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

BARRY W.M. VAN BAKEL<sup>1,6</sup>, DANIELE GUINOT<sup>2</sup>, PEDRO ARTAL<sup>3</sup>,  
RENÉ H.B. FRAAIJE<sup>4</sup> & JOHN W.M. JAGT<sup>5</sup>

<sup>1</sup> Oertijdmuseum De Groene Poort, Bosscheweg 80, NL–5283 WB Boxtel, the Netherlands; and Nederlands Centrum voor Biodiversiteit [Naturalis], P.O. Box 9517, NL–2300 RA Leiden, the Netherlands

E-mail: barryvanbakel@gmail.com

<sup>2</sup> Département Milieux et peuplements aquatiques, Muséum national d'Histoire naturelle, 61 rue Buffon, CP 53, F–75231 Paris Cedex 5, France

E-mail: guinot@mnhn.fr

<sup>3</sup> Museo Geológico del Seminario de Barcelona, Diputación 231, E–08007 Barcelona, Spain

E-mail: partal@optimus.es

<sup>4</sup> Oertijdmuseum De Groene Poort, Bosscheweg 80, NL–5283 WB Boxtel, the Netherlands

E-mail: info@oertijdmuseum.nl

<sup>5</sup> Natuurhistorisch Museum Maastricht, de Bosquetplein 6–7, NL–6211 KJ Maastricht, the Netherlands

E-mail: john.jagt@maastricht.nl

<sup>6</sup> Corresponding author



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BARRY W.M. VAN BAKEL, DANIELE GUINOT, PEDRO ARTAL, RENÉ H.B. FRAAIJE  
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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 Lörenthey *in* Lörenthey & 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-ptyergostome configuration, respiratory physiology and spermathecae, all reveal polarities of the raninoidian clade. The configuration of the sternum with the ptyergostome, 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 Lörenthey *in* Lörenthey & 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 Raninoidia; Ng *et al.* 2008: 42; 2010: 213, as superfamily Raninoidea; De Grave *et al.* 2009: 5, 7, 28, table 1, as section Raninoidia; Ng *et al.* 2009: 16, fig. 5, as section Raninoidia; Karasawa *et al.* 2011: 549, as section Raninoidia). 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.