



PHYLOGENETIC ANALYSIS AND REVISED CLASSIFICATION OF PODOTREMATOUS BRACHYURA (DECAPODA) INCLUDING EXTINCT AND EXTANT FAMILIES

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ABSTRACT

A phylogenetic analysis based upon 30 extinct and extant taxa of podotrematous brachyuran decapods using 74 characters shows that Podotremata sensu Guinot, 1977 is not monophyletic and results in a new classification for these crabs. Four new taxa are recognized at the section-level (Homoloida, Tornyommoida, Etyoida, and Dakoticancroida) as well as two new families (Basinotopidae and Xandarocarcinidae). Dromiacea as historically defined is redefined herein to exclude Homoloidea. New generic names *Noetlingocarcinus* and *Xandarocarcinus*, and *Seorsus millerae* new combination also resulted from the work.

KEY WORDS: Brachyura, classification, Dromiacea, Podotremata, phylogeny, Raninoidea

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INTRODUCTION

Numerous recent studies have focused on the phylogeny of Brachyura, and specifically, the monophyly of Podotremata (Jamieson et al., 1995; Guinot and Tavares, 2001; Brösing et al., 2007; Ah Yong et al., 2007; Scholtz and McLay, 2009). These have included molecular studies and studies using adult morphology, foregut ossicles, and spermatozoal structure, but until now none has included most of the extinct groups, which are known from an extensive fossil record on all continents, from the Early Jurassic to the Pleistocene. Because the podotrematous crabs are considered to be the least derived Brachyura, inclusion of their fossils into any analysis is critical because the fossils represent the earliest history of the group as well as the earliest history of Brachyura. There are numerous extinct lineages within Brachyura, many of which are known with certainty to be podotrematous based upon excellent preservation of fossils, so that phylogenies based upon inclusion of fossils can be interpreted to represent a more realistic representation of the relationships between and among these animals. Interestingly, many of the extant podotrematous families have long and illustrious fossil records and have been on Earth since the time of the dinosaurs. Other families are shorter lived, either originating in the Mesozoic and shortly becoming extinct, or exhibiting what appears to be much greater diversity in modern oceans than in the past. How much of this is due to the vagaries of preservation in the fossil record is not yet known. What we do know is that the record of Brachyura and podotrematous crabs is much better known now than even 20 years ago, and the extensive studies carried out by us and others makes it possible to examine the fossils in

light of biological morphological studies that have also been extensive in recent decades (Guinot and Tavares, 2001, 2003; Guinot et al., 2008). Thus, we present the first comprehensive phylogeny of podotrematous crabs including nearly all extinct and extant representatives.

MATERIALS AND METHODS

Phylogenetic Analysis

Thirty extant and fossil families within Podotremata sensu Guinot (1977) were examined (Table 1). Additionally, two enigmatic podotreme genera, *Basinotopus* M'Coy, 1849, and *Xandarocarcinus* (= *Xandaros* Bishop, 1988c), were also included. The analysis also includes representatives of three eubrachiurans as in-group taxa to test the sister-group relationships of each podotreme family. Two extinct families, Nodoprosopidae Schweitzer and Feldmann, 2009 and Tithonohomolidae Feldmann and Schweitzer, 2009, were excluded from the phylogenetic analyses because they each have a large number of unknown character states. The Gastrodoridae van Bakel et al. 2008, are not included here as they are best considered as members of Anomura.

The analyses were based upon the examination of material deposited in the following institutions: BMNH, The Natural History Museum, London, UK; GSC, Geological Survey of Canada, Eastern Paleontology, Division, Ottawa, Ontario, Canada; HNHM, Hungarian Natural History Museum, Budapest, Hungary; IG, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KSU D, Kent State University Decapod Comparative Collection; KMNH.IVP, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan; LACM, Natural History Museum of Los Angeles County, California, USA; MAB, Oertijdmuseum De Groene Poort, Boxtel, The Netherlands; MAFI, Földani Intézet (Hungarian Geological Survey), Budapest, Hungary; MBA, Museum für Naturkunde Berlin, Paläontologisches Museum, Germany; MCZ, Museo Civico "G. Zannato" di Montecchio Maggiore (Vicenza), Italy; MFM, Mizunami Fossil Museum, Mizunami, Japan; MGSB, Museo Geológico del Seminario de Barcelona, Spain; MGUH, Geologisk Museum University of Copenhagen, Denmark; NHMW, Naturhistorisches Museum Wien (Natural History Museum of Vienna), Austria; NM, Národní

Table 1. Original classification (De Grave et al., 2009; Schweitzer et al., 2010) used to select taxa for this analysis. † indicates extinct taxa (see text for details).

Infraorder Astacidea Latreille, 1802
 Superfamily Nephropoidea Dana, 1852
Nephropidae Dana, 1852
Homarus Weber, 1795 [*H. americanus* H. Milne Edwards, 1837 (in 1834-1840)]

Infraorder Anomura MacLeay, 1838
 Superfamily Eocarcinoidea Withers, 1932
Eocarcinidae † Withers, 1932
Eocarcinus † Withers, 1932 [*E. praecursor* Withers, 1932]

Infraorder Brachyura Linnaeus, 1758
 Section Dromiacea de Haan, 1833
 Superfamily Dakoticancroidea † Rathbun, 1917
Ibericancriidae † Artal et al., 2008
Ibericancer † Artal et al., 2008 [*I. sanchoi* Artal et al., 2008]
Dakoticancridae † Rathbun, 1917
Avitelmessus † Rathbun, 1923b [*A. grapsoideus* Rathbun, 1923b]
Dakoticancer † Rathbun, 1917 [*D. australis* Rathbun, 1935; *D. overanus* Rathbun, 1917]
Tetracarcinus † Weller, 1905 [*T. subquadratus* Weller, 1905]

Superfamily Homolodromioidea Alcock, 1900
Bucculentidae † Schweitzer and Feldmann, 2009a
Bucculentum † Schweitzer and Feldmann, 2009a [*B. bachmayeri* Schweitzer and Feldmann, 2009a; *B. bucculentum* (Wehner, 1988)]
Homolodromiidae Alcock, 1900
Homolodromia A. Milne-Edwards, 1880 [*H. robertsi* Garth, 1973; *H. paradoxa* A. Milne Edwards, 1880]
Dicranodromia A. Milne-Edwards, 1880 [*D. doederleini* Ortmann, 1892]
Goniidromitidae † Beurlen, 1932
Eodromites † Patruilius, 1959 [*E. grande* (von Meyer, 1857)]
Goniidromites † Reuss, 1858 [imprint 1857] [*G. bidentatus* Reuss, 1858 [imprint 1857]; *G. hirotai* Karasawa and Kato, 2007; *G. polyodon* Reuss, 1858 [imprint 1857]; *G. serratus* Beurlen, 1929]
Pithonoton † von Meyer, 1842 [*P. marginatum* von Meyer, 1842; *P. cardwelli* Armstrong et al., 2009]
Sabellidromites † Schweitzer and Feldmann, 2008 [imprint 2007] [*S. inflata* (Collins and Karasawa, 1993); *S. scarabaea* (Wright and Wright, 1950)]
Prosopidae † von Meyer, 1860
Prosopon † von Meyer, 1835 [*P. mammillatum* Woodward, 1868]

Superfamily Glaessneropsoida † Patruilius, 1959
Glaessneropsidae † Patruilius, 1959
Glaessneropsis † Patruilius, 1959 [*G. heraldica* (Moericke, 1889); *G. myrmekia* Schweitzer and Feldmann, 2009a]
Konidromitidae † Schweitzer and Feldmann, 2010b
Konidromites † Schweitzer and Feldmann, 2010b [*K. schneideri* (Stolley, 1924); *K. gibbus* (Reuss, 1858 [imprint 1857])]
Longodromitidae † Schweitzer and Feldmann, 2009a
Antarctiprosopon † Schweitzer and Feldmann, 2011a [*A. chaneyi* (Feldmann and Wilson, 1988)]
Dioratiopus † Woods, 1953 [*D. salebrosus* Woods, 1953]
Glaessnerella † Wright and Collins, 1975 [*G. spinosa* (van Straelen, 1936a)]
Longodromites † Patruilius, 1959 [*L. angustus* (Reuss, 18; 58 [imprint 1857]); *L. excisus* (von Meyer, 1857); *L. ovalis* (Moericke, 1889)]
Planoprosopon † Schweitzer, Feldmann, and Lazăr, 2007 [*P. heydeni* (von Meyer, 1857)]
Vespridromites † Schweitzer and Feldmann, 2011a [*V. hearttailensis* (Bishop, 1985)]
Lecythocaridae † Schweitzer and Feldmann, 2009a
Lecythocaris † von Meyer, 1858 (2) [*L. obesa* Schweitzer and Feldmann, 2009a; *L. paradoxa* (von Meyer, 1858)]

Superfamily Dromioidea de Haan, 1833
Dromiidae de Haan, 1833
Conchoecetes Stimpson, 1858a [*C. artificiosus* (Fabricius, 1798)]
Dromia Weber, 1795 [*D. personata* (Linnaeus, 1758); *D. erythropus* (George Edwards, 1771)]
Epigodromia McLay, 1993 [*E. areolata* (Ihle, 1913)]
Epipedodromia André, 1932 [*E. thomsoni* (Fulton and Grant, 1902)]
Lauridromia McLay, 1993 [*L. dehaani* (Rathbun, 1923a)]
Sphaerodromiidae Guinot and Tavares, 2003
Sphaerodromia Alcock, 1899 [*S. lamellata* Crosnier, 1994]
Dromilites † H. Milne Edwards, 1837 [*D. bucklandi* H. Milne Edwards, 1837 (in 1834-1840); *D. simplex* Quayle and Collins, 1981]
Dynomenidae Ortmann, 1892
Basinotopus † M'Coy, 1849 [*B. lamarckii* (Desmarest, 1822); *B. tricornis* Collins and Jakobsen, 2003]
Dynomene Desmarest, 1822 [*D. hispida* Guérin-Méneville, 1832; *D. pilumnoides* Alcock, 1900; *D. praedator* A. Milne-Edwards, 1878]
Diaulacidae † Wright and Collins, 1972
Diaulax † Bell, 1863 [*D. oweni* (Bell, 1850); *D. feliceps* Wright and Collins, 1972; *D. yokoi* Collins et al., 1993]
Xandaros † Bishop, 1988c [*X. sternbergi* (Rathbun, 1926)]

Superfamily Etyioidea † Guinot and Tavares, 2001
Etyidae † Guinot and Tavares, 2001
Etyus † Mantell, 1822 [*E. martini* Mantell, 1822]
Etyxanthosia † Fraaije, van Bakel, Jagt, and Artal, 2008 [*E. aspera* (Rathbun, 1935); *E. pawpawensis* (Schweitzer, Salva, and Feldmann, 1999)]
Feldmannia † Guinot and Tavares, 2001 [*F. wintoni* (Rathbun, 1935)]
Xanthosia † Bell, 1863 [*X. buchii* (Reuss, 1845); *X. gibbosa* Bell, 1863; *X. granulosa* (M'Coy, 1854); *X. sakoi* Karasawa, Ohara, and Kato, 2008; *X. similis* (Bell, 1863)]

Table 1. Continued.

Superfamily Homoloidea de Haan, 1839

Homolidae de Haan, 1839

Homola Leach, 1816 [imprint 1815] [*H. ranunculus* Guinot and Richer de Forges, 1995; *H. orientalis* Henderson, 1888]

Latreillopsis Henderson, 1888 [*L. bispinosa* Henderson, 1888]

Homolomannia Ihle, 1912 [*H. sibogae* Ihle, 1912]

Paromola Wood-Mason in Wood-Mason and Alcock, 1891 [*P. macrocheira* Sakai, 1961]

Yaldwynopsis Guinot and Richer de Forges, 1995 [*Y. spinimanus* (Griffin, 1965)]

Mithracitidae Števíć, 2005

Mithracites † Gould, 1859

[*M. vectensis* Gould, 1859]

Latreillidae Stimpson, 1858a

Latreillia Roux, 1830 [*L. valida* de Haan, 1839]

Poupiinidae Guinot, 1991

[*Poupinia* Guinot, 1991 [*P. hirsuta* Guinot, 1991]]

Section Raninoida Ahyong et al., 2007

Superfamily Raninoidea de Haan, 1839

Camarocarcinidae † Feldmann, Li, and Schweitzer, 2007

Camarocarcinus † Holland and Cvancara, 1958 [*C. arnesoni* Holland and Cvancara, 1958; *quinquetuberculatus* Collins and Rasmussen, 1992]

Cretacocarcinus † Feldmann, Li, and Schweitzer, 2007 [*C. smithi* Feldmann et al., 2007]

Cenomanocarcinidae † Guinot, Vega, and van Bakel, 2008

Campylostoma † Bell, 1858 [*C. matutiforme* Bell, 1858]

Cenomanocarcinus † Van Straelen, 1936 [*C. vanstraeleni* Stenzel, 1945]

Raninidae de Haan, 1839

Lyreidus de Haan, 1841 [*L. tridentatus* de Haan, 1841]

Ranina Lamarck, 1801 [*R. ranina* (Linnaeus, 1758)]

Palaeocorystidae † Lörenthey in Lörenthey and Beurlen, 1929

Cretacorantina † Martin, 1941 [*C. dichrous* (Stenzel, 1945)]

Eucorystes † Bell, 1863 [*E. broderipi* (Mantell, 1844); *E. carteri* M'Coy, 1854]

Notopocorystes † M'Coy, 1849 [*N. japonicus* (Jimbô, 1894); *N. stokesii* (Mantell, 1844)]

Symethidae Goeke, 1981

Symethis Weber, 1795 [*S. johnsoni* Rathbun, 1935]

Section Cyclodorippoida Ahyong et al., 2007

Superfamily Cyclodorippoidea Ortmann, 1892

Cyclodorippidae Ortmann, 1892

Tymolus Stimpson, 1858b [*T. japonicus* Stimpson, 1858b; *T. uncifer* (Ortmann, 1892)]

Xeinostoma Stebbing, 1920 [*X. eucheir* Stebbing, 1920]

Cymonomidae Bouvier, 1897

Cymonomus A. Milne-Edwards, 1880 [*Cymonomus* sp.]

Cymonomoides Tavares, 1993 [*C. guinotae* (Tavares, 1991)]

Phyllotymolinidae Tavares, 1998

Genkaia Miyake and Takeda, 1970 [*G. gordonae* Miyake and Takeda, 1970]

Phyllotymolinum Tavares, 1993 [*P. crosnieri* Tavares, 1993]

Torynomidae † Glaessner, 1980

Torynomma † Woods, 1953 [*T. dentatum* Glaessner, 1980; *T. flemingi* Glaessner, 1980; *T. quadrata* Woods, 1953]

Section Eubrachyura de Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Dorippoidea MacLeay, 1838

Necrocarcinidae † Förster, 1968

Necrocarcinus † Bell, 1863 [*N. labeschei* (Eudes-Deslongchamps, 1835); *N. wrighti* Feldmann, Tshudy, and Thomson, 1993]

Goniochelidae † Schweitzer and Feldmann, 2011b

Goniochele † Bell, 1858 [*G. angulata* Bell, 1858; *G. madseni* Collins and Jakobsen, 2003]

Superfamily Portunoidea Rafinesque, 1815

Carcinidae MacLeay, 1838

Carcinus Leach, 1814 [*C. maenas* (Linnaeus, 1758)]

Subsection Thoracotremata Guinot, 1977

Superfamily Grapsoidea MacLeay, 1838

Varunidae H. Milne Edwards, 1853

Helice de Haan, 1833 [*H. tridens* (de Haan, 1835)]

Museum, Prague, Czech Republic; OUM, Geological Collections, Oxford University Museum, UK; PI, Charleston Museum Charleston, South Carolina, USA; PRI, Paleontological Research Institution, Ithaca, New York, USA; QMF, uqf, Queensland Museum, Queensland, Australia; SDSM, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; SDSNH, San Diego Museum of Natural History, San Diego, California, USA; SM, Sedgwick Museum, Cambridge University, UK; SMF, Senckenberg Forschungsinstitut und NaturMuseum, Frankfurt, Germany; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; UT, University of Texas at Austin, Texas, USA; UWBM, University of Washington Burke

Museum, Seattle, Washington, USA; and YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA. If actual material was unavailable, the descriptive information for taxa was obtained from the literature; this was necessary for only a few taxa. The genera were selected for the analysis based upon the familial and subfamilial arrangement of De Grave et al. (2009) and Schweitzer et al. (2010) as well as our own observations. The out-groups were chosen from representatives of the astacidean family Nephropidae and the earliest-known anomuran family Eocarcinidae (Feldmann and Schweitzer, 2010).

Two analyses were conducted. Analysis I included only extant taxa. Analysis II included both extinct and extant taxa to examine the impact of

Table 2. Data matrix of podotreme taxa and their character states. See text for details. * indicates extinct taxa.

	0									1									
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Astacidea	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0
*Eocarcinidae	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0
Homolodromiidae	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
*Bucculentidae	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
*Goniodromitidae	0&1	0&1	0&1	0&1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
*Prosopidae	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
*Tanidromitidae	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
*Glaessneropsidae	0	0	0	0	0	0	0	0	1	0	-	0	1	0	0	0	0	0	0
*Konidromitidae	0	0	0	0	0	0	0	0	1	0	-	0	0	0	0	0	0	0	0
*Lecythocaridae	1	0	0	0	0	0	0	0	1	0	-	0	1	0	0	0	0	0	0
*Longodromitidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Dromiidae	1	1	1	1	0&1	0	0	0	1	0	-	0	0	0	0&1	0	0	0	0
Dynomenidae	1	1	1	1	1	0	0	0	1	0	-	0	0	1	1	0	0	0&1	0
Sphaerodromiidae	1	1	1	1	0&1	0	0	0	1	0	-	0	0	1	1	0&1	0&1	0&1	0
*Diaulacidae	1	1	1	1	0	0	0	0	1	0	-	0	0	1	1	0	1	0&1	0
*Xandaros	1	1	1	1	1	0	0	0	1	0	-	0	0	1	1	0	1	1	0
*Basinotopus	0	1	1	1	0	0	0	0	1	0	-	0	0	0	0	0	0	0	0
Homolidae	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
Latreilliidae	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0
Poupiniidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
*Mithracitidae	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
*Etyidae	1	1	1	1	0	0	0	0	1	0	-	1	1	1	1	0	1	0	0
*Dakoticancridae	1	1	0	1	1	0	1	0	1	0	-	0	0	1	1	0	1	0&1	0
*Ibericancridae	1	1	0	1	1	0	1	0	1	0	-	0	1	1	1	0	1	0	0
Raninidae	0	1	0&1	0	1	0	1	0	1	0	-	1	1	1	1	1	1	1	0
Symethidae	0	1	0	0	1	0	1	0	1	0	-	1	1	1	1	1	1	1	0
*Camarocarcinidae	1	1	1	1	1	1	0	0	1	0	-	1	1	1	1	0&1	1	0&1	0
*Cenomanocarcinidae	1	1	1	1	1	0&1	0&1	0	1	0	-	1	1	1	1	0&1	1	0&1	1
*Necrocarcinidae	1	1	1	1	1	0&1	0	0	1	0	-	1	1	1	1	0	1	0&1	1
*Palaeocorystidae	0	1	1	1	1	0	0	0	1	0	-	1	1	1	1	0&1	1	0&1	0&1
Cyclodorippidae	1	1	0&1	0&1	0	0	0	0	1	0	-	0&1	1	1	1	0	1	0	0
Cymonomidae	1	0	0&1	0&1	0	0	0	0	0	0	-	0	0	1	1	0	1	0	0
Phyllotymolidae	1	1	1	1	0&1	0	0	0	1	0	-	0&1	1	1	1	0	1	0	0
*Torynomidae	1	0	0	0	0	0	0	0	1	0	-	0	0	0	1	0	1	0	0
*Goniochelidae	1	1	1	1	1	0	0	0	1	0	-	1	1	1	1	0	1	0	1
Carcinidae	1	1	1	1	1	0	1	0	1	0	-	1	1	1	1	1	1	1	0
Varunidae	1	1	1	1	1	0	1	0	1	0	-	0	0	1	1	1	1	1	0

extinct taxa on the topology of the podotreme relationships. 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, 50 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 decay analyses (Bremer, 1994). The Bremer support was obtained using constraint trees generated in MacClade 4.08 for OSX (Maddison and Maddison, 2005) and analyzed using PAUP*.

Characters

Seventy-four adult morphological characters were used in the analysis. The data matrix is provided in Table 2. Sixty-nine characters were binary; five were multistate characters. The missing, or indeterminable, data were scored as unknown. The rate of missing data within the examined fossil taxa ranged from 6.8 to 68.9 percent. Inapplicable character states were scored as “-” to distinguish them from unknown character states, which 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. Some characters and character states require an explanation, given below. Within many extinct taxa, information on the mouth, sternum, pleon, and pereopods is lacking.

1. Carapace proportions: elongate (0); as long as wide or wider (1).
2. Anterolateral margins: indistinct (0); distinct (1).
3. Spines or teeth on anterolateral margins: absent (0); present (1).
4. Anterolateral margins not well differentiated from posterolateral margins (0); anterolateral margins well differentiated from posterolateral margins (1).
5. Posterolateral margins: rounded, not defined (0); defined (1).
6. Spines on posterolateral margin: absent (0); present (1).
7. Posterior margin: concave (0); straight (1).
8. Re-entrants on posterior margin: absent (0); present (1).

All homolodromioids and homolids have reentrants on the posterolateral margin (8-1), which all other families lack (8-0).

9. Orbit: not defined (0); defined (1).
10. Augenrest: absent (0); present (1).

The augenrest (Schweitzer and Feldmann, 2008 [imprint 2007]) is present in Homolodromioidea, Longodromitidae, and Homoloidea excluding Latreilliidae (10-1). Others lack it (10-0).

11. Augenrest, if present: shallow (0); deep (1).

This character is scored inapplicable for the taxa lacking the augenrest. The tanidromitids, longodromitids, mithracitids, poupiniids, and homolids have a shallow augenrest (11-0), whereas homolodromioids, prosopids, bucculentids, and goniodromitids have a deep augenrest (11-1).

12. Inner orbital angle: not defined (0); defined (1).
13. Upper orbital fissures: absent (0); present (1).
14. Subhepatic swelling: present (0); absent (1).
15. Antennal groove: present (0); absent (1).

Table 2. Extended.

2										3										4												
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	0	0	0	0	0	0	1	-	0	-	-	-	-	0	-	1	0	0	0	0	0	-	-	-	0	0	0	2	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	1	0	0	0	0	1	0	0	1	1	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	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	1	0	1		
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0	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	1	1	0	0	?	1	0	0	0	1	0	1	1	1	1		
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1	1	0	0	0	1	1	0	?	1	1	1	1	?	0	?	1	0	1	?	?	0	-	-	-	?	1	0	1	2	1		
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1	1	0	0	0	1	1	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	-	-	-	1	1	1	2	1	1		

- 16. Cervical groove: distinct (0); indistinct (1).
- 17. Postcervical groove: present (0); absent (1).
- 18. Branchiocardiac groove: distinct (0); indistinct (1).
- 19. Longitudinal ridge or tubercles on branchial region: absent (0); present (1).
- 20. Cervical or branchiocardiac groove: reaching ventral carapace (0); ending at anterolateral margin.
- 21. Intestinal region: very narrow, limited by branchial grooves (0); wide (1).

Within all homolodromioids and glaessneropsoids the intestinal region is very narrow and limited by branchial grooves (21-0), whilst other brachyurans have a relatively wide intestinal region (21-1).

- 22. Homolid lineae: absent (0); present (1).
- 23. Epistomial spine: absent (0); present (1).
- 24. Buccal cavern: wide (0); elongate (1).
- 25. Thoracic sternum: narrow, generally completely covered by pleon (0); wide, not completely covered by pleon (1).

Within most podotrematous crabs, the thoracic sternum is narrow (25-0), but some homoloids, some dakoticancrids, all cyclodorippoids, and eubrachiurans have a relatively wide thoracic sternum (25-1).

- 26. Sternites 1-3: indistinctly indicated ventrally (0); distinct ventrally (1).

Within Homolodromioidea, Glaessneropsoidea, and Dromioidea, the thoracic sternites 1-3 are indistinct ventrally (26-0), whereas within other brachyurans they are distinct ventrally (26-1). However, within homoloids the sternites 1-3 are distinct ventrally but covered by the pleon.

- 27. Posterior sternites: wide (0); narrow, reduced (1).

Most brachyurans have wide posterior thoracic sternites (27-0), whereas within Symethidae and Raninidae, thoracic sternites 6-8 are extremely narrowed posteriorly (27-1).

- 28. Lateral position of posterior sternites: not visible (0); visible (1).

Within most podotreme crabs the posterior thoracic sternites are completely covered by the pleon; therefore, these lateral parts are not visible (28-0). However, within most dakoticancrids, cyclodorippoids, and eubrachiurans, they are visible (28-1).

- 29. Episternites: not clearly defined (0); clearly defined by grooves (1).
- 30. Episternites 4-5: process-like (0); wide (1).

Within most brachyurans the episternites 4 and 5 are wide (30-1), whereas the homolodromiids, longodromitids, and dromioids have narrow, process-like or triangular episternites 4 and 5 (30-0).

- 31. Suture 4-5: only lateral position (0); well developed (1).
- 32. Suture 5-6: only lateral position (0); well developed (1).
- 33. Suture 6-7: incomplete (0); complete (1).
- 34. Sternite 4 with anteriorly protruded plate: absent (0), present (1).
- 35. Median line on sternite 8: absent (0); present (1).
- 36. Sterno-coxal depression: present (0); absent (1).

The homolodromioids, glaessneropsoids, dromioids, and homoloids have a sterno-coxal depression (36-1) (defined by Guinot and Bouchard, 1998), which other brachyurans lack (36-0).

- 37. Sterno-pleonal depression of male: absent (0); present (1).

Table 2. Extended.

5										6									7						
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	
0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
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?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
0	0	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
0	1	0	1	1	0	?	0	?	0	0	0	?	0	?	?	0	1	?	1	0	?	?	?	?	
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0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	0	1	?	1	0	?	?	?	?	
0	1	?	1	1	0	0	0	?	1	1	0	?	0	?	?	0	0	0	0	?	?	?	?	?	
0	0	0	0	?	1	?	0	?	1	0	0	0	0	?	?	0	2	?	2	0	?	?	?	?	
0	1	1	0&1	0	0	0	0	0	0	0&1	0	0	0&1	1	0	0	0	1	1	1	0	0	0	1	1
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0	1	0	0	3	0	0	0	0	1	0	1	1	1	1	1	1	1	0	1	0	0	0	1	1	
?	?	0	?	?	?	0	?	?	1	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	
0	1	0	0	2	0	0	0	?	1	0	1	1	1	0	1	0&1	1	0	1	0	?	?	?	?	
0	1	0	0	2	0	0	0	?	1	0	1	1	1	0	1	1	1	0	1	0	0	?	?	?	
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0	1	0	0	2	0	?	0	?	?	?	?	?	?	?	?	?	2	?	2	0	?	?	?	?	
0	1	?	0	?	0	?	1	?	1	?	0	1	1	?	?	?	0	2	?	?	?	?	?	?	
0	1	1	0	2	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	1	0	0	1	1	
0	1	1	0	1	0	1	1	0	1	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	

Most podotreme crabs have a sterno-pleonal depression (37-0) (Guinot, 1979), which some dakoticancrids and raninids, cyclodorippoids, and eubranchyurans lack (37-1).

38. Sterno-pleonal cavity in male: absent (0); present (1).

The cyclodorippoids and eubranchyurans have a sterno-pleonal cavity (38-1) (Guinot, 1979), which is completely covered by the pleon of male, but most podotremes lack it (38-0).

39. Homolid button: absent (0); present (1).

The homolid button (Guinot and Bouchard, 1998) is only recognized in Homoloidea (39-1).

40. Sella turcica: absent (0); present (1).

The presence of the sella turcica is a feature of the endophragmal skeleton uniting all Eubranchyura (40-1) (Secretan, 1998; Tavares, 2003; Guinot and Tavares, 2001). All podotremes lack the sella turcica (40-0).

41. Spermatheca: absent (0); present (1).

Characters of the spermatheca of podotreme crabs were well studied by Guinot and Quenette (2005). The thoracic sternum of podotremes is specialized in females and bears the spermatheca (41-1). Many workers (i.e., Guinot and Tavares, 2001; Guinot and Quenette, 2005) thought that the presence of spermatheca is one of the unique characters for the monophyly of Podotremata. Actually, Eubranchyura lack spermatheca (41-0).

42. Spermatheca: if present, paired (0); united (1).

This character is scored inapplicable for the taxa without the spermatheca. Within Symethidae and Raninidae the spermatheca is united

and located on a longitudinal median line (42-1), whereas other podotremes have a pair of spermathecae (42-0).

43. Spermatheca position: if present, around level of pereopod 3 coxa (0); much anterior to pereopod 3 coxa (1).

This is also scored inapplicable for the taxa lacking the spermatheca. Within most podotremes the spermathecae are positioned at the level of the coxa of pereopod 3 (43-0), while some dromiids have an elongate, long suture 7-8 and the spermatheca position is located much anterior to the coxa of pereopod 3 (43-1).

44. Aperture of spermatheca: if present, margins not raised (0); raised (1).

This is also scored as inapplicable for the taxa lacking the spermatheca. The margin of the spermathecal aperture is raised within homolodromioids and some dromioids (44-1), but it is not raised within the other podotreme crabs (44-0).

45. Pleon: not folding (0); folding (1).

46. Pleonites: visible dorsally (0); not visible (1).

47. Pleonal pleura: well developed (0); reduced (1).

48. Pleonal locking system: coxal spine (0); sternal lobe (1); absent (2).

Guinot and Bouchard (1998) have studied the pleonal holding system of brachyuran crabs. The pleon is locked by a coxal spine or projection within homolodromioids, homoloids, most dromioids, and longodromitids (48-0); some dynomenids, etyids, necrocarcinids, and dakoticancroids have a sternal lobe or projection, which locks the pleon (49-1); and other taxa lack both locking systems (49-2).

49. Articulating rings of pleon: present (0); absent (1).

50. Fusion of pleonites and telson in males: absent (0); present (1).

Cyclodorippidae and Cymonomidae are the only taxa with fused pleonal somite 6 and telson in males (50-1).

51. Pleonal somite 6 with triangular lateral lobes: present (0); absent (1).
52. Socket on sternite 6: absent (0); present (1).

The homoloids, raninid lyreidines, and eubrachyurans have a socket (Guinot and Bouchard, 1998) on the internal side of pleonal somite 6 (52-1), which others lack (52-0).

53. Telson of male: elongate, much longer than wide (0); about as long as wide or wider than long (1).
54. Anterior end of telson, if folding present: between mxp 3 (0); anterior sternite 4 (1); posterior sternite 4 (2); behind sternite 4 (3).

This character is scored inapplicable for the out-group taxa, symethids and most raninids. The anterior end of the telson is inserted between maxillipeds 3 (54-0) within the homoloids, it reaches the anterior part of thoracic sternite 4 within the homolodromioids, longodromitids, and dromioids (54-1), and within other taxa excluding the cyclodorippids and cymonomids, it is located on the posterior part of sternite 4 (54-2). Within the cyclodorippids, cymonomids, and raninid lyreidines it is located on sternite 5 (54-3).

55. Uropodal plate: absent (0); present (1).

Most brachyurans lacks the uropodal plate at the anterolateral angle of the pleonal somite 6 (55-0), but most dromioids have it (55-1). Characters 39, 53, and 55, although considered by Guinot and Bouchard (1998) to be homologous, are distinct structures and are observed as such in fossils. Thus, we score them separately.

56. Male gonopore position: coxal (0); sternal (1).
57. Female gonopore position: coxal (0); sternal (1).
58. Renal opening of second antennal coxa with beak-like structure: absent (0); present (1).

The homolodromiids and dromioids have the renal opening of the second antennal coxa with a beak-like structure (McLay, 1999; Scholtz and McLay, 2009) (58-0), which other taxa lack (58-1).

59. Maxilliped 3: pediform (0); operculiform (1).
60. Maxilliped 3 much longer than wide: present (0); absent (1).
61. Maxilliped 3 with two planes: absent (0); present (1).
62. Maxilliped 3 with crista dentata: present (0); absent (1).
63. Maxilliped 3 coxa: large, touching (0); small, not touching (1).
64. Palp of maxilliped 3 merus: distal position (0); inner-mesial position (1).
65. Palp of maxilliped 3: different plane (0); same level as merus (1).
66. Pereiopods 3-4 form: normal (0); paddle-like (1).
67. Pereiopods 4-5 condition: normal (0); P5 dorsal (1); P4-5 dorsal (2).
68. Pereiopods 4-5 condition: normal (0); P5 chelate (1); P4-5 chelate (2).
69. Pereiopods 4-5 size: normal (0); P5 reduced (1); P4-5 reduced (2).
70. Coxae of pereiopods: elongate, large (0); short (1).
71. Male coxa P5 with elongation: not modified (0); modified (1).

Within only Homolodromiidae, Sphaerodromiidae, and Dynomenidae the coxa of the pereiopod 5 in males is modified and has a hard, elongate, enclosed penis (Guinot and Tavares, 2003) (71-1).

72. Male coxa P5 with penial tube: absent (0); present (1).

The penial tube of the coxa of pereiopod 5 in males (Guinot and Tavares, 2003) (72-1) is present within only dromiids.

73. Pleopods on segments 3-5 in male: present (0); absent (1).

Most brachyurans lack pleopods on the pleonal segments (73-1), while the homolodromiids, most dromiids, sphaerodromiids, and dynomenids have the pleopods on pleonal segments 3-5 in males (Guinot et al., 1998; McLay, 1999) (73-1).

74. Male second pleopod with exopod: present (0); absent (1).

Most Brachyura lack the exopod of the second pleopods in males (74-1), whereas Sphaerodromiidae and Dynomenidae have it (74-0) (Guinot and Tavares, 2003; Guinot, 2008).

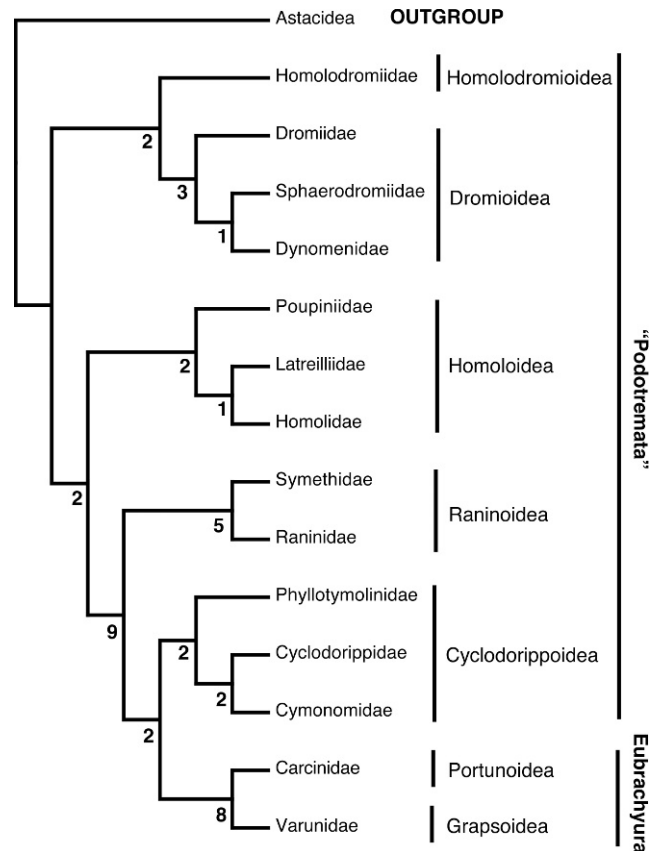


Fig. 1. The single most parsimonious tree from Analysis I (TL = 154 steps, CI = 0.6753, RI = 0.7817, RC = 0.5279). Bremer support for major branches indicated. Superfamilies and section recognized previous to this work are indicated.

RESULTS

Analysis I yielded a single most-parsimonious tree, 154 steps long with a consistency index (CI) of 0.6753, a retention index (RI) of 0.7817, and a rescaled consistency index (RC) of 0.5279. A single most-parsimonious tree indicating Bremer support is given in Fig. 1. Analysis II yielded 39 most-parsimonious trees, 224 steps long with a consistency index (CI) of 0.5938, a retention index (RI) of 0.8030, and a rescaled consistency index (RC) of 0.4768. A strict consensus tree is given in Fig. 2 along with Bremer support values. Character state changes of analysis II are given in Fig. 3. The topologies from analyses I and II were largely matched.

Paraphyly of Podotremata

The present analysis strongly supports the paraphyly of Podotremata shown by many recent works (Schram, 2001; Martin and Davis, 2001; Dixon et al., 2003; Ah Yong and O'Meally, 2004; Brösing et al., 2007; Ah Yong et al., 2007; Chu et al., 2009; Scholtz and McLay, 2009). The topology of analysis I including only extant families (Fig. 1) is consistent with that of Scholtz and McLay (2009) based upon the manual cladistic method. Guinot (1977) divided Podotremata into two subsections, Dromiaceae and Archaeobrachyura. Subsequently, Guinot and Tavares (2001)

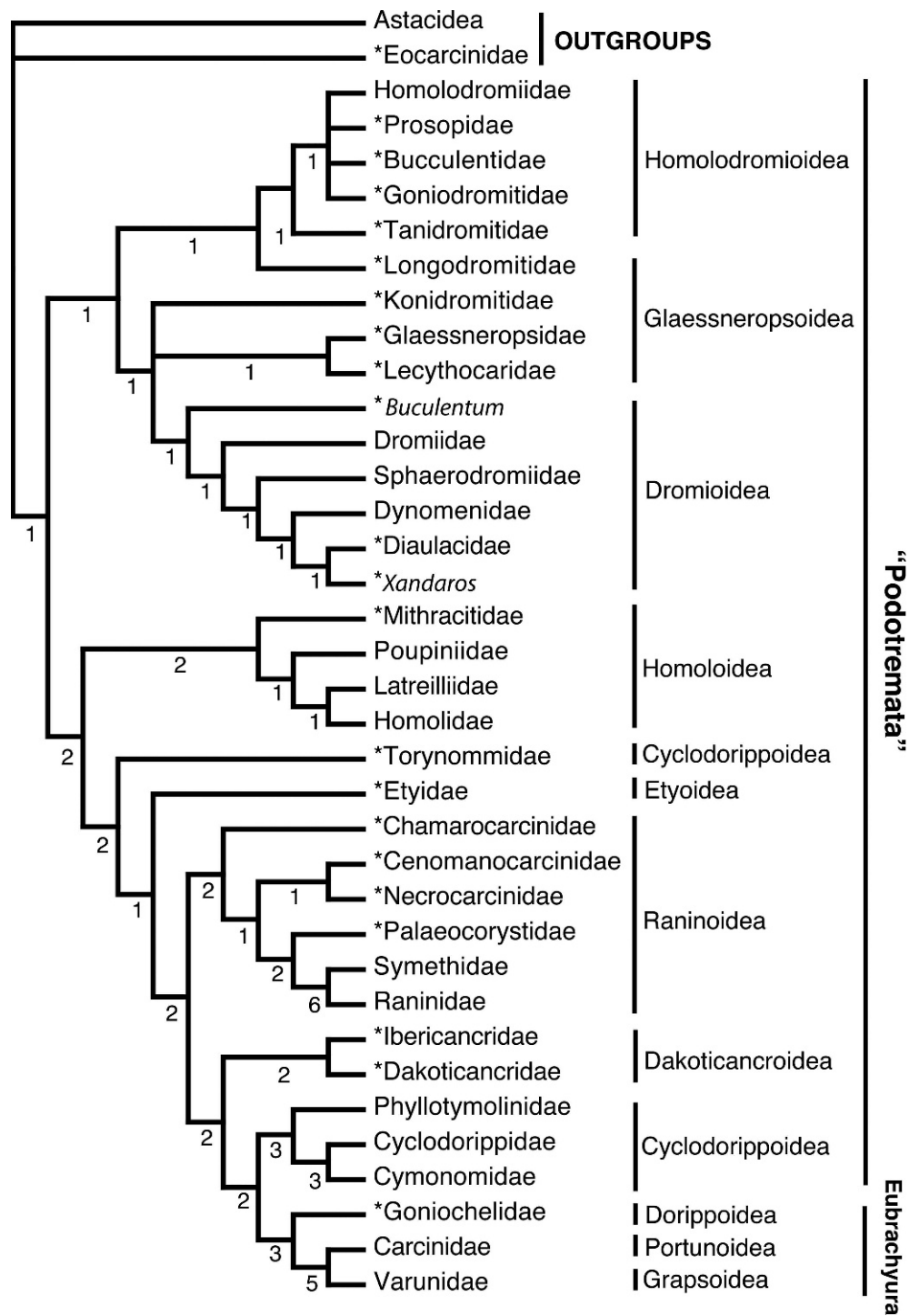


Fig. 2. Strict consensus tree of 39 most parsimonious trees from Analysis II (TL = 224 steps, CI = 0.5938, RI = 0.8030, RC = 0.4768). Bremer support for major branches indicated. Superfamilies and section recognized previous to this work are indicated.

recognized three major clades, the dromiaceans, homoloideans, and archaeobrachyurans, for Podotremata, and Guinot and Quenette (2005) subdivided Podotremata into three subsections, Dromiacea, Homolidea, and Archaeobrachyura. Ahyong et al. (2007) rejected the monophyly of the Podotremata and proposed four sections, Dromiacea, Raninoidea, Cyclodorippoidea, and Eubrachyura for Brachyura based upon molecular analysis. Most recently, Guinot

et al. (2008) proposed four subsections, Dromioidia, Homoloidia, Raninoidia, and Cyclodorippoidea, for Podotremata. De Grave et al. (2009) followed Ahyong et al. (2007) and arranged extant and extinct families within their classification. However, analysis II including extant and extinct families consists of seven major clades A-G (Fig. 3). The basic superfamily-level classification currently in use is largely supported, although the enigmatic

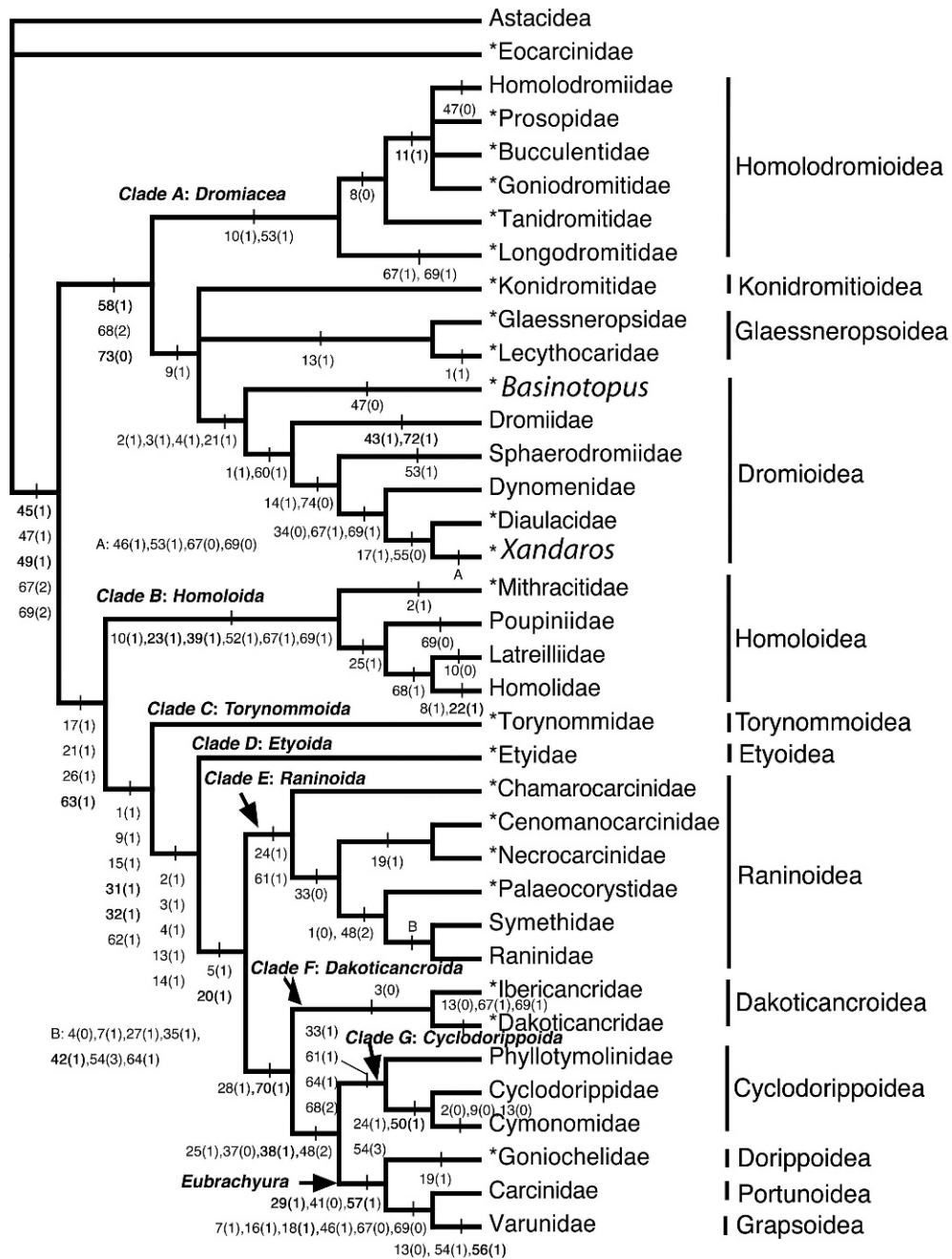


Fig. 3. Strict consensus tree from Analysis II with character state changes mapped onto it. Tree labeled with taxonomy proposed herein including sections, families, and superfamilies.

genera *Basinotopus* and *Xandarocarcinus* represent herein new families. Additionally, the monophyly of Dromiacea and Archaeobrachyura is not supported.

Dromiacea (Clade A).—Dromiacea, the basal, diverse clade A, is the sister group to the rest of the paraphyletic Podotremata, as well as Eubrachyura. This clade is united by three synapomorphies: the renal opening of the second antennal coxa with a beak-like structure (58-1), the presence of chelae of pereopods 4-5 (68-2), and the presence of pleopods on pleonal segments 3-5 in male (73-0). The renal opening of the second antennal coxa with a beak-like structure (McLay, 1999; Scholtz and McLay,

2009) and the presence of pleopods on pleonal segments 3-5 in males (Guinot et al., 1998; McLay, 1999) are unique. Glaessner (1969) placed three superfamilies, Dromioidea, Homoloidea, and Dakoticancroidea, under the section Dromiacea. After that, Guinot (1977) arranged two extant superfamilies, Homolodromioidea and Dromioidea, in the subsection Dromiacea and included Homoloidea within the subsection Archaeobrachyura. Ah Yong et al. (2007) placed Homoloidea in Dromiacea based upon molecular analysis. In the most recent work, De Grave et al. (2009) arranged six superfamilies, Eocarcinoidea, Dromioidea, Glaessneropsoidea, Homolodromioidea, Homoloidea, and Dakoticancroidea, within Dromiacea and, subsequently,

Schweitzer et al. (2010) added Etyoidea to the section. Additionally, Feldmann and Schweitzer (2010) moved Eocarcinoidea to Anomura. The analysis rejects the position of Homoloidea within Dromiacea and suggests that Dromiacea, including the four superfamilies, Homolodromioidea, Konidromitioidea, Glaessneropsoidea, and Dromioidea, be restricted here.

Homolodromioidea is united by two characters, the presence of the augenrest (10-1) and a long, elongate telson of males (53-1). The monophyly of Glaessneropsoidea is not supported and the analysis shows that Glaessneropsoidea is polyphyletic. The glaessneropsoid Longodromitidae clade is derived as the sister to Tanidromitidae and Bucculentidae + Goniodromitidae + Prosopidae + Homolodromiidae clades. Only one character, possession of reentrants on the posterior margin of the carapace, unites the Tanidromitidae and Bucculentidae + Goniodromitidae + Prosopidae + Homolodromiidae clades. A Bucculentidae + Goniodromitidae + Prosopidae + Homolodromiidae relationship is unresolved, and the clade is united by only one character, the presence of a deep augenrest (11-1). The analysis supports the position of four extinct families under Homolodromioidea as referred by Schweitzer and Feldmann (2008 [imprint 2007], 2009a) and strongly suggests that Longodromitidae be moved to Homolodromioidea.

Only one character, the presence of a well-defined orbit (9-1), defines the unresolved clade of Konidromitidae + Glaessneropsoidea + Dromioidea. The clade of Glaessneropsoidea + Lecythocaridae is united by only one character, the presence of upper orbital fissures (13-1). Schweitzer and Feldmann (2009a) gave Glaessneropsinae full family and superfamily status and included four families, Glaessneropsidae, Lecythocaridae, Longodromitidae, and Nodoprosopidae, and subsequently, Schweitzer and Feldmann (2010b) established Konidromitidae within Glaessneropsoidea. However, Konidromitidae lacks synapomorphies of both glaessneropsoids and dromioids; therefore, the family should be given full superfamily status. Glaessneropsoidea including Glaessneropsidae, Lecythocaridae, and Nodoprosopidae is restricted here.

The monophyly of Dromioidea is supported by four characters, well-defined anterolateral margins with lobes or teeth (2-1; 3-1), the carapace with well-differentiated anterolateral and posterolateral margins (4-1), and a wide intestinal region (21-1). Within the dromioid clade, the most basal *Basinotopus* is the sister group of the remainder of the dromioid families. M'Coy (1849) and Collins (2002) placed *Basinotopus* in Dromiidae, while Collins and Jakobsen (2003) moved it to Dynomenidae. Most recently, Guinot (2008) questioned the systematic position of *Basinotopus*. *Basinotopus* lacks two synapomorphies, a short, wide carapace (1-1) and a relatively short maxilliped 3 (60-1), of the remaining dromioid clade. Additionally, *Basinotopus* has one autoapomorphy, well-developed pleonal pleura (47-0). Therefore, it cannot be placed within the previously recognized dromioid families. As a result, a new family is herein erected for *Basinotopus*.

Dromiidae has two unique apomorphies, an anteriorly located spermatheca (43-1) and possession of the penial tube on the coxa of pereopod 5 in males (72-1). The clade

of Sphaerodromiidae + Dynomenidae + Diaulacidae + *Xandarocarcinus* shares two synapomorphies, absence of the subhepatic swellings (14-1) and possession of the exopod of male second pleopods (74-0). Guinot and Tavares (2003) established the subfamily Sphaerodromiinae within Dromiidae and Guinot (2008) showed that Sphaerodromiinae has a close relationship with Dynomenidae. After that, Schweitzer and Feldmann (2010b) gave Sphaerodromiinae full family status. The analysis supports the separate status of Sphaerodromiidae.

The monophyly of the clade including Dynomenidae + Diaulacidae + *Xandarocarcinus* is supported by the synapomorphies: the absence of the anteriorly protruded plate of thoracic sternite 4 (34-0), and the reduced pereopod 5 with dorsal position (67-1; 69-1). Diaulacidae and *Xandarocarcinus* are united by two characters, the absence of the postcervical groove (17-1) and the absence of the uropodal plate (55-0). Bishop (1988c) erected the new genus *Xandaros* (now *Xandarocarcinus*) for *Zanthopsis sternbergi* Rathbun, 1926, and he placed the genus within Xanthidae MacLeay, 1838. Subsequently, Schweitzer et al. (2003) moved *Xandaros* to Dromiidae, and, most recently, Schweitzer et al. (2010) removed it to Dynomenidae. However, the analysis indicates that *Xandarocarcinus* (= *Xandaros*) is the sister to Diaulacidae but has four autoapomorphies, the pleonites not visible dorsally (46-1), a wide telson (53-1), and pereopods 4 and 5 which are not positioned dorsally and are not reduced in size (67-0; 69-0). Therefore, the analysis suggests that *Xandarocarcinus* warrants its own new family (see below for nomenclatural discussion).

Homoloidea (Clade B).—The monophyly of Clade B, with Bremer support of 2, is strongly supported by these synapomorphies: possession of the augenrest (10-1), the presence of the epistomial spine (23-1), possession of the homolid button (39-1), the presence of a socket on pleonal somite 6 (52-1), and the reduced pereopod 5 with dorsal position (67-1; 69-1), of which two (23-1; 39-1) are unique. Clade B is the sister group to the remainder of the in-group taxa. Clades B-G + Eubrachyura, with Bremer support of 2, share four synapomorphies, the absence of the post-cervical groove (17-1), a relatively wide intestinal region (21-1), thoracic sternites 1-3 distinct ventrally (26-1), and relatively small coxae of maxillipeds 3 clearly separated by thoracic sternites 1-3 (63-1), of which one (63-1) is unique. The extinct Mithracitidae is derived as the sister to the three extant homolid families. The monophyly of the three extant families is supported by only one character, a relatively wide thoracic sternum (25-1), and Poupiniidae is the sister to Latreilliidae and Homolidae. Only one character, pereopod 5 with chelae (68-1), supports the sister-group relationship between Homolidae and Latreilliidae.

Torynommidae (Clade C).—The extinct family Torynommidae is the sister to the remaining taxa. Clades C-G + Eubrachyura, with Bremer support of 2, share six synapomorphies: the carapace rather wider than long (1-1), well-defined orbits (9-1), the absence of the antennal groove (15-1), well developed sutures 4-5 and 5-6 on the thoracic sternum (31-1; 32-1), and maxilliped 3 without crista dentata (62-1), of which two (31-1; 32-1) are unique

and never reversed. Glaessner (1980) originally placed Tornyommidae in Cyclodorippoidea and subsequent workers (De Grave et al., 2009; Schweitzer et al., 2010) accepted his opinion. However, the analysis shows that Cyclodorippoidea defined as containing extinct and extant families is polyphyletic and suggests that Tornyommidae be given full superfamily status.

Etyoidea (Clade D).—Clades D-G + Eubrachyura are united by five characters: well-defined anterolateral margins (2-1); anterolateral margins with lobes or teeth (3-1); the carapace with well-differentiated anterolateral and posterolateral margins (4-1); the presence of upper orbital fissures (13-1); and the absence of subhepatic swellings (14-1). Guinot and Tavares (2001) erected the new family Etyidae with *Etyus*, *Feldmannia* Guinot and Tavares, 2001, and *Xanthosia*, and showed its placement within Archaeobrachyura. Subsequently, Števíć (2005) placed the family in Cyclodorippoidea. After that, Karasawa et al. (2008) gave Etyidae superfamily status. De Grave et al. (2009) and Schweitzer et al. (2010) placed Etyidae within Dromiacea. The analysis strongly supports the separate status of Etyoidea.

Raninoidea (Clade E).—The raninoid clade stands as the sister to clades F-G and Eubrachyura. Two characters, an elongate, triangular buccal cavern (24-1) and the maxilliped 3 with two planes (61-1), define Raninoidea with Bremer support of 2. Two synapomorphies, the well defined posterolateral margin (5-1) and the cervical and branchiocardiac grooves not reaching ventrally (20-1), unite clades E-G + Eubrachyura with Bremer support of 2. Within the raninoid clade, Camarocarcinidae represents the most basal clade. *Camarocarcinus*, the type genus of Camarocarcinidae, was originally included in Raninidae (Holland and Cavanaugh, 1958). Most recently, Feldmann et al. (2007) erected the new family Camarocarcinidae with *Camarocarcinus* and *Cretacocarcinus*, and questionably arranged it within Raninoidea. However, Guinot et al. (2008) thought that *Camarocarcinus* belonged to Palaeocorystidae. De Grave et al. (2009) and Schweitzer et al. (2010) accepted the separate status of Camarocarcinidae, which the analysis supports.

Förster (1968) established the new subfamily Necrocarcininae under Calappidae de Haan, 1833, and, subsequently, Schweitzer and Feldmann (2000) elevated it to full family status and placed it in Calappoidea. After that, Schweitzer et al. (2003) moved it to Dorippoidea. Most workers (De Grave et al., 2009; Schweitzer et al., 2010) concurred. However, Guinot and Tavares (2001; 2003) showed that Necrocarcinidae had close affinities with podotreme crabs, and Larghi (2004) placed it in Podotremata. Most recently, Guinot et al. (2008) removed Necrocarcinidae to the podotreme subsection Raninoidea, but they did not arrange it within the known superfamilies. The analysis suggests that Necrocarcinidae be placed in Raninoidea as the sister group to Cenomanocarcinidae.

The clade (Palaeocorystidae + (Raninidae + Symethidae)), with Bremer support of 2, shares two characters, an elongate carapace (1-0) and the absence of the pleonal locking system (48-2). Within some recent works (De

Grave et al., 2009; Schweitzer et al., 2010) Palaeocorystidae was one of the raninid subfamilies, while Guinot et al. (2008) gave it full family status. The analysis strongly supports the separate status of Palaeocorystidae. Palaeocorystidae is derived as the sister to Raninidae and Symethidae. The monophyly of Raninidae and Symethidae, with Bremer support of 6, is well supported by six synapomorphies, of which one, the united spermathecae (42-1), is unique.

Guinot et al. (2008) suggested that the subsection Raninoidea be divided into two superfamilies, Raninoidea containing only extant families and an unnamed superfamily-level group including Palaeocorystidae, Cenomanocarcinidae, and Necrocarcinidae. The analysis rejects their opinion.

Dakoticancroidea (Clade F).—Dakoticancroidea stands as the sister to the Cyclodorippoidea + Eubrachyura. Clades F-G + Eubrachyura, with Bremer support of 2, are united by two synapomorphies, the lateral portion of the posterior thoracic sternites visible ventrally (28-1) and short coxae of pereopods (70-1), of which one (70-1) is unique and never reversed. Two characters, the absence of the anterolateral spines and teeth (3-0) and a nearly straight posterior margin (7-1) define the monophyly of Dakoticancroidea with Bremer support of 2. Within previous works Dakoticancroidea was arranged within Dromiacea (De Grave et al., 2009; Schweitzer et al., 2010). However, Guinot (1993) suggested that Dakoticancroidea represented a fourth lineage within Podotremata, and Guinot and Tavares (2001) suggested that it be included in Archaeobrachyura. The analysis does not support the status of Dakoticancroidea under Dromiacea or Archaeobrachyura and suggests that it represents a separate lineage.

Cyclodorippoidea (Clade G).—The most advanced podotrematous superfamily Cyclodorippoidea is derived as the sister to Eubrachyura. The Cyclodorippoidea + Eubrachyura clade, with Bremer support of 3, is united by four synapomorphies, a wide thoracic sternum (25-1), the absence of the sterno-pleonal depression (37-0), the presence of the sterno-pleonal cavity of males (38-1), and the absence of the pleonal locking system (48-2), of which one (38-1) is unique. The monophyly of Cyclodorippoidea, with Bremer support of 3, is strongly supported by four characters: a complete sternal suture 6-7 (33-1); maxilliped 3 with two planes (61-1); the palp of maxilliped 3 located in an inner-mesial position (64-1); and pereopods 4 and 5 with chelae (68-2). Phyllotymolinidae is the sister to Cyclodorippidae and Cymonomidae. The Cyclodorippidae and Cymonomidae clade, with Bremer support of 3, shares three synapomorphies, an elongate buccal cavern (24-1); the fusion of the telson and pleonal somite 6 (50-1); and the anterior end of the telson not reaching thoracic sternite 4 (54-3), of which one (50-1) is unique. The analysis suggests that Cyclodorippoidea contains only extant families, Phyllotymolinidae, Cymonomidae, and Cyclodorippidae, and excludes Tornyommidae from the superfamily, discussed above.

Eubrachyura.—The monophyly of Eubrachyura, with Bremer support of 3, is strongly supported by three synapomorphies, well-defined episternites (29-1), the absence of

spermathecae (41-0), and the female gonopore located on the sternites (57-1), of which two (29-1, 57-1) are unique.

Classification

As a result of the analysis, we propose the following revised classification of paraphyletic podotremes including the Eubrachyura:

- Infraorder Brachyura Linnaeus, 1758
 - Section Dromiacea De Haan, 1833
 - Homolodromioidea Alcock, 1900
 - Konidromitioidea** n. superfam.
 - Glaessneropsoidea Patruilius, 1959
 - Dromioidea De Haan, 1833
 - Section **Homoloidea** n. section
 - Superfamily Homoloidea De Haan, 1839
 - Section **Torynommoidea** n. section
 - Superfamily Torynommoidea Glaessner, 1980 (new status)
 - Section **Etyoidea** n. section
 - Superfamily Etyoidea Guinot and Tavares, 2001
 - Section Raninoidea Ah Yong et al., 2007
 - Superfamily Raninoidea De Haan, 1839
 - Section **Dakoticancroidea** n. section
 - Superfamily Dakoticancroidea Rathbun, 1917
 - Section Cyclodorippoida Ah Yong et al., 2007
 - Superfamily Cyclodorippoidea Ortmann, 1892
 - Section Eubrachyura de Saint Laurent, 1980

Geologic ranges for families and other higher-level taxa given here are based upon our analysis of the literature; species-level references may be found compiled in Schweitzer et al. (2010). Guinot et al. (2008) replaced the section Dromiacea with Dromioidia. However, the name Dromiacea has been well used since de Haan established it in 1833; therefore, the section name Dromiacea is retained here. Additionally, three subsection names, Homoloidea, Raninoidea, and Cyclodorippoida, established by Guinot et al. (2008), are not used. Two sections, Raninoidea and Cyclodorippoida, named by Ah Yong et al. (2007), have priority. We use the same suffix-*oidea* for the remaining four sections, Homoloidea, Torynommoidea, Etyoidea, and Dakoticancroidea, following Ah Yong et al. (2007).

SYSTEMATICS

Infraorder Brachyura Linnaeus, 1758

Diagnosis.—Carapace shortened and flattened compared to other Decapoda, fused to epistome; last thoracic sternite fused to anterior sternites; peduncles of antennules composed of three articles; peduncle of antenna composed of two articles; maxillae biramous; third maxilliped with well-defined ischium and merus; first pereopods always chelate; second and third pereopods never chelate; fourth and fifth pereopods may be pseudochelate or chelate; pleon reduced, usually held ventral to the carapace but sometimes extending posteriorly from carapace; uropods usually absent but always reduced; telson reduced in size; male pleopods 1 and 2 modified as gonopods, uniramous,

pleopods 3-5 usually absent; female pleopods 2-5 present; gonopores on coxae or sternum.

Section Dromiacea De Haan, 1833

Diagnosis.—Carapace generally longer than wide but sometimes as long as wide or wider than long; orbits well developed, often with an augenrest situated distal to orbit, often ornamented with spines; cervical, branchiocardiac, and usually postcervical groove present; subhepatic region usually inflated, posterior portion of flanks often poorly calcified; renal opening of second antennal coxa with beak-like structure; maxilliped 3 pediform or operculiform with *crista dentata*; pereopods 4 and 5 usually subchelate, pereopod 5 always subdorsal, reduced in size; pereopod 4 sometimes subdorsal, reduced in size; pleon usually with all free somites; male pleonites 3-5 with pleopods, uropodal plates sometimes visible in ventral view; gonopores coxal, spermatheca usually situated posteriorly but may be positioned well anteriorly (Dromiidae); sternum narrow, sterno-coxal depression and sterno-pleonal depression present, sternites 1-3 usually fused, positioned below level of other sternites.

Included Superfamilies.—Dromioidea De Haan, 1833; Glaessneropsoidea Patruilius, 1959; Homolodromioidea Alcock, 1900; Konidromitioidea Schweitzer and Feldmann, 2010b.

Geologic Range.—Late Early Jurassic – Recent.

Remarks.—Dromiacea as herein restricted conforms to that of Scholtz and McLay (2009) but not that of other authors in that we exclude Homoloidea. In light of the fossil record, Dromiacea as defined here is a well-constrained group, united by the synapomorphies discussed above, and characters including a reduced and subdorsal pereopod 5 and cervical and branchiocardiac grooves present. The section appeared by the late Early Jurassic and was well established by the Late Jurassic (Schweitzer and Feldmann, 2010a). The position of Dromiacea as the sister to all other Brachyura is supported by the fossil record as all of the earliest occurrences in Brachyura belong within this section. The section radiated extensively during the later Mesozoic; six of these families crossed the K/Pg boundary, and one originated during the Cenozoic. Four are extant. Interestingly, of the families that originated in the Mesozoic (nearly all of them), only one became extinct during the Maastrichtian. Thus, members of the section are the first occurring members of Brachyura known to date as well as the longest ranging, with extant members of at least one Middle Jurassic family.

Superfamily Homolodromioidea Alcock, 1900

Diagnosis.—Carapace longer than wide or about as long as wide, ovate to hexagonal; with oblique augenrest, sometimes with septum about 2/3 the distance distally; cardiac and branchiocardiac grooves well developed on dorsal carapace and continuing onto and joining one another on lateral flanks, lateral flanks often poorly calcified posteri-

orly; postcervical groove usually present; carapace regions usually moderately to well defined; antennar groove extending forward from junction of cervical and branchiocardiac grooves; subhepatic region generally inflated; telson elongate in males; maxilliped 3 pediform.

Included Families.—Bucculentidae Schweitzer and Feldmann, 2009a; Goniiodromitidae Beurlen, 1932; Homolodromiidae Alcock, 1900; Longodromitidae Schweitzer and Feldmann, 2009a; Prosopidae von Meyer, 1860; Tanidromitidae Schweitzer and Feldmann, 2008 [imprint 2007].

Geologic Range.—Late Early Jurassic – Recent.

Remarks.—The current composition of Homolodromioidea was in part defined by Glaessner (1969) although he did not recognize some of the families we distinguish here. Glaessner (1969) recognized Prosopidae and subdivided it into Pithonotinae Glaessner, 1933; Prosopinae, and Homolodromiinae. Herein, we recognize the same subfamilies, raised to family status and with Pithonotinae as a junior synonym of Goniiodromitidae, and two additional families. Schweitzer and Feldmann (2009a) had originally placed Longodromitidae within Glaessneropsoidea; however, the description of additional species and genera within that family (Schweitzer and Feldmann, 2009b, d) has shown, along with the cladistic analysis herein, that Longodromitidae is better placed within Homolodromioidea. The presence of well-defined augenrests is key in placing Longodromitidae within the superfamily.

Homolodromioidea is a long-lived clade. It embraces the oldest known brachyuran, *Eoprosopon klugi* Förster, 1986, from the Pliensbachian (Early Jurassic), and is not common, but is well established, in modern oceans, represented by one extant family.

Bucculentidae Schweitzer and Feldmann, 2009a

Diagnosis.—Rostrum projected well beyond frontal margin of carapace, may have numerous small spines or be trifid; orbits appearing to be placed under rostrum, augenrest on hepatic region of dorsal carapace or subdorsally on hepatic region, bounded by spines or ridges; frontal margin of carapace may bear spines; hepatic regions strongly inflated and marking widest point on carapace; cervical and branchiocardiac grooves deep; flanks of carapace short.

Included Genera.—*Bucculentum* Schweitzer and Feldmann, 2009a; *Wilmingtonia* Wright and Collins, 1972.

Material Examined.—Specimens of *Bucculentum* spp. listed in Schweitzer and Feldmann (2009a); *Wilmingtonia satyrica* Wright and Collins, 1972, (BMNH) In. 60909 (holotype), In. 61154, In. 63712.

Geologic Range.—Late Jurassic (Oxfordian) – Late Cretaceous (Cenomanian).

Remarks.—Bucculentidae was originally monotypic, and Schweitzer et al. (2010) added *Wilmingtonia*, based upon its possession of dorsally located augenrests.

Goniiodromitidae Beurlen, 1932

Diagnosis.—Carapace slightly longer than wide or about as long as wide; usually moderately vaulted transversely and longitudinally; rostrum simple, bilobed, axially sulcate; eyestalks appearing to arise from beneath rostrum; orbits oblique to axis, directed anterolaterally, elongate, deep, with very long augenrest, orbit and augenrest occupying at least two-thirds the maximum carapace width and often the entire maximum width of carapace, orbit and augenrest separated by ridge; sub-orbital margin may extend farther anteriorly than upper-orbital margin; epigastric regions developed as small swellings; mesogastric region moderately developed, best developed at anterior tip and posteriorly along cervical groove; cervical groove always strong; postcervical groove weak when present; branchiocardiac groove usually well developed but may be interrupted axially; lateral margins usually with spines or rim, especially anteriorly; flanks of carapace well developed, usually with inflated subhepatic region bounded ventrally by antennar groove, with extensions of cervical and branchiocardiac grooves which often merge. Chelae, where known, apparently isochelous, fingers gracile, movable finger longer than fixed finger.

Included Genera.—*Cycloprosopon* Lörenthey in Lörenthey and Beurlen, 1929; *Cyclothyreus* Remeš, 1895; *Distefania* Checchia-Rispoli, 1917; *Eodromites* Patruilius, 1959; *Goniiodromites* Reuss, 1858 [imprint 1857]; *Maurimia* Martins-Neto, 2001; *Microcorystes* Fritsch, 1893; *Palaeodromites* A. Milne-Edwards, 1865; *Pithonoton* Von Meyer, 1842; *Plagiophthalmus* Bell, 1863; *Sabellidromites* Schweitzer and Feldmann, 2008 [imprint 2007]; *Trachynotocarcinus* Wright and Collins, 1972; *Trechmannius* Collins and Donovan, 2006.

Material Examined.—Specimens listed in Schweitzer and Feldmann (2008 [imprint 2007], 2009a, b, c, 2010b, c); *Microcorystes parvulus* Fritsch, 1893, NM 04297; *Plagiophthalmus oviformis* Bell, 1863, (BMNH) In. 31323 (lectotype); (BMNH) In. 63713; (BMNH) In. 31324; (BMNH) In. 61306; SM B 8826.

Geologic Range.—Middle Jurassic (Bajocian) – Paleocene.

Remarks.—Goniiodromitidae is a diverse family, with many species and genera. All are united by an orbit separated from a long, deep augenrest by a transverse ridge about two-thirds the distance laterally. The family ranges from Middle Jurassic to Paleocene. Herein we add three genera to those listed by Schweitzer et al. (2010), *Maurimia*, *Microcorystes*, and *Trechmannius*, based upon possession of a carapace as wide as long or longer than wide, broad orbits with augenrest where well-preserved, cervical and branchiocardiac grooves, and a well-defined mesogastric region. Whereas these three genera are not well-known, they possess the diagnostic features of the family. The addition of *Trechmannius* extends the geologic range from the Late Cretaceous into the Paleocene.

Homolodromiidae Alcock, 1900

Diagnosis.—Carapace longer than wide; lacking well-defined orbits; eyes resting in augenrest formed by orbital

spines or by subhepatic region; two forward-directed lateral rostral spines positioned at base of central rostral spine if present, sometimes fused into a single bifid structure, lateral rostral spines appear to originate on dorsal carapace; central rostral spine variable, may be absent, tiny, downturned, or attenuated; subhepatic region inflated, sometimes markedly so; other subdorsal areas may be well developed; cervical and branchiocardiac grooves moderately well defined, parallel to one another; regions indistinct in extant forms and well developed in most fossil forms; appendages typically slender, sometimes long, pereopod 5 usually carried dorsally, both pereopods 4 and 5 reduced in size; pleonites with triangular, long epimeres; uropodal plate not visible, telson longer than wide; spermatheca placed posteriorly.

Included Genera.—*Antarctidromia* Förster et al., 1985; *Dicranodromia* A. Milne-Edwards, 1880 (extant); *Homolodromia* A. Milne-Edwards, 1880 (extant); *Homolus* Eudes-Deslongschamps, 1835; *Notiodromia* Schweitzer and Feldmann, 2011a; *Palehomola* Rathbun, 1926; *Preclarocarcinus* Schweitzer, Feldmann, Čosović, Ross, and Waugh, 2009; *Rhinodromia* Schweitzer, Nyborg, Feldmann, and Ross, 2004.

Material Examined.—*Dicranodromia doederleini* Ortmann, 1892, SMF unnumbered; *D. felderi* Martin, 1990, USNM acc. no. 226053; *D. ovata*, USNM 81931; *Homolus auduini* Eudes-Deslongchamps, 1835, (BMNH) In 57979 (lectotype); OUM J.71902; *Homolodromia robertsi* Garth, 1973, LACM CR 1980-158.6; *Palehomola gorrelli* Rathbun, 1926, USNM 352912 (holotype); *Preclarocarcinus parvus* Schweitzer et al., 2009, GSC 27176 (holotype); *Rhinodromia richardsoni* (Woodward, 1896); GSC 5995 (holotype).

Geologic Range.—Middle Jurassic (Bathonian) – Recent.

Remarks.—Homolodromiidae is the longest ranging family of Brachyura known to date. The earliest occurrence is the Middle Jurassic *Homolus*, and the family survives in modern oceans, mostly in offshore and slope habitats.

Longodromitidae Schweitzer and Feldmann, 2009a

Diagnosis.—Carapace longer than wide, widest at position of epibranchial or anterior-most branchial region, dorso-ventrally compressed; rostrum projected well beyond orbits, axially sulcate, markedly downturned distally; augenrest shallow or deep, forward-directed, with intra- and outer-augenrest spines as well as subaugenrest spines; protogastric and hepatic regions poorly differentiated; cervical groove deep, originating well posterior to outer-orbital spine; area between cervical and branchiocardiac grooves narrow; postcervical groove present, discontinuous and extending laterally about half the distance to the lateral margins or composed of two discrete segments that meet axially and extend laterally; cardiac region rounded triangular; epibranchial region with rounded or finger-like projection directed toward cardiac region; subhepatic swelling positioned below orbit, bounded by ventral extension of cervical groove and antennar groove; ventral extensions of cervical and branchiocardiac grooves meeting

to form triangular subdorsal extension of epibranchial region; flanks short posteriorly as if they may have been poorly calcified; pleural suture distinct, pterygostome sometimes well calcified; male and female pleonites free, becoming progressively longer and wider toward telson; each somite with three swellings, axial and lateral; telson very long, twice as long as somite 6, extending well beyond coxae of pereopod 1; pereopod 5 subdorsal, small; pereopod 4 ventral, not particularly reduced in size.

Included Genera.—*Abyssopthalmus* Schweitzer and Feldmann, 2009a; *Antarctiprosopon* Schweitzer and Feldmann, 2011a; *Coelopus* Étallon, 1861; *Dioratiopus* Woods, 1953; *Glaessnerella* Wright and Collins, 1975; *Longodromites* Patruilius, 1959; *Planoprosopon* Schweitzer, Feldmann and Lazăr, 2007; *Vespidromites* Schweitzer and Feldmann, 2011a.

Material Examined.—Specimens of *Abyssopthalmus* spp., *Longodromites*, and *Planoprosopon* listed in Schweitzer and Feldmann (2009a, b); *Coelopus* spp. in Schweitzer and Feldmann (2010e) and *Antarctiprosopon* sp., *Dioratiopus* sp., *Glaessnerella* spp. and *Vespidromites* in Schweitzer and Feldmann (2011a).

Geologic Range.—Middle Jurassic (Bajocian) – Eocene.

Remarks.—Longodromitidae is tightly constrained, with deep, parallel grooves and deep, forward-directed augenrests. It ranges from the Middle Jurassic (Bajocian) to Eocene and is nearly cosmopolitan in distribution.

Prosopidae von Meyer, 1860

Diagnosis.—Carapace longer than wide, narrowing anteriorly, widest at branchial regions; regions well defined by grooves; cervical and branchiocardiac groove well developed; postcervical groove usually present; rostrum extending well beyond orbits; augenrest directed anterolaterally, bounded by inflated subhepatic region on suborbital rim and inner- and outer-orbital spine on upper orbital margin; orbit may be situated at base of rostrum as shallow reentrant; lateral margins well defined but not high; grooves deep and well marked, postcervical groove present; posterior margin biconvex, apparently to accommodate fifth pereopods.

Included genera.—*Laeviprosopon* Glaessner, 1933; *Nippopon* Karasawa, Kato and Terabe, 2006; *Prosopon* von Meyer, 1835; *Protuberosa* Schweitzer and Feldmann, 2009a.

Material Examined.—Specimens of *Laeviprosopon* spp. listed in Schweitzer and Feldmann (2008) and *Prosopon* spp. and *Protuberosa* sp. in Schweitzer and Feldmann (2009a).

Geologic Range.—Middle Jurassic (Bathonian) – Early Cretaceous (Aptian).

Remarks.—For many years, Prosopidae was the default family for most Jurassic Brachyura (i.e., Glaessner, 1969). Recent revisions have shown that Jurassic brachyuran

diversity is in fact much higher and that few genera are referable to Prosopidae sensu stricto.

Tanidromitidae Schweitzer and Feldmann, 2008
[imprint 2007]

Diagnosis.—Carapace longer than wide, width 70-85% maximum length; flanks of carapace strongly developed; regions well defined, generally smooth, protogastric and hepatic regions confluent; rostrum downturned, blunt-triangular, axially sulcate; orbit small, directed forward, situated at base of rostrum, rimmed; augenrest usually rimmed, may have small spines or protuberances; fronto-orbital width 50-60% maximum carapace width; lateral margins parallel, subparallel to one another, or diverging slightly posteriorly; subhepatic region may be markedly inflated; large portion of ventral side lies below ventral extension of branchiocardiac groove; ventral extension of cervical groove deep; ventral extension of branchiocardiac groove diminishing ventrally.

Included Genera.—*Gabriella* Collins et al., 2006; *Tanidromites* Schweitzer and Feldmann, 2008 [2007].

Material Examined.—Specimens of *Tanidromites* spp. listed in Schweitzer and Feldmann (2008 [imprint 2007]) and *Gabriella* spp. in Schweitzer and Feldmann (2009d).

Geologic Range.—Middle Jurassic (Bajocian) – Early Cretaceous (Hauterivian).

Konidromitioidea n. superfam.

Diagnosis.—Carapace ovate, longer than wide, widest at position of bifid third lateral spine, about 60% the distance posteriorly on carapace; widening posteriorly, strongly vaulted longitudinally and transversely; rostrum blunt triangular, axially sulcate, with tiny spines on margins, strongly downturned at tip to be oriented almost perpendicular to dorsal carapace; outer suborbital spine extending posteriorly in large, laterally inflated flange; subhepatic region strongly inflated, ornamented with granules arrayed in longitudinal row; lateral margin with five spines; cervical groove sinuous, beginning posterior to outer suborbital spine, deep; branchiocardiac groove much weaker; postcervical groove very short, oblique segments merging with groove defining lateral sides of urogastric region; flanks steep, at right angles to dorsal carapace, posterior to subhepatic region surface of flank concave, perhaps to accommodate merus of first pereopod, posterior to this concavity the surface is corrugated with three parallel oblique concavities perhaps to accommodate meri of pereopods 2-4.

Included Family.—Konidromitidae Schweitzer and Feldmann, 2010b.

Material Examined.—*Konidromites gibbus* (Reuss, 1858 [imprint 1857]), specimens listed in Schweitzer and Feldmann (2010b); *Konidromites bjorki* (Bishop and Williams, 2000), SDSM 11021; *Konidromites izetti* (Bish-

op, 1988b), USNM 418272 (holotype), USNM 418273 (paratype).

Geologic Range.—Late Jurassic (Oxfordian) – Late Cretaceous (Campanian).

Remarks.—Schweitzer and Feldmann (2010b) originally placed Konidromitidae in Glaessneropsoidea based upon its possession of deep orbits with some ornamentation, a long rostrum, cervical groove, and an inflated subhepatic region. Whereas it does share these features with Glaessneropsoidea, our analysis shows that it shares neither the synapomorphies of Glaessneropsoidea nor those of any other superfamilies; thus, we refer it to its own superfamily. Konidromitidae (and the two included genera, *Konidromites* Schweitzer and Feldmann, 2010b, and *Concavilateris* Frantescu, 2010) possess the interesting feature of a crenulate flank, apparently to accommodate the pereopods. It also possesses an outer suborbital spine extending posteriorly in a large, laterally inflated flange, not seen in any other brachyuran. The lateral spines are also unusual, with five spines extending in a flange-like structure.

Superfamily Glaessneropsoidea Patruilius, 1959

Diagnosis.—Carapace longer than wide or wider than long, regions generally well defined by grooves; carapace ornament often well developed, may be composed of tubercles, small spines, large spines, or large swellings; rostrum projecting well beyond orbits, axially sulcate, inflated, or trilobed; orbits well developed; orbit usually ornamented with supra- and sub-orbital spines, fronto-orbital width always occupying entire frontal margin of carapace; augenrest absent; cervical and branchiocardiac grooves usually equally developed, postcervical groove usually present; subhepatic swelling usually present; branchial regions often very short in lateral view; cardiac region always well marked, variable in size (Schweitzer and Feldmann, 2009a, p. 82).

Included Families.—Glaessneropsidae Patruilius, 1959; Leczythocaridae Schweitzer and Feldmann, 2009a; Nodoprosopidae Schweitzer and Feldmann, 2009a.

Geologic Range.—Late Jurassic (Oxfordian) – Late Cretaceous (Maastrichtian).

Remarks.—The superfamily is united mainly by having well defined orbits with orbital fissures, which other Jurassic taxa do not possess. Nodoprosopidae was not included in this analysis due to the large number of missing characters but was originally included in the superfamily (Schweitzer and Feldmann, 2009a), so we retain it here.

Glaessneropsidae Patruilius, 1959

Diagnosis.—Carapace longer than wide, widest at position of branchial region, about half to three-quarters the distance posteriorly; carapace regions flattened or bulbous, may be ornamented with large granules, especially large on branchial regions. Rostrum projected well in advance of

orbits, spatulate, downturned, with longitudinal swellings and sometimes axial sulcus, tip of rostrum may have spines, rostral width usually about half maximum carapace width but rarely as narrow as one-third carapace width. Eyestalk arising beneath rostrum. Orbits bounded on inner angle by rostrum; upper orbital margin with intra-orbital spine that may be rectangular or triangular in shape; intra-orbital spine may be bounded by deep fissures; fissures and spine directed forward or anterolaterally; outer-orbital angle formed of long, triangular, forward-directed spine that wraps around laterally into cup-shaped structure; orbit directed forward; fronto-orbital width 75-95% maximum carapace width. Metagastric region bilobed when well marked. Cervical and branchiocardiac grooves usually well-developed but rarely may be shallow and discontinuous; cervical groove originating at lateral margin just posterior to position of outer-orbital spine; postcervical groove usually present, when present continuous and crossing axis to bound anterior edge of cardiac region. Cardiac region usually small, positioned well anterior of posterior margin but rarely extending toward posterior margin. Subhepatic region markedly inflated, bounded posteriorly by ventral extension of cervical groove, ventrally by antennar groove; anterior margin forms orbital margin. Epibranchial region extending onto flank, bounded by ventral extensions of cervical and branchiocardiac grooves (Schweitzer and Feldmann, 2009a, p. 83).

Included Genera.—*Glaessneropsis* Patrulius, 1959; *Ekalakia* Bishop, 1976; *Rathbunopon* Stenzel, 1945; *Vectis* Withers, 1946; *Verrucarcinus* Schweitzer and Feldmann, 2009a.

Material Examined.—*Glaessneropsis* spp. and *Verrucarcinus* spp., specimens listed in Schweitzer and Feldmann (2009a); *Ekalakia* spp., specimens listed in Feldmann, Schweitzer and Wahl (2008); *Vectis wrighti* Withers, 1946, (BMNH) In. 60908 (holotype); *Vectis echinorum* Wright and Collins, 1972, SM B14291 (holotype), B14292-4 (paratypes); *Rathbunopon polyakron* Stenzel, 1945, UT BEG 21097 (holotype); *Rathbunopon woodsii* Withers, 1951, SM B50799 (holotype); (BMNH) In. 24657.

Geologic Range.—Late Jurassic (Oxfordian) – Late Cretaceous (Maastrichtian).

Remarks.—To the genera originally referred by Schweitzer and Feldmann (2009a) and Feldmann, Schweitzer, and Wahl (2008), Schweitzer et al. (2010) added *Rathbunopon* and *Vectis* based upon the carapace proportions and the ornamentation and conformation of the orbits. The family was well established through the later Mesozoic, ranging from the Oxfordian to the Maastrichtian.

Lecythocaridae Schweitzer and Feldmann, 2009a

Diagnosis.—Generally small crabs, triangular in outline, with widest part in metabranchial region which is extremely large and bears a prominent node or swelling on anterolateral corner; regions strongly inflated and separated by distinct, deep grooves; grooves not necessarily

identifiable as cervical, branchiocardiac, and postcervical. Rostrum broad, spatulate, axially sulcate, and strongly downturned. Orbits circular, rimmed, separated from rostrum by prominent, open notch; with inner suborbital spine. Mesogastric region narrow. Cardiac region very large, extending nearly to posterior border and completely separating metabranchial regions. Hepatic and epibranchial regions developed as globose swellings (Schweitzer and Feldmann, 2009a, p. 94).

Material Examined.—Specimens of *Lecythocaris* spp. listed in Schweitzer and Feldmann (2009a).

Geologic Range.—Late Jurassic (Kimmeridgian-Tithonian).

Remarks.—This monogeneric family is known from central and eastern Europe only from the Late Jurassic (Kimmeridgian-Tithonian). Its distinctive orbits and carapace support its family status.

Nodoprosopidae Schweitzer and Feldmann, 2009a

Diagnosis.—Carapace longer than wide, markedly vaulted transversely, moderately so longitudinally; widest at position of mid-branchial region, about 75% the distance posteriorly, narrowing markedly anteriorly; rostrum trifid, with medial spine and two lateral spines that are directed upward; eyestalk apparently arising from under rostrum; orbits or augenrest not developed; lateral margins spinose; protogastric and hepatic regions differentiated; carapace regions ornamented with large tubercles; cervical groove deep; postcervical groove deep, continuous across axis, extending a short distance laterally; branchiocardiac groove oriented obliquely posteriorly, deep; cardiac region small; posterior margin rimmed, broadly concave; carapace apparently with inflated subhepatic region (Schweitzer and Feldmann, 2009a: 116).

Geologic Range.—Late Jurassic (Kimmeridgian – Tithonian).

Remarks.—Nodoprosopidae and *Nodoprosopon* Beurlen, 1928, the only included genus, are unique in possessing a distinctive trifid rostrum and overall triangular carapace.

Superfamily Dromioidea De Haan, 1833

Diagnosis.—Carapace longer than wide or as long as wide, anterolateral and posterolateral margins usually well-differentiated, anterolateral margins generally with spines or lobes; rostrum typically bilobed or trilobed; orbits without augenrest, deep, circular; orbital margin often with protuberance or rim, outer suborbital spine and sometimes entire suborbital margin visible in dorsal view; cervical groove, postcervical groove, and branchiocardiac grooves variously developed; intestinal region wide; subhepatic swelling marked; sternum narrow, with strong episternal projections, pleonite 6 usually with triangular epimeres, other pleonites always without triangular epimeres; spermatheca posteriorly placed except in most

Dromiidae; maxilliped 3 usually operculiform; uropodal plate usually visible in ventral view but may be concealed or absent; both pereopods 4 and 5 reduced, only pereopod 5 reduced in size, or all pereopods more or less similar in size; pereopod 5 may be subdorsal or dorsal.

Included Families.—Basinotopidae new family; Diaulacidae Wright and Collins, 1972; Dromiidae De Haan, 1833; Dynomenidae Ortmann, 1892; Sphaerodromiidae Guinot and Tavares, 2003; Xandarocarinidae new family.

Geologic Range.—Early Cretaceous (Aptian) – Recent.

Remarks.—Dromioidea has been problematic in the fossil record. Many extinct genera historically referred to Dynomenidae (Glaessner, 1969) cannot be retained there based upon the diagnoses of Guinot (2008) for the various subfamilies. Some have already been removed to Goniodromitidae (Schweitzer et al., 2010; herein), Sphaerodromiidae (Schweitzer and Feldmann, 2010d), or Basinotopidae new family (herein), and others are under study by us and others (Barry van Bakel, personal communication). Part of the problem with many of the remaining genera currently placed within Dromiidae and Dynomenidae is that they lack features of the ventral surface and pereopods, making it very difficult to place them within a family. Thus, many of the genera listed for the two latter families must be considered as provisional until more and better fossil material is recovered to confirm placement within a family.

Basinotopidae n. fam.

Fig. 4

Diagnosis.—Carapace slightly longer than wide, broadly triangular; rostrum broadly triangular, axially sulcate, with well developed median rostral spine; orbits deep, oblique, directed anterolaterally, suborbital margin with large spine; short segment between outer-orbital angle and first anterolateral spine, placing them at same level; lateral margin with three spines anterior to intersection of cervical groove and one very long, posterolaterally directed spine posterior to intersection of cervical groove; cervical, postcervical, and branchiocardiac grooves deep, cervical and branchiocardiac grooves intersecting carapace margin and extending onto flank; carapace with large nodes on regions; sternite 3 at lower level than sternite 4; sternite 4 with long anterior process, pereopod 1 articulating with long, vertically directed episternal projections; sternite 5 long, pereopod 2 articulating with long vertically directed episternal projections; female spermatheca situated posteriorly; female gonopore on coxa 3; male pleon very narrow, with triangular epimeres on pleomere 6 and short epimeres on other pleomeres, uropodal plates visible; female pleon much wider, with triangular epimeres on pleomere 6 and long, rectangular epimeres on pleonites 2-5, bilobed axial swellings on pleonites 2-5, uropodal plates clearly visible, telson very long, much longer than wide; pereopod 5 reduced in size, carried dorsally, pereopod 4 possibly reduced in size.

Included Genera.—*Basinotopus* McCoy, 1849; *Lucanthonisia* van Bakel et al., 2009; *Noetlingocarcinus* (= *Noetlingia* Beurlen, 1928).

Material Examined.—*Basinotopus lamarckii* (Desmarest, 1822): SM C19106-8, 19324, 19326 (female), 19327 (male); (BMNH) In. 34485, 46379 (female), 49849, 48931; 48932 (female); NHMW 854; MB.A.77 (male); PRI K55179 (2 females).

Geologic Range.—Eocene (Ypresian) – Miocene (Langhian).

Remarks.—The analysis shows that Basinotopidae and its type genus, *Basinotopus*, occupy the basal position within Dromioidea, discussed above. *Basinotopus* has many similarities with *Dromilites* sensu stricto, now placed within Sphaerodromiidae, but *Basinotopus* has an elongate, triangular carapace and a well developed median rostral spine, both of which are lacking in Sphaerodromiidae. *Lucanthonisia* was questionably placed within Dynomenidae (van Bakel et al., 2009) and De Grave et al. (2009) and Schweitzer et al. (2010) moved it to Dromiidae. However, *Lucanthonisia* has an elongate, triangular carapace with a well developed median rostral spine. Therefore, we place it within Basinotopidae based upon its close similarity with *Basinotopus*. The family ranges from Eocene to Oligocene of Europe.

***Noetlingocarcinus* n. name**

Noetlingia Beurlen, 1928, p. 164 [preoccupied].

Non *Noetlingia* Hall and Clarke, 1894, p. 229 (Brachiopoda); *Noetlingia* Lambert, 1898, p. 126 (Echinodermata).

Type Species.—*Dromia claudiopolitana* Bittner, 1893, by original designation.

Etymology.—The generic name is derived from the original genus name honoring Noetling and the Greek word *karkinos*, meaning crab, a common stem used for genera within Brachyura.

Material Examined.—*Noetlingocarcinus* (= *Noetlingia*) *claudiopaulitana* (Bittner, 1893), MAFI E9280, MCZ 1212.

Remarks.—Beurlen (1928) erected *Noetlingia* to accommodate *Dromia claudiopolitana* from the Eocene of Italy. That name had been used previously for a brachiopod and for an echinoid. Thus, we provide the replacement name *Noetlingocarcinus* for it. This genus had been placed within Dromiidae but we herein placed it within Basinotopidae based upon its elongate, triangular carapace and long, median rostral spine.

Diaulacidae Wright and Collins, 1972

Fig. 5

Diagnosis.—Orbit deep, directed forward, outer-orbital corner visible in dorsal view; subhepatic swelling absent. Cervical groove may or may not intersect lateral margin of

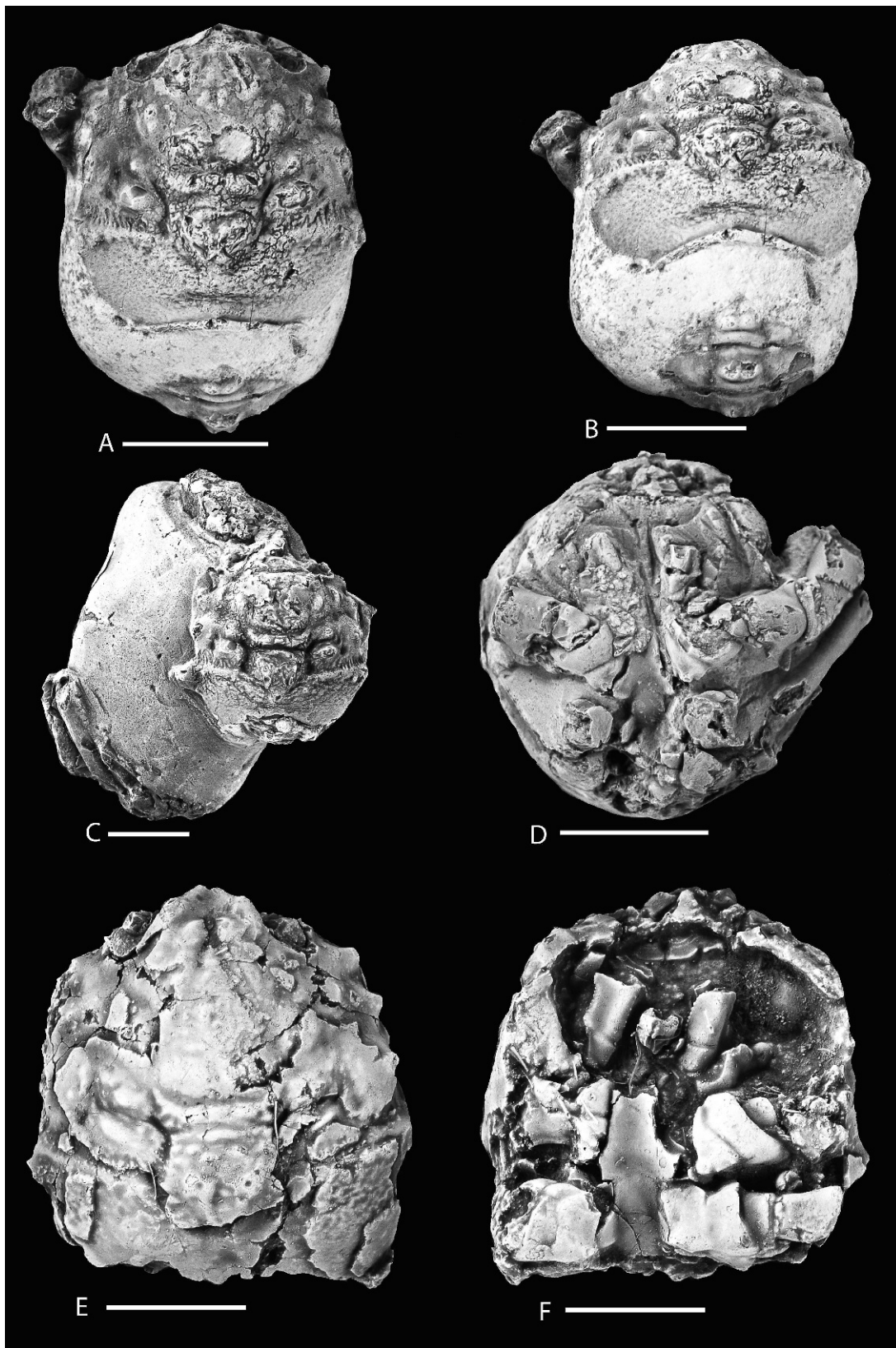


Fig. 4. Dromioidea, Basinotopidae, *Basinotopus lamarckii* (Desmarest, 1822). A-B, (BMNH) In. 48932, female, dorsal carapace (A) and oblique posterior view (B); C-D, (BMNH) 49849, specimen with two individuals, dorsal carapace of one individual (C) and sternum of second individual (D); E-F, (BMNH) unnumbered, dorsal carapace (E) and sternum (F). Scale bars = 1 cm.

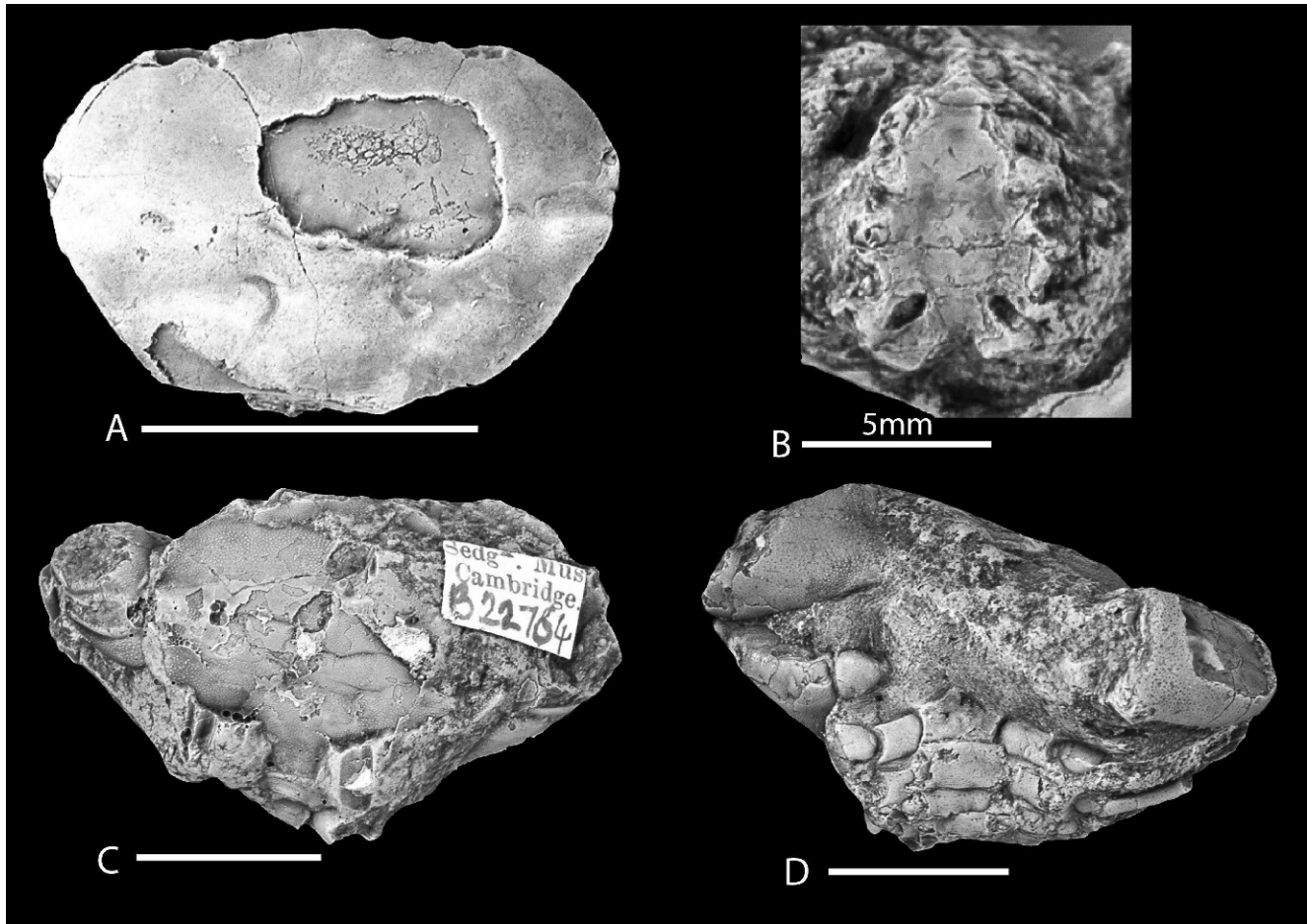


Fig. 5. Dromioidea, Diaulacidae, *Diaulax carteriana* Bell, 1863. A-B, SM B 22799, dorsal carapace (A) and female sternum with large spermatheca (B); C-D, SM B 22784, dorsal carapace (C) and pleon and proximal elements of pereiopods, showing that none are subdorsal (D). Scale bars = 1 cm.

carapace; postcervical groove present; branchiocardiac groove intersecting lateral margin of carapace; grooves not extending or only weakly extending onto flanks; flanks smooth, without swellings. P5 subdorsal. Somites 1-6 of pleon of unknown gender free, none with triangular epimeres, somite 6 and telson long, without uropodal plates. Sternites 1-3 fused, triangular in shape, situated well-below level of other sternites; suture 3/4 complete; sutures 5/6 and 6/7 complete; spermatheca situated posteriorly, large, ovate; episternites long, narrow; sternum narrow, shallow.

Material Examined.—*Diaulax carteriana* Bell, 1863, SM B22784, 22791, 22799, (BMNH) In. 44401, (BMNH) In. 29714; Brussels I.G.8968; *D. feliceps* Wright and Collins, 1972, SM B22794, SM B30706 (paratype), (BMNH) In. 30102 (holotype), (BMNH) I.635, (BMNH) 59810; *D. oweni* Bell, 1850, (BMNH) In. 29803 (holotype), (BMNH) In. 61136.

Geologic Range.—Early Cretaceous (Albian) – Eocene (Ypresian).

Remarks.—Wright and Collins (1972) erected the family for a single genus. Later, Schweitzer et al. (2004) synonymized Diaulacidae with Dynomenidae based on

their distinctive similarities. Some sternal elements and the apparent lack of visible uropodal plates suggest that Diaulacidae should be maintained as a separated family. The range of the family, known only from one genus, is Albian to Eocene.

Dromiidae De Haan, 1833

Diagnosis.—Carapace longer than wide to wider than long; rostrum typically bilobed; orbits without augenrest, deep, circular; orbital margin often with protuberance or rim, subouterorbital spine often visible in dorsal view; cervical groove weak; postcervical groove sometimes present; branchiocardiac groove present; sternum with anteriorly displaced spermatheca in most taxa; pleon without long epimeres on pleonites, somite 6 without triangular epimeres, telson rarely longer than wide, uropodal plates usually visible; both pereiopods 4 and 5 reduced in size, pereiopod 4 subdorsal, pereiopod 5 carried dorsally, penial tube on coxa of pereiopod 5 in males.

Included Fossil Genera.—*Cryptodromia* Stimpson, 1858a (also extant); *Dromia* Weber, 1795 (also extant); *Dromidia* Stimpson, 1858a (also extant); *Dromiopsis* Reuss, 1858 [imprint 1857]; *Epigodromia* McLay, 1993 (also extant);

Kerepesia Müller, 1976; *Pseudodromilites* Beurlen, 1928; *Quinquerugatus* Franțescu et al., 2010.

Material Examined.—*Conchoecetes artificiosus* (Fabricius, 1798), SMF 11511; *Cryptodromiopsis unidentata* (Rüppell, 1830), SMF 24583; *Dromia personata* (Linnaeus, 1758), USNM 258144, 258152; *Dromia dehaani* Rathbun, 1923a, USNM 42218, 57751; *Dromidia antillensis* Stimpson, 1858a, USNM 202878, 241052; *Dromidia australis* Rathbun, 1923a, SMF 4704; *Dromidiopsis orientalis* (Miers, 1880), USNM 70802; *Dromiopsis rugosa* (Schlotheim, 1820), KSU D 801, 803; *Epigodromia areolata* (Ihle, 1913), USNM 282756-58; *Exodromidia spinosa* Studer, 1883, USNM 231224; *Kerepesia viai* Müller, 1976, HNHM M86.420 (holotype); *Petalomera lateralis* (Gray, 1831) USNM 6462; *Quinquerugatus holthuisi* Franțescu et al., 2010, PI 15222 (holotype), PI 15206 (paratype); *Sternodromia spinirostris* (Miers, 1881), USNM 121405; SMF 5922; *Takedromia cristatipes* (Sakai, 1969), USNM 128579, 282762.

Geologic Range.—Early Cretaceous (Aptian) – Recent.

Remarks.—The fossil record of the genera included here in Dromiidae ranges from Late Cretaceous to Holocene. Some of the genera here referred to Dromiidae are provisional, based upon their fragmental nature. *Kerepesia* is fragmental but has a rostrum and orbits similar to that of other dromiids in being trifid and with a suborbital spine respectively. Both *Noetlingicarcinus* and *Pseudodromilites* are based on dorsal carapace material only and lack appendages or ventral aspects of the carapace. They are both longer than wide, have well defined carapace grooves, and a suborbital spine that is visible in dorsal view. Thus, the best placement for them seems to be Dromiidae. *Dromiopsis* is herein moved to Dromiidae from Dynomenidae based upon its possession of well-defined carapace grooves and a suborbital spine that is visible in dorsal view. Members of Dynomenidae have an entire suborbital margin visible in dorsal view. It should be noted that this placement is based upon examination of the type species of *Dromiopsis*, *D. rugosus* Schlotheim, 1820, and that the composition of the genus is likely heterogeneous.

Schweitzer et al. (2010) listed five species of *Dromia*, one questionably referred from the Cretaceous. That Cretaceous species, *Dromia anomala* Rathbun, 1935, is a lobster, possibly a member of *Hoploparia*, based upon examination of the holotype (UT 21200). Thus, the record of *Dromia* is restricted to the Eocene to Holocene.

Dynomenidae Ortmann, 1892

Diagnosis.—Carapace wider than long or longer than wide; surface covered in dense setae; lateral margins with spines or blunt protuberances; front broadly triangular, sulcate; entire suborbital margin visible in dorsal view, subhepatic swelling absent; cervical and branchiocardiac grooves well defined, postcervical groove sometimes present; pleonites 1-5 without long epimeres, somite 6 with triangular epimeres, male telson not longer than wide, uropodal plates visible in ventral view; female spermatheca placed posteriorly on sternum; pereopod 5 reduced in size.

Included Fossil Genera.—*Dynomene* Desmarest, 1823 (also extant); *Graptocarcinus* Roemer, 1887; *Kierionopsis* Davidson, 1966; *Kromtitis* Müller, 1984.

Material Examined.—*Dynomene emiliae* Müller, 1978, HNHM M.86.108; *D. hispida* Latreille in Milbert, 1812, USNM 15593, 189454; *D. lessinea* Beschin et al., 2001, MCZ 2065 (holotype); *D. pilumnoides* Alcock, 1900, SMF 17127, USNM 282761; *D. praedator* A. Milne-Edwards, 1879, SMF 4855; *Graptocarcinus muiri* Stenzel, 1944, UT 21288 (holotype); *G. texanus* Roemer, 1887, OUM K.53173a, b, SM B8845, (BMNH) In. 62020; *Hirsutodynomene ursula* (Stimpson, 1860), USNM 77313; *Kierionopsis nodosa* Davidson, 1966, USNM 649150 (holotype), 649161 (paratype); *Kromtitis koberi* (Bachmayer and Tollmann, 1953), MNHN R03456, NHMW 61/1953 (holotype), *Kromtitis pentagonalis* Müller and Collins, 1991, HMNH M91.133; *Paradynomene tuberculata* Sakai, 1963, USNM 291445.

Geologic Range.—Late Cretaceous (Cenomanian) – Recent.

Remarks.—Guinot (2008) provided diagnoses for Dynomenidae and its constituent subfamilies which she intended to assist paleontologists in evaluating placement of extinct taxa within the family. Her definitions for the family and the conformation of the sternum and pleon of members of the family exclude many of the historically referred genera (Glaessner, 1969; Schweitzer et al., 2003, 2010). This is perhaps not surprising as Dynomenidae is one of the most derived of Dromiacea and a very small group in modern oceans, with few genera and species. Possibly it is a specialized group, having occupied a small niche since its appearance.

The extant genus *Dynomene* is known from Miocene and younger occurrences in the Tethyan and Indo-Pacific realm. Of the extinct genera, the oldest confirmed genus is *Graptocarcinus* from the Late Cretaceous. Placement of the genus in the family is based upon sternal features (personal communication, B. van Bakel, June–July 2009). Guinot (2008) suggested that the Paleocene *Kierionopsis* was a member of Paradynomeninae Guinot, 2008, based upon features of the dorsal carapace. Examination of type material in the USNM suggests that indeed dorsal carapace features indicate such placement but that characters of the pleon are equivocal. Pleonites 3-5 are rectangular, with straight epimeres, whereas pleonite 6 has triangular epimeres. The telson is wide. These are typical features of Dynomenidae (Schweitzer and Feldmann, 2010d, table 1). However, the uropodal plates are not visible. We were unable to determine whether they were obscured by sediment on the USNM specimen; this seems unlikely because all of the other pleomeres and the telson were visible. In Dynomenidae, uropodal plates are visible. Thus, placement of *Kierionopsis* in Dynomenidae must be considered provisional at this time.

Guinot (2008) also considered the Paleocene-Miocene *Kromtitis* to be a clear member of Paradynomeninae based upon dorsal carapace characters. This seems to be the best placement for the genus at this time as there are no ventral characters to further confirm placement.

Sphaerodromiidae Guinot and Tavares, 2003

Diagnosis.—Carapace longer than wide or about as long as wide; rostrum projecting beyond orbits; orbital area composed of two contiguous circular depressions, outer depression deeper, essentially continuous with orbit, poorly separated from orbit; lateral rim merging with or separated only by short distance from outer-orbital angle; subhepatic region inflated; cervical groove weak, postcervical and branchiocardiac grooves well defined; female spermatheca positioned posteriorly on sternum, short female sutures 7/8; male P5 coxa extended into immobile structure; telson long, uropodal plates large and readily visible in ventral view, triangular epimeres on sixth somites, rectangular terminations on remaining pleomeres; long anterior process of sternite 4; pereopods 4 and 5 reduced in size. [See Guinot and Tavares (2003) for additional characters observed from extant specimens.]

Included Fossil Genera.—*Dromilites* H. Milne Edwards, 1837; *Ferricorda* Schweitzer and Feldmann, 2010d.

Material Examined.—Specimens of *Dromilites* spp., *Ferricorda*, and *Sphaerodromia* spp. are listed in Schweitzer and Feldmann (2010d).

Geologic Range.—Late Cretaceous (Maastrichtian) – Recent.

Remarks.—The occurrence of the family in the fossil record was recently summarized (Schweitzer and Feldmann, 2010d) and need not be repeated. Our analysis confirms its distinct family status.

Xandarocarcinidae n. fam.

Fig. 6

Diagnosis.—Carapace wider than long, hexagonal, anterolateral and posterolateral margins well differentiated, both with spines; posterior margin concave, rimmed. Rostrum extending beyond orbits, axially bifid, axial two spines flanked by second pair of spines posterior to them and separated from them by arcuate segment; orbital margin sinuous, first extending posteriorly in segment parallel to axis, then extending convex forward in short arc, then turning strongly concave posteriorly and arcing anteriorly to outer-orbital spine; outer-orbital spine triangular, directed forward; orbit deep, circular, directed forward; eyestalks short, arcuate, arcing concave forward, well calcified. Carapace regions weakly defined, protogastric, hepatic, and epibranchial with large swellings. Cervical groove moderately defined, extending from anterolateral margin just anterior to last anterolateral spine, arcing convex forward, terminating lateral to urogastric region. Branchiocardiac groove obscure laterally, deeper axially, parallel to cervical groove. Postcervical groove present only as weak separation between urogastric and cardiac regions. Sternites 1-3 apparently fused, longer than wide; sternite 4 longer than wide, flattened.

Male pleon moderately wide, with parallel sides, somites without triangular epimeres, uropodal plates not visible, telson reaching middle of sternite 4, all somites free.

Female pleon wide, with convex lateral margins, somites without triangular epimeres, uropodal plates not visible, telson reaching well anterior to sternite 4, all somites free. Female gonopores coxal, ovate, positioned obliquely in distal position on coxae of third pereopods.

Chelipeds strongly sexually dimorphic, much larger in males than in females; chelae ornamented with rows of tubercles on outer surface of manus and carpus; fingers edentulous except for small spine at tip of fixed finger interlocking with movable finger, finger tips black; pereopods 2-5 similar in size, none subdorsal.

Included Genera.—*Acanthodiaulax* Schweitzer et al., 2003; *Xandarocarcinus* new name (type genus).

Material Examined.—*Acanthodiaulax mclayi* Schweitzer et al., 2003, KSU D272, cast of GSC 124804, holotype; KSU D271, cast of GSC124805, paratype; KSU D246; Late Cretaceous (Santonian), British Columbia, Canada.

Remarks.—*Xandarocarcinus* new name is unusual among podotreme crabs in having well-differentiated anterolateral and posterolateral margins, a pleon that is not visible in dorsal view, a wide telson, and no pereopods that are reduced in size and subdorsal. In these respects, this brachyuran is much more similar to most heterotreme crabs. However, the female gonopores are clearly placed on the coxae of the third pereopods, so it is a podotreme with certainty. In spite of the many synapomorphies it shares with other dromioids, no other group possesses this combination of characters. Thus, we place *Xandarocarcinus* within a new family. *Acanthodiaulax*, known from only the type species, is very similar to *Xandarocarcinus* in terms of its dorsal carapace shape, the nature of the orbits and rostrum, and dorsal carapace ornamentation. Only a single appendage is known from *Acanthodiaulax* and no aspects of the ventral surface. Thus, we place it within Xandarocarcinidae based upon its close similarity with *Xandarocarcinus*. All known occurrences of the family are Late Cretaceous from Pacific coastal North America.

Xandarocarcinus n. name

Fig. 6

Xandaros Bishop, 1988c, p. 252 [preoccupied]. Schweitzer et al., 2002, p. 21; De Grave et al., 2009, p. 27; Schweitzer et al., 2010, p. 66.

Non *Xandaros* Maciolek, 1981, p. 827.

Type Species.—*Zanthopsis sternbergi* Rathbun, 1926, by original designation.

Diagnosis.—Carapace wider than long, hexagonal, widest at position of last anterolateral spine about half the distance posteriorly on carapace; carapace strongly vaulted longitudinally, weakly vaulted transversely. Rostrum extending beyond orbits, axially bifid, axial two spines flanked by second pair of spines posterior to them and separated from them by arcuate segment; orbital margin sinuous, first extending posteriorly in segment parallel to axis, then extending convex forward in short arc, then turning strongly concave posteriorly and arcing anteriorly to

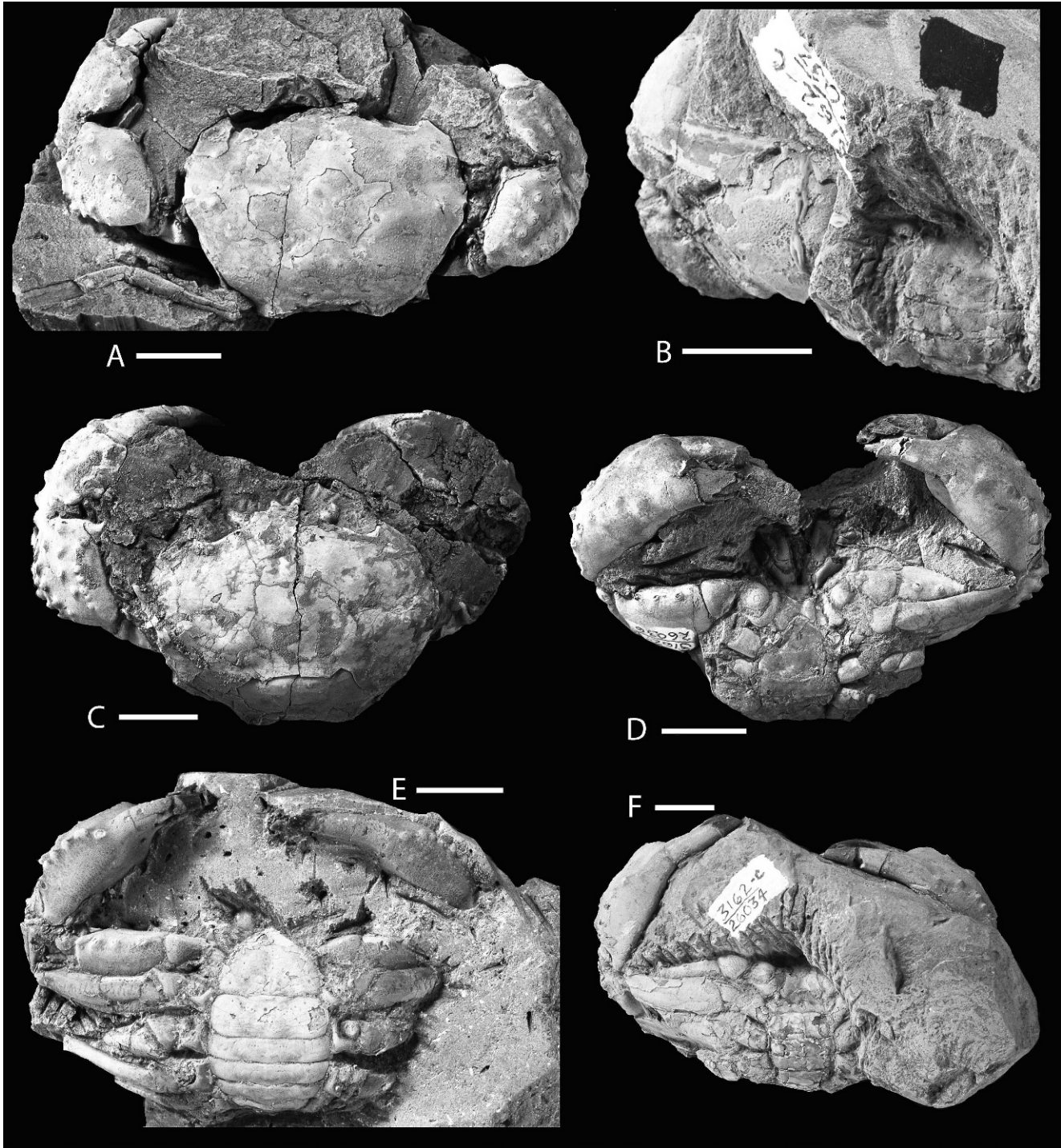


Fig. 6. Dromioidea, Xandarocarcinidae, *Xandarocarcinus sternbergi* (Rathbun, 1926). A-B, SDSNH 26037, hypotype, dorsal carapace (A) and pleon (B) showing completely ventral nature of pleon; C-D, SDSNH 26036, hypotype, dorsal carapace with eyestalks preserved (C) and ventral surface with maxillipeds and showing massive chelipeds; note termination of male pleon in middle of sternite 4 (D); E, SDSNH 26033, hypotype, female pleon, note termination well anterior to sternite 4; F, SDSNH 26034, hypotype, male pleon terminating in middle of sternite 4. Scale bars = 1 cm.

outer-orbital spine; outer-orbital spine triangular, directed forward; orbit deep, circular, directed forward; eyestalks short, arcuate, arcing concave forward, well-calcified. Anterolateral margin tightly convex, with three spines excluding outer-orbital spine, increasing in size posteriorly; posterolateral margin nearly straight, with a few small

projections; posterior margin concave, rimmed. Carapace regions weakly defined, protogastric, hepatic, and epibranchial with large swellings. Cervical groove moderately defined, extending from anterolateral margin just anterior to last anterolateral spine, arcing convex forward, terminating lateral to urogastric region. Branchiocardiac groove

obscure laterally, deeper axially, parallel to cervical groove. Post-cervical groove present only as weak separation between urogastric and cardiac regions.

Sternites 1-3 apparently fused, longer than wide; sternite 4 longer than wide, flattened. Male pleon moderately wide, with parallel sides, somites without triangular epimeres, uropodal plate not visible, telson reaching middle of sternite 4, all somites free. Female pleon wide, with convex lateral margins, somites without triangular epimeres, uropods not visible, telson reaching well anterior to sternite 4, all somites free. Female gonopores coxal, ovate, positioned obliquely in distal position on coxae of third pereopods.

Chelipeds strongly sexually dimorphic, much larger in males than in females; chelae ornamented with rows of tubercles on outer surface of manus and carpus; fingers edentulous except for small spine at tip of fixed finger interlocking with movable finger, finger tips black; pereopods 2-5 similar in size, none subdorsal.

Etymology.—The generic name is derived from the original genus name *Xandaros*, a Greek word meaning a fabulous sea creature, and the Greek word *karkinos*, meaning crab, a common stem within Brachyura.

Material Examined.—SDSNH 26033, 26034, 26036, 26037, all hypotypes, from Point Loma Formation, Late Cretaceous (Campanian); KSU D 659, Rosario Formation (Late Cretaceous), Baja California, Mexico.

Remarks.—Maciolek (1981) named a new genus and species of annelid worm from geothermal vents, *Xandaros acanthodes*. Bishop (1988c) later used the same genus name for a Cretaceous crab. Thus, we herein provide a replacement name for the crab, *Xandarocarcinus*.

Dromiacea incertae sedis

Included Genera.—*Ameridromia* Blow and Manning, 1996; *Cyamocarcinus* Bittner, 1883; *Eotrachynotocarcinus* Beschin et al., 2007; *Gemmellarocarcinus* Checchia-Rispoli, 1905; *Mesodromilites* Woodward, 1900; *Ovamene* Müller and Collins, 1991; *Stephanometopon* Bosquet, 1854.

Material Examined.—*Ameridromia hyneorum* Blow and Manning, 1996, USNM 484532 (holotype); *Cyamocarcinus angustifrons* Bittner, 1883, KSU D 57; *Gemmellarocarcinus loerentheyi* Checchia-Rispoli, 1905, KSU D 107; *Mesodromilites glaber* (Woodward, 1898) (BMNH) I.7990 (holotype).

Remarks.—Several extinct genera have been referred previously either to Dromiidae or Dynomenidae. Examination of these taxa with respect to the most recent diagnoses for these families (Guinot and Tavares, 2003; Guinot, 2008) and other dromiaceans (Schweitzer and Feldmann, 2009a, 2010d) suggests that they cannot be placed confidently within any of them. None of the above genera possess any portion of ventral surface of the carapace or appendages, and in fact, some are quite fragmental as in *Stephanometopon* which is known only from anterior portions of the carapace. *Ameridromia* was

named upon a broken carapace and is referred to the family based upon its small orbits and spined anterolateral margins. Its placement is very problematic. *Ovamene* is about as wide as long and smooth, with little ornamentation. Superficially, it resembles the anomuran group Porcellanidae, but more complete carapace material will be needed to test this hypothesis.

Both *Cyamocarcinus* and *Gemmellarocarcinus* are wider than long and ovate; have very narrow fronto-orbital widths with respect to the maximum carapace width; have entire anterolateral margins that are developed as a thickened rim; and simple, v-shaped fronts. *Gemmellarocarcinus* has distinctive transverse ridges on the hepatic and epibranchial regions, and *Cyamocarcinus* has a row of setal pits parallel to the frontal margins of the carapace. These two genera cannot be accommodated in any known family of Brachyura; recovery of sternal or pleonal elements may help to determine their placement.

Eotrachynotocarcinus is enigmatic. It shares similarities with members of Dynomenidae and with Goniiodromitidae. Like members of Metadynomeninae Guinot, 2008 (Dynomenidae), the carapace grooves are well developed and the carapace is wider than long. However, the orbital margin and rostrum of *Eotrachynotocarcinus* is more like that of many goniiodromitids, with a flared rostrum and rimmed orbital margin. In most dynomenids, the orbit can be seen in dorsal view, which is not the case in *Eotrachynotocarcinus*. Details of the orbits or ventral surface of the carapace would help to determine an appropriate placement for this genus.

Mesodromilites is well preserved but does not fit into any known family based upon dorsal carapace characters, and unfortunately, it lacks a sternum and pleon. It has a trifold front, similar to some dynomenids, and has wide orbits and augenrests, similar to goniiodromitids. Its carapace is long, with distinctive spines and swellings, not unlike sphaerodromiids and some dynomenids. In fact, *Mesodromilites* is quite similar to sphaerodromiids in its cristate lateral margins, wide orbits, and ornamentation. However, it differs from all other dromiaceans in its unusual posterior region that is separated from the remainder of the carapace by a keel and groove. Thus, until sterna or pleons are recovered, it is best placed in Dromiacea incertae sedis.

Homoloidea n. section

Diagnosis.—Carapace longer than wide, usually pseudo-rostral spines present; usually augenrest developed to accommodate eye; epistomial spine present; pereopod 5 usually reduced in size, subdorsal; sternal suture 6/7 complete, separating sternum into two segments; external, paired spermatheca in females; all 7 somites in male and female pleons usually free but female somites sometimes fused; sterno-coxal depression and sterno-pleonal depression present; usually pleonal holding mechanism (homolid press-button) present; female pleonal somite 1 with reduced pleopods; male pleonites 1 and 2 with pleopods with distinct coxae and bases, socket on somite 6.

Included Superfamily.—Homoloidea De Haan, 1839.

Geologic Range.—Late Jurassic (Tithonian) – Recent.

Superfamily Homoloidea De Haan, 1839

Diagnosis.—as for section.

Included Families.—Homolidae De Haan, 1839; Latreilliidae Stimpson, 1858a; Mithracitidae Števíć, 2005; Poupiniidae Guinot, 1991; Tithonohomolidae Feldmann and Schweitzer, 2009.

Geologic Range.—Late Jurassic (Tithonian) – Recent.

Remarks.—Homoloidea is a variable superfamily and by extension, so is the section. Only some members possess a linea homolica, suggesting that it is apomorphic for Homolidae (and Tithonohomolidae, which was not included in our analysis) but also a character that evolved early as it is present in Jurassic forms. Uniting the group are the presence of a sternum divided into 2 parts by a complete suture 6/7 as well as features of the pleons. In addition, our analysis united the Homoloidea by possession of an augenrest, an epistomial spine, the homolid press-button, and a socket on sternite 6. The augenrest in Homoloidea is essentially the same as that seen in Homolodromioidea, except that in Homolidae, the *linea homolica* cuts through it. Although most have a reduced, subdorsal, chelate P5, the Poupiniidae lack this character.

Homolidae De Haan, 1839

Diagnosis.—Carapace rectangular or ovate, longer than wide; linea homolica well developed; rostrum a single spine or bifid, a spine often placed to either side of rostrum; cervical and well-developed branchiocardiac grooves; well-defined carapace regions; pereopod 5 reduced, subchelate or chelate.

Included Genera.—*Antarctomithrax* Feldmann, 1994; *Dag-naudus* Guinot and Richer de Forges, 1995 (also extant); *Doerflesia* Feldmann and Schweitzer, 2009; *Homola* Leach, 1816 [imprint 1815] (also extant); *Homolopsis* Bell, 1863; *Hoplitocarcinus* Beurlen, 1928; *Latheticocarcinus* Bishop, 1988b; *Lignihomola* Collins, 1997; *Londinimola* Collins and Saward, 2006; *Paromola* Wood-Mason in Wood-Mason and Alcock, 1891 (also extant); *Paromolopsis* Wood-Mason in Wood-Mason and Alcock, 1891 (also extant); *Prohomola* Karasawa, 1992; *Zygastrocarcinus* Bishop, 1983b.

Material Examined.—*Doerflesia ornata* Feldmann and Schweitzer, 2009, NHMW 2007z0149/0015 (holotype), NHMW 1912/0006/0696 (paratype); *Latheticocarcinus affinis* (Jakobsen and Collins, 1997), MGUH 24362 (holotype), 24363 (paratype); *L. brightoni* Wright and Collins, 1972, (BMNH) In. 31004 (holotype), SM B23287 (paratype); *L. ludvigseni* Schweitzer et al., 2004, GSC 124842 (holotype); *L. spinigus* Jakobsen and Collins, 1997, MGUH 24359 (holotype), MGUH 24360-61 (paratypes); *L. transiens* Segerberg, 1900, MGUH 256; *Lignihomola etheridgei* (Woodward, 1892) (BMNH) In. 36264; *Londinimola williamsi* Collins and Saward, 2006, (BMNH)

IC453 (holotype); *Homola barbata* (Fabricius, 1793), USNM 273440; *Homola orientalis* (Henderson, 1888), USNM 55131; *Homola ranunculus* Guinot and Richer de Forges, 1995, SMF 22291, USNM 268911; *Paromolopsis boasi* Wood-Mason and Alcock, 1891, USNM 184580; *Prohomola japonica* (Yokoyama, 1911), KMNH.IVP 300,010; *Prohomolopsis piersoni* Schweitzer et al., 2004, UWBM 97178 (holotype), 97179 (paratype); *Zygastrocarcinus cardsmithi* Bishop, 1986, SDSM GAB 23-40; *Z. waagei* Feldmann, Schweitzer, and Green, 2008, YPM 220105 (holotype), YPM 220103-10, 221135 (paratypes).

Geologic Range.—Late Jurassic (Tithonian) – Recent.

Remarks.—Homolidae in the fossil record is very well constrained due to the diagnostic feature of the linea homolica. All of the genera referred to the family here have this feature as well as most of the others listed here. In our analysis, Homolidae is the sister group to Latreilliidae, both of which exhibit a chelate or subchelate P5. However, the latter may be readily distinguished from Homolidae because the latreillids have a very elongate “gastric neck” and lack the linea homolica. Placement of fossil taxa in Homolidae can be problematic because many specimens preserve only the intralinear, dorsal part of the carapace. The flanks, or extralinear elements, are often missing, which gives the false impression that the specimen is narrow and of a form different from that of homolids.

Bell (1863) described a new genus of homolid crab, *Homolopsis*, from Cretaceous rocks of England. Bonaparte (1831) had used that spelling as an apparently unjustified correction or incorrect subsequent spelling of *Homalopsis* Kuhl and Hasselt, 1822, who used that name for a snake. According to ICZN Articles 33.3 and 54.3, incorrect spellings do not enter into homonymy. Thus, *Homolopsis* was an available name when used by Bell in 1863, so we retain it here.

Latreilliidae Stimpson, 1858a

Diagnosis.—Carapace triangular, narrowed and much extended anteriorly into “gastric neck”; linea homolica absent; cervical and branchiocardiac grooves weak; carapace regions poorly developed, sometimes with a spine in mesogastric region and sometimes with branchial spines; eyestalks long; rostrum short, downturned; pseudorostral spines long; male pleon straight; female pleonites 4-6 fused, somites may have spines; female with paired spermatheca; pereopods very long, slender.

Included Fossil Genera: none.

Material Examined.—Cast of *Heeia villersensis* (Hée, 1924), specimen in Oxford University collection; (BMNH) In. 60988, 61137.

Geologic Range.—Recent.

Remarks.—Latreilliids have an elongate “gastric neck,” the region anterior to the metogastric region and leading up to the rostrum, yielding an overall elongate dorsal carapace. *Heeia* Wright and Collins, 1972, from the Cenomanian of Britain originally was placed within Latreilliidae. It possesses the

same overall shape, although its elongate nature is due to its long rostrum and overall elongate carapace rather than a long “gastric neck.” The carapace regions are well-developed from the base of the rostral spine visible in the OU specimen, which is not the case in latreilliids, in which only the mesogastric region is elongate leading up to the rostrum. In addition, in latreilliids, the rostrum is tiny, flanked by two longer pseudorostral spines. In *Heeia*, there appears to be one long rostral spine; it is difficult to determine if it may be broken along the base and may have been bifid. The reconstruction of Wright and Collins (1972: 32) that show a trifid tip cannot be confirmed by any material known to us. We suggest that the elongate carapace, long rostrum, and well-developed carapace regions make *Heeia* similar to the majoid family Priscinachidae Breton, 2009, described from the Cenomanian of northern France. We herein refer it to that family provisionally until more complete specimens can be found to confirm the placement.

Removal of *Heeia* from Latreilliidae renders the family without a fossil record. Castro et al. (2003) summarized the family and that remains the most complete work on it to date. They appear to be a rather specialized group that may carry sea anemones or other objects with the fifth pereopods. Many live in outer-shelf and slope depths, so little is known about their biology. Given the bathymetric distribution of most latreilliids, coupled with their general small size and delicate carapace, it is anticipated that their fossil record will never be substantial.

Mithracitidae Števčić, 2005

Diagnosis.—Carapace about as wide as long, widest in branchial regions; rostrum triangular, simple; orbits narrow, deep, directed forward; augenrest bounded by supra, outer, and subaugenrest spines; lateral margins sinuous, with spines anterior to intersection of cervical groove, convex posterior to it; posterior margin concave, rimmed; linea homolica absent; cervical and branchiocardiac grooves well developed; female pleonites with 4-6 fused or 5-6 fused.

Included Genera.—*Enodicarcinus* Schweitzer and Feldmann, 2011b; *Mithracites* Gould, 1859 (type genus).

Material Examined.—*Mithracites vectensis* Gould, 1859, SM B14268, 14271, 14272, 14282, 14283; (BMNH) In. 28828, In. 28835, In. 28832.

Geologic Range.—Aptian.

Remarks.—Guinot and Tavares (2001) originally suggested the affinity of *Mithracites* with the Homolidae. Števčić (2005) placed the genus within its own family and our analysis bears this out. Thus, we place Mithracitidae within Homoloidea. The family is characterized by the absence of a *linea homolica*, a feature seen only in Homolidae; however, it does possess a reduced, subdorsal P5, and morphological characters of the carapace that are reminiscent of the other Homoloidea. Mithracitidae is distinguished from other families in the superfamily in having a subdorsal P4 as well.

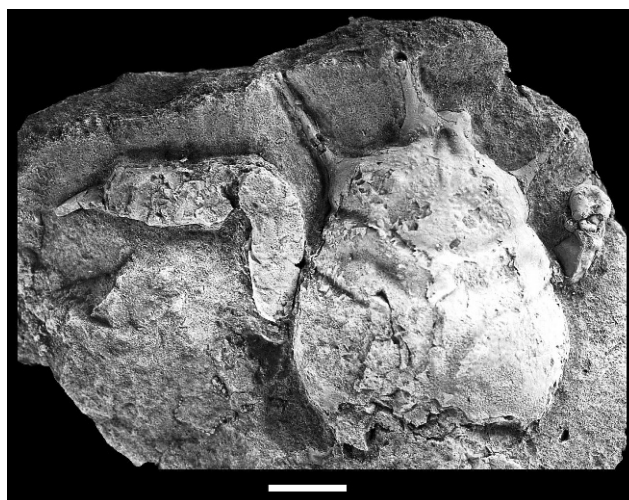


Fig. 7. Homoloidea, Poupiniidae, *Rhinopoupinia bicornis* Feldmann et al., 1993. USNM 457696, holotype. Scale bar = 1 cm.

Poupiniidae Guinot, 1991

Fig. 7

Diagnosis.—Carapace longer than wide, large in overall size, widened posteriorly; large augenrest; small pseudo-rostral spines; without flanks, not covering coxae of pereopods; linea homolica absent; cervical and branchiocardiac grooves moderately defined; all female pleonites free.

Included Fossil Genus: *Rhinopoupinia* Feldmann et al., 1993.

Geologic Range.—Late Cretaceous (Maastrichtian) – Recent.

Remarks.—Guinot (1991) introduced a new family and genus to embrace a single species, *Poupinia hirsuta*, from the South Pacific. To our knowledge, it remains the sole species within the genus. Feldmann et al. (1993) described what remains the sole fossil representative of the family, *Rhinopoupinia bicornis*, from the Maastrichtian of Antarctica. The family is nested well within Homoloidea in our analysis, but is distinguished from other families in possessing a P5 that is subdorsal, as in other homoloids, but is normal in size, not reduced. Further, the propodus and dactylus on P5 are normal and do not form either a subchelate or chelate closure. Other characters of the family on the ventral surface and pleon are less likely to be preserved on fossil forms. The general outline, groove pattern, and flanks are consistent with placement in Homoloidea.

Tithonohomolidae Feldmann and Schweitzer, 2009

Diagnosis.—Inter-lineal portion of carapace longer than wide; extra-lineal regions of cephalothorax not known; *linea homolica* present; rostrum broad and tapering or downturned and blunt; orbits directed anterolaterally, with two prominent orbital eaves; regions well-defined, tumid, often tuberculate or nodose.

Included Genera.—*Tenuihomola* Feldmann and Schweitzer, 2009; *Tithonohomola* Glaessner, 1933.

Material Examined.—Specimens listed in Feldmann and Schweitzer (2009).

Geologic Range.—Late Jurassic (Tithonian).

Remarks.—Tithonohomolidae share the character of possession of a linea homolica with Homolidae that firmly establishes the family as a member of Homoloidea. The representatives of this extinct group cannot be referred to Homolidae because they lack pseudorostral spines; possess a broad, blunt, and downturned rostrum; and exhibit supraorbital eaves separated by a groove. Presence of a linea homolica separates Tithonohomolidae from other families within the superfamily.

Torynommoidea n. section

Diagnosis.—Carapace quadrate; front narrow; orbits extremely broad, forward-directed, with short intraorbital spine and stout, forward directed outer-orbital spine; orbits and frontal margin of carapace nearly straight; cervical groove with hepatic groove extending from it anteriorly and intersecting lateral margin, branchiocardiac groove subparallel to cervical groove and hepatic segment; branchiocardiac groove extending onto flank in long, oblique path; cervical groove weakly extending onto flank and appearing to nearly intersect branchiocardiac groove; hepatic groove appearing to extend onto flank; third maxilliped without crista dentata; anterior sternite 4 broad, with transverse ridge at which female pleon terminates, sternopleonal depression present, well-developed sternal sutures 4/5, 5/6, and 6/7; pleonites of female wide, with moderately developed epimeres; telson much wider than long, terminating before coxae of first pereopods.

Included Superfamily.—Torynommoidea Glaessner, 1980.

Geologic Range.—Early Cretaceous (Aptian) – Late Cretaceous (Maastrichtian).

Superfamily Torynommoidea Glaessner, 1980, n. status

Diagnosis.—As for section.

Included Family.—Torynommidae Glaessner, 1980.

Included Genera.—*Torynomma* Woods, 1953; ?*Withersella* Wright and Collins, 1972.

Material Examined.—*Torynomma quadrata* Woods, 1953, QMF 2877 (holotype), QMF 2880 (paratype), uqf 14924, MFM; *Withersella crepitans* Wright and Collins, 1972, (BMNH) IC15.

Geologic Range.—Early Cretaceous (Aptian) – Late Cretaceous (Maastrichtian).

Results.—*Torynomma* spp. are unusual, and as is reinforced by our analysis, unique among Brachyura. They are clearly podotremes based upon presence of female gonopores on coxae of the third pereopods, but the conformation of the

sternum and pleon as well as the dorsal carapace is different from other podotrematous crabs, and in fact, all other brachyurans. The sternum is relatively wide for a podotreme, and the transverse ridge on the sternum against which the female pleon terminates appears to be unique to the section. These features are of the type species of *Torynomma*; the composition of the genus requires examination, and it may be heterogeneous. *Withersella* is known only from rather poorly preserved dorsal carapace material, with no ventral surfaces. It is similar in some ways to *Torynomma*, especially in the development of carapace grooves and regions. Thus, we place it in Torynommidae until better preserved material can be recovered.

Etyoidea n. section

Diagnosis.—Carapace transversely ovate; rostrum triangular, downturned; orbits circular, directed forward; fronto-orbital width half to three-quarters maximum carapace width; anterolateral margins with spines; posterolateral margin concave; posterior margin narrow; carapace regions often well-marked, generally granular, granules may be all of one size or with interspersed larger tubercles; cervical groove generally extending in sinuous but overall relatively straight path across carapace; if regions developed, well-defined branchial subdivisions may be present; sternopleonal depression present, sternite 3 and sometimes 4 visible even with pleon in place; paired spermatheca long, ovate, situated posteriorly; all pleonites free in males and females, telson long, triangular; all pereopods carried laterally; maxilliped 3 operculiform.

Included Superfamily.—Etyoidea Guinot and Tavares, 2001.

Superfamily Etyoidea Guinot and Tavares, 2001

Diagnosis.—As for section.

Included family.—Etyidae Guinot and Tavares, 2001.

Etyidae Guinot and Tavares, 2001

Fig. 8

Diagnosis.—as for section.

Included Genera.—*Caloxanthus* A. Milne-Edwards, 1864; *Etyus* Mantell, 1822; *Etyxanthosia* Fraaije et al., 2008; *Feldmannia* Guinot and Tavares, 2001; *Guinotosia* Beschin et al., 2007; *Secretanella* Guinot and Tavares, 2001; *Sharnia* Collins and Seward, 2006; *Xanthosia* Bell, 1863, sensu stricto.

Material Examined.—Specimens of *Etyxanthosia*, *Xanthosia*, and *Feldmannia* listed in Schweitzer-Hopkins et al. (1999); *Caloxanthus americanus* Rathbun, 1935, UT BEG 21192 (holotype), BEG 21193-96 (paratypes), (BMNH) In. 60949, 61678; *C. formosus* A. Milne-Edwards, 1864, MNHN R03351 (holotype), (BMNH) In. 61163; *C. ornatus* (von Fischer-Benzoni, 1866), (BMNH) I.8034-6, 16205, 16206; *C. purleyensis* (Withers, 1928), (BMNH) In. 27330

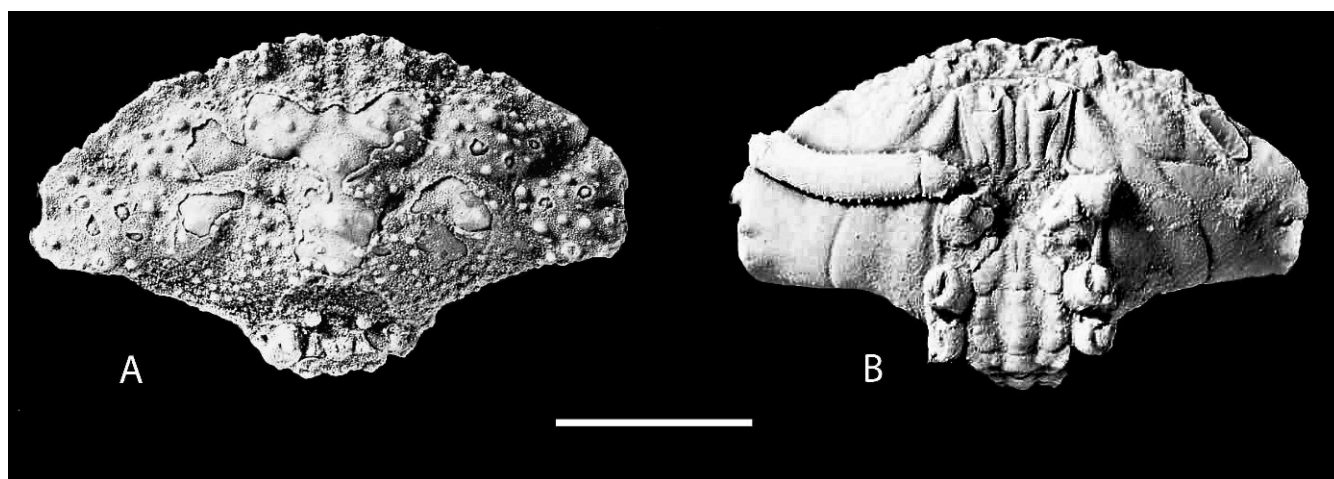


Fig. 8. Etyoidea, Etyidae, *Xanthosia aspera* Rathbun, 1935. Scale bar = 1 cm.

(holotype); *C. simplex* (Secretan, 1964), MNHN R03879 (holotype); *Etyxanthosia fossa* (Wright and Collins, 1972), (BMNH) In. 60996 (holotype), In. 60995, 60997 (paratypes); OUM K.51634; *Secretanella arcuata* (Secretan, 1964), MNHN R03978 (holotype), R03980, A31661 (paratypes); *Sharnia burnhamensis* Collins and Saward, 2006, (BMNH) IC 454 (holotype); *Feldmannia jacksoni* (Wright and Collins, 1972), (BMNH) In. 60957 (holotype); *Xanthosia buchii* (Reuss, 1845), NHMW 1864XL604 (holotype); *Xanthosia gibbosa* Bell, 1863, (BMNH) In. 29964, 29966, 36647, 59523 (syntypes); *Xanthosia similis* Bell, 1863, SM B 22637; *Xanthosia granulosa* (McCoy, 1854), SM B 22656, (BMNH) In. 29736-7. Material of *Xanthosia* sensu lato: *Xanthosia buteonis* Wright and Collins, 1972, (BMNH) In. 60958 (holotype); *X. gracilis* Jakobsen and Collins, 1997, MGUH 24367; *X. occidentalis* Bishop, 1985, SDSM 10037 (paratype), 10036, GAB 36-361, 1376, 886, 895, 1372; *X. robertsi* Secretan, 1964, MNHN R03979 (holotype); *X. semiornata* Jagt et al., 1991, MAB K0020 (holotype).

Geologic Range.—Early Cretaceous (Aptian) – Eocene (Lutetian).

Remarks.—As in *Torynommeidea*, Etyidea are unique among Brachyura. They are clearly podotremes, but unlike all other podotremes, they have a wide, transversely ovate carapace, lacking a well-developed branchiocardiac groove, and apparently are without subdorsal fifth pereopods. In many regards, members of this section are superficially similar to heterotremes in possessing well-developed, forward directed orbits and well-differentiated anterolateral and posterolateral margins. In fact, genera within the section had been placed within Xanthidae sensu lato by various authors (Glaessner, 1969; Schweitzer-Hopkins et al., 1999). Thus, it is perhaps not surprising that our analysis places them as a monotypic group within their own section.

Note that *Feldmannia* Guinot and Tavares, 2001, a member of Etyidae, is a senior homonym of *Feldmannia* Casadío et al., 2001, a trace fossil. Low and Guinot (2010) erected a replacement name for the trace fossil, *Feldmannius*.

To those genera listed by Schweitzer et al. (2010), we add *Secretanella* to the family. Guinot and Tavares (2001) erected the genus to accommodate a species of *Xanthosia* from Madagascar and suggested that it had heterotreme status. Our evaluation of the type material of this taxon suggests that it is best placed within Etyidae based upon its carapace shape and ornamentation, its wide female pleon with all somites free, and telson that extends beyond the coxae of pereopod 1. All of these features are seen in genera within Etyidae, and in fact, there is no other family that can accommodate *Secretanella* at this time. Additional material with preserved gonopores and other aspects of the sternum and pleon could help to confirm the podotreme and family status of this genus.

Xanthosia sensu lato is problematic. Schweitzer et al. (2010) placed many of the species that had originally been placed within the genus into Xanthidae sensu lato. The composition of *Xanthosia* sensu lato is quite variable and requires extensive revision. Those species listed in *Xanthosia* sensu stricto by Schweitzer et al. (2010) are those they considered to be similar to the type species.

The family, like some others within Brachyura, originated in the Cretaceous and persisted well into the Cenozoic. Clear examples of the family are known from the Eocene of Italy, and other genera are known from the Danian and Eocene of northern Europe.

Section Raninoidea Ahyong et al., 2007

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; branchiocardiac groove developed as boundary for urogastric region; maxilliped 3 elongate, merus long; thoracic sternum narrow, sternites 1-3 generally fused, 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; genital openings coxal, spermatheca present.

Included Superfamily.—Raninoidea De Haan, 1839.

Geologic Range.—Early Cretaceous (Berriasian) – Recent.

Superfamily Raninoidea De Haan, 1839

Diagnosis.—As for section.

Geologic Range.—Early Cretaceous (Berriasian) – Recent.

Included Families.—Camarocarcinidae Feldmann, Li, and Schweitzer, 2008; Cenomanocarcinidae Guinot, Vega, and Van Bakel, 2008; Necrocarcinidae Förster, 1968; Palaeocorystidae Lőrenthey *in* Lőrenthey and Beurlen, 1929; Raninidae De Haan, 1839; Symethidae Goeke, 1981.

Remarks.—Raninoidea has been expanded over the past 30 years to include several primarily Cretaceous families. Glaessner (1969) considered all representatives of the superfamily to be referable to Raninidae. Tucker (1998) recognized the distinctive character of *Symethis* and elevated Symethinae to family rank. Subsequently, *Necrocarcinus*, *Camarocarcinus*, and *Cenomanocarcinus*, which were referred to the eubranchyuran family Calappidae De Haan, 1833, were demonstrated to be podotrematous (Larghi, 2004; and others). Thus, Necrocarcinidae Förster, 1968, was removed from the eubranchyurans and has now been referred to Raninoidea (Guinot et al., 2008). Feldmann et al. (2007) erected Camarocarcinidae to include *Camarocarcinus* and a new species, *Cretacocarcinus* Feldmann et al., 2007. Guinot et al. (2008) proposed Cenomanocarcinidae to embrace two other species previously thought to be calappids, *Cenomanocarcinus* and *Campylostoma*. At the same time, they proposed elevating the extant subfamilies of raninids to family rank and considered the section to include two superfamilies, Raninoidea and a second, unnamed superfamily. Our analysis supports a different interpretation. Within the section, Camarocarcinidae is the sister to the remainder of the raninoids; Necrocarcinidae and Cenomanocarcinidae are sister to Palaeocorystidae, Symethidae, and Raninidae. Thus, the inclusion of Necrocarcinidae, Cenomanocarcinidae and Palaeocorystidae, as well as Orithopsidae, within a separate superfamily (Guinot et al., 2008) is unwarranted.

Camarocarcinidae Feldmann, Li, and Schweitzer, 2008

Diagnosis.—Carapace nearly circular in outline, length about 96% maximum width, strongly vaulted transversely and longitudinally. Front narrow, sulcate, down-turned, 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. 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.

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

Material Studied.—The specimens studied are detailed in Feldmann et al. (2008).

Geologic Range.—Late Cretaceous (Campanian) – Paleocene (Danian).

Remarks.—Camarocarcinidae and Necrocarcinidae are similar in terms of overall dorsal morphology and differ from the other families of Raninoidea in possessing spines on the posterolateral margin. However, several characters separate Camarocarcinidae from its most similar taxon, Necrocarcinidae. Whereas the cuticle on camarocarcinids exhibits endocuticular pillars reaching the exocuticle, that is not the case in necrocarcinids. The sternum on species of Camarocarcinidae is extremely narrow, flattened axially, and nearly vertical laterally. The sternum in Necrocarcinidae is not strongly depressed axially, wider, and the lateral portions of the sternum are not vertical, they are oriented at about a 40-degree angle to the axis. The sternum of Necrocarcinidae appears to have a complete suture between sternite 6 and 7, which seems not to be the case in Camarocarcinidae.

Cenomanocarcinidae Guinot, Vega, and van Bakel, 2008
Fig. 9

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 ornamented with longitudinal ridges ornamented with tubercles; 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, pereopod 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 pereopod 2, with two tubercles on each side probably serving to hold pleon in place, directed posterolaterally; sternite 6 inclined at moderate angle to remainder of sternum; sternite 8 directed ventrolaterally, much smaller than sternite 7; 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; pereopod 5 much reduced in size.

Included Genera.—*Campylostoma* Bell, 1858; *Cenomanocarcinus* Van Straelen, 1936.

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

32654-55, 41726, *Cenomanocarcinus vanstraeleni* Stenzel, 1945, UT 21079, 21090, and 21091 (syntypes).

Geologic Range.—Early Cretaceous (Albian) – Eocene (Ypresian).

Remarks.—Guinot et al. (2008) tentatively referred *Campylostoma* to Cenomanocarcinidae. Examination of SM C 19127 (Fig. 9D, E) suggests that its sternum is quite similar to that of *Cenomanocarcinus* spp. and should be referred to the family with confidence. Guinot et al. (2008) also provide a detailed discussion of the interpretations of relationship between *Cenomanocarcinus* and *Necrocarcinus* and that will not be repeated here. The two genera, and the families to which they are referred herein, differ in that species within Cenomanocarcinidae have paddle-like dactyli on pereopods 2-4 and a dorsally carried P5; whereas the necrocarcinids have normally developed P2-P4 and dorsally carried P4-P5. Cenomanocarcinidae have a flattened sternum with reduced sternites 1-3, and very broad, arcuate, and flattened sternite 4 with convex lateral margins. Sternites 1-3 of Necrocarcinidae are quadrate and well-defined, and sternite 4 is narrower, with raised lateral margins that are concave. Sternite 5 in Cenomanocarcinidae is arcuate, oriented convex posteriorly; that of Necrocarcinidae is straight and directed laterally.

Necrocarcinidae Förster, 1968

Fig. 10

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 between 30 and 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 apparently fused, quadrate, anterior two sides at low angle to one another, posterior two sides 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 pereopod 2, directed laterally; sternite 6 similar to sternite 5; sternites 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; pereopods 4 and 5 apparently reduced in size (after Schweitzer and Feldmann, 2000; Schweitzer et al., 2003).

Included genera.—*Necrocarcinus* Bell, 1863; *Corazzatocarcinus* Larghi, 2004; *Cristella* Collins and Rasmussen, 1992; *Paranecrocarcinus* Van Straelen, 1936; *Polycnemidium* Reuss, 1859; *Pseudonecrocarcinus* Förster, 1968; *Shazella* Collins and Williams, 2004.

Material Examined.—*Necrocarcinus labeschei* Eudes-Deslongchamps, 1835, SM B23152, 23210, B80539; *Polycnemidium pustulosum* (Reuss, 1845), NHMW 1864XII666 (holotype);

Geologic Range.—Early Cretaceous (Berriasian) – Paleocene (Danian).

Remarks.—Necrocarcinidae and Camarocarcinidae appear as sister taxa in the present study. Several newly observed features are detailed in the diagnosis.

Palaeocorystidae Lőrenthey in Lőrenthey and Beurlen, 1929

Fig. 11

Diagnosis.—Carapace obovate, widest at position of third or fourth anterolateral spine; frontal margin wide; anterolateral margin with 3 or 4 spines; carapace surface ornamented with ridges, straps, or tubercles; sternites 1-3 fused, 1 and 2 directed downward; sternite 4 long, pereopod 1 articulating near posterior corner, moderately wide, lateral margins concave; sternal suture 4/5 sinuous laterally, then curving abruptly anteriorly parallel to axis; sternite 5 long, moderately wide, with tubercles on episternal projection for attachment of pleon; 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 pereopods; male pleon narrower, telson triangular, somite 6 long, reaching to level of base of coxae of pereopods 2; chelae with long fingers; female gonopore coxal, small, round.

Included Genera.—*Cretacorantina* Mertin, 1941; *Eucozystes* Bell, 1863; *Heus* Bishop and Williams, 2000; *Notopocorystes* M'Coy, 1849.

Material Examined.—*Eucozystes broderipi* (Mantell, 1844), (BMNH) 21331, male, (BMNH) In. 61147, male, 61148-49, 29810-11; SM B30645, 30638, both females; *E. eichhorni* Bishop, 1983b, KSU D1180, cast of holotype SDSM 10007, KSU D1181, cast of paratype, SDSM 10010; *E. harveyi* (Woodward, 1896), KSU D1178, cast of GSC 5817; *E. platys* Schweitzer and Feldmann, 2001, KSU D 240, cast of GSC 124811, KSU D 373, cast of USNM 512163, holotype; *Notopocorystes stokesii* (Mantell, 1844), (BMNH) In. 30376, 61151, syntype, female; (BMNH) 39366, female; SM B30575, male, B30572.

Geologic Range.—Early Cretaceous (Albian) – Late Cretaceous (Maastrichtian).

Remarks.—Customarily considered members of Raninidae, paleocorystids have been recognized as distinctly different from the remainder of the genera within the family. Possession of a bifid rostrum; well developed carapace

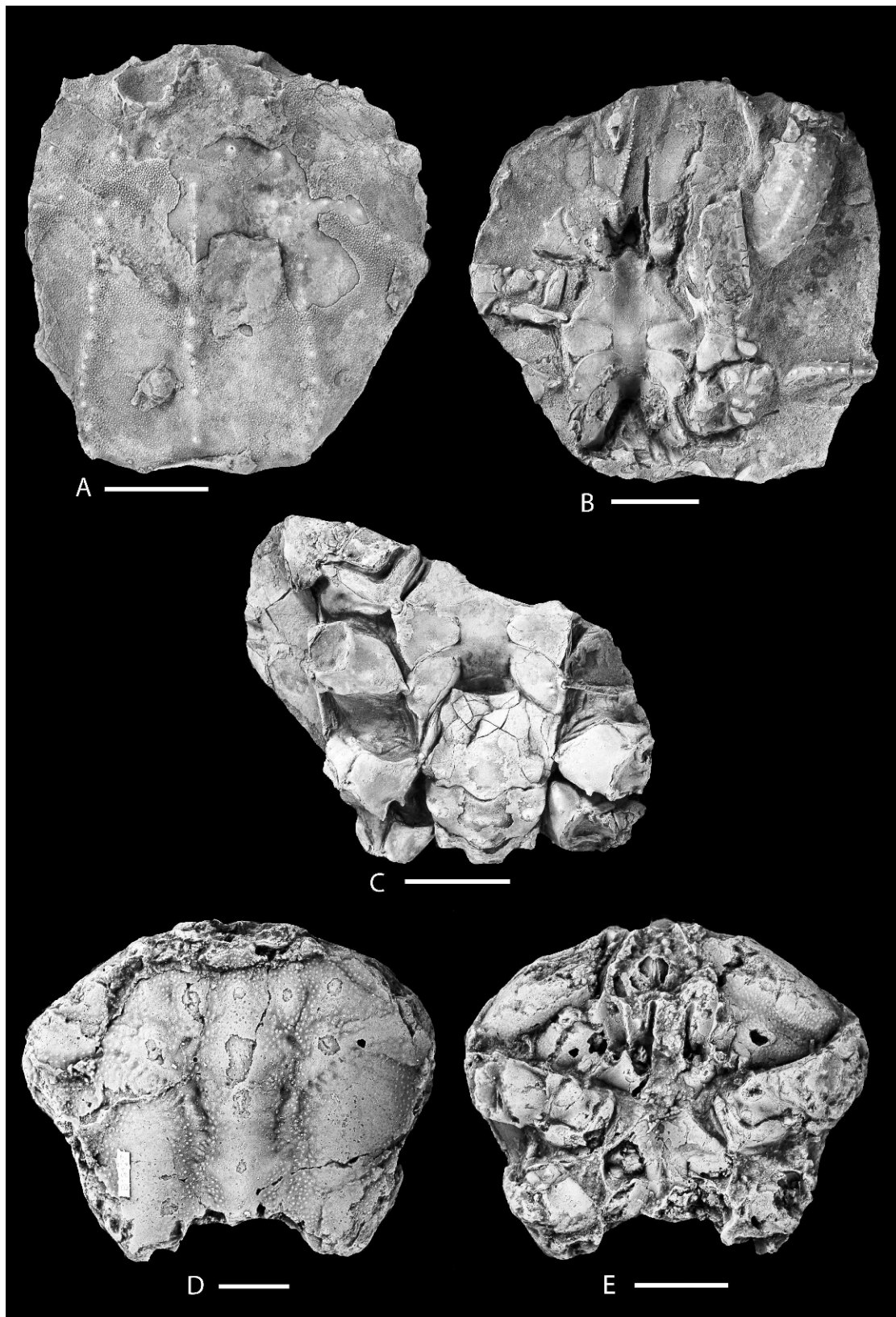


Fig. 9. Raninoidea, Cenomanocarcinidae. A-B, *Cenomanocarcinus vanstraeleni* Stenzel, 1945, UT 2191, syntype, dorsal carapace (A) and sternum; C, *Cenomanocarcinus vanstraeleni* Stenzel, 1945, UT 21090, syntype, sternum, pleon, and enormous coxae of pereiopods 4; D-E, *Campylostoma matutiforme* Bell, 1858, SM C 16127, poorly preserved specimen showing dorsal carapace (D) and ventral surface with anterior sternites (E). Scale bars = 1 cm.

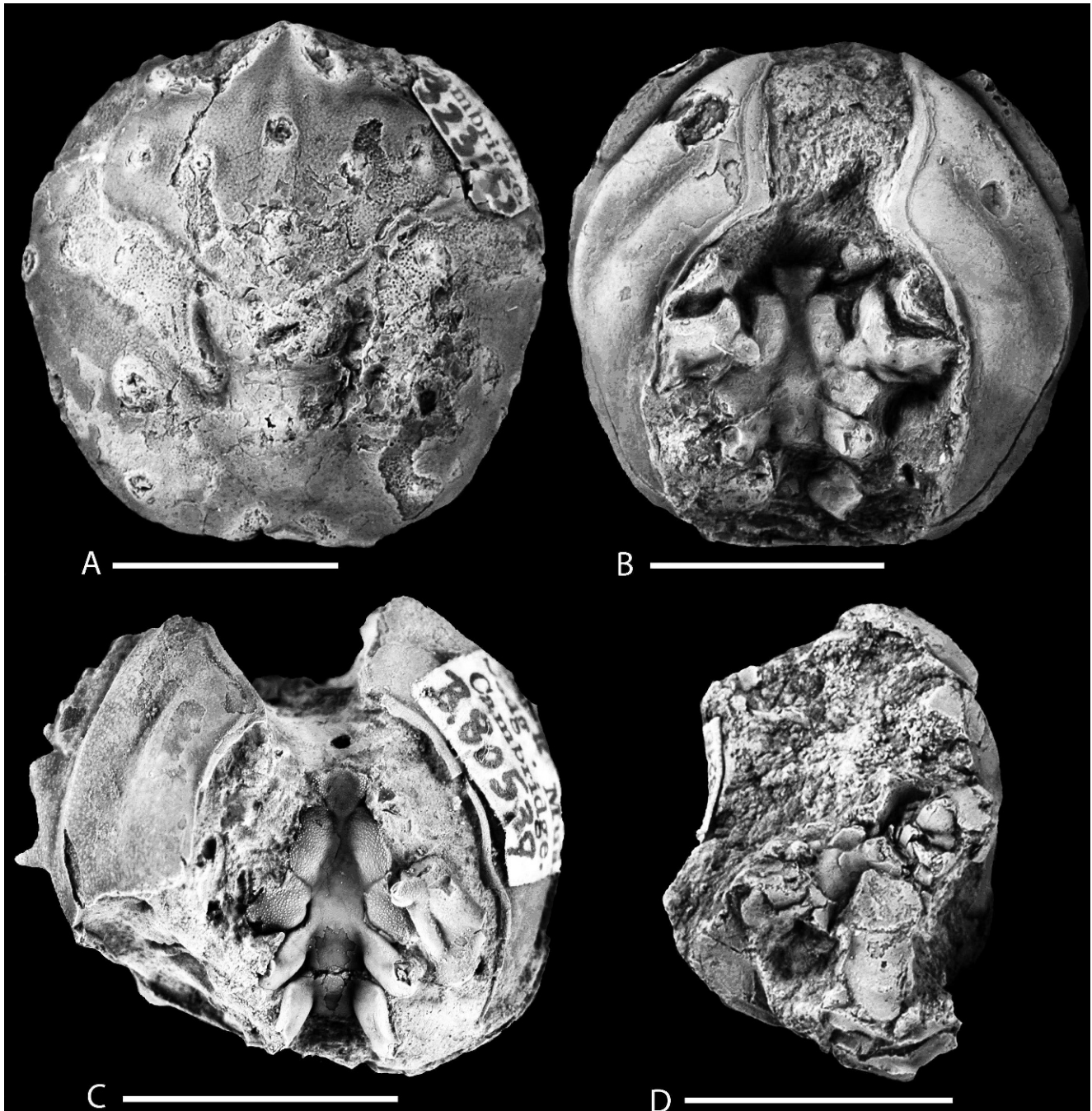


Fig. 10. Raninoidea, Necrocarcinidae, *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835). A-B, SM B 23152, dorsal carapace (A) and sternum (B); C, SM B 80539, excellently preserved sternum; D, SM B 23210, one of the few known pleons of the family. Scale bars = 1 cm.

grooves; and generally coarse ornamentation including straps, ridges, or tubercles readily separates the group from Raninidae as defined herein. On the ventral surface of the carapace, the buccal cavity is broad, rather than elongate and narrow as in Raninidae; and the posterior sternites are broad, as opposed to narrow as they are in raninids.

Raninidae De Haan, 1839

Diagnosis.—Carapace longer than wide; frontal margin short; rostrum typically triangular extending no farther

anteriorly than orbital spines; orbits defined by outer orbital spine, narrow, fissured; anterolateral and posterolateral margins usually distinct; posterior margin straight. Carapace regions indistinct. Buccal cavity elongate, narrow, completely closed by elongate maxilliped 3. Sternum narrow; sternites 1-3 fused, distinct ventrally; sternites 4 and 5 relatively broad; sternites 6-8 narrow, reduced; sutures 4-5, 5-6, and 6-7 complete; episternites 4 and 5 wide; spermatheca united. Pleonites visible dorsally, pleura reduced; male pleonites and telson not fused. Cheliped with carpus/propodus articulation nearly parallel to merus; fixed

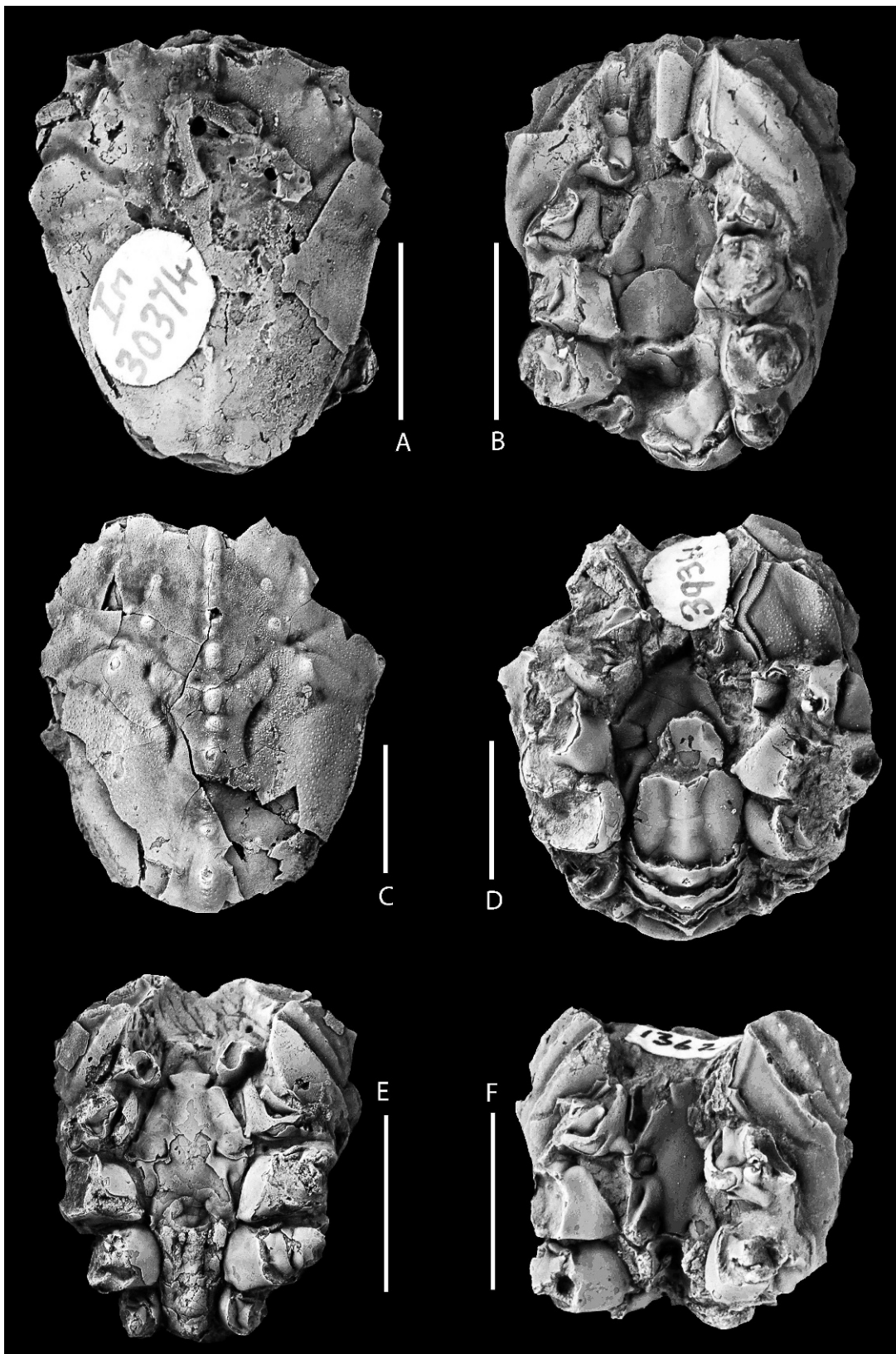


Fig. 11. Raninoidea, Palaeocorystidae. A-B, *Eucorystes broderipi* (Mantell, 1844), (BMNH) In. 30374, female, dorsal carapace (A) and ventral view of sternum and pleon (B); C-D *Notopocorystes stokesii* (Mantell, 1844), (BMNH) In. 39366, female, dorsal carapace (C) and pleon and sternum (D); E, *E. broderipi*, (BMNH) In. 30375, male sternum and pleon; F, *N. stokesii*, (BMNH) In. 61250, male sternum and pleon. Scale bars = 1 cm.

finger and dactylus at approximately right angle to manus. Pereiopods 2-4 with paddle-like dactyli; pereiopod 5 usually reduced, subdorsal.

Included genera.—*Araripecarcinus* Martins-Neto, 1987; *Bicornisranina* Nyborg and Fam, 2008; *Cenocorystes* Collins and Breton, 2009; *Cristafrons* Feldmann, Tshudy, and Thomson, 1993; *Cyrtorhina* Monod, 1956; *Erroranilia* Boyko, 2004; *Eumorphocorystes* Van Binkhorst, 1857; *Hemioon* Bell, 1863; *Lophoranina* Fabiani, 1910; *Lianira* Beschin, Busulini, De Angeli, Tessier, and Ungaro, 1991; *Lovarina* Beschin, Busulini, De Angeli, Tessier, and Ungaro, 1991; *Lyreidina* Fraaye and Van Bakel, 1998; *Lyreidus* De Haan, 1841; *Notopoides* Henderson, 1888; *Notopus* De Haan, 1841; *Notosceles* Bourne, 1922; *Ponotus* Karasawa and Ohara, 2009; *Quasilaeviranina* Tucker, 1998; *Ranidina* Bittner, 1893; *Raniliformis* Jagt, Collins, and Fraaye, 1993; *Ranilia* H. Milne Edwards, 1837 [in 1834-1840]; *Ranina* Lamarck, 1801; *Raninella* A. Milne-Edwards, 1862; *Raninoides* H. Milne Edwards, 1837 [in 1834-1840]; *Remyranina* Schweitzer and Feldmann, 2010f; *Rogueus* Berglund and Feldmann, 1989; *Macroacaena* Tucker, 1998; *Tribolocephalus* Ristori, 1886; *Umalia* Guinot, 1993.

Material Studied.—Specimens described and illustrated in Feldmann and Schweitzer (2007).

Geologic Range.—Early Cretaceous (Albian) – Recent.

Remarks.—Raninidae embraces a readily recognized group of brachyurans based upon the shape of the carapace, the distinctive conformation of the chelipeds, the extension of the pleon posteriorly, and the form of the sternum in which sternites 1-3 form a narrow crown, 4-5 are broad, and 6-8 are extremely narrow and reduced. In other regards, however, genera within the family are different enough that they are currently aligned into six subfamilies; one of which, Palaeocorystinae, is herein elevated to the level of family. Tucker (1998) elevated Symethinae to family rank, a position with which we concur.

Symethidae Goeke, 1981

Diagnosis.—Carapace elongate, ovoid; rostrum extended well beyond anterolateral margin; eyes very small; carapace anterior to cervical groove deeply pitted; buccal cavity elongate, narrow, completely closed by third maxilliped which lies in two planes; sternum with spermatheca well separated, hooded, otherwise as in Raninidae. 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.

Included Genus.—*Symethis* Weber, 1795.

Material Studied.—Specimen described and illustrated in Feldmann and Schweitzer (2007).

Geologic Range.—Recent.

Remarks.—Guinot (1993) retained Symethinae as a subfamily within Raninidae, although noting anecdotally that it might well be elevated to family rank, a position supported by De Grave et al. (2009). Schweitzer et al. (2010) recognized Symethidae as is recognized herein. The conformation of the carapace and pereiopods is markedly different from that of Raninidae sensu stricto although details of the sternum and pleon are similar in the two families. These latter characteristics place the Raninidae and Symethidae clade as the sister group to Palaeocorystidae.

Dakoticancroidea n. section

Diagnosis.—As for superfamily.

Included Superfamily.—Dakoticancroidea Rathbun, 1917.

Superfamily Dakoticancroidea Rathbun, 1917

Fig. 12

Diagnosis.—Carapace quadrate, as wide as long or longer than wide; rostrum narrow, bilobed; orbits well developed, rimmed; eyes sheltered by orbits when retracted; anterolateral margins entire; posterior margin nearly straight; medial part of cervical groove weakly developed; gastric regions poorly separated from cardiac and intestinal regions; branchiocardiac groove well developed; pleural sutures located on sides of carapace; genital openings on coxae, female on third and male on fifth pereiopods; fifth pereiopods reduced; sternum of female without longitudinal grooves; lateral portion of posterior part of sternites visible, coxae of pereiopods at same level as sternum; pair of spermatheca present in females; first pereiopods isochelous (in part after Rathbun, 1917, p. 385; Glaessner, 1969; Bishop, 1983c, p. 424; Bishop et al., 1998, p. 239).

Included Families.—Dakoticancridae Rathbun, 1917; Ibericancridae Artal et al., 2008.

Geologic Range.—Late Cretaceous (Campanian – Maastriichtian).

Remarks.—Our analysis arranged Ibericancridae and Dakoticancridae as sister groups that together are sister to the clade Cyclodorippoida and Eubrachyura. Artal et al. (2008) compared the two families and placed them in the same superfamily also. Despite this, there are several rather major differences between these two families. The shape of the sternum is considerably different. In Dakoticancridae, it is wide and remains wide to the posterior end of the carapace. The sternites are well developed, have episternites, and clearly resemble those of more derived Brachyura. The sterno-pleonal depression is shallow and broad, and *Dakoticancer* has a sterno-pleonal cavity in males. In Ibericancridae, the sternum is narrow and the sterno-pleonal depression is deep and steep-sided. The sternum remains narrow, but is visible laterally, to the posterior end of the carapace. In Ibericancridae, both pereiopods 4 and 5 are much reduced in size compared to the other pereiopods, whereas in Dakoticancridae, only pereiopod 5 is reduced in size. In other regards, the two

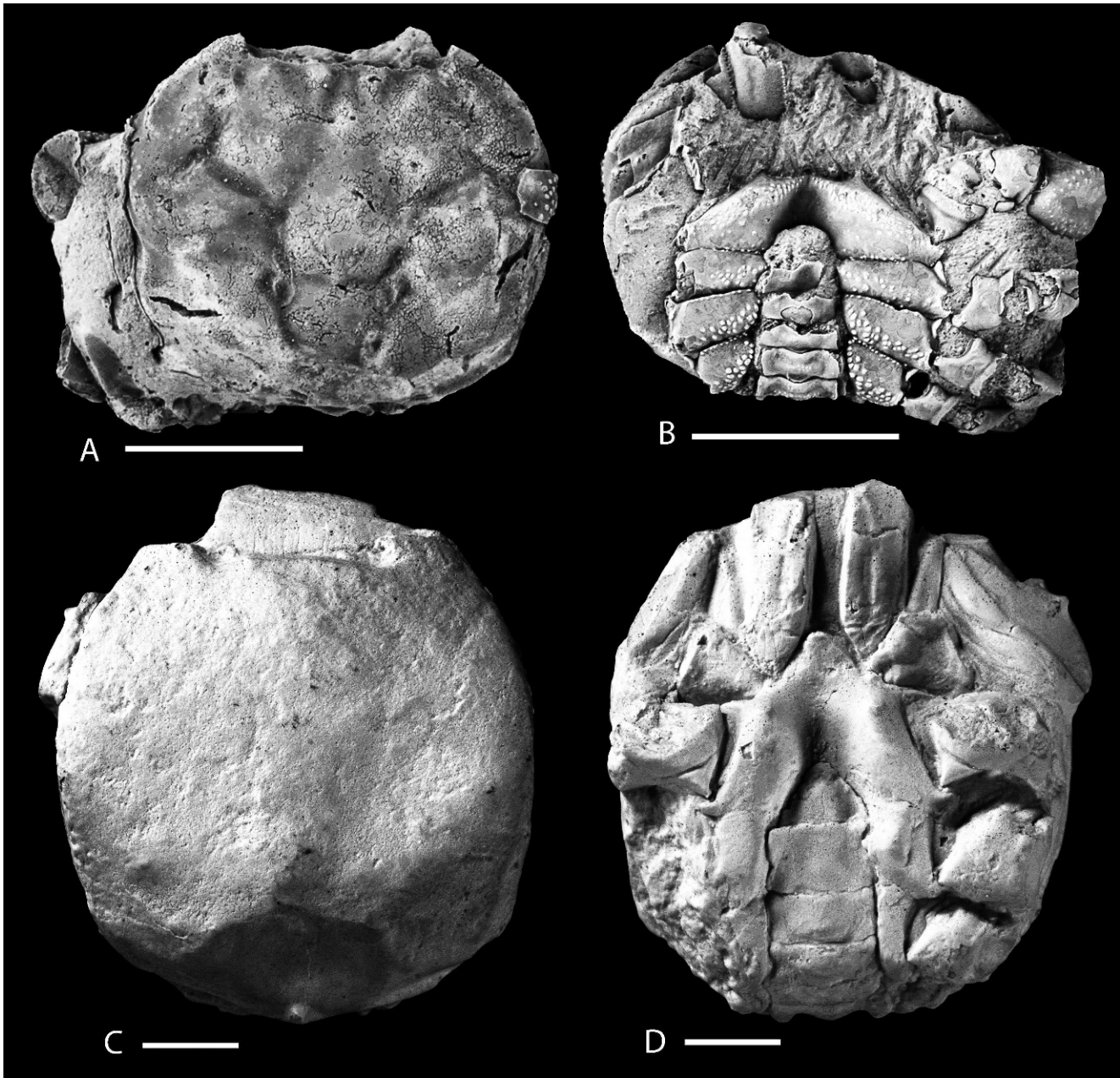


Fig. 12. Dakoticancroidea. A-B, Dakoticancridae, *Dakoticancer overanus* Rathbun, 1917, KSU D 907; C-D, Ibericancridae, *Ibericancer sanchoi* Artal et al., 2008, KSU D 446, cast of MGSB 68572, holotype. Scale bars = 1 cm.

families are similar to one another. As noted below, examination of other Cretaceous genera that are also rectangular and have narrow sterna may eventually indicate that Dakoticancroidea is a more diverse section than is recognized now. To date, few sterna are known for many of the North American genera, but as more material comes to light, this is changing. Dakoticancroidea may be much more robust than currently thought.

Dakoticancridae Rathbun, 1917

Diagnosis.—Carapace quadrate, as wide as long or longer than wide; rostrum narrow, bilobed; orbits well developed, rimmed; eyes sheltered by orbits when retracted; antero-

lateral margins entire; posterior margin nearly straight; medial part of cervical groove weakly developed; gastric regions poorly separated from cardiac and intestinal regions; branchiocardiac groove well developed; pleural sutures located on sides of carapace; genital openings on coxae, female on third and male on fifth pereopods; sternum broad, sternites visible to posterior of carapace, sternite 4 with ridge parallel to anterior end, sternites 5, 6, and 7 with granular transverse ridges, sometimes with sterno-pleonal cavity in males; sternum of female without longitudinal grooves; lateral portion of posterior part of sternites visible; male pleon with all somites free, lateral terminations on pleonites rectangular, telson rounded triangular; female pleon wide, with long epimeres, all

pleonites free; coxae of pereopods at same level as sternum; first pereopods isochelous; fifth pereopods very reduced, subdorsal.

Included Genera.—*Avitelmessus* Rathbun, 1923b; *Dakoticancer* Rathbun, 1917; *Tetracarcinus* Weller, 1905.

Geologic Range.—Late Cretaceous (Campanian – Maastriichtian).

Remarks.—Dakoticancridae traditionally includes rectangular, North American taxa with well-defined axial regions and transverse ridges on the branchial regions. Sterna and pleons are well described (Bishop et al., 1998; Artal et al., 2008), so that even though the sternum is wide and superficially appears heterotreme in nature, the genital openings are coxal in males and females. This mixture of primitive and derived characters is becoming more commonly observed and reported for Cretaceous Brachyura (Feldmann, Schweitzer, and Green, 2008).

Dakoticancer and *Avitelmessus* have very similar sternal, pleonal, and dorsal carapace features. *Tetracarcinus* and *Dakoticancer* are so similar dorsally that we considered synonymizing them. Thus, these three genera seem to form a natural group. However, examination of *Seorsus* Bishop, 1988a, suggests that it may be better placed within Ibericancridae.

The history of *Seorsus* is complicated. Bishop (1988a) described *Seorsus* from Maastriichtian rocks of Mississippi. Later, in 1992a, he described a new species, *Diaulax millerae*, from Campanian rocks of Delaware. Examination of specimens of *D. millerae*, the original descriptions of *Seorsus wadei*, and specimens of the type species of *Diaulax* suggest that *D. millerae* and *Seorsus wadei* are congeneric. Thus, we herein refer *D. millerae* to *Seorsus*, resulting in *Seorsus millerae* new combination. A well-preserved specimen of *S. millerae* under study by the authors has a preserved sternum and pleon. The sternum is narrow, but with well defined sternites and episternites and is visible posteriorly. Thus, we tentatively place *Seorsus* in Ibericancridae until further study can confirm the placement.

Ibericancridae Artal, Guinot, van Bakel, and Castillo, 2008

Diagnosis.—Carapace subrectangular; front broad, with inner-orbital projections; rostrum narrow, downturned, bilobed; orbits small, directed forward; branchiocardiac groove deep; sternum narrow, deep sterno-pleonal cavity, sternites 1-3 at lower level than other sternites, sternite 4 with blunt but marked projection, sternite 5 with pleonal locking mechanism, sternal sutures 4/5 through 7/8 interrupted; female gonopore on coxa of pereopod 3, male gonopore on coxa of pereopod 5, spermatheca of female at sternal suture 7/8; male pleon very narrow, all somites free, female pleon wider, all somites free; pereopods 4 and 5 much reduced in size compared to 1-3, possibly subdorsal.

Included Genera.—*Ibericancer* Artal et al., 2008; tentatively *Seorsus* Bishop, 1988a, and *Sodakus* Bishop, 1978.

Geologic Range.—Late Cretaceous (Campanian – Maastriichtian).

Remarks.—Artal et al. (2008) erected the family for specimens from the Campanian of Spain. There appears to be some variability in the specimens illustrated as belonging to the type and only species of the only genus of the family. There is variation in the fronto-orbital width-to-width ratio, and there seems to be some significant variation in ornamentation of the carapace and some aspects of the sternum. Evaluation of the nature of these variations must await examination of all of the illustrated material.

Comparison of the sternum of the holotype of *Ibericancer sanchoi* (MGSB 68572) with those of *Seorsus millerae* new combination and *Sodakus tatankayotankaensis* Bishop, 1978, reveals some similarities. All are relatively deep, narrow, and composed of distinct sternites with episternites. In *Sodakus*, the male pleon does not reach as far anteriorly as in *Ibericancer*, and the sterno-pleonal depression is not as deep. Thus, we tentatively refer *Sodakus* to Ibericancridae until type and other material can be more carefully examined, following Schweitzer and Feldmann (2011b). *Sodakus* had been referred to Dorippidae, to which it is clearly not referable, because members of Dorippidae have very wide sterna.

Section Cyclodorippoida Ah Yong et al., 2007

Diagnosis.—Carapace ovate to pentagonal; third maxillipeds elongate, covering buccal cavity, palp located at inner portion of merus; buccal cavity elongate; pereopods 2 and 3 long, slender; pereopods 4 and 5 much shorter, subdorsal to dorsal; sternum wide, with short but very deep and clear sternopleonal cavity in males; pleonal locking mechanism absent, pair of spermatheca present in females; genital openings coxal in males and females, pleon in males and females usually with some fusion of somites.

Geologic Range.—Early Cretaceous (Albian) – Recent.

Remarks.—The section is well defined by possession of a distinctive sterno-pleonal cavity which it shares with Eubrachyura. Most taxa are tiny and poorly calcified, at least Holocene ones, which may explain why the fossil record for the group is poor. At this time, *Hillius* is the oldest known member of the section, Early Cretaceous age (Albian). Other fossil occurrences of Cyclodorippoida are Eocene, from Hungary and Washington, USA (Müller and Collins, 1991; Schweitzer, 2001) as well as Miocene occurrences (Conkle et al., 2006, for summary).

Superfamily Cyclodorippoidea Ortmann, 1892

Diagnosis.—As for section.

Geologic Range.—Early Cretaceous (Albian) – Recent.

Cyclodorippidae Ortmann, 1892

Diagnosis.—Carapace ovate to pentagonal; orbits developed; buccal cavity rounded anteriorly, projecting beyond

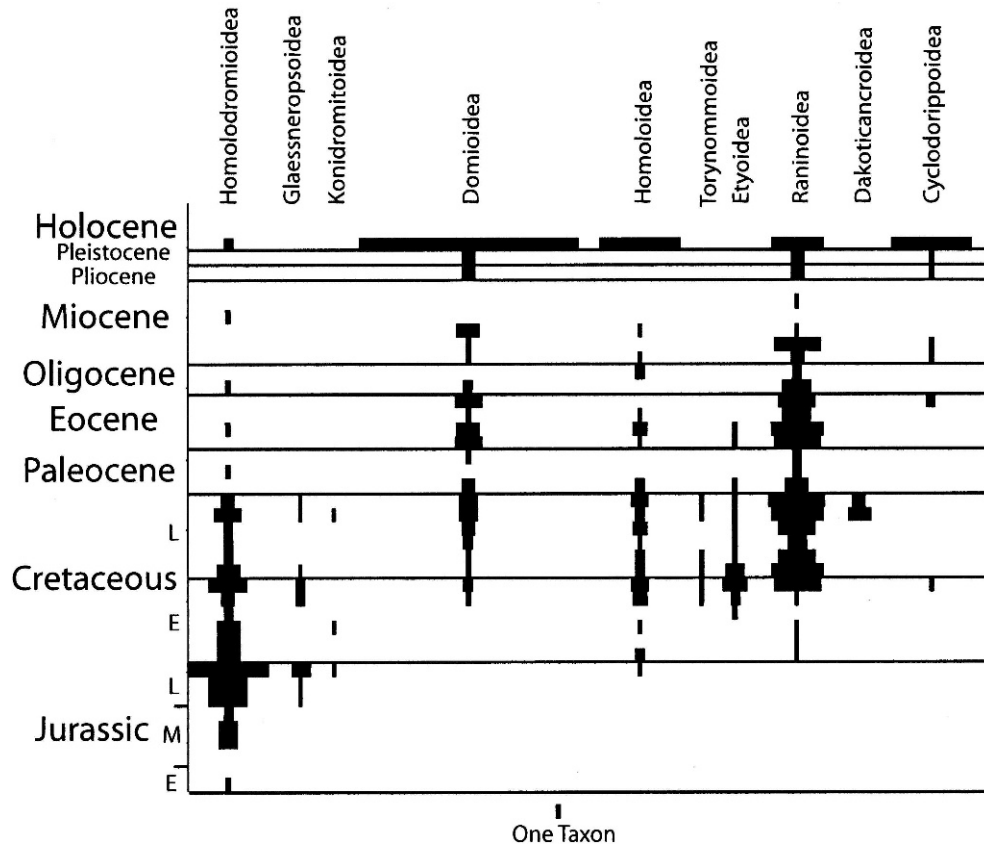


Fig. 13. Spindle diagram of generic occurrences within superfamilies referred to the sections of podotrematous Brachyura. Generic occurrences are tallied by occurrence of a genus within a stage. Where stage data was not known, for only about 10 percent of the data, the genus was assigned to the middle range of the epoch. Number of extant genera from Ng et al. (2008) and De Grave et al. (2010) and number of species from Schweitzer et al. (2010). Spindle diagram generated using PAST version 2.0 (Hammer et al., 2001). Note that spindles are arranged based upon number of stages per epoch and not based on length of time per stage, making the Cenozoic seem longer than the Mesozoic.

epistome; third maxillipeds triangular, covering buccal cavity; pereopods 2 and 3 long, slender; pereopods 4 and 5 much shorter, subdorsal to dorsal; sternum wide, with short but very deep and clear sterno-pleonal cavity; genital openings coxal in males and females, spermatheca at level of genital openings or anterior to them; pleon with some fusion of somites; flagellum of third maxilliped absent.

Included Fossil Genera.—*Hillius* Bishop, 1983a; *Tymolus* Stimpson, 1858b; *Xeinostoma* Stebbing, 1920.

Material Examined.—SDSNH 23643 (holotype), *Hillius youngi* Bishop, 1983a.

Geologic Range.—Early Cretaceous (Albian) – Recent.

Cymonomidae Bouvier, 1897

Diagnosis.—Carapace subquadrate; orbits poorly defined; usually with a rostrum projected beyond frontal margin and often with outer-ocular spines; third maxillipeds long, covering buccal cavity, flagellum present; pereopods 2 and 3 long; pereopods 4 and 5 reduced, subdorsal; genital openings coxal.

Included Fossil Genus.—*Cymonomus* A. Milne-Edwards, 1880.

Geologic Range.—Eocene (Priabonian) – Recent.

Phyllotymolinidae Tavares, 1998

Diagnosis.—Carapace subcircular; buccal cavity rectangular anteriorly, not protruding beyond epistome; third maxillipeds long, covering buccal cavity, merus subrectangular, flagellum present; pereopods 2 and 3 long; pereopods 4 and 5 reduced, subdorsal; genital openings coxal.

Included Fossil Genera.—None, only extant forms are known.

Section Eubrachyura de Saint Laurent, 1980

Diagnosis.—Female gonopores sternal on sternite 6; gonopores coxal or sternal in males; carapace variable in shape and ornamentation; orbits usually well-developed, protective of eye; epistome enclosing base of second antenna, sometimes fused to it; sternites visible even with pleon in place, composed of well-developed sternites separated by sutures that typically extend all the way to the axis or just short of the axis, third maxillipeds separated by sternum, episternites well developed, usually

all but sternite 8 visible and sometimes 8 visible as well; pleonites in males may show fusion, uropods not present in males or females, pleon typically carried so that it is not visible in dorsal view; carapace grooves reduced; pereopods typically not carried subdorsally (except Dorippidae).

Geologic Range.—Early Cretaceous (Albian) – Recent.

Remarks.—Eubrachyura embraces all Brachyura with female gonopores that are sternal. The group is morphologically varied and has a confirmed fossil record extending into at least the Albian (Feldmann, Schweitzer, and Green, 2008). For a list of all currently referred families, genera, and species, see Schweitzer et al. (2010).

DISCUSSION

Podotremata sensu lato is much more diverse than had previously been hypothesized. The various sections, and the superfamilies assigned to them, display a variety of diversity and survivorship patterns through the Mesozoic and Cenozoic (Fig. 13). Of the ten superfamilies now recognized as being podotrematous, six survived the Cretaceous/Paleogene boundary events and five are extant. One did not reach the end of the Cretaceous. All five extant families had origins in the Early Cretaceous. Examination of patterns of diversity and disparity in Decapoda is ongoing.

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