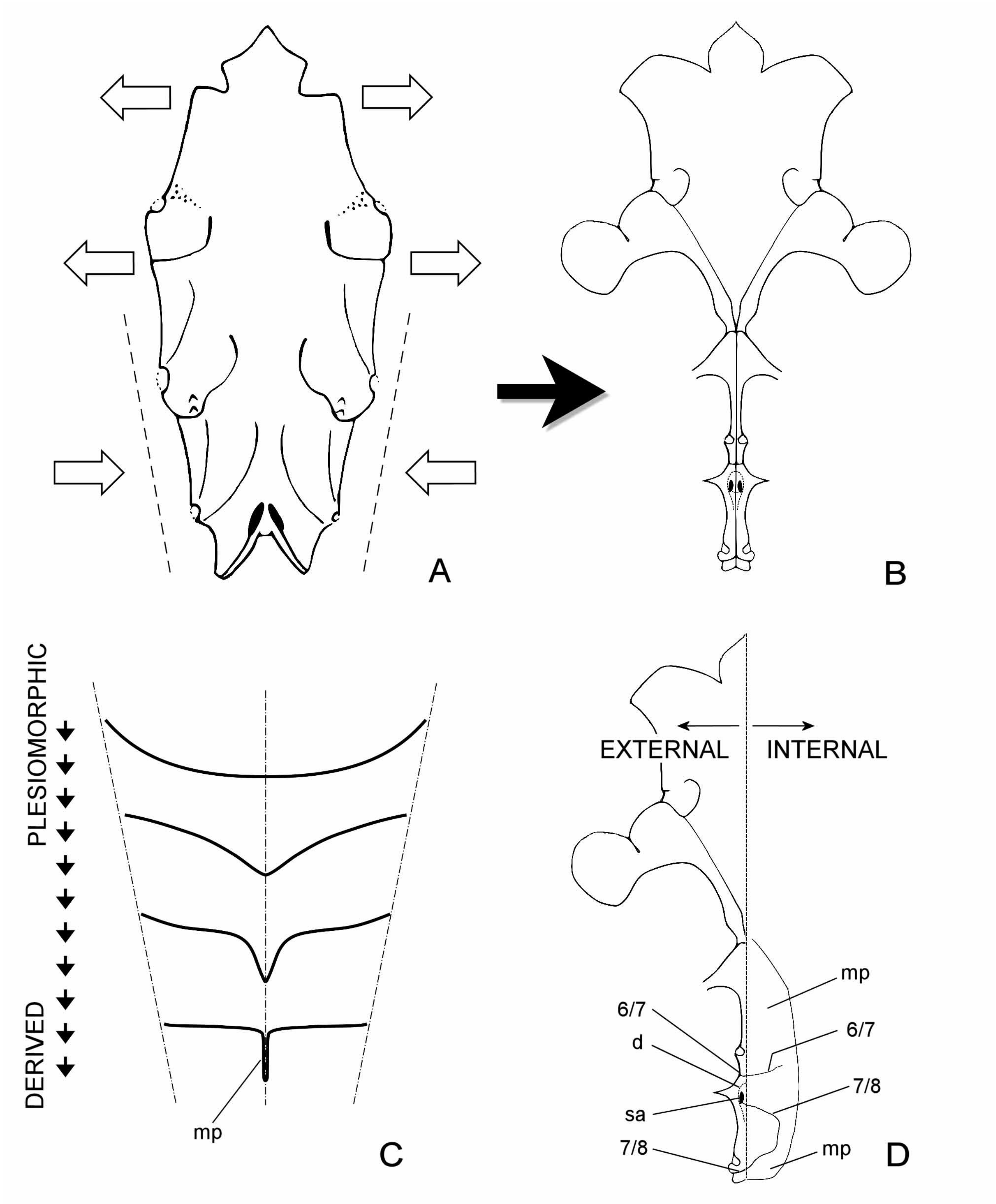

FIGURE 61. Narrowing of thoracic sternum in Raninoidia. A**,** thoracic sternum of *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), reconstructed after several specimens; B, thoracic sternum of *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae); C, hypothetical narrowing of thoracic sternum: transverse cross-section; D, thoracic sternum of *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), left-hand side showing ventral (external) view, right-hand side showing section (internal) view of median plate. **6/7, 7/8,** thoracic sternal sutures 6/7, 7/8; **d,** depression; **mp,** median plate; **sa,** spermathecal aperture.

The Podotremata is very diverse. Morphological patterns shared by podotremes are: the paired and internalised spermatheca depending of phragma 7/8 (see *Spermatheca and spermathecal apertures*), the male abdomen filling entirely in width the space between the pereiopods (but there are exceptions: Cyclodorippoidea, Dakoticancroidea), the shape of the intertagmal phragma that do not form a sella turcica similar to that of Eubrachyura (Guinot *et al.* in press), the shape of suture 4/5. A comparison of Palaeocorystoidea with the other extant and extinct podotreme superfamilies is an important prerequisite to unambiguously clarify the various morphological patterns of Podotremata.

Comparison of the superfamily Palaeocorystoidea with other podotreme superfamilies

Palaeocorystoidea versus Glaessneropsoidea Patrulius, 1959

This comparison considers Glaessneropsoidea *sensu* Schweitzer & Feldmann (2009, 2010b–c) and Schweitzer *et al*. (2010). This assemblage comprises five families: Glaessneropsidae Patrulius, 1959, Lecythocaridae Schweitzer & Feldmann, 2009, Longodromitidae Schweitzer & Feldmann, 2009, Nodoprosopidae Schweitzer & Feldmann, 2009, and Konidromitidae Schweitzer & Feldmann, 2010c. Only carapace material is so far known, and both the composition and diagnosis of the superfamily (Schweitzer & Feldmann 2009: 82) are far from stable at the moment, exemplified by the various rigorous changes recently proposed by Karasawa *et al*. (2011); additional studies are needed to elaborate its status.

Carapace.
– Carapace gently convex in transverse direction in Palaeocorystoidea (strongly convex in Glaessneropsoidea).
– Front as wide as or narrower than orbits in Palaeocorystoidea (much broader, more prominent in Glaessneropsoidea).
– Groove system shallow and subtle in Palaeocorystoidea (acute and prominent in Glaessneropsoidea).
– Cervical groove generally much more strongly incised in Glaessneropsoidea than in Palaeocorystoidea.
– Branchial groove weak, not notching the carapace margins in Palaeocorystoidea (always clearly defined, notching margins in Glaessneropsoidea).

Palaeocorystoidea versus Homolodromioidea Alcock, 1900

Extant Homolodromioidea are discussed and listed by e.g. Baéz & Martin (1989), Martin (1990, 1992, 1994), Guinot (1995), Guinot & Bouchard (1998), Ho & Ng (1999), Martin *et al.* (2001), Dawson (2002), Tavares & Young (2004), Guinot & Quenette (2005), Ng & Naruse (2007), Ahyong *et al.* (2009) and Guinot *et al*. (in press). The fossil record of Homolodromioidea (*sensu* Schweitzer & Feldmann 2009; Schweitzer *et al.* 2010) comprises four families: Bucculentidae Schweitzer & Feldmann, 2009, Goniodromitidae Beurlen, 1932, Prosopidae von Meyer, 1860, and Tanidromitidae Schweitzer & Feldmann, 2009. So far, all four are known solely from carapaces, which demonstrate a highly diverse pattern of carapace bauplan; their suprafamilial assignment remains doubtful. Discovery of ventral morphology may change the taxonomic composition of the extinct portion of this superfamily.

Carapace.
– Carapace varying from elongated (Palaeocorystidae) to subcircular or subhexagonal (Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae and Orithopsidae), always narrowing posteriorly in Palaeocorystoidea (always longer than wide, and generally constant in width or wider posteriorly in Homolodromioidea).
– Front subtriangular to subtrapezoidal in Palaeocorystoidea (two strong triangular teeth in Homolodromioidea).
– Branchial groove not notching the carapace margins in Palaeocorystoidea (notching margins in Homolodromioidea).
Pterygostome, endostome and mxp3.
– Endostome elongated (‘oxystomian mouth’) in Palaeocorystoidea (normal condition in Homolodromioidea).
– Mxp3 with oxystomian condition in Palaeocorystoidea (pediform, never oxystomian in Homolodromioidea).

Appendages.
- – Only P5 dorsal and reduced in Palaeocorystoidea (P4 and P5 reduced in Homolodromioidea).
- – P2–P4 with flattened articles in Palaeocorystoidea (cylindrical articles in Homolodromioidea).
- – Chelae with spiny lower margin in Palaeocorystoidea, an adaptation to burying (smooth in Homolodromioidea).

Thoracic sternum.
- – Sterno-abdominal depression wide, weak in Palaeocorystoidea (Cenomanocarcinidae, Orithopsidae and Palaeocorystidae) or strongly excavated (Camarocarcinidae and Necrocarcinidae) (long, wide and well excavated in Homolodromioidea).
- – Spermathecal apertures large, oval in Palaeocorystoidea (small, circular in Homolodromioidea).
- – Thoracic sternum with crescent-shaped (horizontal outer part, and deep, vertical inner part) sutures 4/5 and 5/6 in Palaeocorystoidea (anterior sutures hidden in sterno-coxal depressions in Homolodromioidea).
- – Sterno-coxal depressions absent in Palaeocorystoidea (present in Homolodromioidea).

Abdomen.
- – Male abdomen not longitudinally filling sterno-abdominal depression with telson partially covering sternite 4, leaving anterior portion of sternites 3 and 4 exposed in Palaeocorystoidea (entirely filling sterno-abdominal depression, with long telson reaching mxp3 in Homolodromioidea, so thoracic sternum not exposed at all).
- – Male abdomen without distinct pleura in Palaeocorystoidea (distinct pleura in Homolodromioidea).
- – Abdominal somite 6 long in both sexes of Palaeocorystoidea (normal in length in Homolodromioidea).
- – Telson rounded in Palaeocorystoidea (elongated, distinctly triangular in Homolodromioidea).

Abdominal holding.
- – Paired tooth on episternite 5 to hold the abdomen in Palaeocorystoidea (only coxal locking structures in Homolodromioidea).
- – Male abdomen in contact with coxae, but no locking by appendages in Palaeocorystoidea (structures on P1 and P2 to hold the abdomen in Homolodromioidea).

Palaeocorystoidea versus Dromioidea De Haan, 1833

Extant Dromioidea are discussed and listed by e.g. Gordon (1950, 1963), Lewinsohn (1977, 1984), McLay & Crosnier (1991), Crosnier (1994), McLay (1991, 1993, 1999, 2001a–c, 2002, 2009), Guinot & Bouchard (1998), Ng *et al.* (2000), Chen & Sun (2002), Guinot & Tavares (2003), Tavares & Franco (2004), Guinot & Quenette (2005), McLay & Ng (2007), Ahyong *et al.* (2009), Ng & McLay (2010) and Guinot *et al*. (in press).

Carapace.
- – Branchial grooves present as scars, or absent in Palaeocorystoidea (carapace mostly with well-defined branchial grooves in Dromioidea).

Pterygostome, endostome and mxp3.
- – Mxp3 oxystomian: distinctly elongated in Palaeocorystoidea (normal/operculiform in Dromioidea).
- – Endostome elongated (‘oxystomian mouth’) in Palaeocorystoidea (normal condition in Dromioidea).

Appendages.
- – Only P5 (sub)dorsal and reduced in Palaeocorystoidea (dorsal P4 and P5 in Dromiidae; only P5 in Dynomenidae).
- – P2–P4 with flattened articles in Palaeocorystoidea (cylindrical in Dromioidea).
- – Chelae always with spiny lower margin in Palaeocorystoidea, an adaptation to burying (non-spinose margins in dromioids).

Thoracic sternum.
- – Sternite 3 visible in Palaeocorystoidea (sternite 3 either dorsally visible at the same level as preceding ones or sternites 1–3 at a lower level in Dromiidae; anterior sternites crown shaped, sternite 3 variable in Dynomenidae).
- – Female suture 7/8 rather long, but not forming a tube in Palaeocorystoidea (forming a spermathecal tube of variable length in Dromioidea, usually conspicuously long in Dromiinae, short in Sphaerodromiinae and Dynomenidae).
- – Thoracic sternum with crescent-shaped sutures 4/5 and 5/6 (sutures short, hidden in sterno-coxal depressions in

Dromiidae and Dynomenidae).

Abdomen.

– Dorsal uropods absent in Palaeocorystoidea (present as dorsal plates in most Dromiidae, in some as ventral lobes, and all Dynomenidae).

Abdominal holding.

– Male abdomen in contact with coxae but no locking by appendages in Palaeocorystoidea (locking by appendages, acting often with uropods, in Dromioidea, except for Dynomeninae, which shows a sternal structure beside the uropod).

– Paired sternal tooth (double peg), on episternite 5 in Palaeocorystoidea (no sternal locking structures in Dromioidea, except in Dynomeninae, where the impaired sternal 'button' is not covered by abdomen, nor by uropod, thus no abdominal socket, the small sternal structure being located aside the abdomen and not facing any abdominal complementary part; e.g., *Dynomene hispida* (Latreille, *in* Milbert 1812)).

Palaeocorystoidea versus Homoloidea De Haan, 1839

Extant Homoloidea are discussed and listed by e.g. Gordon (1950), Serène & Lohavanijaya (1973), Guinot & Richer de Forges (1981, 1995), Wicksten (1985), Guinot & Bouchard (1998), Castro *et al*. (2003), Guinot & Quenette (2005), Richer de Forges & Ng (2007, 2008), Garassino (2009), Ahyong *et al.* (2009), Naruse & Richer de Forges (2010) and Guinot *et al*. (in press).

Carapace.

– Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (invariably elongated or pyriform in Homoloidea).

– Orbits well protected in Palaeocorystoidea (cornea often external: 'false orbit' *sensu* Wright & Collins 1972: 44; 'plage orbitaire' *sensu* Guinot & Richer de Forges 1995: 303, in Homoloidea).

Pterygostome, endostome and mxp3.

– Endostome elongated ('oxystomian mouth') in Palaeocorystoidea (normal condition in Homoloidea).

– Mxp3 oxystomian condition in Palaeocorystoidea (mxp3 pediform to almost operculiform, never oxystomian in Homoloidea).

Appendages.

– Chelae in Palaeocorystoidea with spiny lower margin (adaptation to burying) (margins smooth, granular, or with small spines on the whole surface but never with row of long spines in Homoloidea).

Thoracic sternum.

– Sternite 2 concealed in Palaeocorystoidea (sternites 1–3 forming a triangle, well visible between mxp3 in Homoloidea).

– Suture 6/7 only lateral in Palaeocorystoidea (complete in Homoloidea).

– Sterno-abdominal depression regularly excavated in Palaeocorystoidea (floor of sterno-abdominal depression with distinctive flat surface in Homoloidea).

Abdomen.

– Male abdomen not longitudinally filling sterno-abdominal depression; telson partially covering sternite 4, leaving anterior portion of sternites 3 and 4 exposed in Palaeocorystoidea (male abdomen entirely covering sterno-abdominal depression, so thoracic sternum not exposed in Homoloidea, except for sternites 1–3 visible between mxp3).

– Telson in Palaeocorystoidea not reaching mxp3 (reaching mxp3 in Homoloidea).

Abdominal holding.

– Paired tooth (double peg) on episternite 5 in Palaeocorystoidea for holding the abdomen (coxal holding by mxp3, P1–P3 in Homoloidea (except in Latreilliidae); presence of 'homoloid press-button' on sternite 4 acting with a socket on abdominal somite 6).

– Mxp3 never involved in abdominal holding in Palaeocorystoidea (base of mxp3 may be used in Homoloidea).

Palaeocorystoidea versus Raninoidea De Haan, 1839

Extant Raninoidea are discussed and listed by e.g. Bourne (1922b), Monod (1956), Gordon (1963, 1966), Gomes Corrêa (1970), Griffin (1970), Serène & Umali (1972), Hartnoll (1979), Goeke (1980, 1981, 1984, 1986), Davie (1989), Werding & Müller (1990), Guinot (1993b), Guinot & Bouchard (1998), Dawson & Yaldwyn (1994, 2000, 2002), Guinot & Quenette (2005), Ahyong *et al.* (2009) and Guinot *et al*. (in press).

Carapace.

– Carapace areolated and generally with cervical groove in Palaeocorystoidea, indistinct in Camarocarcinidae (not areolated, obsolete cervical groove in Raninoidea).

– Anterolateral margin of carapace with multiple teeth or tubercles in Palaeocorystoidea, fewer, however, in Camarocarcinidae (unarmed or with a single tooth or two teeth in Raninoidea).

Pterygostome, endostome and mxp3.

– Coxa of mxp3 large, flabelliform in Palaeocorystoidea (small and flat in Raninoidea).

– Antero-lateral corner of sternite 4 not in contact with pterygostome in Palaeocorystoidea, large coxa of mxp3 intercalated between thoracic sternum and pterygostome, presence of Milne-Edwards openings (sternum/pterygostome junction present, absence of Milne-Edwards openings in Raninoidea, except Marylyreidinae **n. subfam.**).

– Pterygostome with groove and blunt crest in Palaeocorystoidea (groove or crest absent in Raninoidea).

Appendages.

– Pereiopods equally spaced, putatively not separated by sternal extensions in Palaeocorystoidea (sterno-pleural extensions separating P1 and P2, and P2 and P3, thus pereiopods unequally spaced, in Raninoidea).

Thoracic sternum.

– No exposed pleurites in Palaeocorystoidea (pleurites 5–7 partially exposed (‘gymnopleurity’) and calcified in Raninoidea).

– Sterno-pleural extensions absent (present between P1 and P2 and between P2 and P3 in Raninoidea).

– Spermathecal apertures large, oval, separate, thus normal podotreme condition in Palaeocorystoidea (embedded in sternite 7, small, close to each other, deeply recessed in Raninoidea, rarely otherwise).

Abdomen.

– Male abdomen rather long, telson reaching sternite 4, completely flexed under the body and locked in Palaeocorystoidea (short and posterior, telson only reaching sternite 6, not completely flexed and not locked in Raninoidea, except Lyreididae).

Abdominal holding.

– Paired sternal tooth (double peg) on episternite 5 in Palaeocorystoidea (absent in Raninoidea, except in Lyreididae, with two teeth at tip of a short or long hook-like projection formed by extended episternite 5).

Palaeocorystoidea versus Cyclodorippoidea Ortmann, 1892

Extant Cyclodorippoidea are discussed and listed by e.g. Tavares (1991, 1992a, b, 1993a, b, 1994, 1996, 1997, 1998, 1999, 2006), Guinot & Bouchard (1998), Guinot & Quenette (2005), Ahyong *et al.* (2009) and Guinot *et al.* (in press).

Carapace.

– Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (varying from longer than wide but never markedly elongated, to subcircular, wider than long, occasionally expanded posteriorly in Cyclodorippoidea).

Pterygostome, endostome and mxp3.

– Epistome normally visible in Palaeocorystoidea (covered by extended endostome in Cyclodorippoidea, having a complete oxystomian condition in most Cyclodorippidae, but epistome present in Phyllotymolinidae).

– Endostome elongated in Palaeocorystoidea (long, extended and reaching the front, sometimes visible dorsally, except in Phyllotymolinidae, Cymonomidae and some Cyclodorippinae).

- No sternum/pterygostome junction and 'normal' Milne-Edwards openings in Palaeocorystoidea (a sternum/pterygostome junction and absence of Milne-Edwards openings in Cyclodorippidae, which has a complete oxystomian condition, but no junction in Phyllotymolinidae and Cymonomidae).

Appendages.

- Only P5 dorsal and reduced in Palaeocorystoidea (P4 and P5 reduced, usually subchelate, mobile, may be placed on dorsal carapace in Cyclodorippoidea; carrying behaviour described in some species, P4 and P5 are vestigial, reduced to an article in *Elassopodus*).

Thoracic sternum.

- Thoracic sternum rather narrow, not exposed laterally in Palaeocorystoidea (thoracic sternum wide, largely exposed laterally in Cyclodorippoidea).
- No sternal extensions in Palaeocorystoidea (a sternum/branchiostegite junction in Cyclodorippoidea due to extension of episternites between P1 and P2, P2 and P3, variable between P3 and P4).
- Presence of a sterno-abdominal depression in Palaeocorystoidea (usually short, posterior sterno-abdominal cavity, occupying only sternites 5–8 or 6–8, in Cyclodorippoidea).

Abdomen.

- All (6 + telson) abdominal somites free in Palaeocorystoidea (a variable number of abdominal somites fused in Cyclodorippoidea, often with a pleotelson, i.e., somite 6 fused to telson).
- Abdomen with continuous margin in Palaeocorystoidea (various arrangements, often with elongated pleura, in Cyclodorippoidea).

Abdominal holding.

- Sternal paired tooth (double peg) on episternite 5 in Palaeocorystoidea ('sliding system' (Cyclodorippidae) or 'block system' (Phyllotymolinidae) to hold the abdomen; no system known in Cymonomidae; absence of sockets in Cyclodorippoidea).

Palaeocorystoidea versus Etyoidea Guinot & Tavares, 2001

Extinct Etyoidea are discussed and listed by e.g. Carter (1898), Rathbun (1935b), Wright & Collins (1972), Schweitzer Hopkins *et al*. (1999), Guinot & Tavares (2001), Van Bakel *et al.* (2005), Fraaije *et al.* (2008b), Karasawa *et al*. (2008a), Collins & Breton (2009) and Klompmaker *et al*. (2011).

Carapace.

- Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (exceptionally wide in Etyoidea).
- Areolation of dorsal carapace weak in Palaeocorystoidea (marked areolation in Etyoidea).
- Orbits medially uninterrupted in Palaeocorystoidea (widely separated through intercalation of antennular fossae in Etyoidea).
- Front narrow in Palaeocorystoidea (wide in Etyoidea).
- No antennular fossa in Palaeocorystoidea (distinct and large fossa for large basal antennular article in Etyoidea).

Pterygostome, endostome and mxp3.

- Endostome elongated (oxystomian condition) in Palaeocorystoidea (normal condition in Etyoidea).
- Mxp3 oxystomian in Palaeocorystoidea (entirely operculiform in Etyoidea).

Appendages.

- Chelae with spiny lower margin in Palaeocorystoidea for burying (chelae long and slender, without spinose lower margin in Etyoidea).
- Pereiopods 2–4 with flattened articles in Palaeocorystoidea (cylindrical articles in Etyoidea).

Thoracic sternum.

- Shallow, lateral sterno-coxal depressions in Palaeocorystoidea (deep, complete sterno-coxal depressions in Etyoidea).

Abdomen.

- Female abdomen not reaching mxp3 in Palaeocorystoidea (reaching mxp3 in female Etyoidea).

Abdominal holding.

– Male abdomen in contact with coxae but no locking by appendages in Palaeocorystoidea (distinct structures on several pereiopods, P1–P3 may be involved, to hold the abdomen in Etyoidea).

Palaeocorystoidea versus Dakoticancroidea Rathbun, 1917

The extinct Dakoticancroidea are discussed and listed by e.g. Weller (1905), Rathbun (1917, 1923), Kesling & Reimann (1957), Roberts (1962), Bishop (1981, 1988), Vega & Feldmann (1991), Guinot (1993b), Bishop *et al.* (1998) and Artal *et al.* (2008).

Carapace.
– Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (subquadrate to subrectangular in Dakoticancroidea).
Pterygostome, endostome and mxp3.
– Endostome elongated (‘oxystomian mouth’) in Palaeocorystoidea (normal condition in Dakoticancroidea).
– Mxp3 oxystomian in condition: distinctly elongated in Palaeocorystoidea (operculiform in Dakoticancroidea).
Appendages.
– Only P5 reduced in Palaeocorystoidea, as in Dakoticancridae (P4 and P5 reduced in Ibericancridae).
– Articles of P2–P4 modified (propodus, dactylus flattened) in Palaeocorystoidea (Cenomanocarcinidae, Palaeocorystidae, unknown condition in others) (pereiopods stronger developed, distal articles not modified in Dakoticancroidea).
Thoracic sternum.
– Thoracic sternum narrow in Palaeocorystoidea (wide in Dakoticancroidea, in which sutures are much longer).
– Thoracic sternum entirely covered in width by abdomen in both sexes in Palaeocorystoidea (laterally exposed in male and even in female Dakoticancroidea).
– Sterno-abdominal depression in Palaeocorystoidea (distinct, rather deep sterno-abdominal cavity in male Dakoticancridae; sterno-abdominal depression towards a cavity in male Ibericancridae).
– Spermathecal apertures elongated, oval in Palaeocorystoidea (circular in Dakoticancroidea).
Abdomen.
– Sexual dimorphism indistinct in Palaeocorystoidea (well-defined, i.e., abdomen much wider in female Dakoticancroidea).
– First abdominal somites in prolongation with the carapace, thus visible in dorsal view, in Palaeocorystoidea (completely folded in Dakoticancroidea).
– Telson as wide as abdominal somite 6 in both sexes of Palaeocorystoidea (telson narrower than abdominal somite 6 in females, but as wide as abdominal somite 6 in males in Dakoticancroidea).
Abdominal holding.
– Sternal paired teeth on episternite 5 near outer lateral margin of thoracic sternum in Palaeocorystoidea (one or more tubercles in the medial part of thoracic sternum, thus at the margin of the sterno-abdominal cavity in Dakoticancroidea).

Monophyly of the Raninoidia

The above comparisons place more emphasis on the considerable diversity displayed by podotremes rather than highlighting the homologous features that they share. With the addition of fossil taxa, both palaeocorystoid and raninoid, the subsection Raninoidia appears to be a diversified, major podotreme subclade which represents a relict fauna, which dates back at least to the Early Cretaceous (Hauterivian, 136.4–130.0 Ma). Modern raninoid faunas comprise merely twelve genera and forty-six species, in contrast with the 196 exclusively fossil species listed by De Grave *et al.* (2009: table 1). The 37 genera listed by Schweitzer *et al.* (2010: 70–78) are, in fact, inaccurate since several podotreme taxa (Necrocarcinidae and Orithopsidae) were included by those authors in Dorippoidea (Eubrachyura; see Schweitzer *et al.* 2010: 80) and therefore not counted. Here counted are 48 extinct genera (see Tables 3 and 6) and 251 nominal extinct species (see Appendix) of Raninoidia; *incertae sedis* are excluded for both.

The Palaeocorystoidea first appears in the Hauterivian with the Necrocarcinidae; the oldest known occurrence of Orithopsidae is late Aptian, that of Palaeocorystidae early Albian, and Cenomanocarcinidae late Albian (Fig. 62). The Palaeocorystidae is assumed to have gone extinct during the late Maastrichtian (Late Cretaceous), whereas Orithopsidae extends into the Oligocene.

Raninoidian diversity is illustrated by the number of new fossil genera (eight) and species (nine) that are erected herein. Moreover, the extinct subfamily Marylyreidinae **n. subfam.** constitutes a transitional form which fills a gap in exhibiting the gymnopleurity of Raninoidea, yet not revealing the junction sternum-pterygostome (and hence exhibiting a different respiratory system from all other raninoids). The Lyreididae is here considered a separate lineage, having retained a relatively long abdomen inserted in the sterno-abdominal depression and held in place by a hook matching a conspicuously long and deep socket (Fig. 36C, D). The socket matching the double peg of Palaeocorystoidea is not exposed in any of the available material.

The interrelationships of the extant Raninoidea have not been studied here but a single family is recognised, as opposed to Lyreididae, namely Raninidae, which comprises Ranininae, Notopodinae, Raninoidinae, Cyrtorhininae and Symethinae. The Cyrtorhininae and Symethinae, which show a number of similarities, are the more basal taxa, and may represent separate sublineages within Raninoidea.

The very long stratigraphic range and diversity of Raninoidia could explain the difficulties encountered when interpreting their morphological organisation and genetics of representatives in nature; many possess derived characters that have evolved since the time of the lineage's divergence and successive radiations.

The paired spermathecae formed by phragma 7/8, the synapomorphy that supports the monophyly of Podotremata (see below), is a trait shared by all raninoidian taxa, both fossil and extant. Tavares & Franco (2004: 132) recognised two additional synapomorphies: (1) the development in a forward direction of the thoracic sternal suture 7/8, leading to the forward displacement of the spermathecae; (2) the intersegmental phragma 7/8 modified to form the spermathecal bulb. A spermathecal bulb is found only in Dromioidia, so it would be better to describe the chamber, which is found in all Podotremata.

The podotreme spermatheca displays several modalities in shape, size and precise location of its apertures on the sternal surface (Guinot & Tavares 2001: fig. 10). That it invariably involves the same two somites and same skeletal parts has not been contradicted so far. The spermathecal apertures that have been found and examined in several fossil podotreme families are no exceptions: Etyidae (Guinot & Tavares 2001: figs. 2, 3, 10J), Dakoticancridae (Guinot 1993a: figs. 7, 8; Guinot & Tavares 2001: fig. 10H; Artal *et al*. 2008: fig. 3D), Ibericancridae (Artal *et al*. 2008: 17), Cenomanocarcinidae and Palaeocorystidae (present paper; Guinot *et al.* 2008: 719). The same is true for the spermathecal apertures recently discovered in several other podotreme taxa (unpublished data).

The spermathecal apertures observed in Palaeocorystoidea are separate, not recessed, normally located at the extremities of sutures 7/8, as usual in Podotremata. They become displaced and cryptic in the more derived Raninoidea, a primitive condition being supplied by archaic forms such as Lyreididae and Symethinae (Goeke 1981: fig. 2A; Davie 1989: fig. 1c). The key problem, the determination of the evolution of the raninoidian spermathecal structure, has been solved by identifying the polarity of the transformation series: from the plesiomorphic palaeocorystoid character-state (Figs. 57, 58, 59) to the apomorphic character-state of Raninoidea (Fig. 53). The evolution of the peculiar raninoid spermathecae beyond the condition found in the other Podotremata, i.e., how the basal condition of the spermatheca could have evolved into the raninoid one, was discussed by Hartnoll (1979: 82, fig. 5). We agree with Hartnoll (1979: 82) who argued for, 'a common spermathecal structure for all early Brachyura', namely Podotremata, including Raninoidea, and concluded that most likely 'the raninids are not on the direct line leading to the higher Brachyura, and that their spermathecal structure is not relevant to the origin of that of the higher forms'. The raninoid spermathecal apertures, however, are not secondarily acquired openings (see *Spermatheca and spermathecal apertures*). Only their apertures are displaced (Fig. 53) and became cryptic as a result of the strong modifications that affected the whole body; the same major transformation that led to the numerous original features of Raninoidea, exemplified by the gymopleurity (Fig. 42B), a unique brachyuran trait.

The acquisition of particular features in the derived Raninoidea, e.g., the lift of the carapace, the narrowing of the carapace and the thoracic sternum, the shortening and unfolding of the abdomen, the modified respiratory structures with a progressive excavation of the plate formed by the exposed and calcified pleurites 5–7, and the increasing implementation of functional cuticle microstructures, may be followed in the transformation series Palaeocorystoidea–Raninoidea. These transformations are considered adaptations to a highly specialised burying mode of life (see *Modifications for a burying mode of life* above). The survival of the raninoidian clade was dependent of its ability to exploit different environments through geological times, and the implementation of novel features permitted its diversification and increased the number of available ecological areas. Such adaptations have evidently involved a more successful reproduction. An oxystomian condition was already present in all families of Palaeocorystoidea, with the endostome only weakly modified in Necrocarcinidae, here considered the most primitive Palaeocorystoidea (see *Respiration in the Brachyura* above). The general morphology of cenomanocarcinids and orithopsids suggests they were able both to bury and swim, whereas palaeocorystidae were the back-burying specialists, in an evolutionary path leading to Raninoidea.

The monophyly of Raninoidia is supported by: (1) the modification of the distal articles of the P2–P4, the propodi and dactyli being flattened and/or enlarged, constantly with a special shape of the P2–P5 dactyli; (2) the crown-shaped anterior sternites; (3) the abdominal-locking system consisting of a double structure on sternite 5, consisting either of a double peg (Palaeocorystoidea) or a hook-like projection ending in two teeth (Lyreididae), or lost (Raninoidea, except Lyreididae) (see *Diagnosis of the Raninoidia* above).

The male abdomen of Raninoidia is either rather long, folded and locked, filling entirely in width the sterno-abdominal depression (Palaeocorystoidea) or moderately elongated, narrow, filling the total width of the sternal plate and locked (Lyreididae), or short, incompletely flexed, not held, virtually not leaving any sternal space exposed laterally (Raninidae). The characters of Raninidae are in fact plesiomorphic, but a strong specialisation has given rise to a considerable modification. It is hoped that the perennial uncertainty about the nature of Raninoidia is now solved thanks to the study of its extinct component, Palaeocorystoidea, in context of their extant representatives.

Glaessner (1960: 46) suggested that *Notopocorystes*, closer to *Necrocarcinus* than to its known descendants, was the most primitive palaeocorystid, with a common ancestor for *Notopocorystes* and *Necrocarcinus* during Early Cretaceous or even Jurassic times (see also Collins 1997). The oldest Lyreididae (Marylyreidinae **n. subfam.**) and Raninidae are known from about the same date, the late Albian.

Carcinisation and secondary elongation

Carcinisation, which is the phenomenon leading to the evolution to a crab-like body form in the higher Decapoda (von Sternberg 1996; McLaughlin & Lemaitre 1997; McLaughlin *et al.* 2004, 2007; Lemaitre & McLaughlin 2009; Guinot *et al.* in press), is a notion not yet addressed in Raninoidia. Carcinisation in Brachyura involves several anatomical readjustments, mainly the reduction of the relative length of the cephalothorax, flattening of the carapace, broadening of the thoracic sternum and its transformation into a wide plastron, cephalic condensation with folding of sensorial organs (antennules and antennae), modification of orbits and eyestalks with formation and closure of the orbits, excavation of a cavity to receive the abdomen, lateral opening of the arthrodial cavities, expansion of sternite 4 linked with increased strength for the chelipeds and expansion of posterior sternites. The female and male gonopores of Podotremata are located on the appendages (P3 and P5 coxae, respectively), thus the widening of the thoracic sternum in Eubrachyura, which increases the distance between the pereopods coxae and the gonopods, is a determining factor in the evolution of the genital region in both sexes. The female gonopore is no longer located on the appendage (P3 coxa); instead, there is formation of a vulva on sternite 6, whereas the broadening of the posterior half (sternites 7 and 8) in males determines the change of the male gonopore, from the P5 coxa (Heterotremata) to sternite 8 (Thoracotremata). It is clear that there are only two different anatomical arrangements in the female and male Brachyura, without a known continuum between the appendicular and sternal positions, respectively (Guinot *et al.* in press).

It is hypothesised here that a different process of carcinisation occurred in Raninoidia. The evolution in Raninoidea led to a narrowing of the body, including a ventral opening of the arthrodial cavities. This contrasts with the broadening of the body in the usual process of carcinisation of Brachyura, a change in polarity. This phenomenon could be regarded as a secondary elongation. An elongated body often characterises burying crabs, podotremes or eubrachyurans such as Corystidae (see *Modifications for a burying mode of life* above).

Evolution induced also a loss of the anterolateral teeth, often developed in Palaeocorystoidea (e.g., Fig. 7C), and changes in cuticle microstructure roughly varying from upright nodes and/or fungiform nodes (Palaeocorystoidea, Symethinae), pits and upright nodes (Lyreididae) to inclined nodes (other Raninoidea) (Waugh *et al.* 2009; see *Respiration in the Brachyura* and *Modifications for a burying mode of life* above).

The monophyly of the Podotremata

Any interpretation of Raninoidea, like that of other podotremes, must take into account that it belongs to the basal brachyuran group, inherently complex, with a long evolutionary history and a high degree of specialisation leading to major changes of many structures. A number of podotreme subclades are extinct, and the surviving ones are most often in decline. The complexity of Podotremata necessarily increases when extinct taxa are added. The Recent Podotremata, with fewer than 400 species in a hundred genera, represents a small percentage of the whole living brachyuran group (approximately 7,000 valid species and more than 1,300 genera), thus only about 13 % of genera and 18 % of the species (Ng *et al*. 2008, updated; Ng *et al*. 2010; Guinot *et al*. in press). Extant podotremes may be regarded as survivors of a once large and widely distributed group, as demonstrated by the fossil record, with a great number of extinct families, and known since the Jurassic. Moreover, the brachyuran plesion is much more diversified than presently assumed, many taxa having not yet been described, consisting of several major clades. The Recent Raninoidea embraces twelve genera and 46 species, currently assigned to two families, Raninidae and Lyreididae, the latter comprising the subfamilies Lyreidinae and Marylyreidinae **n. subfam.** (Table 1).

Assignment of Raninoidea to the group that includes Dromioidia and Homoloidia is contradicted by molecular data (Spears *et al.* 1993; Ahyong *et al.* 2007; Chu *et al.* 2009), and because the paired spermathecae are ignored as synapomorphy, phylogenetic position of the Raninoidea has become one of the core issues of the monophyly of Podotremata. While the monophyly of the section Eubrachyura and of each of its subsections, Heterotremata and Thoracotremata, is supported by most morphological, larval and molecular data, Podotremata is recovered either as polyphyletic or paraphyletic in molecular studies. Molecular data have been used by many workers, both neontologists and palaeontologists, sometimes leading to suppression of the taxon Podotremata. While the first genetic studies (Spears *et al.* 1993) were largely incomplete, more recent ones were based on several different genes and on a wider taxon sampling. Ahyong *et al*. (2007), who sequenced three raninoids (*Ranina ranina*, *Raninoides louisianensis* and *Symethis corallica*), plus three genera of Cyclodorippoidea, provided a similar paraphyletic Podotremata interpretation. The protein-coding gene tree obtained by Chu *et al.* (2009: 95, figs. 1, 3) similarly supported monophyletic Heterotremata and Thoracotremata, but paraphyletic Podotremata. In the first application of two combined nuclear protein-coding genes (Tsang *et al.* 2008), Podotremata was recovered as basal, monophyletic and inclusive of Raninoidea. This monophyly was, however, weakly supported, the tree being based on only one of the two genes and the taxonomic sampling being limited, with only *Ranina* sequenced and Cyclodorippoidea missing.

Morphologists are unable to comprehend or even measure the root underlying the discordance between the diverse molecular phylogenies (Mooi & Gill 2010). The recently proposed molecular classifications of Brachyura suffer (in comparison to a wealth of accurate morphological data) from relying on a too small a number of genes and too few sequenced taxa, and often lack the most significant representatives. A notable example is the incomprehensible absence of Lyreididae from molecular analyses. Its genetic study would be expected to be the most revealing in exploring raninoid relationships, the family Lyreididae retaining the most ancestral features. Lyreidids are abundant in extant faunas, thus their sequencing should not present any problems. In addition, the very diverse, and possibly paraphyletic, Cyclodorippoidea needs to be tested more comprehensively. The ‘accumulating evidence increasingly’ suggestive of a paraphyletic Podotremata (Ng *et al.* 2009: 16, fig. 4) will need to be substantiated by new genetic sequencing efforts. A new molecular estimation including more raninoid taxa and focused on this clade could show its extreme diversification, and would be a beneficial addition to morphological data for reliable phylogenies.

Numerous authors have recently preferred phylogenies based on molecular analyses, including palaeontologists who are experienced morphologists. It is, nevertheless, a challenge to reconstruct the phylogeny by using the morphology of a wealth of completely preserved fossils at our disposal because fossils turn out to be more informative than previously thought. It is evident that Dromioidia and Homoloidia are basal (although their close common ancestor remains unknown) and that Cyclodorippoidia, which combines a wide thoracic sternum with primitive characters, may appear more similar to Eubrachyura. It should be noted that a developed thoracic sternal plate already evolved in the Cretaceous podotremes, for instance in the extinct Dakoticancroidea, in particular Dakoticancridae (Artal *et al.* 2008), which are indisputably true podotremes (see below).

There are additional views against the monophyly of Podotremata. Some authors, e.g., Rice (1980) and von Sternberg & Cumberlidge (2001), refuted the monophyletic status of the Podotremata by arguing that the initial grouping of Guinot (1977) was based on a symplesiomorphy, the possession of both appendicular female and male gonopores being shared by other Malacostraca. The use of a character at a wrong level of generality (Podotremata, instead of Malacostraca) does not deny the monophyletic status of the group, which is supported by a strong synapomorphy, the paired spermathecae (Guinot 1978; de Saint Laurent 1980; Tavares & Secretan 1993; Guinot & Bouchard 1998; Guinot & Tavares 2001, 2003; Tavares 2003; Guinot & Quenette 2005). Additionally Rice (1980) argued for a closer relationship between Anomura and Podotremata based on larval characters. However, the characters put forward to advocate for a closer relationship between Anomura and Podotremata (partially or collectively) should be discarded on the ground that they are shared plesiomorphies (see Tavares & Franco 2004)

Another serious counterargument to a monophyletic Podotremata is that the podotreme spermatheca is considered unsuitable for phylogenetic purposes (e.g., Ahyong & O'Meally 2004; Scholtz & McLay 2009; Ng *et al.* 2009). The data matrix of Ahyong & O'Meally (2004: 691) included the character 'seminal receptacle' as 'medial', 'absent' or 'paired'. 'Paired seminal receptacles' were considered a synapomorphy of Brachyura, whereas 'in other reptants, the seminal receptacle lies on the sternal midline'. The term 'paired spermatheca' was avoided because of 'its specific reference to the podotreme seminal receptacles' and, consequently, the rather different structures, namely the vulvae and spermathecae, have been confused. This leads to an interpretation of all brachyurans as having the same kind of seminal receptacle, which is not correct.

The phylogenetic 'tree' of Scholtz & McLay (2009: 419) was obtained 'by hand and brain following a Hennigian approach', a method that is perhaps too subjective and based too much on *a priori* decisions. Their discussion (Scholtz & McLay 2009: 418, 431, 432) is far from clear, as exemplified by diverse startling assertions: the spermatheca 'is restricted to podotrematan representatives, but it suffers from a problematic polarization because nothing comparable exists in other reptant groups' and 'the seminal receptacle and spermathecae may not be homologous structures, so the derivation of one from other is difficult'. The opinion that the eubrachyuran condition (sternal vulvae) might be derived from that found in podotremate groups (with coxal female gonopores and spermatheca) was discussed and rejected by Hartnoll (1979). We share Hartnoll's conclusion and assume that the separation of Podotremata and Eubrachyura is based on the fact that the female vulva and the spermatheca are not homologous. The region for sperm storage in Brachyura indiscriminately referred to as 'spermatheca' by many authors actually concerns two anatomically different organs. It creates a false homology to group under the same term the two structures for storage of sperm, the spermatheca and seminal receptacle, which only have a similar function. We appeal for restriction of the use of 'spermatheca' to the independent structure of the podotremes, always formed by phragma 7/8 and with its aperture located at the extremity of the sternal suture 7/8. We thus disagree with the statement 'spermathecae connected to the oviducts and internal fertilization' employed for Eubrachyura by Scholtz & McLay (2009: 431). 'Seminal receptacle' must be applied only to the eubrachyuran structure, directly connected to, and thus part of, the female gonad.

To support the molecular results of Ahyong *et al.* (2007) and Chu *et al.* (2009), Ng *et al.* (2009: 16, fig. 5) suggested that the podotreme spermatheca was only 'a feature retained by successive podotreme clades and then lost with derivation of the eubrachyuran synapomorphies' and that 'internalization of the spermatheca is therefore an innovation in the stem brachyuran [*sic*], but not a synapomorphy supporting Podotremata'. The assertion by Ng *et al.* (2009) is insufficient and requires a more detailed explanation. What Ng *et al.* (2009) were referring to were probably the various patterns of the podotreme spermathecae figured by Guinot & Tavares (2001: fig. 10; see also Gordon 1950; Guinot & Quenette 2005), not detracting its homology but only underlining four main patterns: a basal one in Dromioidia, more primitive in Dynomenidae and Sphaerodromiinae than in Dromiinae (see Tavares & Franco 2004); another one, also basal, in Homoloidia (Gordon 1950; Garassino 2009); another one in Raninoidia; and more than one in the poorly known Cyclodorippoidia. All these patterns are variations of the same basic architecture, which is a secondary specialisation of the intersegmental phragma 7/8, a split between its two skeletal plates, one derived from sternite 8 and the other one from sternite 7, leading to sternal modifications at the limit of the two adjacent somites 7 and 8 in females.

Claims that Podotremata is paraphyletic (Ahyong *et al.* 2007; Brösing *et al.* 2007; Ng *et al.* 2009; Scholtz & McLay 2009; Bracken *et al.* 2009; De Grave *et al.* 2009; Karasawa *et al.* 2011), or even polyphyletic (Spears *et al.* 1993) do not provide new information and are not supported by strong data. The conclusion of Scholtz & McLay (2009: 431, 432) that, 'the Cyclodorippoidea is the sister group to the Eubrachyura', is supported only by weak data. The cladistic analysis of Karasawa *et al.* (2011), which includes extinct and extant brachyuran taxa, is based on a data matrix with a great number of unknown character states and several characters that are insufficiently informative since many fossil crabs do not preserve all ventral characters. In addition, several erroneous observations are found in their character matrix. Combined morphological and molecular studies which demonstrate that the podotreme spermatheca is not a synapomorphy have not yet been conducted.

The deliberate use of restricted morphological sources (as opposed to the integration of all characters, i.e., the holomorphology) for phylogenetic inference, such as the foregut-ossicle system (Brösing *et al.* 2007; Brösing 2008), imposes too many limitations (as in some molecular analyses) in attempts to recover monophyly. Despite providing interesting data on foregut ossicles, this interpretation of Podotremata as paraphyletic does not come as a surprise. Some other conclusions concerning Eubrachyura, e.g., the interpretation of Palicidae as a basal taxon of Thoracotremata (Brösing *et al*. 2007: 28; Brösing 2008: 281), are inconsistent with a substantial body of adult and larval morphology and even with recent molecular data, so that some doubt is cast upon the interpretation of the foregut ossicle data, mainly for other higher-level taxa (see Guinot *et al*. in press).

Taxonomic levels

The proposed suppression of Podotremata (Ahyong *et al.* 2007, 2009; Ng *et al.* 2009: 16, figs. 4, 5; see also De Grave *et al.* 2009: 5, 7, 8, table 1; Schweitzer *et al.* 2010: 57) is not only unjustified (see above), but also implies giving a similar rank to the section Eubrachyura and their three podotreme 'sections', Dromiacea, Raninoida and Cyclodorippoida. We do not agree with such a classification structure. From a conceptual and nomenclatural point of view, these three podotreme 'sections', to which a fourth, representing the homoloid clade, must be added, are not equivalent to section Eubrachyura. It is true that the International Code of Zoological Nomenclature (ICZN 1999) does not regulate the 'Section' and 'Subsection' categories, and only mentions five ranks in the 'family-group', from superfamily to subtribe, for which it provides standardised endings (Art. 29, 35.1). For higher-level taxa above the superfamily (suffix -oidea) within the infraorder Brachyura, we use 'subsection' as an additional podotreme rank, as did Guinot *et al*. (2008), to which we apply the oldest available family group name, thus meeting the Principle of Priority of the Code (Art. 23). The same suffix -oidia, applied to these subsections, constituted a mandatory change in spelling (Art. 34.1). It is particularly appropriate to designate as subsections the taxa above the superfamilies within the highly diversified podotreme crabs, and especially when new higher-level taxa, based on a wealth of fossil material, are included.

Proposed scheme

An alternative scheme is therefore proposed herein: a section Podotremata comprising four subsections (Dromioidia, Cyclodorippoidia, Raninoidia, and Homoloidia), alongside a section Eubrachyura, its sister group (Table 2). We consider indispensable the separation of a distinct clade, Homoloidia, distinct from Dromioidia, contrary to recent classifications by Martin & Davis (2001), Ahyong *et al*. (2007, 2009), Ng *et al*. (2009), De Grave *et al*. (2009) and Schweitzer *et al*. (2010), both which were accepted by Števčić (2005), Karasawa *et al*. (2009, 2011) and Scholtz & McLay (2009). A number of morphological characters, as well as spermatological and larval traits, support a homoloidian clade (see *Comparison of the superfamily Palaeocorystoidea with other podotreme superfamilies, Palaeocorystoidea* versus *Homoloidea De Haan, 1839* above). According to Rice (1980: 293, fig. 8), the Homoloidea diverged from the primitive brachyuran line at an early stage, the phylogenetic tree showing 'a close alliance between the raninids and the homolids'. Interestingly, according to Williamson (1965: 394), the short antennal spine of the raninid zoeae resembled that found in most anomurans and dromiids, representing a more primitive state than that of homolids and eubrachyurans, in contrast with many other raninid zoeal characters that indicated a more derived level than the homolids. Other larval characters, however, are in favour of an alliance of Raninidae and Homolidae (Rice 1980: 291, 295). These conflicting traits are indicative of the complex situation of extant Raninoidea, albeit in favour of its podotreme affinities.

Only the future discovery of two or more origins for Podotremata could demonstrate its polyphyly. To determine if Podotremata is paraphyletic, we need to know if Eubrachyura is nested within the podotremes, thus having evolved from within the podotremes, as supported by several molecular studies, but not yet resolved by recent histological and morphological studies (see McLay & López Greco 2011). It should be noted that Linnean classification without paraphyletic taxa is practically impossible. It is well known that paraphyletic taxa are inevitable for classifying earlier representatives of a large group, the early Decapoda, that would evolve into the Brachyura cannot be easily placed in any monophyletically defined podotreme clades. Paraphyletic taxa also provide information on significant changes in morphology, ecology and other aspects of the biology of organisms. A paraphyletic Podotremata is therefore a valuable hypothesis and will continue to generate interesting studies of the most primitive crabs.

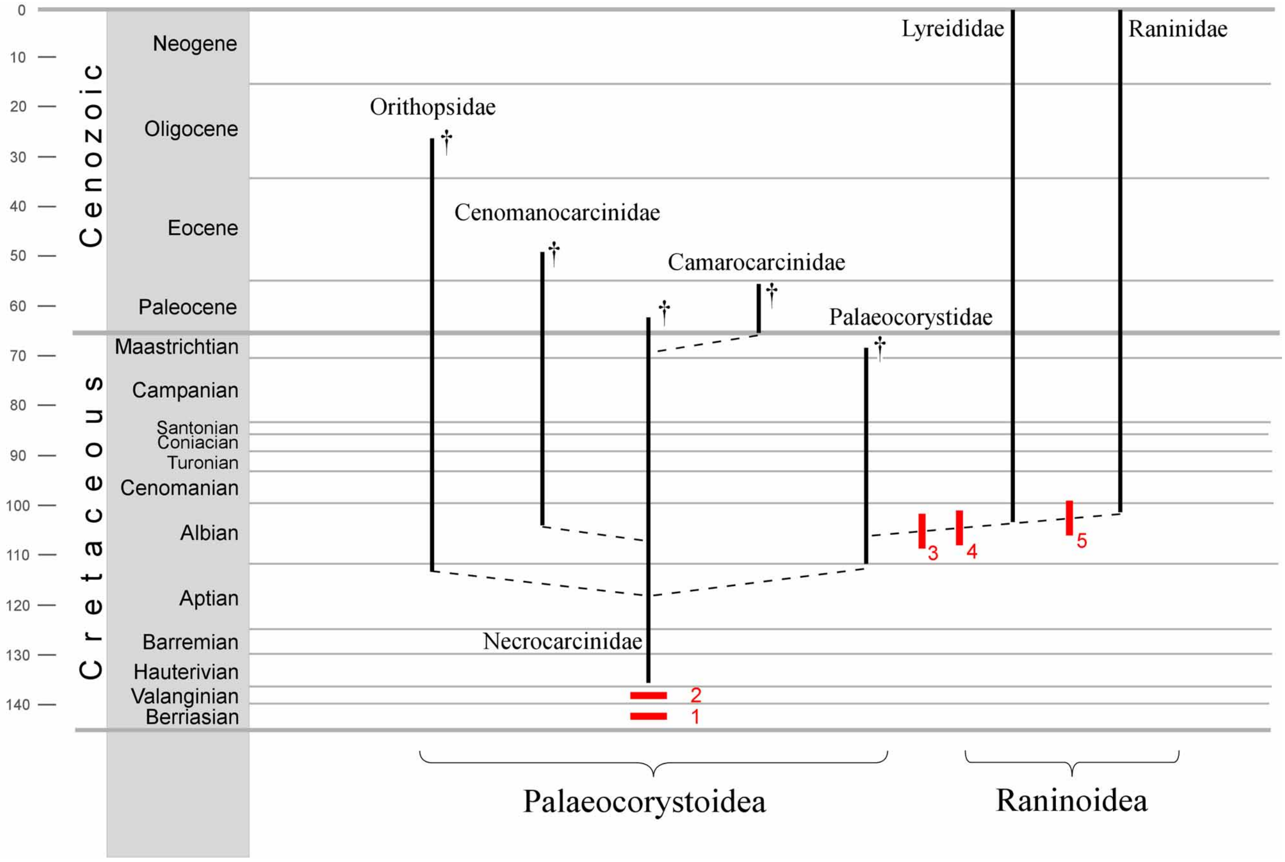

FIGURE 62. Hypothetical phylogeny of Raninoidia, with the various characters numbered as follows: 1. Paired spermathecae dependent of phragma 7/8 (symplesiomorphy of Raninoidia with Podotremata); 2. Paired structure (double peg or hook with two spines) on episternite 5 involved in abdominal holding (preserved in Lyreididae, lost in all other Raninoidea) (synapomorphy of Raninoidia); 3. Gymnopleurity (synapomorphy of Raninoidea); 4. Modified position of spermathecal apertures (synapomorphy of Raninoidea); 5. Abdomen not held against body (synapomorphy of Raninidae).

Podotreme clades

The section Podotremata embraces a number of clades in extant faunas, at least four main large ones, here considered subsection rank: Dromioidia, Homoloidia, Cyclodorippoidia and Raninoidia (Table 2). These subsections are very diverse, Cyclodorippoidia being the least well known and with a very meagre fossil record. Raninoidia consists of two superfamilies, the extinct Palaeocorystoidea (Fig. 56) and Raninoidea, both extinct and extant (Table 1).

The Podotremata had its origins in the Jurassic, and Homolodromioidea, Glaessneropsoidea (Schweitzer & Feldmann 2010c) and Homoloidia (Collins 1998) all have a robust fossil record. Uncertainties nevertheless remain, the ventral surface being largely unknown for these groups. The Dynomenidae is supposed to have appeared during the Late Jurassic (McLay 1999; Guinot 2008; Jagt *et al*. 2010). Despite recent progress, the traits of most fossil Dromiidae remain too poorly known for an accurate placement. This is exemplified by the case of *Basinotopus* McCoy, 1849, traditionally assigned to Dromiidae (McCoy 1849; Bell 1858; Collins 2003; Collins & Jakobsen 2004; Beschin *et al.* 2005), but recently referred to Dynomenidae (De Grave *et al*. 2009; Schweitzer *et al*. 2010) and even to a separate family, Basinotopidae Karasawa, Schweitzer & Feldmann, 2011. The reduced and dorsal P4 and P5 as well as the uropods on the male and female abdomens (McCoy 1849; Bell 1858; see Guinot & Tavares 2001) of the type species, *B. lamarckii* (Desmarest, 1822), could actually belong to a typical dromiid. However, recent discoveries of more complete specimens of the Eocene *B. tricornis* Collins & Jakobsen, 2004, reveal particular sternal characters (Collins & Jakobsen 2004: 69, text-fig. 3, pl. 2, figs. 1–7), so a new interpretation based on all known data is required. It is true that dromiids, with their developed and specialised uropods that are often used for the abdominal holding, are less ‘primitive’ than supposed. However, the Eocene as the earliest occurrence of dromiids suggested by Glaessner (1969) appears too late. The Sphaerodromiinae Guinot & Tavares, 2003 is considered the most ancient; Hypoconchinae Guinot & Tavares, 2003 are hitherto absent in the fossil record.

Schweitzer & Feldmann (2010d) elevated Sphaerodromiinae to family level. These authors nevertheless listed the same plesiomorphic morphological characters of Sphaerodromiidae, which Guinot & Tavares (2003) had defined in establishing the subfamily, and did not recognise any synapomorphies. The hierarchical rank of Sphaerodromiinae must be determined in conformity with the level of generality of characters in the related groups, thus Homolodromiidae, Dromiidae and Dynomenidae. For the time being, we prefer to treat Sphaerodromiinae as a dromiid subfamily.

The relationships between the podotreme clades are poorly understood. The Dromioidia and Homoloidia may be considered as basal, having a long abdomen entirely filling the sterno-abdominal depression transversely (only a narrow exposed space may be present in Dynomeninae and Latreilliidae), and completely in length (Homolodromioidea, Homoloidia, Dromiidae *pro parte*) or nearly so (Dromiidae *pro parte).* The fossil record of podotreme crabs certainly holds the key to clarification of the phylogeny of Podotremata.

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APPENDIX. Systematic list of the subsection Raninoidia.

Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Subsection Raninoidia De Haan, 1839 emend.
Superfamily Palaeocorystoidea† Lőrenthey *in* Lőrenthey & Beurlen, 1929 new status

Family Palaeocorystidae† Lőrenthey *in* Lőrenthey & Beurlen, 1929 new status

Genus *Cenocorystes*† Collins & Breton, 2009
Cenocorystes bretoni† **n. sp.** [lower Cenomanian, northwestern France]
Cenocorystes fournieri† Collins & Breton, 2009 [Collins & Breton 2009: 46, figs. 5–7, lower Cenomanian, northwestern France]

Genus *Cretacoranina* Mertin, 1941
Cretacoranina fritschi† (Glaessner, 1929) [Glaessner 1929a: 155, pl. 10, fig. 5 (as *Notopocorystes*), middle Turonian, Bohemia (Czech Republic), Germany]
Cretacoranina schloenbachi† (Schlüter, 1879) [Schlüter 1879: 612, pl. 18, fig. 2, 2a (as *Raninella*), upper Coniacian–lower upper Maastrichtian; northern Germany, ?southern England, northeastern Belgium, northern Spain]
Cretacoranina cf. *schloenbachi*† sensu Förster 1970 [Förster 1970: 139, text-fig. 4A, pl. 17, fig. 3 (as *Notopocorystes* (*Cretacoranina*)), ?lower Santonian, southern Germany]
Cretacoranina testacea† (Rathbun, 1926) [Rathbun 1926b: 190, pl. 68, figs. 1–4 (as *Raninella*), upper Campanian–Maastrichtian, Delaware, New Jersey, Tennessee, USA, lower Maastrichtian, Mississippi, USA (see Bishop, 1983b)]
Cretacoranina trechmanni† (Withers, 1927) [Withers 1927: 12, text-fig. 1, pl. 7, figs. 1, 2. (as *Ranina*), ?Campanian (Maastrichtian according to Morris 1993), Jamaica (*Raninella trechmanni* in Tucker 1995)]

Genus *Eucorystes* Bell, 1863
Eucorystes carteri† (McCoy, 1854) [McCoy 1854: 118, pl. 4, fig. 3 (as *Notopocorystes*), upper Albian, southern England, France, Switzerland]
Eucorystes eichhorni† (Bishop, 1983) [Bishop 1983a: 905, figs. 5, 6 (as *Notopocorystes* (*Eucorystes*)), upper Campanian, Montana, USA]
Eucorystes intermedius† Nagao, 1931 [Nagao 1931: 207, pl. 14, fig. 4, 4a (as *Notopocorystes* (*Eucorystes*)), Cenomanian–Santonian, Japan]
Eucorystes exiguus† (Glaessner, 1980) [Glaessner 1980: 175, fig. 4, 4a (as *Notopocorystes* (*Cretacoranina*)), Cretaceous (= lower Cenomanian; see Collins 1997), Northern Territory, Australia]
Eucorystes ligulatus† Wright & Collins, 1972 [Wright & Collins 1972: 82, pl. 16, fig. 4 (as *Notopocorystes* (*Eucorystes*) *carteri ligulatus*), uppermost Albian, England [stated to have been overlooked by Tucker (1998) [see Collins, 2003: 84], but synonymised with *E. carteri* by Tucker (1995)]
Eucorystes mangyshlakensis† Ilyin & Pistshikova *in* Ilyin, 2005 [Ilyin 2005: 210, text-fig. 39B, pl. 10, figs. 1, 2 (as *Notopocorystes* (*Eucorystes*)), lower Albian, Kazakhstan]
Eucorystes oxtedensis† Wright & Collins, 1972 [Wright & Collins 1972: 79, text-fig. 11c, pl. 16, figs. 1, 2 (as *Notopocorystes* (*Eucorystes*)), lower Albian, southern England]
Eucorystes iserbyti† **n. sp.** [middle Albian, northern France]
Eucorystes navarrensis† **n. sp.** [Albian, northern Spain]

Genus *Ferroranina*† n. gen.
Ferroranina australis† (Secretan, 1964) [Secretan 1964: 158, text-figs. 90, 91, 92 (right), 97 (left), pl. 18, figs. 1–3 (as *Notopocorystes*), upper Santonian–lower Campanian, Madagascar]
Ferroranina denisae† (Secretan, 1964) [Secretan 1964: 162, text-figs. 93–96, 97 (right), pl. 18, figs. 4–7 (as *Notopocorystes*), lower–upper Campanian, Madagascar]
Ferroranina dichrous† (Stenzel, 1945) [Stenzel 1945: 438, text-fig. 13, pl. 43, figs. 5–7 (as *Notopocorystes*), Turonian, Texas, USA]
Ferroranina cf. *dichrous*† sensu Vega *et al*. 2007 [Vega *et al*. 2007a: 418, figs. 9.6–9.8 (as *Cretacoranina*), lower–middle Turonian, Mexico]

Ferroranina tamilnadu† **n. sp.** [middle Cenomanian, India; see Guinot *et al*. 2008: 712, fig. 9C (as *Cretacoranina* cf. *dichrous*)]

Genus *Joeranina*† n. gen.

Joeranina broderipii† (Mantell, 1844) [Mantell 1844: 532, 534, text-fig. 115/3 (as *Corystes*), middle–upper Albian–?Cenomanian, southern England, northern and central France, Switzerland]

Joeranina gaspari† **n. sp.** [Albian, northern Spain]

Joeranina harveyi† (Woodward, 1896) [Woodward 1896: 225, fig. 4 (as *Palaeocorystes*), Cenomanian, British Columbia, USA (upper Santonian/lower Campanian according to Collins 1997) (Schweitzer *et al*. 2003a: 24, as *Eucorystes harveyi*)]

Joeranina japonica† (Jimbô, 1894) [Jimbô 1894: 101, pl. 9, fig. 7 (as *Eucorystes*), Cenomanian–Santonian, Japan (Collins *et al*. 1993: 300, as *Notopocorystes* (*Notopocorystes*) *japonica*)]

Joeranina paututensis† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 30, fig. 17a, b (as *Notopocorystes* (*Cretacoranina*)), upper Santonian or lower Campanian, West Greenland]

Joeranina platys† (Schweitzer & Feldmann, 2002) [Schweitzer & Feldmann 2002b: 199, figs. 15, 16 (as *Eucorystes*), Albian, Oregon, USA]

Joeranina syriaca† (Withers, 1928) [Withers 1928: 459, pl. 13, figs. 1, 2 (as *Notopocorystes*), Cenomanian, Syria]

Joeranina cf. *syriaca*† sensu Wright & Collins, 1972 [Wright & Collins 1972: 84 (as *Notopocorystes* (*Cretacoranina*)), lower Cenomanian, southern England]

Joeranina sp.† sensu Van Straelen, 1931 [Van Straelen 1931: 56, pl. 2, fig. 39 (as *Notopocorystes* sp.), Cenomanian, Madagascar]

Genus *Notopocorystes*† McCoy, 1849 (= *Palaeocorystes*† Bell, 1863)

Notopocorystes bituberculatus† Secretan, 1964 [Secretan 1964: 155, text-fig. 86; pl. 18, figs. 8, 9, Albian, Madagascar]

Notopocorystes normani† (Bell, 1863) [Bell 1863: 16, pl. 3, figs. 10–12 (as *Palaeocorystes*), Cenomanian, southern England, northern Germany, northern France, Kazakhstan]

Notopocorystes praecox† Wright & Collins, 1972 [Wright & Collins 1972: 75, pl. 13, fig. 4a–c (as *Notopocorystes* (*Notopocorystes*) *stokesii praecox*), lower Albian, southern England]

Notopocorystes serotinus† Wright & Collins, 1972 [Wright & Collins 1972: 76, pl. 14, figs. 3–6, pl. 22, fig. 7 (as *Notopocorystes* (*Notopocorystes*) *stokesii serotinus*), uppermost middle–upper Albian, southern and eastern England]

Notopocorystes stokesii† (Mantell, 1844) [Mantell 1844: 533, text-fig. 115/2 (as *Corystes*), middle Albian, southern England, France, Switzerland]

Notopocorystes xizangensis† Wang, 1981 [Wang 1981: 352, text-fig. 4, pl. 2, fig. 1a–c, upper Lower Cretaceous, Xizang, China; ?lower/middle Albian, central Iran (Yazdi *et al*. 2009: 73, pl. 2, figs. 6–11)]

Family Camarocarcinidae† Feldmann, Li & Schweitzer, 2008

Genus *Camarocarcinus*† Holland & Cvancara, 1958

Camarocarcinus arnesoni† Holland & Cvancara, 1958 [Holland & Cvancara 1958: 499, text-figs. 2, 3a, b, pl. 74, figs. 1–14, Paleocene, North Dakota, USA]

Camarocarcinus obtusus† Jakobsen & Collins, 1979 [Jakobsen & Collins 1979: 63, pl. 1, figs. 3–5, upper Paleocene, eastern Denmark]

Camarocarcinus quinquetuberculatus† Collins & Wienberg Rasmussen, 1992 [Collins & Wienberg Rasmussen 1992: 33, fig. 19a–e, middle Paleocene, West Greenland]

Family Cenomanocarcinidae† Guinot, Vega & Van Bakel, 2008

Genus *Campylostoma*† Bell, 1858

Campylostoma matutiforme† Bell, 1858 [Bell 1858: 23, pl. 3, figs. 8–10, lower Eocene, southern England; Eocene, northern Germany]

Genus *Cenomanocarcinus*† Van Straelen, 1936 (= *Sagittiformosus*† Bishop, 1988)

Cenomanocarcinus beardi† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 [Schweitzer *et al.*

2003a: 38, figs. 12.1–12.4, Cenomanian, Texas, USA; upper Turonian–Santonian, British Columbia, Canada]

Cenomanocarcinus cantabricus† **n. sp.** [Albian, northern Spain]

Cenomanocarcinus dissimilis† Collins, 2010 [Collins 2010: 15, fig. 1.4, lower Cenomanian, southeastern Nigeria]

Cenomanocarcinus inflatus† (A. Milne-Edwards MS *in* Guillier 1886) [Van Straelen 1936: 37, pl. 4, fig. 8, upper Cenomanian–Turonian, northern France (= *Cenomanocarcinus hierosolymitanus*† Avnimelech, 1961 [Avnimelech, 1961: 1, figs. 3, 4, upper Cenomanian, Israel; as *Cenomanocarcinus* cf. *vanstraeleni*† by Remy & Avnimelech, 1955: 314)]

Cenomanocarcinus multituberculatus† (Joleaud & Hsu, 1935) [Joleaud & Hsu 1935: 107, fig. 10 (as *Campylostoma*), 'Senonian', Niger]

Cenomanocarcinus oklahomensis† (Rathbun, 1935) [Rathbun 1935b: 44, pl. 11, fig. 9 (as *Necrocarcinus*), upper Albian, Oklahoma and Texas, USA]

Cenomanocarcinus pierrensis† (Rathbun, 1917) [Rathbun 1917: 389, pl. 33, figs. 4, 5 (as *Campylostoma pierrense*), upper Campanian–lower Maastrichtian, South Dakota, USA (as *Necrocarcinus* by some authors; compare Guinot *et al*. 2008)]

Cenomanocarcinus tenuicarinatus† Collins, 2010 [Collins 2010: 15, fig. 1.3, lower Turonian, southeastern Nigeria]

Cenomanocarcinus vanstraeleni† Stenzel, 1945 [Stenzel 1945: 447, text-fig. 15, pl. 44, figs. 1–6, Cenomanian–lower Turonian, Texas, USA (= *Ophthalmoplax spinosus*† Feldmann, Villamil & Kauffman, 1999 [Feldmann, Villamil & Kauffman, 1999: 96, figs. 3.1, 3.2, 4.1, 4.2, middle Turonian, New Mexico (see Bishop 1986a: 135; Toolson & Kues 1996); lower–middle Turonian, Mexico; upper Albian, Colombia; lower Turonian, Colombia (see Vega *et al*. 2010: 270)]

Cenomanocarcinus aff. *vanstraeleni*† sensu Guinot *et al*. 2008 [Guinot *et al*. 2008: 694, fig. 6, Coniacian, Colombia]

Cenomanocarcinus† sp. sensu Vega *et al*. 2010 [Vega *et al*. 2010: 274, fig. 8.16, Campanian, Mexico]

Genus *Hasaracancer*† Jux, 1971

Hasaracancer cristata† Jux, 1971 [Jux 1971: 158, text-fig. 2, pl. 17, figs. 1–7, upper Campanian, Afghanistan]

Hasaracancer merijaensis† Ossó-Morales, Artal & Vega, 2011 [Ossó-Morales *et al.* 2011: 2, figs. 5, 6, upper Campanian, Morocco]

Hasaracancer renfroae† (Stenzel, 1945) [Stenzel 1945: 443, text-fig. 15, pl. 41, fig. 13 (as *Necrocarcinus*), upper Albian, Texas, USA, Colombia (see Guinot *et al.* 2008: 698, fig. 8A–D; Vega *et al*. 2010: 272, figs. 8.6–8.12)]

Family Necrocarcinidae† Förster, 1968

Subfamily Necrocarcininae† Förster, 1968

Genus *Cretacocarcinus*† Feldmann, Li & Schweitzer, 2008

Cretacocarcinus smithi† Feldmann, Li & Schweitzer, 2008 [Feldmann *et al.* 2008: 1747, figs. 4.1, 4.6, 4.7, Campanian, Manitoba, Canada]

Genus *Marycarcinus*† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

Marycarcinus hannae† (Rathbun, 1926) [Rathbun 1926: 84, pl. 18, figs. 1, 2 (as *Necrocarcinus*), Eocene, Oregon and California, USA (Schweitzer & Feldmann 2000: 242, figs. 11, 12)]

Genus *Necrocarcinus*† Bell, 1863

Necrocarcinus? *bispinosus*† Segerberg, 1900 [Segerberg 1900: 26 (372), pl. 3, fig. 7, lower Paleocene, southern Sweden]

Necrocarcinus davisi† Bishop, 1985 [Bishop 1985: 619, figs. 3.6, 3.10–3.12, lower Campanian, South Dakota, USA]

Necrocarcinus inornatus† Breton & Collins, 2011 [Breton & Collins 2011: 147, fig. 6, lower Cenomanian, northern France]

Necrocarcinus labeschii† (J.A. Deslongchamps, 1835) [J.A. [Eudes-] Deslongchamps 1835: 40, pl. 1, figs. 7, 8 (as *Orythia*, incorrect spelling), (?upper Aptian) lowermost Albian–middle Cenomanian, southern England, northern France; upper Albian, southwestern Crimea, Ukraine (= *N. bodrakensis*† Levitskyi, 1974: 115, pl. 2, fig. 4, pl. 3, fig. 3; see Ilyin 2005: 199]

Necrocarcinus oklahomensis† Rathbun, 1935 [Rathbun 1935b: 44, pl. 11, fig. 9, upper Albian, Texas, USA]

Necrocarcinus olsonorum† Bishop & Williams, 1991 [Bishop & Williams 1991: 452, figs. 1–5, 6B, Turonian, South Dakota and Wyoming, USA]

Necrocarcinus rathbunae† Roberts, 1962 [Roberts 1962: 181, pl. 85, fig. 12, pl. 87, figs. 1, 2, lower Campanian, New Jersey and Delaware, USA]

Necrocarcinus senonensis† Schlüter *in* von der Marck & Schlüter, 1868 [von der Marck & Schlüter 1868: 297, pl. 44, fig. 3, Santonian–upper Campanian, northern Germany; lower Paleocene, central Poland, Denmark (= *N. insignis*† Segerberg, 1900: 26 (372), pl. 3, figs. 1, 6)]

Necrocarcinus cf. *senoniensis*† [*sic*] sensu Mertin 1941 [Mertin 1941: 239, text-fig. 27b, pl. 8, figs. 13, 14, 'Untersenon', northern Germany]

Necrocarcinus tauricus† Ilyin & Alekseev, 1998 [Ilyin & Alekseev 1998: 46, figs. 1a, 2b, upper Albian, southwestern Crimea (see Ilyin 2005: 201–203)]

Necrocarcinus texensis† Rathbun, 1935 [Rathbun 1935b: 45, pl. 11, figs. 20–22 uppermost Albian–?lowermost Cenomanian, Texas, USA]

Necrocarcinus undecimtuberculatus† Takeda & Fujiyama, 1983 [Takeda & Fujiyama 1983: 133, text-fig. 3, pl. 1, figs. 1, 2, upper Aptian, northern Japan]

Necrocarcinus woodwardii† Bell, 1863 [Bell 1863: 20, pl. 4, figs. 1–3 (*non* pl. 5, figs. 4–7), upper Albian–lower Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Necrocarcinus wrighti† Feldmann, Tshudy & Thomson, 1993 [Feldmann *et al.* 1993: 35, figs. 29.1–5, 30, lower Campanian–?lowermost Maastrichtian, James Ross Basin, Antarctica]

Genus *Protonecrocarcinus*† Förster, 1968

Protonecrocarcinus ovalis† (Stenzel, 1945) [Stenzel 1945: 442, text-figs. 14, 15, pl. 41, figs. 7–9 (as *Necrocarcinus*?), upper Cenomanian, Texas, USA; upper Turonian, New Mexico, USA]

Subfamily Paranecrocarcininae† Fraaije, Van Bakel, Jagt & Artal, 2008

Genus *Glyptodynomene*† Van Straelen, 1944

Glyptodynomene alsasuensis† Van Straelen, 1944 [Van Straelen 1944: 10, pl. 1, fig. 4, 4a, upper Albian–lower Cenomanian, northern Spain]

Genus *Paranecrocarcinus*† Van Straelen, 1936 (= *Pseudonecrocarcinus*† Förster, 1968)

Paranecrocarcinus balla† **n. sp.** [Cenomanian, France; see A. Milne-Edwards *in* Guillier 1886: 244, as *Necrocarcinus minutus*† (*nomen nudum*)]

Paranecrocarcinus biscissus† Wright & Collins, 1972 [Wright & Collins 1972: 71, text-fig. 10b, pl. 22, fig. 6 (as *Paranecrocarcinus* (*Pseudonecrocarcinus*)); lower–middle/upper Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Paranecrocarcinus digitatus† Wright & Collins, 1972 [Wright & Collins 1972: 69, text-fig. 10a, pl. 12, fig. 7a–c, lower Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Paranecrocarcinus foersteri† Wright & Collins, 1972 [Wright & Collins 1972: 70, pl. 22, fig. 5a–c, lower–middle Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Paranecrocarcinus gamma† Roberts, 1962 [Roberts 1962: 182, pl. 85, figs. 7, 8, 11, lower Campanian, New Jersey, USA]

Paranecrocarcinus graysonensis† (Rathbun, 1935) [Rathbun 1935b: 45, pl. 11, figs. 23–25 (as *Necrocarcinus*), upper Albian, Texas, USA (= *Necrocarcinus scotti*† Stenzel, 1945: 445, text-fig. 15, pl. 41, figs. 10, 11; see Förster 1968: 173)]

Paranecrocarcinus hexagonalis† Van Straelen, 1936 [Van Straelen 1936: 36, pl. 4, figs. 6, 7, Hauterivian, northern France (see Förster 1970: figs. 2A, 3A)]

Paranecrocarcinus libanoticus† Förster, 1968 [Förster 1968: 171, pl. 13, fig. 1, Cenomanian, Lebanon, northern France, southern England (see Breton & Collins 2011)]

Paranecrocarcinus milbournei† Collins, 2010 [Collins 2010: 16, figs. 1.5–1.8, Cenomanian, southeastern Nigeria]

Paranecrocarcinus moseleyi† (Stenzel, 1945) [Stenzel 1945: 441, text-fig. 15, pl. 41, fig. 12 (as *Necrocarcinus*), uppermost Albian–lowermost Cenomanian, Texas, USA]

Paranecrocarcinus mozambiquensis† Förster, 1970 [Förster 1970: 135, text-figs. 2B, 3B, pl. 17, fig. 4, lower Cenomanian, southern Mozambique]

Paranecrocarcinus olssoni† (Rathbun, 1937) [Rathbun 1937b: 26, pl. 5, fig. 6 (as *Dakoticancer*), Barremian, Colombia (in Feldmann *et al*. 1999: 91 as *Necrocarcinus olssoni*; in Vega *et al.* 2010: 276 as *Orithopsis tricarinata*, age indicated as upper Aptian and upper Albian)]

Paranecrocarcinus pulchellus† (Secretan, 1964) [Secretan 1964: 169, figs. 98, 99, pl. 19, fig. 7 (as *Dromiopsis*), Cenomanian, Madagascar]

Paranecrocarcinus pusillus† Breton & Collins, 2011 [Breton & Collins 2011: 150, figs. 10, 11, lower Cenomanian, northern France, southern England]

Paranecrocarcinus quadriscissus† (Noetling, 1881) [Noetling 1881: 368, pl. 20, fig. 4a, b (as *Necrocarcinus*), upper Maastrichtian, southeastern Netherlands, northeastern Belgium (= *Dromiopsis ubaghsi* Forir, 1889: 452, pl. 14, fig. 3)

Paranecrocarcinus stenzeli† (Bishop, 1983) [Bishop 1983c: 49, text-fig. 8B, pl. 1, figs. 3–5 (as *Pseudonecrocarcinus*), lower Albian, Texas, USA (see Bishop 1986a: 136)]

Paranecrocarcinus vanbirgeleni† Fraaije, 2002 [Fraaije 2002: 916, figs. 1.3, 3.1, 3.2, upper Maastrichtian, southeastern Netherlands]

Genus *Shazella*† Collins & Williams, 2005

Shazella abbotsensis† Collins & Williams, 2005 [Collins & Williams, 2005: 33, fig. 1, ?middle/upper Turonian, southern England]

Family Orithopsidae† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

Genus *Cherpiocarcinus*† Marangon & De Angeli, 1997

Cherpiocarcinus rostratus† Marangon & De Angeli, 1997 [Marangon & De Angeli 1997 : 102, text-fig. 2, pl. 1, figs. 1, 2, middle Oligocene, northern Italy]

Genus *Orithopsis*† Carter, 1872

Orithopsis angelica† (Fraaije, 2002) [Fraaije 2002: 914, figs. 1.1, 1.2 (as *Necrocarcinus*), upper Maastrichtian, southeastern Netherlands]

Orithopsis carinata† (Feldmann, Tshudy & Thomson, 1993) [Feldmann *et al.* 1993: 36, fig. 29.6, lower Campanian, James Ross Basin, Antarctica

Orithopsis? *iserica*† (Fritsch *in* Fritsch & Kafka, 1887) [Fritsch & Kafka 1887: 46, pl. 10, figs. 5, 6 (as *Palaeocorystes*), upper Turonian, Bohemia (Czech Republic) (see Van Straelen 1923a: 118; Collins 1997: table 1; Glaessner 1929a: 156, pl. 10, fig. 7, as *Necrocarcinus isericus*)]

Orithopsis siouxensis† (Feldmann, Awotua & Welshenbaugh, 1976) [Feldmann *et al.* 1976: 986, pl. 1, figs. 1–5 (as '*Necrocarcinus*'), Maastrichtian, North Dakota, USA (as *Cenomanocarcinus* by Schweitzer *et al*. 2003a: 36)]

Orithopsis? *transiens*† (Fritsch *in* Fritsch & Kafka, 1887) [Fritsch & Kafka 1887: 48, pl. 10, fig. 7 (as *Lissopsis*), upper Turonian, Bohemia (Czech Republic)]

Orithopsis tricarinata† (Bell, 1863) [Bell 1863: 21, pl. 4, figs. 9–11, upper Aptian–lower Cenomanian, southern England, northern Spain; lower Cenomanian, Mangyshlak, Kazakhstan (see Ilyin 2005, as *Necrocarcinus tricarinatus*); ?upper Albian, Angola; upper Aptian, Colombia; upper Albian, Oregon (see Vega *et al*. 2010: 275, figs. 8.18–8.23) (= *O. bonneyi*† Carter, 1872, upper Aptian, lower Cenomanian, southern England)]

Orithopsis? *youngi*† (Bishop, 1983) [Bishop 1983c: 46, pl. 1, figs. 8–11 (as *Hillius*), lower Albian, Texas, USA]

Genus *Paradoxicarcinus*† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

Paradoxicarcinus nimonoides† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 [Schweitzer *et al.* 2003a: 43, fig. 14, Santonian, British Columbia, Canada]

Genus *Silvacarcinus*† Collins & Smith, 1993

Silvacarcinus laurae† Collins & Smith, 1993 [Collins & Smith 1993: 263, text-fig. 2 (*non* fig. 3a, b), pl. 2, figs. 1, 2, 4–6 (*non* fig. 3), lower Eocene, central Belgium]

Superfamily Raninoidea De Haan, 1839
Family Lyreididae Guinot, 1993
Subfamily Lyreidinae Guinot, 1993

Genus *Bournelyreidus*† n. gen.

Bournelyreidus carlilensis† (Feldmann & Maxey, 1980) [Feldmann & Maxey 1980: 858, fig. 1a–e (as *Raninella*), upper middle Turonian, Kansas]

Bournelyreidus eysunesensis† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 19, fig. 10a–c (as *Hemioon*), upper Campanian, West Greenland]

Bournelyreidus laevis† (Schlüter *in* von der Marck & Schlüter, 1868) [von der Marck & Schlüter 1868: 298, pl. 44, fig. 2 (as *Palaeocorystes*), upper Turonian, northern Germany (cited after Van Straelen 1923a: 117, 118; Collins 1997: table 1)]

Bournelyreidus manningi† (Bishop & Williams, 2000) [Bishop & Williams 2000: 292, fig. 5 (as *Raninella*), upper Campanian, South Dakota and Colorado, USA]

Bournelyreidus? *oaheensis*† (Bishop, 1978) [Bishop 1978: 615, fig. 5 (as *Raninella*), lower Campanian, South Dakota, USA; ?upper Campanian–Maastrichtian, South Dakota and North Dakota, USA]

Bourneylyreidus teodorii† **n. sp.** [upper Maastrichtian, southwestern France]

Bournelyreidus tridens† (Roberts, 1962) [Roberts 1962: 187, pl. 88, figs. 5, 6 (as *Raninella*), Campanian, New Jersey, Delaware; lower Maastrichtian, Mississippi, USA (see Bishop 1983b)]

Bournelyreidus sp.† sensu Collins & Jakobsen 1995 [Collins & Jakobsen 1995: 39, pl. 10, fig. 10 (as *Lyreidus*), Danian, Denmark]

Genus *Heus*† Bishop & Williams, 2000

Heus foersteri† Bishop & Williams, 2000 [Bishop & Williams 2000: 290, fig. 4, upper Campanian, South Dakota and Colorado, USA]

Genus *Lyreidus* De Haan, 1841

Lyreidus antarcticus† Feldmann & Zinsmeister, 1984 [Feldmann & Zinsmeister 1984: 1048, figs. 3a–k, 4a–i, 5, 6b, 7, lower/upper Eocene, Seymour Island, Antarctica]

Lyreidus bennetti† Feldmann & Maxwell, 1990 [Feldmann & Maxwell 1990: 787, figs. 7.1–7.5, 8, upper Eocene, New Zealand]

Lyreidus brevifrons Sakai, 1937 [Sakai 1937: 171, text-figs. 38b, 41b, 42a, b, pl. 16, fig. 6, Recent, western Indian Ocean, Philippines, Japan, Taiwan, South China Sea]

Lyreidus elegans† Glaessner, 1960 [Glaessner 1960: 16, text-fig. 5, pl. 2, figs. 15, 16 (? = *L. tridentatus*; see Griffin 1970), lower Miocene, New Zealand]

Lyreidus fastigatus† Rathbun, 1919 [Rathbun 1919: 168; Oligocene, Anguilla, West Indies]

Lyreidus hungaricus† Beurlen, 1939 [Beurlen 1939: 146, text-fig. 4, pl. 7, fig. 7, middle Oligocene, Hungary (Feldmann 1992: 954 placed it in *Lyreidus* (*Lysirude*); Tucker 1998: 324 in *Lysirude*)]

Lyreidus lebuensis† Feldmann & Chirono-Gálvez *in* Feldmann, 1992 [Feldmann 1992: 948, fig. 6, Eocene, Chile]

Lyreidus stenops Wood-Mason, 1887 [Wood-Mason 1887: 209, pl. 1, figs. 7, 8 (= *L. integra* Terazaki, 1902: 217, unnumbered figure; *L. politus* Parisi, 1914: 311, pl. 13, fig. 5), Recent, Indo-West Pacific (South China Sea, Philippines, Japan)]

Lyreidus tridentatus† De Haan, 1841 [De Haan 1841: 140, pl. 35, fig. 6, middle Oligocene–Recent, Indo-West Pacific (Japan, South China Sea, Nansha Is., Philippines, eastern and western Australia, New Zealand, Hawaiian Is. (= *L. elongatus* Miers, 1879: 46, as conditional name; *L. australiensis* Ward, 1933: 377; *L. fossor* Bennett, 1964: 24, figs. 5–9; see Griffin 1970, Feldmann 1992, Ng *et al*. 2008)]

Lyreidus waitakiensis† Glaessner, 1980 [Glaessner 1980: 178, fig. 7, 7a, upper middle Eocene, New Zealand (Feldmann 1992: 954 assigned it to *Lyreidus* (*Lysirude*); Tucker 1998: 324 to *Lysirude*)]

Lyreidus† sp. sensu Karasawa 1993 [Karasawa 1993: 42, pl. 7, fig. 4, lower Pliocene, Japan]

Genus *Lysirude* Goeke, 1986

Lysirude channeri (Wood-Mason, 1885) [Wood-Mason 1885: 104 (as *Lyreidus*), see Wood-Mason 1887: 206, pl. 1, figs. 1–6; 1888: 376, Recent, Indo-West Pacific (Arabian Sea, northern Indian Ocean, Bay of Bengal, Philippines, South China Sea) (= *Lyreidus gracilis* Wood-Mason, 1888: 376)]

Lysirude griffini Goeke, 1986 [Goeke 1986: 215, figs. 4, 5, Recent, Philippines]

Lysirude hookeri† Feldmann, 1992 [Feldmann 1992: 953, figs. 12.1–12.5, 13, upper lower Eocene, Seymour I., Antarctica]

Lysirude nitidus (A. Milne-Edwards, 1880) [A. Milne-Edwards 1880: 34, western North Atlantic, from Maine, USA to Caribbean, Venezuela]

Lysirude paronae† (Crema, 1895) [Crema 1895: 671, text-fig. 11, middle Miocene–Pliocene; northern Italy (Feldmann 1992: 954 assigned it to *Lyreidus* (*Lysirude*); see Garassino *et al*. 2004; De Angeli *et al*. 2009b)]

Genus *Macroacaena*† Tucker, 1998 (= *Carinaranina*† Tucker, 1998)

Macroacaena alseana† (Rathbun, 1932) [Rathbun 1932: 239, figs. 3, 4 (as *Lyreidus*), upper Eocene–lower Oligocene, Washington, Oregon, Pacific Northwest of North America (assigned by Feldmann 1992: 951 to *Lyreidus* (*Lysirude*)) (? = *Ranidina teshimai*† Fujiyama & Takeda, 1980 339, pl. 39, figs. 1–5, pl. 40, figs. 1–4, Oligocene, Hokkaido)]

Macroacaena bispinulata† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 27, fig. 16a–d (as *Lyreidus*), middle Paleocene, West Greenland]

Macroacaena chica† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 [Schweitzer *et al.* 2003a: 30, figs. 10.3–10.5, upper Eocene, British Columbia, Canada]

Macroacaena franconica† Schweigert, Feldmann & Wulf, 2004 [Schweigert *et al.* 2004: 62, fig. 2, lower Turonian, southern Germany]

Macroacaena cf. *franconica*† sensu Schweigert *et al*. 2004 [see Gripp 1969; Kümmel 1972; Schweigert *et al*. 2004: fig. 3; ?lower Paleocene, northern Germany (erratic boulders)]

Macroacaena fudoujii† (Karasawa, 2000) [Karasawa 2000b: 806, figs. 2, 3 (as *Carinaranina*), lower Miocene, southern Japan]

Macroacaena johnsoni† (Rathbun, 1935) [Rathbun 1935b: 83, pl. 17, figs 12–17 (as *Symethis*), Paleocene, Alabama; see Armstrong *et al*. 2009: 752, figs. 4.1, 4.2, upper lower Paleocene, central Texas, USA)]

Macroacaena leucosiae† (Rathbun, 1932) [Rathbun 1932: 242, figs. 7, 8 (as *Eumorphocorystes*?), upper Eocene (?Oligocene), Oregon]

Macroacaena marionae† (Tucker, 1998) [Tucker 1998: 338, figs. 8.1–8.4 (as *Carinaranina*), Eocene, Washington]

Macroacaena naselensis† (Rathbun, 1926) [Rathbun 1926a: 100, pl. 24, figs. 9, 10 (as *Eumorphocorystes*), ?middle Oligocene, Washington, Alaska (Waugh *et al*. 2009: 20, table 1, in upper Eocene–Oligocene)]

Macroacaena rosenkrantzi† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 24, figs. 13, 14a–c, 15a, b (as *Lyreidus*), Maastrichtian, West Greenland]

Macroacaena schencki† (Rathbun, 1932) [Rathbun 1932: 242, figs. 5, 6 (as *Eumorphocorystes*), upper Eocene (?Oligocene), Oregon]

Macroacaena succedana† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 23, figs. 11a–c, 12, Campanian–Maastrichtian, West Greenland]

Macroacaena venturai† Vega, Nyborg, Fraaye & Espinosa, 2007 [Vega *et al.* 2007b: 1436, fig. 5.2, Paleocene, northeastern Mexico]

Genus *Rogueus*† Berglund & Feldmann, 1989

Rogueus orri† Berglund & Feldmann, 1989 [Berglund & Feldmann 1989: 70, figs. 2.1–2.6, 3.1, 3.2, lower middle Eocene, Oregon, USA]

Rogueus robustus† Collins & Jakobsen, 1996 [Collins & Jakobsen 1996: 63, fig. 1a, b, middle Paleocene, eastern Denmark]

Subfamily Marylyreidinae† n. subfam.

Genus *Marylyreidus*† n. gen.

Marylyreidus punctatus† (Rathbun, 1935) [Rathbun 1935b: 48, pl. 12, figs. 14–16 (as *Notopocorystes*) (= *Notopocorystes parvus*† Rathbun, 1935, see Rathbun 1935b: 48, pl. 12, figs. 11–13, *Raninella mucronata*† Rathbun, 1935, see Rathbun, 1935b: 50, pl. 14, figs. 32, 33; synonymy after Haj & Feldmann 2002), upper Albian–lower Cenomanian, Texas, USA]

Family Raninidae De Haan, 1839

Subfamily Ranininae De Haan, 1839 emend.

Genus *Lophoranina*† Fabiani, 1910 (= *Palaeonotopus*† Brocchi, 1877)

Lophoranina aculeata† (A. Milne-Edwards, 1881) [A. Milne-Edwards 1881: 7, pl. 22, fig. 4, upper Eocene, southwestern France; lower Oligocene, northern Italy (see Marangon & De Angeli 2007)]

Lophoranina albeshtensis† Schweitzer, Feldmann & Lazăr, 2009 [Schweitzer *et al.* 2009: 7, fig. 4, lower–middle Eocene, Romania]

Lophoranina aldrovandii† (Ranzani, 1818) [Ranzani 1818: 344, pl. 14 (as *Ranina*), ?Eocene, ?northern Italy]

Lophoranina bakerti† (A. Milne-Edwards, 1872) [A. Milne-Edwards 1872: 4 (as *Ranina*), middle Eocene, 'India' (see Withers 1932: 468, pl. 13, figs. 3–5, as *Lophoranina bakeri*), middle Eocene, Pakistan]

Lophoranina barroisii† (Brocchi, 1877) [Brocchi 1877: 4, pl. 29, figs. 6–8 (as *Palaeonotopus*), Eocene, central France]

Lophoranina bishopi† Squires & Demetrion, 1992 [Squires & Demetrion 1992: 44, fig. 130, lower Eocene, Baja California, Mexico]

Lophoranina bittneri† (Lőrenthey, 1902) [Lőrenthey 1902: 104 (809), pl. 1, figs. 1, 2 (as *Ranina*), middle–upper Eocene, northern Italy; Eocene, Sicily, Hungary, Spain]

Lophoranina cf. *bittneri*† sensu Wank 1983 [Wank 1983: 147, figs. 1, 2, lower Eocene, Austria]

Lophoranina cristaspina† Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer & Waugh, 2001 [Vega *et al.* 2001: 933, figs. 4, 5, middle Eocene, southern Mexico]

Lophoranina georgiana† (Rathbun, 1935) [Rathbun 1935b: 97, text-fig. 2, pl. 21, figs. 7, 8 (as *Ranina*), lower Oligocene, Alabama, USA]

Lophoranina aff. *georgiana*† sensu Portell 2004 [Portell 2004: 2, pl. 2, figs. A, B, Eocene, Florida]

Lophoranina kemmerlingi† Van Straelen, 1923 [Van Straelen 1923b: 489 (1), figs. 1, 2a, b, Eocene, Borneo]

Lophoranina laevifrons† (Bittner, 1875) [Bittner 1875: 68, pl. 1, fig. 4 (as *Ranina*), middle Eocene, northern Italy]

Lophoranina levantina† Lewy, 1977 [Lewy 1977: 98, text-figs. 1, 2, pl. 1, figs. 2–9 (as *Ranina* (*Lophoranina*)), middle Eocene, Israel]

Lophoranina marestiana† (König, 1825) [König 1825: 2, pl. 1, fig. 15 (*non* fig. 14) (as *Ranina maresiana* and *R. Maretiana*), lower/upper Eocene, northern Italy, Spain, Israel, Croatia, Egypt, ?Sicily, Kazakhstan]

Lophoranina cf. *marestiana*† sensu Wank 1986 [Wank, 1986: 61, figs. 1–3 (as *Ranina* (*Lophoranina*)), Eocene, Austria]

Lophoranina marestiana var. *avesana*† Bittner, 1883 [Bittner 1883: 301, pl. 2, fig. 2, middle Eocene, northern Italy]

Lophoranina maxima† Beschin, Busulini, De Angeli & Tessier, 2004 [Beschin *et al.* 2004: 110, text-figs. 1, 2, pl. 1, figs. 1–3, pl. 2, figs. 1, 2, middle Eocene, northern Italy]

Lophoranina persica† (Withers, 1932) [Withers 1932: 469, pl. 13, fig. 1 (as *Ranina* (*Lophoranina*)), Eocene, Iran]

Lophoranina porifera† (Woodward *in* Guppy, 1886) [Guppy 1886: 591, pl. 26, fig. 18 (as *Ranina*), lower Oligocene, Trinidad]

Lophoranina? *quinquespinosa*† (Rathbun, 1945) [Rathbun 1945: 375, pl. 55B–E (as *Ranina*), Neogene, Fiji]

Lophoranina raynorae† Blow & Manning, 1996 [Blow & Manning 1996: 7, pl. 2, fig. 3, middle Eocene, North Carolina, USA]

Lophoranina reussi † (Woodward, 1866) [Woodward 1866: 592; middle/upper Eocene, Spain, Italy, Hungary, Slovakia]

Lophoranina rossi† Blow & Manning, 1996 [Blow & Manning 1996: 8, pl. 2, fig. 4 middle Eocene, South Carolina, USA]

Lophoranina soembaensis† (Van Straelen, 1938) [Van Straelen 1938: 95, pl. 1, fig. 3, lower Eocene, Sumba, Indonesia]

Lophoranina straeleni† Vía, 1959 [Vía 1959: 366, text-fig. 7, lower/middle Eocene, Spain, northern Italy]

Lophoranina tchihatcheffi† [d'Archiac MS] (A. Milne-Edwards, 1866) [A. Milne-Edwards 1866: 105, pl. 1, fig. 7 (as *Ranina*), Eocene, Greece (incorrect spelling in Reuss 1859, *tschichatscheffi*; see A. Milne Edwards 1872: 4, 8)]

Lophoranina toyosimai† (Yabe & Sugiyama, 1935) [Yabe & Sugiyama 1935: 2, text-figs. 1, 2, pl. 1, figs. 1-11 (as *Ranina* (*Lophoranina*)); Eocene, Japan

Genus *Lophoraninella*† Glaessner, 1945

Lophoraninella cretacea† (Dames, 1886) [Dames 1886: 553 (Schweitzer *et al*. 2003b: 890, 'as 'likely' in Galatheoidea'), Cenomanian, Lebanon]

Genus *Ranina* Lamarck, 1801 (= *Ranina* (*Eteroranina*)† Fabiani, 1910)

Ranina americana† Withers, 1924 [Withers 1924: 125, pl. 4, figs. 1–3, upper Eocene (Oligocene?), Washington (Waugh *et al*. 2009: 20, table 1, shown as Miocene)]

Ranina bavarica† Ebert, 1887 [Ebert 1887: 264, pl. 8, figs. 5–9, Eocene, southern Germany]

Ranina berglundi† Squires & Demetrion, 1992 [Squires & Demetrion 1992: 43, figs. 128, 129, Eocene, northern and southern Mexico]

Ranina bouilleana† A. Milne Edwards, 1872 [A. Milne Edwards 1872: 6, 9, pl. 8, figs. 2, 2a–c, Oligocene, southwestern France, northern Italy]

Ranina brevispina† Lőrenthey, 1898 [Lőrenthey 1898b: 135, pl. 10, figs. 2, 3, pl. 11, fig. 1, Miocene, Algeria]

Ranina cf. *brevispina*† [= *R. adamsi*† Woodward, *nomen nudum*, lower Miocene, Malta]

Ranina cuspidata† Guppy, 1909 [Guppy 1909: 6, lower Miocene, Trinidad (see Collins *et al*. 2009: 75)]

Ranina elegans† Rathbun, 1945 [Rathbun 1945: 375, pl. 55F, G, Neogene, Fiji]

Ranina granulosa† A. Milne Edwards, 1872 [A. Milne Edwards, 1872: 5, pl. 8, fig. 1, Eocene–?Oligocene, southwestern France (as '*granulata*' on p. 9 and caption to pl. 8)]

Ranina haszlinskyi† Reuss, 1859 [Reuss 1859: 23, pl. 4, figs. 4, 5, Oligocene (?upper Eocene), Hungary]

Ranina hirsuta† Schafhäutl, 1863 [Schafhäutl 1863, middle Eocene, southern Germany]

Ranina lamiensis† (Rathbun *in* Ladd, 1934) [Ladd 1934: 239, pl. 44, fig. 9 (as *Montezumella*) (see Rathbun 1945: 374, pls. 55A, 56A, B), Neogene, Fiji]

Ranina libyca† (Van Straelen, 1935) [Van Straelen 1935: 113, text-figs. A-D (as *Raninella*), Danian, Kurkur Oasis, Egypt]

Ranina molengraaffi† Van Straelen, 1924 [Van Straelen 1924: 777, fig. 1a, b (as *Ranina* (*Hela*)), Miocene, Borneo]

Ranina oblonga† (von Münster, 1840) [von Münster, 1840: 24, pl. 2, fig. 4, Oligocene, Germany]

Ranina palmea† Sismonda, 1846 [Sismonda 1846: 64, pl. 3, figs. 3, 4, lower Miocene, northern Italy]

Ranina propinqua† Ristori, 1891 [Ristori 1891: 11, pl. 1, figs. 4–7, Pliocene, central Italy]

Ranina ranina† (Linnaeus, 1758) [Linnaeus, 1758: 625 (as *Cancer raninus*), middle Pleistocene–Recent, South Africa to Japan, Australia, Norfolk I., New Caledonia, Hawaiian Is.) (= *Ranina dentata* Latreille, 1802; *R. serrata* Lamarck, 1801; ?*Ranina cristata* Desjardins, 1835); some of these names might refer to distinct species]

Ranina speciosa† (von Münster, 1840) [von Münster 1840: 24, pl. 2, figs. 1–3 (as *Hela*), Oligocene (–?Miocene), northern and eastern Germany, northern Italy]

Ranina tejoniana† Rathbun, 1926a [Rathbun 1926a: 90, text-fig. 1, pl. 22, figs. 1, 2, Eocene, California]

Ranina sp.† sensu Hyžný 2007 [Hyžný 2007: 59, fig. 1A–C, lower Oligocene, Slovakia]

Ranina sp.† sensu Remy 1960 [Remy 1960: 58, fig. 3, pl. 1, fig. 12 (as *Ranina* (*Laeviranina*)? sp. indet.), Eocene (probably), Ivory Coast]

Ranina sp.† sensu De Angeli *et al*. 2009 [De Angeli *et al*. 2009a: 120, fig. 2, upper Eocene, northern Italy]

Genus *Raninella*† A. Milne Edwards, 1862 (= *Hemioon*† Bell, 1863)

Raninella? *bidentata*† (Rathbun, 1935) [Rathbun 1935b: 85, pl. 18, figs. 9–12 (as *Symnista bidentata*), lower Paleocene, Alabama, USA]

Raninella circumviator† (Wright & Collins, 1972) [Wright & Collins 1972: 89, text-fig. 12d, pl. 19, fig. 3 (as *Hemioon*), upper Turonian, southern England]

Raninella elongata† A. Milne Edwards, 1862 [A. Milne Edwards 1862: 493 (= *Palaeocorystes callianassarum*† Fritsch *in* Fritsch & Kafka, 1887: 46, text-fig. 69, pl. 10, fig. 9) (see Brocchi 1877: 4, figs. 4, 5, upper Albian–Coniacian, southern England, Czech Republic, northern France, Germany (see Glaessner 1929a: 155, fig. 1a, b); = *Hemioon cunningtonii*† Bell, 1863: 10; = *Raninella atava*† Carter, 1898: 24, pl. 1, fig. 7 [as *Ranina* (*Raninella*?)], ?Cenomanian, England]

Raninella eocenica† Rathbun, 1935 [Rathbun 1935b: 82, pl. 18, figs. 13–16, Eocene, Alabama, USA]

Raninella griesbachi† (Noetling, 1897) [Noetling 1897: 78, pl. 22, fig. 4, Maastrichtian, India]

Raninella novozelandica† (Glaessner, 1980) [Glaessner 1980: 177, fig. 5, 5a (as *Hemioon*), upper Albian, New Zealand (see Feldmann 1993)]

Raninella quadrispinosa† (Collins, Fraaye & Jagt, 1995) [Collins *et al.* 1995: 188, fig. 9a–d (as *Raninoides*?), upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Raninella trigeri† A. Milne Edwards, 1862 [A. Milne Edwards 1862: 493 (compare Brocchi 1877: 2), Cenomanian, southern France]

Raninella yanini† (Ilyin & Alekseev, 1998) [Ilyin & Alekseev 1998: 48, figs. 1b–c, 2d (as *Hemioon*), upper Albian, Crimea (see Ilyin 2005)]

Raninella? n. sp.† sensu Lehmann 2004 [Lehmann 2004, ?Upper Cretaceous/Paleogene, northern Germany (erratics)]

Raninella? *ornata*† (Wright & Collins, 1972) [Wright & Collins 1972: 85, pl. 18, figs. 4, 5 (as *Notopocorystes* (*Cretacoranina*)), lower Cenomanian, southern England (Wright & Collins 1972: pl. 18, fig. 5b, can be attributed to Ranininae but "untraced specimen" and may not be conspecific with fragmentary holotype)]

Genus *Remyranina*† Schweitzer & Feldmann, 2010

Remyranina ornata† (Remy, 1960) [Remy 1960: 57, fig. 2, unnumbered plate, figs. 8, 9, ?Eocene, Ivory Coast (see Schweitzer & Feldmann 2010a: 401, 402)]

Genus *Vegaranina*† n. gen.

Vegaranina precocia† (Feldmann, Vega, Tucker, García-Barrera & Avendaño, 1996) **n. comb.** [Feldmann *et al.* 1996: 297, figs. 3.1–3.3, 4.1, 4.2 [as *Lophoranina precocious*], lower Maastrichtian, southeastern Mexico; Campanian–Maastrichtian, Cuba (see Varela & Rojas-Consuegra 2009), Schweitzer *et al*. (2009c: 7) amended epithet to *precocia*]

Vegaranina cf. *precocia*† sensu Schweitzer *et al*. 2008 [Schweitzer *et al.* 2008: 5, fig. 3 (as *Lophoranina*), lower upper Maastrichtian, Puerto Rico]

Vegaranina sp.† [herein]

Subfamily Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929

Genus *Bicornisranina*† Nyborg & Fam, 2008

Bicornisranina bocki† Nyborg & Fam, 2008 [Nyborg & Fam 2008: 689, figs. 1–6, Upper Cretaceous, British Columbia, Canada (= *Raninoides bocki* Fam & Nyborg, 2003: 57 (*nomen nudum*)]

Genus *Cristafrons*† Feldmann, Tshudy & Thomson, 1993

Cristafrons praescientis† Feldmann, Tshudy & Thomson, 1993 [Feldmann *et al.* 1993: 33, figs. 25, 26, lower Campanian–?lower Maastrichtian, James Ross Basin, Antarctica (type is contained in the collections of the British Antarctic Survey, Cambridge, listed erroneously as a cirripede, under *Cretiscalpellum*)]

Genus *Notopoides* Henderson, 1888

Notopoides exiguus† Beschin, Busulini, De Angeli & Tessier, 1988 [Beschin *et al.* 1998: 188, text-fig. 9, pl. 9, figs. 2, 3, lower–middle Eocene, northern Italy; Eocene, southern Mexico (= *Notopus minutus*† Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer & Waugh, 2001: 936, figs. 6.1, 8, Eocene, southern Mexico)]

Notopoides latus Henderson, 1888 [Henderson 1888: 29, pl. 3, fig. 1, Recent, Indo-West Pacific (Kenya, Somalia ,Indonesia, Philippines, Kei Is., Norfolk I., Hawaiian Is. (see correction of Henderson's original figure by Dawson & Yaldwyn 2002: 202, figs. 1–3)]

Notopoides? *pflugervillensis*† Beikirch & Feldmann, 1980 [Beikirch & Feldmann 1980: 322, text-figs. 5a, b, 11, lower Campanian, Texas, USA]

Notopoides verbeeki† J. Böhm *in* Martin, 1922 [Martin 1922: 527, pl. 63, fig. 11a, b, Miocene, Java]

Genus *Notosceles* Bourne, 1922

Notosceles acanthocolus† (Schweitzer, Feldmann, Gonzáles-Barba & Ćosović, 2007) [Schweitzer *et al.* 2007a: 29, fig. 2.7 (as *Raninoides*), Eocene, Baja California Sur, Mexico]

Notosceles bournei† Rathbun, 1928 [Rathbun 1928: 1, pl. 1, figs. 1–4, Paleocene/Eocene, Texas, Arkansas and Alabama, USA (Rathbun 1935b: 51, pl. 28, fig. 5, recorded 'Navarro Group, Upper Cretaceous'; Bishop 1986a: 136 recorded upper Campanian or lower Maastrichtian of Texas, USA; Armstong *et al.* 2009: 752, figs. 4.3, 4.4 recorded material from the upper lower Paleocene of central Texas, USA)]

Notosceles chimmonis Bourne, 1922 [Bourne 1922b: 74, pl. 4, figs. 2, 3, 24, 40, 41a, 43, pl. 7, figs. 44–47, 57 (= *Raninoides fossor* A. Milne-Edwards & Bouvier, 1923: 300, pl. 1, fig. 10, pl. 2, figs. 2, 3), Recent, Indo-West Pacific (Réunion, India, Philippines, Indonesia, French Polynesia]

Notosceles ecuadorensis (Rathbun, 1935) [Rathbun 1935a: 1 (as *Raninoides*), Recent, Gulf of California, Perú, Galápagos Is.]

Notosceles pepeke Dawson & Yaldwyn, 2000 [Dawson & Yaldwyn 2000: 54, figs. 1–6, Recent, northern New Zealand, Norfolk I., Norfolk Ridge, Kermadec Is.]

Notosceles serratifrons (Henderson, 1893) [Henderson 1893: 408, pl. 38, figs. 10–12 (as *Raninoides*), Recent, Indo-West Pacific (Sri Lanka, Andaman Sea, Japan, Philippines, Nansha Islands, northwestern Australia (Hu & Tao 1999: 219, text-fig. 3, pl. 1, figs. 8, 11, fossil members from Taiwan as *Raninoides serratifrons*†)]

Notosceles viaderi Ward, 1942 [Ward 1942: 47, pl. 4, figs. 5, 6, Recent, Indo-West Pacific, from Réunion and Mauritius to the Hawaiian Is. and French Polynesia]

Genus *Pseudorogueus*† Fraaye, 1995

Pseudorogueus rangiferus† Fraaye, 1995 [Fraaye 1995: 66, figs. 1, 2, lower Eocene, northern Spain]

Genus *Quasilaeviranina*† Tucker, 1998

Quasilaeviranina arzignanensis† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 194, text-fig. 11, pl. 10, figs. 2, 3 (as *Notosceles*), middle Eocene, northern Italy]

Quasilaeviranina keyesi† (Feldmann & Maxwell, 1990) [Feldmann & Maxwell 1990: 784, figs. 3.1, 3.2, 4 (as *Laeviranina*), upper Eocene, New Zealand]

Quasilaeviranina ombonii† (Fabiani, 1910) [Fabiani 1910a: 30, pl. 2, fig. 1 (as *Ranina*), lower Eocene, northern Italy]

Quasilaeviranina ovalis† (Rathbun, 1935) [Rathbun 1935b: 81, pl. 18, figs. 1–8 (as *Raninoides*), Eocene, Alabama, USA]

Quasilaeviranina pororariensis† (Glaessner, 1980) [Glaessner 1980: 177, fig. 6, 6a (as *Ranilia*), upper Eocene, New Zealand]

Quasilaeviranina simplicissima† (Bittner, 1883) [Bittner 1883: 305, pl. 1, fig. 4a, b (as *Ranina*), middle Eocene, northern Italy; upper Eocene, Hungary]

Genus *Raninoides* H. Milne Edwards, 1837 (= *Symnista* Philippi, 1887; *Raninellopsis*† J. Böhm, 1922; *Laeviranina* Lőrenthey *in* Lőrenthey & Beurlen, 1929; ?*Porcellanoidea*† Hu & Tao, 1996)

Raninoides araucana† (Philippi, 1887) [Philippi 1887: 222, pl. 50, fig. 6 (as *Symnista*), lower Eocene, Chile]

Raninoides asper† Rathbun, 1926 [Rathbun 1926a: 98, pl. 23, fig. 5, Oligocene, Oregon, USA]

Raninoides barnardi Sakai, 1974 [Sakai 1974: 87; 1976: 51, text-fig. 24a–d, Recent, Japan and probably South Africa; see *R. serratifrons* sensu Barnard 1950: 399, text-fig. 75e–g, *non* Henderson 1893, which is a species of *Notosceles*; Hu & Tao 1999: 219, text-fig. 2, pl. 1, figs. 2, 4, recorded fossil members from Taiwan]

Raninoides benedicti Rathbun 1935 [Rathbun 1935a: 1; 1937a: 9, text-figs. 4, 5, pl. 1, figs. 7, 8, Recent, Gulf of California, Ecuador]

Raninoides cf. *benedicti*† sensu Todd & Collins 2006 [Todd & Collins 2006: 68, pl. 2, fig. 5, upper Miocene–?lower Pleistocene, Panama]

Raninoides borealis† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 31, fig. 18a–c (as *Laeviranina*), middle Paleocene, West Greenland]

Raninoides bouvieri Capart, 1951 [Capart 1951: 59, fig. 17, Recent, eastern Atlantic (Senegal to Angola)]

Raninoides budapestiniensis† (Lőrenthey, 1897) [Lőrenthey 1897: 153, 166 (as *Ranina*), middle/upper Eocene, northern Italy; upper Eocene, Hungary]

Raninoides crosnieri Ribes, 1990 [Ribes 1990: 908, text-fig. 1a–h, pl. 2, figs. A–D, Recent, Madagascar]

Raninoides dickersoni† Rathbun, 1926a [Rathbun 1926a: 94, text-fig. 3, pl. 20, fig. 5 (= *Cancer* sp. sensu Dickerson 1916: 427, 434, pl. 42, fig. 12), middle Eocene, California (see Schweitzer & Feldmann 2002a: 949, fig. 9)]

Raninoides eugenensis† Rathbun, 1926 [Rathbun 1926a: 96, pl. 24, fig. 4, upper Oligocene, Oregon, USA]

Raninoides fabianii† (Lőrenthey & Beurlen, 1929) [Lőrenthey & Beurlen 1929: 106, pl. 4, fig. 10 (as *Ranina* (*Laeviranina*)), upper Eocene, northern Italy; middle–upper Eocene, Hungary, Germany]

Raninoides cf. *fabianii*† [see Beschin, Busulini, De Angeli, Tessier & Ungaro 1998: 18, text-figs. 7, 9, middle Eocene, northern Italy; see Förster & Mundlos 1982: 156, text-figs. 7, 8, 9B, 10B, pl. 1, figs. 4–6; Lienau 1984, upper Eocene, northern Germany]

Raninoides fulgidus† Rathbun, 1926 [Rathbun 1926a: 96, text-fig. 4, pl. 23, fig. 6, upper Eocene–Oligocene, Washington, Oregon, USA]

Raninoides fulungensis† Hu & Tao, 1999 [Hu & Tao 1999: 218, text-fig. 1, pl. 1, fig. 3, Oligocene–Miocene, Taiwan]

Raninoides glabra† (Woodward, 1871) [Woodward 1871: 90, fig. 1a, b (as *Palaeocorystes*; see *Laeviranina*), lower Eocene, Belgium, southern England]

Raninoides goedertorum† (Tucker, 1998) [Tucker 1998: 348, figs. 13.1–13.7, 14 (as *Laeviranina*), upper Eocene, Washington, USA]

Raninoides gottschei† (J. Böhm, 1928) [Böhm 1928: 563, figs. 1, 2 (as *Raninellopsis*), lower Eocene, northern Germany, southern England]

Raninoides hendersoni Chopra, 1933 [Chopra 1933: 81, text-fig. 1b, pl. 3, fig. 1, 1a, Recent, Indo-West Pacific (Andaman Sea, Philippines, Nansha Is)]

Raninoides hollandica† (Collins, Fraaye, Jagt & van Knippenberg, 1997) [Collins *et al.* 1997: 2, pl. 1, fig. A–D (as *Laeviranina*), ?upper Oligocene, eastern Netherlands]

Raninoides intermedius Dai & Xu, 1991 [Dai & Xu 1991: 1, fig. 1, Recent, South China Sea]

Raninoides javanus† (J. Böhm, 1922) [Böhm 1922: 526, pl. 63, fig. 12a–c (as *Raninellopsis*), lower Miocene, Java]

Raninoides lamarcki A. Milne-Edwards & Bouvier, 1923 [A. Milne-Edwards & Bouvier 1923: 299, pl. 1, figs. 8, 9, pl. 2, figs. 4, 5 (as *Raninoides laevis lamarckii*), Recent, western Atlantic (Gulf of Mexico, Venezuela, Brazil)]

Raninoides laevis (Latreille, 1825) [Latreille 1825: 268 (as *Ranina*), Recent, western Atlantic (eastern USA to Brazil) (= *R. schmitti* Sawaya, 1944: 137)]

Raninoides longifrons Chen & Türkay, 2001 [Chen & Türkay 2001: 332, fig. 1, Recent, western Pacific (Hainan, Nansha Is.)]

Raninoides louisianensis† Rathbun, 1933 [Rathbun, 1933: 186, upper Pleistocene, Jamaica; Recent, Gulf of Mexico, Caribbean, Suriname]

Raninoides madurensis† (Beets, 1950) [Beets 1950: 350, pl. 1, figs. 4–6 (as *Raninellopsis*), lower Miocene, Madura, Indonesia]

Raninoides mexicanus† Rathbun, 1930 [Rathbun, 1930: 8, pl. 4, fig. 1, Miocene, Mexico]

Raninoides morrisi† Collins *in* Collins, Lee & Noad, 2003 [Collins, Lee & Noad 2003: 198, pl. 1, fig. 4, Miocene, Sabah, Brunei]

Raninoides nodai† Karasawa, 1992 [*nodai* Karasawa 1992: 1252, figs. 4.2–4.8, upper middle Eocene, southern Japan]

Raninoides notopoides† (Bittner, 1883) [Bittner 1883: 304, pl. 1, fig. 3 (as *Ranina*), middle Eocene, northern Italy; lower Eocene, England]

Raninoides oregonensis† Rathbun, 1932 [Rathbun 1932: 239, figs. 1, 2, Eocene, Oregon]

Raninoides perarmatus† (Glaessner, 1960) [Glaessner 1960: 15, text-fig. 4, pl. 2, figs. 13, 14 (as *Laeviranina*), upper middle Eocene, New Zealand]

Raninoides personatus (White MS) Henderson, 1888 [Henderson 1888: 27, pl. 2, fig. 5, Recent, Indo-West Pacific (Bay of Bengal, Philippines, Western Australia, Japan, Nansha)]

Raninoides pliocenicus† De Angeli, Garassino & Pasini, 2009 [De Angeli *et al.* 2009b: 171, fig. 5a–d, Pliocene (*s. lat.*), Toscane, Italy]

Raninoides proracanthus† Schweitzer, Feldmann, Gonzáles-Barba & Ćosović, 2007 [Schweitzer *et al.* 2007a: 29, fig. 2.8, Eocene, Baja California, Mexico]

Raninoides pulchrus† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 171, text-fig. 5, pl. 4, figs. 1–3 (as *Laeviranina*), middle Eocene, northern Italy]

Raninoides rathbunae† Van Straelen, 1933 [Van Straelen 1933: 3, fig. 2a, b, lower Miocene, Venezuela (not upper Eocene; see Feldmann & Schweitzer 2004)]

Raninoides sinuosus† (Collins & Morris, 1978) [Collins & Morris 1978: 964, pl. 116, figs. 4–6 (as *Laeviranina*), lower Eocene, Pakistan]

Raninoides slaki† Squires, 2001 [Squires 2001: 22, figs. 47–55, Eocene, California]

Raninoides? *taiwanicus*† (Hu & Tao, 1996) [Hu & Tao 1996: 152, figs. 1, 12 (as *Porcellanoidea*), Miocene, Taiwan]

Raninoides toehoepae† (Van Straelen, 1924) [Van Straelen 1924: 780, fig. 2a–c (as *Raninella*), Miocene, Borneo]

Raninoides treldenaesensis† (Collins & Jakobsen, 2004) [Collins & Jakobsen 2004: 71, text-fig. 4, pl. 3, fig. 5 (as *Laeviranina*), middle Eocene, northern Denmark; Eocene, southern Mexico; upper lower Paleocene, central Texas, USA (see Armstrong *et al*. 2009: 752, figs. 4.5–4.8)]

Raninoides vaderensis† Rathbun, 1926 [Rathbun 1926a: 93, pl. 22, fig. 5 (= *R. lewisanus* Rathbun, 1926a: 94, pl. 22, fig. 4), middle–upper Eocene, Pacific Northwest, North America]

Raninoides washburnei† Rathbun, 1926a [Rathbun 1926a: 95, pl. 22, fig. 6, upper Oligocene, Oregon (Waugh *et al*. 2009: 20, table, indicated as Eocene)]

Raninoides willapensis† (Rathbun, 1926) [Rathbun 1926a: 99, pl. 21, figs. 4, 5 (as *Ranidina*), Eocene (?middle Oligocene), Washington (Tucker 1998: 342 assigned to *Carinaranina*; Waugh *et al.* 2009: 20, table 1, assigned to *Macroacaena*)]

Raninoides sp.† sensu Vega *et al*. 2001 [Vega *et al*. 2001: 935, figs. 6.2, 7 (as *Laeviranina*), Eocene, southern Mexico]

Raninoides sp.† sensu Morris & Collins, 1991 [Morris & Collins 1991: 4, fig. 39, ?upper middle Pleistocene, Brunei (= *R. morrisi*)]

Raninoides sp.† sensu Bachmayer & Mundlos, 1968 [Bachmayer & Mundlos 1968: 670, ?upper Oligocene, northern Germany]

Raninoides sp.† sensu Karasawa *et al*. 2008 [Karasawa *et al*. 2008b: 57, fig. 3S, Pleistocene, Philippines]

Subfamily Notopodinae Serène & Umali, 1972

Genus *Cosmonotus* Adams & White *in* White, 1848 (= *Engonionotus* Rathbun, 1897; *Paralbunea* Hu & Tao, 1996, *non Paralbunea* Serène, 1977)

Cosmonotus chevrona† (Fraaye & Van Bakel, 1998) [Fraaye & Van Bakel 1998: 296, figs. 1d–g, 2c, 3c (as *Raniliformis*), upper Maastrichtian, southeastern Netherlands]

Cosmonotus genkaiae Takeda & Miyake, 1970 [Takeda & Miyake 1970: 199, text-figs. 1b, 2a–f, 3a, b, Recent, East China Sea]

Cosmonotus grayii White, 1847 [White 1847: 129 (*nomen nudum*), 1848: 227, two unnumbered figures (see Adams & White 1849: 60, pl. 13, fig. 3, for publication dates of Adam White's papers, see Clark & Presswell 2001), Recent, Indo-West Pacific (Réunion, East Africa, Persian Gulf, India, Philippines, Nansha Is., Japan, Taiwan, Borneo, Australia)]

Cosmonotus mclaughlinae Tavares, 2006 [Tavares 2006: 534, fig. 1, Recent, Indo-West Pacific (Réunion, Philippines, Indonesia, Solomon Islands, Futuna I., Vanuatu, Loyalty Is., Fiji, Tonga)]

Genus *Eumorphocorystes*† van Binkhorst, 1857

Eumorphocorystes sculptus† van Binkhorst, 1857 [van Binkhorst 1857: 108, pl. 6 (2), figs. 1a, b, 2a, 3a, 5a, *non* 4a, upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Genus *Lianira*† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991

Lianira beschini† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991 [Beschin *et al.* 1991: 197, text-fig. 4, pl. 1, fig. 1a–e, pl. 2, figs. 1, 2a–c, pl. 3, fig. 1a–d, middle Eocene, northern Italy]

Lianira convexa† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991 [Beschin *et al.* 1991: 199, text-fig. 5, pl. 4, figs. 1a, b, 3a–c, middle Eocene, northern Italy]

Lianira isidoroi† Beschin, De Angeli & Checchi, 2007 [Beschin *et al.* 2007: 14, text-fig. 3, pl. 1, figs. 1a–d, 2–4, lower–middle Eocene, northern Italy]

Genus *Lovarina*† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991

Lovarina cristata† Beschin, Busulini, De Angel, Tessier & Ungaro, 1991 [Beschin *et al.* 1991: 202, text-fig. 6, pl. 5, figs. 1a, b, 2, 3, middle Eocene, northern Italy]

Genus *Notopella*† Lőrenthey *in* Lőrenthey & Beurlen, 1929

Notopella vareolata† Lőrenthey *in* Lőrenthey & Beurlen, 1929 [Lőrenthey & Beurlen 1929: 119, pl. 5, fig. 7, middle–upper Eocene, Hungary, northern Spain, northern Italy]

Genus *Notopus* de Haan, 1841 (= *Pseudoraninella*† Lőrenthey *in* Lőrenthey & Beurlen, 1929)

Notopus beyrichi† Bittner, 1875 [Bittner 1875: 72, pl. 1, fig. 6, middle–upper Eocene to lower Oligocene, northern Italy; upper Eocene, Hungary]

Notopus dorsipes (Linnaeus, 1758) [Linnaeus, 1758: 630 (as *Cancer*), Recent, Indo-West Pacific (from Red Sea to Japan, Western Australia) (= *N. rumphii* Rathbun, 1937a: 17)]

Notopus mulleri† (van Binkhorst, 1857) [van Binkhorst 1857: 107, pl. 1, fig. 1a, b (as *Notopocorystes muelleri*), upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Notopus novemdentatus Ortmann, 1892 [Ortmann 1892: 573, pl. 26, fig. 11a, b, k, Recent, New Caledonia]

Notopus vahldieki† (Förster & Mundlos, 1982) [Förster & Mundlos 1982: 159, text-fig. unnumbered (between figs. 10 and 11) (as *Pseudoraninella?*), upper Eocene, northeastern Germany (Waugh *et al.* 2009: 20, table 1, retained this species in *Pseudoraninella*)]

Notopus sp.† sensu Förster & Mundlos 1982 [Förster & Mundlos 1982: 160, text-figs. 9A, 10A, 11, pl. 1, fig. 7a, b (as *Pseudoraninella*), upper Eocene, northeastern Germany]

Genus *Ponotus*† Karasawa & Ohara, 2009

Ponotus shirahamensis† Karasawa & Ohara, 2009 [Karasawa & Ohara 2009: 200, fig. 1, lowermost mid-Miocene, central Japan]

Genus *Ranidina*† Bittner, 1893

Ranidina rosaliae† Bittner, 1893 [Bittner 1893: 33, pl. 2, fig. 2, Miocene, Austria, Bulgaria (see Müller 1984: 71)]

Genus *Ranilia* H. Milne Edwards, 1837 (=*Raninops* A. Milne-Edwards, 1880; *Paralbunea*† Hu & Tao, 1996, pars [*non Paralbunea* Serène, 1977]; *Erroranilia*† Boyko, 2004)

Ranilia angustata Stimpson, 1860 [Stimpson 1860: 240 (112), Recent, eastern Pacific (Gulf of California)]

Ranilia constricta (A. Milne-Edwards, 1880) [A. Milne-Edwards, 1880: 35 (as *Raninops*), Recent, western (Florida to Brazil), central (Ascension I.) and eastern Atlantic (Senegal to Congo) (= *Notopus* (*Raninoides*?) *atlanticus*† Studer, 1883: 17, pl. 1, fig. 5a, b, upper Pleistocene, southern Italy)]

Ranilia fornicata (Faxon, 1893) [Faxon 1893: 162 (as *Raninops*), Recent, eastern Pacific (Gulf of California to Ecuador, Galápagos)]

Ranilia guinotae de Melo & Campos, 1994 [de Melo & Campos 1994: 69, figs. 16–22, Recent, Brazil]

Ranilia muricata H. Milne Edwards, 1837 [H. Milne Edwards 1837: 196, Recent, western Atlantic (from North Carolina, USA, Gulf of Mexico to Colombia and Brazil) (= *Raninops stimpsoni* A. Milne-Edwards, 1880: 35; *R. saldanhai* Rodrigues da Costa, 1970: 33, fig. 1)]

Ranilia punctulata† Beschin, Busulini, De Angeli & Tessier, 1988 [Beschin *et al.* 1988: 196, text-fig. 12, pl. 11, figs. 1, 2, lower middle Eocene, northern Italy]

Ranilia taipeiensis† (Hu & Tao, 1996) [Hu & Tao 1996: 62, pl. 11, figs. 2, 4, 6 (as *Paralbunea*), lower Miocene, Taiwan (see Boyko 2004)]

Ranilia sp.† sensu Portell & Agnew 2004 [Portell & Agnew 2004: 2, pl. 4, fig. E–G, Pliocene, Florida]

Genus *Raniliformis*† Jagt, Collins & Fraaye, 1993

Raniliformis baltica† (Segerberg, 1900) [Segerberg 1900: 22 (368), pl. 2, figs. 9–11 (as *Raninella*), lower Paleocene, eastern Denmark, southeastern Netherlands]

Raniliformis bellini† De Angeli, 2011 [De Angeli 2011: 103, fig. 2/1–5, middle Eocene, northern Italy]

Raniliformis eocenica† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 160, text-fig. 2, pl. 1, figs. 1–4 (as *Cosmonotus*), middle Eocene, northern Italy (Waugh *et al.* 2009: 20, table 1, retain this species in *Cosmonotus*)

Raniliformis occlusa† Collins, Fraaye & Jagt, 1995 [Collins *et al.* 1995: 194, fig. 10d, e, upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Raniliformis ornata† De Angeli & Beschin, 2007 [De Angeli & Beschin 2007: 34, text-fig. 4(3a, b), pl. 2, fig. 3a–c, lower middle Eocene, northern Italy]

Raniliformis prebaltica† Fraaye & Van Bakel, 1998 [Fraaye & Van Bakel 1998: 295, figs. 1b, c, 2b, 3b, upper Maastrichtian, southeastern Netherlands]

Raniliformis rugosa† De Angeli & Beschin, 2007 [De Angeli & Beschin, 2007: 35, text-fig. 4(2a, b), pl. 2, figs. 1a, b, 2, lower middle Eocene, northern Italy]

Genus *Umalia* Guinot, 1993

Umalia chinensis (Chen & Sun, 2002) [Chen & Sun 2002: 184, fig. 78 (1–10), 560 (as *Ranilia*), Recent, South China Sea]

Umalia guinotae† De Angeli & Beschin, 2007 [De Angeli & Beschin 2007: 36, text-fig. 4(4a, b), pl. 3, figs. 2a, b, 3a–c, middle Eocene, northern Italy]

Umalia horikoshii (Takeda, 1975) [Takeda 1975: 139, text-figs. 2, 3, pl. 1, fig. 1 (as *Ranilia*), Recent, East China Sea]

Umalia misakiensis (Sakai, 1937) [Sakai 1937: 176, text-fig. 44 (as *Notopus*), Recent, Indian Ocean (Réunion), Japan]

Umalia orientalis (Sakai, 1963) [Sakai 1963: 226, text-fig. 6 (as *Ranilia*), Recent, Japan]

Umalia ovalis (Henderson, 1888) [Henderson 1888: 31, pl. 2, fig. 6 (as *Notopus*), Recent, Indo-West Pacific (Japan to Indonesia)]

Umalia tenuiocellus (Davie & Short, 1989) [Davie & Short 1989: 165, 171, figs. 5a–g, 7b, 8d–f (as *Ranilia*), Recent, Australia]

Umalia trirufomaculata (Davie & Short, 1989) [Davie & Short 1989: 167, 172, figs. 6a–h, 7a, 8a–c (as *Ranilia*), Recent, Australia]

Subfamily Symethinae Goeke, 1981

Genus *Eosymethis*† n. gen.

Eosymethis aragonensis† **n. sp.** [lower Eocene, northern Spain]

Genus *Symethis* Weber, 1795 (= *Zanclifer* Henderson, 1888)

Symethis corallica Davie, 1989 [Davie 1989: 426, text-fig. 1, pl. 1 (as '*Smethis*', typographical error), Recent, Indo-West Pacific (Australia, New Caledonia, Philippines)]

Symethis garthi Goeke, 1981 [Goeke 1981: 972, text-figs. 1–3, Recent, eastern Pacific (Gulf of California, western Panama)]

Symethis variolosa (Fabricius, 1793) [Fabricius, 1793: 476 (as *Hippa*), Recent, North Carolina, USA to Gulf of Mexico and Brazil (= *Eryon caribensis* de Fréminville, 1832: 273, pl. 8B, figs. 1, 2)]

Genus *Symethoides*† n. gen.
Symethoides monmouthorum† **n. sp.** [lower Danian, New Jersey]

Subfamily Cyrtorhininae Guinot, 1993 emend.
Genus *Antonioranina*† n. gen.
Antonioranina fusseli† (Blow & Manning, 1996) [Blow & Manning 1996: 7, pl. 2, fig. 1 (as *Cyrtorhina*), middle Eocene, North Carolina, USA]
Antonioranina globosa† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 163, text-fig. 3, pl. 2, fig. 1a–d (as *Cyrtorhina*), lower/middle Eocene, northern Italy, Croatia]
Antonioranina? *oblonga*† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 166, text-fig. 4, pl. 3, figs. 1–3 (as *Cyrtorhina*), middle Eocene, northern Italy]
Antonioranina ripacurtae† (Artal & Castillo, 2005) [Artal & Castillo 2005: 34, figs. 2, 3 (as *Cyrtorhina*), lower Ypresian (middle Ilerdian), northeast Spain]

Genus *Cyrtorhina* Monod, 1956
Cyrtorhina balabacensis Serène, 1971 [Serène 1971: 904, pl. 1A, Recent, Indo-West Pacific (South China Sea)]
Cyrtorhina granulosa Monod, 1956 [Monod 1956: 49, figs. 19–31, Recent, Gulf of Guinea from Ghana to Principe I.]

Incertae sedis

Genus *Araripecarcinus*† Martins Neto, 1987
Araripecarcinus ferreirai† Martins Neto, 1987 [Martins Neto 1987: 407, figs. 1, 2, Lower Cretaceous (?Aptian, ?Albian), Brazil (Karasawa *et al*. 2008b noted that this represents a 'raninid' sternum; see Schweitzer *et al.* 2010: 71). The holotype represents a raninoidian, but a palaeocorystoid rather than a raninoidean]

Genus *Corazzatocarcinus*† Larghi, 2004
Corazzatocarcinus hadjoulae† (Roger, 1946) [Roger 1946: 43, text-figs. 32, 33, pl. 8, fig. 1 (as *Geryon*), Cenomanian, Lebanon (interpretation of P4 in text-fig. 32 ('very small and narrow') and P5 (long, 'normal') is inaccurate, as shown by Larghi (2004), P5 being more dorsal and thus easily misinterpreted)]
Corazzatocarcinus cf. *hadjoulae*† sensu Garassino *et al*. 2008 [Garassino *et al*. 2008: 60 (not illustrated), Cenomanian–Turonian, Morocco]

Genus *Cristella*† Collins & Wienberg Rasmussen, 1992
Cristella hastata† Collins & Wienberg Rasmussen, 1992 [Collins & Wienberg Rasmussen 1992: 36, fig. 20a, b, lower Paleocene, West Greenland]

Genus *Lyreidina*† Fraaye & Van Bakel, 1998
Lyreidina pyriformis† Fraaye & Van Bakel, 1998 [Fraaye & Van Bakel 1998: 294, figs. 1a, 2a, upper Maastrichtian, southeastern Netherlands, northeastern Belgium (Waugh *et al*. 2009: 20, table 1, in Lyreidinae)]

Genus *Neoraninella*† Hu & Tao, 1996
Neoraninella tyranna† Hu & Tao, 1996 [Hu & Tao 1996: 64, pl. 11, fig. 13, Oligocene, Taiwan (Hu & Tao 1996: 63 placed in Porcellanidae; see Ng 1999 for comments on the status of new taxa erected therein)]

Genus *Sabahranina*† Collins *in* Collins, Lee & Noad, 2003
Sabahranina trushidupensis† Collins *in* Collins, Lee & Noad, 2003 [Collins, Lee & Noad 2003: 200, pl. 1, fig. 3, Miocene, Sabah, Indonesia]

Genus *Tribolocephalus*† Ristori, 1886
Tribolocephalus laevis† Ristori, 1886 [Ristori, 1886: 128, pl. 2, fig. 19, Pliocene, central Italy (see De Angeli & Garassino 2006b: 39)]

Uncertain placement

'*Cenomanocarcinus*' sp.† sensu Neumann & Jagt 2003 [Neumann & Jagt 2003: 162, fig. 1 (as *Carcineretes* sp.), lower Turonian, northern Germany; probably referable to Cenomanocarcinidae]

'*Necrocarcinus*' *franconicus*† Lehner, 1937 [Lehner 1937: 214, pl. 19, figs. 21, 22, lower Turonian, southern Germany; probably referable to Dynomenidae (Jagt *et al*. 2010)]

Notopocorystes sp.† *sensu* Bishop 1986 [Bishop 1986b: 1099, fig. 2.4, lower Campanian, Montana, USA]

Paranecrocarcinus kennedyi† Wright, 1997 [Wright 1997: 135, figs. 7a, b, 13, Barremian, Zululand, South Africa (removed from Necrocarcinidae and Palaeocorystoidea, see Guinot *et al*. 2008: 707)]

Notopocorystes? *ripleyensis*† Rathbun, 1935 [Rathbun 1935b: 49, pl. 12, figs. 6–10, lower Campanian, Mississippi, USA (see Collins 1997: table 1)]

Necrocarcinidae gen. et sp. indeterminate† sensu Schweitzer *et al*. 2003 [Schweitzer *et al*. 2003b: 890, fig. 1, Cenomanian, Egypt]

Raninella? *armata*† Rathbun, 1935 [Rathbun 1935b: 50, pl. 11, figs. 32, 33, upper Albian, Texas, USA (= *Raninella*? *starkvillensis*† Rathbun, 1935b: 51, pl. 9, figs. 4, 5) (possibly synonymous with *Ferroranina dichrous*†) (Schweitzer *et al*. 2010: 70 as *Cenomanocarcinus armatus*)]

Ranina? *burleighensis*† Holland *in* Holland & Cvancara, 1958 [Holland & Cvancara 1958: 504, text-fig. 3c, pl. 74, fig. 15, Paleocene, North Dakota, USA (indeterminate fragment of chela)]