

## PHYLOGENY AND SYSTEMATICS OF EXTANT AND EXTINCT LOBSTERS

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### ABSTRACT

A phylogenetic analysis including representatives from 44 extinct and 27 extant families of lobsters (Polychelida, Achelata, Glypheidea, and Astacidea), resulted in the recognition of one new superfamily, Glaessnericarioidea, and three new families, Glaessnericariidae, Neoglypheidae, and Litogastroidae. Two families, Protastacidae and Stenochiridae, are elevated to superfamily status. A new classification of Glypheidea is proposed and currently known genera are rearranged based upon the phylogenetic analysis. Palaeopalaemonida is given a separate infraordinal status. Diagnoses for all infraorders, superfamilies, and families are provided.

**KEY WORDS:** Achelata, Astacidea, Decapoda, Glypheidea, Macrura, Palaeopalaemonida, Polychelida, Reptantia

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### INTRODUCTION

Lobsters comprise four decapod infraorders, Polychelida, Achelata, Glypheidea, and Astacidea. At present, lobsters are thought to contain nine extant and 17 fossil families (De Grave et al., 2009). Schweitzer et al. (2010) made lists of currently known fossil species, and Chan (2010) compiled extant species of marine lobsters. Most recently, Feldmann et al. (2012) added three new genera and new species based upon examination of material from the Triassic of China. Within recent works on mostly extant taxa, the higher-level relationships and internal relationships of several families were examined based upon morphological analyses (Scholtz and Richter, 1995; Dixon et al., 2003; Ah Yong and O'Meally, 2004) and molecular analysis (Crandall et al., 2000; Ah Yong and O'Meally, 2004; Porter et al., 2005; Tsang et al., 2008; Bracken et al., 2009; Toon et al., 2009; Boisselier-Dubayle et al., 2010; Yang et al., 2012, and others). Most recently, Bracken-Grissom et al. (in prep.) is working on the phylogeny of lobsters including most known extant genera by molecular analysis. However, the phylogeny of lobsters including fossil taxa has not yet been clear, and there have only been analyses including small numbers of fossil taxa or discrete superfamilies or infraorders (Tshudy and Babcock, 1997; Tshudy and Sorhannus, 2000a, b, 2003; Rode and Babcock, 2003; Amati et al., 2004; Schram and Dixon, 2004; Ah Yong, 2006, 2009; Tshudy et al., 2007; Astrop, 2011). Thus, we present the first comprehensive phylogeny of lobsters including extinct and extant representatives.

### MATERIALS AND METHODS

#### Materials

Representatives of 27 extant and 44 extinct genera were examined with representatives from nine extant and 16 extinct families of the lobster infraorders, Polychelida, Achelata, Glypheidea, and Astacidea (Table 1). Only one family, Tricarinidae, was excluded from the analysis because the single fossil exemplar is missing appendages and other portions of the morphology. Every genus including fossil marine lobsters for which relatively complete specimens are known was included in the analysis. The extinct glypheideans comprise 34 genera within six families (De Grave et al., 2009; Schweitzer et al., 2010; Feldmann et al., 2012). Among these, six erymoid and four glypheoid genera were excluded from the analysis because of their incomplete preservation. Sixteen extinct genera within eight families are currently known in the homaridan fossil record (De Grave et al., 2009; Schweitzer et al., 2010) and almost all of those genera were examined. The extinct astacids are represented by four genera within four families (De Grave et al., 2009; Schweitzer et al., 2010). *Cricoidoscelosus* of Cricoidoscelosidae, an extinct family was included. Polychelida consists of 12 extinct genera within five families (De Grave et al., 2009; Schweitzer et al., 2010). Ah Yong (2009) examined all extant and extinct genera within Polychelida and proposed a phylogeny; therefore, four genera were examined with representatives from four extinct families. The extinct achelatan comprise 11 genera within four families including two extinct families (De Grave et al., 2009; Schweitzer et al., 2010; Feldmann et al., 2012). *Cancrinus*, the sole member of the extinct family Cancrinidae, was used in the analysis to test the sister-group relationship of Palinuridae, Scyllaridae, and Cancrinidae.

In the case of extant marine lobsters, Chan (2010) recognized 55 genera; we examined 27 genera. All extant genera of Nephropidae, Enoplometopidae, and Glypheidea were included. For Achelata, exemplars for the various families were used, in part because we found that within the various families, genera coded the same or nearly the same in terms of the characters we used in the analysis. In Palinuridae, subfamilies are not used, so two representative genera were used as well as a member of the formerly recognized Synaxidae Bate, 1881 (7 genera initially coded at USNM). In the case of Scyllaridae, only a few extant taxa were used in the analysis representing

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Table 1. Taxa used in the analysis. Classification in this table is based on the traditional classification used previous to the revision proposed herein, that of De Grave et al. (2009) and Schweitzer et al. (2010). Selection of taxa was based upon the classification of these two references. † indicates extinct taxa.

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Infraorder Stenopodidea Bate, 1888  
 Family Stenopodoidea Claus, 1872  
 Genus *Stenopus* Latreille, 1819  
*S. hispidus* (Oliver, 1811): Holocene

Infraorder Glypheidea† Winkler, 1882  
 Superfamily Glypheoidea Winkler, 1882  
 Family Chimaerastacidae† Amati, Feldmann, and Zonneveld, 2004  
 Genus *Chimaerastacus*† Amati, Feldmann, and Zonneveld, 2004  
*C. paciflualis* Amati et al., 2004: Middle Triassic

Family Glypheidae† Winkler, 1882  
 Genus *Glyphea*† Von Meyer, 1835  
*G. regleyana* (Desmarest, 1822): Middle-Late Jurassic  
 Genus *Laurentaeglyphea* Forest, 2006  
*L. neocaledonica* (Richer de Forges, 2006): Holocene  
 Genus *Litogaster*† Von Meyer, 1847  
*L. obtusa* Von Meyer, 1847: Middle Triassic  
*L. ornata* Von Meyer, 1851: Middle Triassic  
*L. turnbullensis* Schram, 1971: Early Triassic  
 Genus *Neoglyphea* Forest and Saint Laurent, 1975  
*N. inopinata* Forest and Saint Laurent, 1975: Holocene  
 Genus *Paralitogaster*† Glaessner, 1969  
*P. durlachensis* (Förster, 1967): Early Triassic  
*P. limicola* (König, 1920): Middle Triassic  
 Genus *Squamosoglyphea*† Beurlen, 1930  
*S. dressieri* (Von Meyer, 1840a): Middle Jurassic-Late Jurassic  
 Genus *Trachysoma*† Bell, 1858  
*T. ornata* (Quenstedt, 1858): Middle-Late Jurassic  
*T. pustulosa* (Von Meyer, 1840a): Middle Jurassic  
*T. scabra* Bell, 1858: Eocene

Family Mecochiridae† Van Straelen, 1924 [imprint 1925]  
 Genus *Huhatanka*† Feldmann and West, 1978  
*H. kiowana* (Scott, 1970): Early Cretaceous  
*H. iranica* Yazdi et al., 2010: Early Cretaceous  
 Genus *Mecochirus*† Germar, 1827  
*M. longimanatus* (Schlotheim, 1822): Late Jurassic  
*M. rostratus* Collins and Rasmussen, 1992: Late Cretaceous  
 Genus *Meyeria*† McCoy, 1849  
*M. magna* McCoy, 1849: Early Cretaceous  
*M. ornata* (Phillips, 1829): Early Cretaceous  
*M. rapax* (Harbourt, 1905): Early Cretaceous  
 Genus *Pseudoglyphea*† Opper, 1861  
*P. ancylochelis* (Woodward, 1863): Early Jurassic  
*P. etallonii* Opper, 1862: Early Jurassic  
*P. foersteri* Feldmann et al., 2002: Early Jurassic  
*P. grandis* (Von Meyer, 1837): Early Jurassic  
 Genus *Selenisca*† Von Meyer, 1847  
*S. gratiosa* Von Meyer, 1847b: Late Jurassic

Family Pemphicidae† Van Straelen, 1928a  
 Genus *Pemphix*† Von Meyer, 1840a  
*P. sueurii* (Desmarest, 1822): Middle Triassic  
 Genus *Pseudopemphix*† Wüst, 1903  
*P. albertii* (Von Meyer, 1840a): Middle Triassic  
*P. fritschii* Wüst, 1903: Middle Triassic  
 Genus *Sinopemphix*† Fenglin, 1975  
*S. guizhouensis* Fenglin, 1975: Middle Triassic

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Table 1. (Continued.)

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Family Platychelidae† Glaessner, 1969  
 Genus *Glaessnericaris*† Garassino and Teruzzi, 1993  
*G. dubia* (Pinna, 1974): Late Triassic  
*G. macrochela* Garassino and Teruzzi, 1993: Late Triassic  
 Genus *Platycheila*† Glaessner, 1931  
*P. trauthi* Glaessner, 1931: Late Triassic

Superfamily Erymoidea† Van Straelen, 1924 [imprint 1925]  
 Family Erymidae† Van Straelen, 1924 [imprint 1925]  
 Genus *Clytiopsis*† Bill, 1914  
*C. argentoratensis* Bill, 1914 (type): Early-Middle Triassic  
*C. audax* (Von Meyer, 1834): Early-Middle Triassic  
 Genus *Enoploclytia*† McCoy, 1849  
*E. leachii* (Mantell, 1822): Late Cretaceous  
 Genus *Eryma*† Von Meyer, 1840b  
*E. bedeltum* (Quenstedt, 1857): Late Jurassic  
*E. modestiforme* (Schlotheim, 1822): Late Jurassic  
 Genus *Galicia*† Garassino and Krobicki, 2002  
*G. marianae* Garassino and Krobicki, 2002: Late Jurassic  
*G. veltheimi* (Münster, 1839): Late Jurassic  
 Genus *Lissocardia*† Von Meyer, 1851a  
*L. magna* Von Meyer, 1851a: Middle Triassic  
*L. silesiaca* Von Meyer, 1851a: Middle Triassic  
 Genus *Palaeastacus*† Bell, 1850  
*P. fuciformis* (Schlotheim, 1822): Late Jurassic  
*P. sussexiensis* (Mantell, 1833): Late Cretaceous  
 Genus *Pustulina*† Quenstedt, 1857  
*P. minuta* (Schlotheim, 1822): Late Jurassic  
*P. suevica* Quenstedt, 1857: Late Jurassic

Infraorder Astacidea Latreille, 1802  
 Superfamily Palaeopalaemonoidea Brooks, 1962  
 Family Palaeopalaemonidae† Brooks, 1962  
 Genus *Palaeopalaemon*† Whitfield, 1880  
*P. newberryi* Whitfield, 1880 (type): Late Devonian-Mississippian

Superfamily Enoplometopoidea de Saint Laurent, 1988  
 Family Enoplometopidae de Saint Laurent, 1988  
 Genus *Enoplometopus* A. Milne-Edwards, 1862  
*E. occidentalis* (Randall, 1840): Holocene

Family Uncinidae† Beurlen, 1930a  
 Genus *Malmuncina*† Schweigert and Garassino, 2003  
*M. wulfi* Schweigert and Garassino, 2003: Late Jurassic  
 Genus *Uncina*† Quenstedt, 1850  
*U. posidoniae* Quenstedt, 1850: Early Jurassic

Superfamily Nephropoidea Dana, 1852a  
 Family Chilenophoberidae† Tshudy and Babcock, 1997  
 Genus *Chilenophoberus*† Chong and Förster, 1976  
*C. atacamensis* Chong and Förster, 1976: Jurassic  
 Genus *Palaeophoberus*† Glaessner, 1932b  
*P. suevicus* (Quenstedt, 1867): Middle Jurassic  
 Genus *Pseudastacus*† Opper, 1861  
*P. pustulosus* (Münster, 1839): Late Jurassic  
 Genus *Tillocheles*† Woods, 1957  
*T. kaoriae* Yokoi and Karasawa, 2000: Late Cretaceous  
*T. shannonae* Woods, 1957: Early Cretaceous

Family Protastacidae† Albrecht, 1983  
 Genus *Protastacus*† Albrecht, 1983  
*P. antiquus* (Harbort, 1905): Early Cretaceous  
*P. politus* (Schlüter in Schlüter and Von der Marck, 1868): Early Cretaceous

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Table 1. (Continued.)

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Family Stenochiridae<sup>†</sup> Beurlen, 1928a  
 Genus *Stenochirus*<sup>†</sup> Oppel, 1861a  
*S. angustus* (Münster, 1839): Late Jurassic  
*S. mayeri* Oppel, 1862 (type): Late Jurassic  
*S. vahldieki* Schweigert, Garassino and Riou, 2006: Middle Jurassic

Family Nephropidae<sup>†</sup> Dana, 1852a  
 Genus *Acanthacaris* Bate, 1888  
*A. caeca* A. Milne-Edwards, 1881: Holocene  
*A. tenuimana* Bate, 1888: Holocene  
 Genus *Eunephrops* Smith, 1885  
*E. bairdii* Smith, 1885: Holocene  
 Genus *Homarinus* Kornfield, Williams and Steneck, 1995  
*H. capensis* (Herbst, 1792): Holocene  
 Genus *Homarus* Weber, 1795  
*H. americanus* H. Milne Edwards, 1837: Pleistocene-Holocene  
*H. gammarus* (Linnaeus, 1758): Holocene  
 Genus *Hoplopatria*<sup>†</sup> McCoy, 1849  
*H. longimana* (Sowerby, 1826): Early-Late Cretaceous  
 Genus *Jagtia*<sup>†</sup> Tshudy and Sorhannus, 2000  
*J. kunradensis* Tshudy and Sorhannus, 2000: Late Cretaceous  
 Genus *Metanephrops* Jenkins, 1972  
*M. japonicus* (Tapparone-Caneferi, 1873): Holocene  
 Genus *Nephropoides* Manning, 1969  
*N. caribaeus* Manning, 1969: Holocene  
 Genus *Nephrops* Leach, 1814  
*N. norvegicus* (Linnaeus, 1758): Holocene  
 Genus *Nephropsis* Wood-Mason, 1873  
*N. carpenteri* Wood-Mason, 1885: Holocene  
*N. stewarti* Wood-Mason, 1873: Holocene  
 Genus *Palaeonephrops*<sup>†</sup> Mertin, 1941  
*P. browni* (Whitfield, 1907): Late Cretaceous  
 Genus *Paraclithia*<sup>†</sup> Fritsch, 1877  
*P. nephropica* Fritsch, 1877: Late Cretaceous  
*P. nephropiformis* (Schlüter, 1862): Late Cretaceous  
*P. westfalica* (Mertin, 1941): Late Cretaceous  
 Genus *Thymops* Holthuis, 1974  
*T. birsteini* (Zarenkov and Semenov, 1972): Holocene  
 Genus *Thymopsis* Holthuis, 1974  
*T. nilenta* Holthuis, 1974: Holocene  
 Genus *Thymopoides* Burukovsky and Averin, 1977  
*T. grobovi* (Burukovsky and Averin, 1976): Holocene

Family Thaumastochelidae Bate, 1888  
 Genus *Oncopareia*<sup>†</sup> Bosquet, 1854  
*O. bredai* Bosquet, 1854: Late Cretaceous  
*O. coesfeldiensis* (Schlüter, 1862): Late Cretaceous  
 Genus *Thaumastocheles* Wood-Mason, 1874  
*T. japonicus* Calman, 1913: Holocene  
 Genus *Thaumastochelopsis* Bruce, 1988  
*T. wardi* Bate, 1888: Holocene  
 Genus *Dinochelus* Ah Yong et al., 2010  
*D. ausbeli* Ah Yong et al., 2010: Holocene

Superfamily Astacoidea Latreille, 1802  
 Family Astacidae Latreille, 1802  
 Genus *Astacus* Fabricius, 1775  
*A. astacus* (Linnaeus, 1775): Holocene

Family Cambaridae Hobbs, 1942  
 Genus *Cambarus* Erichson, 1846  
*C. bartonii* (Fabricius, 1798): Holocene  
 Genus *Procambarus* Ortmann, 1905  
*P. clarkii* (Girard, 1852): Holocene

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Table 1. (Continued.)

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Family Cricoidoscelosidae<sup>†</sup> Taylor, Schram and Yan-Bin, 1999  
 Genus *Cricoidoscelosus*<sup>†</sup> Taylor, Schram and Yan-Bin, 1999  
*C. aethus* Taylor, Schram and Yan-Bin, 1999: Early Cretaceous

Superfamily Parastacoidea Huxley, 1879  
 Family Parastacidae Huxley, 1879  
 Genus *Cherax* Erichson, 1846  
*C. albidus* Clark, 1936: Holocene  
 Genus *Parastacus* Huxley, 1879  
*P. pugnax* (Poeppig, 1836): Holocene

Infraorder Polychelida Scholtz and Richter, 1995  
 Superfamily Eryonoidea De Haan, 1841  
 Family Eryonidae<sup>†</sup> De Haan, 1841  
 Genus *Eryon*<sup>†</sup> Desmarest, 1822  
*E. arciformis* Schlotheim, 1822: Late Jurassic

Family Coleiidae<sup>†</sup> Van Straelen, 1924 [imprint 1925]  
 Genus *Coleia*<sup>†</sup> Broderip, 1835  
*C. antiqua* Broderip, 1835: Early Jurassic  
*C. uzume* Karasawa et al., 2003: Late Triassic

Family Palaeopentachelidae<sup>†</sup> Ah Yong, 2009  
 Genus *Palaeopentacheles*<sup>†</sup> Von Knebel, 1907  
*P. roettenbacheri* (Münster, 1839): Late Jurassic

Family Polychelidae<sup>†</sup> Wood-Mason, 1875  
 Genus *Polycheles* Heller, 1862  
*P. typhos* Heller, 1862: Holocene

Family Tetrachelidae<sup>†</sup> Beurlen, 1930a  
 Genus *Tetrachela*<sup>†</sup> Reuss, 1858  
*T. raiblana* Bronn, 1858: Late Triassic

Infraorder Achelata Scholtz and Richter, 1995  
 Superfamily Palinuroidea Latreille, 1802  
 Family Cancrinidae<sup>†</sup> Beurlen, 1930a  
 Genus *Cancrinus*<sup>†</sup> Münster, 1839  
*C. claviger* Münster, 1839: Late Jurassic

Family Palinuridae Latreille, 1802  
 Genus *Palibythus* Davie, 1990  
*P. magnificus* Davie, 1990: Holocene  
 Genus *Palinurus* Weber, 1795  
*P. elephas* (Fabricius, 1787): Holocene  
 Genus *Panulirus* White, 1847a  
*P. japonicus* (Von Siebold, 1824): Holocene

Family Scyllaridae Latreille, 1825  
 Genus *Ibacus* Leach, 1815  
*I. cliatus* (Von Siebold, 1824): Holocene  
 Genus *Scyllarus* Fabricius, 1775  
*S. arctus* (Linnaeus, 1758): Holocene

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two of four subfamilies (all subfamilies were initially coded at USNM, 8 genera). Polychelida is represented by one extant genus in the analysis because the included genera coded similar to one another, but five of six extant genera were examined at USNM. For Astacida, with 30 genera (Gherardi et al., 2011), representative extant genera were used for each family.

The analyses were based upon the examination of material deposited in the following institutions: BAS, British Antarctic Survey, Cambridge, United Kingdom; BMNH, The Natural History Museum, London; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie München (Munich), Germany; CIRGEO, Centro de Investigaciones en Recursos Geológicos, Buenos Aires, Argentina; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; GBA, Geologische Bundesanstalt, Vienna, Austria; GSC, Geological Survey of Canada, Eastern Paleontology, Division, Ottawa, Ontario, Canada; IRB IG, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KSU D, Kent State University Decapod Comparative Collection; LPI, Invertebrate Pale-

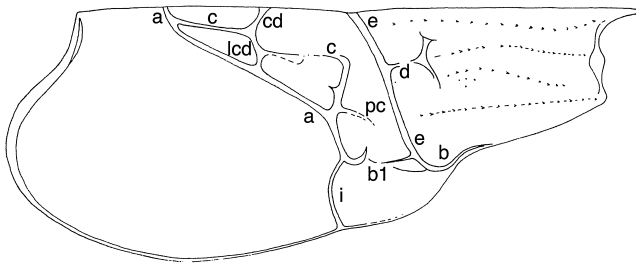


Fig. 1. Glypheidea grooves. Illustration based upon Förster and Matyja (1986). a-a, branchiocardiac groove; b, antennal groove; b1, hepatic groove; c-c, postcervical groove; cd, cardiac groove; d, gastro-orbital groove; e-e, cervical groove; i, inferior groove; lcd, laterocardiac groove; pc, parapostcervical groove (= second intercervical groove of Feldmann et al., 1993, Fig. 3.6).

ontology Collection, Chengdu Institute of Geology and Mineral Resources, Chengdu, Sichuan Province, China; MAFI, Földani Intézet (Hungarian Geological Survey), Budapest, Hungary; MB.A., Museum für Naturkunde Berlin, Paläontologisches Museum, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MFM, Mizunami Fossil Museum, Japan; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MSNB, Museo di Scienze Naturali di Bergamo, Italy; MSNM, Museo Civico di Storia Naturale di Milano, Italy; NHMW, Naturhistorisches Museum Wien (Natural History Museum of Vienna), Austria; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China; NM, Národní Muzeum, Prague, Czech Republic; OU, Department of Geology, Otago University, Dunedin, New Zealand; PE, Field Museum of Natural History, Chicago, Illinois, USA; QMF, Queensland Museum, Queensland, Australia; RGM, Rijks Geologische-Mineralogisch Museum, now the Nationaal Natuurhistorisch Museum, Naturalis, Leiden, Netherlands; RTM, Royal Tyrrell Museum, Drumheller, Alberta, Canada; SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Department of Paleontology and Historical Geology, Frankfurt, Germany; SMMP, Science Museum of Minneapolis, St. Paul, Minnesota, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TRUIPR, Thompson River University Invertebrate Paleontology Repository, Kamloops, British Columbia, Canada; UI, University of Iowa Paleontology Repository, Iowa City, Iowa, USA; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC; UT, University of Texas at Austin, Texas, USA.

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

The genera were selected for the analysis based upon the familial arrangement of De Grave et al. (2009) and Schweitzer et al. (2010). The present analysis examined the taxa of lobster infraorders as the in-group taxa based upon the monophyly of the lobster infraorders shown by molecular analyses (Tsang et al., 2008; Toon et al., 2009; Boisselier-Dubayle et al., 2010). The sister group of the in-group taxa has been identified as Stenopodidea (Scholtz and Richter, 1995; Dixon et al., 2003; Ah Yong and O'Meally, 2004; Schram and Dixon, 2004; Bracken et al., 2009). Therefore, the in-group was rooted to *Stenopus hispidus* (Stenopodidea).

#### Characters

Ninety adult morphological characters were used in the analysis (Table 2). The data matrix is provided in Table 3. Those characters were mainly chosen based upon examination of previous works (Holthuis, 1974; Scholtz and Richter, 1995; Tshudy and Babcock, 1997; Dixon et al., 2003; Ah Yong and O'Meally, 2004; Amati et al., 2004; Schram and Dixon, 2004; Ah Yong, 2006; Ah Yong, 2009). Some new names for groove patterns in Glypheidea that are significant in the analysis are provided here for ease of reference (Fig. 1). Seventy-four characters were binary; sixteen characters were multistate characters. The missing data were scored as unknown. The rate of missing data within the examined fossil taxa ranged from 11.1 to 55.6 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.

#### Phylogenetic Analysis

Two analyses were conducted. Analysis A included only extant taxa. Analysis B included both extinct and extant taxa to examine the impact of extinct taxa on the topology of the 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, unscanned, and equally weighted. Relative stability of clades was assessed using bootstrap (Felsenstein, 1985) and decay analyses (Bremer, 1994). Bootstrapping was realized in PAUP\* based upon 1,000 pseudoreplicates. The Bremer support was obtained using constraint trees generated in MacClade 4.08 for OSX (Maddison and Maddison, 2005) and analyzed using PAUP\*.

#### RESULTS AND DISCUSSION

Analysis A yielded a single most-parsimonious tree, 171 steps long with a consistency index (CI) of 0.5848, a retention index (RI) of 0.8207, and a rescaled consistency index (RC) of 0.4799. The single most-parsimonious tree indicating Bremer support is given in Fig. 2. Analysis B yielded 15 most-parsimonious trees, 292 steps long with a consistency index (CI) of 0.4075, a retention index (RI) of 0.8363, and a rescaled consistency index (RC) of 0.3408. A strict consensus tree is given in Fig. 3 and fifty percent majority consensus tree of 15 trees is shown in Fig. 4. The relationships among the groups indicating Bremer support, bootstrap support exceeding 50 percent, and majority-rule consensus support excluding 100 percent are given in Fig. 4. Character state changes of analysis B are given in Fig. 5 and unambiguous character state changes for each number are shown in Table 4.

#### Higher-level Relationships

There have been several hypotheses concerning the internal relationships at the infraordinal levels within the reptant Decapoda. These hypotheses including only extant groups have been examined based upon morphological analyses (Scholtz and Richter, 1995; Dixon et al., 2003; Ah Yong and O'Meally, 2004) and molecular analyses (Ah Yong and O'Meally, 2004; Porter et al., 2005; Tsang et al., 2008; Bracken et al., 2009; Toon et al., 2009; Boisselier-Dubayle et al., 2010). Analysis A including only extant taxa (Fig. 2) strongly supports the higher-level relationships of Ah Yong and O'Meally (2004) and Bracken-Grissom et al. (in prep.). Polychelida is the most basal, followed by Achelata, Glypheidea, and the most advanced Astacidea.

Our analysis B (Figs. 2-4) contains extant and extinct taxa. The topologies from analyses A and B were largely matched. However, a *Palaeopalaemon* – Polychelida – (Achelata + Astacura) relationship is not resolved. Schram et al. (1978) suggested that *Palaeopalaemon* belonged to the suborder Pleocyemata Burkenrod, 1963, and had affinities with glypheoids and astacideans. Later, Schram and Dixon (2004) gave *Palaeopalaemonida* a new rank, sister to Eurysteralia Dixon et al., 2003, sensu stricto, containing Achelata, Anomura, and Brachyura. De Grave et al.

Table 2. Characters used in the phylogenetic analysis and their states. Characters 17, 24, 28, 29, and 31 are illustrated in Fig. 1.

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1. Carapace: subcylindrical (0), cylindrical (1), dorsoventrally depressed (2)
2. Cephalic ridges: absent (0), present (1)
3. Median Suture of carapace: absent (0), present (1)
4. Intercalated plate of axis of anterior carapace: absent (0), present (1)
5. Cephalic median carina: absent (0), present (1)
6. Cephalic carina or ridges: smooth (0), strongly ornamented with spines or tubercles (1)
7. Thoracic median carina: absent (0), present (1)
8. Thoracic median carina: smooth (0), strongly ornamented with spines (1)
9. Antennal carina: absent (0), present (1)
10. Suborbital carina: absent (0), present (1)
11. Supraorbital carina: absent (0), present (1)
12. Subdorsal carina: absent (0), present (1)
13. Intermediate carina: absent (0), present (1)
14. Branchial carina: absent (0), present (1)
15. Lateral carina: absent (0), present (1)
16. Antennal groove: absent (0), present (1)
17. Gastro-orbital groove: absent (0), present, long (1), present, short, anteriorly bifurcated (2)
18. Cervical groove: long, extending to dorsomedian (0), short, not extending to dorsomedian (1), indistinct (2)
19. Postcervical groove: absent (0), present (1)
20. Postcervical groove, if present: parallel to branchiocardiac groove (0), not parallel to branchiocardiac groove (1)
21. Postcervical groove, if present: originating near dorsomedian (0), originating on dorsomedian (1)
22. Postcervical groove, if present: not reaching cervical groove (0), reaching hepatic groove (1), reaching hepatic groove posteriorly by convex arc (2), reaching cervical groove (3)
23. Postcervical groove, if present: not reaching branchiocardiac groove by groove (0), reaching branchiocardiac groove by groove (1)
24. Intercervical groove: absent (0), present (1)
25. Branchiocardiac groove: present (0), absent or indistinct (1)
26. Branchiocardiac groove angle: gentle, at < 30 degrees to dorsal surface (0), steep, > 30 degrees dorsal surface (1), indistinct (2)
27. Branchiocardiac groove on dorsal thoracic region: joining median suture (0), concave arc (1), indistinct (2)
28. Laterocardiac groove: absent (0), present (1)
29. Parapostcervical groove: absent (0), present (1)
30. Urogastric groove: absent (0), present (1)
31. Parabranchial groove: absent (0), present (1)
32. Inferior groove: absent (0), present (1)
33. Hepatic groove: absent (0), present (1)
34. Omega swelling: weak or absent (0), well defined by grooves (1)
35. Chi swelling: weak or absent (0), well defined by grooves (1)
36. W-shaped groove pattern: absent (0), present (1)
37. Postorbital spine: absent (0), present (1)
38. Antennal spine: absent (0), present (1)
39. Rostrum: simple (0), bifid (1), indistinct (2)
40. Simple rostrum: absent or short (0), well developed (1)
41. Marginal rostral spines: absent (0), present (1)
42. Orbital incision: absent (0), present (1)
43. Cervical incision: absent (0), present (1)
44. Postcervical incision: absent (0), present (1)
45. Lateral margin of carapace: not defined (0), defined (1)
46. Lateral margin of epistome and carapace: not in broad contact (0), in broad contact or fused (1)
47. P1 chelate: dactylus terminal (0), pseudo or subchelate (1), chelate (2)
48. P2 chelate: dactylus terminal (0), pseudo or subchelate (1), chelate (2)
49. P3 chelate: dactylus terminal (0), pseudo or subchelate (1), chelate (2)
50. P4 chelate: dactylus terminal (0), pseudo or subchelate (1), chelate (2)
51. P5 chelate: dactylus terminal (0), chelate (1)
52. P1 type: isochelous (0), heterochelous (1)
53. P1 form: normal (0), bulbous palm with pectinate claws (1)
54. P1 size: not greatly inflated (0), greatly inflated (1)
55. P1 propodus length: normal (0), distinctly elongate (1)
56. P1 dactylus orientation: horizontal or oblique (0), vertical (1)
57. P1 ischial process: absent (0), distinct (1)
58. P1 ischium-merus articulation: oblique (0), vertical (1)
59. P1 basis and ischium: articulate (0), fused (1)
60. Pereiopods ischium hook: absent (0), present (1)
61. Shape of pleuron: rounded (0), rectangular (1), triangular (2)
62. Sharp demarcation between pleonal terga and pleura: absent (0), present (1)

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Table 2. (Continued.)

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63. Pleonal axial keel: absent (0), present (1)
64. Somite 2 pleuron: same size and shape as somite 3 (0), larger than somite 3 (1)
65. Pleonic hinges: lateral (0), mid-lateral (1)
66. Telson: triangular (0), rectangular (1)
67. Telson posterolateral spine: absent (0), present (1)
68. Telson: without diaeresis (0), with incomplete diaeresis (1), with complete diaeresis (2)
69. Telson: calcified distally (0), weakly calcified distally (1), uncalcified and flexible distally (2)
70. Uropod exopod: calcified distally (0), weakly calcified distally (1), uncalcified and flexible distally (2)
71. Uropod exopod diaeresis: absent (0), present (1)
72. Uropod exopod diaeresis: margin not spinose (0), margin spinose (1)
73. Uropod endopod: equal to exopod (0), reduced (1)
74. Second antenna: long, flagellate (0), stout, flagellate (1), modified (2)
75. Second antenna flagellum: elongate (0), short (1), shovel-like (2)
76. Second antenna peduncle: short (0), elongate (1)
77. Scaphocerite: present (0), absent (1)
78. Antennal plate: absent (0), present (1)
79. Antennular stylocerite: present (0), absent (1)
80. Eye: present (0), reduced (1), absent (2)
81. Maxilliped 3 dactylus apex: sharp (0), blunt (1)
82. Maxilliped 3 exopod: present (0), reduced (1)
83. Maxilliped 2 exopod: present (0), reduced (1)
84. Crista dentata: absent (0), present (1)
85. Mandible molar process: weak (0), trapezoidal (1)
86. Sternum: narrow (0), wide (1)
87. Fusion between thoracic sternites 7 and 8: fused (0), articulate (1)
88. Male pleopod 1: present (0), absent (1)
89. Annulus ventralis: absent (0), present (1)
90. Male pleopod 2 endopod: normal (0), with spiral element (1)

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(2009) and Schweitzer et al. (2010) included the superfamily Palaeopalaemonoidea in Astacidea. Most recently, Wahle et al. (2012) reviewed and diagnosed all families within Astacidea and Glypheidea, but they did not recognize Palaeopalaemonidae as an astacidean family. However, the analysis does not support its status as a superfamily within Astacidea and suggests a basal position and separate infraordinal status of Palaeopalaemonida.

Polychelida (clade 1) [clade numbers throughout the following discussion are indicated on Fig. 5].—The monophyly of Polychelida, with Bremer value of 5, is well supported by eight synapomorphies, a dorsoventrally depressed carapace (1-2), the presence of a branchial carina (14-1), the absence of the antennal groove (16-0), an indistinct rostrum (39-2), a well defined lateral margin (45-1), pereopod 5 with a chela (50-2), presence of sharp demarcations between the pleonal terga and pleura (62-1), and presence of a pleonal keel (63-1). Among these, the absence of the antennal groove (16-0) is a unique synapomorphy. Additionally, the extant Polychelida have a characteristic synapomorphy, the eryoneicus larva (Scholtz and Richter, 1995). Although Amati et al. (2004), Tsang et al. (2008), Toon et al. (2009), Boisselier-Dubayle et al. (2010), and Lavalli and Spanier (2011) showed that Polychelida and Achelata were sister taxa, our result supports a more basal position of Polychelida and the sister group relationship of Polychelida and Achelata + (Glypheidea + Astacidea), suggested by Scholtz and Richter (1995), Ah Yong and O'Meally (2004), and Bracken-Grissom et al. (in prep.).

Ah Yong (2009) first examined the phylogeny of Polychelida including extant and extinct genera based upon the morphology-based cladistic analysis. He selected the earliest-known Tetrachelidae as the out-group within Polychelida and indicated that Eryonidae is the most basal, followed by Palaeopentachelidae, and the advanced Coleiidae and Polychelidae. However, our result yields another scheme. The polychelidan clade consists of two major clades. The Tetrachelidae + (Coleiidae + Polychelidae) clade (clade 2) is weakly defined by only one character, the presence of the suborbital carina (10-1), whilst the Eryonidae + Palaeopentachelidae clade (clade 4), with Bremer support of 3, is strongly supported by six synapomorphies, the absence of the cephalic median carina (5-0), and indistinct cervical, postcervical, and branchiocardiac grooves (18-2, 19-0, 25-1, 26-2, 27-2), one (25-1) of which is unique.

Achelata (clade 6).—Scholtz and Richter (1995) demonstrated that Achelata is a well defined monophyletic group. Nine synapomorphies (47-0, 48-0, 49-0, 54-0, 69-2, 70-2, 77-1, 78-1, 86-1) unite Achelata with Bremer Support of 7. Among these characters, the telson and uropodal exopods, which are uncalcified and flexible distally (69-2, 70-2), possession of the antennal plate (78-1), and a wide thoracic sternum (86-1), are unique and never reversed. An additional important character for Achelata is the phyllosoma larvae (Gurney, 1942; Scholtz and Richter, 1995).

Achelata (clade 6) is derived as sister to Glypheidea + Astacidea clade (clade 5). These three infraorders share seven characters, absence of the cephalic and thoracic median carinae (5-0, 7-0), fused lateral margin of the

Table 3. Data matrix used in the analysis.

<i>Stenopus</i>	0000111100	000001000-	--00011000	0000000001	1000002220
	0000000000	0000000000	0000000000	0000000000	
<i>Polycheles</i>	2000101001	0001000111	1300011000	0000000020	0111102222
	10010?0000	0110000000	0000000001	0110000000	
* <i>Coleia</i>	2000101001	0001000111	1300011000	0000000010	01111?2222
	10010?00?0	2110000000	01000000?0	??0?0?????	
* <i>Tetrachela</i>	2000101001	0001000011	1300010000	0000000020	0?111?2222
	00010????0	2110?10000	?10000?0??	????0?????	
* <i>Palaeopentacheles</i>	2000001000	000100020-	--00122000	0000000010	00001?2222
	10010?00?0	2110000000	00000000?0	??0?0?????	
* <i>Eryon</i>	2000001000	000100020-	--00122000	0000000020	00111?2222
	00010?00?0	2110000000	00000000?0	??0?0?????	
<i>Palinurus</i>	1000000010	0100011111	1300011000	0000000110	0000010000
	0000000010	2000010022	0001001110	1001010000	
<i>Panulirus</i>	1000000010	0100011111	1300011000	0000000110	0000010000
	0000000010	2000010022	0001001110	1001010000	
<i>Palibythus</i>	1000000010	0000011111	1300011000	0000000100	1000010000
	0000000010	2000010022	0001001110	1001010000	
* <i>Cancrinus</i>	1000000000	0000010111	1300011000	0000000020	00000?0000
	00000000?0	2000010022	00021011?0	?????1?????	
<i>Ibacus</i>	2000101000	1001010111	1300011000	0000000020	0010110000
	0000000010	2010010022	0002201110	1001010000	
<i>Scyllarus</i>	2000101000	1001010111	1300011000	0000000020	0010110000
	0000000010	2010010022	0002201110	1001010000	
* <i>Palaeopalaemon</i>	1000101010	0000111010	1300010000	0000000000	0?000?2111
	10010?????	2000000000	000?0000??	????0?????	
<i>Astacus</i>	0000000001	0000010111	1300011000	0000000001	0000012220
	0001011110	2001111211	1100000010	1001101001	
<i>Procambarus</i>	0000000001	0000010111	1300011000	0000000001	0000012220
	0001011111	2001111211	1100000010	1001101011	
<i>Cambarus</i>	0000000001	0000010111	1300011000	0000000001	0000012220
	0001011111	2001111211	1100000010	1001101011	
<i>Parastacus</i>	0000000001	0000010111	1300011000	0000000001	0000012220
	0001011110	2001111111	1100000010	1001101100	
<i>Cherax</i>	0000000001	0000010111	1300011000	0000000001	0000012220
	0001011110	2001111111	1100000010	1001101100	
* <i>Protastacus</i>	0000000001	0000010111	1300011000	0000000001	1?000?2????
	?001?????0	2001?11111	11000000??	????0?????	
* <i>Cricoidoscelosus</i>	0000000001	0000010111	1300011000	0000000001	00000?2220
	00010??1?0	2001?11211	11000000?0	????0?01?	
<i>Enoplometopus</i>	0000110000	1100010111	1300122000	0000000101	1000002111
	0001011010	2001111000	1100000010	1001100000	
* <i>Uncina</i>	0010110000	1100010111	1300122000	0000000101	10000?2221
	00010??0?0	1001?00000	11000000?0	????0?????	
* <i>Malmuncina</i>	0010110000	1100010111	1300122000	0000000101	10000?2221
	00010??0?0	1001?00000	11000000?0	????0?????	
* <i>Stenochirus</i>	0000101000	10000110??	?000011000	0?10000001	10000?2220
	00010????0	2001?1?000	11000000?0	????0?????	
* <i>Pseudastacus</i>	0000100000	1000011011	0300011000	0110000001	10000?2220
	00010????0	2001?1?200	11000000?0	????0?????	
* <i>Tillocheles</i>	0000111001	1100011011	0300011000	0110000001	10000?2???
	?0010?10?0	2001?1?000	11000?00?0	????0?????	
* <i>Chilenophoberus</i>	0000111000	1000011011	0300011000	0110000???	?0000?????
	???????????	???????????	???????????	???????????	
* <i>Palaeophoberus</i>	0000111000	1100011011	0300011000	0110000?01	1?000?222?
	?0010??0?0	2001?1?000	11?????????	???????????	
<i>Dinochelus</i>	0000000000	0000011111	1100011000	0010010101	1000012220
	1111011010	1100110000	1110000011	1001100000	
<i>Thymopides</i>	0010000010	1000011111	1100011000	0010011101	1000002220
	0001011010	2111111000	1100000010	1001100000	
<i>Nephrops</i>	0000111111	1110111111	1101011000	0110011101	1000002220
	0101011010	2101111000	1100000010	1001100000	
<i>Metanephrops</i>	0000111111	1011111111	1100011000	0110011101	1000002220
	0001011010	2101111000	1100000010	1001100000	

Table 3. (Continued.)

<i>Homarus</i>	0010000010	1000011111	1101011001	0010011101	1000002220
	0101011010	2101111000	1100000010	1001100000	
<i>Homarinus</i>	0010000010	1000011111	1101011001	0010011101	1000002220
	0101011010	2101111000	1100000010	1001100000	
* <i>Hoploparia</i>	0010000010	1100011111	1101011000	0010011101	10000?2220
	01010????0	2101?11000	11000000?0	????1?0?????	
* <i>Palaeonephrops</i>	0000111111	1110011111	1101011000	0111011101	10000?2220
	01010????0	2111?11000	11000000?0	?????0?????	
* <i>Paraclythia</i>	0000111111	1111111111	1101011000	0111011101	10000?2220
	01010????0	2111?1?000	11000000?0	?????0?????	
<i>Neoglyphea</i>	0110110011	1000010011	0200010000	0110000001	0000011110
	0001100000	1100110000	1100010010	1001101000	
<i>Laurentaeglyphea</i>	0110110011	1000010011	0200010000	0110000001	0000011110
	0001000000	2100110000	1100010010	1001101000	
* <i>Glyphea</i>	01101010011	10000120101	0200000110	0110000001	0000011110
	00010?00?0	2100?10000	11000100?0	1??1?0?????	
* <i>Trachysoma</i>	0110100011	10000100101	0200000100	0110000001	0000011110
	00010??????	2100?10000	11000100?0	????1?0?????	
* <i>Squamosoglyphea</i>	011010100011	10000120101	0200000110	0110000001	00000?1100
	00010??????	2100?10000	11000100?0	?????0?????	
* <i>Selenisca</i>	0110110011	1000010010	0200011000	0????00001	0?000?1100
	00010??????	2100?10000	11000100??	?????0?????	
* <i>Huhatanka</i>	0100100011	100001000-	--00011000	0010000001	0?000?0000
	00010??????	1100?10000	110???00??	?????0?????	
* <i>Mecochirus</i>	0100110011	1000010010	0200011000	0010000001	01000011100
	00011?00?0	2100?10000	11000100?0	1??1?0?????	
* <i>Meyeria</i>	0100110011	1000010010	0200011000	0010000001	01000011100
	00011?00?0	2100?10000	11000100?0	1??1?0?????	
* <i>Pseudoglyphea</i>	0110110011	1000011010	0200000000	0110000001	10000?1110
	00010??????	2100?10000	11000000?0	?????0?????	
* <i>Chimaerastacus</i>	0110100011	1000010010	0000000000	0110100001	00000?2220
	00010??????	2100?10000	11000000?0	?????0?????	
* <i>Litogaster</i>	0110100011	1000011010	0200000000	0110000001	00000?111?
	?0010??????	2100?10000	110?0000?0	?????0?????	
* <i>Paralitogaster</i>	0110111111	1000011010	0200000000	0110000001	10000?1111
	00010??0?0	2100?10000	11000000?0	?????0?????	
* <i>Clytiopsis</i>	0010000010	1000010010	0000000000	0110000101	00000?2220
	00010??0??	1100?10000	11000000?0	?????0?????	
* <i>Lissocardia</i>	0110110001	1000011010	0100000000	0110100001	10000?2221
	00010??????	2100?10000	11000000?0	?????0?????	
* <i>Glaessnericaris</i>	0010000000	00000?0011	0000000000	0000000101	10000?2222
	00010??0?0	2000?11000	11000000?0	?????0?????	
* <i>Platychela</i>	0000000000	0000010010	0200000000	0????00101	0?000?2220
	00010??????	1000?10000	11000000??	?????0?????	
* <i>Eryma</i>	0011000000	00000110101	0010000000	0111100101	1000012221
	00010?00?0	2100?10000	11000000?0	1??110?????	
* <i>Galicia</i>	0011000000	0000011011	0010000000	0110000101	10000?2221
	00010??????	2100?10000	11000000?0	????1?0?????	
* <i>Enoploclytia</i>	0011000000	0000011011	0010000000	0111100101	10000?2221
	00010?00?0	2100?10000	11000000?0	????1?0?????	
* <i>Palaeastacus</i>	0011000000	0000011010	0000000000	0110000101	10000?2221
	00010?00?0	2100?10000	11000000?0	????1?0?????	

carapace and epistome (46-1), a rectangular telson (66-1), absence of the antennular stylocerite (79-1), a blunt dactylus apex of maxilliped 3 (Scholtz and Richter, 1995) (81-1), and the presence of the crista dentata (84-1), three (79-1, 81-1, 84-1) of which are unique synapomorphies.

Recent molecular studies showed Achelata consisting of two major lineages, Palinuridae and Scyllaridae (Palero et al., 2009). Palero et al. (2009), Tsang et al. (2009), Yang et al. (2011), and Bracken-Grissom et al. (in prep.) provided

hypotheses concerning the internal relationships within both families. The present analysis including the extinct Cancrinidae also demonstrates that Achelata comprises two major groups, the palinurid and cancrinid + scyllarid clades. Two characters, the presence of the antennal carina (9-1) and the presence of gastro-orbital groove (17) unite Palinuridae (clade 7). An indistinct rostrum (39-2) weakly defines Cancrinidae + Scyllaridae clade (clade 9). The monophyly of Scyllaridae, with Bremer Support of 4, is strongly supported



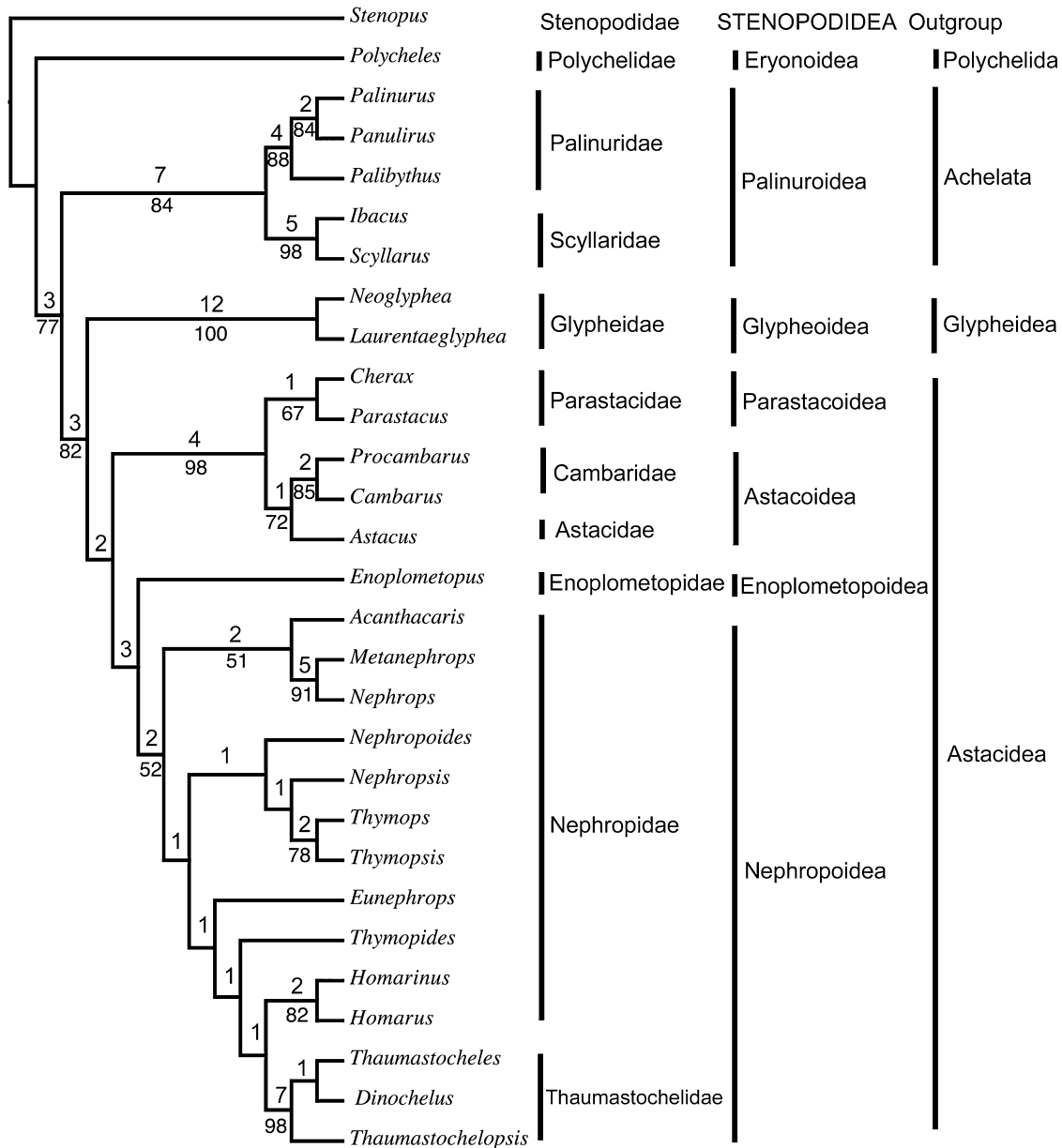


Fig. 2. Single most parsimonious tree recovered from Analysis A; including only extant taxa (TL = 171 steps, CI = 0.5848, RI = 0.8207, RC = 0.4799). Bremer support for major branches indicated. Superfamilies and sections recognized previous to this work are indicated.

by eight characters: a dorso-ventrally depressed carapace (1-2), the presence of a median carina on the cephalic and thoracic regions (5-1, 7-1), the presence of the supraorbital and branchial carinae (11-1, 14-1), the presence of the cervical incision (43-1), a well-defined lateral margin of the carapace (45-1), and the presence of the pleonal axial keel (63-1). The analysis shows the sister group relationship between Cancrinidae and Scyllaridae. Beurlen (1930b) erected Cancrinidae with the sole genus *Cancrinus*. Later, Balss (1957) and George and Main (1967) regarded *Cancrinus* as a genus of Palinuridae, while Glaessner (1969) placed it within its own family, Cancrinidae. Garassino and Schweigert (2006) followed Glaessner's opinion. Most recently, Haug et al. (2009) examined the post-larval morphology of *Cancrinus* and other scyllarids from the Jurassic of Germany and rec-

ognized the sister-group relationship of *Cancrinus* and scyllarids. They included *Cancrinus* in Scyllaridae sensu lato. However, our result shows that Cancrinidae is a valid family, because Scyllaridae is a well-defined family defined by many characters not shared by Cancrinidae.

Glypheidea (clade 12).—Dixon et al. (2003), Schram and Dixon (2004), Ahyong and O'Meally (2004), and Bracken-Grissom et al. (in prep.) showed that Glypheidea was sister to Astacidea. However, Dixon et al. (2003) and Schram and Dixon (2004) did not recognize it as an infraorder and assigned Glypheoidea and Astacidea to Astacura Borradaile, 1907. In contrast, Bracken et al. (2009) demonstrated the sister group relationship between Glypheidea and Achelata. Most recently, Boisselier-Dubayle et al. (2010)

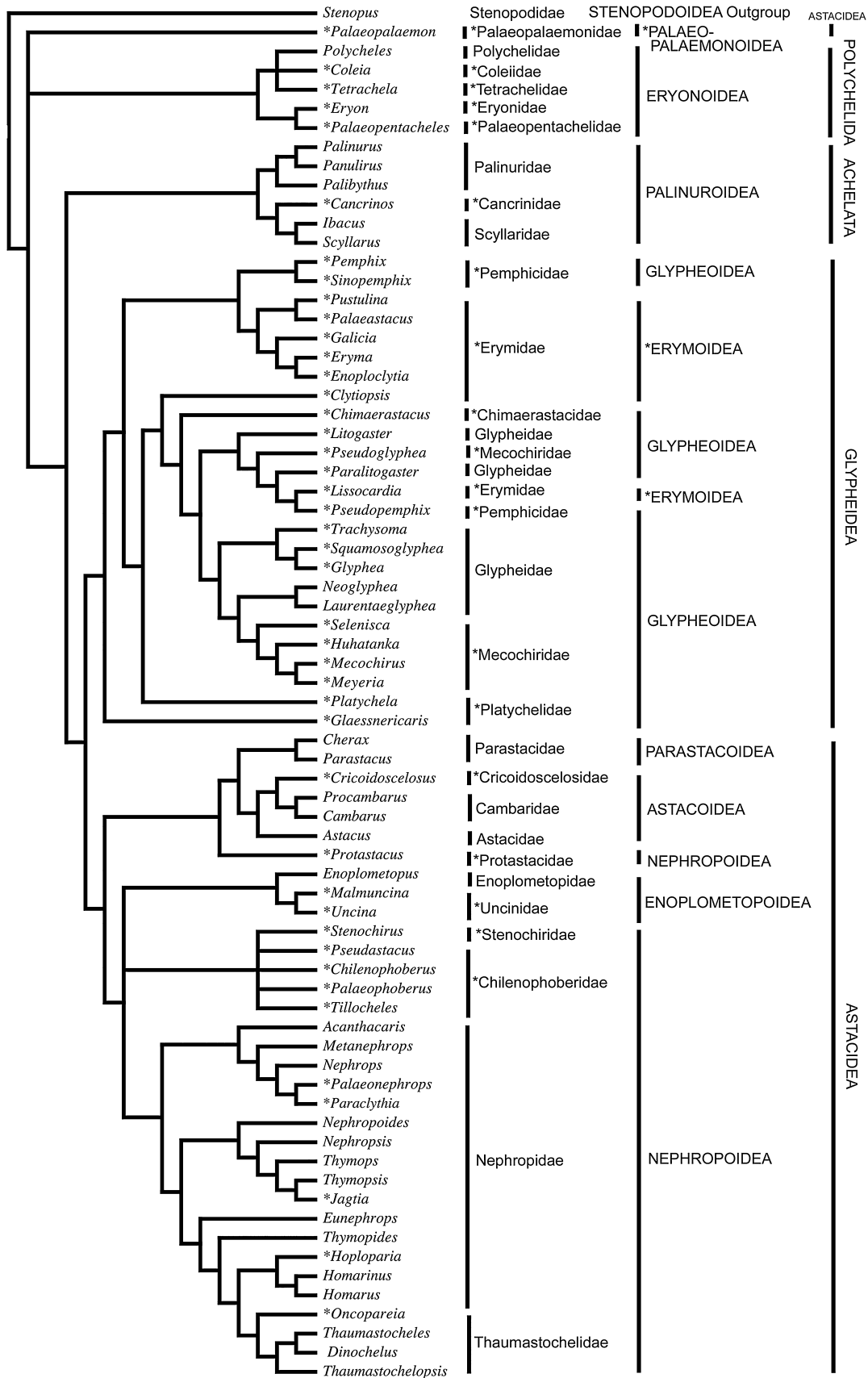


Fig. 3. Strict consensus tree of 15 most parsimonious trees recovered from Analysis B; including extinct and extant taxa (TL = 292 steps, CI = 0.4075, RI = 0.8363, RC = 0.3408). Superfamilies and sections recognized previous to this work are indicated.

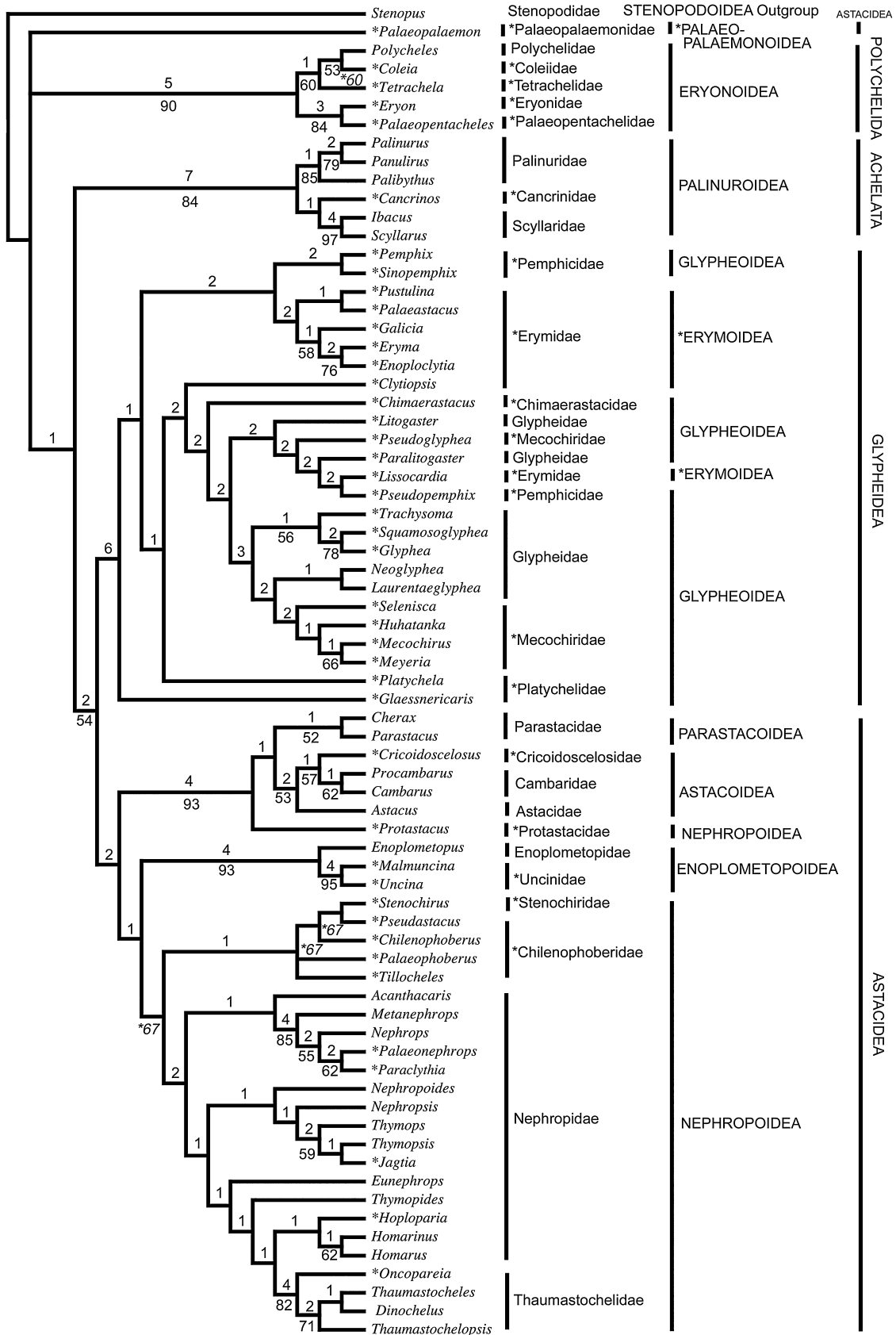


Fig. 4. Fifty percent majority rule consensus tree of 15 trees recovered from Analysis B; indicating Bremer Support (above each branch), bootstrap support exceeding 50 percent (below each branch) and majority-rule consensus support excluding 100 percent (asterisk plus italics below branch). Superfamilies and sections recognized previous to this work are indicated.

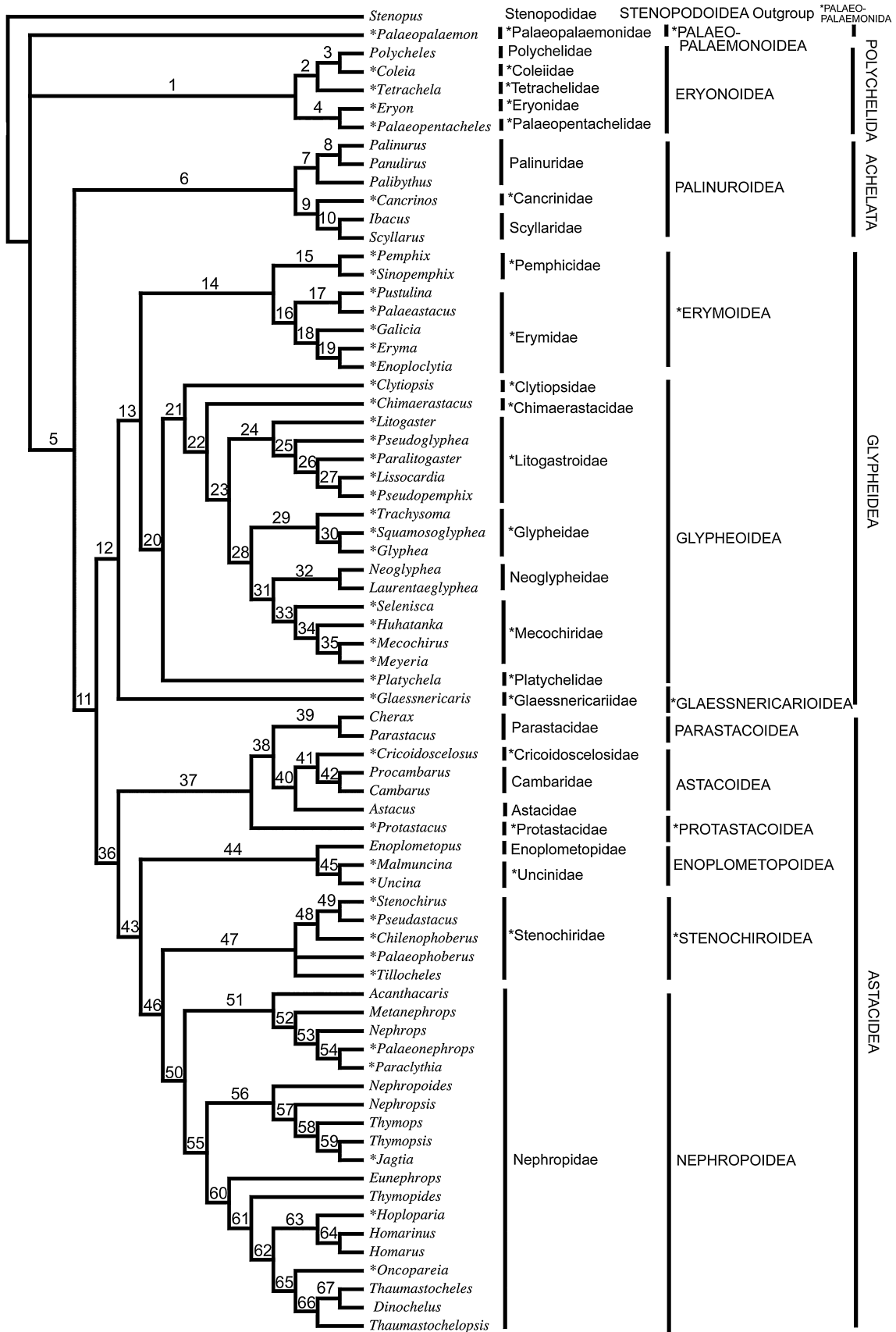


Fig. 5. Fifty percent majority rule consensus tree of 15 trees recovered from Analysis B; indicating character state changes, detailed in Table 4. Superfamilies and sections of proposed classification herein are indicated on this tree.

Table 4. Clade numbers as mapped onto Fig. 5 with their unambiguous character state changes for each number.

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1 (Polychelida). 1: 0/1->2, 14: 0->1, 16: 1->0, 39: 0->2, 45: 0->1, 50: 0->2, 62: 0->1, 63: 0->1
2 (Polychelidae + Coleiidae + Tetrachelidae). 10: 0->1
3 (Polychelidae + Coleiidae). 18: 0->1, 51: 0->1
4 (Eryonidae + Palaeopentachelidae). 5: 1->0, 18: 0->2, 19: 1->0, 25: 0->1, 26: 1->2, 27: 1->2
5 (Achelata + Glypheidea + Astacidea). 5: 1->0, 7: 1->0, 46: 0->1, 66: 0->1, 79: 0->1, 81: 0->1, 84: 0->1
6 (Achelata). 47: 2->0, 48: 2->0, 49: 2->0, 54: 1->0, 69: 0->2, 70: 0->2, 77: 0->1, 78: 0->1, 86: 0->1
7 (Palinuridae). 9: 0->1, 17: 0->1
8 ( <i>Palinurus</i> + <i>Panulirus</i> ). 12: 0->1, 39: 0->1
9 (Cancrinidae + Scyllaridae). 39: 0->2
10 (Scyllaridae). 1: 1->2, 5: 0->1, 7: 0->1, 11: 0->1, 14: 0->1, 43: 0->1, 45: 0->1, 63: 0->1
11 (Glypheidea + Astacidea). 40: 0->1, 41: 0->1, 65: 0->1, 71: 0->1, 72: 0->1, 85: 0->1
12 (Glypheidea). 3: 0->1, 21: 1->0, 22: 3->0, 26: 1->0, 27: 1->0
13 (Erymoidea + Glypheoidea). 32: 0->1, 33: 0->1
14 (Erymoidea). 17: 0->1, 50: 0->1
15 (Pemphicidae). 1: 0->1, 9: 0->1
16 (Erymidae). 4: 0->1, 62: 0->1
17 ( <i>Pustulina</i> + <i>Palaeastacus</i> ). 20: 1->0
18 ( <i>Galicia</i> + <i>Eryma</i> + <i>Enoploclytia</i> ). 23: 0->1
19 ( <i>Eryma</i> + <i>Enoploclytia</i> ). 34: 0->1, 35: 0->1
20 (Glypheoidea). 20: 1->0, 41: 1->0
21 (Clytiopsidae + Chimaerastacidae + Litogastroidae + Glypheidae + Neoglypheidae + Mecochiridae). 9: 0->1, 11: 0->1, 62: 0->1
22 (Chimaerastacidae + Litogastroidae + Glypheidae + Neoglypheidae + Mecochiridae). 2: 0->1, 5: 0->1, 10: 0->1, 38: 1->0
23 (Litogastroidae + Glypheidae + Neoglypheidae + Mecochiridae). 22: 0->2, 47: 2->1, 48: 2->1, 49: 2->1
24 (Litogastroidae). 17: 0->1
25 ( <i>Pseudoglyphe</i> + <i>Paralitogaster</i> + <i>Lissocardia</i> + <i>Pseudopemphix</i> ). 6: 0->1, 41: 0->1
26 ( <i>Paralitogaster</i> + <i>Lissocardia</i> + <i>Pseudopemphix</i> ). 50: 0->1
27 ( <i>Lissocardia</i> + <i>Pseudopemphix</i> ). 9: 1->0, 35: 0->1, 47: 1->2
28 (Glypheidae + Neoglypheidae + Mecochiridae). 76: 0->1
29 (Glypheidae). 28: 0->1
30 ( <i>Squamosoglyphe</i> + <i>Glyphe</i> ). 17: 0->2, 29: 0->1
31 (Neoglypheidae + Mecochiridae). 6: 0->1, 26: 0->1
32 (Neoglypheidae). 20: 0->1
33 (Mecochiridae). 27: 0->1, 49: 1->0
34 ( <i>Huhatanka</i> + <i>Mecochirus</i> + <i>Meyeria</i> ). 3: 1->0
35 ( <i>Mecochirus</i> + <i>Meyeria</i> ). 55: 0->1
36 (Astacidea). 56: 0->1, 57: 0->1, 64: 0->1
37 (Astacida). 10: 0->1, 68: 0->1, 69: 0->1, 70: 0->1
38 (Parastacoidea + Astacoidea). 41: 1->0
39 (Parastacoidea). 88: 0->1
40 (Astacoidea). 68: 1->2, 90: 0->1
41 (Cricoidoscelosidae + Cambaridae). 89: 0->1
42 (Cambaridae). 60: 0->1
43 (Homarida). 5: 0->1, 6: 0->1, 11: 0->1, 12: 0->1, 46: 1->0
44 (Enoplometopoidea). 25: 0->1, 26: 1->2, 27: 1->2, 50: 0->1
45 (Uncinidae). 3: 0->1, 61: 2->1, 66: 1->0, 67: 1->0
46 (Stenochiroidea + Nephropoidea). 17: 0->1, 33: 0->1
47 (Stenochiroidea). 18: 1->0, 21: 1->0, 32: 0->1
48 ( <i>Stenochirus</i> + <i>Pseudastacus</i> + <i>Chilenophoberus</i> ). 12: 1->0
49 ( <i>Stenochirus</i> + <i>Pseudastacus</i> ). 6: 1->0
50 (Nephropoidea). 9: 0->1, 22: 3->1, 36: 0->1, 62: 0->1
51 ( <i>Acanthacaris</i> + <i>Metanephrops</i> + <i>Nephrops</i> + <i>Palaeonephrops</i> + <i>Paraclythia</i> ). 8: 0->1
52 ( <i>Metanephrops</i> + <i>Nephrops</i> + <i>Palaeonephrops</i> + <i>Paraclythia</i> ). 10: 0->1, 13: 0->1, 15: 0->1, 32: 0->1, 37: 0->1
53 ( <i>Nephrops</i> + <i>Palaeonephrops</i> + <i>Paraclythia</i> ). 24: 0->1, 52: 0->1
54 ( <i>Palaeonephrops</i> + <i>Paraclythia</i> ). 34: 0->1, 63: 0->1
55 ( <i>Nephropoides</i> + <i>Nephropsis</i> + <i>Thymops</i> + <i>Thymopsis</i> + <i>Jagtia</i> + <i>Eunephrops</i> + <i>Thymopides</i> + <i>Hoploparia</i> + <i>Homarinus</i> + <i>Homarus</i> + <i>Thaumastocheles</i> + <i>Thaumastochelopsis</i> + <i>Dinochelus</i> ). 3: 0->1, 5: 1->0
56 ( <i>Nephropoides</i> + <i>Nephropsis</i> + <i>Thymops</i> + <i>Thymopsis</i> + <i>Jagtia</i> ). 77: 0->1
57 ( <i>Nephropsis</i> + <i>Thymops</i> + <i>Thymopsis</i> + <i>Jagtia</i> ). 63: 0->1, 80: 0->1
58 ( <i>Thymops</i> + <i>Thymopsis</i> + <i>Jagtia</i> ). 31: 0->1, 83: 0->1
59 ( <i>Thymopsis</i> + <i>Jagtia</i> ). 34: 0->1
60 ( <i>Eunephrops</i> + <i>Thymopides</i> + <i>Hoploparia</i> + <i>Homarinus</i> + <i>Homarus</i> + <i>Oncopareia</i> + <i>Thaumastocheles</i> + <i>Thaumastochelopsis</i> + <i>Dinochelus</i> ). 12: 1->0, 37: 0->1
61 ( <i>Thymopides</i> + <i>Hoploparia</i> + <i>Homarinus</i> + <i>Homarus</i> + <i>Oncopareia</i> + <i>Thaumastocheles</i> + <i>Thaumastochelopsis</i> + <i>Dinochelus</i> ). 6: 1->0

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Table 4. (Continued.)

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62 ( <i>Hoploparia</i> + <i>Homarinus</i> + <i>Homarus</i> + <i>Thaumastocheles</i> + <i>Thaumastochelopsis</i> + <i>Dinochelus</i> ). 52: 0->1
63 ( <i>Hoploparia</i> + <i>Homarinus</i> + <i>Homarus</i> ). 24: 0->1
64 ( <i>Homarinus</i> + <i>Homarus</i> ). 30: 0->1
65 ( <i>Oncopareia</i> + <i>Thaumastocheles</i> + <i>Thaumastochelopsis</i> + <i>Dinochelus</i> ). 3: 1->0, 9: 1->0, 11: 1->0, 53: 0->1, 61: 2->1, 67: 1->0
66 ( <i>Thaumastocheles</i> + <i>Dinochelus</i> + <i>Thaumastochelopsis</i> ). 64: 1->0, 73: 0->1
67 ( <i>Thaumastocheles</i> + <i>Dinochelus</i> ). 37: 1->0

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showed that Glypheidea emerged as the sister to Polyche-  
lida and Achelata. Our result supports the sister group re-  
lationship between Glypheidea and Astacidea. Glypheidea  
and Astacidea (clade 11), with Bremer support of 2, share  
six synapomorphies, a well-developed, simple rostrum with  
marginal spines (40-1, 41-1), mid-lateral pleonic hinges  
(Scholtz and Richter, 1995) (65-1), the uropodal exopod-  
with diaeresis bearing a spinose margin (71-1, 72-2), and  
a trapezoidal mandible molar process (Scholtz and Richter,  
1995) (85-1), three (65-1, 71-1, 85-1) of which are unique  
and never reversed.

The monophyly of Glypheidea (clade 12), with Bremer  
support of 6, is strongly supported by five synapomorphies:  
the presence of a median suture (3-1), the postcervical  
groove originating near dorsomedian (21-0), the postcervical  
groove not reaching the cervical groove (22-0), a steep  
branchiocardiac groove (26-0), and the branchiocardiac  
groove on the dorsal thoracic region joining the median  
suture (27-0). De Grave et al. (2009) and Schweitzer  
et al. (2010) proposed two superfamilies, Glypheoidea  
with five families, Glypheidae, Mecochiridae, Platychelidae,  
Pempficidae, and Chimaerastacidae, and Erymoidea with  
a single family Erymidae, within Glypheidea. However,  
the analysis shows that both superfamilies and the known  
families excluding Chimaerastacidae are polyphyletic.

The extant Glypheidea has only two taxa, *Neoglyphea*  
and *Laurentaeglyphea*, while Glypheidea is represented by  
31 extinct genera (De Grave et al., 2009; Schweitzer et al.,  
2010). Beurlen (1928), Glaessner (1960), and Förster (1966,  
1967) proposed hypotheses of internal relationships within  
Erymidae or Paranephropsidae Beurlen, 1928 (unavailable  
name under 11.7.1 of ICZN, 1999), and Glypheidae, but our  
analysis does not support these hypotheses.

*Glaessnericaris* is a unique, basal lineage within Glyphei-  
dea. *Glaessnericaris* was originally placed under Platyche-  
lidae (Garassino and Teruzzi, 1993). Schram and Dixon  
(2004) showed that the phylogenetic position of the genus  
was uncertain. Most recently, De Grave et al. (2009) and  
Schweitzer et al. (2010) assigned it to Platychelidae. How-  
ever, *Glaessnericaris* lacks a synapomorphy, the presence of  
the inferior and hepatic grooves (32-1, 33-1), of both ery-  
moids and glypheoids (clade 13). Additionally, the genus  
has a unique autapomorphic character, pereopod 4 with true  
chelae (50-2). Therefore, it cannot be placed within the pre-  
viously recognized glypheidean families. As a result, a new  
superfamily and family is herein erected for *Glaessnericaris*.

Amati et al. (2004) and Ah Yong (2006) showed that Ery-  
moidea is sister to Glypheoidea, whereas Schram and Dixon  
(2004) recognized the sister group relationship of Ery-  
moidea and Enoplometopoidea within Astacidea and erected  
the new rank Erymida. Our result supports a sister group

relationship of Erymoidea and Glypheoidea. The erymoid  
clade (clade 14), with Bremer value of 2, shares two synap-  
omorphies, the presence of the gastro-orbital groove (17-1)  
and pereopods 4 with pseudochelae (50-1). Pempficidae  
is derived as the sister to Erymidae. The pempficid clade  
(clade 15), with a Bremer support of 2, is united by two char-  
acters: a cylindrical carapace outline (1-1) and possession of  
the antennal groove (9-1). The erymid clade (clade 16), with  
Bremer index of 2, shares two characters, presence of an in-  
tercalated plate (4-1) and the presence of a sharp demarca-  
tion between pleonal terga and pleura (62-1), of which one  
(4-1) is unique. Traditionally, Pempficidae was recognized  
as a family within Glypheoidea, and Erymidae was placed  
in Astacidea (Glaessner, 1969). Amati et al. (2004) showed,  
using morphology-based cladistic analysis, that Pempfici-  
dae was sister to Erymidae, while Schram and Dixon (2004)  
recognized Pempficidae as the basal position of Astacidea  
and gave it the new rank Pempficida. The present analy-  
sis supports a sister group relationship of Pempficidae and  
Erymidae within Erymoidea.

Two characters support the monophyly of Glypheoidea  
(clade 20): the postcervical groove parallel to the bran-  
chiocardiac groove (20-0), and the rostrum without dis-  
tinct marginal spines (41-0). Platychelidae is the most basal  
within the glypheoid clade. Glaessner (1931) originally  
showed that the systematic position of *Platychele*, the type  
genus of Platychelidae, was uncertain within Paranephrop-  
sidae (= Erymidae). Förster (1967) followed his opin-  
ion. Later, Glaessner (1969) erected Platychelidae under  
Astacidea. Most recently, De Grave et al. (2009) and  
Schweitzer et al. (2010) moved it to Glypheoidea. *Glaess-  
nericaris*, formerly a member of Platychelidae, is moved  
to Glaessnericarioidea, discussed above, within Glypheidea.  
Therefore, Platychelidae is comprised of solely the type  
genus, *Platychele*. The erymid *Clytiopsis* and the remain-  
der of the glypheoid clades (clade 21), with Bremer value  
of 2, share three synapomorphies, presence of the antennal  
carina (9-1), the presence of the supraorbital carina (11-1),  
and a sharp demarcation between pleonal terga and pleura  
(62-1). Beurlen (1927) erected a subfamily, Clytiopsinae,  
with *Clytiopsis* under Paranephropsidae (= Erymidae). Most  
subsequent workers, Förster (1966; 1967), Glaessner (1969),  
and Klompmaker and Fraaije (2011), agreed with his opin-  
ion. Amati et al. (2004) and Feldmann et al. (2012), how-  
ever, gave it full family status and showed that Clytiopsidae  
occupied the basal position within Erymoidea. The present  
analysis supports the family status of Clytiopsidae but sug-  
gests that it be moved to Glypheoidea.

The monophyly of clade 22 (Chimaerastacidae and the re-  
mainder of the glypheoids), with Bremer support of 2, is  
well defined by five synapomorphies, presence of cephalic

ridges (2-1) with median and suborbital carinae (5-1, 10-1), and absence of the antennal spine (38-1). The presence of cephalic ridges (character 5), defined by Amati et al. (2004), is an unambiguous character for clade 22. Clade 23 (remaining glypheoid taxa), with a Bremer index of 2, is united by four unambiguous characters: the postcervical groove reaching the hepatic groove posteriorly by a convex arc (22-2) and pereopods 1-3 pseudochelate (57-1, 48-1, 49-1). Therefore, the present analysis supports Chimaerastacidae as sister group of the remainder of “Glypheidae”.

Our results suggest that the remainder of the “glypheids” consists of three clades, *Litogaster*-, *Glyphea*-, and *Neoglyphea*-groups. The presence of the gastro-orbital groove (17-1) weakly supports monophyly of a *Litogaster*-group containing *Litogaster*, *Pseudoglyphea*, *Paralitogaster*, *Lissocardia*, and *Pseudopemphix*. Within the clade *Litogaster* is most basal, followed by *Pseudoglyphea*, *Paralitogaster*, and the most derived *Lissocardia* and *Pseudopemphix*. Most workers (Glaessner, 1969; De Grave et al., 2009; Schweitzer et al., 2010) placed *Litogaster* and *Paralitogaster* in Glypheidae. *Pseudoglyphea* was assigned to Mecochiridae (see Feldmann et al., 2002); however, most recently, Astrop (2011) indicated that *Pseudoglyphea* is derived as the sister to *Glyphea* and reassigned *Pseudoglyphea* to Glypheidae, as Garassino (1996) had already noted. The systematic placement of *Pseudopemphix* was contentious: van Straelen (1928a) thought that *Pseudopemphix* was a member of Erymidae; Beurlen (1927, 1928) placed it in Clytiopsinae of his Paranephropsidae; Balss (1957) regarded it as a member of Glypheidae; and Förster (1966) assigned it to Pemphicidae. Most workers followed Förster (1966) in placing *Pseudopemphix* in Pemphicidae (Glaessner, 1969; De Grave et al., 2009; Schweitzer et al., 2010), and Amati et al. (2004) supported the position using cladistic analysis, that *Pseudopemphix* was the sister to *Pemphix*. Since the work of van Straelen (1928a), *Lissocardia* was thought to be a member of Erymidae, and Glaessner (1969) followed his opinion. However, a *Litogaster*-group differs significantly from the *Glyphea*-group + (*Neoglyphea*-group + Mecochiridae) clade (clade 28) because it lacks the unique synapomorphy of clade 28, an elongate peduncle of the second antenna (76-1). Therefore, these taxa cannot be placed within previously known families. A new family, Litogastroidea, is erected herein for the *Litogaster*-group. This clade is represented by genera that mainly appeared within the Triassic.

The *Glyphea*-group + (*Neoglyphea*-group + Mecochiridae) clade (clade 28), with Bremer support of 3, shares one unambiguous character, an elongate peduncle of the second antenna (76-1). The presence of the laterocardiac groove (28-1), a unique character, defines the monophyly of a *Glyphea*-group (clade 29). The *Glyphea*-group is comprised of *Trachysoma*, *Squamosoglyphea*, and *Glyphea*, all of which have mainly Jurassic fossil records. The *Glyphea*-group is sister to the *Neoglyphea*-group + Mecochiridae clade (clade 31). Clade 31, with Bremer support of 2, shares two characters, the cephalic carinae ornamented with strong spines (6-1) and a gently sloping branchiocardiac groove (26-1). The *Neoglyphea*-group (*Neoglyphea* + *Laurentaeglyphea*) (clade 32) is united by only one character, the postcervical groove parallel to the branchiocardiac groove

(20-1). Schram and Dixon (2004) examined three genera; *Neoglyphea*, *Glyphea*, and *Mecochirus*, based upon cladistic analysis, and indicated that *Neoglyphea* is derived as the sister to *Glyphea* and *Mecochirus*. Amati et al. (2004) also recognized the monophyly of Glypheoidea, but a *Glyphea* – *Neoglyphea* – (*Mecochirus* + *Pseudoglyphea*) relationship was not resolved. Both works suggested that the family status of Mecochiridae is questionable. However, Astrop (2011) indicated a monophyletic group of Mecochiridae including *Meyeria* and *Mecochirus*, a sister group to Glypheidae. Our analysis also shows that the monophyly of Mecochiridae (clade 33), with Bremer support of 2, is supported by two characters: the branchiocardiac groove on the dorsal thoracic region forming a concave arc (27-1), and pereopods 3 without chelae (49-0); therefore, the family status of Mecochiridae is sustained. Glypheidae should be restricted to a *Glyphea*-group containing *Trachysoma*, *Glyphea*, and *Squamosoglyphea* (clade 29), and a new family, Neoglypheidae, should be erected for a monophyletic *Neoglyphea*-group (clade 32).

Astacidea (clade 36).—Within the recent works, the monophyly of Astacidea is well supported by morphological analyses (Dixon et al., 2003; Ah Yong and O’Meally, 2004) and molecular analyses (Crandall et al., 2000; Ah Yong and O’Meally, 2004; Tsang et al., 2008; Bracken et al., 2009; Toon et al., 2009; Bracken-Grissom et al., in prep.). However, Scholtz and Richter (1995), Amati et al. (2004), and Schram and Dixon (2004) showed, using morphological analyses, that Astacidea was para- or polyphyletic. Our result supports the monophyly of Astacidea. The astacidean clade (clade 36), with Bremer value of 2, shares three synapomorphies, a vertical dactylus orientation of pereopod 1 (Scholtz and Richter, 1995) (56-1), the presence of pereopod 1 with an ischial process (Scholtz and Richter, 1995) (57-1), and a pleuron of pleomere 2 larger than that of pleomere 3 (64-1), two (56-1, 57-1), which are unique and never reversed. Astacidea comprises two major groups, Homarida Scholtz and Richter, 1995 (marine clawed lobsters) and Astacida Scholtz and Richter, 1995 (freshwater crayfishes). The sister group relationship of Homarida and Astacida is well supported by morphological evidence and similarities (Hobbs, 1974), morphological analysis (Ah Yong and O’Meally, 2004), and molecular analyses (Crandall et al., 2000; Ah Yong and O’Meally, 2004; Tsang et al., 2008; Bracken et al., 2009; Toon et al., 2009; Bracken-Grissom et al., in prep.).

The astacidean clade (clade 37) is monophyletic with Bremer Support of 4, and is united by five characters, the presence of the suborbital carina (10-1), the telson with an incomplete diaeresis (68-1), and the telson and uropod exopod weakly calcified distally (69-1, 70-1), three (68-1, 69-1, 70-1) of which are unique. Within the recent work, the sister group relationship of Parastacoidea and Astacoidea was well supported (Crandall et al., 2000; Scholtz, 2002; Rode and Babcock, 2003; Bracken et al., 2009; Toon et al., 2010; Bracken-Grissom et al., in prep.). Albrecht (1983) erected Protastacidae with *Protastacus* and *Pseudastacus* and noted: “They represent a transitional grade between Erymidae and crayfishes”. Shen et al. (2001) and Schram (2001) doubted the systematic position of Protastacidae

under Astacida. Later, Rode and Babcock (2003) showed that *Protastacus*, the type genus of Protastacidae, was included in Astacidae. Most recently, De Grave et al. (2009), Schweitzer et al. (2010), and Wahle et al. (2012) assigned Protastacidae to Nephropoidea. Additionally, Gherardi et al. (2011) did not arrange Protastacidae within the freshwater crayfish. The present analysis suggests that Protastacidae is derived as sister to Parastacoidea and Astacoidea and that *Pseudastacus* is a member of Homarida.

Only one character, rostrum without marginal spines (41-0), unites Parastacoidea and Astacoidea (clade 38). The absence of male pleopod 1 (Hobbs, 1974) (88-1), a unique synapomorphy, defines Parastacidae/Parastacoidea (clade 39). The monophyly of Astacoidea (clade 40), with a Bremer index of 2, is defined by two unique synapomorphies, the telson with a complete diaeresis (69-2) and the male pleopod 2 with a spiral element (90-1). Astacidae as the sister to Cambaridae has been well supported by previous works (Hobbs, 1974; Crandall et al., 2000; Scholtz, 2002; Rode and Babcock, 2003; Bracken et al., 2009; Toon et al., 2010; Bracken-Grissom et al., in prep.). Rode and Babcock (2003) performed morphology-based phylogenetic analysis of extant and fossil genera, but did not examine Cricoidoscelosidae from the Jurassic of China. Our analysis shows the sister-group relationship between Cricoidoscelosidae and Cambaridae (clade 41) with a unique synapomorphy, the presence of the annulus ventralis (89-1). Shen et al. (2001) indicated that Cricoidoscelosidae has close affinities with Cambaridae. We concur. The presence of an ischial hook on pereopods (60-1), a unique character, defines Cambaridae (clade 42). Scholtz (2002) provided additional synapomorphies within extant Astacida and its families.

The monophyly of the extant homaridan group was well supported by both morphological analyses (Scholtz and Richter, 1995; Ah Yong and O'Meally, 2004), and molecular analyses (Ah Yong and O'Meally, 2004; Porter et al., 2005; Bracken-Grissom et al., in prep.). However, within the recent work based upon morphological analysis, the extant homaridans emerge as polyphyletic, consisting of Thaumastocheilida derived as sister to Astacida + Homarida (Dixon et al., 2003). Our analysis suggests that the monophyletic homaridan clade including fossil taxa (clade 43) is united by five characters: the presence of a cephalic median carina (5-1); cephalic carinae or ridges, strongly ornamented with spines or tubercles (6-1); possession of subdorsal and supraorbital carinae (11-1, 12-1); and the lateral margin of epistome and carapace not in broad contact (46-0).

Within our strict consensus tree (Fig. 3) the relationship between Enoplometopoidea (Chilenophoberidae including Stenochiridae), and the remainder of Nephropoidea cannot be resolved. However, the fifty-percent majority consensus tree (Figs. 4 and 5) demonstrates that Enoplometopoidea is the first divergent lineage, Stenochiridae including Chilenophoberidae is the second divergent lineage, and "Nephropoidea" is the most advanced lineage. Within Homarida, the basal position of Enoplometopoidea was also supported by Ah Yong and O'Meally (2004), Chu et al. (2009), Tsang et al. (2009), and Bracken-Grissom et al. (in prep.). The enoplometopoid clade (clade 44), with Bremer support of 4, is well defined by four characters, the

absence of the branchiocardiac groove (25-1, 26-2, 27-2) and pereopods 4 with pseudochelae (50-1). Uncinidae is the sister to Enoplometopidae. Uncinidae (clade 45), with a Bremer value of 4, shares four synapomorphies, the presence of a median suture of carapace (3-1), a rectangular pleon of the pleonal somites (61-1), a triangular telson without posterolateral spines (66-1, 67-0). Traditionally, Uncinidae was considered the sole family of the infraorder Uncinidea Beurlen, 1930a, not "reptant" decapods (Beurlen, 1930a; Balss, 1957; Glaessner, 1969; Karasawa, 2002) because *Uncina*, as well as stenopodids, was thought to have large, elongate pereopods 3. However, Schweigert et al. (2003) showed that *Uncina* had a large, elongated pereopod 1 based upon re-examination of well-preserved material and moved Uncinidae to Astacidea. Later, Ah Yong (2006) showed the sister group relationship between Enoplometopidae and Uncinidae. Our result supports his opinion in placing Uncinidae within Enoplometopoidea.

Clade 47, including *Stenochirus* (Stenochiridae) and four chilenophoberid genera, is united by three characters, the cervical groove extending to the dorsomedian line of carapace (18-0), the postcervical groove reaching near to the dorsomedian line (21-0), and the presence of the inferior groove (32-1). However, a *Tillocheles* – *Palaeophoberus* – *Chilenophoberus* + (*Pseudastacus* + *Stenochirus*) relationship cannot be resolved. Only one character, the absence of the subdorsal carina unites the *Chilenophoberus* + (*Pseudastacus* + *Stenochirus*) clade (clade 48) and the sister-group relationship of *Pseudastacus* and *Stenochirus* (clade 49) is weakly supported by a single character, cephalic carina or ridges not ornamented with strong spines (6-0). When *Stenochirus* is sister to *Pseudastacus*, the chilenophoberids are paraphyletic. Therefore, Chilenophoberidae should be synonymized with Stenochiridae.

The position of Stenochiridae and/or Chilenophoberidae is variable within the previous works. Beurlen (1928) erected Stenochirinae under his Paranephropsidae (= Erymidae). Subsequently, Beurlen (1930a) gave it full family status and arranged it within his tribe Paranephropsidae at the superfamily-level. Subsequently, Stenochiridae has not been used (Glaessner, 1969), but, most recently, Garassino and Schweigert (2006) treated it as a valid family under Astacidea. Additionally, they redefined it based only upon *Stenochirus angustus* (Münster, 1839) and *S. mayeri* (O'p'pel, 1862) (type species), because Beurlen (1928) had established the family along with *Stenochirus suevicus* (Quenstedt, 1867), which Glaessner (1932) subsequently moved to the present chilenophoberid *Palaeophoberus* Glaessner, 1932. Tshudy and Babcock (1997) placed Chilenophoberidae in Nephropoidea and suggested that Chilenophoberidae was the earliest-derived clade within Nephropoidea. Subsequently, Rode and Babcock (2003) documented the paraphyly of Chilenophoberidae. Most recently, Ah Yong (2006) indicated that the family was derived as the sister to Astacidae. Our result supports Tshudy and Babcock (1997) in placing it in the basal position within Nephropoidea and shows the sister-group relationship between Stenochiridae and the remainder of Nephropoidea (clade 46), united by two characters, the presence of the gastro-orbital groove (17-1) and the presence of the hepatic groove (33-1). However, Nephro-



poidea (clade 50), with Bremer support of 2, is well defined by four characters, the presence of the antennal carina (9-1), the postcervical groove reaching the hepatic groove (22-1), the presence of a “W-shaped groove pattern” defined by Scholtz and Richter (1995) (36-1), and a sharp demarcation between pleonal terga and pleura (62-1), one (36-1) of which is unique and never reversed. Therefore, Stenochiridae lacks synapomorphies of Nephropoidea and should be given full superfamily status.

The remainder of the nephropoid clade (clade 50) comprises three major lineages: clade 51 (*Acanthacaris*, *Metanephrops*, *Nephrops*, *Palaeonephrops*, and *Paraclythia*); clade 56 (*Nephropoides*, *Nephropsis*, *Thymopsis*, and *Jagtia*); and clade 60 (*Eunephrops*, *Thymopides*, *Hoploparia*, *Homarinus*, *Homarus*, and four thaumastochelids). The monophyly of Thaumastochelidae (clade 65), with Bremer support of 4, is well supported by six synapomorphies (3-0, 9-0, 11-0, 53-1, 61-1, 67-0). A bulbous palm with pectinate claws (53-1) is an unambiguous synapomorphy of thaumastochelids. When Thaumastochelidae is treated as a separate family, Nephropidae becomes a paraphyletic group. Within the previous works, the family status of Thaumastochelidae was supported by morphological analyses (Tshudy and Sorhannus, 2000a; Dixon et al., 2003; Schram and Dixon, 2004; Ah Yong, 2006) and morphological and molecular analysis (Ah Yong and O’Meally, 2004). In contrast, a separate status of the family is rejected by morphological analyses (Tshudy and Babcock, 1997) and molecular analyses (Tsang et al., 2008; Chu et al., 2009; Tshudy et al., 2009; Bracken-Grissom et al., in prep.). Our result supports the latter hypothesis in placing the known thaumastochelid genera within Nephropidae. The present analysis shows that the “thaumastochelid” clade (clade 65) is derived as sister to the nephropine *Hoploparia* + (*Homarus* + *Homarinus*) clade (clade 63). Interestingly, the sister group relationship between the “thaumastochelids” and *Homarus* has been shown in molecular analyses (Tsang et al., 2008; Chu et al., 2009; Tshudy et al., 2009; Bracken-Grissom et al., in prep.).

The internal relationships among genera within Nephropidae were variable (Tshudy and Babcock, 1997; Tshudy and Sorhannus, 2000a; Ah Yong, 2006; Tshudy et al., 2009; Bracken-Grissom et al., in prep.). The previous workers proposed a subfamilial division for Nephropidae: Mertin (1941) first recognized three nephropoid subfamilies, Phoberinae Mertin, 1941, Nephropsinae (= Nephropinae) Dana, 1852a, and Homarinae Huxley, 1879; Glaessner (1969) divided it into three, Nephropinae, Homarinae, and Neophoberinae Glaessner, 1969 (= Phoberinae); and Holthuis (1974; 1991) recognized Neophoberinae, Nephropsinae, and Thymopinae Holthuis, 1974, as its subfamilies. Tshudy and Babcock (1997) rejected these subfamilial classifications of Nephropidae based upon morphological analysis and subsequent workers (Tshudy and Sorhannus, 2000a; Ah Yong, 2006; Tshudy et al., 2009; Chan, 2010; Bracken-Grissom et al., in prep.) followed their opinion. We concur. However, three weakly defined clades 51, 56, and 60 might correspond to Neophoberinae and Nephropinae, Thymopinae, and Homarinae, respectively. Most recently, Tshudy et al. (2009) and Bracken-Grissom et al. (in prep.) showed using molecular analysis that *Acanthacaris* was the earliest to di-

verge from Nephropidae, while our result as well as the morphological analyses (Tshudy and Babcock, 1997; Tshudy and Sorhannus, 2000b) indicates *Acanthacaris* is the sister to the *Metanephrops* + *Nephrops* + *Palaeonephrops* + *Paraclythia* clade (clade 51).

### Classification

As a result of the analysis above, we propose the following new classification for lobsters (Fig. 5):

- Infraorder Palaeopalaemonida Schram and Dixon, 2004, new status
  - Palaeopalaemonoidea Brooks, 1962
    - Palaeopalaemonidae Brooks, 1962
- Infraorder Polychelida Scholtz and Richter, 1995
  - Eryonoidea De Haan, 1841
    - Eryonidae De Haan, 1841
    - Coleiidae van Straelen, 1925
    - Palaeopentachelidae Ah Yong, 2009
    - Polychelidae Wood-Mason, 1875
    - Tetrachelidae Beurlen, 1930a
    - Tricariniidae Feldmann et al., 2007 (not in phylogeny)
- Infraorder Achelata Scholtz and Richter, 1995
  - Palinuroidea Latreille, 1802
    - Cancrinidae Beurlen, 1930a
    - Palinuridae Latreille, 1802
    - Scyllaridae Latreille, 1825
- Infraorder Glypheidea Winkler, 1882
  - Glaessnericarioidea, new superfamily
    - Glaessnericarididae, new family
  - Erymoidea van Straelen, 1925
    - Erymidae van Straelen, 1925
    - Pempficidae van Straelen, 1928a
- Glypheoidea Winkler, 1882
  - Platychelidae Glaessner, 1969
  - Chimaerastacidae Amati, Feldmann, and Zonneveld, 2004
  - Clytiopsidae Beurlen, 1927
  - Litogastroidae, new family
  - Glypheidae Winkler, 1882
  - Neoglypheidae, new family
  - Mecochiridae van Straelen, 1925
- Infraorder Astacidea Latreille, 1802
  - Section Homarida Scholtz and Richter, 1995
    - Enoplometopoidea de Saint Laurent, 1988
      - Enoplometopidae de Saint Laurent, 1988
      - Uncinidae Beurlen, 1930a
    - Stenochiroidea Beurlen, 1928, new status
      - Stenochiridae Beurlen, 1928
  - Nephropoidea Dana, 1852a
    - Nephropidae Dana, 1852a
- Section Astacida Scholtz and Richter, 1995
  - Protastacoidea Albrecht, 1983, new status
    - Protastacidae Albrecht, 1983
  - Astacoidea Latreille, 1802
    - Astacidae Latreille, 1802
    - Cambaridae Hobbs, 1942
    - Cricoidoscelosidae Taylor, Schram, and Yan-Bin, 1999
  - Parastacoidea Huxley, 1879
    - Parastacidae Huxley, 1879

## SYSTEMATICS

## Infraorder Palaeopalaemonida Schram and Dixon, 2004

Diagnosis.—Carapace dorsoventrally flattened; rostrum distinct, simple; cervical, postcervical, branchiocardiac, antennal, and gastro-orbital grooves distinct; medial ridge and lateral carina present. Pleon without median ridge or keel; pleomere 2 about equal to pleomere 3; pleura triangular, not separated from terga by sharp demarcation. Telson triangular, much longer than wide; exopod of uropod without diaeresis. Scaphocerite present, broad. Pereiopods 1 chelate, much longer than pereiopods 2-5; pereiopods 2-5 subchelate.

Included family.—Palaeopalaemonidae Brooks, 1962.

Remarks.—Palaeopalaemonida is represented by a single superfamily and family. *Palaeopalaemon* is a monotypic genus containing a single species, *P. newberryi* Whitfield, 1880 (Schram et al., 1978). *Palaeopalaemon* is the earliest known macruran decapod, known from the Late Devonian; Schram et al. (1978), Schram and Dixon (2004), and Schram (2009) provided the history of the systematic placement. Most recently, Schram and Dixon (2004) established the new rank Palaeopalaemonida, derived as the sister to Achelata, Anomala, and Brachyura. In contrast, Rolfe and Dzik (2006) suggested that *Angustidontus* Cooper, 1936, had close affinities with *Palaeopalaemon* and that *Angustidontus* might be synonym of *Palaeopalaemon*. Addition-

ally, Shpinev (2010) indicated that Angustidontidae Cooper, 1936, containing the sole genus *Angustidontus*, had uncertain ordinal status within malacostracans. However, De Grave et al. (2009) and Schweitzer et al. (2010) considered that Palaeopalaemonidae belonged to Astacidea and gave it full superfamily status. The present analysis showed that *Palaeopalaemon* was not a member of Astacidea and that the separate infraordinal and superfamilial status of Palaeopalaemonida was given, as discussed above.

## Palaeopalaemonoidea Brooks, 1962

Diagnosis.—As for infraorder.

## Palaeopalaemonidae Brooks, 1962

## Fig. 6

Diagnosis.—As for infraorder.

Included genus.—*Palaeopalaemon* Whitfield, 1880.

Geologic range.—Late Devonian.

## Infraorder Polychelida Scholtz and Richter, 1995

## Fig. 7

Diagnosis.—Carapace dorsoventrally flattened, rostrum indistinct; antennal groove absent; with branchial and thoracic median carinae; epistome and carapace not in broad contact. Pleon with axial keel and sharp demarcation between terga and pleura; telson triangular. Antennular stylocerite present; maxilliped 3 dactylus sharp; pereiopods 1-4 chelate.

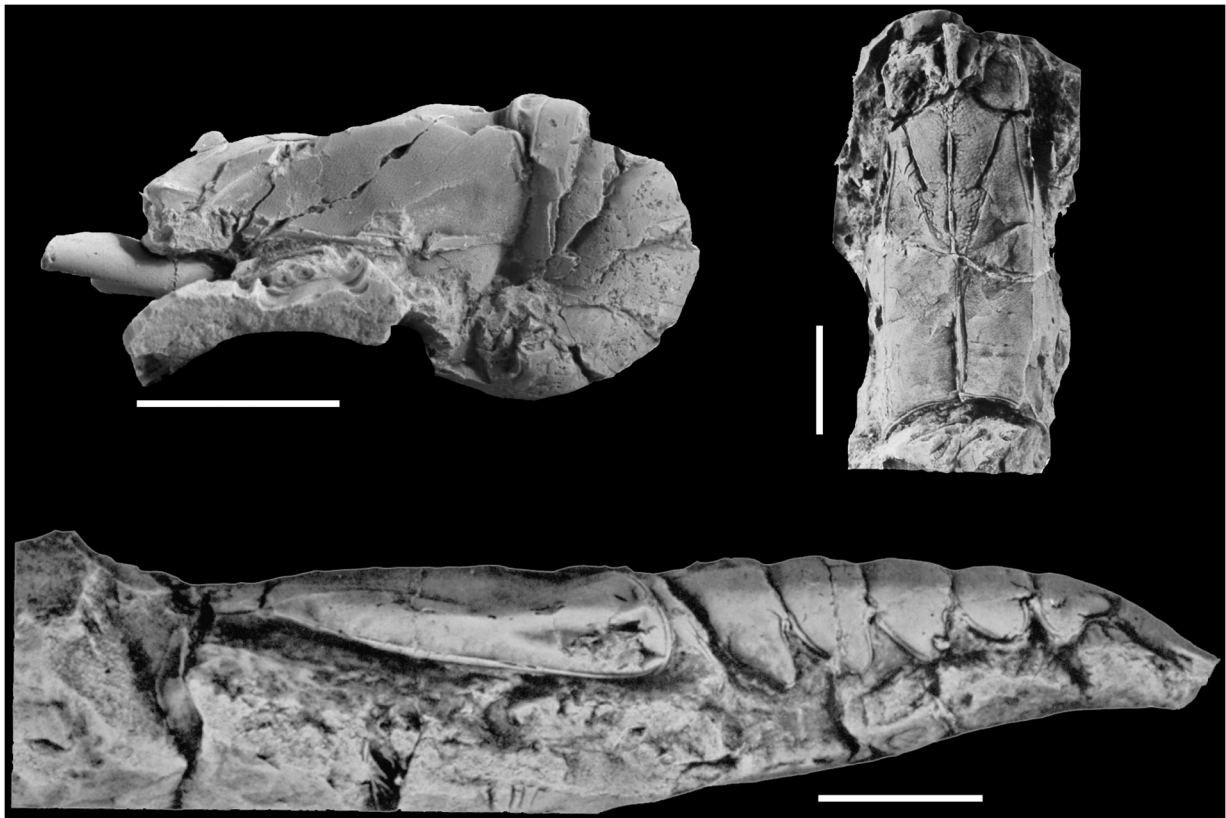


Fig. 6. Infraorder Palaeopalaemonida, Palaeopalaemonidae, *Palaeopalaemon newberryi* Whitfield, 1880. A, B, UI 10752, left lateral view (A) and dorsal view (B); C, UI 10753, left lateral view. Scale bars = 1 cm. A and C reprinted from the Journal of Paleontology, Vol. 54(6), p. 1379-1380, pl. 1, Fig. 5 and pl. 1, Fig. 4 respectively, with permission of the Paleontological Society.

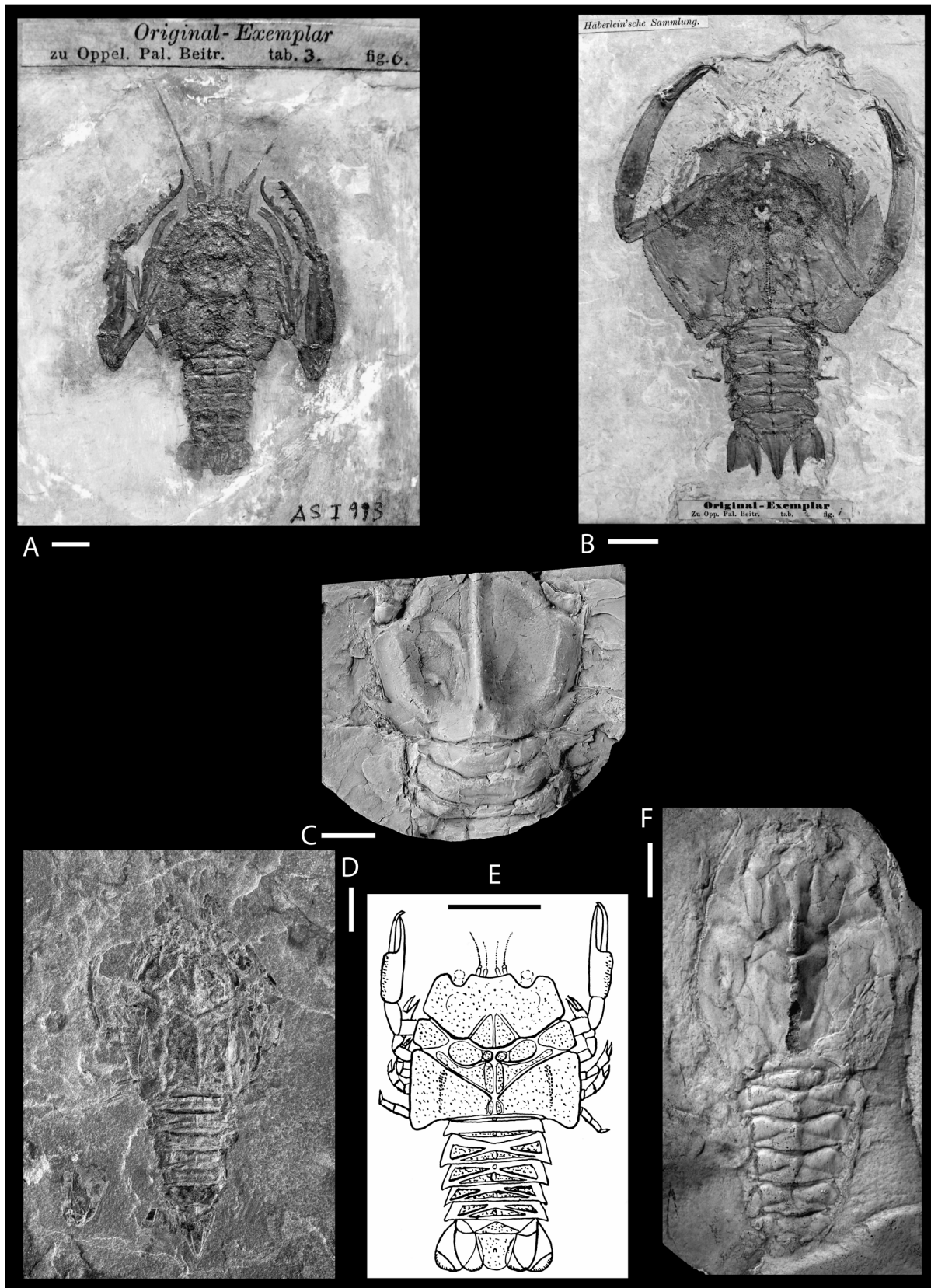


Fig. 7. Infraorder Polychelida. A, Palaeopentachelidae, *Palaeopentacheles roettenbacheri* (Münster, 1839), lectotype BSP AS 1993; B, Eryonidae, *Cycleryon propinquus* (Schlotheim, 1822), CM 34359; C, Tricarinidae, *Tricarina gadvanensis* Feldmann et al., 2007, holotype, CM 54197; D, Coleiidae, *Coleia mediterranea* Pinna, 1968, MSNM/i7665a, part, photo by A. Garassino; E, Tetrachelidae, *Tetrachela raiblana* (Bronn, 1858), digital image of Glaessner (1929: pl. 9, Fig. 1); F, Polychelidae, *Antarcticheles antarcticus* Aguirre-Urreta et al., 1990, cast of holotype CIRGEO 1248. Scale bars = 1 cm.

Included families.—Coleiidae van Straelen, 1925; Eryonidae de Haan, 1841; Palaeopentachelidae Ahyong, 2009; Polychelidae Wood-Mason, 1875; Tetrachelidae Beurlen, 1930a; Tricariniidae Feldmann et al., 2007.

Remarks.—Polychelida is a readily distinguishable group of taxa, perhaps most notably by the possession of a dorsoventrally flattened carapace; triangular, well calcified telson; and chelate pereopods 1-4. However, there are a sufficient number of character differences within the infraorder to warrant recognition of numerous families, more so than the other lobster groups. Each individual branch in the phylogeny has been assigned family status. Three of the families, Polychelidae, Coleiidae, and Tetrachelidae, exhibit strong development of carapace grooves, whereas those grooves are muted or absent in the other families. Characters involving development of a rostrum, form of the pleonal pleura, shape of the telson, and possession or absence of a chelate pereopod 5 are additional characteristics defining families. Of particular interest, each of the groups represented as two distinct clades in the phylogenetic analysis, those with and without well developed carapace grooves, has families with and without a diaeresis on the exopod of the uropods. As defined below, distinctive morphological characters clearly distinguish the family groups.

Geologic Range.—Upper Triassic (Carnian)-Holocene.

Eryonoidea De Haan, 1841

Diagnosis.—As for infraorder.

Included families.—As for infraorder.

Coleiidae van Straelen, 1925  
Fig. 7D

Diagnosis.—Carapace longer than wide, dorsoventrally flattened, rostrum indistinct; antennal groove absent; deep cervical and branchiocardiac grooves extending into lateral carapace indentations; with branchial and thoracic median carinae; epistome and carapace not in broad contact. Pleon long, flattened, with axial keel and sharp demarcation between terga and pleura; exopod of uropods with diaeresis. Antennular stylocerite present; maxilliped 3 dactylus sharp; pereopods 1-4 chelate.

Included genera.—*Coleia* Broderip, 1835; *Hellerocaris* van Straelen, 1925; *Proeryon* Beurlen, 1928; *Pseudocoleia* Garassino and Teruzzi, 1993; *Tropifer* Gould, 1857.

Material examined.—*Hasaracancer cristatus* Jux, 1971, BSP 1988 III 147, cast of holotype.

Geologic Range.—Upper Triassic (Norian)-Upper Cretaceous (Campanian).

Remarks.—Genera retained within Coleiidae exhibit characters that unite them, although some genera are poorly or incompletely preserved. Genera within the family exhibit carapaces that are longer than wide, bearing generally strong longitudinal keels. Both characters tend to distinguish them from genera within Eryonidae, in which the carapace is more circular and in which the keels are less strong. Also definitive, Coleiidae bear a diaeresis on the exopod of the uropods,

a character it shares with Tetrachelidae. That feature is absent in Eryonidae, Palaeopentachelidae, and Polychelidae.

*Hasaracancer* Jux, 1971, previously assigned to Coleiidae (Schweitzer et al., 2010) has an epistome that is fused to the carapace and, as suggested by Guinot et al. (2008) and Ossó-Morales et al. (2011), is better placed within Cenomanocarcinidae. *Hellerocaris* is poorly preserved but exhibits deep orbital notches, characteristic carapace longitudinal ridges, and a keeled pleon with triangular telson. Lateral carapace notches are subtle in *Hellerocaris*. *Proeryon* has an indistinct, triangular rostrum and well developed cervical and branchiocardiac notches on the lateral margins. *Pseudocoleia* is longer than wide, has a truncated front, strong longitudinal carinae, and reduced cervical and branchiocardiac notches on the lateral margins. Axial and lateral carinae are present on the carapace of *Tropifer*, but the branchiocardiac groove and notch are not present. The pleon of *Tropifer* conforms to that of other genera within Coleiidae, thus its placement in the family.

Eryonidae De Haan, 1841  
Fig. 7B

Diagnosis.—Carapace subrectangular or subcircular, dorsoventrally flattened; rostrum indistinct; antennal groove absent; cervical groove moderately deep, extending into lateral indentation, usually with branchiocardiac indentation also; with branchial and thoracic median carinae; epistome and carapace not in broad contact. Pleon flattened, with axial keel and sharp demarcation between terga and pleura; pleura triangular; telson subtriangular; exopod of uropods without diaeresis. Antennular stylocerite present; maxilliped 3 dactylus sharp; pereopods 1-4 chelate; pereopod 5 dactylus achelate.

Included genera.—*Cycleryon* Glaessner, 1965; *Eryon* Desmarest, 1817; *Knebelia* van Straelen, 1922; *Rosenfeldia* Garassino et al., 1996.

Material examined.—*Cycleryon elongatus* (Münster, 1839), SMF I/M 286; *C. propinquus* (Schlotheim, 1822), SMF X/m 73.

Geologic range.—Upper Triassic (Norian)-Lower Cretaceous (Berriasian-Hauterivian).

Remarks.—Eryonids tend to have a nearly circular or equidimensional, rectilinear carapace outline with longitudinal keels that are variously developed, but rarely as strongly as those on Coleiidae. Grooves are not as strongly developed on eryonids as on coleids. Eryonids, along with Palaeopentachelidae and Polychelidae, lack a diaeresis on the exopod of the uropod, a feature possessed by Coleiidae and Tetrachelidae.

*Cycleryon* has a distinctly subcircular carapace, with carapace length and width almost equal, and strong cervical and branchiocardiac notches, although not as strong as those on *Eryon*. Cervical and branchiocardiac grooves are not in evidence. *Knebelia* has a rounded rectilinear carapace lacking carapace grooves and carinae. Cervical and branchiocardiac notches on the lateral margin are shallow notches. The carapace of *Rosenfeldia* is subcircular, wider than long, with axial and lateral carinae, cervical and branchiocardiac notches on the lateral margin but no trace of grooves on the carapace

surface. The telson is subrectangular. The lack of carapace grooves and subcircular carapace place this genus in Eryonidae rather than Coleidae even in the presence of carapace carinae.

Palaeopentachelidae Ah Yong, 2009

Fig. 7A

Diagnosis.—Carapace dorsoventrally flattened; front axially sulcate, bounded by prominent inner orbital spines; antennal groove absent; narrow, u-shaped, deeply incised, dorsal orbits; well-developed eyes; cervical groove only present medially, indistinct; branchiocardiac groove absent; with branchial and thoracic median carinae, median carina absent anterior to cervical groove; posterior margin of carapace much wider than pleon; epistome and carapace not in broad contact; carapace surface coarsely pustulose. Pleon with axial spines and sharp demarcation between terga and pleura; pleonal pleura 2 and 3 similar, pleuron 2 not overlapping 1. Uropodal exopod without diaeresis; telson triangular. Antennular stylocerite present; maxilliped 3 dactylus sharp; pereopods 1-4 [5?] chelate; first pereopod with long dactylus, both fingers with occlusal surfaces with spines.

Included genus.—*Palaeopentacheles* Von Knebel, 1907.

Material examined.—*Palaeopentacheles roettenbacheri* (Münster, 1839), SMF X/M 139. *Palaeopentacheles? starri* Schweitzer and Feldmann, 2001, USNM 512162, holotype.

Geologic range.—Upper Jurassic (Tithonian)-Oligocene.

Polychelidae Wood-Mason, 1875

Fig. 7F

Diagnosis.—Carapace longer than wide, dorsoventrally flattened; rostrum indistinct; deep orbital indentations, eyes reduced; antennal groove absent; cervical groove deep; with branchial and thoracic median carinae; lateral margins denticulate or spinose; epistome and carapace not in broad contact. Pleon with axial keel and sharp demarcation between terga and pleura; telson subtriangular; exopod of uropods without diaeresis. Antennular stylocerite present; maxilliped 3 dactylus sharp; pereopods 1-4 chelate; fingers on pereopod 1 with long, needle-like denticles; pereopod 5 may be chelate.

Included fossil genera.—*Antarcticheles* Aguirre-Urreta et al., 1990; *Willemoesiocaris* van Straelen, 1925.

Material examined.—*Cardus crucifer* (Thomson, 1873), USNM 154313; *Pentacheles laevis* Bate, 1878, USNM 30320; *Polycheles typhlops* Heller, 1862, USNM 1001100; *Stereomastis sculpta* (Smith, 1880), USNM 126089; *Willemoesia leptodactyla* (Thomson, 1873), USNM 210824. *Antarcticheles antarcticus* Aguirre-Urreta et al., 1990, cast of CIRGEO 1248 (holotype) numbered KSU D135.

Geologic range.—Middle Jurassic (Callovian)-Holocene.

Remarks.—As with Eryonidae and *Palaeopentacheles*, Polychelidae lack a diaeresis on the exopod of the uropods. The elongate, ovoid carapace outline, denticulate lateral margins, and strongly denticulate fingers, among other characters, distinguish this family from other Polychelida.

*Antarcticheles* exhibits a carapace that is longer than wide and flattened, but the axial regions are elevated and well defined, and the cervical and branchiocardiac grooves and lateral notches are well developed as is the postcervical groove which crosses the midline. The pleon of *Antarcticheles* is axially keeled. The carapace of *Willemoesiocaris* is subrectangular with weakly convex, denticulate margins and well-developed cervical and branchiocardiac grooves, diagnostic for the family. An axial carina is absent, but lateral carinae extend the length of carapace. Pleon and appendages are not known.

Tetrachelidae Beurlen, 1930a

Fig. 7E

Diagnosis.—Carapace almost quadrangular with orbital emarginations, dorsoventrally flattened, rostrum indistinct; antennal groove absent; cervical and branchiocardiac grooves strongly marked and V-shaped, extending to median; postcervical groove connected with cervical and branchiocardiac grooves; branchial and thoracic median carinae present; epistome and carapace not in broad contact. Pleon with axial keel and sharp demarcation between terga and pleura; telson subrectangular; exopod of uropods with diaeresis. Antennular stylocerite present; maxilliped 3 dactylus sharp; pereopods 1-4 chelate; pereopod 5 unknown.

Included genus.—*Tetrachela* Reuss, 1858.

Geologic range.—Upper Triassic (Carnian).

Remarks.—The family is monotypic, not unusual among Triassic lobster families. It is the oldest member of the infraorder.

Tricarinidae Feldmann, Kolahdouz, Biranvand, and

Schweigert, 2007

Fig. 7C

Diagnosis.—Carapace dorsoventrally flattened; front broad, projected beyond bases of antennae; anterolateral and posterolateral corners with spines; rostrum indistinct; orbits and eyes undeveloped; antennal groove absent; lacking cervical groove and other transverse grooves; with branchial and thoracic median carinae. Pleon lacking axial keel but with sharp demarcation between terga and pleura; antennae arising near anterolateral corners.

Included genus.—*Tricarinata* Feldmann et al., 2007.

Material examined.—*Tricarinata gadvanensis* Feldmann et al., 2007, CM54197, holotype.

Geologic range.—Lower Cretaceous (Barremian-Aptian).

Remarks.—The family is monotypic and represents one of the few fossil decapod taxa known from Iran. Originally, the taxon was placed within Palinuroida which at that time embraced both what is now Achelata and Polychelida. We herein place Tricarinidae with Polychelida, based upon its indistinct grooves, presence of a cephalic median and thoracic carinae, and a dorsoventrally compressed carapace. These features are most characteristic of Polychelida. Within Polychelida, this family seems most allied with Eryonidae and Palaeopentachelidae based upon its indistinct groove pattern.

## Infraorder Achelata Scholtz and Richter, 1995

Fig. 8

Diagnosis.—Carapace subcylindrical, rostrum indistinct or small and bifid; epistome in broad contact with carapace. Pleon with well developed pleura; telson and uropods calcified proximally, distally flexible. Sternum broad. Scaphocerite absent; antennular plate present; maxilliped 3 dactylus blunt; pereopods 1-4 achelate; pereopod 5 sometimes pseudochelate in females; pereopod 1 very rarely pseudochelate.

Included superfamily.—Palinuroidea Latreille, 1802.

Geologic range.—Lower Triassic (Anisian)-Holocene.

Remarks.—Absence of chelate closures on the pereopods, possession of a subcylindrical carapace, and a telson and uropods that are only calcified proximally unite Achelata. The three families within the Infraorder are readily distinguished on the form of the antennae. Those of Palinuridae exhibit long, strong basal segments and relatively long, slender, often somewhat rigid flagellae. The flagellae of Cancrinidae are short, blunt, and strongly inflated. The antennae of Scyllaridae are short, with plate-like structures instead of typical flagellae.

## Palinuroidea Latreille, 1802

Diagnosis.—As for infraorder.

Included families.—Cancrinidae Beurlen, 1930b; Palinuridae Latreille, 1802; Scyllaridae Latreille, 1825.

## Cancrinidae Beurlen, 1930b

Fig. 8B

Diagnosis.—Carapace subcylindrical to subrectangular; rostrum indistinct or small and bifid; cervical groove short; epistome in broad contact with carapace. Pleon finely granulate with well-developed pleura; subrectangular telson and uropods calcified proximally, distally flexible. Sternum broad. Antennae thick with short stalks and 13 to 19 rings, widest in middle part, triangular in cross-section, with long setae on inner edge; Scaphocerite absent; antennular plate present; maxilliped 3 dactylus blunt; pereopods 1-5 achelate; pereopod 1 shorter than others; pereopods 2-5 long and slender.

Included genera.—*Cancrinos* Münster, 1839; *?Praeatya* Woodward, 1868.

Material examined.—*Cancrinos claviger* Münster, 1839, BSP AS I 998; *Praeatya scabrosa* Woodward, 1868, (BMNH) In. 28392, 38418, syntypes.

Geologic range.—?Lower Jurassic (Hettangian-Sinemurian); Upper Jurassic (Tithonian)-Upper Cretaceous (Cenomanian).

Remarks.—Placement of *Praeatya* into this family is definitely tentative. The specimens exhibit achelate pereopod terminations, stout basal articles of the short antennae, and a broad carapace that appears relatively unornamented by grooves. The short but stout antennae seem to best suggest placement in Cancrinidae at this time.

## Palinuridae Latreille, 1802

Fig. 8A

Diagnosis.—Carapace subcylindrical or semirectangular, rostrum indistinct or small and bifid; eyes protected by large supraocular spines (horns); epistome in broad contact with carapace; bearing spines or other carapace ornamentation. Pleon with well-developed pleura; telson rounded subrectangular; telson and uropods calcified proximally, distally flexible. Sternum broad. Antennae very large, thick, antennal bases usually with spines; scaphocerite absent; antennular plate present; maxilliped 3 dactylus blunt; pereopods 1-5 achelate; first pereopods almost always same length or only slightly longer than other pereopods, very rarely pseudochelate; pereopod 5 sometimes pseudochelate in females.

Included fossil genera.—*Archaeocarabus* M'Coy, 1849; *Archaeopalinurus* Pinna, 1974; *Astacodes* Bell, 1863; *Eurycarpus* Schlüter in Schlüter and von der Marck, 1868; *Jasus* Parker, 1883 (extant); *Justitia* Holthuis, 1946 (extant); *Linuparus* White, 1847 (extant); *Palaeopalinurus* Bachmayer, 1954; *Palinurina* Münster, 1839; *Palinurus* Weber, 1795 (extant); *Panulirus* White, 1847 (extant); *Rugafarius* Bishop, 1985; *Yunnanopalinura* Feldmann et al., 2012.

Material examined.—*Archaeocarabus bowerbanki* M'Coy, 1849, (BMNH) 64621, I.63380, 38388, 24621, 46358; *Astacodes falcifer* Bell, 1863, (BMNH) 42238, lectotype; *Jasus paulensis* (Heller, 1862), USNM 228796; *Linuparus canadensis* (Whiteaves, 1885), USNM 529228 (as *L. atavus*, holotype); *L. tarrantensis* Davidson, 1963, USNM 132020, 132021, holotype; *L. vancoverensis* (Whiteaves, 1895), USNM 73706, holotype; *L. wilcoxensis* Rathbun, 1935, USNM 336020, holotype; *Palinurellus wieneckii* (De Man, 1881), USNM 107345; *Palinurus elephas* (Fabricius, 1787), USNM 1151684; *Panulirus argus* (Latreille, 1804), USNM 13996; *Projasus parkeri* (Stebbing, 1902), USNM 221819; *Puerulus angulatus* (Bate, 1888), USNM 104636; *Rugafarius fredrichi* Bishop, 1985, SDSM 10029, holotype; *Sagmariasus verreauxi* (H. Milne Edwards, 1851), USNM 240250, 240252; Synaxiidae indet, USNM ST #RW88-28; *Yunnanopalinura schrami* Feldmann et al., 2012, LPI-40169 (holotype), LPI-41667 (paratype).

Geologic range.—Middle Triassic (Anisian)-Holocene.

Remarks.—In addition to the characters defining the section and family, the included fossil genera bear clear distinguishing features. *Archaeocarabus* bears a carapace with a moderate-sized rostrum separated from large supraorbital spines by a straight, spinose front; supraorbital carinae extend to a well-developed, arcuate cervical groove. The pleon is smooth, and the sternum has four pairs of tubercles flanking the midline. Pereopod 1 is stout and possibly pseudochelate. *Archaeopalinurus* is incompletely known; however, possession of long, stout antennae, an incompletely calcified telson and uropods, and achelate pereopods places the genus within Palinuridae. Supraorbital spines on *Astacodes* are prominent, widely spaced, and laterally compressed; spinose postantennal keels extend to the cervical groove; the thoracic part of the carapace lacks keels. The pleura are without transverse grooves in *Astacodes* and with a posteroventrally directed, curved spine on the anterior mar-

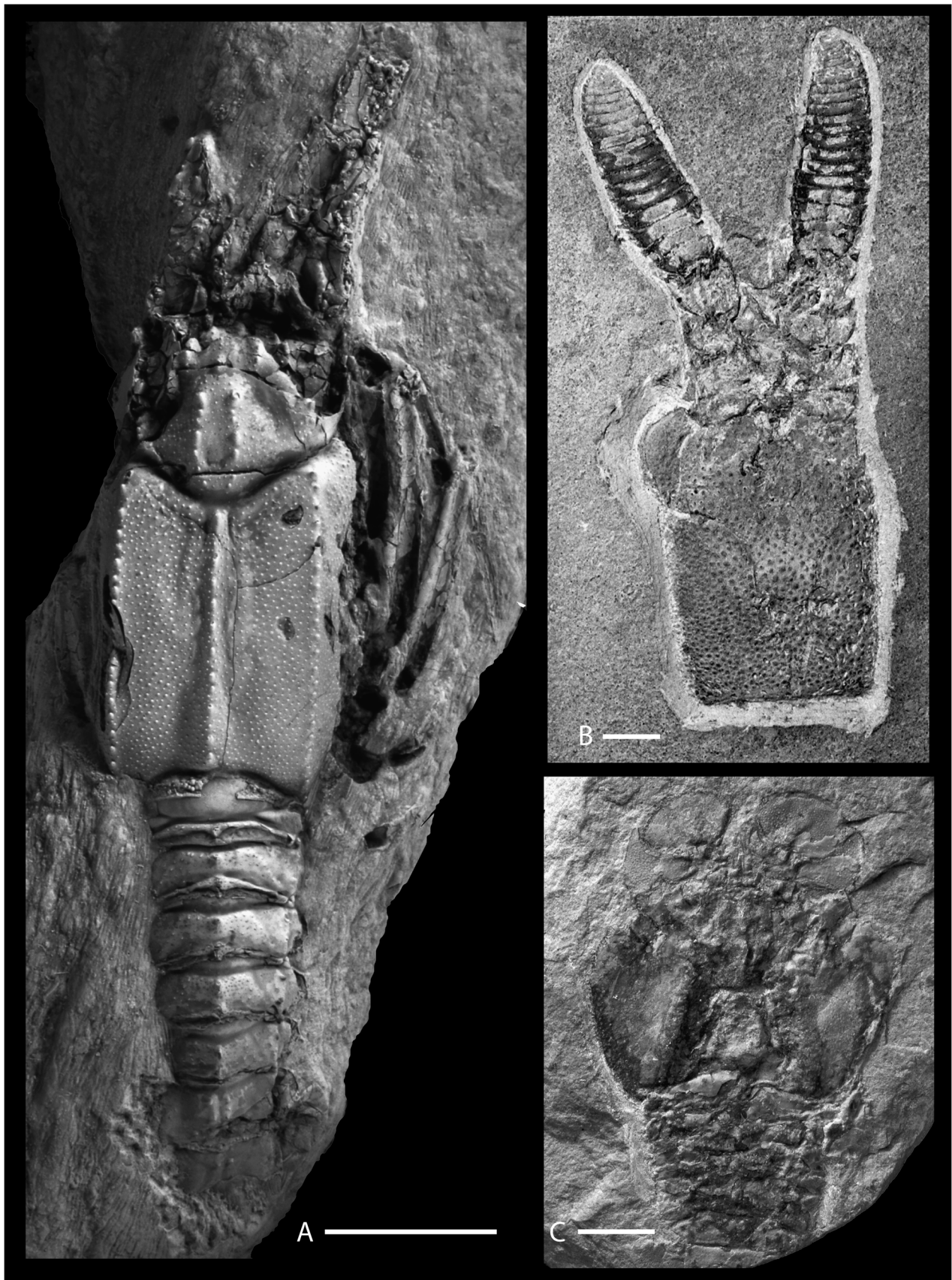


Fig. 8. Infraorder Achelata. A, Palinuridae, *Linuparus grimmeri* Stenzel, 1945, USNM Acc. #259571; B, Cancrinidae, *Cancrinos claviger* Münster, 1839, holotype, BSP AS I 998; C, Scyllaridae, *Palibacus praecursor* (Dames, 1886), BSP 1966 XXV 4-7. Scale bars = 1 cm.

gin of pleura 4-6; the uropods are lanceolate. *Eurycarpus* is only known from a single specimen with long antennal stalks and long, slender pereopods, which secure its place within Palinuridae until better material is recovered. The triangular rostrum on *Jasus* is clasped by hooked processes of the ophthalmic somite and extends anteriorly almost to level of strong, ridged supraorbital spines. Pereiopod 1 is stout. *Justitia* is characterized by denticulate supraorbital spines and a squamose carapace ornament; pleomeres 2-5 have transverse grooves on the terga and sharp, posteroventrally directed spines on the pleura. The most widely distributed palinurid in the fossil record, *Linuparus*, exhibits a carapace that is subquadrate in cross-section and has three longitudinal keels; a rostrum is lacking and supraorbital spines lie near the midline. A prominent, ridged swelling lies on the flank just posterior to the cervical groove, and the pleon has keeled terga and variously spined lateral margins on well-developed pleura. Pereiopod 1 is stout, and pereopods 1-5 are achelate. *Palaeopalinurus* is poorly preserved but bears large supraorbital spines and other carapace spines, a well-developed cervical groove, and transversely grooved and a ridged thoracic region. In addition to the characters of Palinuridae, *Palinurus* bears large, obliquely flattened, supraorbital spines and pereiopod 1 is shorter than pereopods 2-5. *Palinurina* exhibits a very small, triangular rostrum set between widely spaced supraorbital spines; the antennal spines are well developed and the suborbital spine is weak. The pleon is longer than the carapace. Pereiopod 1 is shorter and stronger than pereopods 2-5. The carapace of *Panulirus* lacks an axial keel but bears long pointed supraorbital spines. The pleon is smooth, with one transverse groove on the terga and a single terminal spine on the pleura. Pereiopods are generally smooth and pereiopod 1 is not enlarged. *Yunnanopalinura* bears stout antennae; stout, pseudochele first pereiopods; and a granular carapace that place it into the Palinuridae. Originally identified as a galatheid (Bishop, 1985, p. 614), *Rugafarius* is known only from a single carapace. It bears an antennal spine, closely spaced cervical and postcervical grooves, a granular axial keel on the thoracic region, and coarse scabrous ornamentation. Placement in Palinuridae is tenuous.

Scyllaridae Latreille, 1825  
Fig. 8C

Diagnosis.—Carapace subcylindrical to subrectangular, dorsoventrally more or less flattened, with sharp lateral margins; rostrum indistinct or small and bifid; orbits in anterior margin; supraorbital spines absent; epistome in broad contact with carapace. Pleon wide, well developed, with well-developed pleura; telson and uropods calcified proximally, distally flexible. Sternum broad. Antennae short, wide, flattened into plates with dentate or lobulate margins; scaphocerite absent; antennular plate present; maxilliped 3 dactylus blunt; pereopods 1-5 generally achelate but pereiopod 5 sometimes pseudochele in females.

Included fossil genera.—*Acanthophoenicides* Audo and Charbonnier, 2012 (extinct); *Biarctus* Holthuis, 2002 (extant); *Palibacus* Förster, 1984; *Parribacus* Dana, 1852a (extant); *Scyllarella* Rathbun, 1935; *Scyllarides* Gill, 1898 (extant); *Scyllarus* Fabricius, 1775 (extant).

Material examined.—*Acantharctus posteli* (Forest, 1963), USNM 126156; *Ibacus alticrenatus* Bate, 1888, USNM 98873; *Palibacus praecursor* (Dames, 1886), BSP 1966 XXV 4-7, neotype BSP 1975 I 66; *Parribacus antarcticus* (Lund, 1793), USNM 100823; *Scammarctus batei* (Holthuis, 1946), USNM 1004698; *Scyllarella gardneri* (Woods, 1925), (BMNH) In. 22414, holotype; *Scyllarella gibbera* Rathbun, 1935, USNM 336005, paratype; *Scyllarides nodifer* (Stimpson, 1866), USNM 14476, 274950, 274952; *Scyllarides punctatus* (Woods, 1926), (BMNH) In. 22411, holotype; *Scyllarus caparti* Holthuis, 1952, USNM 126150; *Thenus orientalis* (Lund, 1793), USNM 104398.

Geologic Range.—Lower Cretaceous (Albian)-Holocene.

Remarks.—In addition to the characters typifying the family, species of *Biarctus* have only two medial spines in advance of the cervical groove. The pleon lacks an axial keel and has an anastomosing pattern of narrow, deep grooves on the terga of somites 2-5, and bluntly triangular, downturned pleura. Pereiopod 2 has an elongated propodus and dactylus (extracted from Holthuis, 2002, p. 629). *Palibacus* has a wider than long carapace; orbits nearer to the midline than to the anterolateral corner; a deep cervical notch; two blunt spines just posterior to the cervical notch; and smooth lateral margins that converge posteriorly. The pleon is much narrower than the carapace, and the margin of the pleon is weakly convex with a strong narrow, granular, axial crest. The orbits on *Parribacus* lie midway between the midline and the anterolateral corner; and the carapace surface is generally scabrous and lacking definition of carapace grooves. The lateral margin has six or seven anterolaterally directed spines. The pleon has an axial carina and prominent anterolaterally directed spines that terminate the pleura of somites 2-5. *Scyllarella* has a rectilinear carapace with anterolateral margin about 75% of the maximum width and a strongly elevated axis with two prominent nodes. The lateral margins are upturned with small, rounded projections, and nodose lateral carinae diverge slightly posteriorly. The carapace of *Scyllarides* is moderately vaulted, longer than wide, and has orbits situated at the anterolateral corners. The shallow cervical and branchiocardiac notches are situated on generally smooth lateral margins. The pleon has a broad axial crest, but it is not otherwise strongly ornamented. Pereiopod 5 may be chelate in *Scyllarides*. *Scyllarus* has a carapace that is longer than wide, not strongly vaulted, and with eyes set near the anterolateral corner. Two or three axial spines are placed anterior to the cervical groove, and the lateral margin is finely denticulate. The pleon has a longitudinal carina and arborescent sculpture. The terminal antennal plate has a few large spines.

*Ibacus* Leach, 1815, is included in the phylogenetic analysis based solely upon extant specimens. A single fossil species, *I. praecursor*, was named by Dames (1886) for material from the Cretaceous of Lebanon. Subsequently, Förster (1984) restudied the material and reassigned the species to *Palibacus*, so that *Ibacus* is now confined to present-day occurrences.



Infraorder Glypheidea Winkler, 1882  
Figs. 9-12

Diagnosis.—Subcylindrical carapace; well-developed rostrum; cervical, postcervical, and branchiocardiac grooves present and generally well developed; pleonal somites with triangular or rectangular pleural terminations, subrectangular telson; exopod of uropods with diaeresis; third maxillipeds long, pediform; pereopod 1 pseudochelate or chelate, rarely achelate; pereopods 2-4 chelate, pseudochelate, or achelate; pereopod 5 with terminal dactylus.

Included superfamilies.—Erymoidea van Straelen, 1925; Glaessnericarioidea new superfamily; Glypheoidea Winkler 1882.

Geologic Range.—Permian-Recent.

Discussion.—Glaessner (1969) referred Glypheoidea to Palinura Latreille, 1802, perhaps due to their achelate nature, and Erymidae to Astacidea, probably due to their possession of claws. Glaessner's conception of Glypheoidea was different than that construed herein because he included Pemphicidae, which we herein refer to Erymoidea. He also included Platychelidae in Astacidea, whereas we place it within Glypheoidea. Garassino and Schweigert (2006) referred Erymidae, Glypheidae, and Mecochiridae to Astacidea.

Ahyong and O'Meally (2004) showed that Glypheidea were distinct from Astacidea, and this arrangement has been recovered in phylogenies since then (Bracken et al., 2009; Boisselier-Dubayle et al., 2010). De Grave et al. (2009) and Schweitzer et al. (2010) provided what were at that time the most up-to-date generic and species, respectively, arrangements of the taxa within what was by then recognized as Glypheidea, a group that could embrace the living glypheids and a large array of extinct lobsters that belonged neither to Astacidea, Achelata, or Polychelida. They referred Glypheidae, Erymidae, Mecochiridae, Pemphicidae, and Platychelidae to Glypheidea. Our analysis shows that Glypheidea is in fact monophyletic but that the superfamily and family level generic arrangements are somewhat different than those presented in De Grave et al. (2009) and Schweitzer et al. (2010).

Erymoidea van Straelen, 1925  
Fig. 9

Diagnosis.—Subcylindrical carapace; well developed rostrum; cervical, postcervical, and branchiocardiac grooves present and generally well developed; gastroorbital, hepatic, and inferior grooves present; exopod of uropods with diaeresis; pereopods 1 always strongly developed, chelate (Erymidae) or pseudochelate (Pemphicidae); pereopods 2-3 chelate or pseudochelate; pereopods 4 and 5 generally achelate, 4 may be pseudochelate.

Included families.—Erymidae van Straelen, 1925; Pemphicidae van Straelen, 1928a.

Geologic range.—Middle Triassic-Eocene (Bartonian).

Remarks.—Erymoidea as defined by De Grave et al. (2009) and Schweitzer et al. (2010) included only the Erymidae. The analysis of Amati et al. (2004) suggested that the Pemphicidae were closely related to Erymidae as does our analysis. They are sister groups in our analysis as they were

in the analysis of Amati et al. (2004). Erymoids always have a strongly developed first pereopod, which may be chelate or pseudochelate; the other chelae are variable. The carapace is ornamented by well-developed grooves but lacks cephalic ridges.

Erymidae van Straelen, 1925  
Fig. 9A

Diagnosis.—Subcylindrical carapace with very deep cervical groove, with intercalated plate in anterior axial portion of carapace; gastroorbital, hepatic, and inferior grooves present; branchiocardiac and postcervical grooves almost parallel; moderately spined rostrum; flat pleon with triangular somites, sharp demarcation between tergites and pleurites, exopod of uropods with diaeresis; pereopod 1 with large chelae, upper margin of fixed finger often concave; carpus short, rectangular; pereopods 2 and 3 chelate or pseudochelate; pereopods 4 and 5 with terminal dactyli; carapace and first pereopod surfaces finely or coarsely granular.

Included genera.—*Enoploclytia* M'Coy, 1849; *Eryma* von Meyer, 1840b; *Galicja* Garassino and Krobicki, 2002; *Olinnaecaris* van Straelen, 1925; ?*Oosterinkia* Klompmaker and Fraaije, 2011; *Palaeastacus* Bell, 1850; *Pustulina* Quenstedt, 1857; ?*Stenodactylina* Beurlen, 1928.

Material examined.—*Eryma bedelta* (Quenstedt, 1857), KSU D 68, 1427; *E. bordenensis* (Copeland, 1960), KSU D 1444; *E. jungostrix* Feldmann and Titus, 2006, cast of USNM 530027, holotype, numbered KSU D 799; *E. modestiforme* (Schlotheim, 1822), KSU D 67, cast of SMF x/m 100 numbered KSU D 462, MB.A.1042, MB.A.407, MB.A.404; *E. mosquensis* Lahusen, 1894, BSP 1988 III 83 numbered KSU D 586; *E. sulcatum* Harbort, 1905, KSU D 1434. *Eryma ventrosa* (von Meyer, 1835), KSU D 1438. *Palaeastacus foersteri* Taylor, 1979, cast of (BAS) KG.50.4, holotype, numbered KSU D 843, KSU D 1788; *P. fuciformis* (Schlotheim, 1822), KSU D 64, cast of SMF x/m 101 numbered KSU D 464, KSU D 1433; *P. scaber* (Bell, 1863), KSU D 1428; *P. sussexiensis* (Mantell, 1833), KSU D 1787, 1895; *P. terraereginae* (Etheridge, Jr., 1914), cast of (BAS) KG.3.11 numbered KSU D 833, cast of (BAS) KG.11.4 numbered KSU D 842, KSU D 1792; *P. trisulcatus* Schweitzer and Feldmann, 2001, cast of USNM 512150, holotype, numbered KSU D 367; *Pustulina dawsoni* (Woodward, 1900), cast of GSC 5969 numbered KSU D 1447.

Geologic range.—?Middle Triassic (Anisian); Early Jurassic (Hettangian)-Eocene (Bartonian).

Remarks.—As discussed by Feldmann et al. (2012), Erymidae had become unwieldy and too broadly construed over the past years to be useful for classification and distinguishing among lobster groups. They removed several genera from Erymidae, namely those that lacked the intercalated plate anteriorly along the axis. Herein, we concur with this definition for Erymidae, restricting it to those genera possessing the intercalated plate as well as chelate first pereopods with rectangular carpi and well developed carapace grooves. Those genera that had previously been placed within Erymidae that lacked the intercalated plate were placed by Feldmann et al. (2012) into Clytiopsidae,

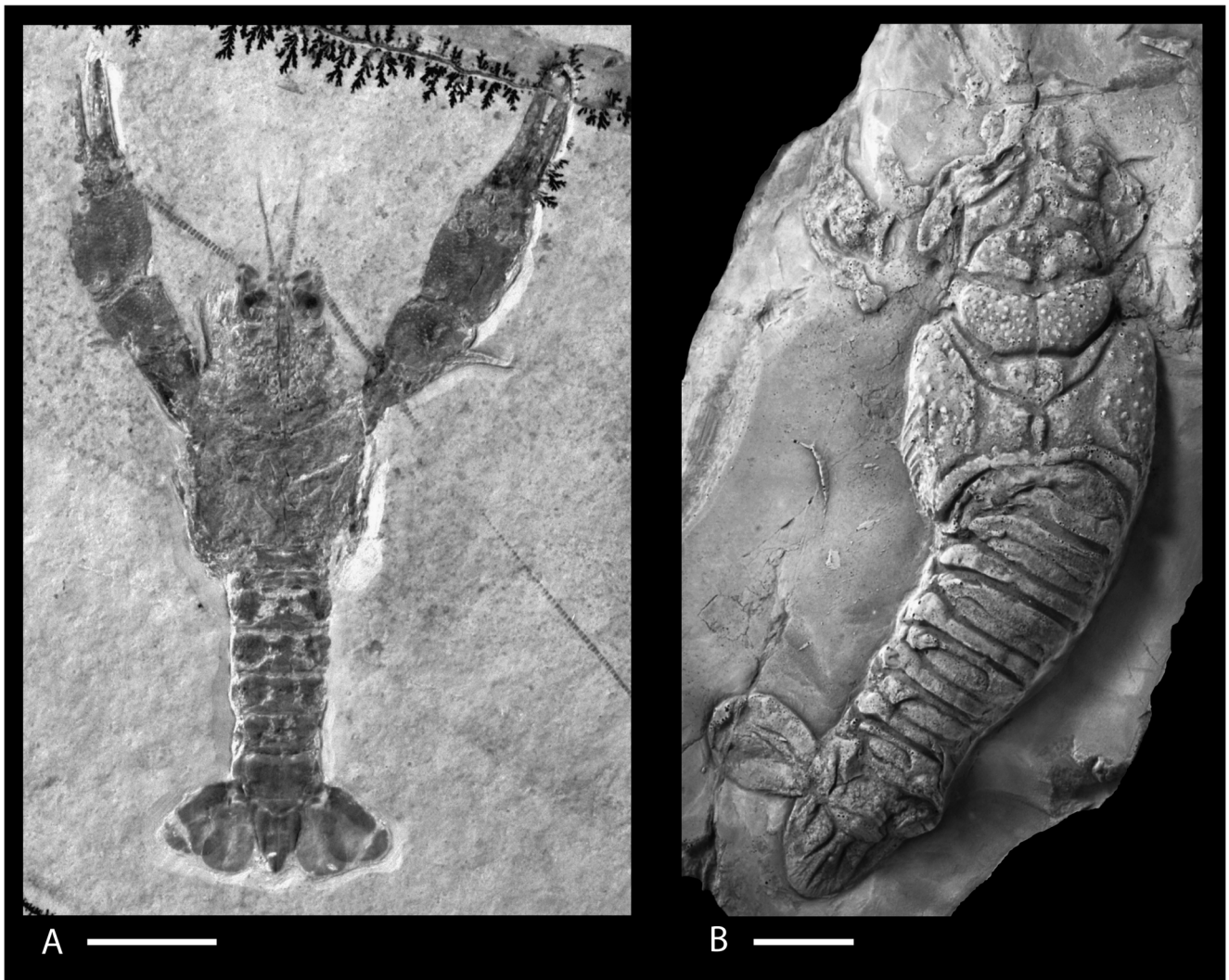


Fig. 9. Infraorder Glypheidea, Superfamily Erymoidea. A, Erymidae, *Eryma modestiforme* (Schlotheim, 1822), MB.A. Inv. Nr. 1995.4; B, Pemphicidae, *Pemphix sueurii* (Desmarest, 1822), cast of SMNS 4701. Scale bars = 1 cm.

which was recovered in our analysis, discussed below. Thus, Erymidae is now quite reduced in size and restricted morphologically.

Herein we also restrict the range of Erymidae by removing the Late Permian *Eryma hoerstgenensis* (Bachmayer and Malzahn, 1983) from the genus and the family. This species is based upon a tiny claw that cannot be referred to *Eryma* based upon its angular manus and fingers that lack the concave upper surfaces seen on species of *Eryma* and other erymids. In addition, the referral of this species to *Eryma* constitutes a nearly 150 million year range extension from the next oldest member of the genus. Thus, we herein remove *E. hoerstgenensis* to Decapoda incertae sedis. Erymidae occurs from the Middle Triassic to Eocene, although the Middle Triassic occurrence is also debatable, as discussed below.

Nearly all of the genera placed within this family herein have intercalated plates and chelae and carapace groove patterns diagnostic for the family. However, two genera are fragmentary. *Olinacaris* is only a portion of a cephalotho-

rax, but it possesses two deep, well-developed grooves (van Straelen, 1925, pl. 9, Figs. 4, 5) that make placement in Erymidae appear to be most parsimonious at this time. *Stenodactylina* is only a portion of a chela, characterized by a spiny manus and an edentulous, long fixed finger (Beurlen, 1928, pl. 6, Fig. 4). It is reminiscent of those of *Enoplocyrtia*; thus, placement in Erymidae seems best at this time.

*Oosterinkia* is problematic and was not included in the phylogenetic analysis due to its incomplete nature. Its features are rather difficult to interpret. It has a broad, triangular rostrum, not like those of other erymids. The structure interpreted as the intercalated plate is much longer and narrower than those in other erymids, and examination of illustrations suggests that it may actually be a broken axial ridge. The groove pattern is also different from other erymids; it has deep cervical and branchiocardiac grooves and another deep groove, possibly a gastroorbital groove, extending anteroventrally. The carapace also appears to have moderate hepatic and epibranchial swellings. These features are reminiscent of Pemphicidae, members of which can have

an axial ridge, carapace swellings, and wider rostra than Erymidae. *Oosterinkia* is also the same age, Middle Triassic, as other pemphicids, and is older than other confirmed erymids (Sinemurian) by nearly 40 million years. However, until we can examine type material, *Oosterinkia* will remain in Erymidae.

The intercalated plate in Erymidae is certainly distinctive and has been traditionally considered to be of taxonomic significance (Schram and Dixon, 2004). Although van Straelen (1925) did not include the plate as a definitive character of the family, he did note its presence in *Eryma*. Glaessner (1969) considered it to be one of the family-level characters, but placed Clytiopsinae within the family. Clytiopsinae lack the intercalated plate, which prompted Amati et al. (2004) and Feldmann et al. (2012) to elevate the subfamily to family status.

The functional significance of the intercalated plate is problematic. Some Paleozoic phyllocarid arthropods, including *Ceratiocarina* Clarke in Zittel, 1900, and *Rhinocarina* Clarke in Zittel, 1900, possessed a rostral plate intercalated along the medial axis and extending anteriorly into a simple rostrum. However, other than these occurrences within Phyllocarida and that of the plate in Erymidae, no other accessory plates in Malacostraca are known to us. It is tempting to suggest that the intercalated plate in erymids is a vestige of the rostral plate seen in the Paleozoic phyllocarids, but there is no clear evidence for such a relationship. Thus, the plate remains a taxonomically significant marker with a murky history and function.

#### Pemphicidae van Straelen, 1928a

##### Fig. 9B

Diagnosis.—Subcylindrical carapace with antennal carina; gastro-orbital, hepatic, and inferior grooves present; cervical, postcervical, and branchiocardiac grooves all well developed, the latter two joining on flank; cervical groove deepest and widest of the three; gastric and hepatic regions differentiated; carapace ornamented with coarse or fine granules; long, spatulate rostrum; subrectangular pleonal somites, exopod of uropods with diaeresis, subrectangular telson; pereopod 1 strongly developed and subchelate, merus rectangular, short; pereopods 2-3 slender and subchelate; pereopods 4-5 with terminal achelate dactylus.

Included genera.—*Pemphix* von Meyer, 1840a; *Sinopemphix* Li, 1975.

Material examined.—*Pemphix sueurii* (Desmarest, 1822), cast of NHMW 1848 I 430 numbered KSU D 491; cast of NHMW 1844 III 52 numbered KSU D 490; cast of RGM 244988 numbered KSU D 428; cast of IRB IG 9229 numbered KSU D 543; cast of IRB IG 9271 numbered KSU D 544; cast of BSP 1988 III 156 numbered KSU D 579; cast of molted specimen in SMNS numbered KSU D 396; cast of SMNS 4701 numbered KSU D 397. *Sinopemphix guizhouensis* Li, 1975, cast of cast of holotype, BSP III 126 numbered KSU D 563.

Geologic range.—Middle Triassic (Anisian-Ladinian).

Remarks.—Pemphicids are easily recognized by the well-defined regions on the dorsal carapace that are reminiscent of, but not the same as, the carapace regions of brachyurans.

The broad spatulate rostrum of these lobsters is distinctive, as are the well-defined, deep carapace grooves. The carpus of the only member of the Pemphicidae, *Pemphix*, in which it is preserved, is short and rectangular. Whereas *Pemphix* has a postcervical groove that extends to the dorsal surface that of *Sinopemphix* lacks the anterodorsal segment of that groove. The rostrum of *Pemphix* is not downturned, but it is downturned in *Sinopemphix*.

#### Glaessnerarioidea New Superfamily

##### Fig. 10

Diagnosis.—Cylindrical carapace with cervical, postcervical, and branchiocardiac grooves, median suture present; long rostrum bearing three suprarostal teeth; dorsal margin of carapace with spines arranged in two longitudinal parallel rows; exopod of uropods with diaeresis; pereopods 1-4 chelate.

Included family.—Glaessnericarididae new family.

#### Glaessnericarididae New Family

Diagnosis.—As for superfamily.

Included genus.—*Glaessnericaris* Garassino and Teruzzi, 1993.

Geologic range.—Late Triassic (Norian).

Discussion.—*Glaessnericaris* was originally referred to Platychelidae. However, that family was originally defined as having, and the type genus possesses, chelate pereopods 1-3 with very small chelae and achelate pereopods 4 and 5. *Glaessnericaris* has chelate pereopods 1-4. In addition, Platychelidae has cervical, postcervical, and branchiocardiac grooves, but the latter two are weak, whereas in *Glaessnericaris*, all three are more or less equal. *Glaessnericaris* has rows of spines on the dorsal carapace, which Platychelidae lack. These differences have resulted in *Glaessnericaris* occupying an entirely separate clade from all other lobsters, warranting a distinct family and superfamily to accommodate it.



Fig. 10. Infraorder Glypheidea, Superfamily Glaessnerarioidea. *Glaessnericaris macrochela* Garassino and Teruzzi, 1993, holotype MSNB 4202, image by A. Paganoni.

Glypheoidea Winkler, 1882  
Figs. 11, 12

Diagnosis.—Subcylindrical carapace; short or long rostrum usually without spines (except Litogastroidea); cephalic carinae present; gastroorbital, hepatic, and inferior grooves present; cervical groove well developed, postcervical and branchiocardiac grooves present, variously developed; postcervical groove generally parallel to branchiocardiac groove; pleonal somites with triangular or rectangular pleural terminations, sharp demarcation between pleura and terga, exopod of uropods with diaeresis; subrectangular telson; third maxillipeds long, pediform; pereopod 1 pseudo-chelate or chelate, pereopods 2–4 pseudo- or achelate, pereopod 5 with terminal dactylus.

Included families.—Chimaerastacidae Amati et al., 2004; Clytiopsidae Beurlen, 1927; Glypheidae Winkler, 1882; Litogastroidea new family; Mecochiridae van Straelen, 1925; Neoglypheidae new family; Platychelidae Glaessner, 1969.

Geologic range.—Permian–Recent.

Chimaerastacidae Amati, Feldmann, and Zonneveld, 2004  
Fig. 11A, B

Diagnosis.—Carapace subcylindrical, with distinct longitudinal cephalic ridges including antennal, suborbital, and median carinae; median suture present posteriorly; cervical, postcervical, and branchiocardiac grooves well defined, subparallel; cervical groove long, extending to dorsomedian, steeply inclined at 65–70° to dorsal surface; postcervical groove parallel to branchiocardiac groove, originating near dorsomedian, not reaching cervical groove or hepatic groove; intercervical groove absent; branchiocardiac groove at less than 30° angle to dorsal surface, joining median suture; urogastric and supplementary grooves absent; gastroorbital, inferior, and hepatic grooves present; antennal spine absent; long and prominent rostrum; chi swelling (attachment site of adductor testis muscle) well defined by grooves; sharp demarcation between pleura and terga, exopod of uropods with diaeresis; pereopods 1–3 chelate, pereopods 4 and 5 with terminal dactyli.

Included genus.—*Chimaerastacus* Amati, Feldmann, and Zonneveld, 2004.

Geologic range.—Middle Triassic.

Remarks.—Amati et al. (2004) discussed this family and the included genus at length. The type material was examined by one of us (RMF) during the original description of the taxon.

Clytiopsidae Beurlen, 1927  
Fig. 11C–E

Diagnosis.—Carapace with antennal and suborbital carinae; cervical, postcervical, and branchiocardiac grooves well defined, subparallel, cervical groove long, extending to dorsomedian; postcervical groove parallel to branchiocardiac groove, originating near dorsomedian, not reaching cervical groove or hepatic groove; intercervical groove and chi swelling absent; branchiocardiac groove at less than 30° angle to dorsal surface, joining median suture; urogastric and supplementary grooves absent; gastroorbital, inferior, and hepatic grooves present; antennal spine absent; short, well-developed rostrum, without supra- and subrostral spines; sharp demarcation between pleura and terga, exopod of uropods with diaeresis; pereopods 1–3 chelate, pereopods 4 and 5 achelate.

Included genera.—*Clytiella* Glaessner, 1931; *Clytiopsis* Bill, 1914; *Koryncheiros* Feldmann et al., 2012; *Paraclytiopsis* Oravecz, 1962; *Protoclytiopsis* Birshtein, 1958.

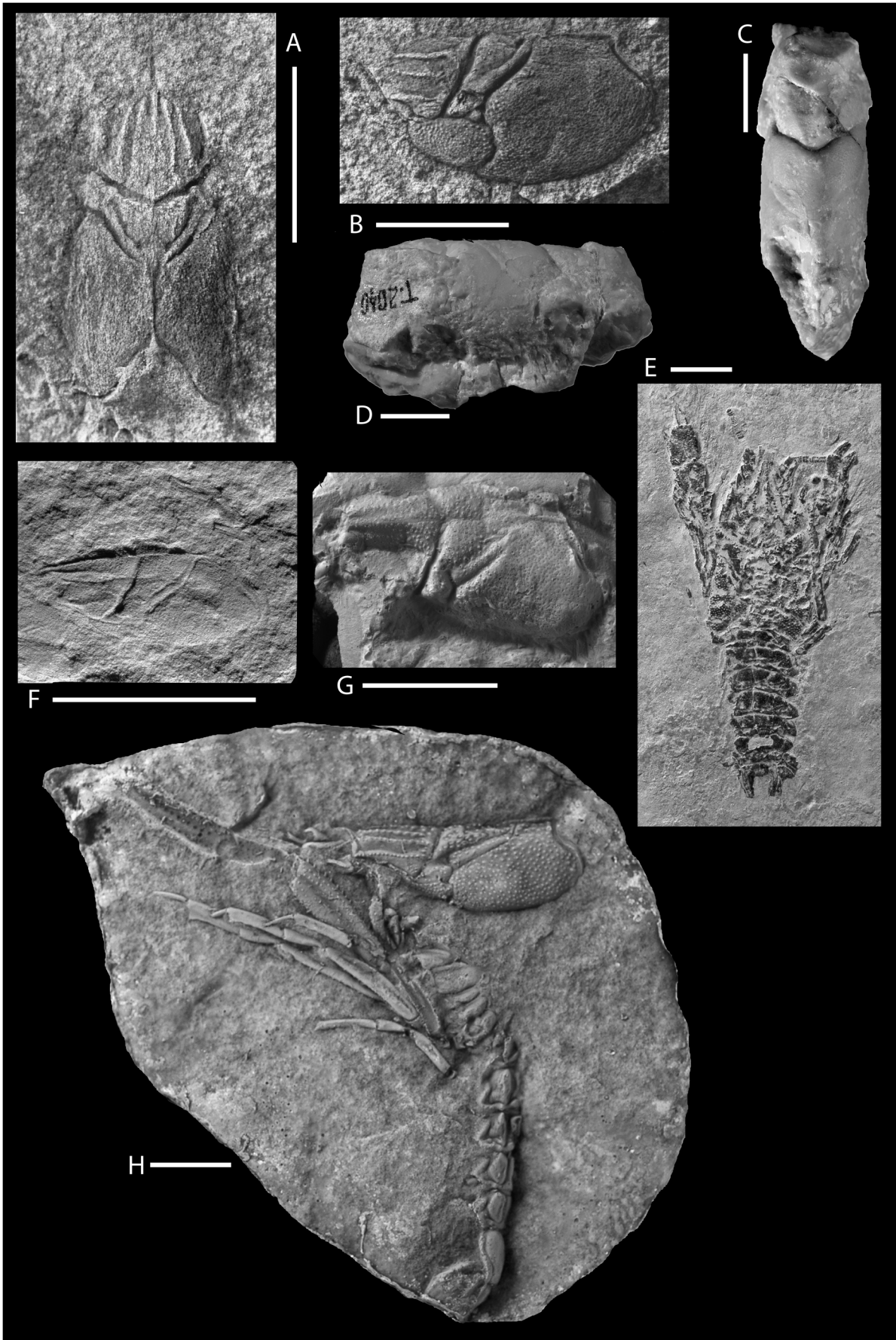
Material examined.—*Clytiella spinifera* Glaessner, 1931, photos of GBA 1931/003/0001, holotype; *Koryncheiros luopingensis* Feldmann et al., 2012, holotype, LPI 41171 and paratypes, LPI-40503a, 40505, 40535, 40550, 41793, 40542. *Paraclytiopsis hungaricus* Oravecz, 1962, KSU D 1599, cast of holotype MAFI T. 2040. *Protoclytiopsis antiqua* Birshtein, 1958, cast of a cast of holotype, BSP 1988 III 321 numbered KSU D 570.

Geologic range.—Late Permian–Late Triassic (Carnian).

Remarks.—Amati et al. (2004) and later Feldmann et al. (2012) resurrected Clytiopsidae to embrace members of Erymidae that lacked an axial intercalated plate. They placed that family within Erymoidea. Our analysis demonstrates that the possession of cephalic carinae, parallel postcervical and branchiocardiac grooves, and pleonal somites with triangular or rectangular pleural terminations and sharp demarcation between pleura and terga place this family within Glypheoidea.

*Koryncheiros* and *Clytiella* are referable to Clytiopsidae based upon their chelate pereopods 1–3, groove pattern, and lack of an intercalated plate. Some genera are only known from dorsal carapaces, *Paraclytiopsis* and *Protoclytiopsis*. However, both of these taxa are incomplete and placement within Clytiopsidae is rather provisional. *Paraclytiopsis* has a broken frontal area but enough appears to be preserved to show that it lacks an axial anterior intercalated plate. The broken nature of the anterior portion of the carapace also makes it difficult to determine whether or not the sole species had anterior cephalic ridges; none is visible. The cervical and branchiocardiac grooves of *Paraclytiopsis* are

Fig. 11. Infraorder Glypheoidea, Superfamily Glypheoidea. A, Chimaerastacidae, *Chimaerastacus paciflualis* Amati et al., 2004, RTM 97.121.535, dorsal view; B, Chimaerastacidae, *Chimaerastacus paciflualis* Amati et al., 2004, RTM 97.121.15, left lateral view; C, Clytiopsidae, *Paraclytiopsis hungaricus* Oravecz, 1962, holotype, MAFI type collection T. 2040; dorsal view, photo by Zoltan Lantos of MAFI, Budapest, Hungary; D, Clytiopsidae, *Paraclytiopsis hungaricus* Oravecz, 1962, holotype, MAFI type collection T. 2040; right lateral view, photo by Zoltan Lantos of MAFI, Budapest, Hungary; E, Clytiopsidae, *Koryncheiros luopingensis* Feldmann et al., 2012, LPI-40503, paratype; F, Litogastroidea, *Litogaster turnbullensis* Schram, 1971, PE 16215, photo courtesy F. Schram; G, Litogastroidea, *Litogaster obtusa* Von Meyer, 1847a, cast of SMNS 4401/653; H, Glypheidae, *Glyphea robusta* Feldmann and McPherson, 1980, holotype GSC 61398, molting specimen in Salter's position. Scale bars = 1 cm. A and B reprinted from the Journal of Paleontology, Vol. 78, p. 150–168, Figs. 9.1 and 9.5, with permission from the Paleontological Society.



deep, and the post-cervical groove is short and parallels the branchiocardiac groove.

In *Protoclytiopsis*, only half of the cephalothorax is preserved. Thus, it is difficult to know for certain whether or not an anterior axial intercalated plate was present, but it appears not to have been. There is no indentation along the dorsal surface where such a plate would have been inserted. *Protoclytiopsis* lacks cephalic ridges, although because the specimens known to us are casts, we do not know if they are internal molds or casts of cuticle. Thus, it is uncertain as to whether or not the original material may have possessed ridges. The well-developed omega and chi swellings are distinctive on this taxon and may help to more definitively place it in the future. For now, both *Paracltytiopsis* and *Protoclytiopsis* are placed in Clytiopsidae.

#### Glypheidae Winkler, 1882

Fig. 11H

Diagnosis.—Subcylindrical carapace, slightly compressed laterally, with longitudinal cephalic carinae; short or long rostrum; well-developed cervical groove, oriented at over 70° angle to dorsal surface of carapace, extending from dorsal surface to position beyond half-height of cephalothorax; postcervical groove variable, converging with branchiocardiac groove either dorsally and ventrally or only ventrally; branchiocardiac groove at less than 30° angle to dorsal carapace; laterocardiac groove present and parapostcervical groove sometimes present; pleonal somites generally smooth, rarely with transverse keels, with triangular pleural terminations, sharp demarcation between pleura and terga, subrectangular telson, exopod of uropods with diaeresis; third maxillipeds long, pediform; second antennal peduncle elongate; pereopods 1 and 2 pseudochele, pereopod 3 pseudo- or achelate, pereopods 4 and 5 with terminal dactylus.

Included genera.—*Cedrilloxia* Garassino, Artal, and Pasini, 2009; *Glyphea* von Meyer, 1835; *Squamosoglyphea* Beurlen, 1930a; *Trachysoma* Bell, 1858.

Material examined.—*Glyphea regleyana* (Desmarest, 1822), KSU D 795; cast of Paris VI, no. 30 in MNHN, numbered KSU D 797. In addition, one of us (RMF) has described numerous new species of *Glyphea*. *Squamosoglyphea dresseri* (von Meyer, 1840a), cast of holotype, Universitäts Museum Tübingen, Tübingen, Germany (holotype is apparently lost), cast of cast of holotype numbered KSU D 542. *Trachysoma rostrata* (Phillips, 1829), KSU D 1695.

Geologic range.—Triassic-Eocene.

Remarks.—Our analysis greatly restricts Glypheidae and eliminates the extant members from the family. This arrangement was also suggested by the analysis of Amati et al. (2004). Glypheidae are most clearly defined by possession of the laterocardiac groove and a quite variable postcervical groove. These features are not seen in other members of Glypheoidea. The first and second pereopods within Glypheidae *sensu stricto* are pseudochele, but pereopod 3 is variable, being pseudo- or achelate, and pereopods 4 and 5 have a terminal dactylus. This is a quite stereotypical pattern within the superfamily, actually, with very little variability.

*Cedrilloxia* is unusual in possessing a gastroorbital groove with two convex forward arcs. No other genus has such an unusual form. It also has several extensions of the branchiocardiac groove that are unlike those seen in other genera. The anterior narrowing of the carapace and very steep cervical groove are similar to those seen in glypheids. It is difficult to determine from the illustrations if the carapace has cephalic ridges; an antennal ridge is mentioned in the description. Thus, Glypheidae seems to be the best placement for *Cedrilloxia* at this time.

Squamoso carapace ornamentation distinguishes *Squamosoglyphea* from confamilial genera, and orientation of the cervical groove, at right angles to the dorsal surface, is unique to *Trachysoma* spp.

The restriction of the family herein limits the range of the family to the Triassic to Eocene. By far the most speciose genus within of the family is *Glyphea*. Revision of that genus is currently ongoing (A. Garassino, pers. commun. March 2012).

#### Litogastroidae New Family

Fig. 11F, G

Diagnosis.—Carapace subcylindrical, with cephalic ridges and antennal spine, rostrum usually with marginal spines; cervical, postcervical, and branchiocardiac grooves all present and well-developed, gastroorbital, hepatic, and inferior grooves present; postcervical groove usually reaching hepatic groove by arcuate groove (except *Lissocardia*); cervical groove at or less than 70° to dorsal surface; branchiocardiac groove at less than 30° angle to dorsal surface; sharp demarcation between pleura and terga, exopods of uropod with diaeresis; pereopods 1 chelate or pseudochele, pereopods 2 and 3 pseudochele (except *Lissocardia*, where they are chelate) pereopods 4 pseudo- or achelate; pereopod 5 achelate.

Included genera.—*Lissocardia* von Meyer, 1851 (= *Piratella* Assmann, 1927); *Litogaster* von Meyer, 1847a; *Paralitogaster* Glaessner, 1969; *Pseudoglyphea* Opper, 1861a; *Pseudopemphix* Wüst, 1903; *Tridactylastacus* Feldmann et al., 2012.

Material examined.—*Litogaster obtusa* von Meyer, 1847a, cast of SMNS 4401/653, numbered KSU D 406. *Pseudopemphix alberti* (von Meyer, 1840a), cast of SMNS plastyotype, possibly of holotype, numbered KSU D 398; cast of SMNS 22109 number KSU D 399; cast of SMNS 4401/650 numbered KSU D 400; cast of NHMW 1852 XIV 237 numbered KSU D 494. *Tridactylastacus sinensis* Feldmann et al., 2012, holotype, LPI-40546, and paratypes LPI-40140, 40503b, 41446, 41545, 41548, 41670, 41671, 41672, 41674, 41675, 41676, 41677, and 41764.

Etymology.—The etymology of constructing the family name was rather confusing. *Gaster* is Greek for stomach, and can terminate in the noun form as either *gastero-*, or *gastro-* (Brown, 1956, p. 26).

Geologic range.—Early Triassic (Olenekian)-Late Jurassic (Oxfordian).

Remarks.—Members of this new family were originally scattered amongst Erymidae, Glypheidae, Mecochiridae,

and Pemphicidae (De Grave et al., 2009; Schweitzer et al., 2010). They are united into Litogastroidae by their possession of cephalic ridges which differentiates them from Erymidae and Pemphicidae; lacking the laterocardiac groove which differentiates them from Glypheidae; branchiocardiac groove at less than 30° angle which differentiates them from Mecochiridae; and a variable combination of chelate, pseudo-chelate, or achelate pereopods, which differentiates them from Chimaerastacidae, Clytiopsidae, Mecochiridae, and Neoglypheidae, in which the chela pattern is very well defined. Thus, the new family brings together several genera that were not well accommodated in the families to which they had been historically placed.

*Tridactylastacus* was originally placed with Glypheidae based upon its similarities with *Paralitogaster*, *Pseudoglyphea*, *Trachysoma*, and *Squamosoglyphea*. Our analysis herein has rearranged the systematics of Glypheidae, and *Tridactylastacus* has most close affinities with members now referred to Litogastroidae. Both *Paralitogaster* and *Pseudoglyphea* have pseudo-chelate pereopods 1-4 and spinose ornamentation on the mani of pereopod 1 as does *Tridactylastacus*. The pleons of all three of these genera are delicate in size and small compared to the claws and carapace. Thus, because *Tridactylastacus* is missing carapace characters and could not be analyzed with the other genera, we place it with Litogastroidae at this time.

*Lissocardia* appears in this clade, although it is exceptional in many regards, having chelate second and third pereopods and lacking the postcervical groove reaching hepatic groove by arcuate groove. Interestingly, Förster (in Glaessner, 1969) had considered that *Lissocardia* was an intermediate form, apparently sharing features of Erymidae, Glypheidae, and Pemphicidae. Our analysis shows *Lissocardia* to fall within a new family, Litogastroidae, with Glypheidae but with characters unique within that family, perhaps foreshadowed by Förster's comments.

#### Mecochiridae van Straelen, 1925

##### Fig. 12B

Diagnosis.—Subcylindrical carapace slightly compressed laterally, median suture absent, with cephalic carinae usually ornamented with spines or tubercles but sometimes smooth; short rostrum lacking supra- and subrostral teeth; cervical, postcervical, and well-developed branchiocardiac grooves; cervical groove less than 70° angle to dorsal surface, branchiocardiac groove at over 30° angle to dorsal surface, expressed as concave arc; subrectangular pleonal somites; sharp demarcation between pleura and terga; exopod of uropods with diaeresis; second antennal peduncle elongate; pereopod 1 strongly elongate and pseudo-chelate or achelate; pereopod 2 pseudo- or achelate; pereopods 3-5 always with terminal dactyli.

Included genera.—*Huhatanka* Feldmann and West, 1978; *Jabaloya* Garassino, Artal, and Pasini, 2009; *Mecochirus* Germar, 1827; *Meyeria* M'Coy, 1849; *Selenisca* von Meyer, 1847b.

Material examined.—*Huhatanka kiwana* (Scott, 1970), KSU D 693, 1430, 1453, 1495, 1498, 1499. *Mecochirus longimanus* (Schlothheim, 1822), KSU D 1376, 1445; mold of USNM 20341, numbered KSU D 1388 and 1389. *Meyeria*

*ornata* (Phillips, 1829), KSU D 1440. *Selenisca gratiosa* von Meyer, 1847b, MCZ Invertebrate Paleontology 109949, holotype.

Geologic range.—Early Jurassic (Hettangian)-Late Cretaceous (Maastrichtian).

Remarks.—Mecochiridae is largely unchanged from the way it has been construed historically (Glaessner, 1969) and recently (De Grave et al., 2009; Schweitzer et al., 2010). From these generic lists, *Pseudoglyphea* has been removed to the Litogastroidae based upon its multiply pseudo-chelous appendages. *Praeatya* Woodward, 1869, which appears in all three lists mentioned above, is herein suggested to be a possible member of the Cancrinidae based upon its broad and flattened carapace, achelate appendages, and moderately stout antennae. *Jabaloya* was not included in the phylogeny due to its incomplete nature but is referable to Mecochiridae based upon its gently sloping cervical and branchiocardiac grooves and cephalic ridges.

Mecochiridae are united in possession of steep branchiocardiac grooves, pereopod 1 strongly elongate and pseudo-chelate or achelate, pereopod 2 pseudo- or achelate, and pereopods 3-5 always with terminal dactyli. No other members of the superfamily have pereopods 3-5 with terminal dactyls, and only Neoglypheidae have both the cervical and branchiocardiac grooves steep. These similarities with Neoglypheidae make the two sister groups, at odds with the hypothesis of Forest and de Saint Laurent (1989) that Mecochiridae not by included within Glypheoidea.

Genera within Mecochiridae are distinguished on the basis of presence or absence (*Huhatanka*) of a postcervical groove; development of cephalic carinae (*Mecochirus*, *Meyeria*, and *Selenisca*); development of spinose branchial carinae (*Selenisca*); and presence of a spinose rostrum (*Meyeria*).

Schweigert (personal communication, 8/2012) suggested that *Selenisca gratiosa* is the junior synonym of *Glyphea pseudoscyllarus* (Schlothheim, 1822), based upon a newly discovered specimen from the Nusplinger Plattenkalk (Dietl et al., 2002). However, the morphology of the pleon of the new specimen does not seem to be the same as that of *Selenisca gratiosa* and comparative details of the carapace are difficult to work out because of preservational differences. Further, Schlothheim (1822) did not illustrate his species and the present authors are not aware of the existence of the holotype. Thus, for now we retain *Selenisca* within Mecochiridae as suggested by the phylogenetic analysis.

#### Neoglypheidae New Family

##### Fig. 12A

Diagnosis.—Subcylindrical carapace slightly compressed laterally, median suture absent, with cephalic carinae usually ornamented with spines or tubercles but sometimes smooth; short rostrum lacking supra- and subrostral teeth; cervical, postcervical, and well-developed branchiocardiac grooves, both cervical and branchiocardiac grooves steep, cervical groove at over 70° angle and branchiocardiac groove at over 30° angle to dorsal surface, expressed as concave arc; subrectangular pleonal somites, sharp demarcation between pleura and terga, exopod of uropods with diaeresis; second

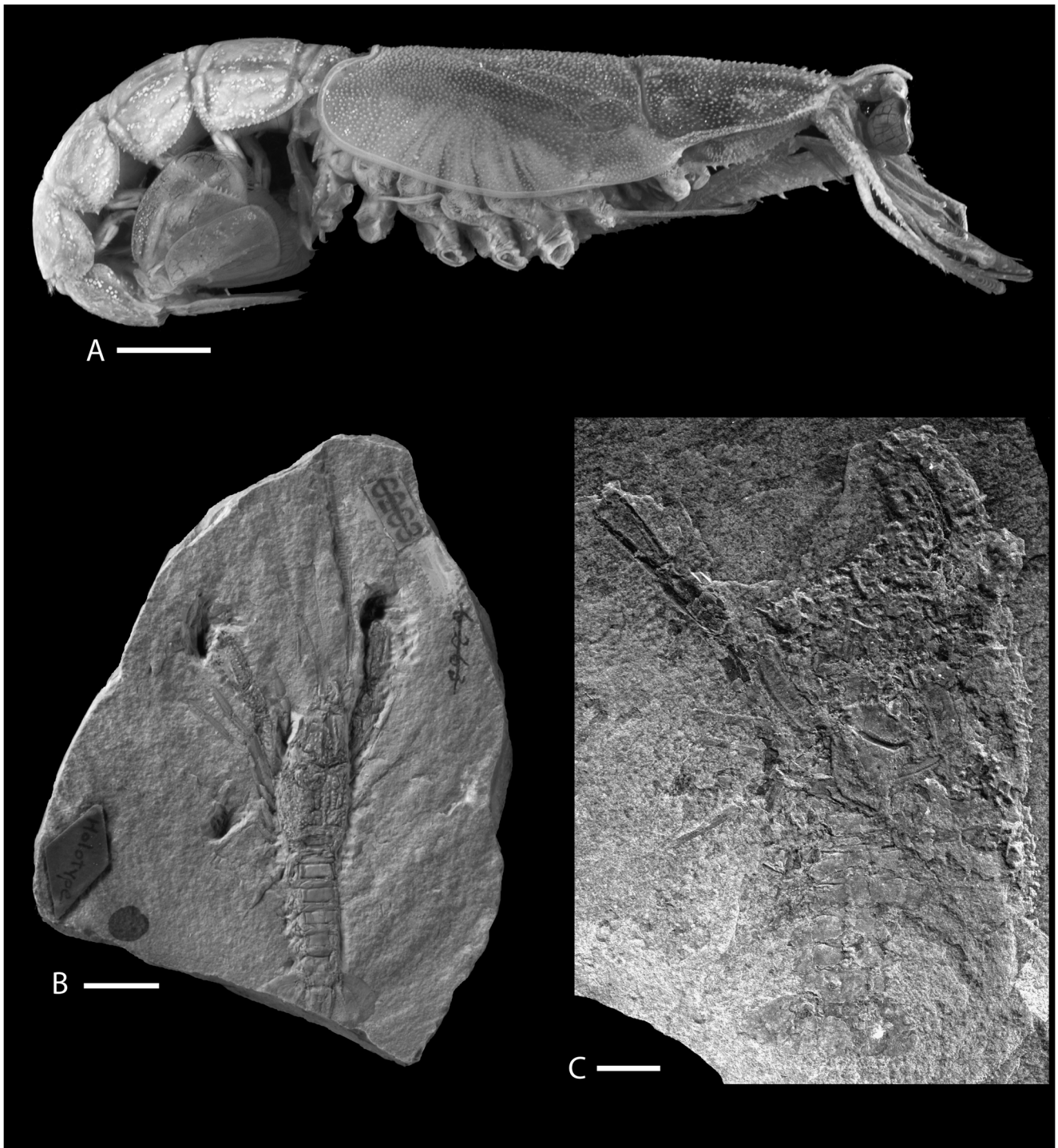


Fig. 12. Infraorder Glypheidea, Superfamily Glypheoidea. A, Neoglypheidae, *Neoglypheia inopinata* Forest and De Saint Laurent, 1975, holotype USNM 152650; B, Mecochiridae, *Selenisca gratiosa* Von Meyer, 1847b, holotype MCZ 109949; C, Platychelidae, *Platycheila trauthi* Glaessner, 1931; specimen originally labeled as *P. kahleri* Glaessner, 1931, holotype, NHMW 1887.IX.105, 107, photo by A. Kroh of NHMW; the two species subsequently synonymized by Förster (1967). Scale bars = 1 cm.

antennal peduncle elongate; pereiopods 1-4 pseudochelate; pereiopod 5 with terminal dactylus.

Included genera.—*Laurentaeglypheia* Forest, 2006; *Neoglypheia* Forest and de Saint Laurent, 1975.

Material examined.—*Neoglypheia inopinata* Forest and de Saint Laurent, 1975, holotype, USNM 152680.

Geologic range.—Recent.

Remarks.—Our analysis demonstrates that the extant genera form a clade with closest affinities to Mecochiridae,



not Glypheidae as might be expected. Neoglypheidae is characterized by ornamented cephalic ridges, cervical and branchiocardiac grooves at a high angle; and pereopods 1-4 pseudochelate and pereopod 5 with terminal dactylus. This combination of characters makes them distinct among Glypheoidea and thus warranting their own family.

Platychelidae Glaessner, 1969  
Fig. 12C

Diagnosis.—Carapace dorsoventrally flattened, median suture absent; short rostrum with suprarostal teeth; deep cervical groove and weak postcervical and branchiocardiac grooves, post-cervical and hepatic grooves connected by arcuate groove; pleonal somites 1-6 smooth with well developed pleura, subrectangular telson, subrectangular pleonal somites, sharp demarcation between pleura and terga, exopod of uropods with diaeresis; pereopods 1-3 chelate, pereopod 1 with long and slender chelae; chelae of pereopods 2-3 smaller than those of pereopod 1, pereopods 2-5 shorter than pereopod 1; pereopods 4 and 5 with terminal dactyli.

Included genera.—*Platycheila* Glaessner, 1931; *Platypleon* van Straelen, 1936.

Material examined.—*Platycheila kohleri* Glaessner, 1931, NHMW 1887 IX 105, 107, holotype.

Geologic range.—Late Triassic.

Remarks.—Glaessner (1969) erected the family, apparently to accommodate the large chelate first pereopods, smaller chelate second and third pereopods, and well-developed groove pattern typical of glypheoids. He placed *Platypleon*, which is based upon a fragmentary pleon, with *Platycheila* based upon the resemblance of the pleon to that of *Platycheila* (Glaessner, 1969, p. R458). We elect to accept Glaessner's placement of this incomplete material.

Infraorder Astacoidea Latreille, 1802  
Figs. 13, 14

Diagnosis.—Carapace subcylindrical; frontal portion of carapace not fused with epistome; long or short rostrum bearing suprarostal and subrostral spines; antennae with five segmented stalk and scale; third maxilliped pediform; pereopods 1-3 chelate or pseudochelate; pereopods 4-5 with a terminal dactylus, rarely pereopod 4 pseudochelate; pleon with somite 2 larger than somite 3; exopod of uropods with diaeresis; genital openings coxal.

Included sections.—Astacida Scholtz and Richter, 1995; Homarida Scholtz and Richter, 1995.

Geologic range.—Early Jurassic (Pliensbachian)-Recent.

Section Astacida Scholtz and Richter, 1995  
Fig. 13

Diagnosis.—Carapace subcylindrical; frontal portion of carapace not fused with epistome; long or short rostrum bearing suprarostal and subrostral spines; antennae with five segmented stalk and scale; third maxilliped pediform; pereopods 1-3 chelate; pereopods 4-5 with a terminal dactylus; pleon with somite 2 larger than somite 3; exopod of uropods with diaeresis; genital openings coxal.

Included superfamilies.—Astacoidea Latreille, 1802; Parastacoidea Huxley, 1879; Protastacoidea Albrecht, 1983.

Geologic range.—Late Jurassic (Kimmeridgian-Tithonian)-Recent.

Astacoidea Latreille, 1802  
Fig. 13C-E, G

Diagnosis.—Carapace subcylindrical; frontal portion of carapace not fused to epistome; rostrum long or short, bearing suprarostal and subrostral spines; genital openings coxal. Telson and exopod of uropods with diaereses. Antennae with five-segmented stalk and scale; pereopods 1-3 chelate; pereopods 4 and 5 with a terminal unmodified dactylus.

Included families.—Astacidae Latreille, 1802; Cambaridae Hobbs, 1942; Cricoidoscelosidae Taylor, Schram, and Yan-Bin, 1999.

Geologic range.—Late Jurassic (Kimmeridgian-Tithonian)-Recent.

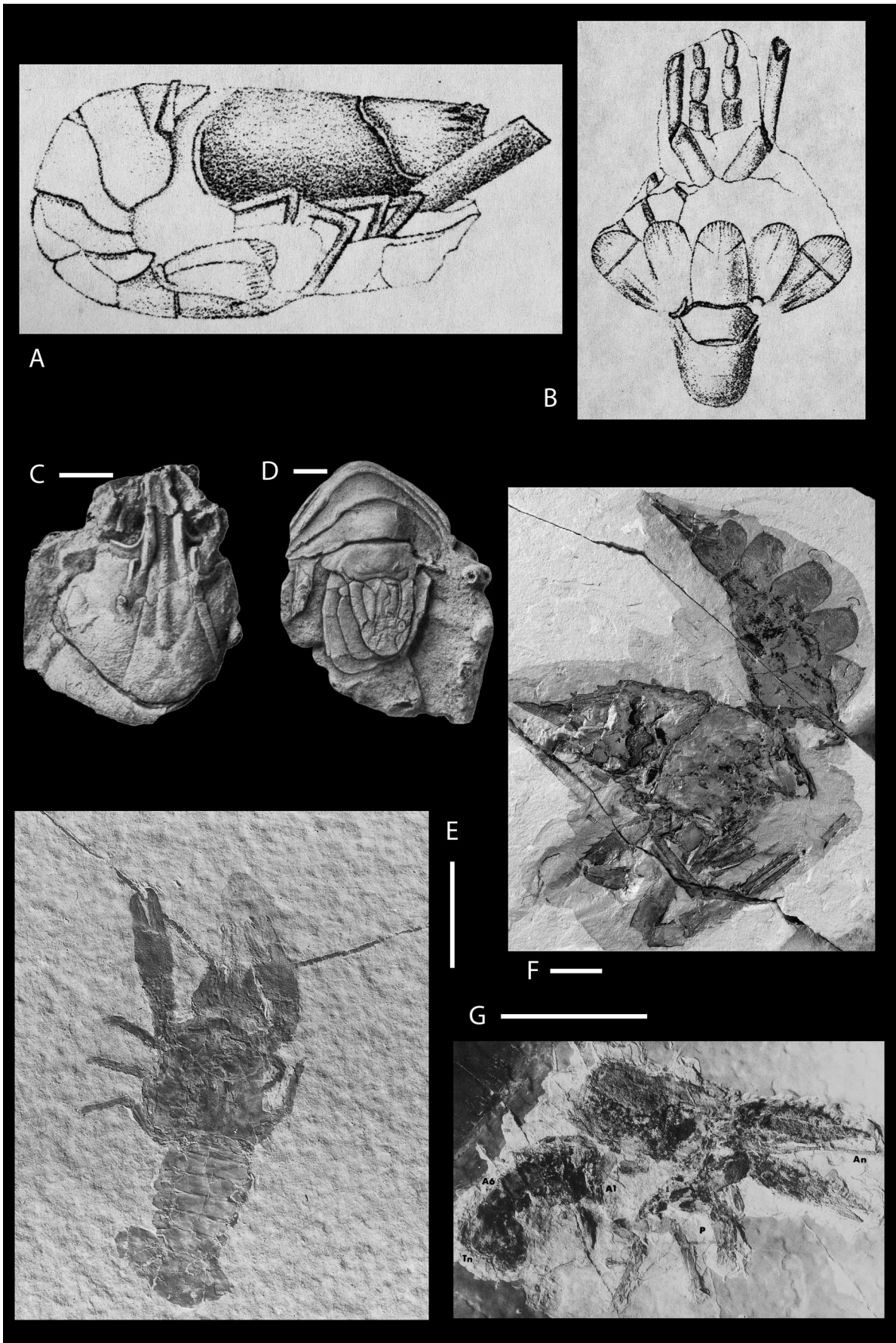
Astacidae Latreille, 1802  
Fig. 13C, D

Diagnosis.—Cylindrical carapace with deep cervical and postcervical grooves; short rostrum with one or two supra-rostral teeth; strong scaphocerite with pointed distal extremity. Pleon with rounded pleura; subrectangular telson with diaeresis, longitudinally subdivided by a carina with one pair of lateral spines; telson and exopod of uropods with diaeresis. Pereopod 1 with strong chelae; ischial hooks absent in males; annulus ventralis absent in females.

Included fossil genera.—*Astacus* Fabricius, 1775; *Austropotamobius* Skorikov, 1907; *Pacificastacus* Bott, 1950; *Palaecambarus* Taylor, Schram, and Yan-bin, 1999.

Geologic range.—Upper Jurassic (Kimmeridgian-Tithonian)-Recent.

Remarks.—As with other fresh water decapods, the fossil record of Astacidae is sparse. Astacids and cambarids are similar in many respects with regard to the dorsal carapace; however, lack of ischial hooks on the males and an annulus ventralis on females within Astacidae serves to distinguish them. Distinguishing fossil genera within the family can be based upon dorsal carapace characters. *Astacus* exhibits a deep cervical groove with one or two postcervical spines, a long rostrum with one suprarostal tooth on the distal part and two postorbital spines. The telson is subrectangular with a strong median spine on the lateral margins and a diaeresis dividing the telson into two more or less identical parts. The fixed finger of pereopod 1 lacks a marked step at the level of articulation with the dactylus as is present on *Austropotamobius*. *Austropotamobius* bears a strong cervical groove extending into a weak antennal groove; the long rostrum has one suprarostal spine and has only one postorbital spine at the base of the rostrum. The telson is subrectangular with a strong spine in the distal part of the lateral margins and a Y-shaped dorsal carina. The fixed finger of pereopod 1 has a marked step in the proximal part at the level of articulation with the dactylus. The carapace



of *Pacifastacus* has a weak postcervical as well as a deep cervical groove; the rostrum is long, tapering distally, and laterally carinate, and the first pereopods are heterochelous.

*Palaeocambarus* was placed within Cambaridae (Taylor et al., 1999), but the absence of ischial hooks supports placement in Astacidae. The dorsal part of the carapace is covered by fine granules, and the rostrum bears basal lateral spines. The telson has a pair of large lateral spines and a rounded distal margin. Pereiopod 1 bears long, narrow, pitted and spinose chelae. Interestingly, Rode and Babcock (2003) showed using morphological analysis that *Astacus spinirostris* Imaizumi, 1938, a junior synonym of *Palaeocambarus licenti* (van Straelen, 1928b), was included in Astacidae.

Cambaridae Hobbs, 1942  
Fig. 13E

Diagnosis.—Cylindrical carapace with deep cervical groove and weak postcervical groove; short or long rostrum with or without suprarostal teeth. Pleon with rounded pleura; telson subrectangular; telson and exopod of uropod with diaeresis. Pereiopod 1 with short or long equal chelae, occlusal surface of both dactylus and propodus bearing a row of equal or irregular teeth; ischial hooks on pereopods 3 and 4 of males, and annulus ventralis on females.

Included fossil genera.—*Procambarus* Ortmann, 1905.

Geologic range.—Eocene-Recent.

Remarks.—Although Cambaridae has a cosmopolitan distribution in modern fresh-water environments, they are not common in the fossil record. The fossil record is limited to *Procambarus*, known only from a single species, *P. primaevus* (Packard, 1880), from the Eocene of western North America.

Distinguishing between species of Cambaridae and Astacidae is difficult, but one character useful in the fossil record that seems to provide a reliable means of placement within one or the other family is the presence of a meral hook on males in Cambaridae and its absence in Astacidae. Presence or absence of the annulus ventralis in females is not as useful because the ventral region is rarely exposed in fossils. Many other features of the two families overlap sufficiently that their application is limited. Cambarids are generally New World crayfish, whereas astacids are Old World. Taylor et al. (1999) placed *Palaeocambarus* within Cambaridae, which was followed by Schweitzer et al. (2010); however, the absence of ischial hooks suggests that it be better placed within Astacidae. Thus, *Palaeocambarus* has been placed within Astacidae herein.

Cricoidoscelosidae Taylor, Schram, and Yan-bin, 1999  
Fig. 13G

Diagnosis.—Rostrum with rounded base, lateral spines; scaphocerite bladelike; pleura rounded; gonopod 1 in males styliform, remainder of pleopods annulate; telson large, with lateral spines, not divided by transverse suture; well-developed chelae, appearing to be equal; pereopods without ischial hooks (after Taylor et al., 1999).

Included genus.—*Cricoidoscelosus* Taylor, Schram, and Yan-bin, 1999.

Geologic range.—Early Cretaceous.

Parastacoidea Huxley, 1879  
Fig. 13F

Diagnosis.—Cylindrical carapace with deep cervical groove and weak postcervical groove; short or long rostrum with or without suprarostal teeth; keeled anterior region on cephalothorax. Pleon with pleonite 1 lacking pleopods; subrectangular telson not subdivided by a longitudinal carina and lacking diaeresis; telson may exhibit membraneous termination; exopod of uropods with diaeresis. Pereiopod 1 with strong, stout chelae; occlusal surface of both dactylus and propodus with irregular teeth; bearing hook on inner margin of carpus; inner margin of propodus longer than dactylus.

Included family.—Parastacidae Huxley, 1879.

Geologic range.—Early Cretaceous (Albian)-Recent.

Parastacidae Huxley, 1879  
Fig. 13F

Diagnosis.—As for superfamily.

Included fossil genera.—*Aenigmastacus* Feldmann, Schweitzer, and Leahy, 2011; *Astacopsis* Huxley, 1879; *Lammastacus* Aguirre-Urreta, 1992; *Palaeoechinastacus* Martin et al., 2008; *Paranephrops* White, 1842.

Material examined.—*Aenigmastacus crandalli* Feldmann et al., 2011, holotype TRUIPR L-018 F-1146 and F-1147 (part and counterpart) and 11 paratypes, TRUIPR L-018 F-1143 and F-1144 (part and counterpart), F-1145, F-1148- F-1151, F-1152 and 1153 (part and counterpart), F-1154, F-1155, F-1156 and F-1157 (part and counterpart) and F-1158. *Paranephrops fordycei* Feldmann and Pole, 1994, holotype, OU 39695a-c.

Geologic range.—Early Cretaceous (Albian)-Recent.

Remarks.—Although Parastacidae are widespread in Australia, South America, and Madagascar in the Southern Hemisphere, they are poorly known in the fossil record.

Fig. 13. Infraorder Astacidea, Section Astacida. A, B, Protastacoidea, Protastacidae, *Protastacus politus* (Schlüter in Schlüter & Von der Marck, 1868), right lateral view (A), ventral view showing incomplete telson diaeresis (B), digital images from Schlüter & Von der Marck, 1868, pl. 44, Fig. 4 (A) and 5 (B); C, D, Astacoidea, Astacidae, *Pacifastacus chenoderma* (Cope, 1871), USNM 353343, digital images from Rathbun (1926), pl. 33, Fig. 3 (C), pl. 32, Fig. 2 (D); E, Astacoidea, Cambaridae, *Procambarus primaevus* (Packard, 1880), SMMP 78.9.41; F, Parastacoidea, Parastacidae, *Paranephrops fordycei* Feldmann and Pole, 1994, OU 39695a, holotype, photo by Ewan Fordyce, University of Otago; G, Astacoidea, Cricoidoscelosidae, *Cricoidoscelosus aethus* Taylor, Schram, and Yan-bin, 1999, NIGP 126355 digital image of Taylor et al. (1999: Fig. 8a; reprinted from Paleontological Research, Vol. 3 (2), with permission from the Paleontological Society of Japan). Scale bars = 1 cm.

*Aenigmastacus* bears a smooth carapace with a weak cervical groove and smooth chelipeds. Placement of this genus within Parastacidae is problematic because it is the only parastacoid known from the Northern Hemisphere, but the sole species bears all the diagnostic characters of the family and superfamily. *Astacopsis*, known from a single specimen, has a cylindrical, tuberculate and punctate carapace; the rostrum is long and bears a single suprarostal tooth; and the telson is triangular and lacks a diaeresis. *Lammuas-tacus* has deep cervical, postcervical, and branchiocardiac grooves; the rostrum is long and broad with 5-6 suprarostal spines; the pleon has a chordate pleuron on somite 2 and triangular pleura on somites 3-5, decreasing in size posteriorly. The specimens representative of *Palaeoechinastacus* are partial; however, the pleon exhibits blunt spines on pleura 2-4, a quadrate telson without diaeresis, and long, slender uropods with a diaeresis on the exopod. Pereiopod 1 is moderately heterochelous, with spines on the upper margin of the manus and dactylus; the outer surfaces of the chelae are granular, and the occlusal surfaces of the fingers bear small spines. The carapace of *Paranephrops* has a strong rostrum with suprarostal teeth, strong cervical and weak postcervical and branchiocardiac grooves, and a finely pustulose surface. The pleon exhibits subrectangular pleura. Pereiopod 1 has strong chelae, a merus and carpus bearing a few sharp, distally directed spines in a row on the upper surface, and a propodus bearing rows of slender spines on the upper and lower surfaces.

Protastacoidea Albrecht, 1983 New Status  
Fig. 13A, B

Diagnosis.—As for family.

Included family.—Protastacidae Albrecht, 1983.

Geologic range.—Early Cretaceous (Berriasian-Hauterivian).

Protastacidae Albrecht, 1983  
Fig. 13A, B

Diagnosis.—Subcylindrical carapace with deep cervical groove at less than 70° angle to dorsal surface; postcervical and branchiocardiac grooves absent; subrectangular telson with incomplete diaeresis developed as posterolaterally directed marginal slits; exopod of uropods with diaeresis; pereiopod 1 stronger than the others and chelate.

Included genus.—*Protastacus* Albrecht, 1983.

Geologic range.—Early Cretaceous (Berriasian-Hauterivian).

Remarks.—Albrecht (1983) included *Pseudastacus* Opper, 1861b, in Protastacidae; however, our analysis supports placement of *Pseudastacus* within Stenochiridae. *Pseudastacus* possesses cephalic median and supraorbital carinae,

neither of which is evident on Protastacidae, and the telson of *Pseudastacus* bears a complete diaeresis. Thus, it is not referable to Protastacidae.

Section Homarida Scholtz and Richter, 1995  
Fig. 14

Diagnosis.—Carapace subcylindrical; frontal portion of carapace not fused with epistome; long or short rostrum bearing suprarostal and subrostral spines; antennae with five segmented stalk and scale; third maxilliped pediform; pereiopods 1-3 chelate or pseudochelate; pereiopods 4-5 with a terminal dactylus, rarely pereiopod 4 pseudochelate; pleon with somite 2 larger than somite 3; exopod of uropods with diaeresis; genital openings coxal.

Included superfamilies.—Enoplometopoidea de Saint Laurent, 1988; Stenochiroidea Beurlen, 1928; Nephropoidea Dana, 1852a.

Enoplometopoidea de Saint Laurent, 1988  
Fig. 14A, D

Diagnosis.—Cephalothorax cylindrical, rostrum well developed, with rostral spines, cephalothorax with cephalic ridges; cervical groove short, weak; branchiocardiac groove indistinct; pleon with small first and large second somite, with pleura expanded anteriorly and posteriorly, pleura rounded or rectangular; telson with or without movable spines; exopod of uropods usually with diaeresis; first pereiopods large, chelate; pereiopods 2-4 pseudochelate or chelate; pereiopod 4 rarely achelate; pereiopod 5 with terminal dactyli.

Included families.—Enoplometopidae de Saint Laurent, 1988; Uncinidae Beurlen, 1930a.

Geologic range.—Early Jurassic (Pliensbachian)-Recent.

Enoplometopidae de Saint Laurent, 1988  
Fig. 14D

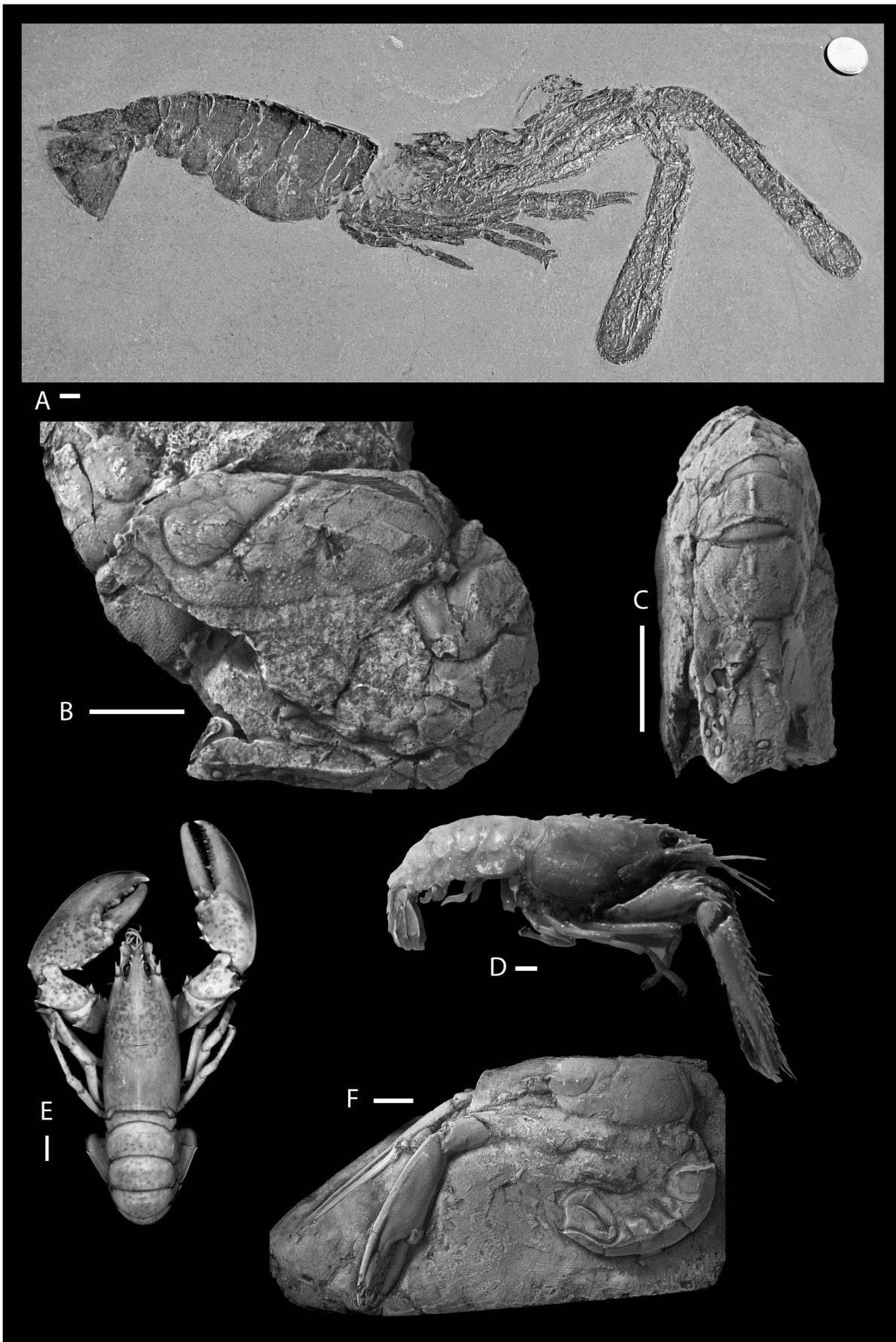
Included genus.—*Enoplometopus* A. Milne-Edwards, 1862.

Diagnosis.—Cephalothorax cylindrical, well-developed rostrum, cephalic ridges present; cervical groove weak, branchiocardiac groove indistinct; pleonal pleura rounded, pleon with small first and large second somite; pleura rounded and expanded anteriorly and posteriorly, sometimes with spines; well-calcified tailfan; telson rounded, with movable spines, exopod of uropods with diaeresis; first pereiopods large, chelate, pereiopods 2-5 pseudochelate.

Material examined.—*Enoplometopus debelius* Holthuis, 1983, USNM 252577; *E. gracilipes* (de Saint Laurent, 1988), USNM 268823.

Geologic range.—Recent.

Fig. 14. Infraorder Astacidea, Section Homarida. A, Enoplometopoidea, Uncinidae, *Uncina posidoniae* Quenstedt, 1851, Urwelt-Museum Hauff Holzmaden specimen, one Euro coin for scale (diameter = 23.25 mm); B-C, Stenochiroidea, Stenochiridae, *Tillocheles shannonae* Woods, 1957, cast of QMF 3252, holotype, left lateral view (B) and pleon and telson (C); D, Enoplometopoidea, Enoplometopidae, *Enoplometopus occidentalis* (Randall, 1840), unnumbered specimen in L. B. Holthuis Collection, Naturalis, Leiden, Netherlands, photo by D. Tshudy, Edinboro University, PA; E, Nephropoidea, Nephropidae, *Homarus americanus* H. Milne Edwards, 1837 [in 1834-1840], KSU unnumbered specimen; F, Nephropoidea, Nephropidae, *Hoploparia stokesi* (Weller, 1903), cast of BAS DJ 231.9 numbered KSU D1041. Scale bars = 1 cm.



Uncinidae Beurlen, 1930a  
Fig. 14A

Diagnosis.—Cephalothorax short, cervical groove short; median suture present; branchiocardiac groove indistinct. Pleon with small first and large second somite, with pleura expanded anteriorly and posteriorly, rectangular; telson triangular, without movable posterolateral spines, exopod of uropods with diaeresis; pereopod 1 long, strong, and spinose, with elongate propodus and strong curved dactylus; pereopods 2-3 with small chelae, pereopods 4 with chelae or terminal dactyli; pereopod 5 with terminal dactyli.

Included genera.—*Malmuncina* Schweigert and Garassino, 2003; *Uncina* Quenstedt, 1851.

Material examined.—*Uncina posidoniae* Quenstedt, 1851, Urwelt-Museum Hauff Holzmaden specimen.

Geologic range.—Early (Pliensbachian)-Late (Tithonian) Jurassic.

Remarks.—The members of Uncinidae share several features with Enoplometopidae, making them sister groups in the phylogeny recovered here, but there are some important differences that should be mentioned. The general shape of the chelipeds differs between the two groups. In Enoplometopidae, the claws have long mani and fingers, whereas in Uncinidae, the mani are long but the fingers are short and highly arched. The shape of the fingers in uncinids is, in fact, very distinctive.

Stenochiroidea Beurlen, 1928 New Status  
Fig. 14B, C

Diagnosis.—As for family.

Included family.—Stenochiridae Beurlen, 1928.

Stenochiridae Beurlen, 1928  
[= Chilenophoberidae Tshudy and Babcock, 1997]  
Fig. 14B, C

Diagnosis.—Subcylindrical carapace, cephalic carinae present; cervical groove extending anteroventrally from dorsal midline to antennal groove; postcervical groove extending anteroventrally from near dorsal midline, joining cervical groove at approximately midheight on carapace; branchiocardiac groove subparallel to dorsal midline dorsally; hepatic groove looping to cervical groove; inferior groove extending ventrally; pleonal somite 2 larger than somite 3; exopod of uropods with diaeresis; pereopods 1 long, isochelous or heterochelous, dactylus held vertically, ischial process distinct, claws usually longer than carapace; propodus of the chelae usually unsculptured; pereopods 2 and 3 chelate; pereopods 4 and 5 with terminal dactylus.

Included genera.—*Chilenophoberus* Chong and Förster, 1976; *Palaeophoberus* Glaessner, 1932; *Pseudastacus* Opperl, 1861b; *Stenochirus* Opperl, 1861a; *Tillocheles* Woods, 1957.

Material examined.—*Stenochirus mayeri* Opperl, 1862, holotype (BMNH) 44765. *Stenochirus angustus* (Münster, 1839), (BMNH) 44822, In. 28982. *Tillocheles shannonae* Woods, 1957, cast of QMF 3247 numbered KSU D 739; KSU D 1801.

Geologic range.—Middle Jurassic (Bajocian)-Late Cretaceous (Cenomanian-Turonian).

Remarks.—The composition of the family differs little from its definition by Tshudy and Babcock (1997) (as Chilenophoberidae), only with the addition of *Stenochirus*. At the time they performed their analysis, *Stenochirus* was only known from claws and poorly preserved carapace material. However, in 2003, Schweigert et al. named a new species that was well preserved. Interestingly, Glaessner (1969: R460) had noted that Beurlen (1928a) had named Stenochiridae largely on the basis of a species that Beurlen thought was a member of *Stenochirus* but was later to become the type for *Palaeophoberus*. *Palaeophoberus* was included in Chilenophoberidae and is herein embraced in Stenochiridae. Thus, the synonymy of Chilenophoberidae with Stenochiridae seems to have historic precedence.

Tshudy and Babcock (1997) inferred that their Chilenophoberidae, now Stenochiridae, was closely related to Erymididae, but this seems to be an artifact of the reduced number of taxa included in their analysis. It now seems that Stenochiridae is nested fully within Astacidea, sister to Nephropidae, as they found, but not closely related to Erymididae. Claws in lobsters appear to have evolved more than once.

Nephropoidea Dana, 1852a  
Fig. 14E, F

Included family.—Nephropidae Dana, 1852a.

Nephropidae Dana, 1852a  
Fig. 14E, F

Diagnosis.—Subcylindrical carapace; typically with longitudinal carina; tuberculate longitudinal carinae in the antennal region; deep cervical groove extending ventrally from level of orbit to antennal groove; postcervical groove typically curving anteroventrally from dorsal midline toward, or to, cervical groove at approximately midheight on carapace; branchiocardiac groove dorsally subparallel or parallel to dorsal midline, joining postcervical groove at level of orbit; rostrum usually large and spinose. Pleonal somites usually ending in a point and with a transverse median carina; telson quadrangular, entirely hardened, lacking diaeresis; uropods entirely hardened, exopod of uropod with diaeresis. Antennae with long, whip-like flagella and well developed scaphocerite; pereopod 1 with elongate and strong equal or unequal chelae with variable shaped denticles along the interior margins of dactylus and index; pereopods 1-3 chelate, pereopod 5 sometimes chelate.

Included fossil genera.—*Cardirynchus* Schlüter, 1862; *Dinocheilus* Ahyong et al., 2010; *Homarus* Weber, 1795; *Hoploparia* M'Coy, 1849; *Jagtia* Tshudy and Sorhannus, 2000b; *Metanephrops* Jenkins, 1972; *Nephrops* Leach, 1814; *Nephropsis* Wood-Mason, 1873; *Palaeonephrops* Mertin, 1941; *Paraclythia* Fritsch, 1877; *Pseudohomarus* van Hoepen, 1962.

Material examined.—*Acanthacaris caeca* A. Milne-Edwards, 1881, USNM 181790; *Eunephrops cadenasi* Chace, 1939, USNM 170677; *Homarus americanus* H. Milne Edwards, 1837, USNM 99746; *Hoploparia stokesi* (Weller,

1903), BAS DJ 231.9; *Metanephrops binghami* (Boone, 1927), USNM 170705; *M. velutinus* Chan and Yu, 1991, USNM 106039; *Nephropsis aculeata* Smith, 1881, USNM 180458; *Paraclythia nephropica* Fritsch, 1877, NMP O2227a, 3462, 3464, 3458, 3459, 3460, 3461, 3465, 3466, 4045, 4047, 4057, 4058, 4059, O3462, *Thaumastocheles zaleucus* (Thomson, 1873), USNM 170683; *Thymopsis nilenta* Holthuis, 1974, USNM 291288.

Geologic range.—Early Cretaceous (Berriasian-Hauterivian)-Recent.

Remarks.—Nephropidae comprise a large, distinct, and distinguishable group of lobsters, and in addition to those genera with a fossil record, every extant genus within the family was analyzed. Superficially, they may appear similar to the fresh-water crayfish; however, they may be distinguished on the bases that Nephropidae possess a fully calcified telson and uropods; the telson lacks a diaeresis, whereas Astacidae and Cambaridae possess a diaeresis on the telson. These characters, in addition to the observation that most Nephropidae exhibit better developed groove patterns and carapace carinae than do the crayfish, are morphological aspects that are readily observable in the fossil record. Another significant distinguishing feature, but one that is not commonly visible in fossils, is the presence of a completely fused sternum in Nephropidae, whereas that of crayfish is not fused between sternites 7 and 8. This condition led Scholtz and Richter (1995) to erect the Fractosternalia to embrace Astacidea, Thalassinidea, Anomala, and Brachyura. Although this classification has not been widely accepted (De Grave et al., 2009), the feature is certainly distinctive and significant, possibly having functional significance by providing additional flexibility for those exhibiting a sternum that is not fully fused.

Fritsch (1877) originally established the new monotypic genus *Paraclythia* with *Paraclythia nephropica* Fritsch, 1877. After that, Zittel (1885) modified the generic name *Paraclythia* to *Paraclytia* without any reason. Fritsch and Kafka (1887) used the generic name *Paraclytia* with the author, Fritsch. Therefore, *Paraclytia* has often been attributed to “Fritsch, 1887” (Mertin, 1941; McCobb and Hairapetian, 2009). However, *Paraclythia* Fritsch, 1877, is clearly the available name and *Paraclytia* should be attributed to Zittel (1885) and became the unjustified emended spelling of *Paraclythia* (ICZN, 1999, art. 33.2.3).

Distinguishing between genera known from the fossil record can be accomplished when material is reasonably complete. *Cardirynchus* is, unfortunately, not known well enough to make comparisons with other nephropids. *Dinochelus* Ahong et al., 2010, is known from the fossil record from a single, newly named species from the Eocene of England (Tshudy and Saward, 2012) as well as from an extant occurrence in the Philippines. Closely related to the extant *Thaumastocheles* Wood-Mason, 1874, and *Thaumastochelopsis* Bruce, 1988, *Dinochelus* has a long, slightly downturned rostrum with spinose margins; the carapace is cylindrical with some granules, but otherwise has a smooth surface, lacking a median groove or carina; the orbital notch is absent; the postcervical groove is the most prominent one and is continuous with branchiocardiac, cervical, and antennal grooves; the epistome is fused anteriorly with the cara-

pace. The pleon is smooth and depressed, and the pleura are rectilinear and lacking prominent terminal spine; the telson is subquadrate, complete, and calcified throughout. The first pereopods are strongly heterochelous, with the major claw bearing a bulbous, spinose hand and acicular denticles on the fingers. The minor claw is more elongate and compressed with a spinose hand and denticles on the fingers similar to those of the major claw. Pereopods 2, 3, and 5 are chelate.

*Homarus* exhibits a generally smooth carapace bearing a long rostrum with suprarostal spines, and a strong supraorbital spine. Cervical and postcervical grooves are well developed, and the latter extends from midline to about midheight of carapace where it approaches or joins cervical groove. The branchiocardiac groove is weak. Pleon with weakly ornamented or smooth terga and prominent triangular pleura with thickened margins and terminal spine; telson is rectilinear, complete, fully calcified; exopod of uropods with diaeresis. The first pereopods are strongly heterochelous with a strong, deep propodus and domal denticles on occlusal surface; minor cheliped with finer, spinose denticles; and pereopods 1-3 chelate. The genus *Hoploparia* is similar to *Homarus*, but the former exhibits a subdorsal carina, which *Homarus* lacks. The postcervical groove in *Hoploparia* is longer than that in *Homarus* and it joins to hepatic groove to encircle the “adductor testis” muscle attachment. *Hoploparia* is the most speciose nephropid and, although it has been suggested to be a form genus (Tshudy and Sorhannus, 2003), Feldmann et al. (2007) concluded that the genus, as herein distinguished from *Homarus*, was well constrained.

*Jagtia* has well developed cervical and postcervical grooves, but the latter does not approach the cervical groove as it does in *Homarus* nor does it join the hepatic groove as in *Hoploparia*. In addition, *Jagtia* has a smooth pleon with a large, quadrate pleuron on somite 2; pleura of somites 3-5 are chordate. In our cladistic analysis, *Jagtia* emerged in a clade with *Thymops* and *Nephropsis*, among others based upon the absence of a scaphocerite. The clade embracing *Homarus*, *Hoploparia*, and *Dinochelus*, among others, bears a scaphocerite.

*Metanephrops* exhibits a weak cervical and strong postcervical groove, a long rostrum with suprarostal and subrostral spines, a supraorbital carina with three spines, and three pairs of thoracic carinae. The pleomeres have a narrow, transverse furrow posteriorly and a subrectangular telson. Pereiopod 1 tends to be isochelous. The genus differs from *Nephrops* in that the latter has a long rostrum with three pairs of suprarostal spines; an intercervical groove is present, but there is no branchial carina. Pereiopods 1 are heterochelous. *Nephropsis* bears a long, triangular rostrum with one or more pairs of prominent lateral spines and a subdorsal carina that extends onto the cephalic region. Supraorbital and antennal spines are strong; dorsomedian, cervical, postcervical, and hepatic grooves are well developed. The pleon bears a median carina and ventrally sharp pleura on somites 2-5; somite 1 is smooth. Chelipeds are isochelous. Although recorded in the fossil record, the evidence is sparse and not convincing. *Nephropsis midwayensis* Rathbun, 1935, is represented by a partial propodus which is not unlike that of extant forms, whereas *Nephropsis* sp. from Italy (Garassino

and De Angeli, 2004) is keeled and coarsely scabrous on the outer surface and has domal denticles on the proximal part of the dactylus; none of these features is characteristic of *Nephropsis*. In fact, that morphology is more like chelae of *Eunephrops*, but much better and more complete material is necessary to identify the specimen with certainty.

*Oncopareia* has a carapace similar to that of *Hoploparia* in that the cervical and postcervical grooves are well developed, and inferior and antennal grooves are also present on a generally smooth, well-calcified carapace. The pleon has relatively smooth terga and short, quadrate pleura. Chelipeds are strongly heterochelous; the major claw has a bulbous propodus and long, slender fingers with acicular denticles much like that of *Thaumastocheles*. The minor claw is similar to the minor, cutter, claw of *Homarus*. Whereas *Thaumastocheles* has strongly reduced eyes and no orbital notches, a well-developed orbital notch is present on species of *Oncopareia*.

*Palaeonephrops* is characterized by deep cervical and postcervical grooves, presence of an intercervical groove, a row of strong spines on the dorsal midline, and a prominent rostrum with suprarostal spines. The pleon is strongly ornamented with a median keel and transverse grooves. Chelipeds are heterochelous. *Paraclithia* is distinctive in that it bears a pair of strong, spinose or nodose subdorsal ridges on the cephalic region and four pairs of ridges on the thoracic region. The rostrum bears suprarostal spines, and there is a spinose antennal carina. The pleon is strongly ornamented with deep transverse grooves and longitudinal ridges, including a prominent ridge separating terga from pleura. The heterochelous chelae are very long, bearing rows of spines. Partial preservation and rough preparation of the sole specimen of *Pseudohomarus* make characterization difficult. The rostrum is long and apparently smooth, and the carapace is generally smooth with only an incomplete cervical groove. The pleon is finely granular. Chelipeds are extremely long, slender, and heterochelous. The major cheliped, based upon the length of the propodus, bears a few domal denticles whereas the minor cheliped has smooth occlusal surfaces.

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