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PHYLOGENY AND CLASSIFICATION OF RANINOIDA (DECAPODA: BRACHYURA)

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ABSTRACT

Phylogenetic analysis of most genera within fossil and extant Raninoida (Brachyura) based on 72 adult morphological characters yielded a new superfamily and family level classification for the section. The section was most diverse at the family level during the Late Cretaceous but remains diverse at the genus and species level in the Holocene. New subfamilies include Bicornisranininae, Macroacaeninae, and Rogueinae within Lyreididae. New genera include *Colombicarcinus*, *Alessandranina*, *Claudioranina*, *Giulianolyreidus* and *Italianira*, and one new species, *Colombicarcinus laevis*, is described. New combinations include *Alessandranina ornata* (Wright and Collins, 1972), *Claudioranina oblonga* (Beschin, Busulini, de Angeli, and Tessier, 1988), *Heus manningi* (Bishop and Williams, 2000), *Italianira punctulata* (Beschin, Busulini, de Angeli, and Tessier, 1988), *Giulianolyreidus bidentatus* (Rathbun, 1935a), *G. johnsoni* (Rathbun, 1935a), *Lyreidus teodorii* (van Bakel et al., 2012), *Macroacaena tridens* (Roberts, 1962), *M. teshimai* (Fujiyama and Takeda, 1980), *M. yanini* (Ilyin and Alekseev, 1998) and *Quasilaeviranina eocenica* (Rathbun, 1935a).

KEY WORDS: Lyreididae, Necrocarcinoidea, Palaeocorystidae, phylogeny, Raninidae, Raninoidea

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INTRODUCTION

Raninoida, also known as "frog crabs," is one of the most bewildering groups of Brachyura or true crabs, characterized by an unusual morphological disparity. It is a diverse group of crabs ranging in age from Early Cretaceous to the present. Their relationship to other decapod groups and their internal arrangement has been the subject of considerable controversy. Most recently, van Bakel et al. (2012), and Guinot et al. (2013) have considered various aspects of the group and have proposed classifications based upon traditional systematic procedures that support the monophyly of the Podotremata. These arrangements contrast with the classifications of Martin and Davis (2001) based upon traditional systematic and phylogenetic methods who rejected the monophyly of Podotremata. That position was sustained by De Grave et al. (2009) and Schweitzer et al. (2010), although arrangements of taxa therein considered within Raninoida differ. Karasawa et al. (2011) performed a cladistic analysis of fossil and extant representatives of the so-called primitive crabs and demonstrated that the Podotremata was paraphyletic. Raninoida was demonstrated to be a monophyletic section within the group studied. The essential issue that has resulted in the different classifications of Raninoida is centered around selection of bases for analysis, ranging from emphasis on single characters to inclusion of a wide range of morphological characters, molecular analyses, spermatozoal structures, and foregut ossicle studies, for example. It is clear that controversy continues to rage over placement of Raninoida in the broad scheme of decapod classification and, more specifically, the arrangement of taxa within the group. In attempting to address these questions, we use raninoidan's broad phenotypic disparity and relatively abundant fossil record to examine their internal phylogenetic relationships under a cladistic framework. Based on a broad range of adult morphological characters, here we propose a phylogenetic hypothesis or their ancestral-descendent relationships, which, in turn, forms the basis for a re-classification of the section, allowing the study of general trends in their evolution and diversity throughout geological time.

MATERIALS AND METHODS

Materials

From the 54 Raninoida taxa examined, 42 are exclusively fossil and 12 are extant taxa (Table 1). Their initial generic and family placement was mainly based upon Schweitzer et al. (2010) and van Bakel et al. (2012) although some placements have been changed herein. The generic status for some species belonging to three genera differed in both works; hence, we included in the phylogenetic analysis five species of *Macroacaena* Tucker, 1998, three species of *Notopus* de Haan, 1841, and two species of *Ranilia* H. Milne Edwards, 1837. Prior to this study, seventy-two raninoidan genera within seven families were known (De Grave et al., 2009; Schweitzer et al., 2010; Luque et al., 2012; Schweitzer et al., 2012; van Bakel et al., 2012; Beschin et al., 2013). Among those, twelve necrocarcinoid, two lyreidid, and nine raninoid genera were excluded from the analysis because of their incomplete preservation. Most of the excluded taxa are known only from dorsal carapace material, making their analysis difficult because of large numbers of missing characters. All extant genera were included, and in all families except Necrocarcinidae, at least half of the genera were included in the analysis.

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Table 1. Taxa used in the analysis. Classification in this table is based on van Bakel et al. (2012). Dagger (†) indicates extinct taxa.

Section Dromiacea
Superfamily Homolodromioidea Alcock, 1900
Family Homolodromiidae Alcock, 1900
Genus *Homolodromia* A. Milne-Edwards, 1880
Homolodromia paradoxa A. Milne Edwards, 1880
Section Homoloida
Superfamily Homoloidea de Haan, 1839
Family Homolidae de Haan, 1839
Genus *Homola* Leach, 1816
Homola orientalis Henderson, 1888
Section Raninoida
Superfamily Palaeocorystoidea† Lőrenthey *in* Lőrenthey and Beurlen, 1929
Family Palaeocorystidae† Lőrenthey *in* Lőrenthey and Beurlen, 1929
Genus *Cenocorystes*† Collins and Breton, 2009
Cenocorystes bretoni† van Bakel et al., 2012, lower Cenomanian
Cenocorystes fournieri† Collins and Breton, 2009, lower Cenomanian
Genus *Cretacoranina* Mertin, 1941
Cretacoranina schloenbachi† (Schlüter, 1879), upper Coniacian-upper Maastrichtian
Cretacoranina testacea† (Rathbun, 1926), upper Campanian-Maastrichtian
Genus *Eucorystes* Bell, 1863
Eucorystes carteri† (McCoy, 1854), upper Albian
Eucorystes ligulatus† Wright and Collins, 1972, uppermost Albian
Eucorystes oxtedensis† Wright and Collins, 1972, lower Albian
Genus *Ferroranina*† van Bakel et al., 2012
Ferroranina dichrous† (Stenzel, 1945), Turonian
Genus *Joeranina*† van Bakel et al., 2012
Joeranina broderipii† (Mantell, 1844) middle Albian-?Cenomanian
Joeranina japonica† (Jimbô, 1894), Cenomanian-Santonian
Genus *Notopocorystes*† McCoy, 1849
Notopocorystes normani† (Bell, 1863), Cenomanian
Notopocorystes stokesii† (Mantell, 1844), middle Albian
Family Camarocarcinidae† Feldmann, Li, and Schweitzer, 2008
Genus *Camarocarcinus*† Holland and Cvancara, 1958
Camarocarcinus arnesoni† Holland and Cvancara, 1958, Paleocene
Camarocarcinus quinquetuberculatus† Collins and Wienberg Rasmussen, 1992, middle Paleocene
Family Cenomanocarcinidae† Guinot, Vega and Van Bakel, 2008
Genus *Campylostoma*† Bell, 1858
Campylostoma matutiforme† Bell, 1858, Eocene
Genus *Cenomanocarcinus*† van Straelen, 1936
Cenomanocarcinus vanstraeleni† Stenzel, 1945, Cenomanian-lower Turonian
Family Necrocarcinidae† Förster, 1968
Genus *Cretacocarcinus*† Feldmann, Li and Schweitzer, 2008
Cretacocarcinus smithi† Feldmann, Li, and Schweitzer, 2008, Campanian
Genus *Necrocarcinus*† Bell, 1863
Necrocarcinus labeschei† (J. A. Deslongchamps, 1835), Albian-middle Cenomanian
Genus *Hadrocarcinus*† Schweitzer, Feldmann, and Lamanna, 2012
Hadrocarcinus carinatus† (Feldmann, Tshudy, and Thomson, 1993), Santonian-Campanian
Hadrocarcinus tectilacus† Schweitzer, Feldmann, and Lamanna, 2012, Coniacian
Hadrocarcinus wrighti† (Feldmann, Tshudy, and Thomson, 1993), Santonian-Campanian
Genus *Paranecrocarcinus*† van Straelen, 1936
Paranecrocarcinus hexagonalis† van Straelen, 1936, Hauterivian
Paranecrocarcinus libanoticus† Förster, 1968, Cenomanian
Genus *Planocarcinus* Luque et al., 2012
Planocarcinus olssoni† (Rathbun, 1937a), Aptian
Planocarcinus johnjagti† Bermudez et al., 2013, Aptian-Albian
Family Orithopsidae† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003
Genus *Orithopsis*† Carter, 1872
Orithopsis tricarinata† (Bell, 1863), upper Aptian-lower Cenomanian
Genus *Silvacarcinus*† Collins and Smith, 1993
Silvacarcinus laurae† Collins and Smith, 1993, lower Eocene

Table 1. (Continued.)

Superfamily Raninoidea De Haan, 1839
Family Lyreididae Guinot, 1993
Subfamily Lyreidinae Guinot, 1993
Genus *Bournelyreidus*† van Bakel et al., 2012
Bournelyreidus eysunesensis† (Collins and Wienberg Rasmussen, 1992), upper Campanian
Bournelyreidus tridens† (Roberts, 1962), Campanian
Genus *Lyreidus* De Haan, 1841
Lyreidus brevifrons Sakai, 1937
Lyreidus stenops Wood-Mason, 1887
Lyreidus tridentatus De Haan, 1841
Genus *Lysirude* Goeke, 1985
Lysirude channeri (Wood-Mason, 1887)
Lysirude griffini Goeke, 1985
Lysirude nitidus (A. Milne Edwards, 1880)
Genus *Macroacaena*† Tucker, 1998
Macroacaena alseana† (Rathbun, 1932), upper Eocene-lower Oligocene
Macroacaena fudoujii† (Karasawa, 2000), lower Miocene
Macroacaena johnsoni† (Rathbun, 1935), upper lower Paleocene
Macroacaena naselensis† (Rathbun, 1926), middle Oligocene
Macroacaena succedana† (Collins and Wienberg Rasmussen, 1992), Campanian-Maastrichtian
Genus *Rogueus*† Berglund and Feldmann, 1989
Rogueus orri† Berglund and Feldmann, 1989, lower middle Eocene
Subfamily Marylyreidinae† van Bakel et al., 2012
Genus *Marylyreidus*† van Bakel et al., 2012
Marylyreidus punctatus† (Rathbun, 1935), upper Albian-lower Cenomanian
Family Raninidae De Haan, 1839
Subfamily Ranininae De Haan, 1839
Genus *Lophoranina*† Fabiani, 1910
Lophoranina aculeata† (A. Milne-Edwards, 1881), upper Eocene
Lophoranina marestiana† (König, 1825), lower Eocene
Lophoranina maxima† Beschin, Busulini, de Angeli, and Tessier, 2004, middle Eocene
Genus *Ranina* Lamarck, 1801
Ranina ranina (Linnaeus, 1758)
Genus *Raninella*† A. Milne Edwards, 1862
Raninella elongata† A. Milne Edwards, 1862, upper Albian-Coniacian
Raninella trigeri† A. Milne Edwards, 1862, Cenomanian
Genus *Vegaranina*† van Bakel et al., 2012
Vegaranina precocia† (Feldmann, Vega, Tucker, Garciá-Barrera, and Avendanö, 1996), lower Maastrichtian
Subfamily Raninoidinae Lőrenthey *in* Lőrenthey and Beurlen, 1929
Genus *Bicornisranina*† Nyborg and Fam, 2008
Bicornisranina bocki† Nyborg and Fam, 2008, Upper Cretaceous
Genus *Notopoides* Henderson, 1888
Notopoides latus Henderson, 1888
Genus *Notosceles* Bourne, 1922
Notosceles chimmonis Bourne, 1922
Notosceles serratifrons (Henderson, 1893)
Genus *Quasilaeviranina*† Tucker, 1998
Quasilaeviranina arzignanensis† (Beschin, Busulini, de Angeli, and Tessier, 1988), middle Eocene
Quasilaeviranina ombonii† (Fabiani, 1910), lower Eocene
Quasilaeviranina simplicissima† (Bittner, 1883), middle Eocene
Genus *Raninoides* H. Milne Edwards, 1837
Raninoides louisianaensis Rathbun 1933
Raninoides goedertorum† (Tucker, 1998), upper Eocene
Raninoides laevis (Latreille, 1825)
Raninoides willapensis† (Rathbun, 1926), Eocene
Subfamily Notopodinae Serène and Umali, 1972
Genus *Cosmonotus* Adams and White *in* White, 1848
Cosmonotus grayii White, 1847
Genus *Eumorphocorystes*† van Binkhorst, 1857
Eumorphocorystes sculptus† van Binkhorst, 1857, upper Maastrichtian
Genus *Lianira*† Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991
Lianira beschini† Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991, middle Eocene
Genus *Lovarina*† Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991
Lovarina cristata† Beschin, Busulini, De Angel, Tessier, and Ungaro, 1991, middle Eocene

Table 1. (Continued.)

Genus *Notopella*† Lőrenthey *in* Lőrenthey and Beurlen, 1929
Notopella vareolata† Lőrenthey *in* Lőrenthey and Beurlen, 1929, middle-upper Eocene
Genus *Notopus* de Haan, 1841
Notopus beyrichi† Bittner, 1875, middle Eocene-lower Oligocene
Notopus dorsipes (Linnaeus, 1758)
Notopus muelleri† (van Binkhorst, 1857), upper Maastrichtian
Genus *Ponotus*† Karasawa and Ohara, 2009
Ponotus shirahamensis† Karasawa and Ohara, 2009, Miocene
Genus *Ranidina*† Bittner, 1893
Ranidina rosaliae† Bittner, 1893, Miocene
Genus *Ranilia* H. Milne Edwards, 1837
Ranilia muricata H. Milne Edwards, 1837
Ranilia punctulata† Beschin, Busulini, de Angeli, and Tessier, 1988, lower middle Eocene
Genus *Raniliformis*† Jagt, Collins, and Fraaye, 1993
Raniliformis baltica† (Segerberg, 1900), lower Paleocene
Raniliformis eocenica† (Beschin, Busulini, de Angeli, and Tessier, 1988), middle Eocene
Raniliformis ornata† de Angeli and Beschin, 2007, lower middle Eocene
Raniliformis prebaltica† Fraaye and Van Bakel, 1998, upper Maastrichtian
Raniliformis rugosa† de Angeli and Beschin, 2007, middle Eocene
Genus *Umalia* Guinot, 1993
Umalia misakiensis (Sakai, 1937)
Umalia orientalis (Sakai, 1963)
Subfamily Symethinae Goeke, 1981
Genus *Symethis* Weber, 1795
Symethis garthi Goeke, 1981
Symethis variolosa (Fabricius, 1793)
Subfamily Cyrtorhininae Guinot, 1993
Genus *Antonioranina*† van Bakel et al., 2012
Antonioranina globosa† (Beschin, Busulini, de Angeli, and Tessier, 1988), lower Eocene
Genus *Cyrtorhina* Monod, 1956
Cyrtorhina balabacensis Serène, 1971
Cyrtorhina granulosa Monod, 1956
Incertae sedis
Genus *Corazzatocarcinus*† Larghi, 2004
Corazzatocarcinus hadjoulae† (Roger, 1946), Cenomanian

Guinot et al. (2013) discussed the nomenclature problems of Raninoida De Haan, 1841, Raninoidia De Haan, 1841, and Gymnopleura Bourne, 1922, the latter of which contained Palaeocorystoidea and Raninoidea in their view, and suggested the usage of the subsection Gymnopleura for both superfamiles. However, the gymnopleuran condition; i.e. reduced branchiostegites and exposed pleurae of the cephalothorax (Bourne, 1922), is a synapomorphy seen only in those genera and families within Raninoidea, and is not seen in any other raninoidan clade, including Palaeocorystoidea. Gymnopleura seems best applied only to Raninoidea, and cannot embrace the other superfamilies within the section. Thus, within the present analysis, we use section Raninoida based upon the higher-level phylogenetic classification proposed by Karasawa et al. (2011).

The material examined for the phylogenetic analyses and systematic descriptions is deposited in the following institutions: ANSP, Academy of Natural Sciences of Philadelphia, Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA; AR, DSIR Geology and Geophysics collection, Lower Hutt, New Zealand; BAS, British Antarctic Survey, Cambridge, UK; BMNH, The Natural History Museum, London; BSP, Bayerische Staatsammlung für Paläontologie und historische Geologie München, Munich, Germany; CBM, Natural History Museum and Institute of Chiba, Chiba, Japan; CIRGEO, Centro de Investigaciones en Recursos Geológicos, Buenos Aires, Argentina; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; GAB, Gale A. Bishop collection, now largely housed at South Dakota School of Mines and Technology, Rapid City, SD, USA; GSC, Geological Survey of Canada Eastern Paleontology Division, Ottawa, ON, Canada; IG, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; IGM, Colombian Geological Survey, Bogotá, Colombia; IHNCH, Instituto de Historia Natural de Chiapas, Tuxtla Gutiérrez, Chiapas, Mexico; JSH Collins, Joe S. H. Collins Private Collection, London, UK; KMNH.IVP, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan; KSU D, Kent State University Decapod Comparative Collection, Kent, OH, USA; LPBart, Laboratory of Paleontology, Department of Geology and Paleontology, University of Bucharest, Bucharest, Romania; MAFI, Földani Intézet (Hungarian Geological Survey), Budapest, Hungary; MAK, Oertijdmuseum De Groene Poort, Boxtel, The Netherlands; MBA, Humboldt-Universitat zu Berlin Museum, Berlin, Germany; MFM, Mizunami Fossil Museum, Japan; MGSB, Museo Geológico del Seminario de Barcelona, Barcelona, Spain; MGUH, Geologisk Museum University of Copenhagen, Copenhagen, Denmark; MCZ, Museo Civico "G. Zannato" di Montecchio Maggiore (Vicenza), Vicenza, Italy; MHN-UABCS, Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Mexico; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MSNM, Museo Civico di Storia Naturale di Milano, Italy; NHMW, Naturhistorisches Museum Wien (Natural History Museum of Vienna), Vienna, Austria; NJSM, New Jersey State Museum, Trenton, NJ, USA; OU, Department of Geology, Otago University, Dunedin, New Zealand; OUM, Geological Collections, Oxford University Museum, Oxford, UK; RE, Ruhrlandmuseum der Stadt Essen, Essen, Germany; RGM, Rijks Geologische-Mineralogisch Museum, now the Nationaal Natuurhistorisch Museum, Naturalis, Leiden, The Netherlands; SDSM, SDSMT, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, SD, USA; SM, Sedgwick Museum, Cambridge University, Cambridge, UK; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Department of Paleontology and Historical Geology, Frankfurt, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SMU, Southern Methodist University, Dallas, TX, USA; TX, Texas Memorial Museum of the University of Texas at Austin, Austin, TX, USA; UND, Department of Geology and Geological Engineering, University of North Dakota, Grand Forks, ND, USA; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UT, University of Texas at Austin, Austin, TX, USA; zcf, Canterbury Museum, Christchurch, New Zealand.

If actual material was unavailable, the descriptive information for taxa was obtained from the literature.

Characters

Seventy-two adult morphological characters were used in the analysis (Table 2) (Figs. 1, 2). The data matrix is provided as supplementary material in Table S1 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x. Those characters were mainly chosen based upon examination of previous works

Table 2. Characters used in the phylogenetic analysis and their states.

1. Carapace proportions: elongate (0), as long as wide or wider (1)
2. Carapace widest position: mid-length (0), anterior (1)
3. Carapace with spinose ornamentations: absent (0), present (1)
4. Carapace with coarsely punctate ornamentations: absent (0), present (1)
5. Carapace with terrace ornamentations: absent (0), present (1)
6. Anterior carapace region: smooth (0), with distinct tubercles (1)
7. Cervical groove: distinct (0), indistinct (1)
8. Ventral aspect of cervical groove: well developed (0), ending at pleural suture (1), absent (2)
9. Anterior portion of rostrum: simple (0), bifid or trifid (1), absent (2)
10. Postfrontal depression: absent (0), present (1)
11. Fronto-orbital margin: narrower or as wide as half the carapace width (0), wider than half the carapace width (1)
12. Branchiocardiac groove: distinct (0), indistinct (1)
13. Longitudinal median carina: absent (0), present (1)
14. Branchial groove: absent (0), present (1)
15. Epibranchial ridge: absent or weak (0), present (1)
16. Branchial ridges: absent (0), present, (1)
17. Inner orbital fissure: absent (0), weak (1), well developed (2)
18. Outer orbital fissure: absent (0), weak (1), well developed (2)
19. Intra- or inner orbital lobes or spines: obsolete or rather faint (0), well developed (1)
20. Supra-orbital lobe or spine: absent (0), defined but poorly developed (1), well developed (2)
21. Outer orbital lobe or spine: absent (0), defined but poorly developed (1), well developed (2)
22. Orientation of orbital margin: horizontal (0), oblique backwards (1)
23. Supra- and outer orbital margins forming loop: absent (0), present (1)
24. Teeth or spines on anterolateral margins: absent (0), present with single spine (1), present with 2 or more spines (2)
25. Anterolateral spine: simple (0), with subspine (1)
26. Last anterolateral teeth: absent (0), short, shorter or equal to outer orbital teeth (1), longer than outer orbital tooth (2)
27. Epibranchial tooth or spine: absent (0), faint (1), well developed (2)
28. Junction between anterolateral and posterolateral margins: not defined (0), well defined (1)
29. Spines or teeth on posterolateral margins: absent (0), present (1)
30. Spine or tubercle at posterior corner: absent (0), present (1)
31. Oxystomatous condition: absent (0), present (1)
32. Maxilliped 3 merus: shorter than or as long as ischium (0), longer than ischium (1)
33. Maxilliped 3 merus with longitudinal furrow: absent (0), present (1)
34. Coxa of maxilliped 3: large or flabelliform (0), small, flat (1)
35. Ischium of maxilliped 3 with oblique crest: absent (0), present (1)
36. Maxilliped 3 basis: defined (0), fused to ischium (1)
37. Notopodine chela: absent (0), present (1)
38. Pereiopods 2 to 4 form: normal (0), wide, flattened (1)
39. Pereiopod 4 propodus: longer than wide (0), wider than long (1)
40. Pereiopod 5 coxa: large (0), small (1)
41. Pereiopods 2-4 dactyli: normal (0), strongly modified (1)
42. Branchiostegite: normal (0), reduced (1)
43. Pleurites 5-7: completely concealed (0), exposed (1)
44. Sterno-pleonal depression: present (0), absent (1)
45. Spermatheca opening: thoracic sternal suture 7/8 (0), endosternite 7/8 (1)
46. Episternites 4-7 sterno-coxal depression: present (0), absent (1)
47. Episternites: weakly or moderately raised (0), strongly raised (1)
48. Sternite 3: clearly divided from sternite 4 (0), not divided from sternite 4 (1)
49. Sternites 3-4 anterior margin: simple, triangular (0), crown shaped (1), narrow (2)
50. Sternite 4: wide (0), narrow (1)
51. Sternite 4: medially concave (0), nearly flattened (1), rather convex (2)
52. Sternite 5 posterior line: indistinct (0), forming V-shaped (1)
53. Sternite 5: medially concave (0), nearly flat (1), raised (2)
54. Sternite 5 with foliaceous extension: absent (0), present (1)
55. Sternites 5 and 6 with lateral extension: absent (0), present (1)
56. Sternite 6: medially concave (0), nearly flat (1), raised (2)

Table 2. (Continued.)

57. Sternite 6: wide (0), extremely narrowed (1)
58. Junction between sternite 6 and pleurite 6: narrow (0), wide (1)
59. Sternite 7: wide (0), extremely narrowed (1)
60. Sternite 7: medially concave (0), raised (1)
61. Suture 5/6: incomplete (0), complete (1)
62. Suture 6/7: incomplete (0), complete (1)
63. Median line on sternites: absent (0), reaching sternite 7 (1), reaching sternite 5 (2)
64. Sternum/pterygostome junction: absent (0), present, narrow (1), present, wide (2)
65. Pleonal locking system of abdomen: present (0), absent (1)
66. Position of locking system, if present: maxilliped coxae (0), sternite 4 (1), sternite 5 (2)
67. Sternite with double peg system: absent (0), present (1)
68. Sternite with lyreidid hook: absent (0), present (1)
69. Pleon: long, reaching sternite 4 (0), reaching sternite 5 (1), short (2)
70. Pleon: folded (0), not folded (1)
71. Pleonal somite 4 with spine: absent (0), present (1)
72. Pleonal somite 6: as long as somite 5 (0), longer than somite 5 (1)

(Tucker, 1998; Karasawa et al., 2011; van Bakel et al., 2012; Guinot et al., 2013). From these 72 characters, 55 are binary and 17 are multistate. Missing data were scored as unknown "?". The rate of missing data within the examined fossil taxa ranged from 0 to 56.9 percent. Inapplicable character states were scored as "-". In the text, characters and character states are indicated by numbers in parentheses, e.g., (1-0) = character 1 + character state 0.

Phylogenetic Analysis

The present analysis examines the previously suggested monophyly of the in-group Raninoida (Guinot et al., 2008; Karasawa et al., 2011; van Bakel et al., 2012; Guinot et al., 2013). The in-group was rooted to the out-group sister brachyuran clades *Dicranodromia* A. Milne-Edwards, 1880 (Dromiacea), and *Homola* Leach, 1816 [imprint 1815] (Homoloida) (Scholtz and McLay, 2009; Karasawa et al., 2011).

The phylogenetic analysis used PAUP* 4.0b10 (Swofford, 1999), utilizing a data matrix originating in MacClade 4.08 for OS X (Maddison and Maddison, 2005). Heuristic search analyses were performed with the following options in effect: random addition sequence, 1000 replications with random input order; one tree held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch stepping performed; MulTrees option activated; steepest descent option not in effect; branches having maximum length zero collapsed to yield polytomies; topological constraints not enforced; multistate taxa interpreted as polymorphism; character state optimization by accelerated transformation (ACCTRAN). All characters were unordered, unscaled, and equally weighted. Relative stability of clades was assessed using parsimony jackknifing (Farris et al., 1996) and Bremer support (Bremer, 1994). Jackknife frequencies were calculated in PAUP* using 1000 pseudoreplicates under a heuristic search with 33% character deletion. Bremer support was obtained using constraint trees generated in MacClade 4.08 for OS X (Maddison and Maddison, 2005) and analyzed using PAUP*.

Results and Discussion

Results

The analysis yielded two most parsimonious trees, 180 steps long with a consistency index (CI) of 0.5444, a retention index (RI) of 0.9045, and a rescaled consistency index (RC) of 0.4925 (NB: Matrix and Trees available in Treebase: http://purl.org/phylo/treebase/phylows/study/TB2:S15066). The strict consensus tree for the two most parsimonious trees showing the relationships among the clades as classified previously (van Bakel et al., 2012) is given in Fig. 3 (left) and as classified in the scheme provided here in Fig. 3 (right). The tree topology is well resolved, with only two soft polytomies recovered for four terminals for Necrocarcinidae and three for Lyreididae. Branch supports are indicated by Bremer support exceeding 1 and Jackknife proportions exceeding 50%. Character optimizations for labeled clades (Fig. 3) are given in Table 3.

Raninoida (Clade 1).—The present analysis strongly supports the monophyly of Raninoida shown by many recent works (Ahyong et al., 2007; Guinot et al., 2008; Scholtz and McLay, 2009; Karasawa et al., 2011; van Bakel et al., 2012; Guinot et al., 2013; Števčić, 2013). Raninoida is well united by nine unambiguous characters: the cervical groove ending at the pleural suture (8-1), well-developed inner orbital and outer orbital fissures (17-2; 18-2), well-defined intra- or inner- and supra-orbital lobes or spines (19-1, 20-1), presence of anterolateral spines (24-1), the buccal frame with the oxystomatous condition (31-1), absence of the sterno-coxal depression (46-1), and the pleon bearing a long somite 6 (72-1). Bremer support of 9 and 100% Jackknife support endorse the monophyletic status of Raninoida.

Guinot et al. (2008) suggested that raninoidans were comprised of the superfamily Raninoidea and an unnamed superfamily containing Palaeocorystidae, Necrocarcinidae, and Cenomanocarcinidae. Later, De Grave et al. (2009), Schweitzer et al. (2010), and Karasawa et al. (2011) considered the section Raninoida to be monotypic, comprised solely by a superfamily Raninoidea, while van Bakel et al. (2012), Guinot et al. (2013), and Števčić (2013) recognized two superfamilies, Raninoidea and Palaeocorystoidea, following Guinot et al. (2008). The present analysis shows that Raninoida consists of three major clades, each of them with unique combinations of morphological characters, and each deserving superfamily-level status (Fig. 4). Under this scenario, Palaeocorystoidea *sensu* van Bakel et al. (2012) is paraphyletic, consisting of two major clades: Clade 2 (Camarocarcinidae + (Cenomanocarcinidae + (Necrocarcinidae + Orithopsidae))) and Clade 11 (Palaeocorystidae), but excluding Raninoidea. For Palaeocorystoidea to be monophyletic, it must include all the taxa derived from their most recent common ancestor, and exclusion of Raninoidea would suggest that raninoideans had a different

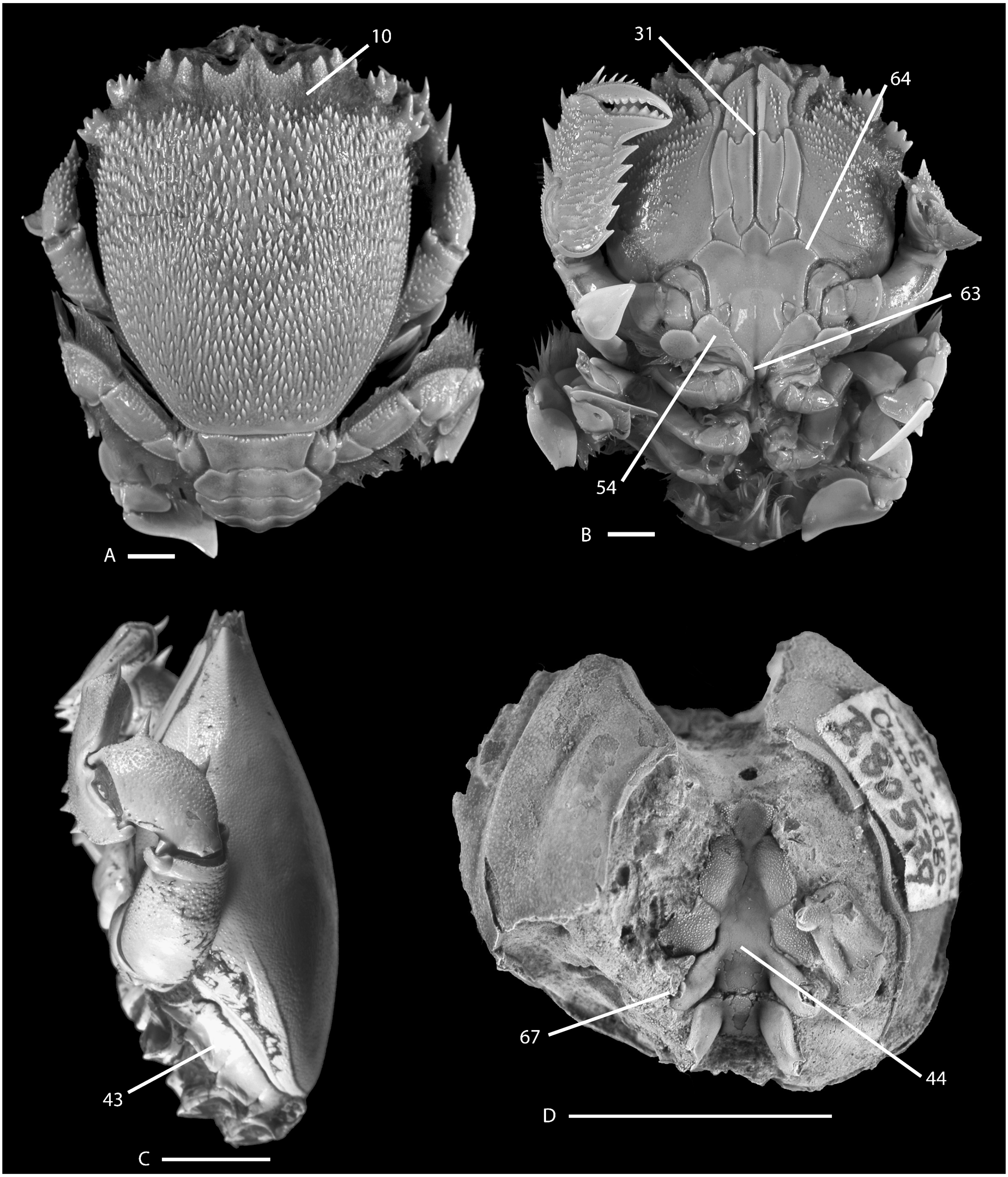

Fig. 1. Illustration of selected character states. A-B, *Ranina ranina* (Linnaeus, 1758), USNM 2044, 10 = postfrontal depression, 31 = oxystomatous condition, 54 = sternite 5 with foliaceous extension, 63 = median line on sternites, 64 = sternum and pterygostome junction present; C, *Lyreidus tridentatus* De Haan, 1841, MFM, 43 = pleurites exposed laterally; D, *Necrocarcinus labeschei* Eudes-Deslongchamps, 1835, SM B 80539, 44 = sterno-pleonal depression, 67 = sternite with double-peg pleonal locking system. Scale bars = 1 cm.

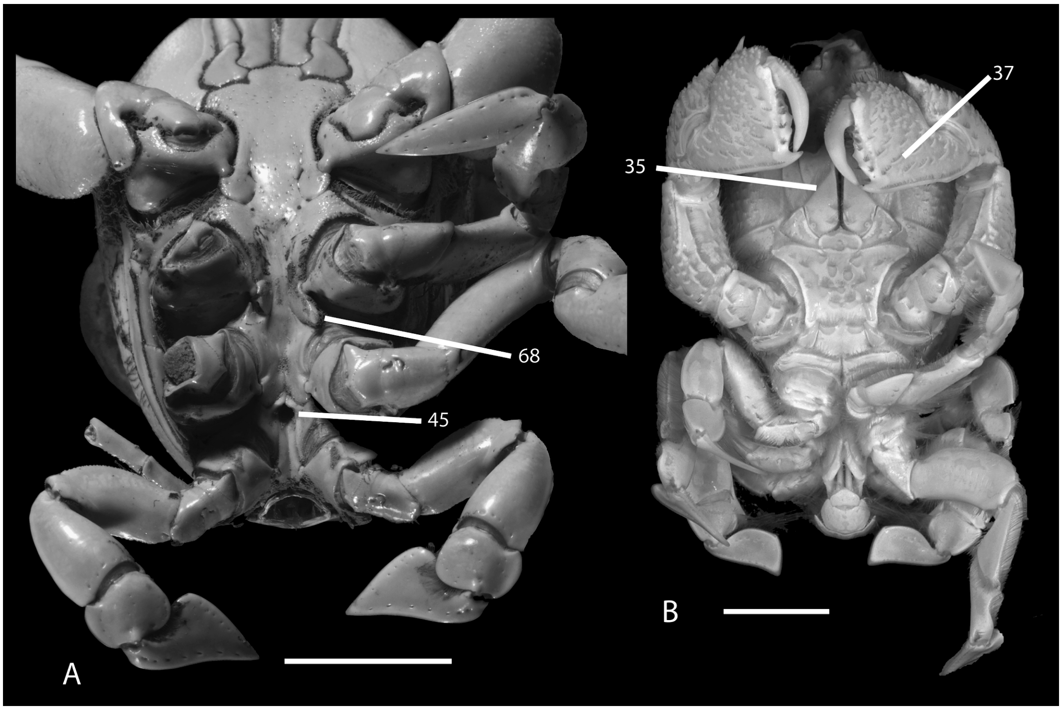

Fig. 2. Illustration of selected character states. A, *Lyreidus tridentatus* De Haan, 1841, MFM 192111, 45 = spermatheca opening on endosternite 7/8, 68 = sternite with lyreidid hook; B, *Ranilia muricata* H. Milne Edwards, 1837 [in 1834-1840], USNM unnumbered, 35 = oblique crest on ischium of third maxilliped, 37 = notodopine-type chela. Scale bars = 1 cm.

common ancestor than necrocarcinoideans + palaeocorystoideans.

Necrocarcinoidea New Status (Clade 2).—The first branching Clade 2 (Camarocarcinidae + Cenomanocarcinidae + Orithopsidae + Necrocarcinidae), is the sister group to the clade formed by Palaeocorystidae and Raninoidea. This clade is supported by Bremer support of 4 and 89% Jackknife support, and is well united by six unambiguous characters: the carapace about as long as wide (1-1), a narrow fronto-orbital margin (11-0), presence of the epibranchial ridge (15-1), presence of a well developed epibranchial spine (27-2), a well defined junction between anterolateral and posterolateral margins (28-1), and the presence of spines on the posterolateral margins (29-1). The well-defined junction between anterolateral and posterolateral margins and the presence of spines on posterolateral margins are unique and never reversed. Van Bakel et al. (2012) and Guinot et al. (2013) assumed that the double peg system on thoracic sternite 5, acting as a pleonal locking mechanism, is a diagnostic trait to warrant the monophyly of Palaeocorystoidea. However, the presence of double peg pleonal locking mechanisms are not present in the most derived raninoidans, indicating that this might represent the plesiomorphic condition for Raninoida, and not a synapomorphy that would support the presumed monophyletic status of Palaeocorystoidea *sensu* van Bakel et al. (2012) and Guinot et al. (2013).

Camarocarcinidae (Clade 3) is recovered as sister taxon to Clade 4 (Cenomanocarcinidae + (Orithopsidae + Necrocarcinidae)). Karasawa et al. (2011) recognized Camarocarcinidae as the first branching lineage within Raninoida. Van Bakel et al. (2012) and Guinot et al. (2013) placed it in Palaeocorystoidea. Under maximum parsimony, such phylogenetic affiliation is not supported, deeming Palaeocorystoidea as paraphyletic. Camarocarcinidae is herein recovered as a monophyletic family, constituted by the terminals *Camarocarcinus* and *Cretacocarcinus*, and mainly united by the strongly raised episternites (47-1). *Cretacocarcinus* was originally placed in Camarocarcinidae (Feldmann et al., 2008) while van Bakel et al. (2012) included it within Necrocarcinidae.

Clade 4 (Cenomanocarcinidae + (Orithopsidae + Necrocarcinidae)) is united by the presence of a longitudinal median carina (13-1) and the longitudinal branchial ridges (16-1), the latter being unique among raninoidans. Orithopsidae is sister taxon to Necrocarcinidae (Clade 6), and they are only united by the presence of the branchial groove. Orithopsidae was originally placed in Dorippoidea MacLeay, 1838 (Schweitzer et al., 2003). De Grave et al. (2009) and Schweitzer et al. (2010) followed their opinion. Therefore, Karasawa et al. (2011) excluded Orithopsidae from their analysis. Guinot et al. (2008) and Vega et al. (2010) noted that Orithopsidae was closer to Necrocarcinidae and Cenomanocarcinidae than to Dorippoidea. Such systematic proximity was also recognized by others (Vega et al., 2010; van Bakel et al., 2012; Guinot et al., 2013), although in those works the three genera were included in the paraphyletic Palaeocorystoidea. The present analysis supports the recognition of Orithopsidae within the monophyletic Necrocarcinoidea instead of Palaeocorystoidea.

Necrocarcinidae (Clade 8) is supported by a single character, the strongly raised episternites (47-1). *Hadrocarcinus* is derived as the sister terminal to the remaining

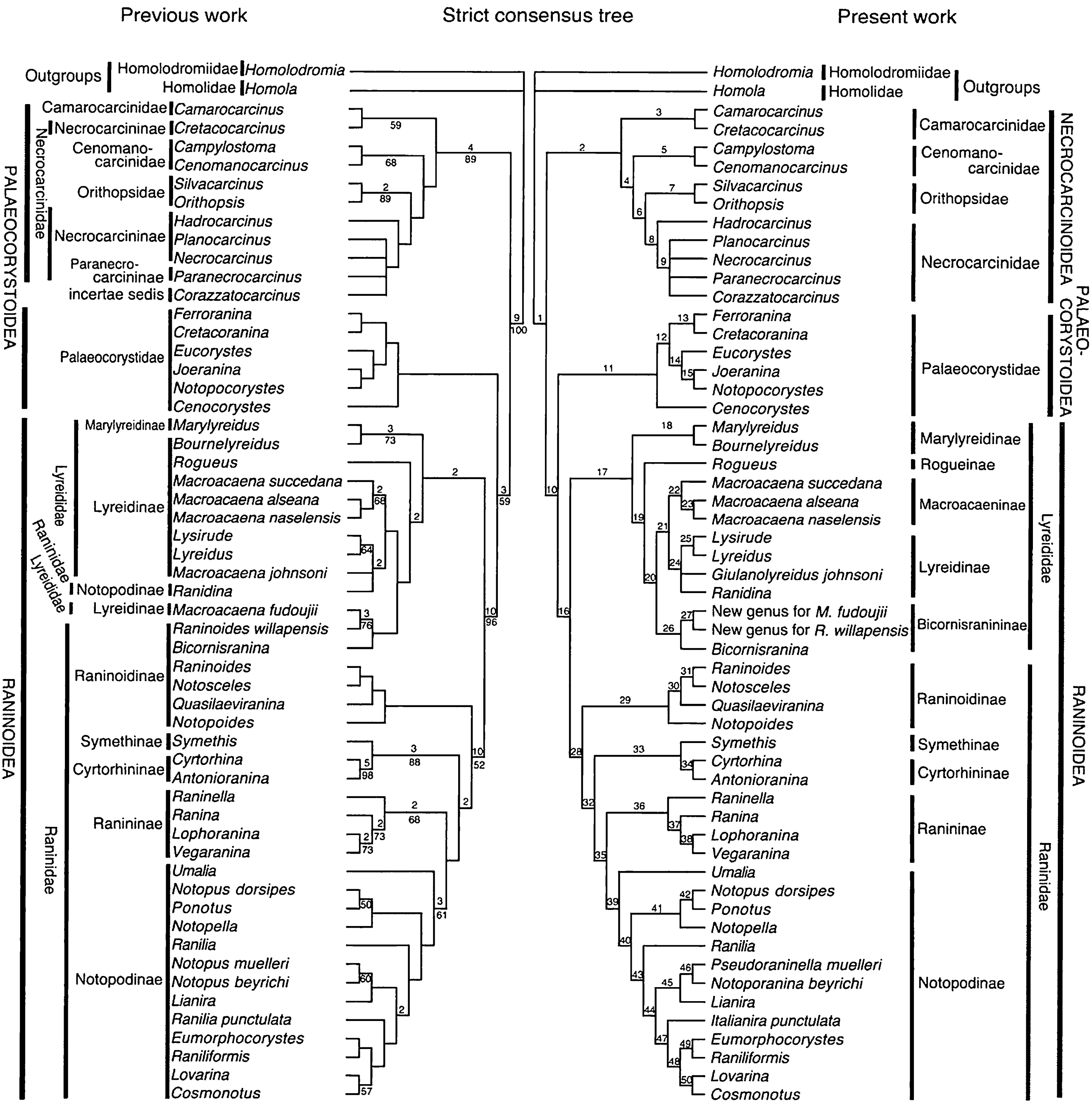

Fig. 3. Strict consensus tree of two most parsimonious trees (TL = 180 steps, CI = 0.5444, RI = 0.9045, RC = 0.4925). Left tree showing Bremer support exceeding 1 indicated above each branch, and Jackknife support exceeding 50% indicated below each branch. Classification was followed by van Bakel et al. (2012), Luque et al. (2012), and Schweitzer et al. (2012). Right tree indicating clade numbers, detailed in Table 3. Classification presented on right tree is that as revised by the present analysis.

four necrocarcinid genera, *Corazzatocarcinus*, *Necrocarcinus*, *Planocarcinus*, and *Paranecrocarcinus*, which lie in a soft polytomy and share the possession of a weak epibranchial spine (27-1). *Corazzatocarcinus* was first included within Necrocarcinidae by Larghi (2004), a placement also followed by later authors (De Grave et al., 2009; Schweitzer et al., 2010). Van Bakel et al. (2012) regarded the genus as Palaeocorystoidea *incertae sedis*. Additionally, Fraaije et al. (2008), van Bakel et al. (2012) and Števčić (2013) recognized two subfamilies within Necrocarcinidae, i.e., Necrocarcininae and Paranecrocarcininae. Our analysis shows that *Corazzatocarcinus* is a member of Necrocarcinidae, and although the separate status of Paranecrocarcininae is not supported by the present analysis due to the unresolved soft polytomy, it is possible that there are more than two subclades within Necrocarcinidae. Future phylogenetic analyses at the species level are necessary to test this hypothesis.

Table 3. Clade numbers as mapped onto Fig. 4 with their unambiguous character state changes for each number.

1 (Raninoida). 8: 0->1, 17: 0->2, 18: 0->2, 19: 0->1, 20: 0->1, 24: 0->2, 31: 0->1, 46: 0->1, 72: 0->1
2 (Chamarocarcinidae + Cenomanocarcinidae + Orithopsidae + Necrocarcinidae). 1: 0->1, 11: 1->0, 15: 0->1, 27: 0->2, 28: 0->1, 29: 0->1
3 (Camarocarcinidae). 47: 0->1
4 (Cenomanocarcinidae + Orithopsidae + Necrocarcinidae). 13: 0->1, 16: 0->1
5 (Cenomanocarcinidae). 48: 0->1, 49: 0->1
6 (Orithopsidae + Necrocarcinidae). 14: 0->1
7 (Orithopsidae). 9: 1->0, 29: 1->0, 31: 1->0
8 (Necrocarcinidae). 47: 0->1
9 (*Corazzatocarcinus* + *Planocarcinus* + *Necrocarcinus* + *Paranecrocarcinus*). 27: 2->1
10 (Palaeocorystidae + Lyreididae + Raninidae). 2: 0->1, 6: 1->0, 38: 0->1, 39: 0->1, 48: 0->1, 49: 0->1
11 (Palaeocorystidae). 27: 0->1, 33: 0->1
12 (*Ferroranina* + *Cretacoranina* + *Eucorystes* + *Notopocorystes* + *Joeranina*). 46: 1->0
13 (*Ferroranina* + *Cretacoranina*). 12: 0->1
14 (*Eucorystes* + *Notopocorystes* + *Joeranina*). 14: 0->1, 15: 0->1
15 (*Notopocorystes* + *Joeranina*). 13: 0->1
16 (Raninoidea: Lyreididae + Raninidae). 7: 0->1, 8: 1->2, 12: 0->1, 24: 2->1, 34: 0->1, 42: 0->1, 43: 0->1, 45: 0->1, 55: 0->1, 60: 0->1, 62: 0->1, 64: 0->2
17 (Lyreididae). 32: 0->1, 68: 0->1
18 (*Marylyreidus* + *Bournelyreidus*). 2: 1->0, 50: 0->1
19 (*Rogueus* + *Macroacaena* spp. + *Bicornisranina* + *Ranidina* + *Lysirude* + *Lyreidus* + *Raninoides willapensis*). 20: 1->0, 26: 1->2
20 (*Macroacaena* spp. + *Raninoides willapensis* + *Ranidina* + *Lysirude* + *Lyreidus*). 9: 2->0, 21: 1->2
21 (*Macroacaena succedana* + *Macroacaena alseana* + *Macroacaena naselensis* + *Macroacaena johnsoni* + *Ranidina* + *Lysirude* + *Lyreidus*). 11: 1->0, 17: 2->1, 71: 0->1
22 (*Macroacaena succedana* + *Macroacaena alseana* + *Macroacaena naselensis*). 24: 1->2
23 (*Macroacaena naselensis* + *Macroacaena alseana*). 4: 0->1
24 (*Macroacaena johnsoni* + *Ranidina* + *Lysirude* + *Lyreidus*). 19: 1->0, 26: 2->1
25 (*Lysirude* + *Lyreidus*). 2: 1->0
26 (*Macroacaena fudoujii* + *Raninoides willapensis* + *Bicornisranina*). 20: 0->2
27 (*Macroacaena fudoujii* + *Raninoides willapensis*). 4: 0->1, 13: 0->1
28 (Raninidae). 36: 0->1, 44: 0->1, 51: 0->1, 53: 0->1, 56: 0->2, 59: 0->1, 61: 0->1, 65: 0->1, 70: 0->1, 72: 1->0
29 (Raninoidinae). 58: 0->1
30 (*Raninoides* + *Quasilaeviranina* + *Notosceles*). 9: 1->0
31 (*Raninoides* + *Notosceles*). 20: 1->2
32 (Symethinae + Cyrtorhininae + Ranininae + Notopodinae). 40: 1->0, 57: 0->1
33 (Symethinae + Cyrtorhininae). 2: 1->0, 11: 1->0, 41: 0->1, 53: 1->2, 64: 2->1
34 (Cyrtorhininae). 9: 1->0, 24: 1->2, 49: 1->2, 50: 0->1, 51: 1->2
35 (Ranininae + Notopodinae). 52: 0->1
36 (Ranininae). 21: 1->2, 24: 1->2
37 (*Ranina* + *Lophoranina* + *Vegaranina*). 3: 0->1, 54: 0->1
38 (*Lophoranina* + *Vegaranina*). 5: 0->1
39 (Notopodinae). 9: 1->0, 35: 0->1, 37: 0->1, 56: 2->1
40 (*Notopus dorsipes* + *Ponotus* + *Notopella* + *Ranilia* + *Notopus muelleri* + *Notopus beyrichi* + *Lianira* + *Ranilia punctutata* + *Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*). 18: 2->0
41 (*Notopus dorsipes* + *Ponotus* + *Notopella*). 20: 1->0
42 (*Notopus dorsipes* + *Ponotus*). 13: 0->1
43 (*Ranilia* + *Notopus muelleri* + *Notopus beyrichi* + *Lianira* + *Ranilia punctutata* + *Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*). 22: 0->1
44 (*Notopus muelleri* + *Notopus beyrichi* + *Lianira* + *Ranilia punctutata* + *Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*). 21: 1->0
45 (*Notopus muelleri* + *Notopus beyrichi* + *Lianira*). 23: 0->1
46 (*Notopus muelleri* + *Notopus beyrichi*). 10: 0->1
47 (*Ranilia punctutata* + *Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*). 20: 1->0
48 (*Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*). 18: 0->1
49 (*Eumorphocorystes* + *Raniliformis*). 23: 0->1
50 (*Lovarina* + *Cosmonotus*). 2: 1->0

Clade 10 (Palaeocorystidae + (Lyreididae + Raninidae)), with Bremer support of 3 and 59% jackknifing support, shares six unambiguous characters: carapace anteriorly widest without dorsal tubercles (2-1, 6-0), wide and flattened pereiopods 2-4 (38-1), a short, wide propodus of pereiopod 4 (39-1), sternite 3 not divided from sternite 4 (48-1), and crown-shaped sternites 3-4 (49-1), of which one (39-1) is unique. Therefore, Palaeocorystoidea is redefined here as a monotypic taxon that only includes the family Palaeocorystidae, and is sister to Raninoidea.

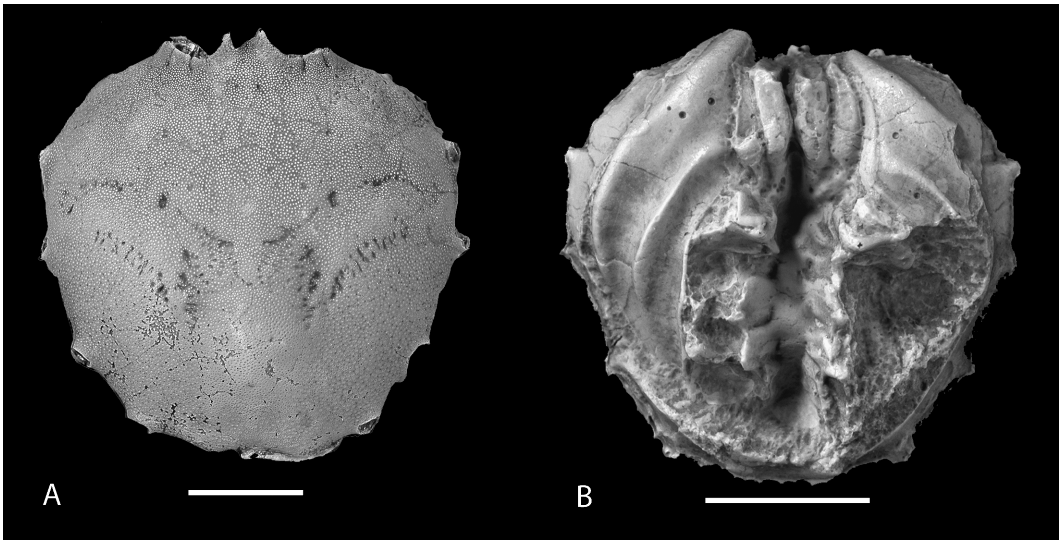

Fig. 4. Camarocarcinidae. A, *Camarocarcinus arnesoni* Holland and Cvancara, 1958, holotype USNM 562093, dorsal carapace; B, *Camarocarcinus quinquetuberculatus* Collins and Rasmussen, 1992, cast of holotype numbered KSU D 762, ventral surface including sternum. Scale bars = 1 cm.

Palaeocorystoidea (Clade 11).—The monophyly of Palaeocorystoidea containing a sole family, Palaeocorystidae, is supported by only two characters: the possession of a faint epibranchial tooth (27-1) and the possession of a longitudinal furrow on the merus of maxilliped 3 (33-1). *Cenocorystes* stands as the sister to the remainder of the palaeocorystoid genera (Clade 12), which are united by the presence of the sterno-coxal depression on the thoracic sternum (46-0). The indistinct branchiocardiac groove unites Clade 13 (*Ferroranina* + *Cretacoranina*). Clade 14 (*Eucorystes* + *Notopocorystes* + *Joeranina*) shares two unambiguous characters, the possession of a branchial groove (14-1) and the possession of an epibranchial ridge (15-1). The presence of a longitudinal median carina (13-1) unites Clade 15 (*Notopocorystes* + *Joeranina*).

Raninoidea (Clade 16).—The monophyly of Raninoidea is well supported by 12 synapomorphies (7-1, 8-2, 12-1, 24-1, 34-1, 42-1, 43-1, 45-1, 55-1, 60-1, 62-1, 64-2). Among these, eight characters are unique and never reversed: the cervical groove not reaching the ventral carapace (8-1); a small, flattened coxa of maxilliped 3 (34-1); a reduced branchiostegite (42-1); the presence of gymnopleurity as exposed pleurites 5-7 (van Bakel et al., 2012; Guinot et al., 2013) (43-1); the spermatheca opening on the endosternite 7/8 (45-1); sternites 5 and 6 with lateral extensions (55-1); raised sternite 7 (60-1); and a complete sternal suture 6/7 (62-1). Bremer support of 10 and Jackknife proportions of 96% strongly support the monophyly of Raninoidea. Brösing et al. (2007) had previously shown the monophyly of Raninidae based upon a foregut-based cladistic analysis.

Guinot (1993) recognized six extant subfamilies under Raninidae: Cyrtorhininae (nom. correct. Tucker, 1998, p. 322; ex Cyrtorhinae Guinot, 1993, p. 1325), Lyreidinae, Notopodinae, Ranininae, Raninoidinae, and Symethinae, a classification followed by other workers (Ng et al., 2008; De Grave et al., 2009). Additionally, Tucker (1998) and Schweitzer et al. (2010) granted Symethinae full family status. Based on a cladistic analysis, Tucker (1998) examined the phylogeny of Raninidae containing all known fossil and extant genera, and included Palaeocorystidae as a subfamily. Within her work *Symethis* was excluded from the analysis because she argued that *Symethis* belonged to its own family Symethidae. She concluded that within Raninidae, the palaeocorystine clade was the most basal, followed by the lyreidine, raninoidine, cyrthorhine, and the most advanced, raninine + notopodine clades. Števčić (2005) only recognized the extant subfamilies Cyrtorhininae, Lyreidinae, Notopodinae, Ranininae, with the tribes Raninini and Raninoidini, and Symethinae, but included Palaeocorystinae. Recently, Karasawa et al. (2011) gave Palaeocorystinae separate family status, and van Bakel et al. (2012) elevated Lyreidinae to a full family. Although Števčić (2013) agreed on the separate family status for the paleocorystids, he retained Lyreidinae as a subfamily within Raninidae, containing the tribes Lyreidinini and Marylyreidinini. Herein, our analysis supports the recognition of the families Lyreididae and Raninidae, the latter containing five subfamilies: Cyrtorhininae, Notopodinae, Ranininae, Raninoidinae, and Symethinae. The topology for the main lineages is consistent with the work of Tucker (1998), but internal relationships among genera are not matched.

Lyreididae (Clade 17).—The lyreidid clade, with Bremer support of 2, shares two unique synapomorphies: the maxilliped 3 merus longer than the ischium (32-1) and sternite 5 with a lyreidid hook (Guinot, 1979) (68-1). The analysis suggests that some taxa should be moved to Lyreididae from Raninidae.

Within Lyreididae, Clade 18 (*Marylyreidus* + *Bournelyreidus*), with Bremer support of 3 and 73% Jackknife support, is the first diverging lineage and shares two characters, a carapace widest portion at mid-length (2-0) and a narrow sternite 4 (50-1). Van Bakel et al. (2012) erected a new subfamily Marylyreidinae with a sole genus *Marylyreidus*. Števčić (2013) did not recognize the validity of the subfamilial status of Marylyreidinae; however, Marylyreidinae is retained based upon our analysis. Additionally, the analysis suggests that *Bournelyreidus* should be moved to Marylyreidinae.

The remainder of the lyreidid clade (Clade 19), with Bremer support of 2, is united by two characters: the absence of the supra-orbital lobe (20-0) and a long, elongate last anterolateral spine (26-2). Within this clade, *Rogueus* is the first branching terminal, sister to Clade 20, which includes the remaining lyreidids. *Rogueus* lacks two ambiguous characters (9-0: a simple tip of the rostrum; 21-2: the well-developed outer orbital spine) that unite Clade 20. Additionally, *Rogueus* exhibits an autapomorphic character, the anterolateral spine with a subspine (25-1). Therefore, a new subfamily should be erected for the sole genus *Rogueus*. Within Clade 20, Clade 26 (*Bicornisranina* + *Macroacaena fudoujii* + *Raninoides willapensis*) was recovered as sister to Clade 21, which includes the most derived lyreidids, i.e., Clade 22 (*Macroacaena succedana* + *Macroacaena alseana* + *Macroacaena naselensis*) and Clade 24 (*Macroacaena johnsoni* + *Ranidina* + *Lysirude* + *Lyreidus*). Only one character, the presence of a single anterolateral spine (24-1), unites Clade 26 (*Bicornisranina* + *Macroacaena fudoujii* + *Raninoides willapensis*). *Bicornisranina* is the sister to the *Macroacaena fudoujii* + *Raninoides willapensis* clade (Clade 26), united by two characters, the coarsely punctuated carapace (4-1) and the possession of a longitudinal median carina (20-1). *Bicornisranina* was originally placed in Raninoidinae (Nyborg and Fam, 2008; Schweitzer et al., 2010; van Bakel et al., 2012). However, this analysis suggests that *Bicornisranina* should be moved to Lyreididae. Additionally, *Macroacaena* is a heterogeneous group and a new genus should be erected for *Macroacaena fudoujii* and *Ranidina willapensis*. The placement of species within *Macroacaena* has been complex. Schweitzer et al. (2002) synonymized *Carinaranina* Tucker, 1998, with *Macroacaena* Tucker, 1998, and transferred most species previously assigned to *Carinaranina* to *Macroacaena* and moved what Tucker (1998) referred to as *Carinaranina willapensis* (originally referred to *Ranidina*) to *Raninoides*. Subsequent workers (Schweitzer et al., 2010; van Bakel et al., 2012) followed their opinions for the placement of *Carinaranina* within *Macroacaena*. *Ranidina willapensis* has been variously placed within *Macroacaena* (Waugh et al., 2009; Schweitzer et al., 2010) and *Raninoides* (van Bakel et al., 2012).

The remainder of Lyreididae (Clade 21) has three unique characters, a relatively narrow fronto-orbital margin (11-0), the possession of a weak inner orbital fissure (17-1), and the possession of pleonal somite 4 with a distinct spine (71-1), being (71-1) unique among raninoidans. However, Clade 26 lacks these unique characters defining Clade 21. Therefore, a new subfamily should be proposed for Clade 26 (*Bicornisranina* + *Macroacaena fudoujii* + *Raninoides willapensis*). Clade 22 (*Macroacaena succedana* + *Macroacaena alseana* + *Macroacaena naselensis*), with Bremer support of 2 and 58% Jackknife support, is defined by the possession of two anterolateral spines (24-2). Only one character, the coarsely punctate carapace (4-1), unites the *Macroacaena naselensis* + *Macroacaena alseana* clade (Clade 23). This clade comprises a species group of *Macroacaena s.s.*, supporting the referral of these species to the genus. Other species included in our analysis must be removed to other genera. Clade 24 (*Macroacaena johnsoni* + *Ranidina* + *Lysirude* + *Lyreidus*), with Bremer support of 2, is derived as the sister to the restricted *Macroacaena* clade and is supported by two characters, the presence of an obsolete intraorbital tooth (19-0) and a short anterolateral spine (26-1). Therefore, the monophyly of Clades 23 and 24 is well supported. The analysis strongly suggests that *Macroacaena s.s.* (Clade 23) represents its own subfamily and that Lyreidinae *s.s.* is restricted here. A *Macroacaena johnsoni* + *Ranidina* + (*Lysirude* + *Lyreidus*) relationship is not resolved. *Macroacaena johnsoni* was originally assigned to *Symethis* (Symethinae) (Rathbun, 1935a) and most subsequent workers (Glaessner, 1969; Schweitzer et al., 2010) agreed with her opinion. However, Armstrong et al. (2009) and van Bakel et al. (2012) transferred the species to *Macroacaena*. The analysis supports that *Macroacaena johnsoni* is a member of Lyreidinae, but suggests that the species should be removed to a separate new genus. Within the previous works (Tucker, 1998; Schweitzer et al., 2010) *Ranidina* was assigned to Notopodinae, while the analysis suggests the subfamilial placement of *Ranidina* under Lyreidinae.

Raninidae (Clade 28).—The monophyly of Raninidae, with Bremer support of 10 and 52% Jackknife support, is well defined by ten unambiguous characters (36-1, 44-1, 51-1, 53-1, 56-2, 59-1, 61-1, 65-1, 70-1, 72-0). Six characters are never reversed: the maxilliped 3 basis fused to the ischium (36-1); the absence of the sterno-pleonal depression (44-1); the extremely narrowed sternite 7 (59-1); a complete sternal suture 5/6 (61-1); the absence of the pleonal locking system (65-1); and the unfolded pleon (70-1).

Clade 29 (Raninoidinae) is unambiguously united by only one character, a wide contact between the sternite 6 and pleurite 6 (58-1). Within the raninoidine clade *Notopoides* is the first branching, followed by *Quasilaeviranina* and the derived, *Raninoides* and *Notosceles*. Števčić (2005) placed the tribe Raninoidini in Ranininae, but the analysis reinforces the subfamilial status of Raninoidinae.

The remainder of Raninidae (Clade 32), with Bremer support of 2, shares two unambiguous characters, a relatively large coxa of pereiopod 5 (40-1) and an extremely narrowed sternite 6 (57-1). A narrow sternite 6 is never reversed. Within this clade Symethinae + Cyrtorhininae (Clade 33) is recovered as the first branching clade, united by five unambiguous characters (2-0, 11-0, 41-1, 53-2, 64-1). Three characters, the strongly modified dactyli of pereiopods 2-4 (40-1), possession of strongly raised sternite 5 (53-2), and a narrow sternum/pterygostome junction (64-1), are never reversed. Bremer support of 3 and Jackknife values of 88% strongly support the monophyly of Symethinae and Cyrtorhininae. Symethinae has five autapomorphic characters: the absence of an inner orbital fissure (17-0), presence of a weak outer orbital fissure (18-1), absence of an inner orbital lobe (19-0), absence of a supra-orbital lobe (20-0), and a clearly defined sternite 3 (48-0). Goeke (1981) established Symethinae with a single genus *Symethis*; Guinot (1993), Davie (2002), Ahyong et al. (2007), Ng et al. (2008), De Grave et al. (2010), van Bakel et al. (2012) and Guinot et al. (2013) concurred. However, Tucker (1998), Martin and Davis (2001), Schweitzer et al. (2010), and Karasawa et al. (2011) gave it full family status. Within the phylogenetic analysis Karasawa et al. (2011) examined only three extant raninoid genera, *Ranina*, *Lyreidus* and *Symethis*; therefore, the analysis of Karasawa et al. (2011) resulted in two families, Raninidae and Symethidae. Within the present analysis many representatives of all extant raninoid subfamilies were included, and as a result, Symethidae became one of the subfamilies under Raninidae. Cyrtorhininae is recovered as the sister to Symethinae. The monophyly of the cyrtorhinine clade (Clade 34), with Bremer support of 5 and 98% Jackknife support, is unambiguously united by five characters (9-0, 24-2, 49-2, 50-1, 51-2). Only one character, a strongly convex sternite 4 (51-2), is unique and never reversed.

Clade 35 (Raninidae + Notopodinae) is defined by a single synapomorphy, a V-shaped posterior sternite 5 (52-1). Ranininae (Clade 36), with Bremer support of 2 and 88% Jackknife support, is well supported by two unambiguous characters: the outer orbital spine with well developed lobes (21-2) and the presence of two anterolateral spines (24-2). Within the raninine clade, *Raninella* is the first branching terminal. Tucker (1998) showed, using cladistic analysis, that the genus was the sister to the lyreidine genus *Macroacaena*. However, De Grave et al. (2009), Schweitzer et al. (2010), and van Bakel et al. (2012) assigned it to Ranininae. The analysis supports the subfamilial placement of *Raninella* under Ranininae. Clade 37 (*Ranina* + *Lophoranina* + *Vegaranina*), with Bremer support of 2 and 73% Jackknife support, shares two unambiguous characters, a spinose carapace (3-1) and sternite 5 with a foliaceous extension (54-1), of which one (54-1) is unique and never reversed. *Ranina* is sister to *Lophoranina* and *Vegaranina*. Only one unambiguous character, the carapace with terrace ornamentation (5-1), unites the clade of *Lophoranina* + *Vegaranina* (Clade 38).

Clade 39 (Notopodinae), with Bremer support of 3 and 61% Jackknife support, is united by three unambiguous characters (9-1, 35-1, 37-1, 56-1). The unique and never reversed characters are the ischium of maxilliped 3 with an oblique crest (35-1), the presence of the Notopodine chela (37-1), and a nearly flattened sternite 6 (56-1). Števčić (2005) recognized two tribes, Notopodini and Cosmonotini, under Notopodinae. However, *Cosmonotus*, the type genus of Cosmonotini, is placed in the most advanced clade and is sister to *Lovarina*. When Cosmonotini is regarded as a valid rank, other notopodine relationships become paraphyletic. Therefore, Števčić's subdivisions are rejected here. *Umalia* stands as the sister to the remaining notopodines (Clade 40), united by the absence of the outer orbital fissure (18-0). *Notopus dorsipes*, *Ponotus*, and *Notopella* (Clade 41), a second diverse group, share the unambiguous absence of a supra-orbital spine (20-0). *Notopella* stands as the sister to *Notopus dorsipes* + *Ponotus* clade (Clade 43). *Notopella*, a monotypic genus, was sometimes synonymized with *Ranilia* (Müller and Collins, 1991; Waugh et al., 2009; Schweitzer et al., 2010). The present analysis recognizes it as a valid genus. Clade 43 (*Ranilia* + *Notopus muelleri* + *Notopus beyrichi* + *Lianira* + *Ranilia punctulata* + *Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*) is defined by only one character, an oblique upper orbital margin (22-1). *Ranilia* is sister to the remainder of Notopodinae (Clade 44) united by one unambiguous character, the absence of a clearly defined outer orbital lobe (21-0). Clade 45 (*Notopus muelleri* + *Notopus beyrichi* + *Lianira*) shares one unambiguous character, the supra-orbital and outer orbital margins forming a loop (23-1). *Lianira* stands as sister to *Notopus muelleri* and *Notopus beyrichi*, sharing the presence of a postfrontal depression (10-1). The analysis suggests the polyphyly of *Notopus* based upon examination of three species. Herein, we restrict the monotypic genus *Notopus* to a single species, *Notopus dorsipes*. Schweitzer et al. (2010) synonymized *Pseudoraninella* with *Eumorphocorystes*, and van Bakel et al. (2012) synonymized *Pseudoraninella* with *Notopus*, transferring *Pseudoraninella muelleri* to *Notopus*. Since Bittner (1875) originally described *Notopus beyrichi*, subsequent workers (Schweitzer et al., 2010; van Bakel et al., 2012) have accepted that generic status for it. However, Lörenthey *in* Lörenthey and Beurlen (1929) erected a new monotypic genus *Notoporanina* for *N. beyrichi* but *Notoporanina* was considered a junior synonym of *Notopus* by Glaessner (1969). The present analysis suggests the validity of the two genera, *Pseudoraninella* and *Notoporanina*, which we reestablish herein.

Clade 47 (*Ranilia punctulata* + *Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*) is defined by the absence of the supra-orbital lobes or spines (20-1). A weak outer orbital fissure (18-1) unites the most derived Clade 48 (*Eumorphocorystes* + *Raniliformis* + *Lovarina* + *Cosmonotus*) within the notopodine clade. *Ranilia punctulata* has been known as the oldest fossil record of *Ranilia* (Beschin et al., 1988; Beschin et al., 2007). However, the analysis shows that *Ranilia punctulata* is the sister to *Eumorphocorystes*, *Raniliformis*, *Lovarina*, and *Cosmonotus*. Therefore, a new genus should be erected for *Ranilia punctulata*.

Classification

As a result of the above analysis, we propose the following higher-level classification for Raninoida crabs as shown on Fig. 3 (right). A species level version is provided in Table S2 in the supplementary material in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x.

Section Raninoida Ahyong et al., 2007
Superfamily Necrocarcinoidea Förster, 1968
    Camarocarcinidae Feldmann, Li, and Schweitzer, 2008
    Cenomanocarcinidae Guinot, Vega, and van Bakel, 2008
    Necrocarcinidae Förster, 1968
    Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003
Superfamily Palaeocorystoidea Lőrenthey *in* Lőrenthey and Beurlen, 1929
    Palaeocorystidae Lőrenthey *in* Lőrenthey and Beurlen, 1929
Superfamily Raninoidea De Haan, 1839
    Lyreididae Guinot, 1993
    Raninidae De Haan, 1839

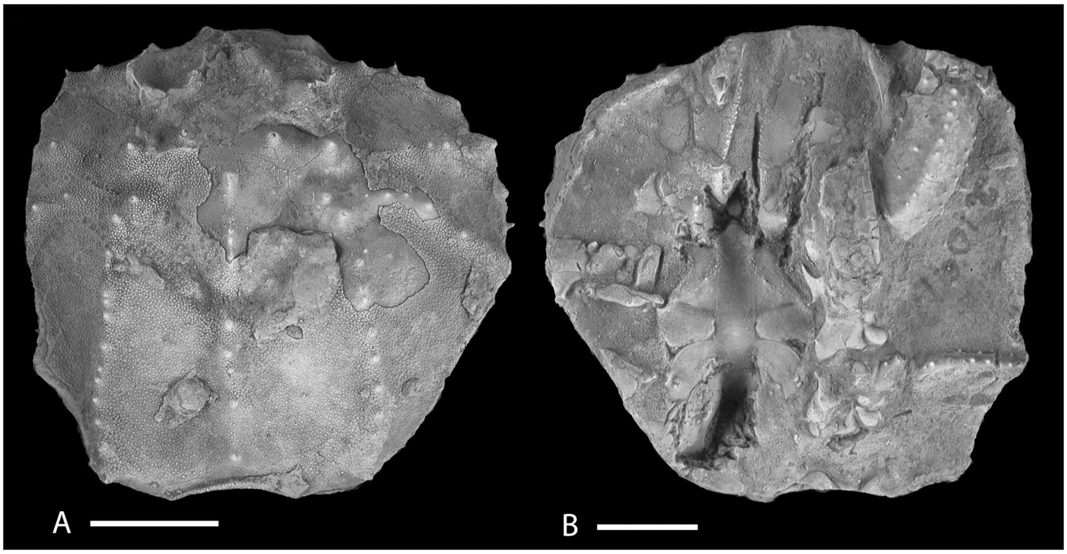

Fig. 5. Cenomanocarcinidae, *Cenomanocarcinus vanstraeleni* Stenzel, 1945, syntype UT 21091, dorsal carapace (A) and ventral surface including sternum and some elements of pereiopods (B). Scale bars = 1 cm.

Systematics

Section Raninoida Ahyong et al., 2007

Diagnosis.—Elongate or equidimensional brachyurans, usually vaulted transversely; regions generally poorly defined; cervical groove ending at pleural suture. Inner orbital and outer orbital grooves well developed; intra- or inner orbital and supra-orbital lobes or spines present; anterolateral spines generally present. Mouthparts taper anteriorly (oxystomatous condition). No sterno-pleonal cavity, elongate pleonal somite 6. Pleon narrow in males and females with reduced but clear dimorphism. Genital openings coxal; spermatheca present.

Included Superfamilies.—Necrocarcinoidea Förster, 1968; Palaeocorystoidea Lőrenthey *in* Lőrenthey and Beurlen, 1929; Raninoidea De Haan, 1839.

Remarks.—The plexus of eight characters in the present analysis reaffirm the conclusion of numerous recent studies, cited above, that Raninoida is monophyletic.

Superfamily Necrocarcinoidea Förster, 1968
Figs. 4-8

Included Families.—Camarocarcinidae Feldmann, Li, and Schweitzer, 2008; Cenomanocarcinidae Guinot, Vega, and Van Bakel, 2008; Necrocarcinidae Förster, 1968; Orithopsi-

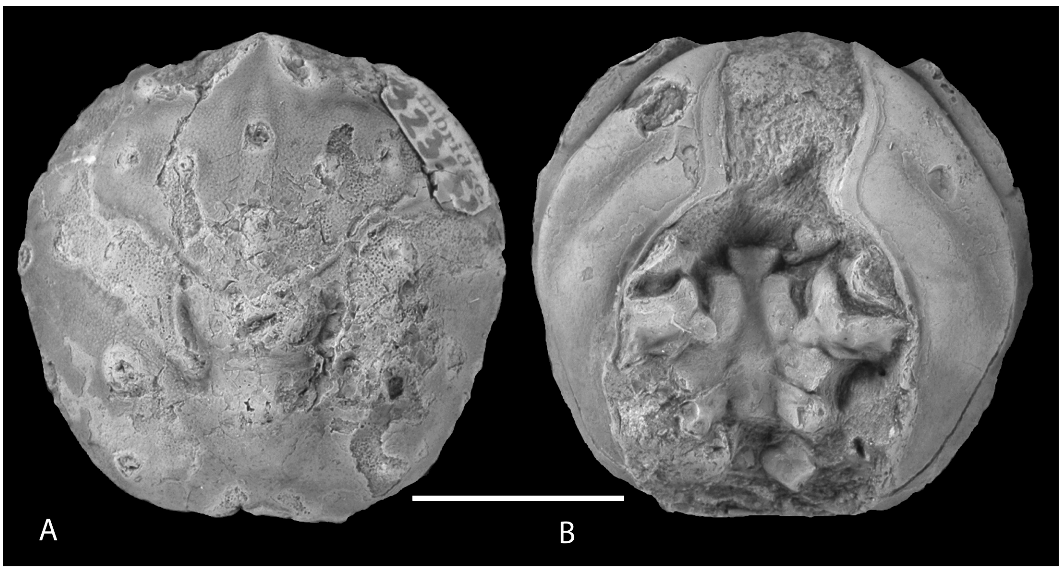

Fig. 6. Necrocarcinidae, *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835), SM B 23152, dorsal carapace (A) and ventral surface including sternum (B). Scale bar = 1 cm.

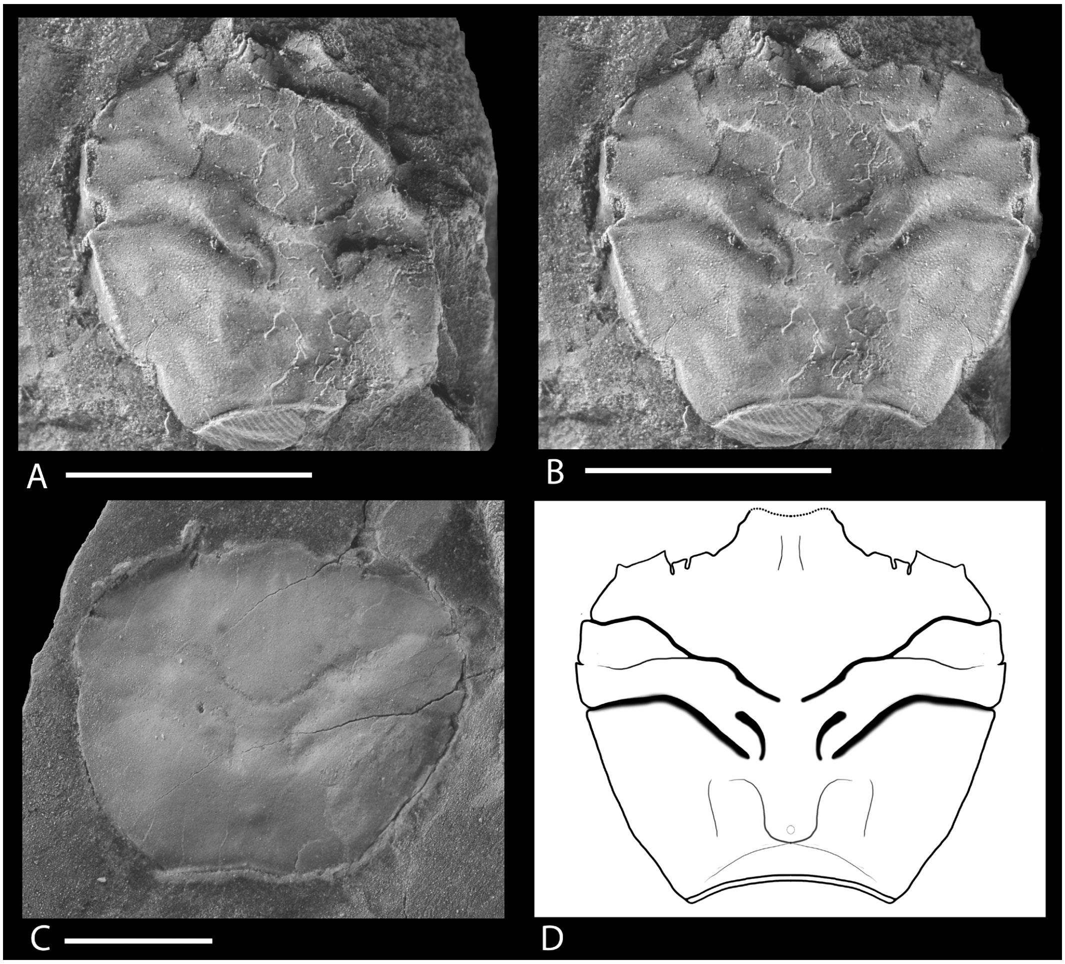

Fig. 7. Necrocarcinidae, *Colombicarcinus laevis* new genus, new species. A, Holotype IGM p881167, partial dorsal carapace of female showing orbital fissures and wide posterior margin; B, reconstruction of holotype; C, paratype IGM p881105, male, showing narrower posterior margin; D, line drawing reconstruction based upon both specimens. Scale bars = 5 mm.

dae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003.

Diagnosis.—Carapace about as wide as long or wider; fronto-orbital margin usually narrow (except Orithopsidae), orbits with 2 fissures; epibranchial ridge and well-developed epibranchial spine present; branchial ridges present, tubercular or granular (except Camarocarcinidae (16-1)); anterolateral and posterolateral margins well-differentiated; both anterolateral and posterolateral margins with spines; sternum narrow, flattened axially, sternites 1-3 fused, sternite 4 longer than wide, pleonal locking mechanism composed of double peg where known, pleonal somites free, may have axial spines; pereiopod 5 and sometimes 4 reduced in size.

Camarocarcinidae Feldmann, Li, and Schweitzer, 2008
Fig. 4

Included Genera.—*Camarocarcinus* Holland and Cvancara, 1958; *Cretacocarcinus* Feldmann, Li, and Schweitzer, 2008.

Diagnosis.—Carapace nearly circular in outline, length about 96% maximum width, strongly vaulted transversely and longitudinally. Front narrow, sulcate, downturned, with axial projection and two smaller lateral spines. Orbits directed forward, deepest axially; upper margin of orbits quadrate to circular, rim flared upward, with two orbital fissures; orbits elevated on carapace well above anterolateral margin; fronto-orbital width ranging from 25% to 40% maximum carapace width. Anterolateral and posterolateral margins with spines. Branchiocardiac groove defined by row of obliquely directed, elongate pits; cervical groove less strongly developed to obscure; branchial ridges absent. Cuticle with endocuticular pillars extending up to or through exocuticle surface; cuticle surface nearly smooth to granular.

Third maxillipeds much longer than wide, oriented in two planes, one nearly perpendicular to dorsal surface of carapace, other parallel to ventral surface of carapace; sternum very narrow, sternal elements flattened axially, nearly vertical laterally (Karasawa et al., 2011, p. 550).

Remarks.—Our analysis reiterates the finding of Karasawa et al. (2011) that the family is distinctive and composed of the two referred genera. Inclusion of more Raninoida taxa in the analysis places Camarocarcinidae within Necrocarcinoidea instead of as sister to the remainder of the raninoidans. Van Bakel et al. (2012) moved *Cretacocarcinus*

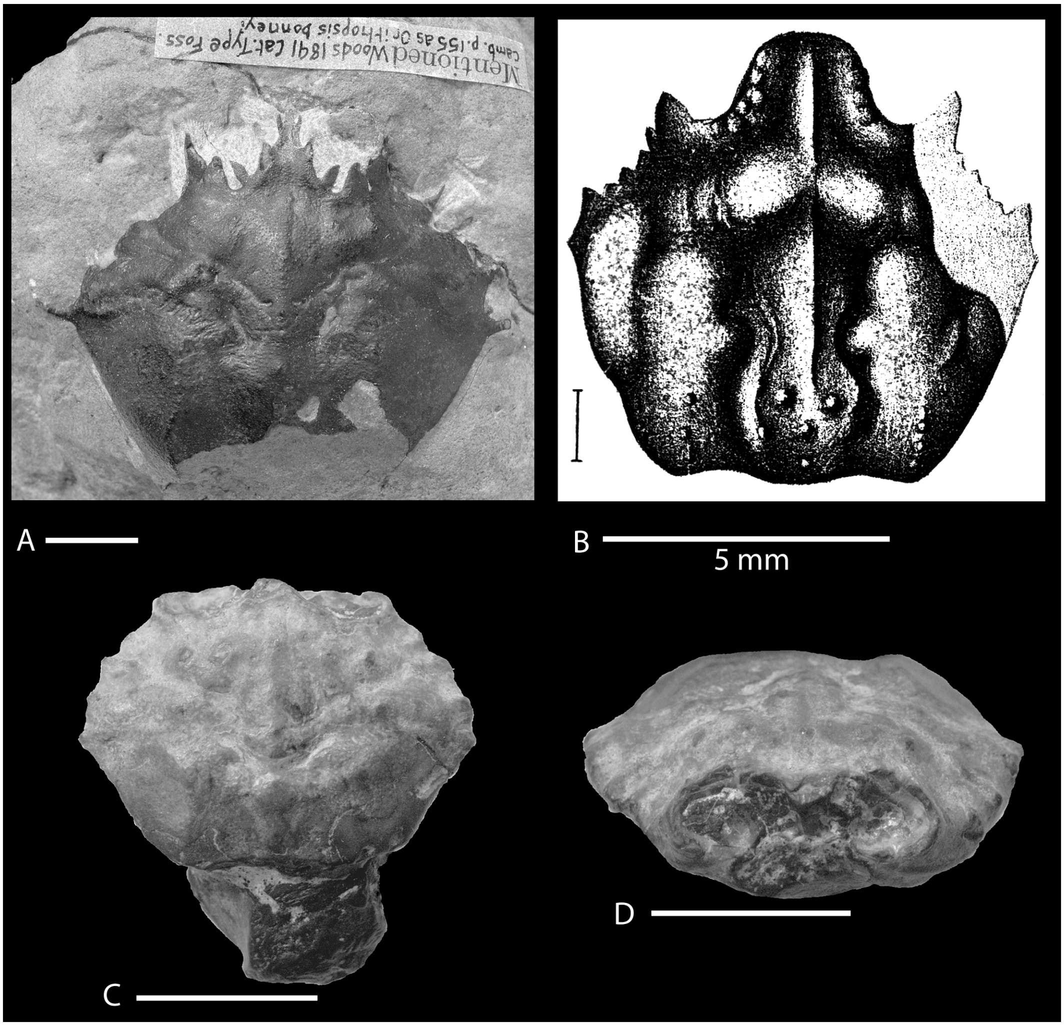

Fig. 8. Orithopsidae. A, *Orithopsis bonneyi* Carter, 1872, holotype SM B 58557; B, *Paradoxilissopsa transiens* (Frič and Kafka, 1887), digital image Frič and Kafka (1887: pl. 10, Fig. 7a); C-D, *Orithopsis tricarinata* Bell, 1863, SM B 23259, dorsal view (C) and anterior view (D). Scale bars = 1 cm except B.

to the Necrocarcinidae, but our analysis clearly allies *Camarocarcinus* and *Cretacocarcinus* as distinct from that family.

Camarocarcinus Holland and Cvancara, 1958
Fig. 4

Type Species.—*Camarocarcinus arnesoni* Holland and Cvancara, 1958, by original designation.

Other Species.—*Camarocarcinus obtusus* Jakobsen and Collins, 1979; *C. quinquetuberculatus* Collins and Rasmussen, 1992.

Diagnosis.—Carapace about as wide as long, narrowing posteriorly, widest at about midlength; rostrum narrow, deflexed, sulcate; orbits directed forward, with two fissures; anterolateral and posterolateral margins confluent, armed with four discrete, long, forward-curved spines; remainder of margins smooth; regions very poorly developed; cervical and branchiocardiac grooves well defined; chelipeds isochelous.

Material Examined.—*Camarocarcinus arnesoni*, UND 705, 710, 711; *C. quinquetuberculatus* Collins and Rasmussen, 1992, cast of holotype specimen numbered KSU D 762.

Range.—Paleocene.

Cretacocarcinus Feldmann, Li, and Schweitzer, 2008

Type Species.—*Cretacocarcinus smithi* Feldmann, Li, and Schweitzer, 2008, by original designation.

Diagnosis.—Carapace nearly circular in outline, length about 96% maximum width, carapace width widest about 40% the distance posteriorly, strongly vaulted transversely and longitudinally. Front narrow, sulcate, downturned, with axial projection and two smaller lateral spines. Orbits directed forward and upward, orbits deepest axially; upper margin of orbits quadrate to circular, rim flared upward, with two orbital fissures; orbits elevated on carapace well above anterolateral margin; fronto-orbital width great for family, about 46% maximum carapace width. Spines present on both anterolateral and posterolateral margins. Branchiocardiac groove defined by row of obliquely directed, elongate pits; cervical groove well developed, nearly as strong as branchiocardiac groove. Carapace ornamented with nodes and spines, not arrayed in rows. Cuticle with endocuticular pillars extending up to or through exocuticle surface; cuticle surface nearly smooth to granular. Pterygostomial region with stridulating ridge. Third maxillipeds much longer than wide, oriented in two planes, one nearly perpendicular to dorsal surface of carapace, other parallel to ventral surface of carapace; sternum very narrow, sternal elements flattened axially, nearly vertical laterally (Feldmann et al., 2008, p. 1747).

Material Examined.—*Cretacocarcinus smithi* Feldmann, Li, and Schweitzer, 2008, holotype, Manitoba Museum I-4077, Winnipeg, Manitoba, Canada.

Range.—Campanian.

Cenomanocarcinidae Guinot, Vega, and Van Bakel, 2008
Fig. 5

Included Genera.—*Campylostoma* Bell, 1858; *Cenomanocarcinus* van Straelen, 1936; *Hasaracancer* Jux, 1971.

Diagnosis.—Carapace hexagonal to rounded; wider than long; orbits closely spaced, with two fissures; rostrum projected weakly beyond orbits, with five spines; anterolateral margins spinose; posterolateral margins with one or two spines; carapace moderately vaulted transversely and longitudinally; cervical and branchiocardiac grooves weak; carapace bearing longitudinal ridges ornamented with tubercles; maxillipeds very long; male sternum ovate, broadly concave; sternites 1-3 fused, forming a triangular shape; sternite 4 trapezoidal, longer than wide, with projections extending from anterior end, pereiopod 1 articulating from concavity at about midlength; sternal suture 4/5 deep, concave posteriorly laterally, becoming straight and oriented parallel to axis of animal axially; sternite 5 wider than long, articulating with pereiopod 2, with two tubercles on each side probably serving to hold pleon in place, directed posterolaterally; sternite six inclined at moderate angle to remainder of sternum; sternites 7 and 8 unknown; sternal sutures 5/6 and 6/7 complete; pleon of male moderately wide, telson much longer than wide, somites 5 and 6 with three spines, one axial and one on each side; pereiopod 5 much reduced in size (Karasawa et al., 2011, p. 550).

Range.—Early Cretaceous (Albian)-Eocene (Ypresian, ?Priabonian).

Campylostoma Bell, 1858

Type and Sole Species.—*Campylostoma matutiforme* Bell, 1858, by monotypy.

Diagnosis.—Carapace about as long as wide, ovate, weakly vaulted transversely and longitudinally; front narrow, bifid, axially sulcate, with a large node at the base on either side; orbits elongate-oval, directed antero-dorsally, upper margin with blunt intra-orbital spine and outer orbital spine, lower orbital margin with suborbital spine, entire suborbital margin visible dorsally; fronto-orbital width about half maximum carapace width. Anterolateral margin with four spines excluding outer orbital spine; first two directed anterolaterally; third directed laterally; last one largest, directed posterolaterally; posterolateral margin nearly straight; posterior margin narrow, rimmed, concave.

Material Examined.—*Campylostoma matutiforme* Bell, 1858, SM C19125-7, (BMNH) 35231, I.7314, In. 29083, 32654-55, 41726.

Range.—Eocene (Ypresian, ?Priabonian).

Cenomanocarcinus van Straelen, 1936
Fig. 5

Sagittoformosus Bishop, 1988b, p. 379.

Type Species.—*Cenomanocarcinus inflatus* van Straelen, 1936, by monotypy.

Other Species.—*Cenomanocarcinus? armatus* (Rathbun, 1935a); *C. beardi* Schweitzer, Feldmann et al., 2003; *C. cantabricus* van Bakel et al., 2012; *C. carabus* (Bishop, 1988b); *C. disimmilis* Collins, 2010; *C. hierosolymitanus* Avnimelech, 1961; *C. multituberculatus* (Joleaud and Hsu, 1935); *C. nammourensis* Beschin and de Angeli, 2013; *C. oklahomensis* (Rathbun, 1935a); *C. robertsi* Feldmann et al., 2013; *C. siouxensis* (Feldmann et al., 1976); *C. tenuicarinatus* Collins, 2010; *C. vanstraeleni* Stenzel, 1945; questionably *C. renfroae* (Stenzel, 1945).

Diagnosis.—Carapace ovate or hexagonal, wider than long; two orbital fissures; rostrum sulcate, downturned, usually with trifid tip; tubercles of carapace arranged in ridges; three longitudinal ridges, one axial and one on each branchial region; two transverse gastric ridges.

Material Examined.—*Cenomanocarcinus beardi*, GSC 124820, holotype, GSC 12481, paratype; *Cenomanocarcinus robertsi*, holotype NJSM 23309, paratype NJSM 23310; *Cenomanocarcinus vanstraeleni*, UT 21079, 21090, and 21091 (syntypes); *Necrocarcinus siouxensis*, holotype USNM 218090; *Necrocarcinus oklahomensis*, holotype USNM 73713; *Sagittiformosus carabus*, holotype USNM 418277.

Remarks.—We include *Cenomanocarcinus siouxensis* within the genus, following Schweitzer et al. (2003, 2010); van Bakel et al. (2012) placed it within *Orithopsis*. This species has the diagnostic branchial and gastric ridges of *Cenomanocarcinus*, which are not present in *Orithopsis*. The flattened sternum, albeit poorly preserved, is typical of Cenomanocarcinidae. Van Bakel et al. (2012) included *Necrocarcinus pierrensis* in *Cenomanocarcinus*; we retain it in *Necrocarcinus* based upon its lack of the transverse gastric ridges diagnostic of *Cenomanocarcinus*. *Cenomanocarcinus vanstraeleni* was reported from the Albian of Colombia (Vega et al., 2010; Bermudez et al., 2013). That specimen seems to be of a somewhat different shape, being much wider than long as compared to the type material of *C. vanstraeleni*; it may be a different species.

Range.—Early Cretaceous (Albian)-Late Cretaceous (Maastrichtian).

Hasaracancer Jux, 1971

Type Species.—*Hasaracancer cristatus* Jux, 1971, by original designation.

Other Species.—*Hasaracancer merijaensis* Ossó, Artal, and Vega, 2011.

Diagnosis.—Carapace as wide as long or slightly longer than wide; cervical groove deep; axial keel with tubercles; two lateral keels; posterolateral margin straight to slightly convex; posterior margin convex; pleonal somites with three large tubercles each; pleurae long, with sharp terminations directed posteriorly.

Material Examined.—*Hasaracancer cristatus*, cast of a cast of holotype BSP 1988 III 147 numbered KSU D 560.

Range.—Late Cretaceous (Campanian).

Necrocarcinidae Förster, 1968
Fig. 6

Included Genera.—*Colombicarcinus* new genus; *Corazzatocarcinus* Larghi, 2004; *Cristella* Collins and Rasmussen, 1992; *Glyptodynomene* van Straelen, 1944; *Hadrocarcinus* Schweitzer et al., 2012; *Necrocarcinus* Bell, 1863; *Paranecrocarcinus* van Straelen, 1936; *Planocarcinus* Luque et al., 2012; *Polycnemidium* Reuss, 1859; *Pseudonecrocarcinus* Förster, 1968; *Shazella* Collins and Williams, 2004; tentatively *Araripecarcinus* Martins-Neto, 1987; new genus, Luque, in press a, b.

Diagnosis.—Carapace circular or ovate, about as long as wide or slightly wider than long, widest at position of last anterolateral spine, moderately vaulted longitudinally and transversely; regions well-defined, usually with longitudinal ridges or rows of tubercles on axial and branchial regions; rostrum narrow, sulcate at tip or with small spines; orbits small, circular, with two fissures, directed forward; inner orbital, intra-orbital, and outer orbital spines well developed; fronto-orbital width typically between 30-45% maximum carapace width but rarely over half in some species; anterolateral margins long, usually with numerous spines; posterolateral margin entire or with spines; cervical and branchiocardiac grooves well developed, usually parallel to one another. Sternum narrow, sternites 1-3 fused and quadrate; anterior portion of sternum at low angles to one another, sternum deep posteriorly, with flanks at high angle to one another, lateral margins raised and granular; sternite 4 long, with widely raised lateral margins, axially deep, episternal projections short, suture 4/5 incomplete; sternal suture 4/5 deep, concave posteriorly laterally, becoming straight and oriented parallel to axis of animal axially; sternite 5 wider than long, articulating with pereiopod 2, directed laterally; sternite 6 similar to sternite 5; sternite 7 directed ventrolaterally; sternite 8 directed ventrolaterally, much smaller than sternite 7; sternal sutures 5/6 and 6/7 complete. All pleonites free, with blunt axial spines, somite 6 much longer than wide, telson long; pereiopods 4 and 5 apparently reduced in size (after Karasawa et al., 2011, p. 551).

Remarks.—Several of the contained genera were not included in the phylogenetic analysis due to a very high percentage of missing characters. Each of these is only known from dorsal carapace material and partial appendage remains. However, each genus exhibits the carapace characters diagnostic of the family; thus, the family composition is the same as in Karasawa et al. (2011) with the addition of two new genera named since then, both of which were included in the analysis (*Hadrocarcinus* and *Planocarcinus*).

Our conception of Necrocarcinidae is quite similar to that of Schweitzer et al. (2010) and Karasawa et al. (2011), but it differs from that of van Bakel et al. (2012). Some of the differences are due to our use of phylogeny based upon parsimony, which grouped *Corazzatocarcinus*, *Hadrocarcinus*, and *Planocarcinus* within the family, none of which were included by van Bakel et al. (2012). The latter two were published at about the same time, accounting for that discrepancy. We also include *Shazella* and *Polycnemidium*, which while incomplete, seem to fit best within the family at this time. We also differ from van Bakel et al. (2012) in not utilizing subfamilies for Necrocarcinidae. A more in-depth analysis at the species level will be necessary to resolve subfamilial relationships within this group.

Range.—Early Cretaceous (Barremian)-Paleocene (Danian).

Corazzatocarcinus Larghi, 2004

Type and Sole Species.—*Geryon hadjoulae* Roger, 1946, by original designation.

Diagnosis.—Carapace ovate, about as wide as long; front projecting slightly beyond orbits, trifid; orbits rimmed, directed forward; anterolateral margins with several short, sharp spines; posterolateral margin with several small spines; axial regions with keel bearing tubercles; protogastric region with central tubercles; epibranchial region with arcuate, tubercled keel connecting to transverse keel at level of cardiac region; oblique arcuate keel extending from cardiac region to posterolateral corner; chelipeds short; pereiopods 2 and 3 long, slender; pereiopods 4 and 5 short, dactyl curved and short; female pleon with straight sides, telson triangular, somites with transverse swellings.

Range.—Late Cretaceous (Cenomanian).

Cristella Collins and Rasmussen, 1992

Type and Sole Species.—*Cristella hastata* Collins and Rasmussen, 1992, by original designation.

Diagnosis.—Carapace hexagonal, about as wide as long; front with long central spine, possibly a smaller spine on either side; orbits deep, closely spaced; orbital margin with several spines; anterolateral margin with at least two spines, last spine (may be equivalent to epibranchial spine) longer than carapace width.

Material Examined.—Cast of holotype and sole specimen of *Cristella hastata*, MGUH 21.611, numbered KSU D 1807.

Remarks.—The genus can be accommodated within Necrocarcinidae based upon its narrow orbits and strongly vaulted carapace. Cenomanocarcinidae and Orithopsidae have a more flattened carapace. The very long spines at the anterolateral corners in this taxon are unusual within the family. Material with a preserved sternum could help verify its family-level placement.

Range.—Paleocene (Danian).

Glyptodynomene van Straelen, 1944

Type Species.—*Glyptodynomene alsasuensis* van Straelen, 1944, by monotypy.

Diagnosis.—Carapace wider than long, hexagonal, vertically high; orbits closely spaced, carapace highly domed over orbits; front downturned between orbits; anterolateral margin flared, rimmed; cervical groove deep, broadly concave forward; postcervical groove deep, discontinuous; protogastric and hepatic regions with marginal, longitudinal swellings; posterior margin broad, rimmed.

Material Examined.—*Glyptodynomene alsasuensis*, cast of MGSB 28130 numbered KSU D 207.

Remarks.—Glaessner (1969) placed *Glyptodynomene* within Dynomenidae Ortmann, 1892. Schweitzer et al. (2010) placed it within Necrocarcinidae followed by van Bakel et al. (2012), although Karasawa et al. (2011) did not consider it a member of the family. The carapace exhibits development of regions quite unlike other members of Necrocarcinidae, but the orbits are small and forward directed and the cervical and post-cervical grooves are well-developed as in members of the family. The orbits seem to lack the two fissures typical of Necrocarcinidae and the carapace lacks the ridges or rows of tubercles diagnostic for the family. Thus, placement within Necrocarcinidae must be considered provisional at this time.

Range.—Late Cretaceous (Cenomanian).

Hadrocarcinus Schweitzer, Feldmann, and Lamanna, 2012

Type Species.—*Hadrocarcinus tectilacus* Schweitzer, Feldmann, and Lamanna, 2012, by original designation.

Other Species.—*Hadrocarcinus carinatus* (Feldmann, Tshudy, and Thomson, 1993); *H. wrighti* (Feldmann, Tshudy, and Thomson, 1993).

Diagnosis.—Carapace about as wide as long, widest about 40% the distance posteriorly on carapace; rostrum trifid, middle spine downturned, outer two spines directed upward; orbits directed anteriorly or axially; fronto-orbital width about 44% maximum carapace width; anterolateral margins set below level of rostrum and orbits, with between 4 and 6 spines excluding outer orbital spine, most appearing to be broad, triangular, last spine long, directed laterally; posterolateral margin with two spines near posterolateral corner; posterior margin narrow, convex; carapace regions very well defined, most ornamented with stout spines; cervical groove deep, sinuous, bounding posterior margins of protogastric and hepatic regions; branchiocardiac groove shallower than cervical groove, bounding posterior margin of epibranchial region; postcervical groove only present as deep lateral margin of metagastric region; chelipeds appearing to be heterochelous at least in terms of length; sternum deep, narrow; sternites 1-3 fused, long sternite 4 with steep lateral sides, deep axially; pleon with axial keel, somite 6 very long (Schweitzer et al., 2012, p. 152).

Material Examined.—*Necrocarcinus carinatus*, cast of holotype BAS In. 2238 numbered KSU D 1016; *N. wrighti*, cast of holotype BAS In. 2237 numbered KSU D 2237, cast of paratype CIRGEO 882 numbered KSU D 1014; *Hadrocarcinus tectilacus*, holotype CM 56700.

Range.—Late Cretaceous (Santonian-Maastrichtian).

Necrocarcinus Bell, 1863
Fig. 6

Type Species.—*Orithya labeschei* Eudes-Deslongchamps, 1835, by subsequent designation of Withers, 1928.

Other Species.—*N. avicularis* Frič and Kafka, 1887 (chelae only); *N. bispinosus* Segerberg, 1900; *N. brodrakensis* Levitski, 1974; *N. davisi* Bishop, 1985; *N. franconicus* Lehner, 1937; *N. inornatus* Breton and Collins, 2011; *N. insignis* Segerberg, 1900; *N. olsonorum* Bishop and Williams, 1991; *N. ornatissimus* Forir, 1887; *N. pierrensis* Rathbun, 1917; *N. rathbunae* Roberts, 1962; *N. senonensis* Schlüter and Von der Marck, 1868; *N. tauricus* Ilyin and Alekseev, 1998; *N. texensis* Rathbun, 1935a; *N. undecimtuberculatus* Takeda and Fujiyama, 1983; *N. woodwardi* Bell, 1863; questionably *N. perlatus* Frič and Kafka, 1887.

Diagnosis.—Carapace ovate, hexagonal, or subquadrate, wider than long; rostrum downturned, weakly projecting beyond orbits, with three or four small spines; orbits round, forward directed, often with intra-orbital and outer orbital spines and two fissures; anterolateral margin with two or more spines; posterolateral margin sometimes with spines; protogastric region well-marked, wider than long; cervical groove deep, sinuous, forms reentrant where it intersects lateral margin; branchiocardiac groove less well-developed; post-cervical groove deep, short, straight across midline, then with segments at each end at nearly right angles to axial segment; axial regions well-marked, cardiac region elongate-ovate; dorsal carapace with large tubercles or spines often arranged into longitudinal rows, sometimes not arranged into rows (Feldmann et al., 2013, p. 22).

Material Examined.—*Necrocarcinus labeschei*, SM B 23152, 23170-83, 23210, B 80539; *Necrocarcinus davisi*, KSU D 1679, 1689; *N. pierrensis*, KSU D 1464, 1472, 1480; *N. rathbunae*, NJSM 9517, 22692-94, 23299, 23300, 23304, 23305, 23311, 23312, 23319, 23320, 23333; *Necrocarcinus texensis*, paratype USNM 75989.

Remarks.—*Necrocarcinus* is quite speciose. Some species have been recently verified as members of the genus (*N. rathbunae*, Feldmann et al., 2013; *N. texensis*, Franţescu, 2013). Specimens of *Necrocarcinus davisi* (KSU D 1679, 1689) and *N. pierrensis* (KSU D 1464, 1472, 1480) exhibit the strong cervical, post-cervical, and branchiocardiac grooves, narrow front, spinose anterolateral margins, and well-marked axial regions diagnostic for the genus. Other species, especially the older European occurrences, probably should be reevaluated.

Range.—Early Cretaceous (Aptian)-Paleocene (Danian).

Paranecrocarcinus van Straelen, 1936

Protonecrocarcinus Förster, 1968, p. 178.

Type Species.—*Paranecrocarcinus hexagonalis* van Straelen, 1936, by monotypy.

Other Species.—*Paranecrocarcinus balla* van Bakel et al., 2012; *P. digitatus* Wright and Collins, 1972; *P. foersteri* Wright and Collins, 1972; *P. graysonensis* (Rathbun, 1935a); *P. kennedyi* Wright, 1997; *P. libanoticus* Förster, 1968; *P.*

milbournei Collins, 2010; *P. moseleyi* (Stenzel, 1945); *P. mozambiquensis* Förster, 1970; *P. ovalis* (Stenzel, 1945); *P. pulchellus* (Secretan, 1964); *P. pusillus* Breton and Collins, 2011; *P. vanbirgeleni* Fraaije, 2002.

Diagnosis.—Carapace ovate, ornamented with large tubercles not arranged in rows, moderately to strongly vaulted longitudinally and transversely; fronto-orbital width broad, orbits rimmed, forward directed; anterolateral margins with few spines, posterolateral margin with 1 spine or entire; protogastric regions with large swellings; epigastric regions with slit-like depressions not extending all the way through the cuticle; epibranchial regions with swellings.

Material Examined.—*Paranecrocarcinus foersteri*, holotype (BMNH) In. 60969; *Dromiopsis pulchellus*, holotype MNHN R03929.

Remarks.—Feldmann et al. (2013) discussed the rationale for maintenance of separation of *Paranecrocarcinus* and *Pseudonecrocarcinus*, which we maintain herein. One of the main bases upon which the two genera were synonymized was the presence of epigastric slit-like depressions in the carapace (Fraaije, 2002); however, we know of at least three genera in which these slits occur. A species level investigation of the Necrocarcinidae might yield a better understanding of the importance of these slit-like depressions.

Range.—Early Cretaceous (Albian)-Late Cretaceous (Cenomanian).

Planocarcinus Luque, Feldmann, Schweitzer, Jaramillo, and Cameron, 2012

Type and Species.—*Dakoticancer olssoni* Rathbun, 1937a, by original designation.

Other Species.—*Planocarcinus johnjagti* Bermudez, Gómez-Cruz, and Vega *in* Bermudez et al., 2013.

Diagnosis.—Carapace subcircular, slightly wider than long; with distinct cervical, postcervical, and branchiocardiac grooves; fronto-orbital margin as long as posterior margin; rostrum bilobate, spatulate, wider than long; orbits narrow, upturned, with two short orbital fissures; anterolateral margin convex, with at least five spines; posterolateral margin convex, entire; posterior margin straight to concave; hepatic region depressed; metabranchial region swollen, lacking nodules or ridges (after Luque et al., 2012).

Material Examined.—*Dakoticancer olssoni*, holotype USNM 495104.

Remarks.—*Planocarcinus johnjagti* seems to differ from the type species of the genus in having a longer carapace, a straighter posterolateral margin, a much more concave posterior margin, and more square orbits. The relationship of that species to the type species should be tested further.

Range.—Early Cretaceous (Aptian).

Polycnemidium Reuss, 1859

Type and Sole Species.—*Dromilites pustulosus* Reuss, 1845, by monotypy.

Diagnosis.—Carapace wider than long, length about three-quarters maximum width, maximum width about at mid-length, flattened transversely and longitudinally; regions defined by swellings. Front downturned, axially keeled; orbits directed forward, lower orbital margin visible in dorsal view, upper orbital margin upturned, outer orbital angle with weak projection; fronto-orbital width about half maximum carapace width. Anterolateral and posterolateral margins confluent, small projections on anterolateral portion, one large projection at point of maximum width; posterior margin with granular rim. Epigastric regions with oblique slit-like depressions not extending through cuticle; mesogastric region long, slender; with prominent axial node posteriorly; metagastric region weakly defined by cervical and concave forward postcervical groove; cardiac region transversely ovoid with central node; intestinal region broad, short. Protogastric region with two tubercles arranged transversely, innermost largest; hepatic region small, triangular, granular. Cervical groove extending from margin anteromesially to inner hepatic region, curving concave-forward around posterior margin of mesogastric region; post-cervical groove short, concave-forward, continuous across axis. Epibranchial region with two small tubercles arrayed in oblique line; mesobranchial region with two prominent tubercles arrayed transversely; metabranchial region uniformly inflated. Entire surface of carapace granular. Buccal frame appearing to be broad, quadrate. Manus of first pereiopod longer than high, outer surface strongly inflated, granular; lower surface nearly straight; articulation with carpus at steep angle to long axis of hand; upper margin short, with triangular flange extending inward almost at right angle, flange rimmed; inner surface smooth, undulate. Fingers short, stout; fixed finger weakly downturned.

Material Examined.—*Polycnemidium pustulosus*, holotype, NHMW 1864 XII 666.

Remarks.—*Polycnemidium* can be referred to Necrocarcinidae based upon its possession of a wider than long carapace; epigastric slit-like depressions; well-defined cervical and post-cervical groove; tubercles arranged into rows; anterolateral and posterolateral margins with spines or granules. It lacks the moderately vaulted carapace seen in other members of the family. Recovery of specimens with sterna could help verify its family level placement.

Range.—Late Cretaceous (Coniacian).

Pseudonecrocarcinus Förster, 1968

Type Species.—*Necrocarcinus quadriscissus* Noetling, 1881, by original designation.

Other Species.—*Pseudonecrocarcinus biscissus* Wright and Collins, 1972; *P. gamma* (Roberts, 1962); *P. scotti* (Stenzel, 1945); *P. stenzeli* Bishop, 1983a.

Diagnosis.—Carapace about as wide as long, hexagonal, weakly vaulted transversely and longitudinally; front produced beyond orbits, with four projections; orbits rimmed, projected forward; anterolateral margins spinose; posterolateral margins with spines; posterior margin concave; epigastric region with 2 or 4 slit-like depressions in cuticle, slits not extending through cuticle; cervical groove moderately deep;

protogastric region with several tubercles; epibranchial region with several tubercles, arcuate; remainder of branchial region undifferentiated, with tubercles loosely arranged into row.

Material Examined.—*Pseudonecrocarcinus biscissis*, holotype, (BMNH) In. 61166; *P. gamma* (Roberts, 1962), holotype, ANSP 20031.

Remarks.—*Pseudonecrocarcinus* can be referred to Necrocarcinidae based upon its spinose anterolateral and posterolateral margins that are well-differentiated, well-defined axial regions, deep cervical groove and arcuate epibranchial region, and narrow fronto-orbital width. Recovery of specimens with sterna could help verify its family level placement.

Range.—Early Cretaceous (Albian)-Late Cretaceous (Maastrichtian).

Shazella Collins and Williams, 2004

Type and Sole Species.—*Shazella abbotsensis* Collins and Williams, 2004, by original designation.

Diagnosis.—Carapace hexagonal, with large, inflated, pustulose, mesogastric region; cervical groove extending onto flanks, very deep except axially; branchial region undifferentiated, strongly inflated, with central elongate swelling and swelling at lateral margin; cardiac region elongate, inflated; branchiocardiac groove parallels lateral margins of cardiac region; posterior margin deeply concave.

Material Examined.—*Shazella abbotsensis*, holotype, (BMNH) IC. 306.

Remarks.—*Shazella* is referred to Necrocarcinidae based upon its hexagonal carapace, deep cervical groove and branchiocardiac grooves, and well-defined axial regions. Recovery of specimens with sterna could help verify its family level placement.

Range.—Late Cretaceous (Turonian).

Araripecarcinus ferreirai Martins-Neto, 1987

Type and Sole Species.—*Araripecarcinus ferreirai* Martins-Neto, 1987, by original designation.

Diagnosis.—Carapace subcircular, nearly as wide as long. Pterygostome broad, vaulted, crest inconspicuous. Cervical groove reaching ventral carapace; buccal cavity elongated, about half the carapace length. Thoracic sternum narrow; S3 distinct ventrally, wider than long; S4 flattened mesially, lateral margins sub-parallel and slightly convex; E4 longer than wide, slightly ovate distally, forming with lateral margins of S4 an angle of $\sim$120 degrees. Chelipeds isochelous; P2 and P3 the longest of all pereiopods, similar in size; P4 nearly half P2-P3; P5 the smallest, very reduced, apparently subdorsal (after Luque, in press).

Material Examined.—Cast of the holotype USP (GP/1T 1477), deposited in the Instituto de Geociências da Universidade São Paulo, São Paulo, Brazil.

Remarks.—The sternal architecture of raninoidans varies considerably among families and genera, and *Araripecarcinus* seems to follow that pattern. Although its thoracic sternum has no match among raninoidans, it is more similar to *Planocarcinus johnjagti*, also from the Early Cretaceous of Colombia (Bermudez et al., 2013; Luque, in press). Thus, we place it within Necrocarcinidae.

Range.—Early Cretaceous (Albian).

Colombicarcinus n. gen.
Fig. 7

Type Species.—*Colombicarcinus laevis* n. sp., by original designation and monotypy.

Diagnosis.—Carapace nearly equidimensional, maximum width in anterior third; maximum length about 80% carapace width, measured from posterior margin to base of rostrum. Fronto-orbital margin broad, about 55% carapace width. Orbits relatively wide for a necrocarcinid, directed forward, with two short, widely spaced orbital fissures; intra-orbital spine short, broad, truncated. Anterolateral margin with at least 3 short, unequal spines, excluding outer orbital spine; posterolateral margins long, slightly convex, finely granulated, lacking posterolateral spines; posterior margin concave, rimmed, shorter than fronto-orbital margin, apparently sexually dimorphic, about 50% carapace width in female, and about 40% in male. Postrostral slits absent; cervical and branchiocardiac grooves distinct, well developed, reaching anterolateral margins; postcervical groove absent. Dorsal carapace smooth, weakly ornamented, lacking axial ridge or row of tubercles; branchial region lacking conspicuous longitudinal ridge.

Etymology.—The genus name is derived from Colombia, the country from which the type material was collected.

Colombicarcinus laevis n. sp.
Fig. 7

Diagnosis.—As for genus.

Description.—Dorsal carapace nearly equidimensional, with maximum width in anterior third. Fronto-orbital margin broad, about 55% the carapace width; rostrum poorly preserved but apparently broader at the base, narrowing anteriorly, with lateral sides straight, converging antero-mesially, extending beyond level of outer orbital spine; postrostral slits absent. Orbits relatively wide for a necrocarcinid, directed forward, bearing two short and widely spaced orbital fissures; inner orbital spine is short, truncated, subtrapezoidal in appearance, intra-orbital spine short, truncated, nearly half as broad as inner orbital spine, subrectangular, outer orbital spine poorly preserved in holotype or paratype, but apparently short, subtriangular. Anterolateral margin shorter than posterolateral margin, stringly convex, apparently bearing at least 3 short, unequal spines excluding the outer orbital spine, with one very small spine between outer orbital spine and lateral expression of cervical groove, and two short, broad spines, straight laterally, directed anteriorly; posterolateral margin long, slightly convex, finely granulated, but lacking posterolateral spines; posterior margin concave, rimmed, shorter than fronto-orbital margin, apparently sexually dimorphic, about 50% carapace width in female, and about 40% in male.

Cervical groove distinct, well developed, sinuous, with smooth deflections, slightly interrupted axially, reaching anterolateral margin; postcervical groove absent; branchial grooves present; branchiocardiac groove distinct, well developed, sub-parallel to cervical groove. Dorsal carapace smooth, poorly ornamented. Epigastric, protogastric, mesogastric and hepatic regions poorly delimited, lacking tubercles or conspicuous ornamentations; hepatic region wide, somewhat depressed; mesogastric region weakly defined anteriorly, more so posteriorly; metagastric and urogastric regions delimited laterally by branchial grooves; cardiac region moderately developed, wider anteriorly, bearing a small tubercle posteriorly near contact with intestinal region; intestinal region wide. Dorsal carapace lacking axial ridge or row of tubercles; branchial regions lacking conspicuous longitudinal ridges. Dorsal carapace finely granulated.

Etymology.—The trivial name derives from the Latin 'levis' (smooth, light), referring to its smooth and unornamented dorsal carapace.

Types.—Holotype IGM p881167, and paratype IGM p881105, deposited in the paleontological collections of the Colombian Geological Survey, Bogotá, Colombia.

Remarks.—Among necrocarcinids, the diagnostic lack of axial and branchial longitudinal rows of tubercles of *Colombicarcinus* is shared with *Planocarcinus olssoni* and *P. johnjagti*, as well as the absence of posterolateral spines. The type specimens of *Colombicarcinus laevis* were collected in association with the holotype of *Joeranina kerri* (Luque et al., 2012).

Range.—Early Cretaceous (Aptian).

Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003
Fig. 8

Included Genera.—*Cherpiocarcinus* Marangon and de Angeli, 1997; *Marycarcinus* Schweitzer et al., 2003; *Orithopsis* Carter, 1872; *Paradoxilissopsa* Schweitzer, Dworschak, and Martin, 2011 (= *Lissopsis* Frič and Kafka, 1887); *Paradoxicarcinus* Schweitzer et al., 2003; *Silvacarcinus* Collins and Smith, 1993.

Diagnosis.—Carapace hexagonal, angular, wider than long or about as wide as long excluding orbital and rostral spines, length averaging about 90% carapace width, widest at position of last anterolateral spine, about one-third to one-half the distance posteriorly on carapace; flattened; rostrum projected well beyond orbits, with two to four spines; orbits broad; inter-, intra-, and outer orbital spines well developed, outer orbital spine sometimes bifid; fronto-orbital width 50-70% maximum carapace width; anterolateral margin short, about half maximum carapace length, with several spines; protogastric regions narrow, sometimes with small nodes or elongate, reniform swellings; hepatic regions wide, sometimes with small nodes or elongate, reniform swellings; cervical and branchiocardiac grooves shallow, not well defined; branchial regions sometimes with longitudinal ridges and small nodes anteriorly; axial regions may have longitudinal ridge; sternite 2 small, pentagonal; sternite 3 triangle, separate from sternite 4 by axial grooves; sternite 4 flattened axially and raised laterally, sternal suture 4/5 incomplete, deep, straight, then turning at nearly right angle and oriented parallel to axis of animal axially; sternite 5 wider than long, articulating with pereiopod 2, directed laterally, sternal suture 5/6 incomplete, deep, straight, then turning at nearly right angle and oriented parallel to axis of animal axially; sternite 6 directed posterolaterally, sternal suture 6/7 incomplete, deep, arcuate and oriented parallel to axis of animal axially; sternite 7 reduced with bulge anteriorly and axially, suture 7/8 appearing to be complete; sternite 8 reduced, vertical, visible only in posterior view; all pleonites free in females, with blunt axial ridge on each somite, somite 6 much longer than wide, telson extending to level of middle of somite 4 in female (after Karasawa et al., 2011).

Range.—Early Cretaceous (Albian)-Oligocene.

Remarks.—Orithopsidae clearly belongs within Necrocarcinoidea after being referred to Dorippoidea MacLeay, 1838 (Schweitzer et al., 2003), as discussed above. *Goniochele* Bell, 1858, which previously had been referred to the family, is now a member of its own nominal family, Goniochelidae Schweitzer and Feldmann, 2011, within Dorippoidea (Schweitzer and Feldmann, 2011). Many of the currently referred genera lack sternal and appendage elements and their family level placement will be tested when these can be recovered.

Cherpiocarcinus Marangon and de Angeli, 1997

Type and Sole Species.—*Cherpiocarcinus rostratus* Marangon and de Angeli, 1997, by original designation.

Diagnosis.—Carapace hexagonal, as long as wide with three anterolateral spines; front triangular with long axial spine and lateral spines; orbits with two very long fissures bounding two very long intra-orbital spines; outer orbital spine bifid, longer than rostrum; regions variously defined; one gastro-cardiac keel and three longitudinal protogastric keels; surface granular.

Remarks.—*Cherpiocarcinus* is placed within Orithopsidae based upon its possession of long orbital and anterolateral spines, hexagonal carapace, deep cervical groove, and keels on the protogastric region. The only known material lacks sternal characters.

Range.—Oligocene (Rupelian).

Marycarcinus Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003

Type and Sole Species.—*Necrocarcinus hannae* Rathbun, 1926b, by original designation.

Diagnosis.—Carapace about as wide as long, widest about one-third the distance posteriorly on carapace; rostrum with four small spines; intra-orbital spine bounded on either side by deep, open orbital fissure; outer orbital spine bifid, outer tip longer than inner tip; fronto-orbital width about 65% maximum carapace width; anterolateral margin with two or three small spines; branchial regions with arcuate ridge convex axially, terminating in a tubercle (Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003, p. 40).

Material Examined.—*Marycarcinus hannae*, CM 45974.

Remarks.—*Marycarcinus* was originally placed within Orithopsidae and is retained there herein based upon its deep orbital grooves and well-developed orbital spines, cervical groove and arcuate epibranchial region, and wide fronto-orbital margins. Unfortunately, the only known material lacks sternal characters.

Range.—Eocene.

Orithopsis Carter, 1872
Fig. 8A, C, D

Type Species.—*Orithopsis bonneyi* Carter, 1872, by monotypy.

Other Species.—*Orithopsis angelicus* (Fraaije, 2002); ? *O. isericus* (Frič and Kafka, 1887); *Orithopsis tricarinatus* (Bell, 1863).

Diagnosis.—Carapace hexagonal, about as wide as long; front projecting well beyond orbits, central spine trifid, with two spines on either side of central spine, largest forming inner orbital spine; large, triangular intra-orbital spine; outer orbital spine stout, wrapping around outer orbital angle; anterolateral margins with 4 spines excluding outer orbital spine; carapace axially keeled; protogastric regions ornamented with tubercles; epibranchial region arcuate; branchial region with longitudinal keel subparallel to axial keel.

Material Examined.—*Orithopsis bonneyi*, holotype SM B 58857; *Orithopsis tricarinatus*, Bell, 1863, paralectotype SM B 23259, B 30733-4.

Remarks.—Composition of *Orithopsis* has been somewhat variable. Van Bakel et al. (2012) concurred with the long held synonymy of *O. bonneyi* with *O. tricarinatus*. Two of us (RMF, CES) examined type or illustrated material of those two species at the Sedgwick Museum (Cambridge University). The two species, while both referable to *Orithopsis*, differ in the ornamentation of the carapace. *Orithopsis tricarinatus* (SM B 23259, the illustrated specimen of Bell, 1863, pl. IV, Fig. 10), has broad swellings on the carapace that are ornamented with tubercles at the highest point. That of *O. bonneyi* (SM B 58557, holotype), is smooth, without such inflated regions and tubercles. Thus, we have elected since Schweitzer et al. (2010) to maintain them as separate species.

Van Bakel et al. (2012) placed several other species within *Orithopsis* with which we do not concur. They placed *Palaeocorystes isericus* Frič and Kafka, 1887, within *Orithopsis*. The drawing of that taxon (Frič and Kafka, 1887: pl. 10.5) shows that it seems to have had spinose orbits and a relatively unornamented carapace. However, it is also reminiscent to us of *Cenocorystes*. Thus, placement within *Orithopsis* must be considered provisional, until type material can be examined and illustrated. *Paradoxilissopsa transiens* is discussed below, and *Cenomanocarcinus siouxensis* was discussed under *Cenomanocarcinus*. Schweitzer and Feldmann (2011) placed *Hillius youngi* (Bishop, 1983a) within the Cyclodorippidae Ortmann, 1892, based upon examination of type material.

Range.—Early (Albian)-Late (Maastrichtian) Cretaceous.

Paradoxilissopsa Schweitzer,
Dworschak, and Martin, 2011
Fig. 8B

Lissopsis Frič and Kafka, 1887, p. 48, pl. 10, Figs. 7a-b.

Type and Sole Species.—*Lissopsis transiens* Frič and Kafka, 1887, by monotypy.

Diagnosis.—Carapace about as long as wide, angular; rostrum projected well beyond orbits, spatulate; orbits deep, rimmed, with stout outer orbital spine; anterolateral margin short, with several spines; posterolateral margin longer than anterolateral margin; posterior margin long, sinuous; carapace with axial keel; regions broadly inflated; branchial regions with longitudinal keels.

Remarks.—Glaessner (1929, p. 235) placed what was then called *Lissopsis* within "Brachyuridea inc. sedis" and later (1969: R532) into "Brachyura of uncertain systematic position or status." Schweitzer et al. (2010, p. 145) placed it within Decapoda Incertae sedis. Van Bakel et al. (2012, p. 205) questionably referred the type and only species of *Lissopsis* to *Orithopsis*. Meanwhile, Schweitzer et al. (2011) had erected a replacement name for *Lissopsis* Frič and Kafka, 1887, *Paradoxilissopsa*, because *Lissopsis* was preoccupied. Examination of the figures of *Paradoxilissopsa* in Frič and Kafka (1887, Fig. 10.7), suggests an affinity with *Orithopsis* and Orithopsidae, but we support retention of separate generic status of *Paradoxilissopsa* until examination and illustration of type material can be accomplished. Frič and Kafka's illustration differs rather substantially from *Orithopsis* species, which have very spinose rostral and orbital margins; that of *Paradoxilissopa* are smooth and entire. The drawing of the anterolateral margin of *Paradoxilissopsa* is unusual in showing it to be rather concave and spinose; examination of the actual specimen will be necessary to determine its nature. The distinct differences between the orbits and rostra between the two taxa, at least as illustrated, suggest that they should be maintained as separate for now.

Range.—Late Cretaceous (Turonian).

Paradoxicarcinus Schweitzer, Feldmann, Fam, Hessin,
Hetrick, Nyborg, and Ross, 2003

Type and Sole Species.—*Paradoxicarcinus nimonoides* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003, by original designation.

Diagnosis.—Carapace about as long as wide excluding spines; cervical groove very deep, branchiocardiac groove deep axially and not developed laterally; front bifid; anterolateral margin with three long, attenuated spines; gastric regions with longitudinal swellings; branchial regions with one transverse and one longitudinal swelling (Schweitzer et al., 2003, p. 42).

Material Examined.—*Paradoxicarcinus nimonoides*, holotype GSC 124826, and paratype, GSC 124827.

Remarks.—*Paradoxicarcinus* is referred to Orithopsidae based upon its hexagonal carapace; long rostral, orbital, and anterolateral spines; and its gastric and branchial swellings. Unfortunately, the only known material lacks sternal characters.

Range.—Late Cretaceous (Santonian).

Silvacarcinus Collins and Smith, 1993

Type and Sole Species.—*Silvacarcinus laurae* Collins and Smith, 1993, by original designation.

Diagnosis.—Carapace hexagonal, about as wide as long; apparently with a narrow intra-orbital spine; outer orbital spine stout; anterolateral margins with 3 or 4 spines excluding outer orbital spine; carapace axially keeled; protogastric regions ornamented with tubercles; epibranchial region arcuate; branchial region with longitudinal keel subparallel to axial keel; male sternum narrowly ovate.

Range.—Eocene (Ypresian).

Superfamily Palaeocorystoidea Lőrenthey *in* Lőrenthey and Beurlen, 1929
Fig. 9

Diagnosis.—As for family.

Remarks.—Our analysis yields a single group within Palaeocorystoidea. Van Bakel et al. (2012) referred several families to the superfamily; those additional families have been referred to Necrocarcinoidea in our analysis.

Palaeocorystidae Lőrenthey *in* Lőrenthey and Beurlen, 1929
Fig. 9

Included Genera.—*Alessandranina* new genus; *Cenocorystes* Collins and Breton, 2009; *Cretacoranina* Mertin, 1941; *Eucorystes* Bell, 1863; *Ferroranina* van Bakel et al., 2012; *Joeranina* van Bakel, 2012; *Notopocorystes* M'Coy, 1849.

Diagnosis.—Carapace obovate, usually longer than wide, widest at position of third or fourth anterolateral spine; frontal margin wide; anterolateral margin with 2 to 4 spines; carapace surface ornamented with ridges, straps, tubercles or unornamented; epibranchial region with weak tooth; fronto-orbital margin and orbits wide, orbital margin with two fissures; rostrum generally long, with two spines at tip; orbits with inner, intra-, and outer orbital spines, some of which may be bifid; gymnopleuran condition absent; sternites 1-3 fused, 1 and 2 directed downward; sternite 4 long, pereiopod 1 articulating near posterior corner, moderately wide, lateral margins concave; sternal suture 4/5 sinuous laterally, then turning abruptly anteriorly parallel to axis; episternite 4 usually laterally directed but may be posteriorly directed (*Notopocorystes*); sternites 4/5 usually in broad contact (except *Notopocorystes*); sternite 5 long, moderately wide, with double peg structure on episternal projection for attachment of pleon, episternites directed laterally or posterolaterally (*Notopocorystes*); sternal suture 5/6 complete; all female pleonites free, pleonite 6 long, pleonites 2-5 with central spine, entire pleon reaching to level of base of coxae of first pereiopods; male pleon narrower, telson triangular, somite 6 long, reaching to level of base of coxae of pereiopods 2; pleonal holding mechanism consisting of a double-peg structure; longitudinal furrow on merus of maxilliped 3; chelae with long fingers; female gonopore coxal, small, round; spermatheca at end of suture 7/8, separated from one another; pereiopod 5 reduced in size (after Karasawa et al., 2011, p. 551; van Bakel et al., 2012, p. 17).

Remarks.—The family was recently extensively revised and diagnosed by van Bakel et al. (2012), who erected two new genera and several new species. They also reassigned many genera previously placed within *Cretacoranina* or *Eucorystes*. We follow some of their revision, but do not concur with some generic placements as discussed below.

Range.—Early Cretaceous (Aptian)-Late Cretaceous (Maastrichtian).

Cenocorystes Collins and Breton, 2009

Type Species.—*Cenocorystes fournieri* Collins and Breton, 2009, by original designation.

Other Species.—*Cenocorystes bretoni* van Bakel et al., 2012.

Diagnosis.—Carapace about as long as wide, strongly vaulted; orbits shallow, directed forward; rostrum apparently trifid or with four spines; intra-orbital spine long; outer orbital spine longer than intra-orbital spine, spines separated by wide fissures; anterolateral margin with three short spines; posterolateral margin with one short spine anteriorly; regions not well delimited; cervical and branchiocardiac grooves weak; fifth pereiopod small, subdorsal.

Range.—Late Cretaceous (Cenomanian).

Cretacoranina Mertin, 1941

Type Species.—*Raninella*? *schloenbachi* Schlüter, 1879, by original designation.

Other Species.—*Cretacoranina denisae* (Secretan, 1964); *C. fritschi* (Glaessner, 1929); *C. testacea* (Rathbun, 1926a); *C. trechmanni* (Withers, 1927).

Diagnosis.—Carapace obovate, wide in anterolateral third; posterolateral margin narrowing considerably; rostrum extending beyond orbital margin, tip bifid, with spine just posterior to each spine at tip for a total of four, short spines on either side of rostrum forming inner orbital spines, rostrum sometimes rimmed; intra-orbital spine bifid, bounded by fissures; outer orbital spine bifid; anterolateral margin with 3 or 4 spines; spines becoming smaller posteriorly, last one nearly obsolete; cervical groove absent; branchiocardiac groove developed as arcs on either side of axis; dorsal carapace ornamentation developed as fungiform pillars overall but ending in indistinct scalloped termination to base of orbital margin or just barely onto orbital margin and anterolateral spines; sternite 3 appearing triangular; sternite 4 wide, episternite 4 wide, in broad contact with sternite 5, directed laterally, suture 4/5 incomplete, straight; sternite 5 narrower than sternite 4.

Material Examined.—*Cretacoranina schloenbachi*, cast of RE 551.763.333A 3963 numbered KSU D 444; *C. testacea*,

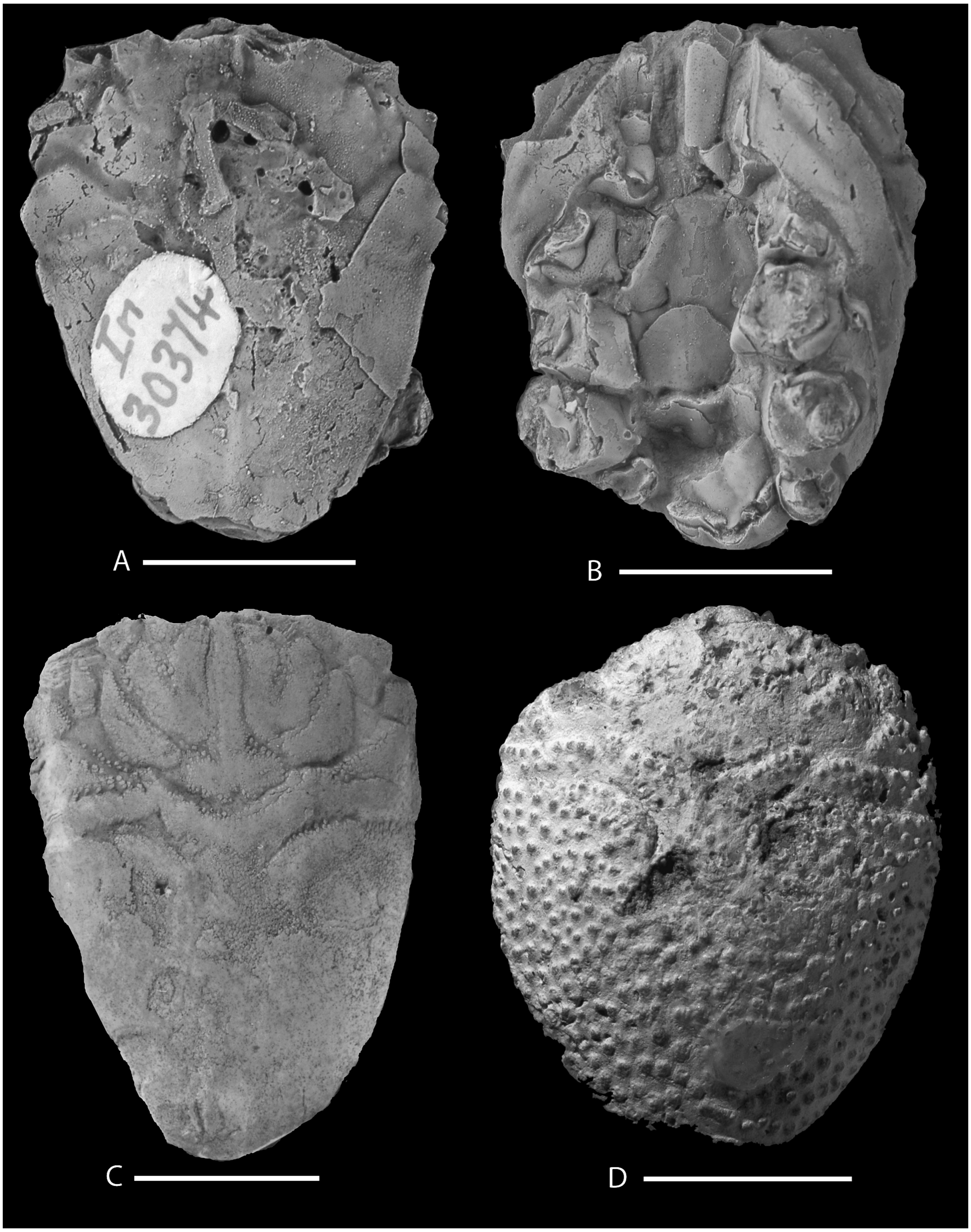

Fig. 9. Palaeocorystidae. A-B, *Joeranina broderipi* (Mantell, 1844), (BMNH) In. 30374, dorsal carapace (A) and ventral view showing some sternal and pleonal elements (B); C, *Eucorystes carteri* M'Coy, 1854, cast of J. S. H. Collins Collection 2319f numbered D1509 showing distinctive strap-like ornamentation; D, *Alessandranina ornata* (Wright and Collins, 1972), holotype (BMNH) In. 61111, dorsal carapace. Scale bars = 1 cm.

NJSM 23313; holotype USNM 73121 and USNM 355986 from the Coon Creek locality of the Ripley Formation, Tennessee; USNM 327238, illustrated specimen of Roberts (1962); *C. trechmanni*, holotype (BMNH) In. 26011.

Remarks.—Constituent species within *Cretacoranina* had been quite divergent in morphology (i.e., Haj and Feldmann, 2002; Schweitzer et al., 2010). Van Bakel et al. (2012) limited the genus to those species exhibiting distinctive hexagonal ornamentation overall, terminating at the base of the orbits and anterolateral spines, and lacking a cervical groove.

Range.—Late Cretaceous (Cenomanian-Maastrichtian).

Eucorystes Bell, 1863
Fig. 9C

Type Species.—*Eucorystes carteri* M'Coy, 1854, by monotypy.

Other Species.—*Eucorystes eichhorni* Bishop, 1983b; *E. exiguus* (Glaessner, 1980); *E. harveyi* (Woodward, 1896); *E. iserbyti* van Bakel et al., 2012; *E. intermedius* Nagao, 1931; *E. mangyshlakensis* Ilyin and Pistshikova *in* Ilyin, 2005; *E. navarrensis* van Bakel et al., 2012; *E. oxtedensis* Wright and Collins, 1972; *E. paututensis* (Collins and Rasmussen, 1992); *E. platys* Schweitzer and Feldmann, 2001a.

Diagnosis.—Carapace longer than wide; rostrum long, with trifid central spine, central spine of three very short; two short spines to either side of rostrum forming inner orbital spines; intra-orbital spine short, blunt, bounded by fissures; outer orbital spine bifid, wide; anterolateral margin with two or three spines and possibly various tubercles of varying degrees of development; posterolateral margin may have one anterior spine; anterior half of carapace ornamented with distinctive strap-like ornamentation, with the general arrangement as follows: epibranchial strap extends across the carapace, including the metabranchial region; arcuate straps posterior to it bound urogastric and cardiac regions; mesogastric region developed into strap-like structures. Protogastric region ornamented with U-shaped strap. Posterior and lateral to it is an arcuate strap. Hepatic region generally has a series of smaller, raised swellings. Sternites 1-3 small; sternite 4 wide, episternite 4 wide, directed laterally, in broad contact with sternite 5, suture 4/5 incomplete, initially straight, then turning at right angles and parallel to axis; sternite 5 wide, episternite directed posteriorly, suture 5/6 complete; sternite 6 smaller than five.

Material Examined.—*Eucorystes carteri*, KSU D 1509, 1530, 1713; *E. eichhorni*, KSU D 1180, cast of holotype SDSM 10007, KSU D 1181, cast of paratype, SDSM 10010; *E. harveyi* (Woodward, 1896), KSU D1178, cast of GSC 5817; *E. paututensis*, cast of holotype MGUH 21.604 numbered KSU D 1802; *E. platys*, KSU D 240, cast of GSC 124811, KSU D 373, cast of USNM 512163, holotype.

Remarks.—Van Bakel et al. (2012) restricted *Eucorystes* to those species with very well developed, raised, strap-like ornamentation. Those with subdued strap-like ornamentation were referred to *Joeranina* (Fig. 9A, B) Examination of casts of holotype and referred material of *Eucorystes platys* and *Eucorystes harveyi* and illustrations of all species referred to the two genera suggests that most should remain in *Eucorystes*. Species of *Eucorystes* possess strap-like ornamentation in a pattern that can be generalized to all species. An epibranchial strap extends across the carapace, including the metabranchial region. Posterior to it, arcuate straps bound the urogastric and cardiac regions. The mesogastric region is developed into strap-like structures. The protogastric region is ornamented with a U-shaped strap, and posterior and lateral to it is an arcuate strap. The hepatic region generally has a series of smaller, raised swellings. All species of *Eucorystes* have these straps to some degree. In some species, they are developed as raised, somewhat rounded straps separated by deep grooves (type species). In others, they are more discrete, rounded, granular, and separated by wide, shallower grooves (*E. iserbytei*). Still others possess subdued straps separated by shallow grooves (*E. platys*). This is as opposed to species of *Joeranina*, in which the straps are essentially absent. In species of *Joeranina*, the cervical groove is deep and sinuous, and a disjunct postcervical groove or row of pits lies posterior to it. The branchiocardiac groove is composed of arcuate grooves as in most Raninoida. Straps are absent, and the hepatic region possesses a pair of forward directed, low, dull spines.

The range of variation in strap-like ornamentation within *Eucorystes* as it currently stands is wide. There are some other differences, including maximum width of the carapace (very wide in *E. platys*, for example) and other aspects of carapace ornamentation. *Eucorystes iserbyti* is quite different from other genera in possessing rounded straps and a very different sternum than the type species; its sternum has sternites four and five not in broad contact, for example, more like that of *Notopocorystes*. Revision of that species must await examination of type material.

Range.—Early Cretaceous (Albian)-Late Cretaceous (Campanian).

Ferroranina van Bakel, Guinot, Artal, and Jagt, 2012

Type Species.—*Notopocorystes dichrous* Stenzel, 1945, by original designation.

Other Species.—*F. australis* (Secretan, 1964); *F. tamilnadu* van Bakel et al., 2012.

Diagnosis.—Carapace ovate, not much longer than wide; widest at penultimate anterolateral spine, about 33% the distance posteriorly; fronto-orbital width wide, about 75% maximum width of carapace; rostrum composed of three elements, axially keeled, rimmed and bifid axially element and rimmed inner orbital spines; intra-orbital spines flanked by orbital fissures, spine may be itself bifid; outer orbital spine may be bifid, long; anterolateral margin with many spines with broad bases, usually four; posterolateral margin straight, can have beaded rim; cervical groove developed as short sinuous segments on either side of axis; branchiocardiac groove developed as arcuate segments on either side of axis; dorsal carapace ornamentation developed as fungiform pillars overall but ending in distinctive scalloped termination just before orbits and anterolateral spines; sternites 1-3 small; sternite 4 wide, episternite 4 wide, directed laterally, in broad contact with sternite 5, suture 4/5 incomplete, initially straight, then turning at right angles and parallel to axis; pleon with broad axial ridge.

Material Examined.—*Ferroranina dichrous*, cast of UT 21076 numbered KSU D 872, several hundred unnumbered specimens from SDSMT; cast of holotype of *Ferroranina tamilnadu*, OUM ky.2861 numbered KSU D 445; *Notopocorystes australis*, cast of MNHN R03874 numbered KSU D 42.

Remarks.—Van Bakel et al. (2012) placed all those species previously referred to *Cretacoranina* or *Notopocorystes* with a distinctive scalloped termination in ornamentation on the anterior of the carapace into *Ferroranina*.

Range.—Late Cretaceous (Cenomanian-Campanian).

Joeranina van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012
Fig. 9A, B

Type Species.—*Corystes broderipi* Mantell, 1844, by original designation.

Other Species.—*Joeranina colombiana* Bermudez, Gómez-Cruz, and Vega *in* Bermudez et al., 2013; *J. gaspari* van Bakel et al., 2012; *J. goshourajimensis* Karasawa and Komatsu, 2013; *J. houssineaui* van Bakel, 2013; *J. japonica* (Jimbô, 1894); *J. kerri* (Luque et al., 2012); *J. syriaca* (Withers, 1928); *J. xizangensis* (Wang, 1981).

Diagnosis.—Carapace longer than wide, widest at position of penultimate anterolateral spine about 30% the distance posteriorly; fronto-orbital margin wide, about 75% maximum width of carapace; rostrum composed of three elements, axially keeled, rimmed and bifid axially element and rimmed inner orbital spines; simple or bifid intra-orbital spines flanked by orbital fissures; outer orbital spine may be bifid, long; anterolateral margin with many spines with broad bases; posterolateral margin straight, may have beaded rim; cervical groove sinuous, developed as three arcs and terminating before crossing midline; branchiocardiac groove developed as arcuate segments on either side of axis; hepatic region with distinct pair of swellings anteriorly just posterior to orbit; branchial region with weak, arcuate, strap-like ornament that may be developed as muscle scars; sternites 1-3 small; sternite 4 wide, episternite 4 wide, directed laterally, in broad contact with sternite 5, suture 4/5 incomplete, initially straight, then turning at right angles and parallel to axis; sternite 5 wide, episternite directed posteriorly, suture 5/6 incomplete, initially straight, then turning at right angles and parallel to axis; suture 6 smaller than five, suture 6/7 incomplete, sternite 7 directed posterolaterally; sternite 8 appearing to be positioned perpendicular to sternite 7.

Material Examined.—*Notopocorystes broderipi* (Mantell, 1844), (BMNH) 21331, male, (BMNH) In. 61147, male; 31313, 35074, 59055, 59796, 61148-49, 29810-11; SM B 30645, 30638, both females; SM B 30646-48; KSU D 1505, 1696, 1746; *N. kerri*, holotype IGM p881128; *N. syriacus*, holotype (BMNH) I.8407.

Remarks.—Van Bakel et al. (2012) placed those species previously referred to *Cretacoranina* or *Eucorystes* with weakly developed strap-like ornamentation and a distinct pair of hepatic swellings within *Joeranina*. Herein we restrict *Joeranina* to those species with deep cervical grooves, a pair of dull, forward-directed, hepatic spines, an axial keel, and lacking strap-like ornamentation of any degree of development. This results in *Eucorystes* being quite speciose but the species are all united by a clear set of characters.

Range.—Early Cretaceous (Aptian)-Late Cretaceous (Campanian).

Notopocorystes M'Coy, 1849

Type Species.—*Corystes stokesi* Mantell, 1844, by subsequent designation.

Other Species.—*Notopocorystes bituberculatus* Secretan, 1964; *N. normani* (Bell, 1863); *N. ripleyensis* Rathbun, 1935a (claws only).

Diagnosis.—Carapace longer than wide; rostrum long, bifid, axially sulcate, sometimes with small spine posterior to rostral tip, bounded on either side by short spines serving as inner orbital spines; intra-orbital spine short, bounded by fissures; outer orbital spine wide, bifid; anterolateral margin with three short, triangular spines; posterolateral margins granular; carapace with axial keel ornamented with large tubercles; protogastric, hepatic, and epibranchial regions ornamented with tubercles; cervical groove deep axially, fading at lateral edges; branchiocardiac and postcervical grooves moderately deep. Sternite 2 long; sternite 3 short; sternite 4 long, episternites directed posteriorly; suture 4/5 incomplete, initially straight, then turning at right angles and paralleling axis; sternite 5 about as wide as 4, episternites directed posterolaterally, with double peg structure on episternal projection; suture 5/6 incomplete, initially straight, then turning at right angles and paralleling axis; pleon with blunt axial keel.

Material Examined.—*Notopocorystes normani*, SM B 8823; *Notopocorystes stokesii* (Mantell, 1844), (BMNH) I.7479, In. 30376, 30377, 61151, syntype, female; (BMNH) 39366, female; SM B 22902, B 30575, male; B 30572, 30645-48.

Remarks.—Most of the species referred to *Notopocorystes* by Schweitzer et al. (2010) were referred to other genera by van Bakel et al. (2012) in their revision of Palaeocorystidae. They restricted the genus to only those with large tubercles on the axial keel and on the various carapace regions. *Notopocorystes* has a somewhat different sternal architecture than other genera in the family. Sternite 4 is narrow and in less broad contact with sternite 5, and episternite 4 is directed posteriorly rather than laterally. This results in an overall narrower sternum than in other genera. Interestingly, *Notopocorystes* was recovered as one of the more derived genera within Palaeocorystidae. Narrowing of the sternum seems to be a trend in the evolution of Raninoida.

Range.—Early Cretaceous (Albian)-Late Cretaceous (Maastrichtian).

Alessandranina n. gen.
Fig. 9D

Type and Sole Species.—*Notopocorystes* (*Cretacoranina*) *ornatus* Wright and Collins, 1972, by present designation.

Diagnosis.—Carapace elongate, widest in anterior one-third; anterolateral margin appearing to have about four or five short, triangular, forward directed spines; epibranchial region developed as a strap-like arc extending from anterolateral margin about two-thirds the distance axially; metagastric region a wide, strap-like region; mesogastric and protogastric regions not well defined; hepatic regions with two triangular subregions; branchial regions broad, undifferentiated; all regions ornamented with large granules, most densely spaced on branchial regions.

Etymology.—The genus name honors the contribution of Alessandra Busulini, Venezia Mestre, Italy, to the study of fossil decapod crustaceans, particularly from the Eocene of Italy. The gender is feminine.

Material Examined.—*Notopocorystes* (*Cretacoranina*) *ornatus*, holotype, (BMNH) In. 61111.

Remarks.—We place this new genus and its sole species, *Alessandranina ornata* new combination, within Palaeocorystidae, based upon its possession of strap-like ornamentation, overall granular ornamentation, and multiple anterolateral spines. No other raninidean family can accommodate this array of characters. The species had originally been placed within *Notopocorystes* (*Cretacoranina*), which are now two separate genera. *Notopocorystes* lacks the overall granular ornamentation and instead has isolated, large tubercles, some placed on ridges, unlike *Alessandranina*. *Cretacoranina* and *Ferroranina* have very densely spaced granules over the entire carapace and no strap-like ornamentation. *Cenocorystes*, *Joeranina*, and *Eucorystes* do not have the large granular ornamentation displayed by *Alessandranina*.

We base our new genus and diagnosis on the holotype and sole specimen of *Alessandranina ornata*. Wright and Collins (1972: pl. 18.5) reported another untraced specimen of which there were photographs in The Natural History Museum (Britain). That specimen looks like *Ranina* spp., and in any event, the specimen's whereabouts is unknown.

Range.—Late Cretaceous (Cenomanian).

Superfamily Raninoidea De Haan, 1839
Figs. 10-19

Included Families.—Lyreididae Guinot, 1993; Raninidae De Haan, 1839.

Diagnosis.—Carapace longer than wide or about as wide as long, generally ovate, usually vaulted transversely, regions poorly defined; usually with well-developed rostrum and orbital spines; anterolateral margins usually with one spine but can have none or more than one; posterolateral margin lacking spines; cervical groove not reaching ventral edge of carapace; branchiocardiac groove indistinct, developed as boundary of urogastric region; branchial ridges absent; junction between sternum and pterygostome usually wide; coxa of third maxilliped small, flattened; sternum narrow, sternites 1-3 generally fused, sternites 5 and 6 with lateral extensions, sternal suture 6/7 complete, sternites 7 and 8 often reduced and at lower level than other sternites; where known, pleon narrow in males and females, showing reduced but clear dimorphism, never reaching sternite 4; genital openings coxal, spermatheca present on endosternite 7/8; branchiostegite reduced; gymnopleuran condition present.

Remarks.—Raninoidea has long been viewed as a superfamily, embracing multiple families (i.e., De Grave et al., 2009; Schweitzer et al., 2010; Karasawa et al., 2011) or two families (van Bakel et al., 2012). Our analysis supports the position of van Bakel et al. (2012), that Raninoidea should embrace two families.

Range.—Lower Cretaceous (Albian)-Holocene.

Lyreididae Guinot, 1993
Figs. 10-14

Included Subfamilies.—Bicornisranininae new subfamily; Lyreidinae Guinot, 1993; Macroacaeninae new subfamily; Marylyreidinae van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012; Rogueinae new subfamily.

Diagnosis.—Carapace much longer than wide, oblanceolate; dorsal surface smooth or punctate, regions undefined; anterior margin narrow or wide; rostrum trifid, middle spine generally much longer than other two which serve as inner orbital spines; orbit with intra- and outer orbital spines; anterolateral margins may be entire or with one or two spines; sternum-pterygostome junction poorly to well-developed or absent; gymnopleuran condition present; sternites 1-3 fused, forming a cap-like shape; sternite four large, with lateral

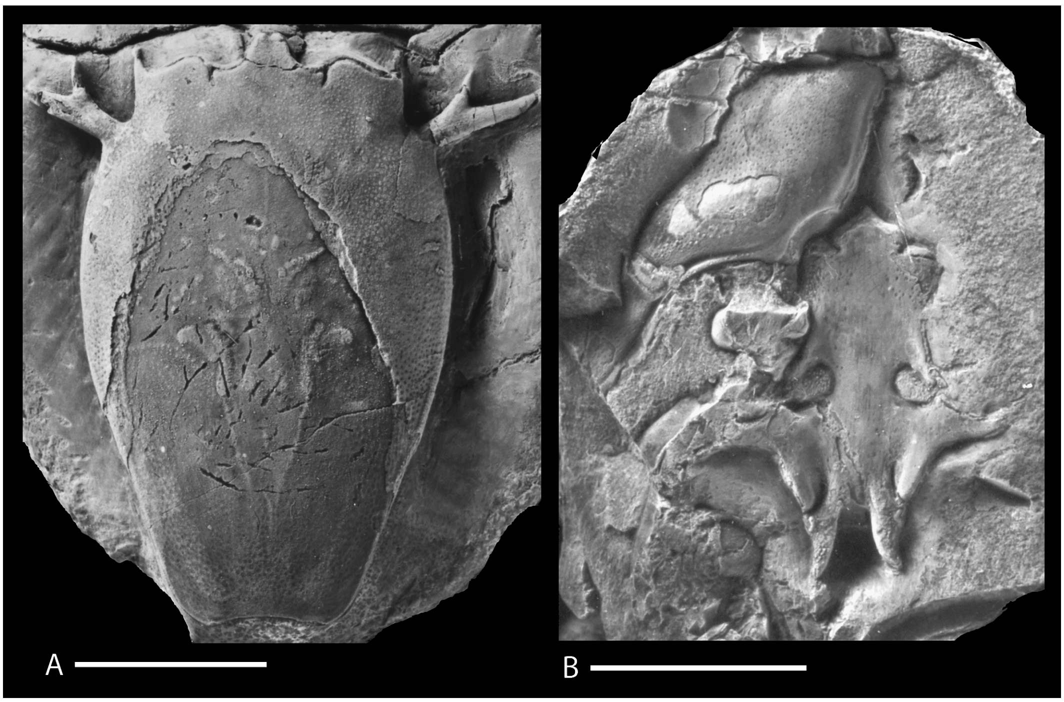

Fig. 10. Lyreididae, Rogueinae, *Rogueus orri* Berglund and Feldmann, 1989. A, holotype USNM 430027, dorsal carapace; B, paratype USNM 430038. Scale bars = 1 cm.

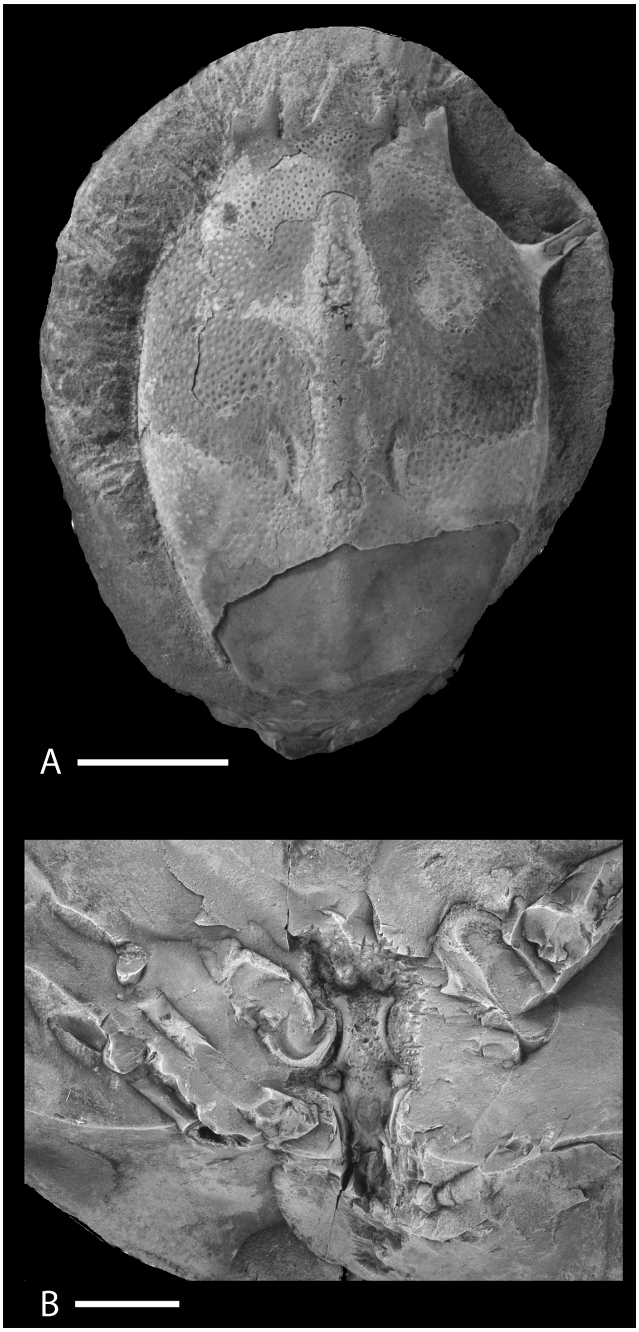

Fig. 11. Lyreididae, Macroacaeninae, *Macroacaena naselensis* (Rathbun, 1926b). A, USNM 493448; B, USNM 493446 showing sternal elements.

extensions anteriorly, concave laterally; sternite 5 of similar shape but smaller, with lyreidid hook (Guinot, 1979) and double peg pleonal locking mechanism; sternite 6 much smaller, sometimes with ridge; sternites 7 and 8 much reduced in size, median one reaching sternite 7; pleon narrow in both males and females, telson short, somite 6 long; pleon sexually dimorphic, somites 2 and 5 proportionally wider in females than males, somite 6 proportionally longer in females than males; spermatheca placed on sternite 7, separated by wall; merus of maxilliped three longer than ischium.

Remarks.—Composition of Lyreididae herein differs somewhat from that of Schweitzer et al. (2010, as Lyreidinae) and van Bakel et al. (2012). This is in part due to use of inclusion of as many genera as possible in this analysis, which suggested movement of *Ranidina* and *Bicornisranina* into the family. We also included several species that at various times had been referred to *Macroacaena*. Examination of type and referred material at USNM, KMNH, and MFM suggested that these species might not be congeneric; thus, we included them individually in our analysis. Three species clustered into a genus group, including the type, *M. succedana*, and *M. alseana* and *M. naselensis*, all of which remain in *Macroacaena*. New genera are erected below for the others.

Van Bakel et al. (2012) considered Lyreididae to be composed of two subfamilies, Lyreidinae and Marylyreidinae. Examination of the phylogeny and the characters of the genera within each clade within Lyreididae (Table 4) suggests that further subfamily division is in order. Each clade has its own unique combination of diagnostic characters; thus, we herein erect subfamilies for each. Distinctive among the subfamilies is the presence of three sternal types, lyreidine-type, a macroacaenine-type and marylyreidine-type sterna (Table 4).

Range.—Early Cretaceous (Albian)-Holocene.

Rogueinae n. subfam.
Fig. 10

Included Genus.—*Rogueus* Berglund and Feldmann, 1989.

Diagnosis.—As for genus.

Remarks.—This new subfamily is distinctive in its possession of a wide fronto-orbital width, a bifid rostral tip, a lack of intra-orbital spines and orbital fissures, and possession of a lyreidine-like sternum. This combination of characters is unique in the family.

Range.—Paleocene (Selandian)-Eocene (Lutetian-Bartonian).

Rogueus Berglund and Feldmann, 1989
Fig. 10

Type Species.—*Rogueus orri* Berglund and Feldmann, 1989, by original designation.

Other Species.—*Rogueus robustus* Collins and Jakobsen, 1996.

Diagnosis.—Carapace much longer than wide, oblanceolate; dorsal surface smooth or punctate, regions undefined; anterior margin wide, about 75% maximum carapace width; rostrum overall trifid, middle spine generally much longer than other two which serve as inner orbital spines, inner spine itself bifid at tip; orbital margin sinuous, intra-orbital spine absent; supra-orbital spine absent; anterolateral margins with one bifid spine; sternum-pterygostome junction apparently present; sternites 1-3 fused, forming a cap-like shape; sternite four large, with short lateral extensions anteriorly, concave laterally, sternal suture 4/5 incomplete, curling into a coiled shape; sternite 5 with wide lateral extensions anteriorly; sternite 6 much smaller, with ridge laterally; chela flattened, with spines on lower margin.

Material Examined.—*Rogueus orri*, holotype USNM 430027; paratypes USNM 430028-430044; *Rogueus robustus*, cast of holotype MGUH 22370 numbered KSU D 816, cast of paratype MGUH 22371 numbered KSU D 817.

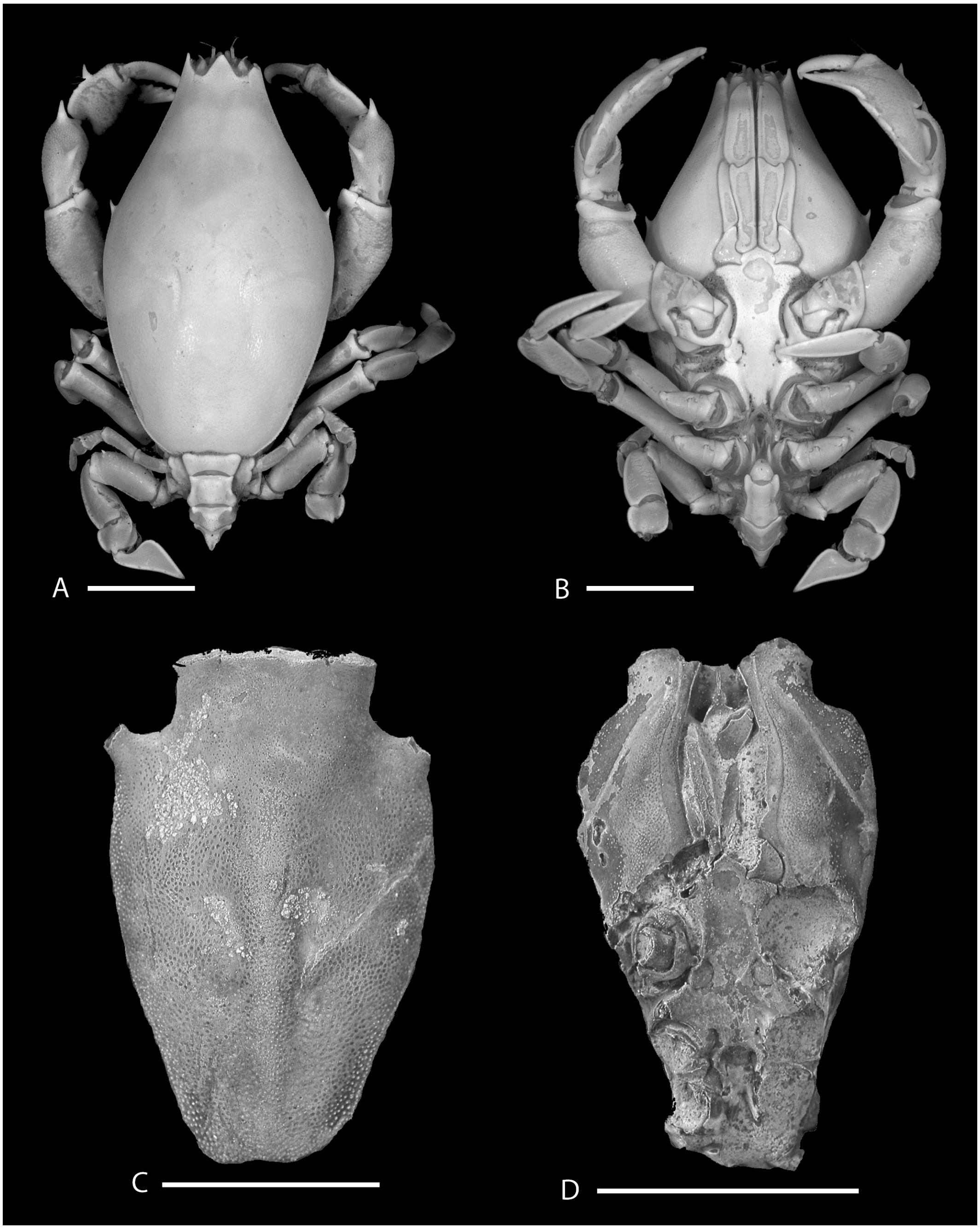

Fig. 12. Lyreididae, Lyreidinae. A-B, *Lyreidus tridentatus* De Haan, 1841, USNM 48278, dorsal (A) and ventral (B) views; C-D, *Giulianolyreidus johnsoni* (Rathbun, 1935a), C, holotype USNM 328799, dorsal view; D, paratype USNM 371691, ventral view including sternal elements, maxillipeds, and pereiopods bases. Scale bars = 1 cm.

Range.—Paleocene (Selandian)-Eocene (Lutetian-Bartonian).

Macroacaeninae n. subfam.
Fig. 11

Diagnosis.—As for genus.

Included Genus.—*Macroacaena* Tucker, 1998.

Remarks.—The narrow fronto-orbital width, singular rostrum, and macroacaenine-type sternum typifies this new subfamily.

Range.—Paleocene (Selandian)-Eocene (Priabonian).

Macroacaena Tucker, 1998
Fig. 11

Carinaranina Tucker, 1998 (part).

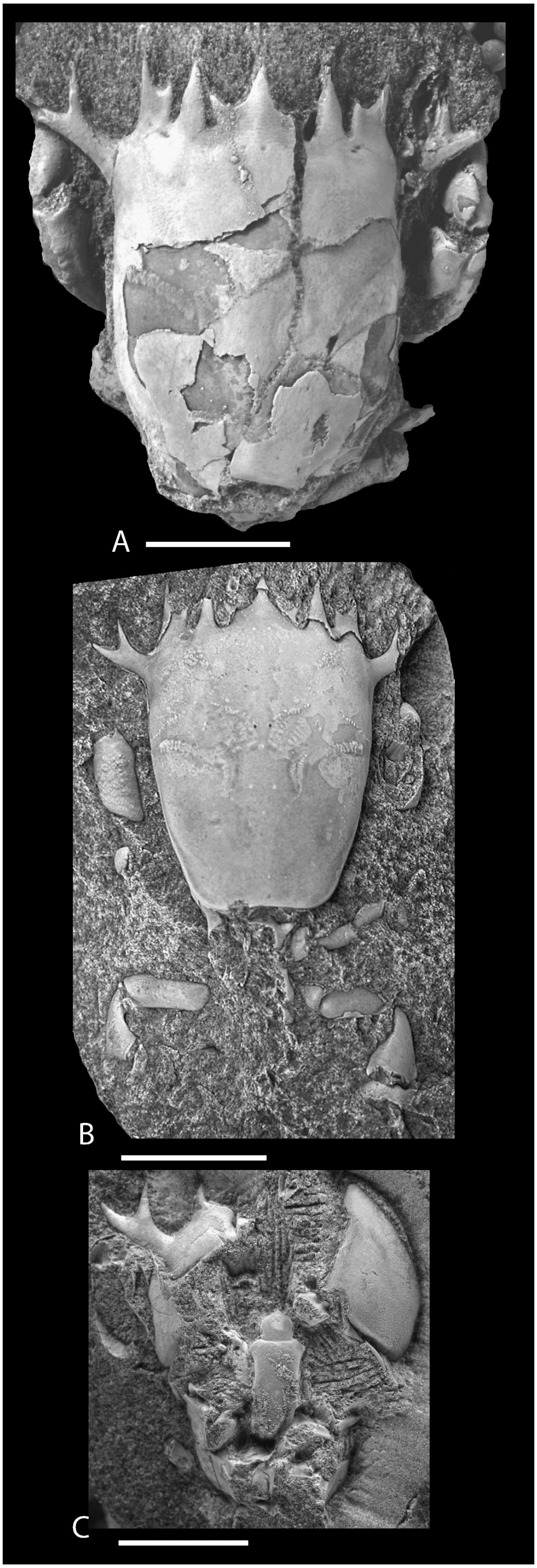

Fig. 13. Lyreididae, Bicornisranininae, *Bicornisranina bocki* Nyborg and Fam, 2008. A, holotype GSC 57082, dorsal carapace; B, paratype VIPM 2000, dorsal carapace and some elements of appendages; C, paratype CDM 039, ventral surface including elements of sternum. B and C courtesy of Torrey Nyborg. Scale bars = 1 cm.

Type Species.—*Lyreidus succedanus* Collins and Rasmussen, 1992, by original designation.

Included species.—*Macroacaena alseana* (Rathbun, 1932); *M. bispinulata* (Collins and Rasmussen, 1992); *M. chica* Schweitzer et al., 2003; *M. franconia* Schweigert et al., 2004; *M. leucosiae* (Rathbun, 1932); *M. marionae* (Tucker, 1998); *M. naselensis* (Rathbun, 1926b); *M. rosenkrantzi* (Collins and Rasmussen, 1992); *M. schencki* (Rathbun, 1932); *M. teshimai* (Fujiyama and Takeda, 1980) new combination; *M. tridens* (Roberts, 1962) new combination; *M. venturai* Vega et al., 2007; *M. yanini* (Ilyin and Alekseev, 1998) new combination.

Diagnosis.—Maximum carapace width about 60% the distance posteriorly, carapace coarsely punctate; rostrum trifid, fronto-orbital width about half maximum carapace width; orbits with two fissures, fissures open, narrow, or nearly closed; intra-orbital spine defined by fissures, ranging from very short to about half as long as outer orbital spine; entire frontal area directed forward or flared anterolaterally; anterolateral spine very long, may be a small anterolateral protuberance between anterolateral spine and outer orbital spine; carapace may have longitudinal keel. Sternites 1-3 fused, crown-shaped; sternite 4 long, with concave lateral margins along which coxa of first pereiopod lies, short anterolaterally directed spine-like projection anteriorly, short episternal projection posteriorly; sternal suture 4/5 incomplete, curling into a coiled shape; sternite 5 with wide projection anteriorly, depressed axially, short episternal projections posteriorly; sternites 6 and 7 narrow, deep axially. Pterygostome barely in contact with sternite 4 at short anterior projections. Pleon narrow, somite 6 very long. Fifth pereiopod appearing to be reduced in size.

Material Examined.—*Macroacaena alseanus*, hypotype, USNM 431293; *M. bispinulata*, cast of holotype MGUH 21.602, numbered KSU D 122; *M. chica*, holotype GSC 124818, paratype GSC 124819; *M. marionae*, holotype USNM 494628, paratype USNM 494629; *M. naselensis*, USNM 593446-8, 2 unnumbered KSU specimens; *M. rosenkrantzi* cast of paratype MGUH 21.600 numbered KSU D 1813, also casts KSU D 1804 and 1809 of MGUH specimens; *M. succedana*, cast of holotype MGUH 21.595 numbered KSU D 120; *M. tridens*, ANSP 19737; *Raninella tridens* sensu Bishop, 1983c, casts of specimens numbered GAB 37-832 and 833 numbered KSU D 1685.

Remarks.—*Macroacaena* is herein restricted to those genera with a fronto-orbital width of about 50% maximum carapace width; a carapace reaching maximum width at about the position of the last anterolateral spine and maintaining that width to about 50 or 60% the distance posteriorly on carapace; a fourth sternite with small projections anteriorly; and a fifth sternite with wide projections anteriorly. This includes nearly all of the species, including the type, that had been originally referred to *Carinaranina*, so the

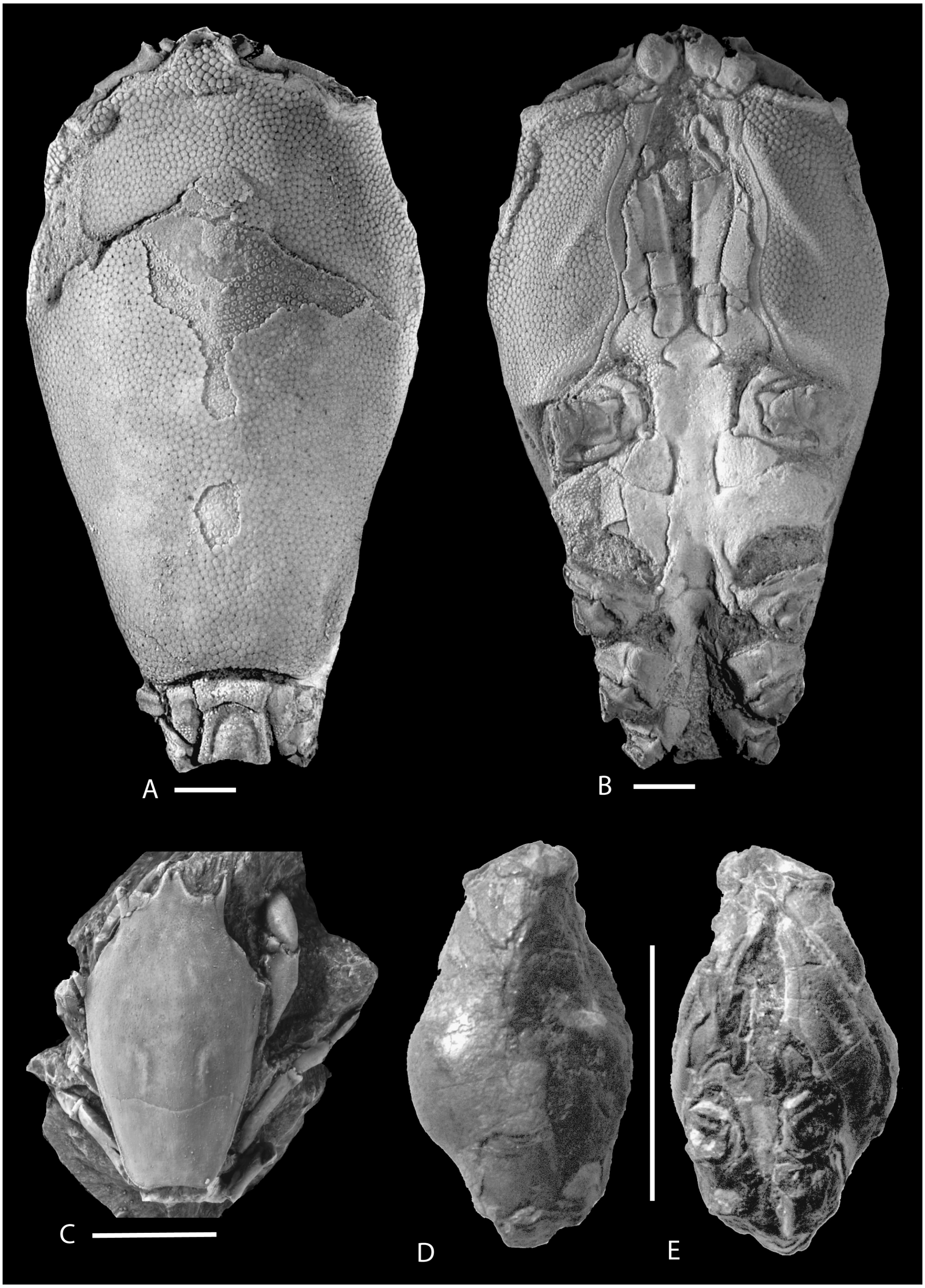

Fig. 14. Lyreididae, Marylyreidinae. A-B, *Marylyreidus punctatus* (Rathbun, 1935a), USNM 559038, dorsal view clearing showing hexagonal cuticular pattern (A) and ventral view showing sternal architecture (B); C, *Bournelyreidus eysunesensis* (Collins and Rasmussen, 1992), cast of MGUH 21593, dorsal carapace; D-E, *Hemioon cunningtoni* Bell, 1863, syntype SM B 23289, dorsal carapace with large bopyrid swelling in left branchial chamber (D) and ventral view showing sternum (E). Scale bars = 1 cm.

synonymy of *Macroacaena* and *Carinaranina* still stands (see Schweitzer et al., 2000, 2003). We remove several species to new genera that diverge from these characters, described below.

Roberts (1962) originally named *Raninella tridens* from the Late Cretaceous of New Jersey. Van Bakel et al. (2012) illustrated specimens from the Maastrichtian of Mississippi that they referred to *Bournelyreidus tridens* (Roberts, 1962),

Fig. 15. Raninidae, Raninoidinae, *Raninoides fulgidus* Rathbun, 1926b. A, KSU D 667, dorsal carapace; B, KSU D 2161; both specimens from Eocene Hoko River Formation, Washington, USA. Scale bars = 1 cm.

thus transferring the species to that genus. This was followed by Feldmann et al. (2013), who questioned the standing of *Bournelyreidus*. Examination of casts of the Mississippi specimens suggests that they cannot be referred to *Bournelyreidus* because they lack the very long extensions on sternite 5, have a hook-like structure on sternite 5 that does not

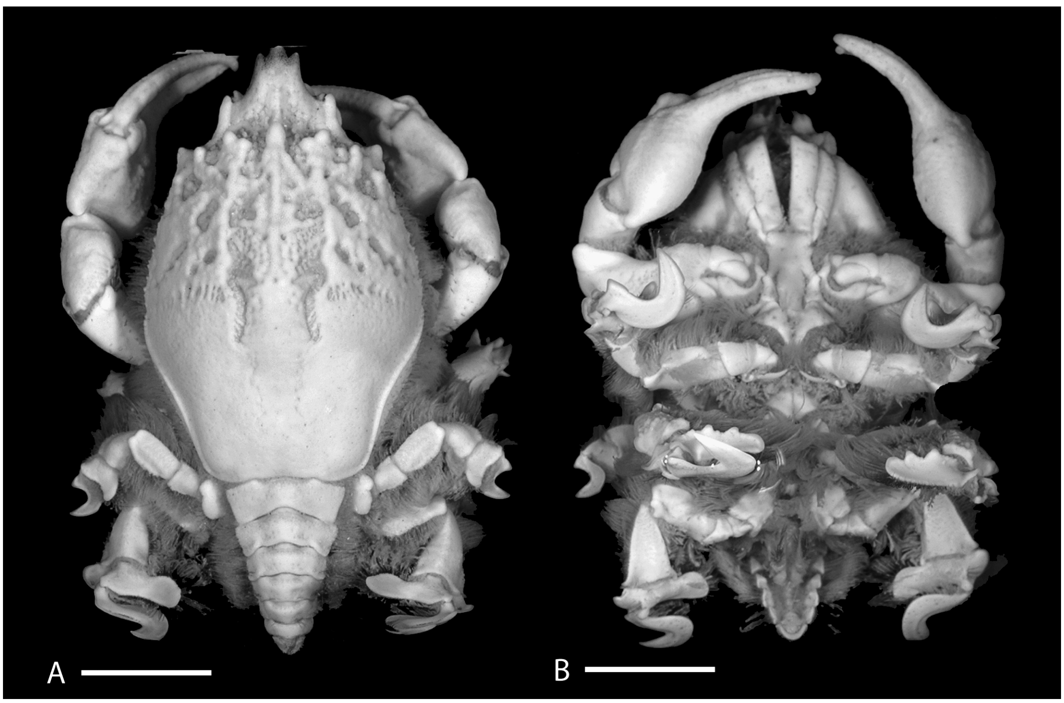

Fig. 16. Raninidae, Symethinae, *Symethis variolosa* (Fabricius, 1798), USNM 273398, dorsal view (A) and ventral view (B). Scale bars = 1 cm.

Fig. 17. Raninidae, Cyrtorhininae. *Claudioranina oblonga* new combination (Beschin, Busulini, de Angeli, and Tessier, 1988), cast of holotype MCZ 1100 numbered KSU D 14. Scale bar = 1 cm.

appear to be present in *Bournelyreidus*, and have an articulation of sternites 4 and 5 similar to that of Lyreidinae and not Marylyreidinae. Those specimens also differ somewhat from the holotype of *Raninella tridens* in being more elongate and in not maintaining their maximum width along the lateral margin. Because none of the specimens has a well-preserved front, and the type material of *R. tridens* lacks a sternum, it is difficult to determine if they are conspecific. Thus, we place *Raninella tridens sensu* Roberts within *Macroacaena*, based upon its possession of an anterior margin about half the maximum carapace width, two anterolateral spines, and what appears to be a flared anterior margin. Recovery of specimens with sternal material could help settle the question of the generic placement of this species. The identity of the Mississippi taxon is currently under study by two of us, who have actual material from the Bishop locality at hand (RMF, CES).

Ilyin and Alekseev (1998) described a new species of raninid that they placed within *Hemioon*, *H. yanini*. Van Bakel et al. (2012) placed that species within *Raninella* based upon their synonymy of *Hemioon* with *Raninella*. Based upon examination of the figures of *H. yanini* (Ilyin and Alkeseev, 1998; Ilyin, 2005), it seems best to place it within *Macroacaena*. The carapace is incomplete, but narrows anteriorly and posteriorly, and retains evidence of two acicular anterolateral spines, intra- and outer orbital spines, and a fronto-orbital width occupying about half the maximum carapace width. This morphology cannot be accommodated in *Bournelyreidus*, which has a wider fronto-orbital width; in *Hemioon*, which seems to lack anterolateral spines; or in *Raninella*, which has a wider carapace anteriorly, wider anterolateral spines, and a distinct postfrontal ridge.

Fujiyama and Takeda (1980) described *Ranidina teshimai*, a new raninid from the upper Eocene Poronai Formation of Japan. Feldmann (1992) suggested that *R. teshimai* might be the junior synonym of *Lyreidus alseanus*. Therefore, Tucker (1998) and van Bakel et al. (2012) synonymised *R. teshimai* with *Macroacaena alseana*. However, Schweitzer et al. (2010) removed *R. teshimai* to *Lyreidus*. *Macroacaena teshimai* new combination appears to differ from *M. alseana* based upon the detailed characters of fronto-orbital and anterolateral margins (Kato and Ando, peronal communication, 2013).

Range.—Paleocene (Selandian)-Eocene (Lutetian-Bartonian).

Lyreidinae Guinot, 1993
Fig. 12

Included Genera.—*Giulianolyreidus* new genus; *Lyreidus* De Haan, 1841; *Ranidina* Bittner, 1893; *Symethoides* van Bakel et al., 2013; *Tribolocephalus* Ristori, 1886.

Diagnosis.—Carapace much longer than wide, oblanceolate; dorsal surface smooth or punctate, regions undefined; anterior margin narrow, rostrum trifid, middle spine generally much longer than other two which serve as inner orbital spines; orbit with intra- and outer orbital spines, supraorbital spine absent; fronto-orbital width less than half to two-thirds maximum carapace width in most taxa; anterolateral margins may be entire or with one or two spines, last spine long; sternum-pterygostome junction poorly to well-developed; gymnopleuran condition present; sternites 1-3 fused, forming a cap-like shape; sternite four large, with lateral extensions anteriorly, concave laterally; sternite 5 of similar shape but smaller, with lyreidid hook (Guinot, 1979) and double peg pleonal locking mechanism composed of curved hooks; sternite 6 much smaller, sometimes with ridge; sternites 7 and 8 much reduced in size; pleon narrow in both males and females, telson short, somite 6 long; spermatheca placed on sternite 7, separated by wall; merus of maxilliped three longer than ischium.

Remarks.—This is the only subfamily within Lyreididae with both fossil and extant genera. It is diagnosed most distinctly by its narrow fronto-orbital width and lyreidinae-type sternum.

Range.—Paleocene (Danian)-Holocene.

Lyreidus De Haan, 1841
Fig. 12A, B

Lysirude Goeke, 1985.

Type Species.—*Lyreidus tridentatus* De Haan, 1841, by monotypy.

Other fossil species.—*Lyreidus antarcticus* Feldmann and Zinsmeister, 1984; *L. bennetti* Feldmann and Maxwell, 1990; *L. elegans* Glaessner, 1960; *L. fastigatus* Rathbun, 1919 (only pereiopod); *L. hookeri* Feldmann, 1992; *L.*

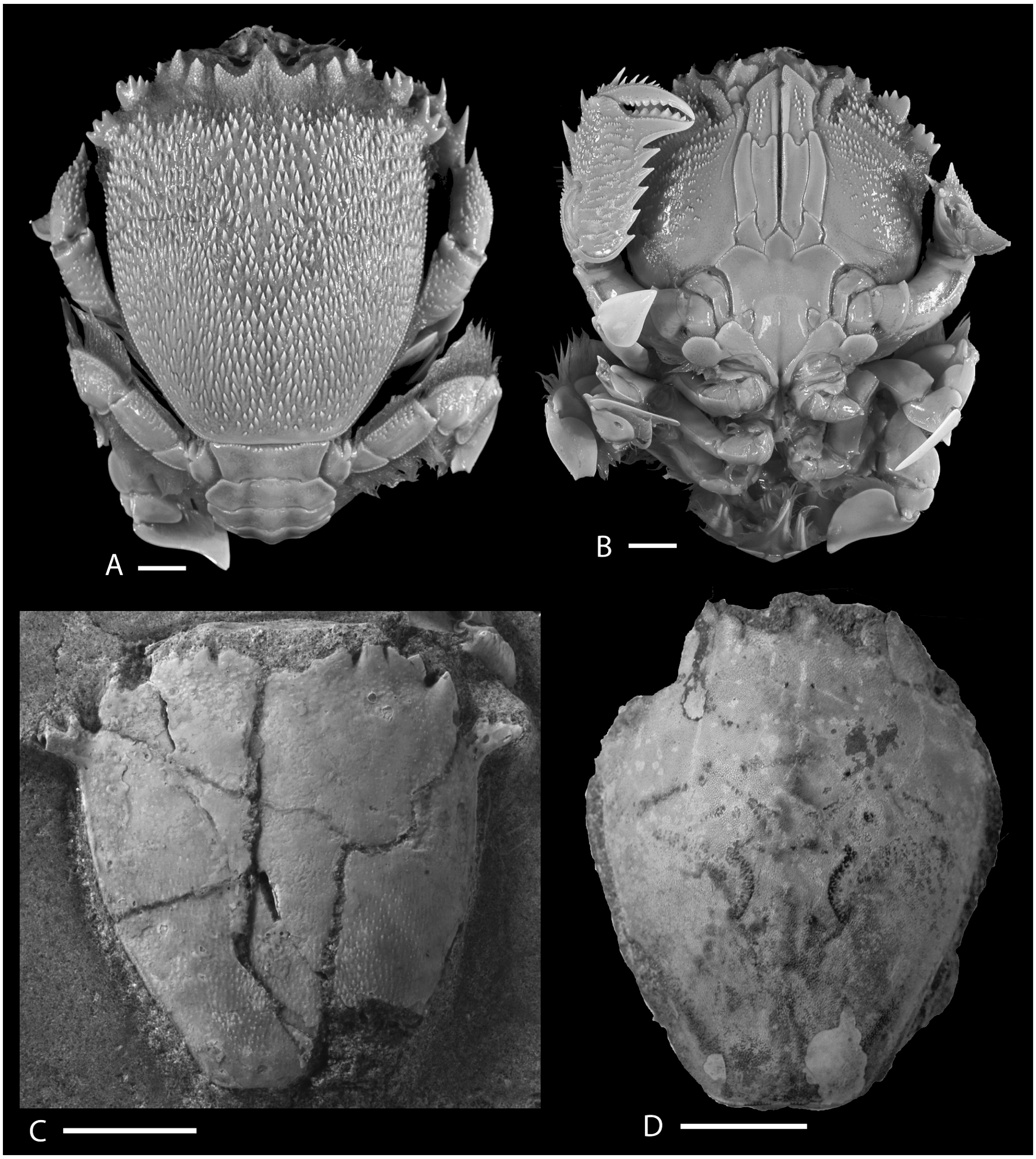

Fig. 18. Raninidae, Ranininae. A-B, *Ranina ranina* (Linnaeus, 1758), USNM 2044, dorsal view (A) and ventral view (B); C, *Ranina americana* Withers, 1924, KSU D 677, dorsal carapace, Eocene Hoko River Formation, Washington, USA; D, *Raninella elongata* A. Milne-Edwards, 1862b, (BMNH) In. 63689, dorsal carapace. Scale bars = 1 cm.

hungaricus Beurlen, 1939; *L. lebuensis* Feldmann, 1992; *L. paronae* Crema, 1895; *L. teodorii* (van Bakel et al., 2012) new combination; *L. waitakiensis* Glaessner, 1980.

Diagnosis.—Carapace elongate, very smooth; anterior margin narrow; rostrum trifid, axial spine much larger than outer spines which serve as inner orbital spines, triangular; outer two spines serving as inner orbital spines; orbit with one fissure and outer orbital spine, fronto-orbital width half or less maximum carapace width; anterolateral margins with one or no spines. Sternites 1-3 fused, short, crown-shaped; sternite 4 long, with concave lateral margins along which coxa of first pereiopod lies, triangularly projected anteriorly, short episternal projection posteriorly; sternal suture 4/5 incomplete, curling into a coiled shape; sternite 5 with wide projections anteriorly, flattened axially, short episternal projections posteriorly; sternites 6 and seven narrow, deep axially. Pterygostome in contact with sternite 4. Pleon narrow, somite 6 very long, sometimes with spines axially on somites.

Material Examined.—*Lyreidus alseanus*, holotype USNM 371901, USNM 431289-431303, CM 35530-35555; *L. antarcticus*, cast of paratype USNM 365450 numbered KSU D 1056; cast of paratype USNM 365444 numbered KSU D 1057; *L. bennetti*, holotype AR 1932, paratype AR 960, cast of paratype AR 955 numbered KSU D 1053; *L. elegans*, holotype DC 123 and paratype DC 108; *L. hookeri*, holotype BAS IN 2397, paratypes BAS IN 2398, 2399, 2401, 2402; *L. hungaricus*, KSU D 1737; *L. lebuensis*, holotype and three paratypes; *L. nitidus* (A. Milne-Edwards, 1880) (as *L. bairdii*), USNM unnumbered; *L. paronae*, KSU D 1673;

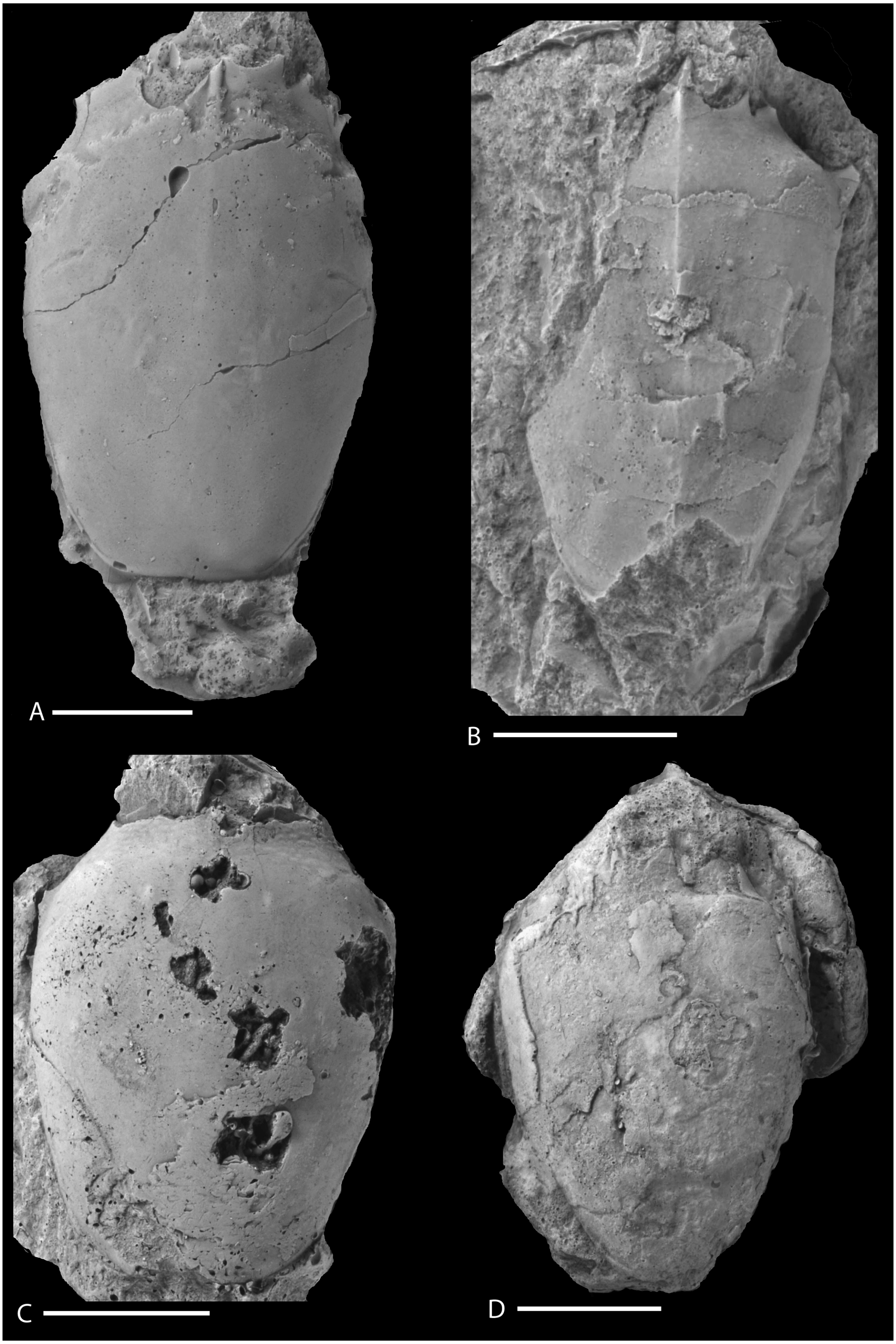

Fig. 19. Raninidae, Notopodinae. A, *Pseudoraninella muelleri* (Van Binkhorst, 1857), cast of holotype MBA 238 numbered KSU D 86; B, *Notopella vareolata* Lőrenthey *in* Lőrenthey and Beurlen, 1929, cast of syntype MAFI Lőrenthey Collection 37 numbered KSU D 55; C, *Raniliformis baltica* (Segerberg, 1900), cast of MGUH 257 numbered KSU D 2162; D, *Notoporanina beyrichi* (Bittner, 1875), cast of Miocene, Hungary, specimen numbered KSU D 1590. Scale bars = 1 cm.

Table 4. Characters and their states for subfamilies within Lyreididae. Abbreviations: Bicorn = Bicornisranininae; Macro = Macroacaeninae; Mary = Marylyreidinae.

Character	Mary	Rogueinae	Macro	Lyreidinae	Bicorn
Fronto-orbital width/width	66-80%	75%	50%	50-60%	60-85%
Rostral tip	Bifid	Bifid	Singular	Singular	Singular
Intra-orbital spines and fissures	Present	Absent	Present	Present	Present
Anterolateral spines	Two	One	Two, one is obscure	None, one, two, one is obscure	One
Sternum type	Mary	Lyreidine	Macro	Lyreidine	Macro
Sternum-Pterygostome articulation	Absent	Present	Present	Present	Present
Sternite 4 anterior projections	Poorly developed	Spine-like	Spine-like	Triangular	Spine-like
Episternal projections on sternite 4	Short, triangular, directed laterally	Short, triangular, directed slightly posterolaterally	Short, triangular, directed slightly posterolaterally	Very short	Short, triangular, directed slightly posterolaterally
Sternal suture 4/5	Incomplete, turning perpendicular to axis	Incomplete, curling into a coiled shape	Incomplete, curling into a coiled shape	Incomplete, curling into a loose coiled shape	Incomplete, curling into a coiled shape
Sternite 5 anterior projection	Very wide, arcuate, usually in contact with pleurite	Wide, triangular, directed laterally	Wide, triangular, directed laterally	Wide, triangular, directed weakly posterolaterally	Wide, triangular, directed laterally
Sternite 6	With lateral ridge		Without lateral ridge	With lateral ridge	

L. tridentatus de Haan, 1841, USNM 63689, 48278; *L. waitakiensis*, Zfc 30.

Remarks.—Many authors consider *Lysirude* as a separate genus from *Lyreidus*. We have been unable to discern a means by which to convincingly distinguish these genera. We place *Bournelyreidus teodorii* van Bakel et al., 2012, within *Lyreidus* herein based upon its fusiform shape, very narrow fronto-orbital margins, which are less than half the maximum carapace width, and reduced anterolateral spines. In *Bournelyreidus*, the fronto-orbital width is at least half of the maximum carapace width. Recovery of ventral material could help confirm placement of this species.

Range.—Eocene (Lutetian)-Holocene.

Ranidina Bittner, 1893

Type and Sole Species.—*Ranidina rosaliae* Bittner, 1893, by monotypy.

Diagnosis.—Carapace elongate-ovate; rostrum small, triangular, with triangular orbital spine; small, triangular anterolateral spine about one-third the distance posteriorly; carapace axially keeled; sternites 1-3 fused; sternites 4 and 5 narrow; pleon narrow.

Remarks.—The material is poorly known and illustrated.

Range.—Miocene.

Giulianolyreidus n. gen.
Fig. 12C, D

Type Species.—*Symethis johnsoni* Rathbun, 1935a, by present designation.

Other Species.—*Giulianolyreidus bidentatus* (Rathbun, 1935a) new combination, as *Symnista*.

Diagnosis.—Maximum carapace width about 35% the distance posteriorly, carapace coarsely punctate; fronto-orbital width about 60% maximum carapace width; orbits and rostrum poorly known, appearing to have had an intra-orbital spine defined by fissures; entire frontal area flared slightly anterolaterally; anterolateral margin short, with one stout anterolateral spine; carapace may have longitudinal keel. Sternites 1-3 fused, short, crown-shaped; sternite 4 long, with concave lateral margins along which coxa of first pereiopod lies, triangularly projected anteriorly, short episternal projection posteriorly; sternal suture 4/5 incomplete, curling into a coiled shape; sternite 5 with wide projections anteriorly, depressed axially, short episternal projections posteriorly; sternites 6 and 7 narrow, deep axially. Pterygostome in contact with sternite 4. Pleon narrow, somite 6 very long. Coxae indicate pereiopods 1-3 reducing in size posteriorly.

Etymology.—The generic name honors the contribution of Giuliano Tessier, Lido de Venezia, Italy, to the study of fossil decapod crustaceans, particularly from the Eocene of Italy. The gender is masculine.

Material Examined.—*Symethis johnsoni*, holotype USNM 328799; paratypes USNM 371691 (20 specimens), 371693; *Symnista bidentata*, holotype USNM 371742.

Remarks.—This genus has a frontal margin occupying about 60% the maximum width, one stout anterolateral spine, a fourth sternite with concave lateral margins and lacking the short anterior projections. Its sternum is more similar to that of *Lyreidus* than that of *Macroacaena*.

Symnista bidentata was named by Rathbun (1935) for a single, poorly preserved, incomplete specimen, collected from the same formation as *Giulianolyreidus johnsoni* new combination. Schweitzer et al. (2010) placed the species within *Macroacaena*. *Symnista bidentata* has a tiny anterolateral spine and a granule between the anterolateral spine and the anterior margin. The anterior margin is very narrow. It differs from *Giulianolyreidus johnsoni* in having additional ornamentation between the anterolateral spine and anterior margin. However, the poor preservation makes it difficult to make additional observations. Thus, at this time is seems best to refer the species to *Giulianolyreidus* based upon its overall similarity to the type species and the fact that they were collected from the same formation.

Range.—Paleocene (Thanetian).

Symethoides van Bakel, Guinot, Artal, Fraiije, and Jagt, 2012

Type and Sole Species.—*Symethoides monmouthorum* van Bakel, Guinot, Artal, Fraiije, and Jagt, 2012, by original designation.

Diagnosis.—Carapace fusiform, longer than wide, granular; front narrow; anterolateral and posterolateral margins about equal in length, anterolateral appearing to be beaded, posterolateral rimmed; carapace axially keeled anteriorly; strongly vaulted transversely, flattened longitudinally.

Remarks.—This genus was originally placed within Symethidae and reasons for exclusion from Lyreididae were given at that time (van Bakel et al., 2012). We herein place it within Lyreidinae, similar in many regards to *Lyreidus*. It has a very narrow fronto-orbital width, similar, for example, to some *Lyreidus tridentatus* in which the fronto-orbital width may be a quarter to one-third the maximum width. The posterolateral margin on species of *Lyreidus* may be rimmed as it is on *Symethoides*. The axial ridge exhibited on *Symethoides* does not appear on any Symethinae, but appears to varying degrees in some Lyreididae including *Macroacaena* and also in other raninoids (Schweitzer et al., 2003). They may be due to preservational biases (Schweitzer et al., 2003, p. 29). Granular ornamentation is not seen in Symethinae; those taxa have very distinctive pitted cuticle with no distinct structures and otherwise exhibit fungiform nodes (Waugh et al., 2009). Marylyreidinae exhibit ornamented carapaces including straps and upright nodes. Thus, Lyreididae (Lyreidinae) seems a better fit for the morphology of *Symethoides*.

Range.—Paleocene (Danian).

Tribolocephalus Ristori, 1886

Type Species.—*Tribolocephalus laevis* Ristori, 1886, by monotypy.

Diagnosis.—Carapace longer than wide; rostrum triangular; outer orbital spines triangular, equal in length to rostrum; carapace with longitudinal keel, granular.

Remarks.—The type material for this taxon has not been located.

Range.—Pliocene.

Bicornisranininae n. subfam.
Fig. 13

Included Genera.—*Bicornisranina* Nyborg and Fam, 2008; a new genus in progress (A. Franţescu, personal communication, September 2013).

Diagnosis.—Carapace ovate; rostrum trifid, lateral two spines forming inner orbital spines, tip singular; intra-orbital spines and fissures present; fronto-orbital width ranging from 60-85% maximum carapace width; one anterolateral spine, which may be bifid; carapace widest at position of anterolateral spine and maintaining that width for anterior quarter of carapace; sternites 1-3 fused, crown-shaped; sternite 4 long, with concave lateral margins along which coxa of first pereiopod lies, short anterolaterally directed spine-like projection anteriorly, short episternal projection posteriorly; sternum and pterygostome articulating; fifth pereiopods with flattened propodi.

Material Examined.—*Ranidina willapensis*, USNM 494633-494643; *Raninoides nodai*, holotype, KMNH IVP 300,0113, paratypes, KMNH IVP 300,014, 300,015; *Carinaranina fudoujii*, holotype, MFM83061, paratypes, MFM83062-83065, KMNH IVP 300,024-300,026.

Remarks.—The subfamily is united by several features of the frontal area and sternum (Table 4). The wide nature of the front and the macrocaenine-type sternum render this subfamily distinctive. A second genus within the family has been submitted for publication, to embrace *Carinaranina fudoujii* Karasawa, 2000, *Raninoides nodai* Karasawa, 1992, and *Ranidina willapensis* Rathbun, 1926b (A. Franţescu, personal communication, September 2013). Karasawa (2000) reported an earliest early Miocene age for *Carinaranina fudoujii*. However, Matsubara et al. (2010) suggested that the formation containing *C. fudoujii* was Oligocene in age based upon molluscan fossils.

Range.—Late Cretaceous (Santonian)-Oligocene.

Bicornisranina Nyborg and Fam, 2008
Fig. 13

Type and Sole Species.—*Bicornisranina bocki* Nyborg and Fam, 2008, by original designation.

Diagnosis.—Carapace ovate; rostrum trifid, lateral two spines forming inner orbital spines; intra-orbital spine very long, as long as rostrum, bounded by open fissures; outer orbital spine bifid, outer branch longer than inner; fronto-orbital width about 85% maximum carapace width; anterolateral spine bifid; carapace widest at position of anterolateral spine and maintaining that width for anterior quarter of carapace; sternites 1-3 fused; sternite 4 long, narrow, with concave lateral margins; fifth pereiopods with flattened propodi.

Remarks.—The genus had been placed within Raninoidinae (De Grave et al., 2009; Schweitzer et al., 2010; van Bakel et al., 2012). Our analysis placed it within Lyreidinae, based upon features of the rostrum and orbits and the macrocaenine-type sternum.

Range.—Late Cretaceous (Santonian).

Marylyreidinae van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012
Fig. 14

Included Genera.—*Bournelyreidus* van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012; *Hemioon* Bell, 1863; *Heus*

Bishop and Williams, 2000; *Marylyreidus* van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012.

Diagnosis.—Carapace much longer than wide, oblanceolate, widest at about mid-length; dorsal surface smooth, regions undefined, ornamented with upright nodes or fungiform nodes; fronto-orbital margin wide, ranging from about two-thirds to 80% maximum carapace width; rostrum trifid, middle spine generally much longer than other two serving as inner orbital spines, middle spine bifid; orbit with intra- and outer orbital spines; anterolateral margins with one or two spines; sternum-pterygostome junction absent; gymnopleuran condition present; sternites 1-3 fused, forming a cap-like shape; sternite 4 narrow, with blunt-triangular episternite directed laterally; sternite 5 with very large lateral projections, arcuate, extending as far as lateral margin of carapace, with lyreidid hook (Guinot, 1979) and double peg pleonal locking mechanism composed of short pegs; sternite 6 much smaller, sometimes with ridge; sternites 7 and 8 much reduced in size; pleon narrow in both males and females, telson short, somite 6 long; spermatheca placed on sternite 7, separated by wall; merus of maxilliped 3 longer than ischium.

Range.—Early Cretaceous (Albian)-Miocene.

Bournelyreidus van Bakel, Guinot, Artal,
Fraaije, and Jagt, 2012
Fig. 14C

Type Species.—*Hemioon eysunesensis* Collins and Rasmussen, 1992, by original designation.

Other Species.—*B. carlilensis* (Feldmann and Maxey, 1980); *B. laevis* (Schlüter *in* Schlüter and Von der Marck, 1868); *B. oaheensis* (Bishop, 1978).

Diagnosis.—Carapace much longer than wide, oblanceolate, widest at about mid-length; dorsal surface smooth, regions undefined; fronto-orbital margin wide, ranging about half to two-thirds maximum carapace width; rostrum overall trifid, middle spine generally much longer than other two which serve as inner orbital spines, central spine bifid at tip; orbit with intra- and outer orbital spines; anterolateral margins with two spines; sternum-pterygostome junction absent, sternite 4 articulating with third maxilliped; sternites 1-3 fused, forming a cap-like shape; sternite four narrow, with short arcuate projections anteriorly, concave laterally, with blunt-triangular episternites directed laterally; sternite 5 with moderate lateral projections, arcuate; chelae flattened, lower margin with spines.

Material Examined.—*Hemioon eysunesensis*, MGUH 86-1983; cast of holotype MGUH 21.592 numbered KSU D 121, cast of paratype MGUH 21.593 numbered KSU D 1806; images of MGUH 21.592-4, provided by Sten Jakobsen; *Raninella oaheensis*, holotype USNM 173589, paratype 173584, cast of CM 34565 numbered KSU D 1722.

Remarks.—*Bournelyreidus* was originally placed within Lyreidinae, but our analysis placed it within Marylyreidinae. *Bournelyreidus* shares some characters with *Marylyreidus*, including the apparent articulation of the sternum with the third maxillipeds (Collins and Rasmussen, 1992, Fig. 10C) and a wide anterior margin of the carapace. The main distinguishing feature of *Bournelyreidus*, based upon the dorsal carapace, seems to be the possession of two anterolateral spines or protuberances. Many lyreidids have a long spine and a short protuberance on the anterolateral margin (species of *Lyreidus*, *Macroacaena*) but not two spines.

Range.—Late Cretaceous (Turonian-Maastrichtian).

Hemioon Bell, 1863
Fig. 14D, E

Type Species.—*Hemioon cunningtoni* Bell, 1863, by monotypy.

Other Species.—*Hemioon callianassarum* (Frič and Kafka, 1887); *H. novozelandicum* Glaessner, 1980.

Material Examined.—*Hemioon cunningtoni*, SM B 23289, herein designated as lectotype for that species, paralectotypes (BMNH) In. 60137, In. 29965; *Raninella atava* Carter, 1898, syntypes (BMNH) 59527; *Hemioon circumviator* Wright and Collins, 1972, holotype (BMNH) In. 60986.

Diagnosis.—Carapace ovate, longer than wide, generally smooth on interior molds, appears to lack anterolateral ornamentation, may have an axial keel; some swellings on carapace mark position of cervical and branchiocardiac grooves on molds of the interior; cuticle ornamented with strap-like ornamentation and nodes; widest about one-third the distance posteriorly; fronto-orbital width about half maximum carapace width; sternites 1-3 fused, cap-shaped; sternite 4 long, with short projections anteriorly, concave laterally, appearing to have short projections posteriorly; sternal suture 4/5 incomplete; sternum appears to be separated from pterygostome by third maxilliped.

Remarks.—Bell (1863) erected *Hemioon cunningtoni*, the type species, for three syntypes, as briefly mentioned by Waugh et al. (2009). The specimens appear dissimilar because two lack cuticle, and the one retaining cuticle is crushed on the right anterolateral margin and has a bopyrid swelling on the left branchial region. Thus, direct comparison of the material is difficult. Since the material named by Bell (1863), no further material has been referred to *H. cunningtoni*. Thus, we elect to retain all three specimens within the species, naming the specimen with cuticle and a sternum as the lectotype. The ornamentation on the carapace, the wide posterior projection on sternite 4, and the apparent articulation of the sternum with the third maxillipeds suggest placement of the genus in Marylyreidinae at this time. It is the only subfamily of Lyreididae in which these features appear and in which the carapace exhibits distinctive ornamentation.

Hemioon and its type species have had a convoluted history, undoubtedly due to the poor nature of the type material. Glaessner (1969, p. R498) maintained the genus as distinct, with Bell's type species, but in the addendum (1969, p. R626), synonymized it with *Raninella* on the advice of Wright and Collins. Wright and Collins (1972) synonymized *Hemioon cunningtoni* with *Raninella elongata*, based on their interpretation that syntype (BMNH) In. 60137 of *Hemioon cunningtoni* was conspecific with *Raninella elongata*. That opinion was followed by van Bakel et al. (2012), who, based upon that species-level synonymy, synonymized the genera *Hemioon* and *Raninella*, following Glaessner (1969).

We do not concur that (BMNH) In. 60137 of *Hemioon cunningtoni* is conspecific with *Raninella elongata*. That syntype of *H. cunningtoni* lacks the depressed frontal margin seen in *Raninella*, and lacks distinct, wide anterolateral spines as seen in *Raninella*. Further, none of the other syntypes of *Hemioon* is referable to *Raninella*, either. The strap-like ornamentation seen in SM B 23289 is not seen in *Raninella*, and the sternum of the specimen is typical of Lyreididae, not Raninidae, which embraces *Raninella*. Thus, *Hemioon* is not synonymous with *Raninella* and, furthermore, belongs in a separate family.

Other taxa, such as *Raninella atava* Carter, 1898, were synonymized with *Hemioon cunningtoni* (Wright and Collins, 1972, p. 87). The type specimen of *Raninella atava* is very poorly preserved, and its sternum, although poorly preserved, seems similar to that of *Raninella trigeri*, the type species of *Raninella*. Thus, we retain *R. atava* in *Raninella*. *Palaeocorystes callianassarum* is similar in appearance, at least in the drawing, to our designated paralectotypes of *Hemioon cunningtoni*. Thus, it seems best to place this species within *Hemioon* until type material can be examined.

Hemioon circumviator, although poorly preserved, is best placed within *Raninella* based upon its possession of anterolateral spines and a wide, inflated, rimmed pterygostomial region, both seen in *Raninella* spp. *Hemioon novozelandicum* is a wide species, maintaining a wide carapace toward the fronto-orbital margin of the carapace, which appears to occupy about 62% the maximum carapace width. Glaessner (1980) reported two spines on the anterolateral margin of this taxon. Feldmann (1993) later illustrated a partial sternum for it, exhibiting clear lyreidid affinities. It also demonstrates muscle scars on the mold of the interior where the cervical and branchiocardiac grooves might be placed as seen in the paralectotypes of *H. cunningtoni*. Thus, this species seems best retained in *Hemioon*.

Range.—Early Cretaceous (Albian)-Late Cretaceous (Maastrichtian).

Heus Bishop and Williams, 2000

Type and Sole Species.—*Heus foersteri* Bishop and Williams, 2000, by original designation.

Other Species.—***Heus manningi*** (Bishop and Williams, 2000) new combination.

Diagnosis.—Carapace obovate, width about 68% length; widest about one-third the distance posteriorly; frontal margin narrow, rostrum triangular, sulcate, with axial keel; orbits with an open fissure and broad outer orbital spine, fronto-orbital width about 58% maximum carapace width; small spine about one-third the distance posteriorly on anterolateral margin; dorsal surface with weak oblong swelling on protogastric region on mold of interior.

Material Examined.—*Heus foersteri*, holotype SDSM 11016 and paratype 11017; *H. manningi*, holotype SDSM 11018 and paratypes 11019-11020.

Remarks.—Placement of *Heus* among the subfamilies of Lyreididae is rather difficult, because the material lacks sternum and pleon. Its dorsal carapace is similar to members of both Lyreidinae and Marylyreidinae in some regards. Van Bakel et al. (2012) differentiated their new genus *Bournelyreidus* from *Heus* by the former having a narrower carapace. Both genera have a carapace that is about 62-68% as wide as long. *Bournelyreidus* was reported to have a wide, bifid front, which we interpret to be the rostrum; that structure appears axially sulcate, axially keeled, and otherwise poorly preserved in *Heus*. The axial keel in *Heus* barely extends onto the dorsal carapace; such a structure is not seen in *Bournelyreidus* spp. Both taxa have orbital fissures, either open or closed. The swellings attributed to *Heus* by van Bakel et al. (2012) are seen on a mold of the interior, which may not be evident if the cuticle were present. Thus, the differences between *Bournelyreidus* and *Heus* are minor and may be species-level differences. In addition, the dorsal carapace of *Heus foersteri* and *Bournelyreidus carlilensis* sensu van Bakel et al. (2012) are very similar. For now, we keep the two genera separate, as many of the main defining characters of *Bournelyreidus* are on the sternum, which *Heus* lacks.

Bishop and Williams (2000) named *Heus* for a species whose holotype lacked cuticle, *Heus foersteri*. Comparison of the photographs and illustrations of *Heus foersteri* and *Raninella manningi* Bishop and Williams, 2000, named in the same paper, strongly suggests that *R. manningi* is a congeneric specimen with preserved cuticle. It may even be conspecific with *H. foersteri*. For now, we maintain the two as separate species of *Heus*. The latter species lacks the wide carapace in the anterior one quarter as seen in *Raninella*. Van Bakel et al. (2012) placed *R. manningi* in *Bournelyreidus*, but for now, we find it more parsimonious to consider it as *Heus*, given its remarkable similarity to the type species of that genus.

Range.—Late Cretaceous (Maastrichtian).

Marylyreidus van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012
Fig. 14A, B

Type and Sole Species.—*Notopocorystes punctatus* Rathbun, 1935a, by original designation.

Diagnosis.—Carapace much longer than wide, oblanceolate, widest at about mid-length; dorsal surface smooth, regions undefined, cuticle composed of fungiform cuticular structures; fronto-orbital margin wide, ranging about half to two-thirds maximum carapace width; rostrum overall trifid, middle spine generally much longer than other two which serve as inner orbital spines, central spine bifid at tip; orbit with intra- and outer orbital spines; anterolateral margins with one spine; sternum-pterygostome junction absent; third maxilliped apparently articulating with sternite 4; sternites 1-3 fused, forming a cap-like shape; sternite four narrow, with blunt-triangular episternites directed laterally; sternite 5 with very large lateral projections, arcuate, reaching to lateral edge of dorsal carapace; posterior pereiopod flattened.

Material Examined.—*Notopocorystes punctatus*, holotype UT 210; *Notopocorystes parvus*, holotype UT 284 (junior subjective synonym of *N. punctata*); SMU-I 50049-68.

Remarks.—*Marylyreidus* is unusual in its very wide lateral projections on sternite 5 and its fungiform cuticular structures.

Range.—Early Cretaceous (Albian).

Lyreididae incertae sedis
Lyreidina Fraaye and van Bakel, 1998

Type and Sole Species.—*Lyreidina pyriformis* Fraaye and van Bakel, 1998, by monotypy.

Diagnosis.—Carapace ovate, longer than wide, widest about two-thirds the distance posteriorly on carapace, moderately vaulted longitudinally and strongly vaulted transversely; rostrum blunt-triangular, with axial carina; inner orbital spines very short. Orbits directed forward, intra-orbital spine very short, rounded, not projecting much beyond orbital rim, longer than outer orbital spine; outer orbital spine very short, rounded; intra-orbital spine bounded by closed fissures. Lateral margins convex, rimmed posteriorly; posterior margin narrow; carapace surface coarsely punctate posteriorly; very subtle Y-shaped epibranchial and cardiac swelling.

Material Examined.—*Lyreidina pyriformis*, holotype, MAK k.2251.

Remarks.—This genus is problematic, and it is unclear as to where to place it. Indeed, van Bakel et al. (2012) placed it as incertae sedis. The ovate carapace is widest about two-thirds the distance posteriorly and exhibits distinctive punctate ornamentation. We place the genus within Lyreididae at this time largely as there is no other family to accommodate it.

Range.—Late Cretaceous (Maastrichtian).

Raninidae de Haan, 1839
Figs. 15-19

Included Subfamilies.—Cyrtorhininae Guinot, 1993; Notopodinae Serène and Umali, 1972; Ranininae de Haan, 1839; Raninoidinae Lőrenthey *in* Lőrenthey and Beurlen, 1929; Symethinae Goeke, 1981.

Diagnosis.—Carapace longer than wide, generally ovate, usually vaulted transversely; usually with rostrum and orbital spines; anterolateral margin generally with between 1 and 3 spines; posterolateral margin long, usually entire; carapace regions generally undifferentiated; branchiocardiac groove developed as boundary of urogastric region; gymnopleuran condition present; sternum narrow, sternites 1-3 generally fused, sternites 4 and 5 flattened, sternite 6 raised, sternites 7 and 8 often reduced and at lower level than other sternites, sternite 7 extremely narrow, sternal suture 5/6 complete; pleon narrow in males and females, showing reduced but clear dimorphism, sterno-pleonal depression absent, pleonal locking mechanism absent, pleon unfolded and often extending posteriorly from carapace, pleonal somite 6 as long as somite 5; genital openings coxal, spermatheca present; basis of third maxilliped fused to ischium; chelipeds usually with distinct chelae with finger oriented at nearly right angles to manus; fifth pereiopod may be modified for burrowing.

Range.—Late Cretaceous (Cenomanian)-Holocene.

Raninoidinae Lőrenthey *in* Lőrenthey and Beurlen, 1929
Fig. 15

Included Genera.—*Bonizzatoides* Beschin, Busulini, and Tessier, 2013; *Cristafrons* Feldmann et al., 1993; *Notopoides* Henderson, 1888; *Notosceles* Bourne, 1922; *Pseudorogueus* Fraaye, 1995; *Quasilaeviranina* Tucker, 1998; *Raninoides* H. Milne Edwards, 1837 [in 1834-1840].

Diagnosis.—Carapace elongate; frontal margin generally wide, rostrum and orbital spines well-developed, generally long, orbit often with long orbital fissures; anterolateral margin with one spine; sternites 1-4 fused, 1-3 forming cap-like structure, sternite four with lateral projections anteriorly and posteriorly; sternite five reduced; sternite six very long, wide contact between sternite 6 and pleurite 6; sternites 7 and 8 narrow, long; spermathecae very closely spaced; sternum often with longitudinal groove on sternites 5-8; pleon markedly sexually dimorphic, all somites wider in females than in males.

Remarks.—Schweitzer et al. (2010) placed *Notopoides*, *Notosceles*, *Quasilaeviranina*, and *Raninoides* within Raninoidinae, which this analysis confirmed. *Bicornisranina* and *Cenocorystes*, also placed in the subfamily in that work, have been placed elsewhere as discussed. *Cristafrons* and *Pseudorogueus*, not included in our analysis, are also placed within Raninoidinae here, following Schweitzer et al. (2010) and van Bakel et al. (2012).

Range.—Late Cretaceous (Santonian)-Holocene.

Bonizzatoides Beschin, Busulini, and Tessier, 2013

Type and Sole Species.—*Bonizzatoides tuberculatus* Beschin, Busulini, and Tessier, 2013.

Diagnosis.—"Long transversally convex carapace. Wide fronto-orbital margin; wide rostrum with three well developed triangular teeth; the middle one the largest; small triangular upper orbital tooth enclosed, outer orbital tooth pointed. Short convex anterolateral margins with a small spine; long weakly concave convergent posterolateral margins. Short fronto-orbital region bounded by a weak sinuous ridge concave in the middle part. Dorsal regions not defined. Smooth surface with one tubercle on each protogastric region, two on the mesogastric and the cardiac ones and other isolated ones on the branchial region. Wide thoracic sternite 4 with transverse anterior margin, very wide sternite 5, axially sulcate sternites 5 and 6. Arched and smooth upper margins of the chelipeds." (Beschin, Busulini, and Tessier, 2013, p. 118.)

Range.—Eocene (Lutetian).

Cristafrons Feldmann, Tshudy, and Thomson, 1993

Type and Sole Species.—*Cristafrons praescientis* Feldmann et al., 1993, by original designation.

Diagnosis.—Carapace ovate; rostrum with long triangular central spine, axially broadly sulcate and with keel in sulcus, two spines to either side of central rostral spine, short, forming inner orbital spines; intra-orbital spine not projecting beyond orbital rim, bounded by open fissures; outer orbital spine long, as long as or longer than rostrum; anterolateral spine stout at base, drawing into more slender spine distally; post-frontal ridge sinuous; cervical groove deep.

Material Examined.—*Cristafrons praescientis*, holotype BAS.IN. 2225, paratypes BAS.IN. 2206, 2207, 2220-2222, 2224, 2226-2234, 2247, 2427, 2429, and 2432.

Range.—Late Cretaceous (Santonian).

Notopoides Henderson, 1888

Type Species.—*Notopoides latus* Henderson, 1888, by monotypy.

Included Fossil Species.—*Notopoides exiguus* Beschin et al., 1988; *N. nantoensis* Beschin, Busulini, and Tessier, 2013; *N. pflugervillensis* Beikirch and Feldmann, 1980; *N. verbeeki* Böhm, 1922.

Diagnosis.—Carapace obovate, widest in anterior third; rostrum triangular, two spines on either side of central rostral spine, short, forming inner orbital spines; intra-orbital spine triangular, bounded by open fissures; outer orbital spine triangular; anterolateral margins entire or with tiny serrations; postfrontal ridge very well developed.

Material Examined.—*Notopoides latus*, RGM 28567; *N. pflugervillensis*, holotype 1238TX23, paratypes 1238TX22, 25-28; *N. verbeeki*, cast of holotype RGM 11738 numbered KSU D 434.

Range.—Late Cretaceous (Campanian)-Holocene.

Notosceles Bourne, 1922

Type Species.—*Notosceles chimmonis* Bourne, 1922, by monotypy.

Included Fossil Species.—*Notosceles bournei* Rathbun, 1928; *N. serratifrons* (Henderson, 1893).

Diagnosis.—Carapace elongate-rectangular; rostrum with triangular central spine that is itself serrate, two spines to either side of central rostral spine, short, forming inner orbital spines, serrate; intra-orbital spine triangular, short, bounded by short open fissures; outer orbital spine triangular; anterolateral spine positioned only a short distance from outer orbital spine.

Material Examined.—*Notosceles bournei*, holotype USNM 369608, paratype USNM 371525, hypotype USNM 371696; *N. chimmonis*, USNM 134655.

Remarks.—*Notosceles serratifrons* was reported by Hu and Tao (1999, as *Raninoides*) from the late Pliocene of Taiwan. Several extant species are known from the Indo-Pacific region.

Range.—Paleocene/Eocene-Holocene.

Pseudorogueus Fraaye, 1995

Type and Sole Species.—*Pseudorogueus rangiferus* Fraaye, 1995, by original designation.

Diagnosis.—Carapace ovate; rostrum trifid, lateral two spines forming inner orbital spines; intra-orbital spine long, bounded by open fissures; outer orbital spine bifid, outer branch longer than inner; anterolateral spine long, with three small spines on upper surface.

Remarks.—This genus had been synonymized with *Raninoides*, but the outer orbital spines that are themselves spinose suggest a unique generic status. Lack of sternal anatomy makes placement in Raninoidinae the best placement for the genus at this time.

Range.—Eocene (Ypresian).

Quasilaeviranina Tucker, 1998

Type Species.—*Ranina simplicissima* Bittner, 1883, by original designation.

Other Species.—*Q. arzignanensis* (Beschin, Busulini, de Angeli, and Tessier, 1988); *Q. eocenica* (Rathbun, 1935a) new combination; *Q. keyesi* (Feldmann and Maxwell, 1990); *Q. miniscula* Beschin et al., 2012; *Q. ombonii* (Fabiani, 1910); *Q. ovalis* (Rathbun, 1935a); *Q. pororariensis* (Glaessner, 1980); *Q. simplicissima* (Bittner, 1883).

Diagnosis.—Carapace ovate, wide for subfamily; rostrum triangular, two spines to either side of central rostral spine, short, forming inner orbital spines; intra-orbital spine triangular, bounded by closed fissures; outer orbital spine triangular; postfrontal ridge well-developed.

Material Examined.—*L. keyesi*, cast of AR 958 numbered KSU D 11323; *Raninella eocenica*, holotype USNM 371701, paratypes USNM 371700 (2 specimens); *Raninella ovalis*, cotypes USNM 371689; *Raninoides simplicissima*, KSU D 1652.

Remarks.—To the published lists of species in *Quasilaeviranina* (Schweitzer et al., 2010; van Bakel et al., 2012), we add *Q. eocenica*, originally referred to *Raninella* and maintained by those authors in that genus. Examination of type material suggests that it is better placed in *Quasilaeviranina* based upon its tiny anterolateral spines which are short and needle like, different than the usually broad, flattened anterolateral spines of *Raninella*. *Quasilaeviranina eocenica* is not well preserved and lacks sternal material which could help confirm its generic placement.

Range.—Paleocene-Eocene (Priabonian).

Raninoides H. Milne Edwards, 1837 [in 1834-1840]
Fig. 15

Laeviranina Lőrenthey *in* Lőrenthey and Beurlen, 1929.
Raninellopsis Böhm, 1922.

Type Species.—*Ranina laevis* Latreille, 1825, by monotypy.

Fossil Species.—*R. acanthocolus* Schweitzer, Feldmann, Gonzalez-Barba, and Ćosović, 2006; *R. araucana* (Philippi, 1887); *R. asper* Rathbun, 1926b; *R. barnardi* Sakai, 1974 (also extant); *R. benedicti* Rathbun, 1935b (also extant); *R. borealis* (Collins and Rasmussen, 1992); *R. budapestiniensis* (Lőrenthey, 1897); *R. dickersoni* Rathbun, 1926b; *R. eugenensis* Rathbun, 1926b; *R. fabianii* (Lőrenthey *in* Lőrenthey and Beurlen, 1929); *R. fulgidus* Rathbun, 1926b; *R. fulungensis* Hu and Tao, 1999; *R. glabra* (Woodward, 1871) *R. goedertorum* (Tucker, 1998); *R. gottschei* Böhm, 1927; *R. hollandica* (Collins et al., 1997); *R. javanus* (Böhm, 1922); *R. louisianensis* Rathbun, 1933 (also extant); *R. madurensis* Beets, 1950; *R. mexicanus* Rathbun, 1930; *R. morrisi* Collins et al., 2003; *R. notopoides* (Bittner, 1883); *R. oregonensis* Rathbun, 1926b; *R. perarmata* (Glaessner, 1960); *R. pliocenicus* de Angeli et al., 2009; *R. proracanthus* Schweitzer, Feldmann, Gonzalez-Barba, and Ćosović, 2006; *R. pulchra* (Beschin, Busulini, de Angeli, and Tessier, 1988); *R. rathbunae* van Straelen, 1933; *R. rioturbiensis* Schweitzer et al., 2012; *R. sinuosus* (Collins and Morris, 1978); *R. slaki* Squires, 2001; *R. treldenaesensis* Collins and Jakobsen, 2003; *R. vaderensis* Rathbun, 1926b (= *Laeviranina lewisana* Rathbun, 1926b); *R. toehoepae* (van Straelen, 1924 [imprint 1923]) *R. washburnei* Rathbun, 1926b.

Diagnosis.—Carapace longer than wide, length about 70% maximum carapace width but may be as low as 60% and as high as 90%; rostrum with triangular central spine and triangular lateral spines which also form inner orbital spines, rostral width about 30-40% maximum carapace width; upper orbital margin with open grooves, narrow grooves, or fissures; intra-orbital spine well-developed; outer orbital spine bifid; one-anterolateral spine; carapace with or without post-frontal ridge; sternites 1-3 fused; sternite 4 long, with anterior and posterior lateral projections, concave between projections; sternite 5 very short and narrow; sternite 6 widening posteriorly, with arcuate, biconcave posterior margin; posterior portion of sternite 4 and sternites 5 and 6 with longitudinal groove.

Material Examined.—*Laeviranina borealis*, cast of MGUH 21.590 numbered KSU D 125; *L. sinuousa*, holotype (BMNH) In. 48241; *Raninellopsis javanus*, cast of holotype RGM st.11737 numbered KSU D 433; *Raninoides acanthocolus*, holotype MHN-UABCS/Ba12-6; *R. budapestiniensis*, KSU D 1538; *R. gottschei*, cast of JSH Collins coll. 1708 numbered KSU D 1522; *R. permarmata*, cast of OU 12920 numbered KSU D 689; *R. proracanthus*, holotype MHN-UABCS/Ba12-7, paratype MHN-UABCS/Ba12-8; *R. rathbunae*, cast of paratype SM X/m 3/a (2 specimens); *R. vaderensis*, KSU D 665, 672

Range.—Eocene (Ypresian)-Holocene.

Symethinae Goeke, 1981
Fig. 16

Included Genera.—*Eosymethis* van Bakel et al., 2013; *Symethis* Weber, 1795.

Diagnosis.—Carapace elongate, ovoid, widest at midlength; rostrum extended well beyond anterolateral margin; eyes very small; fronto-orbital width about half maximum carapace width, inner orbital fissure absent, outer orbital fissure weak, inner and outer orbital lobes absent; carapace anterior to cervical groove deeply pitted; buccal cavity elongate, narrow, completely closed by third maxilliped which lies in two planes; pterygostome-sternum junction very narrow; sternum with spermathecae well separated, hooded; sternite 3 clearly divided from sternite 4; sternite 5 medially raised; sternite 6 very narrow; pleon sexually dimorphic, triangular in males, broad and parallel sided in females. Cheliped with carpus/propodus articulation transverse to long axis of arm, fixed finger and dactylus not strongly deflected; pereiopods 2-5 with crescentic dactyli; pereiopod 5 subdorsal, coxa large.

Remarks.—New genera have been named subsequent to the list in Schweitzer et al. (2010). The sole fossil species of *Symethis* is now recognized as a lyreidid. *Symethoides* has been placed here within Lyreidinae. Thus, the fossil record of the subfamily is sparse.

Range.—Eocene (Ypresian)-Holocene.

Eosymethis van Bakel, Guinot, Artal, Fraiije, and Jagt, 2012

Type and Sole Species.—*Eosymethis aragonensis* van Bakel, Guinot, Artal, Fraiije, and Jagt, 2012, by original designation.

Diagnosis.—Carapace ovate, longer than wide if rostral length included, carapace surface punctate; anterolateral margin longer than posterolateral margin, anterolateral margin sinuous, posterolateral margin concave; axial region of carapace somewhat inflated; branchiocardiac groove developed as arcs on either side of axis, straight groove segment on either side of carapace extending anteriorly from anterolateral corner; rostrum with straight margin at base, terminating in triangular tip; at least one of pereiopods with sickle-like dactyl.

Range.—Eocene (Ypresian).

Symethis Weber, 1795
Fig. 16

Type Species.—*Hippa variolosa* Fabricius, 1787.

Diagnosis.—"Carapace ovate, convex from side to side and from before backward, its surface partly uneven. Fronto-orbital border very narrow, considerably less than half the width of carapace, frontal region trilobate produced anteriorly. Eyes rudimentary, placed in ill-defined orbits; the peduncles short, and the corneae of small size though pigmented. Antennal peduncle massive, first segment fused with carapace, second with a very prominent external prolongation; flagellum short. Antennules small, completely concealed by the antennal peduncles, which meet in the middle line. Outer maxillipeds moderately broad, ischium twice the length of the merus. Sternal thoracic shield narrow, becoming linear between ambulatory legs of first pair, but slightly dilating again between first and second pairs. Chelipeds of considerable length, propodus swollen laterally, fingers long. Ambulatories with uncinate dactyli, last pair of small size but not filiform. Male generative appendages similar to but shorter than those of *Raninoides*." (Rathbun, 1937b, p. 24)

Material Examined.—*Symethis variolosa*, USNM 273398.

Range.—Holocene.

Cyrtorhininae Guinot, 1993 [Cyrthorhinae Guinot, 1993]
Fig. 17

Included Genera.—*Cyrtorhina* Monod, 1956; *Antonioranina* van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012; *Claudioranina* new genus.

Diagnosis.—Carapace ovate, longer than wide, bulbous, widest at about mid-length; rostrum trifid, central spine longest, outer two spines also forming inner orbital spines; orbits with intra- and outer orbital spines; entire frontal area including rostrum and orbits set at lower level than remainder of carapace, fronto-orbital width about half maximum carapace width; anterolateral margin with at least two spines excluding outer orbital spine; carapace surface granular in post-frontal region, remainder relatively smooth; junction between pterygostome and sternum narrow; sternites 1-3 fused, small; sternites 3 and 4 narrow; sternite 4 long, with two grooves parallel to lateral margins, flattened; sternite 5 wider, with axial groove, raised; sternite six diamond shaped, with axial groove, sternum very narrow between sternites 5 and 6; sternites 7 and 8 reduced; male pleon triangular; coxa of pereiopod 5 large.

Range.—Eocene (Ypresian)-Holocene.

Cyrtorhina Monod, 1956

Type Species.—*Cyrtorhina granulosa* Monod, 1956, by monotypy.

Diagnosis.—Carapace ovate, approaching circular in shape; anterolateral margin with multiple spines and granules; anterior areas of carapace granular; chelae may have long spines on fixed finger and upper margin of propodus; sternites 1-3 fused T-shaped; sternite 4 narrow, with arcuate lateral grooves; sternite 5 wide anteriorly, with rounded lateral margins, narrowing posteriorly, sternite 6 short, wide.

Remarks.—Van Bakel et al. (2012) restricted *Cyrtorhina* to only the extant species, based largely upon sternal features. Indeed, *Antonioranina* is very similar to it based upon dorsal carapace features.

Range.—Holocene.

Antonioranina van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012

Type Species.—*Cyrtorhina globosa* Beschin, Busulini, de Angeli, and Tessier, 1988, by original designation.

Other Species.—*A. fusseli* (Blow and Manning, 1996); *A. ripacurtae* (Artal and Castillo, 2005).

Diagnosis.—Carapace ovate, approaching circular in shape; fronto-orbital margins continuous with anterolateral margins; anterolateral margins with two or three spines; anterior portion of carapace may be granular; chelae appearing to lack long spines; sternites 1-3 fused, flattened; sternite 4 with straight lateral grooves; sternite 5 moderately wide anteriorly, with straight to slightly concave lateral margins, narrowing posteriorly, sternite 6 moderately long, wide, with triangular lateral extensions.

Material Examined.—*Antonioranina fusseli*, CM 36010, 36011.

Remarks.—Van Bakel et al. (2012) placed the fossil species previously assigned to *Cyrtorhina* into *Antonioranina*. They questioned the placement of *Cyrtorhina oblonga* within *Antonioranina* based upon its different sternum and dorsal carapace. Herein we place it in a new genus.

Range.—Eocene (Ypresian-Lutetian).

Claudioranina n. gen.
Fig. 17

Type Species.—*Cyrtorhina oblonga* Beschin, Busulini, de Angeli, and Tessier, 1988, by present designation.

Diagnosis.—Carapace oblong, anteriorly and posteriorly narrowed; frontal margin set distinctly below level of remainder of carapace, fronto-orbital margin not grading smoothly into anterolateral margin, forming about 120° angle between outer orbital spine and anterolateral margin; anterolateral margin with 2 spines; posterolateral margin sinuous, centrally concave; sternite 3 wide; sternite 4 wide, with arcuate lateral grooves; sternite 5 moderately widened anteriorly, with a slight projection anteriorly that articulates with or slightly overlaps posterior margin of sternite 4; with straight to lateral margins, narrowing posteriorly, sternite 6 moderately long and wide, with straight lateral margins.

Etymology.—The genus name honors the contribution of Claudio Beschin, Montecchio Maggiore, Italy, to the study of fossil decapod crustaceans, particularly from the Eocene of Italy. The gender is feminine.

Material Examined.—*Cyrtorhina oblonga*, cast of holotype MCZ 1100 numbered KSU D 14.

Remarks.—*Claudioranina* differs from the other genera in the family in having a carapace that narrows anteriorly and posteriorly, a fronto-orbital region that does not merge confluently with the anterolateral margins, and different shapes of sternites 3-5. Van Bakel et al. (2012) had already noted that the type and sole species herein referred to *Claudioranina* differed from other members of the family.

Range.—Eocene (Lutetian-Bartonian).

Subfamily Ranininae de Haan, 1839
Fig. 18

Included Genera.—*Lophoranina* Fabiani, 1910; *Lophoraninella* Glaessner, 1946; *Ranina* Lamarck, 1801; *Raninella* A. Milne-Edwards, 1862; *Remyranina* Schweitzer and Feldmann, 2010; *Vegaranina* van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012.

Diagnosis.—Carapace ovate, wide; orbits well-ornamented with many spines, which themselves may be complex, outer orbital spine well developed; usually two anterolateral spines which may be complex, anterolateral spines may exhibit sexual dimorphism (see Feldmann and Schweitzer, 2007, for example); dorsal surface scabrous or terraced; sternites 1-4 forming a distinctive trifid form anteriorly and with concave sides laterally; sternite 5 coming to a V-shape posteriorly; sternites 5-8 very reduced, spermatheca very closely spaced; pleon sexually dimorphic, somites 1 and 2 equal in width in males, somite 2 wider than 1 in females.

Range.—Late Cretaceous (Cenomanian)-Holocene.

Lophoranina Fabiani, 1910

Type Species.—*Ranina marestiana* König, 1825, by original designation.

Other Species.—*Lophoranina aculeata* (A. Milne-Edwards, 1881); *L. albeshtensis* Schweitzer, Feldmann, and Lazăr, 2009; *L. aldrovandii* (Ranzani, 1820); *L. bakerti* (A. Milne-Edwards, 1872); *L. barroisi* (Brocchi, 1877); *L. bishopi* Squires and Demetrion, 1992; *L. bittneri* (Lőrenthey, 1902); *L. cinquecrista* Feldmann, Schweitzer, Bennett, Franţescu, Resar, and Trudeau, 2011; *L. cristaspina* Vega, Cosma et al., 2001; *L. georgiana* (Rathbun, 1935a); *L. kemmelingi* van Straelen, 1924 [imprint 1923]; *L. laevifrons* (Bittner, 1875); *L. levantina* Lewy, 1977; *L. maxima* Beschin et al., 2004; *L. persica* Withers, 1932; *L. porifera* (Woodward, 1866); *L. quinquespinosa* (Rathbun, 1945); *L. raynorae* Blow and Manning, 1996; *L. reussi* (Woodward, 1866); *L. rossi* Blow and Manning, 1996; *L. soembaensis* van Straelen, 1938; *L. straeleni* Vía, 1959; *L. tchihatcheffi* (A. Milne-Edwards, 1866); *L. toyosimai* Yabe and Sugiyama, 1935.

Diagnosis.—Carapace generally widest in anterior one-quarter, narrowing posteriorly; rostrum trifid, axial two spines serving as inner orbital spines, central spine itself may be trifid; intra- and outer orbital spines triangular or bifid; anterolateral margin generally with two spines that may be bifid or themselves ornamented with granules or spinelets; postfrontal region depressed slightly below level of remainder of carapace, can be granular or scabrous; carapace surface with well-developed, transverse terraces; terraces relatively narrowly spaced, usually parallel to one another anteriorly, often interfingered with one another or intersecting posteriorly; terraces ornamented with tiny, forward directed spines; pterygostome, pleonal somites, and appendages ornamented with terraces; sternites 1-5 with scattered scabrous ornamentation.

Material Examined.—*Lophoranina albeshtensis*, holotype LPBIIIart007; *L. bishopi*, MHN-UABCS/Te14/66-65, 66-66; *L. bittneri*, KSU D 1606; *L. cinquecristata*, holotype SMNS 67887; *L. cristaspina*, holotype IHNCH 3428, paratypes IHNCH 3429-3460; *L. marestiana*, cast of MNHN R03371 numbered KSU D 45, cast of LPBIIIar021 numbered KSU D 231; *L. raynorae*, CM 36004-36009; *L. tchihatcheffi* cast of MNHN specimen numbered KSU D 46.

Range.—Eocene (Ypresian)-Miocene.

Lophoraninella Glaessner, 1946

Type and Sole Species.—*Ranina cretacea* Dames, 1886, by original designation.

Diagnosis.—Carapace with short, scabrous ornamentation in anterior third, serrate transverse ornamentation on remainder of carapace; sternite 4 appearing widened anteriorly, narrowing posteriorly.

Remarks.—Van Bakel et al. (2012) placed the genus within Ranininae based upon the sternum and buccal frame. The material is crushed and poorly preserved, but the apparent raninoid-type sternum and transverse, spinose ridges seems to confirm placement in Ranininae.

Range.—Late Cretaceous (Cenomanian).

Ranina Lamarck, 1801
Fig. 18A-C

Type Species.—*Cancer raninus* Linnaeus, 1758, by subsequent designation.

Other Species.—*Ranina americana* Withers, 1924; *R. bavarica* Ebert, 1887; *R. berglundi* Squires and Demetrion, 1992; *R. bouilleana* A. Milne-Edwards, 1872; *R. brevispina* Lőrenthey, 1898b; *R. burleighensis* Holland and Cvancara, 1958 (claw only); *R. cuspidata* Guppy, 1909; *R. elegans* Rathbun, 1945; *R. granulosa* A. Milne-Edwards, 1872; *R. griesbachi* Noetling, 1897; *R. haszlinskyi* Reuss, 1859; *R. hirsuta* Schafhäutl, 1863; *R. lamiensis* Rathbun, 1945; *R. libyca* (van Straelen, 1935 [imprint 1934]); *R. molengraaffi* van Straelen, 1924 [imprint 1923]; *R. oblonga* Münster, 1840; *R. ornata* de Angeli and Beschin, 2011; *R. palmea* E. Sismonda, 1846; *R. pellattieroi* de Angeli and Beschin, 2011; *R. propinqua* Ristori, 1891; *R. ranina* (Linnaeus, 1758) (type, fossil and extant); *R. speciosa* (Münster, 1840); *R. tejoniana* Rathbun, 1926b.

Diagnosis.—Carapace generally widest in anterior one-quarter, narrowing posteriorly; rostrum trifid, with axial two spines serving as inner orbital spines, central spine triangular; intra- and outer orbital spines triangular; anterolateral margin generally with two spines that are bifid or trifid, often larger and more complexly ornamented in males; postfrontal region depressed slightly below level of remainder of carapace, can be granular or scabrous; remainder of carapace ornamented with forward directed spines; appendages and pterygstome ornamented with less densely-spaced spines; sternum smooth.

Material Examined.—*Ranina granulosa*, holotype (BMNH) I. 8085; *R. americana*, holotype (BMNH) In. 23798, KSU D 675-678; *R. berglundi*, MHN-UABCS/Ba7-3, MHN-UABCS/Ba10-10, MHN-UABCS/Ba10-9; *R. ranina*, USNM 2044; *R. speciosa*, cast of Humboldt-Universität zu Berlin specimen numbered KSU D 81.

Remarks.—*Ranina* is the only extant genus within the family. *Ranina griesbachi* Noetling, 1897, had at some point been transferred to *Raninella* (Glaessner, 1929; Schweitzer et al., 2010; van Bakel et al., 2012), perhaps because of its Late Cretaceous age. Its wide anterolateral margins; wide, bifid outer orbital spine; and scabrous carapace ornamentation (Noetling, 1897: pl. 22.4) can be best accommodated in *Ranina*, which has all of these characteristics. Furthermore, *Ranina griesbachi* seems to lack the narrower fronto-orbital width and postfrontal ridge seen in *Raninella*.

Range.—Late Cretaceous (Maastrichtian)-Holocene.

Raninella A. Milne-Edwards, 1862
Fig. 18D

Type Species.—*Raninella trigeri* A. Milne-Edwards, 1862, by original designation.

Other Species.—*Raninella atava* Carter, 1898; *R. circumviator* (Wright and Collins, 1972); *R. elongata* A. Milne-Edwards, 1862; questionably *R. quadrispinosa* Collins et al., 1995.

Diagnosis.—Carapace ovate, widest about half the distance posteriorly, surface covered by densely spaced inclined nodes; fronto-orbital width about two-thirds the maximum carapace width, rostrum trifid, axial two spines serving as inner orbital spines, central spine triangular; intra-orbital spine blunt; outer orbital spine triangular, may be directed forward or outer edge curved axially; anterolateral margin generally with two spines that are flattened, triangular or more narrow; postfrontal region depressed below level of remainder of carapace, forming a postfrontal ridge; pterygostome with closely spaced nodes; chelipeds may have granular or scabrous ornamentation.

Material Examined.—*Hemioon circumviator*, holotype (BMNH) In. 60986; *H. elongata*, (BMNH) In. 31302, 63689; *Raninella elongata*, (BMNH) In. 61371-72.

Remarks.—Herein we restrict the composition of *Raninella* as compared to recent authors (Schweitzer et al., 2010; van Bakel et al., 2012). The maintenance of *Hemioon* as a distinct genus removes several species from *Raninella*, and several others have been placed in other taxa as discussed above. *Raninella quadrispinosa* is only questionably referred to *Raninella* and probably does not belong within it. The specimens exhibit a carapace that is widest at about the midlength, but they seem to lack the postfrontal ridge seen in *Raninella*. The poor preservation of the front as illustrated for this species makes it difficult to determine a generic placement for it.

Range.—Late Cretaceous (Cenomanian-Maastrichtian).

Remyranina Schweitzer and Feldmann, 2010

Type and Sole Species.—*Raninella ornata*, Remy, 1960, by original designation.

Diagnosis.—Small raninine; carapace ovate, widest about half the distance posteriorly on carapace; fronto-orbital width about two-thirds maximum carapace width, fronto-orbital margin set below level of remainder of carapace; anterolateral margins appearing to have had two projections; carapace ornamentation granular in anterior half and strongly terraced in posterior half, terraces with small, anteriorly projecting spines.

Material Examined.—*Raninella ornata*, holotype MNHN R03847.

Range.—Eocene.

Vegaranina van Bakel, Guinot, Artal, Fraaije, and Jagt, 2012

Type and Sole Species.—*Lophoranina precocious* Feldmann, Vega, Tucker, García-Barrera, and Avendaño, 1996, by original designation.

Diagnosis.—Carapace generally widest in anterior one-quarter, narrowing posteriorly; rostrum trifid, axial two spines serving as inner orbital spines, central spine itself trifid; intra-orbital spine blunt, outer orbital spine bifid; anterolateral margin generally with three triangular, flattened spines; postfrontal region depressed slightly below level of remainder of carapace, with scattered granules; carapace surface with well-developed, broadly spaced transverse terraces, parallel to one another posteriorly, interfingered with one another or intersecting anteriorly; terraces ornamented with tiny, forward directed spines; pterygostome and appendages ornamented with terraces; sternites 1-5 smooth.

Material Examined.—*Lophoranina precocia*, holotype Instituto de Historia Natural de Estado de Chiapas 1703, paratypes 1702, 1621.

Range.—Late Cretaceous (Maastrichtian).

Notopodinae Serène and Umali, 1972
Fig. 19

Included Genera.—*Cosmonotus* Adams and White, 1848; *Erroranilia* Boyko, 2004; *Eumorphocorystes* van Binkhorst, 1857; *Italianira* new genus; *Lianira* Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991; *Lovarina* Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991; *Notopella* Lőrenthey *in* Lőrenthey and Beurlen, 1929; *Notoporanina* Lőrenthey *in* Lőrenthey and Beurlen, 1929; *Notopus* De Haan, 1841; *Ponotus* Karasawa and Ohara, 2009; *Pseudoraninella* Beurlen *in* Lőrenthey and Beurlen, 1929; *Raniliformis* Jagt, Collins, and Fraaye, 1993; *Ranilia* H. Milne Edwards, 1837 [in 1834-1840]; *Umalia* Guinot, 1993.

Diagnosis.—Carapace wide for family, strongly vaulted transversely; often with deep reentrant at position of antennae interpreted to be in axis of rostrum, usually without outer orbital fissures (except *Umalia*); rostrum bifid or trifid; post-frontal region often ornamented; anterolateral margins with one spine; often with a straight segment which could be interpreted as a lateral margin so that carapace is essentially octagonal; sternites 1-3 fused, cap-like, sternite 4 wide, with short antero-lateral projections, concave laterally; posterior portion of sternite 5, and sternites 6, 7 and 8 very narrow; sternite 5 with broad anterior projections; sternite 6 flattened; sternite 8 very reduced; spermathecae very closely situated so that they are almost united; ischium of third maxilliped with oblique crest; notopodine-type chelae present (chela very high, with very reduced fixed finger and long movable finger, large gape between two fingers).

Remarks.—Notopodinae is a large clade but is well-united by the diagnostic characters listed here.

Range.—Late Cretaceous (Maastrichtian)-Holocene.

Umalia Guinot, 1993

Type Species.—*Notopus misakiensis* Sakai, 1937, by original designation.

Fossil Species.—*Umalia guinotae* de Angeli and Beschin, 2007, questionably.

Diagnosis.—Carapace widest near front; lateral margins parallel, straight, converging posteriorly; rostrum triangular; frontal margin concave on either side of rostrum, concavities followed by nearly straight segment with two fissures; frontal margin then sloping obliquely to base of short anterolateral spine; carapace surface ornamented with small tubercles; pereiopod 5 much reduced, subdorsal.

Range.—Eocene (Lutetian)?-Holocene.

Notopella Lőrenthey *in* Lőrenthey and Beurlen, 1929
Fig. 19B

Type and Sole Species.—*Notopella vareolata* Lőrenthey *in* Lőrenthey and Beurlen, 1929, by monotypy.

Diagnosis.—Carapace elongate-trapezoidal, widest in anterior 20% at position of anterolateral spines; rostrum triangular; orbital margins apparently with two spines; fronto-orbital width about 65% maximum carapace width; anterolateral margins very short; lateral margins converging posteriorly, nearly straight, rimmed; carapace axially keeled.

Material Examined.—Cast of *Notopella variolata*, syntype MAFI Lőrenthey Collection 37 numbered KSU D 55.

Remarks.—*Notopella* had been synonymized with *Ranilia* (Glaessner, 1969, p. R501), and that opinion had been followed by subsequent workers (Müller and Collins, 1991; Waugh et al., 2009; Schweitzer et al., 2010). Our analysis indicates that it should be maintained as a separate genus. It differs rather substantially from the type species of *Ranilia*, *R. muricata*, in its more angular carapace, whereas *R. muricata* is more ovate. *Ranilia muricata* has three spines along the orbital margins instead of two and lacks the axial keel seen in *N. vareolata*. Thus, there are many differences to warrant maintenance of the original genus, *Notopella*.

Range.—Eocene (Priabonian).

Notopus De Haan, 1841

Type Species.—*Cancer dorsipes* Linnaeus, 1758, by monotypy.

Included Fossil Species.—*Notopus dorsipes*, RGM 24916; *Notopus minutus* Vega et al., 2001.

Diagnosis.—Carapace widest anteriorly, with weak longitudinal keel; rostrum triangular; orbits with triangular inner orbital spine, outer orbital spine, and serrate margin between the spines; fronto-orbital width about 65% maximum carapace width; long spine placed at anterolateral corner; post-frontal ridge well-developed, may be serrate; lateral margins parallel, may be weakly serrate; posterolateral margins converging; sternites 1-3 fused, caplike, sternite 4 wide, with short antero-lateral projections, concave laterally; posterior portion of sternite 5, and sternites 6, 7, and 8 narrow; sternite 5 with broad anterior projections; sternite 6 flattened; sternite 8 reduced; spermatheca very closely situated so that they are almost united; ischium of third maxilliped with oblique crest; notopodine-type chelae present (chela very high, with reduced fixed finger and long movable finger, large gape between two fingers).

Material Examined.—*Notopus minutus*, holotype IHNCH 3462.

Range.—Eocene (Lutetian)-Holocene.

Discussion.—Vega et al. (2008) synonymized *Notopus minutus* with *Notopoides exiguus*. Examination of illustrations of specimens they illustrated of *Notopoides exiguus* (Vega et al., 2008, pl. 2, Figs. 4-6) suggests that they are not conspecific and probably not congeneric with those of *Notopus minutus*. *Notopus minutus* has moderately convex lateral margins and is widest in the anterior one-third of the carapace; its frontal margin is poorly preserved. The specimens referred to *Notopoides exiguus* are strongly convex laterally and are maximally wide at least half the distance posteriorly. Thus, we retain the taxa as separate at this time.

Ponotus Karasawa and Ohara, 2009

Type and Sole Species.—*Ponotus shirahamensis* Karasawa and Ohara, 2009, by original designation.

Diagnosis.—Carapace long, widest just posterior to anterolateral spine; rostrum broadly triangular; orbits with small triangular inner orbital spine, followed by short fissure, followed by broad segment and small outer orbital spine; fronto-orbital width about 70% maximum carapace width; small anterolateral spine; carapace axially keeled, with large pores; post-frontal ridge absent; lateral margin with short transverse terraces; sternites 1-3 fused, cap-like, sternite 4 wide, with short antero-lateral projections, concave laterally; posterior portion of sternite 5 narrow; notopodine-type chelae present (chela very high, with very reduced fixed finger and long movable finger, large gape between two fingers).

Range.—Miocene (Langhian).

Ranilia H. Milne Edwards, 1837 [in 1834-1840]
Raninops A. Milne-Edwards, 1880a.

Type Species.—*Ranilia muricata* H. Milne Edwards, 1837 [in 1834-1840], by monotypy.

Included Fossil Species.—*Ranilia constricta* (A. Milne-Edwards, 1880); *R. misakiensis* (Sakai, 1937), RGM 31997; *R. muricata*, USNM unnumbered.

Diagnosis.—Carapace ovate; rostrum sharp, needle-like, frontal margin concave on either side of rostrum; upper orbital margin oblique; triangular inner orbital spines followed by smaller, triangular intra- and outer orbital spines, outer margins of spines serrate; small, needle-like anterolateral spine placed about one-quarter the distance posteriorly, anterolateral margin weakly serrate; post-frontal region scabrous; lateral margins parallel, very weakly serrate anteriorly; posterolateral margin weakly concave, sinuous; sternites 1-3 fused, caplike, sternite 4 wide, with short anterolateral projections, with tufts of short setae, concave laterally; posterior portion of sternite 5 narrow; notopodine-type chelae present (chela very high, with very reduced fixed finger and long movable finger, large gape between two fingers), ornamented with tufts of short setae.

Remarks.—Herein we restrict the fossil occurrence of *Ranilia* to the Pleistocene occurrence of *Ranilia constricta* in Italy.

Range.—Pleistocene-Holocene.

Pseudoraninella Beurlen *in* Lőrenthey and Beurlen, 1929
Fig. 19A

Type Species.—*Notopocorystes muelleri* van Binkhorst, 1857, by subsequent designation of Glaessner (1969).

Other Species.—*Pseudoraninella vahldieki* (Förster and Mundlos, 1982).

Diagnosis.—Rostrum long, needlelike, extending onto carapace as a clear axial ridge; orbits with sharp inner, intra-, and outer orbital spines, margins serrate between spines; fronto-orbital width 78% maximum width; long, slender anterolateral spine positioned a short distance posteriorly on margin; lateral and posterolateral margins confluent, converging posteriorly; carapace with tubercles anteriorly, posterior to tubercles a well-defined, scabrous post-frontal ridge.

Remarks.—*Pseudoraninella* was synonymized with *Eumorphocorystes* (Schweitzer et al., 2010) and later *Notopus* (van Bakel et al., 2012). Our analysis indicates that it should retain separate generic status based upon its oblique orbital margins; post-frontal ridge; three needle-like spines along the orbital margins; serrate margins between spines; and wide fronto-orbital width with respect to maximum carapace width. This combination of characters sets it apart from *Notopus* and *Notopella*, which have fewer orbital spines and straight lateral segments. *Pseudoraninella vahldieki* is poorly preserved. The carapace is very wide anteriorly, narrows posteriorly, and appears to have somewhat serrate lateral margins. At this time, we retain it in *Pseudoraninella* until more complete material can be collected.

Material Examined.—Cast of *Notopocorystes muelleri* van Binkhorst, 1857, holotype MBA 238, numbered KSU D 86; *Pseudoraninella vahldieki*, holotype BSP 1981 XI 31.

Range.—Late Cretaceous (Maastrichtian)-Eocene (Priabonian).

Notoporanina Lőrenthey *in* Lőrenthey and Beurlen, 1929
Fig. 19D

Type and Sole Species.—*Notopus beyrichi* Bittner, 1875, by monotypy.

Diagnosis.—Carapace ovate, widest in anterior one-quarter; rostrum trifid, central spine singular, with double groove axially; outer two spines serving as inner orbital spines; intra-orbital spine bounded by closed fissures; outer orbital spine short, directed axially; fronto-orbital width about 77% maximum carapace width; anterolateral spine very short, forward directed anterolateral spine; post-frontal ridge discontinuous, interrupted axially; lateral margins and posterolateral margins confluent, arcuate, rimmed; sternites 1-3 fused, cap-like, sternite 4 wide, with short antero-lateral projections, concave laterally; chelipeds with transverse ridges, large granules on upper margin of manus of chela.

Material Examined.—Cast of Miocene, Hungary specimen numbered KSU D 1590.

Remarks.—*Notoporanina* has been synonymized with *Notopus* since Glaessner (1969). Our analysis indicates that it should be maintained as a separate genus. The orbital margin, even though poorly preserved, does not seem to indicate the presence of any intra-orbital spines as seen in *Notopus*. Thus, we reinstate it.

Range.—Eocene.

Lianira Beschin, Busulini, de Angeli,
Tessier, and Ungaro, 1991

Type Species.—*Lianira beschini* Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991, by original designation.

Other Species.—*Lianira convexa* Beschin et al., 1991; *L. isidoroi* Beschin et al., 2007.

Diagnosis.—Carapace oblong, flared anteriorly, widest along anterior margin of carapace; frontal margin very wide; rostrum sharp, triangular, well developed; long triangular inner orbital spine, remainder of orbital margin a long, flared, spinose projection; lateral spine just distal to outer orbital angle, stout; lateral margins parallel, then converging posteriorly; surface punctate; sternites 1-3 fused, cap-like, sternite 4 wide, with wide antero-lateral projections, concave laterally; chelipeds with transverse setal pores or ridges.

Range.—Eocene (Ypresian-Lutetian).

Italianira n. gen.

Type and Sole Species.—*Ranilia punctulata* Beschin, Busulini, de Angeli, and Tessier, 1988, by present designation.

Etymology.—The genus name is derived from *Lianira*, an anagram of *Ranilia*, and Italy, the area from which the type and species has been recovered.

Diagnosis.—Carapace elongate, widest in anterior one-fifth of carapace at position of anterolateral spine; rostrum trifid, middle spine singular, lateral two spines serving as inner orbital spines; remainder of anterior margin arcuate, sinuous, merging smoothly into anterolateral spine; lateral and posterolateral margins confluent, weakly convex; carapace punctate; sternites 1-3 fused, caplike, sternite 4 wide, with long antero-lateral projections, concave laterally; sternite 5 wide; notopodine-type chelae present (chela very high, with very reduced fixed finger and long movable finger, large gape between two fingers), proximal elements with transverse ridges.

Remarks.—*Ranilia punctulata* cannot be retained within *Ranilia* or any other existing genus within Nopodinae based upon its arcuate, smooth, anterior margin; trifid rostrum; and maximum width at the anterior of the carapace. This is a unique combination of characters within the subfamily.

Range.—Eocene (Ypresian).

Eumorphocorystes Van Binkhorst, 1857

Type and Sole Species.—*Eumorphocorystes sculptus* Van Binkhorst, 1857, by monotypy.

Diagnosis.—Carapace elongate, widest in anterior one-fifth at position of anterolateral margin; front trifid, central spine much longer than lateral spines; orbits with two fissures, intra, and outer orbital spines; fronto-orbital width about 64% maximum carapace width; long spine at anterior corner; carapace surface with distinctive strap-like ornamentation over entire surface, with longitudinal, axial keel.

Material Examined.—Cast of *Eumorphocorystes sculptus*, Museum Maastricht specimen, numbered KSU D 443.

Range.—Late Cretaceous (Maastrichtian).

Raniliformis Jagt, Collins, and Fraaye, 1993
Fig. 19C

Type Species.—*Raninella baltica* Segerberg, 1900, by original designation.

Other Species.—*R. bellini* de Angeli, 2011; *R. chevrona* Fraaye and van Bakel, 1998; *R. eocaenica* (Beschin, Busulini, de Angeli, and Tessier, 1988); *R. occlusa* Collins, Fraaye and Jagt, 1995; *R. ornata* de Angeli and Beschin, 2007; *R. prebaltica* Fraaye and Van Bakel, 1998; questionably *R. rugosa* de Angeli and Beschin, 2007.

Diagnosis.—Carapace ovate, very strongly vaulted transversely, triangular in cross-section, flattened longitudinally; carapace widest in anterior one-third; rostrum triangular, axially keeled; with triangular inner orbital spine, followed by fissure; broad intra-orbital projection, highest axially, followed by short fissure; followed by long, straight segment, followed by long outer orbital projection; all orbital margins serrate; fronto-orbital width about 60% maximum carapace width; stout, long anterolateral spine directed anterolaterally; postfrontal region with short scabrous ridges, remainder of carapace punctate.

Material Examined.—*Raninella baltica*, cast of MGUH 257 numbered KSU D 2162.

Remarks.—Jagt et al. (1993) erected the genus largely based upon material from the early Paleocene of The Netherlands that they considered to be conspecific with *Raninella baltica* Segerberg, 1900, from the Danian of Sweden and Denmark. Examination of photographs of the holotype, a translation of the original description of the type species, and published photos of the Dutch material suggests that assumption that the material is conspecific is the best interpretation at this time. The Dutch material retains cuticle, spines, and ornamentation and is very much better preserved than the holotype, which is a mold of the interior. *Raniliformis rugosa* differs from other species of the genus in possessing overall rugose ornamentation and in being longer and narrower than other species. The known specimens have broken fronts, at least as illustrated, so more complete material will be necessary to test their generic placement.

Range.—Late Cretaceous (Maastrichtian)-Eocene (Lutetian).

Lovarina Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991

Type and Sole Species.—*Lovarina cristata* Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991, by original designation.

Diagnosis.—Carapace ovate, much longer than wide, apparently widest in anterior one-quarter, strongly vaulted transversely; frontal margin strongly concave at position of antennae, rimmed, apparently outer orbital spines; no anterolateral spines apparent; carapace and chelae ornamented by transverse, closely spaced, sub-parallel ridges.

Range.—Eocene (Lutetian).

Cosmonotus Adams and White, 1848

Type Species.—*Cosmonotus grayii* White, 1848, by monotypy.

Fossil Species.—*Cosmonotus grayii*, questionably, from the early Miocene of Taiwan, identified as paratypes 1 and 2 of *Paralbunea taipeiensis* Hu and Tao, 1996 (see Boyko, 2004).

Diagnosis.—Carapace longer than wide, angular, widest about one-third the distance posteriorly at position of anterolateral spine, highly vaulted transversely; front with deep reentrant for antennae; one fissure distal to reentrant; anterolateral margins confluent with orbital margins, oblique, sloping to anterolateral spine; anterolateral spine followed by straight, lateral margins that are parallel; posterolateral margins converging posteriorly; posterior margin sinuous; fifth pereiopod with sickle-shaped dactylus.

Remarks.—Boyko (2004) referred two specimens that had been placed with *Paralbunea taipeiensis* Hu and Tao (1996) to *Cosmonotus grayii*. Those specimens are poorly preserved, and have one anterolateral spine, parallel lateral margins, and may have anterolateral margins that converge axially. That placement is accepted until better material can be recovered. Van Bakel et al. (2012) referred *Raniliformis chevrona* to *Cosmonotus*. That species cannot be retained in *Cosmonotus* because it has a very wide fronto-orbital margin and a very short anterolateral margin that does not converge axially.

Range.—Miocene-Holocene.

Erroranilia Boyko, 2004

Type and Sole Species.—*Paralbunea taipeiensis* Hu and Tao, 1996, by original designation.

Diagnosis.—Carapace longer than wide, widest anteriorly. Specimen very poorly preserved.

Remarks.—Boyko (2004) designated *Erroranilia* based upon the species of Hu and Tao (1996) but only on the holotype. The paratypes 1 and 2 were questionably placed within *Cosmonotus grayii*. *Erroranilia taipeiensis* is very poorly preserved. Van Bakel et al. (2012) synonymized the genus with *Ranilia*, but because of its poor preservation, we elect to maintain it as a separate genus until better material is recovered.

Range.—Miocene.

Raninidae incertae sedis

Sabahranina Collins, Lee, and Noad, 2003

Type and Sole Species.—*Sabaharanina trushidupensis* Collins, Lee, and Noad, 2003, by monotypy.

Diagnosis.—Carapace longer than wide, orbitofrontal margin straight, upturned; a sharp constriction behind orbits, followed by small, obliquely directed spine; anterolateral margins sinuous, posterolateral margins weakly concave; dorsal surface with postero-median depression (Collins et al., 2003).

Remarks.—This genus is problematic, and its subfamilial placement is unclear. Indeed, Collins et al. (2003), De Grave et al. (2009) and Schweitzer et al. (2010) placed it within Incertae sedis under Raninidae.

Range.—Early Miocene (Burdigalian)?.

Diversity Patterns

Diversity curve

All taxa were counted, including singletons. Singletons comprise a very large percentage of the raninoidan record.

Occurrences of geologic ranges were compiled using the range through method for genera (following Aberhan and Kiessling, 2012), with some exceptions. Extant taxa with a single occurrence prior to the Miocene were not extended into the Holocene. Extant genera with scattered occurrences through the record prior to the Oligocene and including the post-Oligocene (Eocene, Oligocene and Miocene), were extended into the Holocene; these include *Lyreidus*, *Ranina* and *Raninoides*. Other extant genera had insufficiently continuous records or lacked sterna to verify generic and family placement. For taxa in 19th Century literature noted "Senonian," or other poorly constrained times, every attempt was made to more narrowly pinpoint the time stage. In the few cases where this was not possible, the taxon was assigned to the youngest time interval so as not to inflate the range of the lineage, recognizing that this might inflate diversity in the latest stage in an epoch. For taxa with ranges of occurrences or age ranges for rock units, we assigned the taxon to each time unit. This may have artificially inflated the diversity slightly for some intervals, notably Coniacian-Maastrichtian, the units to which this relates most significantly.

A significant proportion of the identifications, taxonomy, and phylogeny of the Raninoida have been verified by the authors with colleagues and students. Nearly all southern hemisphere raninoidans have been examined by one (RMF; JL) or some of us (Feldmann and Schweitzer, 2006). North Pacific raninoidans have been examined and summarized (Collins et al., 1993; Karasawa, 1993, 1997, 2000; Schweitzer, 2001; Karasawa et al., 2006; Karasawa and Ohara, 2009). Central American decapods have been summarized and described (Schweitzer et al., 2002). Thus, the problems of the taxic approach (Aberhan and Kiessling, 2012) can be avoided because the authors have personally verified as much of the dataset as possible. Potential biases to the decapod record are discussed by Schweitzer and Feldmann (submitted).

Family Diversity

Family-level diversity in Raninoida reached its peak in the Campanian, when all seven families were present. Six families were present throughout the entire Late Cretaceous. Ypresian time was the most diverse Cenozoic time period, with four families present. Modern oceans only embrace two families (Fig. 20).

Generic diversity.—Peak generic diversity occurred in the Maastrichtian, with 23 recorded genera (Fig. 20). The entire Late Cretaceous ranges from 16-23 genera within each stage.

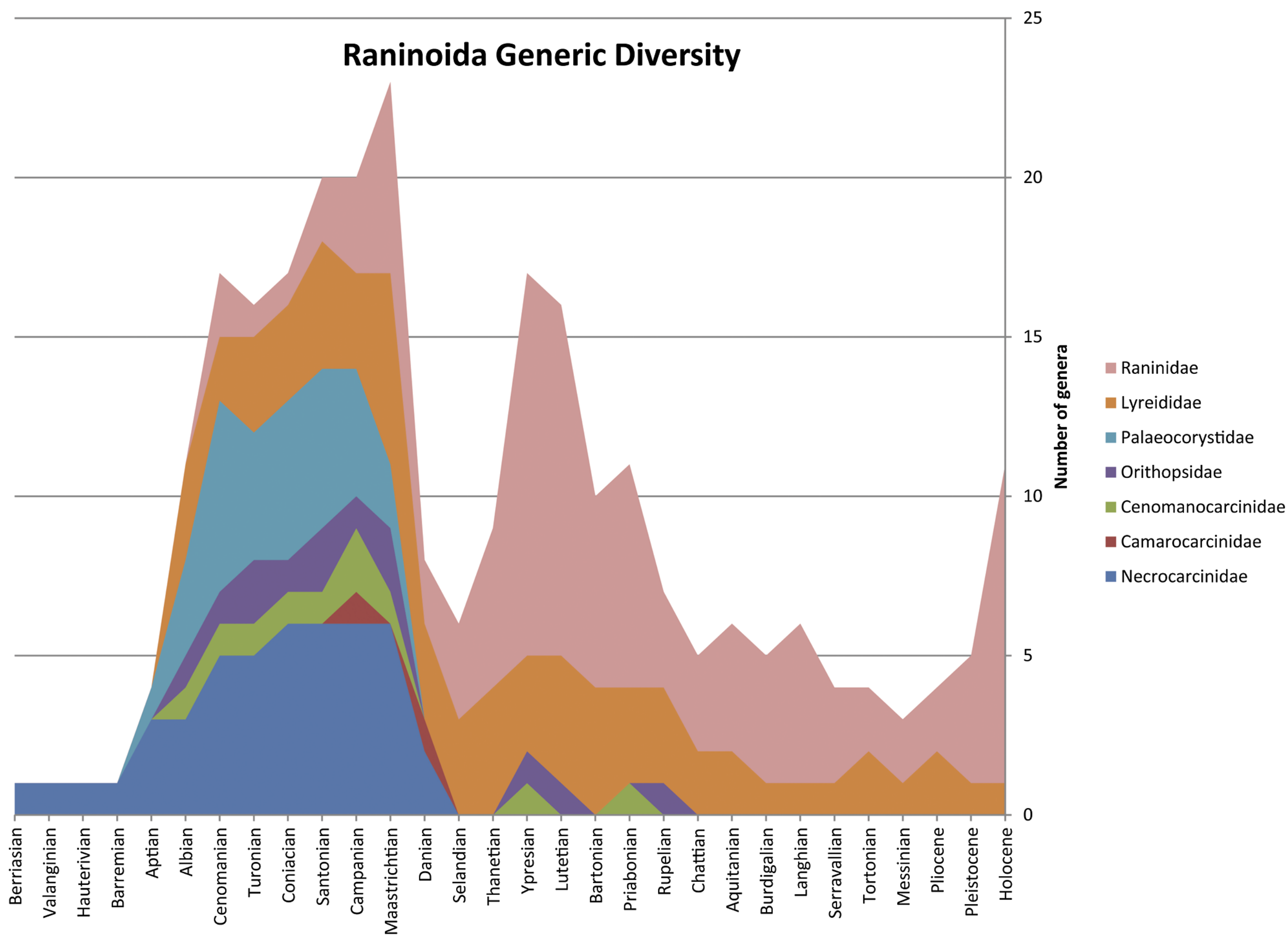

Fig. 20. Diversity curve at genus level for all raninoidans, extinct and extant. Note that the *x*-axis is not to scale.

Table 5. Four major body plans within Raninoida.

Bauplan	Necrocarcinid	Cenomanocarcinid	Palaeocorystid	Raninoid (Gymnopleuran)
Included families	Necrocarcinidae Camarocarcinidae	Cenomanocarcinidae Orithopsidae	Paleocorystidae	Raninidae Lyreididae
Carapace shape	Equidimensional	Equidimensional	Elongate	Elongate
Gymnopleuran condition	Non-gymnopleuran	Non-gymnopleuran	Non-gymnopleuran	Gymnopleuran
Sternum shape	Deep sterno-pleonal depression	Flattened, wider sternites	Flattened, moderate width of sternites	Reduced width of sternites
Pleonal locking mechanism	Double peg	Double peg	Double peg	Double peg (Lyreididae) or absent (Raninidae)
Pleonal position	Held tightly against sternum where known	Held tightly against sternum where known	Held to level of second pereiopods	Not reaching level of sternite 4; often held posteriorly

The Ypresian and Lutetian are nearly as diverse, with 17 and 16 genera respectively. Modern oceans embrace 11 recorded genera.

Species Diversity

Species diversity for Raninoida is highest in modern oceans with the Lutetian close behind, with 46 and 43 species respectively. The Maastrichtian, the time of highest generic diversity, had 34 species recorded.

Raninoida Body Plans

Raninoida, unlike the pattern seen in lobsters (Schweitzer and Feldmann, in revision), decreased in body plans through time. Four major body plans are found within the group (Table 5) and all were present by the late Early Cretaceous. Several trends can be seen in the four body plans, their order of appearance, and their order of extinction. The first to appear was the necrocarcinoid body plan, characterized by an equidimensional carapace, a deep sterno-pleonal depression, and a pleon held tightly to the sternum. The next body plan to appear were the paleocorystid and cenomanocarcinid, which show trends toward a flattening of the sternum, an elongation of the carapace, and a migration of the pleon to a more posteriorly-held position. The raninoid body plan appeared nearly at the same time, with an elongate carapace, the gymnopleuran condition, and a pleon held more loosely to the sternum and more posteriorly. In addition, the sternum itself is much more reduced in this body plan. These features have been considered to be adaptations to burrowing (van Bakel et al., 2012). However, that interpretation may not reflect the timing of introduction of characters and does not consider the possibility that reproductive strategy played a significant role in the selection of some of these characters.

Our analysis demonstrates that elongation of the carapace and development of flattened pereiopods into what has commonly been held to reflect a burrowing habit (Schäfer, 1972, 1976), among other characters, unites palaeocroystoids and raninoids and precedes the appearance of gymnopleury and extension of the pleon. This decoupling of the characters cited by van Bakel et al. (2012) as being adaptions for burrowing introduces the possibility that quite different selective pressures resulted in the evolution of these features. Indeed, it is reasonable to speculate that the extension of the pleon behind the carapace, rather than tucked beneath it, might serve a useful function for egg holding. It is difficult to understand its function for burrowing as other elongate burrowers, such as corystids and hippids do not possess an extended pleon. Gymnopleury remains enigmatic. To the best of our knowledge, no clear functional significance of this feature has been articulated. Although it would appear to be unsuited for a burrowing or burying life habit, and is not shared with other burrowers, gymnopleury does not seem to be detrimental to this life style. At present, its adaptive significance must remain a mystery. Additionally, we suggest that they may be related to reproduction.

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Supporting Information

Additional information can be found online. Extinct taxa marked with a dagger (†).

Table S1. PDF of the data matrix.

									1										2										3										4										5										6										7		
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Homolodromia	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homola	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cenocorystes†	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	2	2	1	1	1	0	0	2	0	1	1	0	0	0	1	0	1	0	0	0	?	?	?	?	?	0	0	0	?	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	?	0	0	?	0	1
Notopocorystes†	0	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	2	2	1	1	1	0	0	2	0	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Eucorystes†	0	1	0	0	0	0	0	1	1	0	1	0	0	1	1	0	2	2	1	1	1	0	0	2	0	1	1	0	0	0	1	0	1	0	0	0	0	1	?	0	0	0	0	0	?	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Joeranina†	0	1	0	0	0	0	0	1	1	0	1	0	1	1	1	0	2	2	1	1	1	0	0	2	0	1	1	0	0	0	1	0	1	0	0	0	0	1	?	?	?	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Cretacoranina†	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0	2	2	1	1	1	0	0	2	0	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	?	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Ferroranina†	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	2	2	1	1	1	0	0	2	0	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	?	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Necrocarcinus†	1	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	2	2	1	1	1	0	0	2	0	1	1	1	1	0	1	0	?	0	0	0	0	0	?	1	?	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Corazzatocarcinus†	1	0	0	0	0	1	0	?	1	0	0	0	1	?	1	1	2	2	1	1	1	0	0	2	0	1	1	1	1	0	1	0	?	?	?	0	0	0	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
Paranecrocarcinus†	1	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	2	2	1	1	1	0	0	2	0	1	1	1	1	0	1	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Planocarcinus†	1	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	2	2	1	1	1	0	0	2	0	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	1	1	0	0	0	0	0	0	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	?	?
Hadrocarcinus†	1	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	2	2	1	1	1	0	0	2	0	1	2	1	1	0	?	?	?	0	0	0	0	0	?	?	?	0	0	0	?	1	1	0	0	0	0	0	0	0	0	?	?	?	?	?	0	?	0	0	?	?	?	?	?	0	0	1
Camarocarcinus†	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	2	2	1	1	1	0	0	2	0	1	2	1	1	1	1	0	0	0	0	0	0	0	?	1	0	0	0	0	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	?	1
Cretacocarcinus†	1	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	2	2	1	1	1	0	0	2	0	1	1	1	1	1	1	0	0	0	0	0	0	?	?	?	?	0	?	?	?	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cenomanocarcinus†	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	2	2	1	1	1	0	0	2	0	1	2	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Campylostoma†	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	2	2	1	1	1	0	0	2	0	1	2	1	1	?	1	0	0	0	0	0	0	?	?	1	?	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Orithopsis†	1	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	2	2	1	1	1	0	0	2	0	1	2	1	0	0	0	?	?	0	0	?	0	?	?	?	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1
Silvacarcinus†	1	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	2	2	1	1	1	0	0	2	0	1	2	1	0	0	0	?	?	0	0	?	0	?	?	?	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	?	1
Lyreidus	0	0	0	0	0	0	1	2	0	0	0	1	0	0	0	0	0&1	0	0	0	2	0	0	0&1	0	0&1	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	2	0	2	0	1	1	0	1	1
Lysirude	0	0	0	0	0	0	1	2	0	0	0	1	0	0	0	0	0&1	0	0	0	2	0	0	1&2	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	2	0	2	0	1	1	0	1	1
Ranidina†	0	1	0	0	0	0	1	2	0	0	0	1	1	0	0	0	0	0	0	0	2	0	0	1	0	1	0	0	0	0	1	?	?	?	0	0	0	?	?	?	?	1	?	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	?	2	?	?	?	?	1	0	?	1
Macroacaena johnsoni†	0	1	0	1	0	0	1	2	?	0	1	1	0	0	0	0	1	0	0	0	?	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	?	?	?	1	0	1	?	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	?	2	0	2	0	1	1	0	1	?
Macroacaena succedana†	0	1	0	0	0	0	1	2	0	0	0	1	0	0	0	0	1	1	1	0	2	0	0	2	0	2	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	1	1	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	1	2	0	2	0	1	1	0	1	1
Macroacaena alseana†	0	1	0	1	0	0	1	2	0	0	0	1	0	0	0	0	1	1	1	0	2	0	0	2	0	2	0	0	0	0	1	1	0	1	0	0	0	1	?	?	?	1	?	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	1	2	0	2	0	1	1	0	1	1
Macroacaena naselensis†	0	1	0	1	0	0	1	2	0	0	0	1	1	0	0	0	1	1	1	0	2	0	0	2	0	2	0	0	0	0	1	1	0	1	0	0	0	1	?	?	?	1	?	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	1	2	0	2	0	1	1	0	1	1
Raninoides willapensis†	0	1	0	1	0	0	1	2	0	0	1	1	1	0	0	0	2	2	1	2	2	0	0	1	0	2	0	0	0	0	1	1	0	1	0	0	0	1	1	?	?	1	?	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	1	2	0	2	0	1	?	?	?	?
Macroacaena fudoujii†	0	1	0	1	0	0	1	2	0	0	1	1	1	0	0	0	2	2	1	2	2	0	0	1	0	2	0	0	0	0	1	1	0	1	0	0	0	1	1	?	?	1	?	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	1	2	0	2	0	1	1	0	0	1
Bicornisranina†	0	1	0	0	0	0	1	2	0	0	1	1	0	0	0	0	2	2	1	2	2	0	0	1	1	2	0	0	0	0	?	?	?	?	?	?	0	?	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rogueus†	0	1	0	0	0	0	1	2	1	0	1	1	0	0	0	0	2	0	1	0	1	0	0	1	1	2	0	0	0	0	1	?	0	1	0	?	0	?	?	?	?	1	?	0	?	1	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	1	2	0	2	0	1	?	?	?	?
Marylyreidus†	0	0	0	0	0	0	1	2	1	0	1	1	0	0	0	0	2	2	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	?	1	0	1	1	0	?	1	0	1	1	1	0	0	0	0	1	0	0	0	?	?	?	?	1	?	0	2	0	1	1	0	?	1
Bournelyreidus†	0	0	0	0	0	0	1	2	1	0	1	1	0	0	0	0	2	2	1	1	1	0	0	2	0	1	0	0	0	0	1	1	0	1	0	0	0	1	?	1	0	1	1	0	?	1	0	1	1	1	0	0	0	0	1	0	0	0	?	?	?	?	1	2	0	2	0	1	1	0	?	1
Lophoranina†	0	1	1	0	1	0	1	2	1	1	1	1	0	0	0	0	2	2	1	1	2	0	0	2	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	2	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Vegaranina†	0	1	1	0	1	0	1	2	1	1	1	1	0	0	0	0	2	2	1	1	2	0	0	2	0	1	0	0	0	0	1	0	0	1	0	1	0	1	?	0	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	2	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Raninella†	0	1	0	0	0	0	1	2	1	1	1	1	0	0	0	0	2	2	1	1	2	0	0	2	0	1	0	0	0	0	1	0	0	1	0	1	0	1	?	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	2	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Ranina	0	1	1	0	0	0	1	2	0	1	1	1	0	0	0	0	2	2	1	2	2	0	0	2	1	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	2	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Raninoides	0	1	0	0	0	0	1	2	0	0&1	1	1	0	0	0	0	2	2	1	2	2	0	0	1	0	1&2	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0	1	2	0	1	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Quasilaeviranina†	0	1	0	0	0	0	1	2	0	1	1	1	0	0	0	0	2	2	1	1	1	0	0	1	0	1	0	0	0	0	1	?	?	?	?	1	0	1	1	1	0	1	?	1	?	1	0	1	1	0	1	0	1	0	1	2	0	1	?	?	1	?	2	2	1	-	0	0	2	1	?	?
Notopoides	0	1	0	0	0	0	1	2	1	1	0	1	0	0	0	0	2	2	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0	1	2	0	1	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Notosceles	0	1	0	0	0	0	1	2	0&1	1	1	1	0	0	0	0	2	2	1	2	1&2	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0	1	2	0	1	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Ranilia	0	1	0	0	0	0	1	2	0	0	1	1	0	0	0	0	2	0	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Umalia	0	1	0	0	0	0	1	2	0	0	0	1	0	0	0	0	2	2	1	1	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Cosmonotus	0	0	0	0	0	0	1	2	2	0	1	1	1	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Notopus dorsipes	0	1	0	0	0	0	1	2	0	1	1	1	1	0	0	0	2	0	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Ponotus†	0	1	0	0	0	0	1	2	0	0	1	1	1	0	0	0	2	0	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	?	?	1	1	1	?	1	0	1	1	0	1	1	1	0	1	1	1	0	?	1	1	1	2	2	1	-	0	0	2	1	0	0
Notopella†	0	1	0	0	0	0	1	2	0	0	1	1	0	0	0	0	2	0	1	0	1	0	0	1	0	1	0	0	0	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lianira†	0	1	0	0	0	0	1	2	0	0	1	1	0	0	0	0	2	0	1	1	0	0	1	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Raniliformis†	0	1	0	0	0	0	1	2	0	0	1	1	0	0	0	0	2	1	1	0	0	1	1	1	0	1	0	0	0	0	?	?	?	?	?	1	1	1	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eumorphocorystes†	0	1	0	0	0	0	1	2	0	0	1	1	1	0	0	0	2	1	1	0	0	1	1	1	0	1	0	0	0	0	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notopus muelleri†	0	1	0	0	0	0	1	2	0	1	1	1	0	0	0	0	2	0	1	1	0	1	1	1	0	1	0	0	0	0	1	?	?	?	?	1	1	1	1	0	0	1	1	?	?	?	?	?	1	0	?	?	?	?	1	?	?	?	?	?	?	?	2	?	1	-	0	0	2	1	0	0
Notopus beyrichi†	0	1	0	0	0	0	1	2	0	1	1	1	0	0	0	0	2	0	1	1	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1	1	1	?	?	?	?	1	1	1	?	1	0	1	1	0	1	1	1	0	1	1	1	0	?	?	?	?	2	2	?	?	?	?	?	?	?	?
Ranilia punctulata†	0	1	0	0	0	0	1	2	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	?	1	0	1	1	0	1	1	1	0	1	1	1	0	?	?	?	?	2	2	1	-	0	0	2	1	0	0
Lovarina†	0	0	0	0	1	0	1	2	0	0	1	1	0	0	0	0	2	1	1	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	2	2	1	-	0	0	2	1	0	0
Symethis	0	0	0	0	0	0	1	2	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	0	1	0	1	0	2	0	1	2	1	0	1	1	1	1	2	1	1	-	0	0	2	1	0	0
Cyrtorhina	0	0	1	0	0	0	1	2	0	0	0	1	0	0	0	0	2	2	1	1	1	0	0	2	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	2	1	2	0	2	0	1	2	1	0	1	1	1	1	2	1	1	-	0	0	2	1	0	0
Antonioranina†	0	0	0	0	0	0	1	2	0	0	0	1	0	0	0	0	2	2	1	1	1	0	0	2	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	2	1	2	0	2	0	1	2	1	0	1	1	1	1	2	1	1	-	0	0	2	1	0	0

Table S2. Classification of species of fossil Raninoida, based upon the results of this study. † indicates that the taxon is extinct and extant; †† indicates that the group is extinct. If a higher level taxon is extinct, embraced taxa are not labeled as extinct as that is implied.

Section **Raninoida**† Ahyong et al., 2007
Superfamily **Necrocarcinoidea**†† De Haan, 1839
Family **Camarocarcinidae** Feldmann, Li, and Schweitzer, 2007
Camarocarcinus Holland and Cvancara, 1958
C. arnesoni Holland and Cvancara, 1958 (type)
C. obtusus Jakobsen and Collins, 1979
C. quinquetuberculatus Collins and Rasmussen, 1992
Cretacocarcinus Feldmann, Li and Schweitzer, 2007
C. smithi Feldmann et al., 2007 (type)
Family **Cenomanocarcinidae** Guinot, Vega, and van Bakel, 2008
Campylostoma Bell, 1858
C. matutiforme Bell, 1858 (type)
Cenomanocarcinus van Straelen, 1936 (= *Sagittiformosus*†† Bishop, 1988)
C.? armatus (Rathbun, 1935a)
C. beardi Schweitzer, Feldmann et al., 2003
C. cantabricus van Bakel et al., 2012
C. carabus (Bishop, 1988)
C. disimmilis Collins, 2010
C. hierosolymitanus Avnimelech, 1961
C. inflatus van Straelen, 1936 (type)
C. multituberculatus (Joleaud and Hsu, 1935)
C. oklahomensis (Rathbun, 1935)
?*C. renfroae* (Stenzel, 1945)
C. robertsi Feldmann et al., 2013
C. siouxensis (Feldmann et al., 1976)
C. tenuicarinatus Collins, 2010
C. vanstraeleni Stenzel, 1945
Hasaracancer Jux, 1971
H. cristatus Jux, 1971 (type)
H. merijaensis Ossó, Artal, and Vega, 2011
Necrocarcinidae Förster, 1968
?*Araripecarcinus* Martins-Neto, 1987
A. ferreirai Martins-Neto, 1987 (type)
Colombicarcinus new genus
C. laevis new species (type)
Corazzatocarcinus Larghi, 2004
C. hadjoulae (Roger, 1946) (type)
Cristella Collins and Rasmussen, 1992
C. hastata Collins and Rasmussen, 1992 (type)
Glyptodynomene van Straelen, 1944
G. alsasuensis van Straelen, 1944 (type)
Hadrocarcinus Schweitzer et al., 2012
H. carinatus (Feldmann, Tshudy, and Thomson, 1993)
H. tectilacus Schweitzer et al., 2012
H. wrighti (Feldmann, Tshudy, and Thomson, 1993)
Necrocarcinus Bell, 1863
N. avicularis Fritsch and Kafka, 1887
N. bispinosus Segerberg, 1900
N. bodrakensis Levitski, 1974
N. davisi Bishop, 1985
‘*Necrocarcinus*’ *franconicus* Lehner, 1937
N. inornatus Breton and Collins, 2011
N. insignis Segerberg, 1900
N. labeschei (Eudes-Deslongchamps, 1835) (type)
N. olsonorum Bishop and Williams, 1991
N. ornatissimus Forir, 1887
?*N. perlatus* Fritsch and Kafka, 1887
N. pierrensis (Rathbun, 1917)
N. rathbunae Roberts, 1962
N. senonensis Schlüter *in* Schlüter and Von der Marck, 1868
N. tauricus Ilyin and Alekseev, 1998
N. texensis Rathbun, 1935a
N. undecimtuberculatus Takeda and Fujiyama, 1983

Table S2. (Continued.)

N. woodwardi Bell, 1863
Paranecrocarcinus van Straelen, 1936
P. balla van Bakel et al., 2012
P. digitatus Wright and Collins, 1972
P. foersteri Wright and Collins, 1972
P. graysonensis (Rathbun, 1935)
P. hexagonalis van Straelen, 1936 (type)
P. kennedyi Wright, 1997
P. libanoticus Förster, 1968
P. milbournei Collins, 2010
P. moseleyi (Stenzel, 1945)
P. mozambiquensis Förster, 1970
P. ovalis (Stenzel, 1945)
P. pulchellus (Secretan, 1964)
P. pusillus Breton and Collins, 2011
P. vanbirgeleni Fraaije, 2002
Planocarcinus Luque, Feldmann, Schweitzer, Jaramillo, and Cameron, 2012
P. johnjagti Bermudez et al., 2013
P. olssoni (Rathbun, 1937) (type)
Polycnemidium Reuss, 1859
P. pustulosus (Reuss, 1845) (type)
Pseudonecrocarcinus Förster, 1968
P. biscissus Wright and Collins, 1972
P. gamma (Roberts, 1962)
P. quadriscissus (Noetling, 1881) (type)
P. scotti (Stenzel, 1945)
P. stenzeli Bishop, 1983
Shazella Collins and Williams, 2004
S. abbotsensis Collins and Williams, 2004 (type)
New genus in press
Orithopsidae Schweitzer, Feldmann et al., 2003
Cherpiocarcinus Marangon and de Angeli, 1997
C. rostratus Marangon and de Angeli, 1997 (type)
Marycarcinus Schweitzer, Feldmann et al., 2003
M. hannae (Rathbun, 1926) (type)
Orithopsis Carter, 1872
O. angelicus (Fraaije, 2002)
?*O. isericus* (Fritsch and Kafka, 1887)
O. bonneyi Carter, 1872 (type)
O. tricarinatus (Woodward, 1868)
Paradoxicarcinus Schweitzer, Feldmann et al., 2003
P. nimonoides Schweitzer et al., 2003 (type)
Paradoxilissopsa Schweitzer, Dworschak, and Martin, 2011 [= *Lissopsis* Fritsch and Kafka, 1887]
P. transiens (Fritsch and Kafka, 1887) (type)
Silvacarcinus Collins and Smith, 1992
S. laurae Collins and Smith, 1992 (type)
Superfamily **Palaeocorystoidea**†† Lőrenthey *in* Lőrenthey and Beurlen, 1929
Palaeocorystidae Lőrenthey *in* Lőrenthey and Beurlen, 1929
Alessandranina new genus
A. ornata (Wright and Collins, 1972)
Cenocorystes Collins and Breton, 2009
C. bretoni van Bakel et al., 2012
C. fournieri Collins and Breton, 2009 (type)
Cretacoranina Mertin, 1941
C. denisae (Secretan, 1964)
C. fritschi (Glaessner, 1929)
C. schloenbachi (Schlüter, 1879) (type)
C. testacea (Rathbun, 1926)
C. trechmanni (Withers, 1927)
Eucorystes Bell, 1863
E. carteri McCoy, 1854 (type)
E. eichhorni Bishop, 1983
E. exiguus (Glaessner, 1980)
E. harveyi (Woodward, 1896)

Table S2. (Continued.)

E. iserbyti van Bakel et al., 2012
E. intermedius Nagao, 1931
E. mangyshlakensis Ilyin and Pistshikova *in* Ilyin, 2005
E. navarrensis van Bakel et al. 2012
E. oxtedensis Wright and Collins, 1972
E. paututensis (Collins and Rasmussen, 1992)
E. platys Schweitzer and Feldmann, 2001
Ferroranina van Bakel et al., 2012
F. australis (Secretan, 1964)
F. dichrous (Stenzel, 1945) (type)
F. tamilnadu van Bakel et al., 2012
Joeranina van Bakel et al., 2012
J. broderipi (Mantell, 1844)
J. colombiana Bermudez et al., 2013
J. gaspari van Bakel et al., 2012
J. goshourajimensis Karasawa and Komatsu, 2013
J. houssineaui van Bakel, 2013
J. japonica (Jimbô, 1894)
J. kerri (Luque et al., 2012)
J. syriaca (Withers, 1928)
J. xizangensis (Wang, 1981)
Notopocorystes McCoy, 1849
N. bituberculatus Secretan, 1964
N. normani (Bell, 1863)
N. ripleyensis Rathbun, 1935 (claws only)
N. stokesii (Mantell, 1844) (type)
Superfamily **Raninoidea**† **de Haan, 1839**
Family **Lyreididae**† **Guinot, 1993**
Subfamily Bicornisranininae†† new subfamily
New genus in preparation
Carinaranina fudoujii Karasawa, 2000
Raninoides nodai Karasawa, 1992
Ranidina willapensis Rathbun, 1926
Bicornisranina Nyborg and Fam, 2008
B. bocki Nyborg and Fam, 2008 (type)
Subfamily Lyreidinae† Guinot, 1993
Giulianolyreidus†† new genus
G. bidentatus (Rathbun, 1935)
G. johnsoni (Rathbun, 1935)
Lyreidus† De Haan, 1841 (= *Lysirude* Goeke, 1985)
L. antarcticus†† Feldmann and Zinsmeister, 1984
L. bennetti†† Feldmann and Maxwell, 1990
L. elegans†† Glaessner, 1960
L. fastigatus†† Rathbun, 1919 (only pereiopod)
L. hookeri†† Feldmann, 1992
L. hungaricus†† Beurlen, 1939
L. lebuensis†† Feldmann, 1992
L. paronae†† Crema, 1895
L. teodorii†† (van Bakel et al., 2012)
L. waitakiensis†† Glaessner, 1980
Ranidina†† Bittner, 1893
R. rosaliae Bittner, 1893 (type)
Symethoides†† van Bakel et al., 2012
S. monmouthorum van Bakel et al., 2012
Tribolocephalus†† Ristori, 1886
T. laevis Ristori, 1886 (type)
Subfamily Rogueinae†† new subfamily
Rogueus Berglund and Feldmann, 1989
R. orri Berglund and Feldmann, 1989 (type)
R. robustus Collins and Jakobsen, 1995
Subfamily Macroacaeninae†† new subfamily
Macroacaena Tucker, 1998 (= *Carinaranina* Tucker, 1998)
M. alseana (Rathbun, 1932)
M. bispinulata (Collins and Rasmussen, 1992)

Table S2. (Continued.)

M. chica Schweitzer, Feldmann et al., 2003
M. franconia Schweigert et al., 2004
M. leucosiae (Rathbun, 1932)
M. marionae (Tucker, 1998)
M. naselensis (Rathbun, 1926)
M. rosenkrantzi (Collins and Rasmussen, 1992)
M. schencki (Rathbun, 1932)
M. succedana (Collins and Rasmussen, 1992) (type)
M. teshimai (Fujiyama and Takeda, 1980)
M. tridens (Roberts, 1962)
M. venturai Vega et al., 2007
M. yanini (Ilyin and Alekseev, 1998)
Subfamily Marylyreidinae†† van Bakel et al., 2012
Bournelyreidus van Bakel et al., 2012
B. eysunesensis (Collins and Rasmussen, 1992) (type)
B. carlilensis (Feldmann and Maxey, 1980)
B. laevis (Schlüter *in* Schlüter and von der Marck, 1868)
B. oaheensis (Bishop, 1978)
Hemioon Bell, 1863
H. cunningtoni Bell, 1863 (type)
H. callianassarum (Fritsch and Kafka, 1887)
H. novozelandicum Glaessner, 1980
Heus Bishop and Williams, 2000
H. foersteri Bishop and Williams, 2000 (type)
H. manningi (Bishop and Williams, 2000)
Marylyreidus van Bakel et al., 2012
M. punctatus (Rathbun, 1935a) = *Notopocorystes parvus* Rathbun, 1935a; *Raninella mucronata* Rathbun 1935a (type)
Lyreididae incertae sedis
Lyreidina†† Fraaye and van Bakel, 1998
L. pyriformis Fraaye and van Bakel, 1998 (type)
Family **Raninidae**† De Haan, 1839
Subfamily Cyrtorhininae† Guinot, 1993
Antonioranina†† van Bakel, Guinot, Artal, Fraiije, and Jagt, 2012
A. fusseli (Blow and Manning, 1996)
A. globosa (Beschin, Busulini, de Angeli, and Tessier, 1988)
A. ripacurtae (Artal and Castillo, 2005)
Claudioranina†† new genus
C. oblonga (Beschin, Busulini, de Angeli, and Tessier, 1988)
Subfamily Notopodinae† Serène and Umali, 1972
Cosmonotus† Adams and White, 1848
C. grayii† White, 1848 (type)
Erroranilia†† Boyko, 2004
E. taipeiensis (Hu and Tao, 1996) (type)
Eumorphocorystes†† van Binkhorst, 1857
E. sculptus Van Binkhorst, 1857 (type)
Italianira†† new genus
I. punctulata Beschin, Busulini, de Angeli, and Tessier, 1988
Lianira†† Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991
L. beschini Beschin et al., 1991 (type)
L. convexa Beschin et al., 1991
L. isidoroi Beschin, de Angeli and Checchi, 2007
Lovarina†† Beschin, Busulini, de Angeli, Tessier, and Ungaro, 1991
L. cristata Beschin et al., 1991 (type)
Notopella†† Lőrenthey *in* Lőrenthey and Beurlen, 1929
R. vareolata Lőrenthey *in* Lőrenthey and Beurlen, 1929 (type)
Notoporanina†† Lőrenthey *in* Lőrenthey and Beurlen, 1929
N. beyrichi Bittner, 1875 (type)
Notopus† De Haan, 1841
N. dorsipes† (Linnaeus, 1758) (*Dorippe dorsipes* [*sensu*] Glaessner, 1929)
N. minutus†† Vega, Cosma et al., 2001
Ponotus†† Karasawa and Ohara, 2009
P. shirahamensis Karasawa and Ohara, 2009 (type)
Pseudoraninella†† Beurlen *in* Lőrenthey and Beurlen, 1929
P. muelleri (van Binkhorst, 1857) (type)

Table S2. (Continued.)

P. vahldieki (Förster and Mundlos, 1982)
Raniliformis†† Jagt, Collins, and Fraaye, 1993
R. baltica (Segerberg, 1900) (type)
R. bellini de Angeli, 2011
R. chevrona Fraaye and van Bakel, 1998
R. eocaenica (Beschin, Busulini, de Angeli, and Tessier, 1988)
R. occlusa Collins, Fraaye, and Jagt, 1995
R. ornata de Angeli and Beschin, 2007
R. prebaltica Fraaye and van Bakel, 1998
R. rugosa de Angeli and Beschin, 2007
Ranilia† H. Milne Edwards, 1837 [in 1834-1840] (= *Raninops* A. Milne-Edwards, 1880a)
R. constricta† (A. Milne-Edwards, 1880)
Umalia† Guinot, 1993
U. guinotae†† de Angeli and Beschin, 2007
U. misakiensis† (Sakai, 1937)
Subfamily Ranininae† De Haan, 1839
Lophoranina†† Fabiani, 1910
L. aculeata (A. Milne-Edwards, 1881)
L. albeshtensis Schweitzer, Feldmann, and Lazăr, 2009
L. aldrovandii (Ranzani, 1820)
L. bakerti (A. Milne-Edwards, 1872)
L. barroisi (Brocchi, 1877)
L. bishopi Squires and Demetrion, 1992
L. bittneri (Lőrenthey, 1902)
L. cinquecrista Feldmann, Schweitzer, Bennett, Franţescu, Resar, and Trudeau, 2011
L. cristaspina Vega, Cosma et al., 2001
L. georgiana (Rathbun, 1935)
L. kemmelingi van Straelen, 1924 [imprint 1923]
L. laevifrons (Bittner, 1875)
L. levantina Lewy, 1977
L. marestiana (König, 1825) (type)
L. maxima Beschin et al., 2004
L. persica Withers, 1932
L. porifera (Woodward, 1866)
L. quinquespinosa (Rathbun, 1945)
L. raynorae Blow and Manning, 1996
L. reussi (Woodward, 1866)
L. rossi Blow and Manning, 1996
L. soembaensis van Straelen, 1938
L. straeleni Vía, 1959
L. tchihatcheffi (A. Milne-Edwards, 1866)
L. toyosimai Yabe and Sugiyama, 1935
Lophoraninella†† Glaessner, 1946
L. cretacea (Dames, 1886) (type)
Ranina† Lamarck, 1801
R. americana†† Withers, 1924
R. bavarica†† Ebert, 1887
R. berglundi†† Squires and Demetrion, 1992
R. bouilleana†† A. Milne-Edwards, 1872
R. brevispina†† Lőrenthey, 1898
R. burleighensis†† Holland and Cvancara, 1958
R. cuspidata†† Guppy, 1909
R. elegans†† Rathbun, 1945
R. granulosa†† A. Milne-Edwards, 1872
R. griesbachi†† Noetling, 1897
R. haszlinskyi†† Reuss, 1859
R. hirsuta†† Schafhäutl, 1863
R. lamiensis†† Rathbun, 1945
R. libyca (van Straelen, 1935 [imprint 1934])
R. molengraaffi†† van Straelen, 1924 [imprint 1923]
R. oblonga†† Münster, 1840
R. ornata†† de Angeli and Beschin, 2011
R. palmea†† E. Sismonda, 1846
R. pellattieroi†† de Angeli and Beschin, 2011

Table S2. (Continued.)

R. propinqua†† Ristori, 1891
R. ranina† (Linnaeus, 1758) (type)
R. speciosa†† (Münster, 1840)
R. tejoniana†† Rathbun, 1926
Raninella†† A. Milne-Edwards, 1862
R. atava Carter, 1898
R. circumviator (Wright and Collins, 1972)
R. elongata A. Milne-Edwards, 1862
R.? quadrispinosa (Collins, Fraaye, and Jagt, 1995)
R. trigeri A. Milne-Edwards, 1862 (type)
Remyranina†† Schweitzer and Feldmann, 2010
R. ornata (Remy, 1960) (type)
Vegaranina†† van Bakel et al., 2012
L. precocia (Feldmann et al., 1996)
Subfamily Raninoidinae† Lőrenthey *in* Lőrenthey and Beurlen, 1929
Bonizzatoides†† Beschin, Busulini, and Tessier, 2013
B. tuberculatus Beschin, Busulini, and Tessier, 2013 (type)
Cristafrons†† Feldmann, Tshudy, and Thomson, 1993
C. praescientis Feldmann et al., 1993 (type)
Notopoides† Henderson, 1888
N. exiguus†† Beschin, Busulini, de Angeli, and Tessier, 1988
N. nantoensis†† Beschin, Busulini, and Tessier, 2013
N. pflugervillensis†† Beikirch and Feldmann, 1980
N. verbeeki†† Böhm, 1922
Notosceles† Bourne, 1922
N. bournei†† Rathbun, 1928
N. serratifrons† (Henderson, 1893)
Pseudorogueus†† Fraaye, 1995
P. rangiferus Fraaye, 1995
Quasilaeviranina†† Tucker, 1998
Q. arzignanensis (Beschin, Busulini, de Angeli, and Tessier, 1988)
Q. eocenica (Rathbun, 1935)
Q. keyesi (Feldmann and Maxwell, 1990)
Q. miniscula Beschin et al., 2012
Q. ombonii (Fabiani, 1910)
Q. ovalis (Rathbun, 1935)
Q. pororariensis (Glaessner, 1980)
Q. simplicissima (Bittner, 1883)
Raninoides† H. Milne Edwards, 1837 [in 1834-1840] (= *Laeviranina* Lőrenthey *in* Lőrenthey and Beurlen, 1929; = *Raninellopsis* Böhm, 1922)
R. acanthocolus†† Schweitzer, Feldmann, Gonzalez-Barba, and Ćosović, 2006
R. araucana†† (Philippi, 1887)
R. asper†† Rathbun, 1926
R. barnardi† Sakai, 1974
R. benedicti† Rathbun, 1935
R. borealis†† (Collins and Rasmussen, 1992)
R. budapestiniensis†† (Lőrenthey, 1897)
R. dickersoni†† Rathbun, 1926
R. eugenensis†† Rathbun, 1926
R. fabianii†† (Lőrenthey *in* Lőrenthey and Beurlen, 1929)
R. fulgidus†† Rathbun, 1926
R. fulungensis†† Hu and Tao, 1999
R. glabra†† (Woodward, 1871)
R. goedertorum†† (Tucker, 1998)
R. gottschei†† Böhm, 1927
R. hollandica†† (Collins et al., 1997)
R. javanus†† (Böhm, 1922)
R. louisianensis† Rathbun, 1933
R. madurensis†† Beets, 1950
R. mexicanus†† Rathbun, 1930
R. morrisi†† Collins et al., 2003
R. notopoides†† (Bittner, 1883)
R. oregonensis†† Rathbun, 1926
R. perarmata†† (Glaessner, 1960)

Table S2. (Continued.)

R. pliocenicus†† de Angeli et al. 2009
R. proracanthus†† Schweitzer, Feldmann, Gonzalez-Barba, and Ćosović, 2006
R. pulchra†† (Beschin, Busulini, de Angeli, and Tessier, 1988)
R. rathbunae†† van Straelen, 1933
R. rioturbioensis†† Schweitzer et al., 2012
R. sinuosus†† (Collins and Morris, 1978)
R. slaki†† Squires, 2001
R. treldenaesensis†† Collins and Jakobsen, 2003
R. vaderensis†† Rathbun, 1926b (= *Laeviranina lewisana* Rathbun, 1926b)
R. toehoepae†† (van Straelen, 1924 [imprint 1923])
R. washburnei†† Rathbun, 1926b
Subfamily Symethinae† Goeke, 1881
Eosymethis†† van Bakel et al., 2012
E. aragonensis van Bakel et al., 2012 (type)
Subfamily indeterminate
Sabahranina†† Collins et al., 2003
S. trushidupensis Collins et al., 2003 (type)