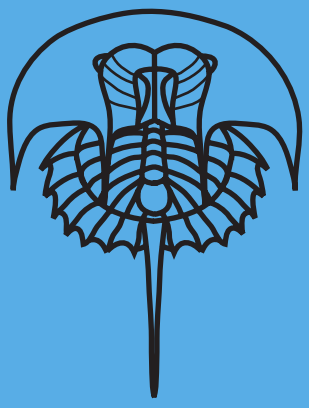

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PART R, REVISED, VOLUME 1, TREATISE ONLINE 190:

CLASSIFICATION AND PHYLOGENY OF THE DECAPODA: INTRODUCTION TO SYSTEMATICS CHAPTERS

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The bases for the classification used in this volume are summarized here, in addition to a brief overview of the history of classification of the group. This chapter is not intended to be an exhaustive discussion of the phylogeny of each group; rather, it is intended to provide a justification for the classification used in the systematics chapters. In general, our classification follows the consensus classification to the family level presented in Schram and Koenemann (2021) (extinct and extant), Poore and Ahyong (2023) (extant), and DecaNet (2024, extant; extinct classification in DecaNet follows the *Treatise* Online chapters). Discrepancies and reasons for them are discussed where appropriate. Our arrangement of superfamilies and families largely mirrors that of DecaNet through December 2022, the arbitrary but necessary cut-off date for our classification. Exceptions include a few findings published in 2023 that extended the range of extant families into the fossil record.

ORDER DECAPODA

Decapoda has long been considered to be a monophyletic group, confirmed by multiple phylogenomic analyses (Wolfe & others, 2016, 2019, 2024). Early on, it was divided into a swimming group (Natantia) and a crawling or walking group (Reptantia) (Boas, 1880). At present, Decapoda is broadly recognized to be composed of two suborders, Dendrobranchiata Bate, 1888, and Pleocyemata Burkenroad, 1963. Dendrobranchiata are characterized by branching gills. They release tiny eggs into the water, and they have a short adult lifespan compared with time spent in the larval form (Abele & Felgenhauer, 1986). Pleocyemata have a variety of gill structures, females always brood eggs on the pleopods, and the time spent as a larval form is short compared with that spent as an adult (Abele & Felgenhauer, 1986). Dendrobranchiata includes the penaeoid and sergestoid shrimp, and Pleocyemata includes all other decapods. Within Pleocyemata, 12 infraorders are nested, one of which is extinct.

The current arrangement of infraorders is a combination of old and new ideas about classification of pleocyemate decapods. Most infraorders date back to the 19th century, but a few have been more recently recognized. The general history of classification schemes for Decapoda has been summarized several times. Glaessner's (1969) original decapod volume of the *Treatise* referenced the summaries of Balss (1940, 1957). Glaessner (1969) presented an array of classifications that had been used up to the 1960s, and his *Treatise* classification was used by paleontologists for many years.

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The next major classification of Decapoda that received broad usage was that provided by Martin and Davis (2001). They provided a classification for all extant Crustacea, down to the family level, summarizing the history of various classification schemes up until 2001 and providing extensive commentary for every level to superfamily. They did not include fossil groups in their classification, although they provided an introduction into the crustacean fossil literature. This work provided the basis for the molecular revolution that commenced in the 2000s, as well as the foundation for several checklists and classifications of Decapoda that were subsequently published. The basic sub- and infraordinal classification for Decapoda used by Martin and Davis (2001), and later by De Grave and others (2009), is largely intact; some of their recognized infraorders are now composed of two discrete infraorders (Table 1).

By 2010, numerous morphological and/or molecular phylogenies of Decapoda had been published (Dixon, Ahyong, & Schram, 2003; Schram & Dixon, 2004; Ahyong & O'Meally, 2004; Porter, Pérez-Losada, & Crandall, 2005; Tsang & others, 2008). These supported the monophyly of the three major shrimp clades, Dendrobranchiata, Stenopodea, and Caridea. Bracken and others (2010) showed that Procaridea should be maintained as a separate infraorder from Caridea. The separate standing of the infraorders Polychelida and Achelata, as proposed by Scholtz and Richter (1995), received wide support. Most analyses supported Glypheidea as a separate clade from Astacidea. Robles and others (2009) recognized that Thalassinidea, as it had been construed, should be separated into Axiidea and Gebiidea, as originally suggested by de Saint Laurent (1979a). Anomura (sometimes called Anomala) was usually recovered as sister to the Brachyura.

A 2013 mitogenomic study of Decapoda found support for most infraorders as construed here (Shen, Braband, & Scholtz, 2013) (Fig. 1). In 2019, phylogenomic analysis demonstrated that all extant suborders and infraorders recognized in this volume (except Palaeopalaemonida and Glypheidea, which were not included in the analysis) are monophyletic (Wolfe & others, 2019) (Fig. 2). Schram and Koenemann (2021) integrated both extinct and extant forms into their treatment of all crustaceans, and Poore and Ahyong (2023) provided diagnoses for every extant marine

Table 1. Comparison of the suprafamilial Decapoda classification of Martin & Davis (2001) and that used herein. SO, suborder; I, infraorder; S, section; SS, subsection. References for taxa are provided in Table 2.

Martin & Davis (2001)	Current
SO Dendrobranchiata	SO Dendrobranchiata
SO Pleocyemata	SO Pleocyemata
I Stenopodidea	I Stenopodidea
I Caridea	I Procarididea I Caridea
Not included	I Palaepalaemonida (extinct)
I Palinura	I Polychelida I Achelata
I Astacidea	I Glypheidea I Astacidea S Astacida S Homarida
I Thalassinidea	I Gebiidea I Axiidea
I Anomura	I Anomura
I Brachyura	I Brachyura
S Dromiacea	S Dromiacea S Homoloidea
Not included	S Callichimaeroidea (extinct)
Not included	S Torynommoida (extinct)
Not included	S Etyoida (extinct)
SS Raninoda within Eubrachyura	S Raninoida
Not included	S Dakoticancroida (extinct)
Nested within Raninoida	S Cyclodorippoida
S Eubrachyura	S Eubrachyura
SS Heterotremata	Not included
SS Thoracotremata	Thoracotremata

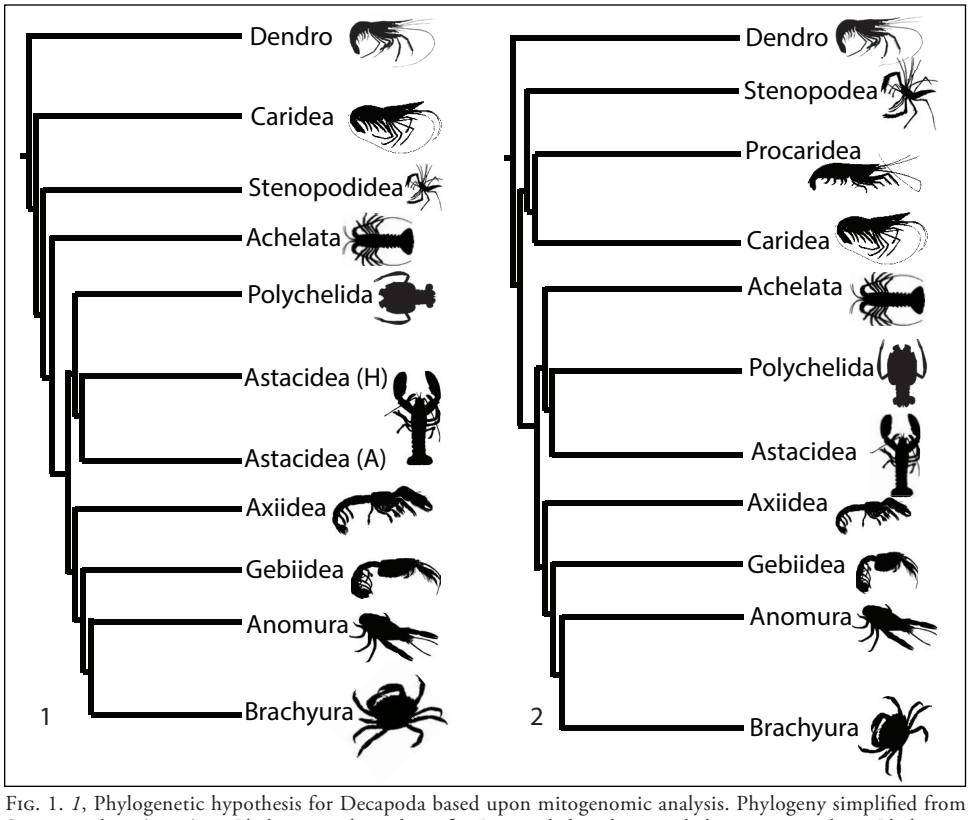

Fig. 1. *1*, Phylogenetic hypothesis for Decapoda based upon mitogenomic analysis. Phylogeny simplified from Shen & others (2013). *2*, Phylogenetic hypothesis for Decapoda based upon phylogenomic analysis. Phylogeny simplified from Wolfe & others (2019). A = Astacida, Dendro = Dendrobranchiata, H = Homarida. Silhouettes from PhyloPic (phylopic.org) or new.

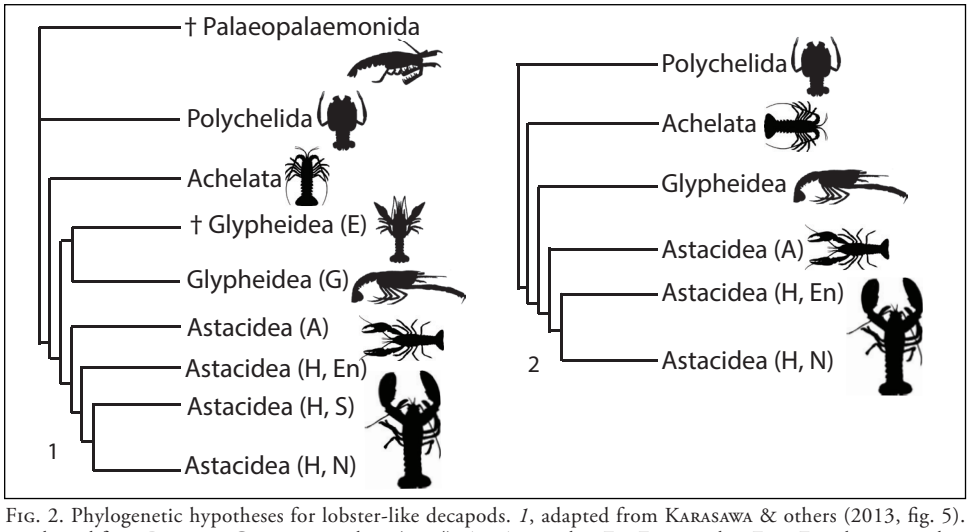

Fig. 2. Phylogenetic hypotheses for lobster-like decapods. *1*, adapted from Karasawa & others (2013, fig. 5). *2*, adapted from Bracken-Grissom & others (2014). A = Astacoidea, E = Eryomoidea, En = Enoplometopoidea, G = Glypheoidea, H = Homarida, N = Nephropoidea, S = Stenochiroidea. † = extinct. Silhouettes from PhyloPic (phylopic.org) or new.

decapod crustacean to the genus level. These two recent works, as well as DecaNet, have been instrumental in guiding the systematics of this volume. Thus, the infraordinal subdivisions used in this volume have received strong support from morphologic, genetic, and phylogenomic analyses. The classification used herein, to family, is presented in Table 2. Authorships for all taxa to family may be found therein and are not repeated elsewhere.

Table 2. Treatise Classification. †, extinct group; ♦, group with no fossil record. All other groups are represented by both fossil and extant taxa.

Suborder Dendrobranchiata Bate, 1888
Superfamily Penaeoidea Rafinesque, 1815
Aciculopodidae † Feldmann & Schweitzer, 2010b
Aegeridae † Burkenroad, 1963
Aristeidae ♦ Wood-Mason in Wood-Mason & Alcock, 1891
Benthesicymidae Wood-Mason, 1891
Carpopenaeidae † Garassino, 1994
Penaeidae Rafinesque, 1815
Sicyoniidae Ortmann, 1898
Solenoceridae Wood-Mason, 1891
Superfamily Sergestoidea Dana, 1852a
Luciferidae De Haan, 1849
Sergestidae Dana, 1852a
Suborder Pleocyemata Burkenroad, 1963
Infraorder Stenopodea Claus, 1872
Stenopodidae Claus, 1872
Infraorder Procaridea Felgenhauer & Abele, 1983
Procarididae ♦ Chace & Manning, 1972
Udorellidae † Van Straelen, 1925
Infraorder Caridea Dana, 1852a
Superfamily Alpheoidea Rafinesque, 1815
Alpheidae Rafinesque, 1815
Barbouriidae ♦ Christoffersen, 1987
Bythocarididae ♦ Christoffersen, 1987
Hippolytidae Bate, 1888
Lysmatidae ♦ Dana, 1852b
Merguiidae ♦ Christoffersen, 1987
Ogyrididae ♦ Holthuis, 1955
Thoridae ♦ Kingsley, 1878
Superfamily Atyoidea De Haan, 1849
Atyidae De Haan, 1849
Superfamily Bresilioidea Calman, 1896
Agostocarididae ♦ Hart & Manning, 1986

Table 2 (*Continued*)

Alvinocarididae † Christoffersen, 1986
Bresiliidae ♦ Calman, 1896
Disciadidae ♦ Rathbun, 1902
Pseudochelidae ♦ De Grave & Moosa, 2004
Superfamily Campylonotoidea ♦ Sollaud, 1913
Bathypalaemonellidae ♦ de Saint Laurent, 1985
Campylonotidae ♦ Sollaud, 1913
Superfamily Crangonoidea Haworth, 1825
Crangonidae Haworth, 1825
Glyphocrangonidae Smith, 1884
Superfamily Nematocarcinoidea ♦ Smith, 1884
Eugonatononotidae ♦ Chace, 1937
Nematocarcinidae ♦ Smith, 1884
Rhynchocinetidae ♦ Ortmann, 1890
Xiphocaridae ♦ Ortmann, 1895
Superfamily Oplophoroidea Dana, 1852b
Acanthephyridae ♦ Bate, 1888
Oplophoridae Dana, 1852b
Superfamily Palaemonoidea Rafinesque, 1815
Desmocarididae ♦ Borradaile, 1915
Euryrhynchidae ♦ Holthuis, 1950
Palaemonidae Rafinesque, 1815
Typhlocarididae ♦ Annandale & Kemp, 1913
Superfamily Pandaloidea Haworth, 1825
Chlorotocellidae ♦ Komai, Chan, & De Grave, 2019
Pandalidae Haworth, 1825
Superfamily Pasiphaeoidea Dana, 1852b
Pasiphaeidae Dana, 1852b
Superfamily Physetocaridoidea ♦ Chace, 1940
Physetocarididae ♦ Chace, 1940
Superfamily Pleopteryxoidea † Schweigert & Garassino, 2006
Pleopteryxidae † Schweigert & Garassino, 2006
Superfamily Processoidea ♦ Ortmann, 1896
Processidae ♦ Ortmann, 1896
Superfamily Psalidopodoidea ♦ Wood-Mason & Alcock, 1892
Psalidopodidae ♦ Wood-Mason & Alcock, 1892
Superfamily Stylodactyloidea ♦ Bate, 1888
Stylodactylidae ♦ Bate, 1888

Table 2 (*Continued*)

Infraorder Palaeopalaemonida † Schram & Dixon, 2004
Palaeopalaemonidae † Brooks, 1962
Infraorder Polychelida Scholtz & Richter, 1995
Superfamily Eryonoidea De Haan, 1841
Coleiidae † Van Straelen, 1925
Eryonidae † De Haan, 1841
Palaeopentachelidae † Ahyong, 2009
Polychelidae Wood-Mason, 1874
Tetrachelidae † Beurlen, 1930
Infraorder Glypheidea Winkler, 1881
Superfamily Erymoidea † Van Straelen, 1925
Erymidae † Van Straelen, 1925
Pemphicidae † Van Straelen, 1928
Superfamily Glaessnericaroidea † Karasawa, Schweitzer, & Feldmann, 2013
Glaessnericaridae † Karasawa, Schweitzer, & Feldmann, 2013
Superfamily Glypheoidea Winkler, 1881
Chimaerastacidae † Amati, Feldmann, & Zonneveld, 2004
Clytiopsidae † Beurlen, 1927
Glypheidae Winkler, 1881
Litogastroidae † Karasawa & others, 2013
Mecochiridae † Van Straelen, 1925
Neoglypheidae ♦ Karasawa, Schweitzer, & Feldmann, 2013
Platychelidae † Glaessner, 1969
Infraorder Achelata Scholtz & Richter, 1995
Cancrinidae † Beurlen, 1930
Palinuridae Latreille, 1802
Scyllaridae Latreille, 1825
Infraorder Astacidea Latreille, 1802
Section Astacida Scholtz & Richter, 1995
Superfamily Astacoidea Latreille, 1802
Astacidae Latreille, 1802
Cambaridae Hobbs, 1942
Cambaroididae ♦ Villalobos, 1955 (= **Cricoidoscelosidae** † Taylor, Schram, & Yanbin, 1999) (see Audo & others, 2023)
Superfamily Parastacoidea Huxley, 1879
Parastacidae Huxley, 1879
Superfamily Protastacoidea Albrecht, 1983
Protastacidae † Albrecht, 1983
Section Homarida Scholtz & Richter, 1995
Superfamily Enoplometopoidea de Saint Laurent, 1988

Table 2 (*Continued*)

Enoplometopidae ♦ de Saint Laurent, 1988
Uncinidae † Beurlen, 1928
Superfamily Stenochiroidea † Beurlen, 1928
Stenochiridae † Beurlen, 1928
Superfamily Nephropoidea Dana, 1852b
Nephropidae Dana, 1852b
Infraorder Axiidea de Saint Laurent, 1979a
Anacalliacidae Manning & Felder, 1991
Axiidae Huxley, 1879
Callianassidae Dana, 1852b
Callianideidae Kossmann, 1880
Callianopsidae Manning & Felder, 1991
Callichiridae Manning & Felder, 1991
Ctenochelidae Manning & Felder, 1991
Eucalliacidae Manning & Felder, 1991
Micheleidae Sakai, 1992
Paracalliacidae Sakai, 2005
Strahlaxiidae ♦ Poore, 1994
Infraorder Gebiidea de Saint Laurent, 1979
Axianassidae Schmitt, 1924
Laomediidae Borradaile, 1903
Thalassinidae Latreille, 1831
Upogebiidae Borradaile, 1903
Infraorder Anomura MacLeay, 1838
Superfamily Aegloidea Dana, 1852a
Aeglidae Dana, 1852a
Superfamily Chirostyloidea Ortmann, 1892a
Chirostylidae Ortmann, 1892a
Eumunididae ♦ A. Milne-Edwards & Bouvier, 1900
Kiwaidae ♦ Macpherson, Jones, & Segonzac, 2005
Pristinaspinidae † Ahyong & Roterman, 2014
Superfamily Eocarcinoidea † Withers, 1932
Eocarcinidae † Withers, 1932
Platykottidae † Chablais, Feldmann, & Schweitzer, 2011
Superfamily Galatheoidea Samouelle, 1819
Catillogalatheidae † Robins and others, 2016
Galatheidae Samouelle, 1819
Munididae Ahyong and others, 2010
Munidopsidae Ortmann, 1898
Paragalatheidae † Robins and others, 2016
Porcellanidae Haworth, 1825
Superfamily Hippoidea Latreille, 1825

Table 2 (*Continued*)

Albuneidae Stimpson, 1858a
Blepharipodidae Boyko, 2002
Hippidae ♦ Latreille, 1825
Superfamily Uncertain
Retrorsichelidae † Feldmann, Tshudy, & Thomson, 1993
Superfamily Gastrodoroidea † Van Bakel and others, 2008
Gastrodoridae † Van Bakel and others, 2008
Superfamily Lithodoidea Samouelle, 1819
Hapalogastridae Brandt, 1850
Lithodidae Samouelle, 1819
Superfamily Lomisoidea ♦ Bouvier, 1895
Lomisidae ♦ Bouvier, 1895
Superfamily Paguroidea Latreille, 1802
Annuntidiogenidae † Fraaije, 2014
Calcinidae ♦ Fraaije, van Bakel, & Jagt, 2017
Coenobitidae Dana, 1851a
Diogenidae Ortmann, 1892a
Paguridae Latreille, 1802
Parapaguridae Smith, 1882
Pilgrimchelidae † Fraaije, 2014
Probeebeidae Boone, 1926
Pylochelidae Bate, 1888
Pylojacquesidae ♦ McLaughlin & Lemaitre, 2001
Schobertellidae † Schweigert and others, 2013
Xylopaguridae Gašparič and others, 2016
Infraorder Brachyura Linnaeus, 1758
Section Dromiacea De Haan, 1833
Superfamily Homolodromioidea Alcock, 1900
Bucculentidae † Schweitzer & Feldmann, 2009
Goniodromitidae † Beurlen, 1932
Homolodromiidae Alcock, 1900
Jurellanidae † Klompmaker & Robins in Robins & Klompmaker, 2019
Longodromitidae † Schweitzer & Feldmann, 2009
Prosopidae † Von Meyer, 1860
Tanidromitidae † Schweitzer & Feldmann, 2008
Superfamily Glaessneropsoidea † Patrulius, 1959
Glaessneropsidae † Patrulius, 1959
Lecythocaridae † Schweitzer & Feldmann, 2009

Table 2 (*Continued*)

Nodoprosopidae † Schweitzer & Feldmann, 2009
Viaiidae † Artal and others, 2012
Superfamily Konidromitioidea † Schweitzer & Feldmann, 2010
Konidromitidae † Schweitzer & Feldmann, 2010
Superfamily Dromioidea De Haan, 1833
Basinotopidae † Karasawa, Schweitzer, & Feldmann, 2011
Diaulacidae † Wright & Collins, 1972
Dromiidae De Haan, 1833
Dynomenidae Ortmann, 1892b
Sphaerodromiidae Guinot & Tavares, 2003
Xandarocarcinidae † Karasawa, Schweitzer & Feldmann, 2011
Section Homoloida De Haan, 1839
Superfamily Homoloidea De Haan, 1839
Homolidae De Haan, 1839
Latreillidae Stimpson, 1858a
Mithracitidae † Števčić, 2005
Poupiniidae Guinot, 1991
Tithonohomolidae † Feldmann & Schweitzer, 2009
Section Callichimaeroida † Luque & others, 2019
Superfamily Callichimaeroidea † Luque & others, 2019
Callichimaeridae † Luque & others, 2019
Section Torynommoida † Glaessner, 1980
Superfamily † Torynommoidea Glaessner, 1980
Torynommidae † Glaessner, 1980
Section Etyoida † Guinot & Tavares, 2001
Superfamily † Etyoidea Guinot & Tavares, 2001
Etyidae † Guinot & Tavares, 2001
Feldmanniidae † Schweitzer & others, 2012
Section Raninoida Ahyong & others, 2007
Superfamily Necrocarcinoidea † Förster, 1968
Camarocarcinidae † Feldmann, Li, & Schweitzer, 2008
Cenomanocarcinidae † Guinot, Vega, & Van Bakel, 2008
Necrocarcinidae † Förster, 1968
Orithopsidae † Schweitzer & others, 2003

Table 2 (*Continued*)

Paranecrocarcinidae † Fraaije & others, 2008
Superfamily Palaeocorystoidea † Lőrenthey *in* Lőrenthey & Beurlen, 1929
Palaeocorystidae † Lőrenthey *in* Lőrenthey & Beurlen, 1929
Superfamily Raninoidea De Haan, 1839
Lyreididae Guinot, 1993
Raninidae De Haan, 1839
Section Dakoticancroida † Rathbun, 1917
Superfamily Dakoticancroidea † Rathbun, 1917
Dakoticancridae † Rathbun, 1917
Ibericancridae † Artal & others, 2008
Section Cyclodorippoida Ortmann, 1892b
Superfamily Cyclodorippoidea Ortmann, 1892b
Cyclodorippidae Ortmann, 1892b
Cymonomidae Bouvier, 1897
Phyllotymolinidae ♦ Tavares, 1998
Quadratoplanidae † Franţescu, 2014
Section Eubrachyura de Saint Laurent, 1980
Marocarcinidae † Guinot, De Angeli & Garassino, 2008
Superfamily Aethroidea Dana, 1851b
Aethridae Dana, 1851b
Superfamily Bellioidea ♦ Dana, 1852a
Belliidae ♦ Dana, 1852a
Superfamily Bythograeoidea ♦ Williams, 1980
Bythograeidae ♦ Williams, 1980
Superfamily Calappoidea De Haan, 1833
Calappidae De Haan, 1833
Superfamily Cancroidea Latreille, 1802
Atelecyclidae Ortmann, 1893
Cancridae Latreille, 1802
Montezumellidae † Ossó & Dominguez, 2021
Superfamily Carpilioidea Ortmann, 1893
Arabicarcinidae † Schweitzer & Feldmann, 2017
Carpiliidae Ortmann, 1893
Palaeoxanthopsidae † Schweitzer, 2003
Tumidocarcinidae † Schweitzer, 2005
Zanthopsidae † Vía, 1959
Superfamily Cheiragonoidea ♦ Ortmann, 1893
Cheiragonidae ♦ Ortmann, 1893

Table 2 (*Continued*)

Superfamily Componocancroidea † Feldmann, Schweitzer, & Green, 2008
Componocancridae † Feldmann, Schweitzer, & Green, 2008
Superfamily Corystoidea Samouelle, 1819
Corystidae Samouelle, 1819
Superfamily Dairoidea Serène, 1965
Dacryopilumnidae ♦ Serène, 1965
Dairidae Ng & Rodriguez, 1986
Superfamily Dorippoidea MacLeay, 1838
Dorippidae MacLeay, 1838
Ethusidae Guinot, 1977
Goniochelidae † Schweitzer & Feldmann, 2011
Telamonocarcinidae † Larghi, 2004
Superfamily Eriphioidea MacLeay, 1838
Dairoididae Števčić, 2005
Eriphiidae MacLeay, 1838
Hypothalassiidae Karasawa & Schweitzer, 2006
Menippidae Ortmann, 1893
Oziidae Dana, 1851b
Platyxanthidae Guinot, 1977
Superfamily Gecarcinucoidea ♦ Rathbun, 1904
Gecarcinucidae ♦ Rathbun, 1904
Parathelphusidae ♦ Alcock, 1910
Superfamily Goneplacoidea MacLeay, 1838
Acidopsidae ♦ Števčić, 2005
Carinocarcinoididae † Karasawa & Kato, 2003
Chasmocarcinidae Serène, 1964
Conleyidae ♦ Števčić, 2005
Euryplacidae Stimpson, 1871a
Goneplacidae MacLeay, 1838
Litocheiridae Kinahan, 1856
Magyarcarcinidae † Domínguez & Ossó, 2016
Martinocarcinidae † Schweitzer, Feldmann, & Bonadio, 2009
Mathildellidae Karasawa & Kato, 2003
Progeryonidae ♦ Števčić, 2005
Scalopidiidae ♦ Števčić, 2005
Sotoplacidae ♦ Castro, Guinot, & Ng, 2010
Vultocinidae Ng & Manuel-Santos, 2007
Superfamily Hexapodoidea Miers, 1886
Hexapodidae Miers, 1886

Table 2 (*Continued*)

Superfamily Hymenosomatoidea ♦ MacLeay, 1838
Hymenosomatidae ♦ MacLeay, 1838
Superfamily Leucosioidea Samouelle, 1819
Folguerolesiidae † Artal & Hyžný, 2016
Iphiculidae Alcock, 1896
Leucosiidae Samouelle, 1819
Matutidae de Haan, 1841
Superfamily Majoidea Samouelle, 1819
Epialtidae MacLeay, 1838
Inachidae MacLeay, 1838
Inachoididae Dana, 1851b
Macrocheiridae Dana, 1851d
Majidae Samouelle, 1819
Oregoniidae Garth, 1958
Priscinachidae † Breton, 2009
Superfamily Orithyioidea Dana, 1852a
Orithyiidae Dana, 1852a
Superfamily Palicoidea Bouvier, 1898
Crossotonotidae Moosa & Serène, 1981
Palicidae Bouvier, 1898
Superfamily Parthenopoidea MacLeay, 1838
Parthenopidae MacLeay, 1838
Superfamily Pilumnoidea Samouelle, 1819
Galenidae Alcock, 1898
Pilumnidae Samouelle, 1819
Tanaochelidae ♦ Ng & Clark, 2000
Superfamily Portunoidea Rafinesque, 1815
Carcineretidae † Beurlen, 1930
Carcinidae MacLeay, 1838
Geryonidae Colosi, 1924
Lithophylacidae † Van Straelen, 1936
Longusorbiidae † Karasawa, Schweitzer, & Feldmann, 2008
Portunidae Rafinesque, 1815
Psammocarcinidae † Beurlen, 1930
Superfamily Potamoidea Ortmann, 1896
Potamidae Ortmann, 1896
Potamonautidae Bott, 1970
Superfamily Pseudocarcinoidea Ng & Davie, 2020
Pseudocarcinidae Ng & Davie, 2020
Superfamily Pseudothelphusoidea Ortmann, 1893
Epiloboceridae ♦ Smalley, 1964
Pseudothelphusidae Ortmann, 1893
Superfamily Pseudozioidea Alcock, 1898
Christmaplacidae ♦ Naruse & Ng, 2014
Pilumnoididae ♦ Guinot & Macpherson, 1987

Table 2 (*Continued*)

Planopilumnidae ♦ Serène, 1984
Pseudoziidae Alcock, 1898
Superfamily Retroplumoidea Gill, 1894
Archaeopidae † Karasawa & others, 2019
Retroplumidae Gill, 1894
Superfamily Trapezioidea Miers, 1886
Domeciidae Ortmann, 1893
Tetraliidae Castro, Ng, & Ahyong, 2004
Trapeziidae Miers, 1886
Vicetitrapeziidae † Beschin, Busulini, & Tessier, 2021
Superfamily Trichodactyloidea H. Milne Edwards, 1853
Trichodactylidae H. Milne Edwards, 1853
Superfamily Trichopeltarioidea Tavares & Cleva, 2010
Trichopeltariidae Tavares & Cleva, 2010
Superfamily Xanthoidea MacLeay, 1838
Linnaeoxanthidae ♦ Števčić, 2005
Panopeidae Ortmann, 1893
Pseudorhombiliidae Alcock, 1900
Xanthidae MacLeay, 1838
Subsection Thoracotremata Guinot, 1977
Superfamily Cryptochiroidea ♦ Paul'son, 1875
Cryptochiridae ♦ Paul'son, 1875
Superfamily Grapsoidea MacLeay, 1838
Gecarcinidae MacLeay, 1838
Glyptograpsidae ♦ Schubart, Cuesta, & Felder, 2002
Grapsidae MacLeay, 1838
Leptograpsodidae ♦ Guinot, Ng, & Rodriguez Moreno, 2018
Percnidae Števčić, 2005
Plagusiidae Dana, 1851c
Sesarmidae Dana, 1851c
Varunidae H. Milne Edwards, 1853
Xenograpsidae ♦ N. K. Ng and others, 2007
Superfamily Ocypodoidea Rafinesque, 1815
Camptandriidae Stimpson, 1858b
Dotillidae ♦ Stimpson, 1858b
Heloeciidae ♦ H. Milne Edwards, 1852
Macrophthalmidae Dana, 1851c
Mictyridae ♦ Dana, 1851c
Ocypodidae Rafinesque, 1815
Xenophthalmidae Stimpson, 1858b
Superfamily Pinnotheroidea De Haan, 1833
Aphanodactylidae ♦ Ahyong & Ng, 2009
Pinnotheridae De Haan, 1833

Table 2 (*Continued*)

Brachyura incertae sedis
Cretapsaridae † Luque *in* Luque & others, 2021
Montemagrechiridae † Klompmaker, Portell, & van der Meij, 2016
Decapoda incertae sedis
Amazighopsidae † Garassino & Pasini, 2018

Decapoda Checklists

During the 2000s, the publication of generic and species level checklists for most decapod groups, some including fossils (Table 3), in addition to the constantly updated DecaNet, a subregister of WoRMS, greatly streamlined work on decapods. Fossil taxa have been integrated into DecaNet. These provide an excellent entry into the alpha taxonomy of Decapoda.

SHRIMP: INFRAORDERS DENDROBRANCHIATA, CARIDEA, STENOPODEA, AND PROCARIDEA

Felgenhauer and Abele (1983) provided a historical summary of the classification of all shrimp-like decapods. Tavares and Martin (2010) provided a brief summary of classification of dendrobranchiate shrimp. Our classification of the Dendrobranchiata follows Tavares and Martin (2010), supported by the work of Robalino and others (2016). Most analyses of Decapoda have found that Dendrobranchiata is monophyletic and a basally derived sister group to the Pleocyemata (Tavares, Serejo, & Martin, 2009, and references therein). Mitogenomic analysis of an array of decapods also confirmed monophyly of Dendrobranchiata (Shen, Braband, & Scholtz, 2013). Within Dendrobranchiata, the analysis of Tavares, Serejo, and Martin (2009) found that Sergestoidea and Penaeoidea were monophyletic groups. A more recent phylogenetic analysis based on a combined data set, including morphologic, genetic, and behavioral characters, found that Penaeoidea was monophyletic and included Penaeidae, Benthesicymidae, Aristeidae, and Solenoceridae, with Sicyoniidae apparently embedded within Penaeidae (Robalino & others, 2016). Sergestoidea included Sergestidae and Luciferidae and was found to be sister to Penaeoidea (Robalino & others, 2016). Another analysis suggested that Sergestoidea may be further subdivided into multiple families (Vereshchaka, 2017), but this has not yet been incorporated into mainstream classification (DecaNet, 2024). Benthesicymidae was recovered as monophyletic (Vereshchaka, Kulagin, & Lunina, 2021). At this time, we recognize Penaeidae, Benthesicymidae, Aristeidae, Solenoceridae, Sicyoniidae, Sergestidae, and Luciferidae, as well as the extinct Aegeridae, Aciculopodidae, and Carpopenaeidae. Ongoing work is focused on determining monophyly at the generic level and the species-level composition within genera. For generic and species composition of extant families and genera, we follow De Grave and Fransen (2011), Poore and Ahyong (2023), and DecaNet (2024).

Extinct dendrobranch families have been defined based on morphological criteria and have received little phylogenetic attention (except Robalino & others, 2016). Aegeridae was erected by Burkenroad (1963) based on an array of characteristics he considered suggestive of Aristeidae, Penaeidae, Sergestidae, and Solenoceridae. This led him to place Aegeridae as a basally derived group, characterized by a narrow first pleonal somite, a ventral rostral spine, and spinose cuticle, and he reported a petasma (Burkenroad, 1963). Glaessner (1969) did not recognize Aegeridae, instead placing its constituent genera within Penaeidae. Aegeridae was extensively diagnosed by Schweitzer and others (2014), who noted that whereas it clearly shared affinities with other dendrobranch shrimp, Aegeridae did not necessarily belong within an established superfamily. They tentatively placed it within Penaeoidea. Aegeridae was later recovered as

Table 3. Checklists of Decapoda. All lists are to species level and extant only unless otherwise noted. All include global records.

Taxa covered	Authors
Brachyura	Ng & others (2008)
Chirostylidae, Galatheidae, Kiwaidae	Baba & others (2008)
Decapoda genera (extinct and extant)	De Grave & others (2009)
Extinct Decapoda	Schweitzer & others (2010)
Anomura (Lithodoidea, Lomisoidea, Paguroidea)	McLaughlin & others (2010)
Anomura (Porcellanidae)	Osawa & McLaughlin (2010)
Anomura (Aegloidea)	McLaughlin, Lemaitre, & Crandall (2010)
Anomura (Hippoidea)	Boyko & McLaughlin (2010)
Marine Lobsters (Astacidea, Glypheidea, Achelata, Polychelida)	Chan (2010)
All decapod shrimp (Dendrobranchiata, Caridea, Procaridea, Stenopodidea)	De Grave & Fransen (2011)
Extant Crustacea (to family)	Ahyong & others (2011)
Freshwater crayfish (extinct and extant)	Crandall & De Grave (2017)
All Decapoda (to family)	Schram & Koenemann (2021)
All marine Decapoda (to genus)	Poore & Ahyong (2023)

polyphyletic (Robalino & others, 2016), but as only two species within two of the four genera were analyzed, we elect to retain the family as currently construed (Schweitzer & others, 2014). Shared characters of Aegeridae include the spinose third maxillipeds and a very short first pleonal somite.

Aciculopodidae was based on an incomplete fossil of Devonian age exhibiting shrimp morphology; thus, we retain it as a separate family here, as it is chronologically separated from other shrimp occurrences by nearly 100 million years. Carpopenaeidae was erected by Garassino (1994), for *Carpopenaeus*, placed by Glaessner (1945) within Penaeidea (=Dendrobranchiata). Garassino (1994) noted that the multiarticulate carpus of pereiopod 2 and 3 was completely unknown within Dendrobranchiata but occurred often in caridean shrimp. The lack of overlap of pleonal somite 2 over somites 1 and 3 clearly places Carpopenaeidae within Dendrobranchiata, and the well-developed 5 pairs of pereiopods suggest placement in Penaeoidea.

Caridea, like Dendrobranchiata, has repeatedly been found to be monophyletic (Bracken & others, 2010; Wolfe & others, 2019). Over the decades, Caridea embraced a wide array of families, with a proliferation of names, many of which recently have been synonymized. Wicksten (2010) summarized classifications up to that time, mostly following Christoffersen (1990), Chace (1992), and Holthuis (1993). Subsequently, several families have been synonymized, and the classification used here follows the arrangement of infraorders, superfamilies, families, and genera in several recent works (De Grave & others, 2009; Chan & others, 2010; De Grave, Chu, & Chan, 2010; Schweitzer & others, 2010; De Grave & Fransen, 2011; Li & others, 2011; De Grave & others, 2014; De Grave, Fransen, & Page, 2015; Davis & others, 2018; Liao & others, 2019; Chow, DeGrave, & Tsang, 2020; Schram & Koenemann, 2021; Poore & Ahyong, 2023; DecaNet, 2024).

Fossil carideans can be difficult to place within families. The only extinct caridean family is Pleopteryxidae, erected by Schweigert and Garassino (2006) to accommodate its caridean affinities, as well as its unique long, feather-like pleopods. Most fossil carideans are placed either within

Palaemonidae or Caridea incertae sedis, as the tiny details used to classify extant caridean shrimp typically are not seen in fossils.

Goy (2010) summarized the history of classification of Stenopodea. Our classification of Stenopodea follows Chen and others (2016), who showed that the three constituent families recognized for the infraorder were not monophyletic. They suggested placing all of the genera within one family, Stenopodidae, until further analysis was completed. Bracken and others (2009) summarized placement of procarid shrimp and recovered Procaridea as a separate infraorder from Caridea (Bracken & others, 2009), later confirmed by mitogenomic analysis (Wang & others, 2021). Herein, Procaridea includes the extinct Udorellidae, a group exhibiting a caridean second pleonal somite overlapping both pleonal somites 1 and 3 and lacking chelipeds. Felgenhauer and Abele (1983) proposed that Udorellidae and procarid shrimp were similar in the nature of the third maxilliped, and Fransen and De Grave (2009) compared the achelate pereiopods of udorellids with procarids. Our own examination of specimens attributed to the sole contained genus *Udorella* Oppel, 1862, confirms the lack of chelae on the pereiopods. Thus, Udorellidae is placed within Procaridea, an otherwise extant infraorder with the same characteristics.

INFRAORDER PALAEOPALAEMONIDA

This extinct group is composed of one family, genus, and species. Schram and Dixon (2004) recovered Palaeopalaemonidae, for which they introduced the name Palaeopalaemonida, as the sister to a clade containing Achelata, Anomura, and Brachyura. Karasawa, Schweitzer, & Feldmann (2013) and Jones and others (2018) recovered the group as sister to the Polychelida and basal within Decapoda (Fig. 2). Herein, we consider Palaeopalaemonida as a distinct infraorder, following these previous works.

INFRAORDER POLYCHELIDA

Polychelida has had a rather strange history of placement within Decapoda. De Haan in 1833–1850 (1841) erected Eryonidae as a family within the Astacidea, which he considered to also include scyllarid, palinurid, and astacid lobsters. He only referenced extinct genera by noting the work of Münster (1839), and indeed the extant family Polychelidae was not recognized until later (Wood-Mason, 1874). Wood-Mason (1874) noted the similarities between Polychelidae and the extinct Eryonidae. Many subsequent workers considered Polychelidae to be similar to palinurid and scyllarid lobsters, and Borradaile (1907) erected the name Palinura to include all three types of lobsters. Drach (1950) examined extant polychelid lobsters and suggested that eryonid lobsters as a group be separated from the palinurids, based on the endophragmal skeleton. Glaessner (1969) conceived Palinura as including glypheoid, some erymoid, eryonoid, palinurid, and scyllarid lobsters, an arrangement not recognized today. Palinura as construed by Borradaile (1907) has remained in use by some workers (Lavalli & Spanier, 2010) (see discussion below). Glaessner (1969) appears to have

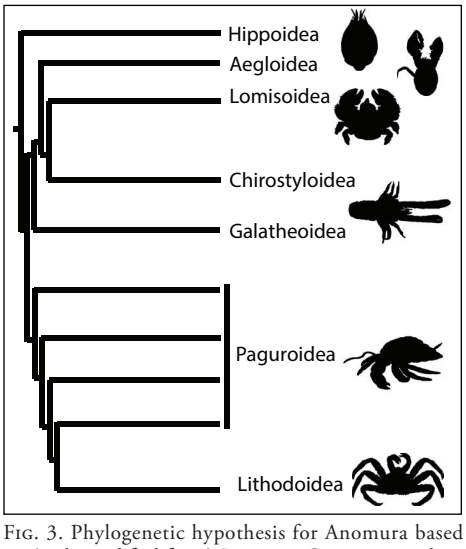

Fig. 3. Phylogenetic hypothesis for Anomura based on (and simplified from) Bracken-Grissom & others (2013, fig. 1, simplified). Silhouettes from PhyloPic.

been one of the first authors to formalize the relationship among the extinct Eryonidae, Coleiidae, Tetrachelidae, and Polychelidae by placing these families within Eryonoidea. Scholtz and Richter (1995) demonstrated that Palinura as construed by Borradaile (1907) was not monophyletic, erecting Polychelida for polychelidan lobsters and Achelata to embrace Palinuridae and Scyllaridae. Ahyong (2009) placed Eryonidae, Coleiidae, and Tetrachelidae and the extinct and extant Polychelidae within Polychelida.

The monophyly of Polychelida and its clear distinction from Achelata have been recovered repeatedly in phylogenetic analyses of morphology and molecular data (Ahyong, 2009 and references therein up to 2009; Karasawa, Schweitzer, & Feldmann, 2013; Bracken-Grissom & others, 2014; Wolfe & others, 2019) (Fig. 2). In this volume, we follow the arrangement of Ahyong (2009), Schweitzer and others (2010), Schram and Koenemann (2021), and Poore and Ahyong (2023) for genera within families of Polychelida.

INFRAORDER GLYPHEIDEA

Perhaps no group within Decapoda has been subject to as much uncertainty in taxonomic placement as the glypheoid and erymoid lobsters, undoubtedly due to their being almost completely extinct. Only two extant genera of Glypheidea currently are recognized (Chan, 2010; Karasawa, Schweitzer, & Feldmann, 2013). Glaessner (1969) adopted the view that Glypheoidea was allied with Palinura, and that Erymoidea was nested with Astacidea, probably due to the nature of the pereiopod terminations in each group. Beginning in the 2000s, morphological and molecular phylogenies of extant taxa demonstrated that glypheidean lobsters were not part of a monophyletic group including Palinura (Dixon, Ahyong, & Schram, 2003; Ahyong & O'Meally, 2004). There was no consensus as to whether *Neoglyphea* and its extinct congeners were more closely related to the Polychelida or the Astacidea, both groups of clawed lobsters.

At the same time, other analyses included fossil taxa of both the Glypheoidea and Erymoidea, the latter of which is completely extinct. Glypheoid lobsters were recovered as monophyletic and sister to the erymoid lobsters, as part of a larger clade including astacid lobsters (Amati, Feldmann, & Zonneveld, 2004). Another analysis recovered erymoid lobsters as part of a clade with astacid lobsters, and glypheoid lobsters were found in a clade with pemphicid lobsters (Schram & Dixon, 2004). By the time of publication of the checklists of extinct and extant decapod genera (De Grave & others, 2009) and extinct decapod species (Schweitzer & others, 2010), a consensus view was adopted in which Glypheidea was recognized as including Glypheidae, Erymidae, Mecochiridae, Pemphicidae, and Platychelidae. This view was followed by Wahle and others (2012).

The state of lobster classification up to the present was summarized by Karasawa, Schweitzer, and Feldmann (2013), who conducted a morphology-based phylogenetic analysis with representatives of all extinct and extant families but one, in some cases including every genus within a family, for a total of 27 extant and 44 extinct genera. Their analysis recovered three superfamilies, Erymoidea, Glypheoidea, and the monotypic Glaessnericaridoidea, in one monophyletic clade, Glypheidea. Their analysis resulted in the resurrection of one family that had gone out of usage, Clytiopsidae, as well as some new ones, Glaessnericaridae, Litogastroidae, and Neoglypheidae. Bracken-Grissom and others (2014) analyzed 173 species of extant lobsters, and their molecular phylogeny resulted in the extant glypheideans in a clade sister to the astacid lobsters. Charbonnier and others (2015) recovered a somewhat different topology in examining a subset of extinct and extant lobsters, with Pemphicidae as part of Glypheoidea instead of Erymoidea, and a different arrangement of genera within

constituent families. Devillez, Charbonner, and Barriel (2019) summarized the history of placement of Erymidae among lobsters and its generic composition and examined a subset of extinct and extant lobsters. They recovered a phylogeny in which the erymoid lobsters were nested with the astacid lobsters, an arrangement followed in DecaNet (February 2024). Because Karasawa, Schweitzer, and Feldmann (2013) used the broadest array of extinct and extant lobsters among these recent analyses, we retain the infraorder, superfamily, and family level classification therein (Fig. 2), following Schram and Koenemann (2021). Generic placement in families and of species in genera follows several recent works (Karasawa, Schweitzer, & Feldmann, 2013; Charbonnier & others, 2013, 2015; Devillez & Charbonnier, 2017, 2019; Devillez & others, 2016, 2017; Devillez, Charbonnier, & Pezy, 2018; Devillez, Charbonner, & Barriel, 2019; Feldmann, Schweitzer & Haggart, 2020). Our classification and that of Schram and Koenemann (2021) recognize Neoglypheidae as embracing the two extant glypheid genera, whereas Poore and Ahyong (2023) and DecaNet place the extant genera in Glypheidae.

INFRAORDER ACHELATA

Palinuridae and Scyllaridae have been recognized as related families at least since Borradaile (1907) grouped them together within Palinura. Glaessner (1969) placed the two families along with the extinct Cancrinidae within Palinuroidea. Scholtz and Richter (1995) demonstrated that Palinura as construed by Borradaile (1907) was polyphyletic and erected Achelata to embrace Palinuridae and Scyllaridae, separating it from Polychelida (discussed above). Martin and Davis (2001) and Lavalli and Spanier (2011) retained Palinura *sensu* Borradaile, including Polychelida within it. Palero and others (2009) summarized the placement of Achelata and its constituent families to that time and recovered the extant achelatans as a monophyletic group, including monophyletic Palinuridae and Scyllaridae. The monophyly of Achelata *sensu* Scholtz and Richter (1995) has been recovered repeatedly in phylogenetic analyses of morphology and molecular data (Karasawa, Schweitzer, & Feldmann, 2013; Bracken-Grissom & others, 2014; Wolfe & others, 2019) (Fig. 2). Karasawa, Schweitzer, and Feldmann (2013) recovered Cancrinidae within Achelata in an analysis of morphology, and Haug and others (2016) considered cancrinids as closely related to scyllarids. Thus, we place the three families, Cancrinidae, Palinuridae, and Scyllaridae, within Achelata, echoing Schram and Koenemann (2021), Poore and Ahyong (2023), and DecaNet.

INFRAORDER ASTACIDEA

Borradaile (1907) united the astacid crayfish and homarid lobsters into Astacura. Scholtz and Richter (1995) regarded this group as polyphyletic and recommended retention of two separate taxa for them, the Astacida, composed of the freshwater crayfish, and the Homarida, including the marine clawed lobsters. Martin and Davis (2001) considered both astacids and homarids as part of the Infraorder Astacida. Karasawa, Schweitzer, and Feldmann (2013) recognized Sections Astacida and Homarida, each monophyletic, as part of a larger monophyletic infraorder Astacidea. The analysis of Bracken-Grissom and others (2013) also supported monophyly of Astacida and Homarida within Astacidea.

Within Astacida, Karasawa, Schweitzer, and Feldmann (2013) recovered two extant families, Astacidae and Cambaridae, as well as the extinct Cricoidoscelosidae, within Astacoidea, in addition to the extant Parastacoidea and the extinct Protastacoidea as monotypic superfamilies. Crayfish classification and arrangement of families, genera, and species were recently compiled by Crandall and De Grave (2017) based on the

phylogeny of Stern and others (2017). Crandall and De Grave (2017) summarized the history of classification of crayfish, and they supported the superfamily arrangement of Karasawa, Schweitzer, and Feldmann (2013) for extant taxa, in addition to recognizing Cambaroididae, a monotypic family within Astacoidea. Most recently, Audo and others (2023) synonymized Cricoidoscelosidae with Cambaroididae, extending the geologic range of that family into the Cretaceous, but not changing its geographic range. Thus, our Astacida classification essentially follows Karasawa, Schweitzer, and Feldmann (2013), Crandall and De Grave (2017), and Schram and Koenemann (2021) (Fig. 2).

Within Homarida, Karasawa, Schweitzer, and Feldmann (2013) and Bracken-Grissom and others (2013) found the same monophyletic extant families, Enoplometopidae and Nephropidae, and Karasawa, Schweitzer, and Feldmann (2013) recognized two extinct families, one allied with Enoplometopidae (Uncinidae) and one comprising a monotypic superfamily Stenochiroidea. These groups were recognized by Schram and Koenemann (2021), and we recognize all of these homarid taxa herein (Fig. 2).

INFRAORDERS GEBIIDEA AND AXIIDEA

Until recently, taxa referred to these infraorders were commonly referred to as "callianassids" or "thalassinids." Most fossil literature has used these terms, and indeed, dozens of fossil species have been referred to *Callianassa sensu lato* which have never been revised (see list of species in Schweitzer & others, 2010). Revision of fossils referred to this group has received renewed attention (summarized by Hyžný & Klompmaker, 2015). At this time, fossil taxa are placed within the classification scheme developed for extant forms; no fossil axiideans or gebiideans have been analyzed phylogenetically.

Extant axiideans and gebiideans have recently received renewed attention. de Saint Laurent (1979a, 1979b) originally proposed two major groups, Gebiidea and Axiidea. Martin and Davis (2001) recognized the infraorder Thalassinidea, which included the mud and ghost shrimp, noting that the group was unlikely to be monophyletic. Robles and others (2009) demonstrated that Thalassinidea was not monophyletic and separated the taxa into two infraorders, Gebiidea and Axiidea, based on nuclear and mitochondrial genetic analysis, as originally suggested by de Saint Laurent (1979a, 1979b), based on morphology. They recovered Gebiidea as sister to a larger clade composed of a monophyletic Axiidea sister to a clade of astacids, achelatans, anomurans, and brachyurans. Tsang and others (2008), using two protein-coding nuclear genes, recovered Axiidea sister to a clade containing all lobster groups, and Gebiidea as sister to Anomura + Brachyura, basically the opposite of Robles and others (2009). Wolfe and others (2019), in a phylogenomic analysis, found Axiidea sister to a clade comprising a monophyletic Gebiidea as sister to the Anomura + Brachyura. Thus, although the relative placement of Gebiidea and Axiidea varies somewhat in comparison to other decapods, both are repeatedly recovered as separate clades.

Dworschak, Felder, & Tudge (2012) recognized two monophyletic infraorders, Gebiidea and Axiidea. Poore and others (2019) summarized the state of callianassoid systematics at that time and provided diagnoses for the families and genera they recognized, as well as a key to all axiidean families. They extensively revised callianassoid systematics, based on the phylogeny of Robles and others (2020). We follow the family and generic level classification for extant axiideans presented by Poore and others (2019) and Poore and Ahyong (2023), noting that a subsequent mitogenomic phylogeny has suggested that Strahlaxiidae may not be monophyletic (Kou & others, 2020). As yet, there are no

extinct axiidean families, although there are extinct genera and species. Gebiidean classification follows the family arrangement of Robles and others (2009).

INFRAORDER ANOMURA

Anomura, sometimes called Anomala (see McLaughlin & Holthuis, 1985, for discussion of the two terms), has historically been composed of hermit crabs, squat lobsters, mole crabs, and porcelain crabs, in addition to sometimes including axiidean and gebiidean shrimp and even the brachyuran dromiacean and raninoid crabs. Tudge, Asakura, and Ahyong (2012) noted the instability within the taxonomic arrangements of Anomura, and the history of placement of taxa within Anomura was summarized by Martin and Davis (2001) and McLaughlin, Lemaitre, and Sorhannus (2007). Burkenroad (1963) and Scholtz and Richter (1995) suggested that Anomura (=Anomala) exclude axiideans, gebiideans, and brachyurans. Bracken-Grissom and others (2013), using molecular and morphologic data, analyzed members of all but one anomuran family plus dendrobranch and caridean shrimp, axiideans, gebiideans, and brachyurans. They found that Anomura as construed by Scholtz and Richter (1995) is monophyletic, thus excluding axiideans, gebiideans, and brachyurans (Fig. 3).

In this work, we have separated the group into hermit crabs and relatives (Paguroidea, Lithodoidea, Gastrodoroidea) in one systematic chapter and all other anomurans (galatheoids, chirostyloids, hippoids, and others) into a second systematic chapter. This reflects the way these groups tend to be treated in the fossil record; it is also supported by molecular and morphological phylogeny (Bracken-Grissom & others, 2013). Hippoidea was found to be monophyletic and sister to the remaining anomurans (Bracken-Grissom & others, 2013). A large clade including Aegloidea, Lomisoidea, Chirostyloidea, and Galatheoidea comprised a second clade, sister to a clade that included all Paguroidea and Lithodoidea. Lithodoidea is considered by many to be a derived group within Paguroidea and thus is not recognized as a superfamily in some works. Paguroids and relatives are thus placed within a separate chapter from the other anomurans (Fig. 3).

The classification of hermit crabs and their relatives has undergone rapid changes in the past 20 years. Several recent phylogenies have shown that the hermit crabs may be polyphyletic. Indeed, Bracken-Grissom and others (2013) found that when morphological and molecular data were combined, hermit crabs formed a monophyletic group. However, when morphology was excluded, they were clearly polyphyletic. Some members of Pylochelidae were found to be sister to Galatheoidea (Tsang & others, 2011; Bracken-Grissom & others, 2013, molecular only). Other members of Pylochelidae were found in a distinct clade sister to Parapaguridae and Chirostyloidea + Aeglidae + Lomisidae

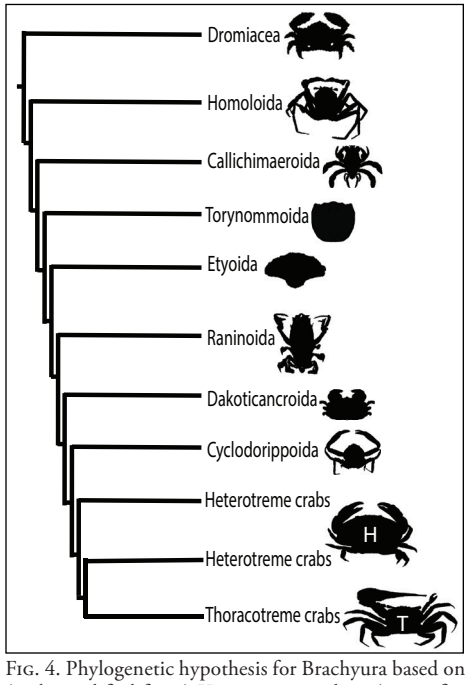

Fig. 4. Phylogenetic hypothesis for Brachyura based on (and simplified from) Karasawa & others (2011, fig. 3), Luque & others (2019, fig. 5), and Wolfe & others (2024, fig. 2). Silhouettes from Phylopic.

(Tsang & others, 2011; Bracken-Grissom & others, 2013, molecular only). Including morphology, Bracken-Grissom and others (2013) recovered Pylochelidae as monophyletic and sister to all other hermit crabs. Diogenidae, Coenobitidae, Paguridae, and Lithodidae were recovered as part of a large monophyletic clade (Tsang & others, 2011; Bracken-Grissom & others, 2013, including morphology); however, a molecular-only analysis found Diogenidae as polyphyletic and Paguridae as paraphyletic (Bracken-Grissom & others, 2013). Tan and others (2018) also found polyphyletic hermit crabs, whereas Wolfe and others (2019) recovered them as monophyletic. The most recent summary classification placed all the extant hermit crab families within Paguroidea for convenience, recognizing that the group may be polyphyletic (Poore & Ahyong, 2023). Our classification differs from this somewhat in recognizing Lithodoidea to include Lithodidae and Hapalogastridae, following Bracken-Grissom and others (2013), with the remaining hermit crab families placed within Paguroidea.

Recent work has recognized additional hermit crab families (Fraaije & others, 2022). These have not yet been widely adopted in the literature on extant forms, but we recognize most herein, especially as they are largely based on extinct forms. Gastrodoroidea, with the sole family Gastrodoridae, has been suggested to be closely related to hermit crabs. Annuntidiogenidae, Pilgrimchelidae, and Schobertellidae are extinct families known primarily from the Mesozoic of Europe (Fraaije, 2014), with only Annuntidiogenidae ranging into the Cenozoic (Yost, Feldmann, & Schweitzer, 2023). In addition, the previously extant-only Pylochelidae has been recognized in the fossil record. Probeebeidae has been resurrected recently based on an excellently preserved fossil, showing that the group has an extensive history ranging from the Cretaceous to Holocene (Fraaije & others, 2024). Xylopaguridae is a small group including extinct forms. The composition of Calcinidae as construed by Fraaije, van Bakel, and Jagt (2017) received no support in the analysis of Bracken-Grissom and others (2013); however, some aspects of their concept of the family were supported by Craig and Felder (2021). Thus, we recognize it as a monotypic family at this time. Poore and Ahyong (2023) noted the need to revise and analyze extant hermit crabs to determine the monophyly and generic composition of all proposed families and even the monophyly of genera, with which we strongly agree. In addition, phylogenetic analysis of extinct forms in concert with extant forms is crucial to attempt to resolve relationships between and among extinct and extant families, as well as monophyly of extinct families.

It is notable that in the fossil record, paguroid dorsal carapaces and pleonal somites only recently have been recognized (van Bakel & others, 2008; Fraaije, Klompmaker, & Artal, 2012; Fraaije & others, 2012); previous to this, hermit crabs were almost exclusively recognized from claws and pereiopods. Generally, taxa were placed within families based on which first cheliped was larger.

Among the remaining anomurans, which comprise a separate systematics chapter in this volume, Ahyong and others (2011) summarized the history of phylogenies and systematics of extant forms. They noted that the "squat lobsters," long hypothesized to be related, were actually composed of two major clades that evolved independently, the Chirostyloidea and Galatheoidea (Schnabel, Ahyong, & Maas, 2011). The arrangement of non-paguroid anomuran superfamilies and constituent families in this volume follows Tudge, Asakura, and Ahyong (2012) and Bracken-Grissom and others (2013), including Hippoidea, Aegloidea, Lomisoidea, Chirostyloidea, and Galatheoidea.

There are several extinct anomuran groups. Eocarcinoidea was recognized as an anomuran, based on features of the pereiopods and pleon (Feldmann & Schweitzer,

2010a). Scholtz (2020) considered it to be a basal brachyuran. We retain Eocarcinoidea within Anomura, based on the similarity of the pleon with other anomurans. Within Chirostyloidea, the extinct Pristinaspinidae is monotypic. The rich fossil record of Galatheoidea includes members of Catillogalatheidae and Paragalatheidae, known primarily from dorsal carapaces. Retrorsichelidae is a monotypic family with unusual carapace and pereiopod morphology. Luque and others (2019) suggested placement with the brachyuran group Callichimaeroida. For now, it is placed with the non-hermit crab Anomura until more data can resolve its taxonomic placement.

INFRAORDER BRACHYURA

Brachyura historically has been recognized as a discrete unit, with the most notable controversies being over whether podotrematous crabs or crabs with pleons extending posteriorly should be included within the group (see Davie, Guinot, & Ng, 2015a, for summary).

Davie, Guinot, and Ng (2015a) provided a summary of the historical subdivisions within Brachyura. The work of Bouvier (1896), Gordon (1963, 1966) and Hartnoll (1979) on the internal skeleton and the sternal and reproductive morphology suggested that two main groups existed, the peditremes (=Podotremata *sensu* Guinot) and the sternitremes (=Eubrachyura *sensu* de Saint Laurent). Guinot (1977, 1979) proposed the sections Podotremata, Heterotremata, and Thoracotremata, the latter two for sternitreme crabs. Heterotremata was characterized by female gonopores on the sternum and male gonopores on the coxae of pereiopods five. Thoracotremata included those crabs with both male and female gonopores on the sternum. Guinot also proposed Archaeobrachyura (1977, 1978) as a subset of podotrematous crabs to accommodate Homoloidea, Raninoidea, and Tymoloidea, which she regarded as a "natural group." de Saint Laurent (1980) suggested that the term Eubrachyura be applied to all brachyurans with sternal gonopores (i.e., heterotremes and thoracotremes), as in her opinion this could only have evolved once.

The placement of brachyuran genera as podotremes, heterotremes, or thoracotremes had largely been unquestioned, as the position of the gonopores is readily observed in extant forms and sometimes seen in fossils. However, the monophyly of Podotremata is no longer widely accepted, and the monophyly of heterotremes is now questioned. In addition, the generic composition of families and superfamilies within Eubrachyura has undergone major modifications over the past decades. The classification presented in this volume is therefore a reflection of the state of matters at this time.

Status of Podotremata

Ahyong and others (2007), Scholtz and McLay (2009), and Davie, Guinot, and Ng (2015a) summarized the understanding of Podotremata to that time, including the previous placement of some members within Anomura and the composition of various included superfamilies. It seems to us that a pervasive issue in analyzing the status of Podotremata as monophyletic and the relationship of constituent groups within Podotremata to one another and to Eubrachyura is that any studies only including extant forms are inherently incomplete. The overwhelming majority of podotremes are extinct; thus, any examination that excludes the extinct groups eliminates several lineages within the group. It would be like trying to reconstruct the history of dinosaurs without looking at birds, or vice versa.

Ahyong and others (2007) recognized a paraphyletic Podotremata based on 18S sequences. They noted that Podotremata had been recognized as presumably monophyletic based on four apomorphies: 1) possession of gonopores on the pereiopods in both males and females, 2) sperm morphology, 3) reduction of posterior pereiopods, and 4) absence of a *sella turcica* (part of the endophragmal

skeleton). The position of the gonopores in both males and females now is recognized as a plesiomorphic condition shared by all Decapoda and most Malacostraca (Gordon, 1963; de Saint Laurent, 1980; Scholtz & McLay, 2009; Luque & others, 2019). Posterior pereiopods are reduced or modified in many non-podotrematous groups, including Hexapodidae (Gordon, 1971) and Dorippoidea (Sin & others, 2009). Guinot, Tavares, and Castro (2013) noted that the *sella turcica* was indeed present in all brachyurans, supporting monophyly of Brachyura in its entirety. Although analysis of sperm morphology has resulted in a monophyletic Podotremata, most likely due to limited sampling across the wide array of brachyuran morphology, numerous other features have suggested that the group is not monophyletic (Ahyong & others, 2007; Karasawa, Schweitzer, & Feldmann, 2011; Luque & others, 2019; Wolfe & others, 2023, and references therein).

The possession of spermathecae in podotrematous crabs has more recently been posited as an apomorphy uniting the group (Guinot & Quenette, 2005; Davie, Guinot, & Ng, 2015a), but as noted by Gordon (1963) and later Scholtz and McLay (2009), the spermathecae in raninoids and other podotreme crabs are not in the same position. In dromiaceans, the spermathecae are positioned between the seventh and eighth sternites and have separate chambers, whereas in raninoids, they are on the seventh sternite and lead into a single chamber (Scholtz & McLay, 2009). Thus, there are no synapomorphies that unite Podotremata into a monophyletic group.

As early as 1980, monophyly of Podotremata was questioned (de Saint Laurent, 1980). Martin and Davis (2001) abandoned the Podotremata on the basis that molecular phylogenies did not support its monophyly, and that raninoids and dromiaceans were clearly not part of the same clade in such studies. Phylogenetic analyses over the past two decades have repeatedly recovered Podotremata *sensu* Guinot as para and/or polyphyletic. Ahyong and others (2007) analyzed ribosomal DNA using maximum parsimony analyses and found that extant podotrematous crabs comprised three separate clades for which they recognized the sections Dromiacea, Raninoida, and Cyclodorippoida. Cyclodorippoida was sister to the Eubrachyura. Scholtz and McLay (2009) recovered a paraphyletic Podotremata in a phylogenetic analysis "by hand" of morphology of extant forms, using several character sets. Both molecular (i.e., Tsang & others, 2014, and Ma & others, 2019) and morphological (i.e., Luque & others, 2019 and 2021) analyses used maximum likelihood and Bayesian inference methodologies and recovered podotremes as paraphyletic. Chen and others (2019) used maximum likelihood and Bayesian inference methodologies in a phylomitogenomic study and recovered Raninoida as sister to Eubrachyura, as well as a distinctly paraphyletic Podotremata, as did Liu and others (2021), Xing and others (2021), and Xu and others (2021). Wolfe and others (2024) reiterated the paraphyletic nature of the podotremes in the largest analysis to date of Brachyura.

In an analysis of morphology of extant and extinct podotrematous brachyurans using parsimony analysis, Karasawa, Schweitzer, and Feldmann (2011) found Podotremata to be paraphyletic and composed of seven clades for which they recognized sections Dromiacea, Homoloida, Torynommoida, Etyoida, Dakoticancroida, and Cyclodorippoida, the latter of which was sister to all Eubrachyura. This supported the findings of Ahyong and others (2007) with respect to the extant groups. Luque and others (2019) recovered the same groups with an additional section Callichimaeroida, analyzing morphology of extinct and extant crabs using Maximum Parsimony, Maximum Likelihood, and Bayesian Inference. Archaeobrachyura *sensu* Guinot was found to be paraphyletic by Ahyong and others (2007), Karasawa, Schweitzer,

and Feldmann (2011), Tsang and others (2014), Ma and others (2019), and Luque and others (2019, 2021).

A contrary view of podotreme monophyly was proposed by Guinot, Tavares, and Castro (2013) and Davie, Guinot, and Ng (2015a). Guinot, Tavares, and Castro (2013) suggested a series of subsections for podotreme crabs that largely paralleled the proposals of Ahyong and others (2007), Karasawa, Schweitzer, and Feldmann (2011), and Luque and others, (2019), with different names. As summarized by Davie, Guinot, and Ng (2015a), Guinot, Tavares, and Castro (2013) proposed Dynomeniformia for Dromiacea as recognized by Karasawa, Schweitzer, and Feldmann (2011) and Luque and others (2019). Homoliformia was proposed for Homoloida of Karasawa, Schweitzer, and Feldmann (2011) and Luque and others (2019). Ahyong and others (2007) had included the homoloid groups within Dromiacea. Cyclodorippiformia was proposed for Cyclodorippoida of Ahyong and others (2009), Karasawa, Schweitzer, and Feldmann (2011), and Luque and others (2019). Guinot, Tavares, and Castro (2013) advocated for the use of Gymnopleura rather than Raninoida, as used by Ahyong & others (2009), Karasawa, Schweitzer, and Feldmann (2011) and Luque and others (2019). The term Gymnopleura was introduced by Bourne (1922) to include the group that contains all of the crown groups of frog crabs in the superfamily Raninoidea De Haan, 1839 in 1833–1850, which share the presence of exposed or "naked" pleura (hence the name Gymnopleura). As indicated by Luque and others (2019), this synapomorphy that defines the clade Gymnopleura is not seen in least inclusive phylogenetic stem lineages to crown Raninoidea (e.g., palaeocorystoids, necrocarcinoids). Thus, "Gymnopleura" is a junior synonym of Raninoidea. As the ICZN does not regulate names above the family level, we retain usage of Raninoida for the total group or section that unites Raninoidea, Palaeocorystoidea, and Necrocarcinoidea (see Karasawa & others, 2014). Guinot, Tavares, and Castro (2013) did not include the various extinct lineages in their hypothesized cladogram, but listed them in their table 5, with Etyoida, Dakoticancroida, Torynommoida, and several dromiacean families of Karasawa, Schweitzer, and Feldmann (2011) listed as *incertae sedis*. Jagt and others (2015) followed the Guinot, Tavares, and Castro (2013) classification of subsections and included taxa. The classification of Davie, Guinot, and Ng (2015b) did not use the podotreme subsections of Guinot, Tavares, and Castro (2013) and instead listed the five extant superfamilies within Podotremata, including Raninoidea.

Noting that "Podotremata" is broadly shown to be paraphyletic, Poore and Ahyong (2023) used the sections Cyclodorippoida, Dromiacea, Homoloida, and Raninoida for extant podotrematous crabs. Schram and Koenemann (2021) recognized all of the podotrematous sections of Karasawa, Schweitzer, and Feldmann (2011) and Luque and others (2019). Because the overwhelming number of podotremes are extinct, the analyses of Karasawa, Schweitzer, and Feldmann (2011) and Luque and others (2019) included both extinct and extant podotreme groups, and molecular phylogenies including podotremes support the divisions of Karasawa, Schweitzer, and Feldmann (2011) and Luque and others (2019) with respect to the extant podotreme crabs. We thus retain the series of sections proposed by Karasawa, Schweitzer, and Feldmann (2011) and Luque and others (2019) (Fig. 4).

Eubrachyura, "Heterotremata," and Thoracotremata

Monophyly of Eubrachyura has been supported by most phylogenies until recently. Ahyong and others (2007) found some thoracotreme families nested within a heterotreme clade; however, their coverage of thoracotremes was not broad. Shen, Braband, and Scholtz (2013) recovered a

monophyletic Eubrachyura but paraphyletic Heterotremata. Tsang and others (2014), and then later Zhang and others (2020), recovered the Eubrachyura as a monophyletic group, and both heterotremes and thoracotremes were monophyletic in their analyses.

However, more recent morphological, phylogenomic, and mitogenomic phylogenies by Ma and others (2019), Wang and others (2020), and Luque and others (2021) recovered a monophyletic Eubrachyura but a paraphyletic Heterotremata, with Thoracotremata nested within the heterotremes. Chen and others (2019) analysed a wide range of brachyurans and found that Eubrachyura and Thoracotremata were monophyletic, but that Heterotremata was not, based on a phylomitogenomic study using Bayesian and Maximum likelihood. Liu and others (2021) and Xing and others (2021), Xu and others (2021), and Lu and others (2020) also recovered a similar topology. Wolfe and others (2019) recovered Eubrachyura, Heterotremata, and Thoracotremata as monophyletic, but the aim of that work was to resolve the higher relationships among the main crown decapod infraorders and not among brachyuran superfamilies and sections, for which the taxon coverage was low. Most recently, Wolfe and others (2024) recovered a paraphyletic Heterotremata in an analysis of 10 gene sequences for members of 88 crab families, the largest analysis to date. Most evidence now suggests that Heterotremata is not monophyletic, but the term "heterotreme" is useful to designate its evolutionary grade of gonopore position. In this work, we have used the term Eubrachyura to embrace all non-podotrematous brachyurans, and the term Thoracotremata is used for the chapter including all decapods with only sternal gonopores.

The family arrangement within Eubrachyura has evolved through time. Davie, Guinot, and Ng (2015a) summarized the work of H. Milne Edwards (1834–1840), De Haan (1833–1845), and Borradaile (1903, 1907) as well as other early subdivisions within Heterotremata and Thoracotremata. However, no well-supported arrangement of superfamilies has yet been posited nor have relationships between and among the families of Eubrachyura been established. In part, this is due to the immense size of the group, with thousands of species, and the resulting enormous data matrix. Many superfamilies used previously, such as Xanthoidea, have been found to be para- or polyphyletic, as have the families and subfamilies within it (Lai & others, 2011; Thoma, Guinot, & Felder, 2014). Other paraphyletic families include Epialtidae, Carcinidae, Corystidae, Leucosiidae, and Pilumnidae (Wolfe & others, 2023). Polyphyletic superfamilies include Eriphioidea and Goneplacoidea among heterotremes, and Grapsoidea and Ocypodoidea among thoracotremes (Wang & others, 2020; Liu & others, 2021; Wolfe & others, 2023). Polyphyletic families include Majidae, Platyxanthidae, and Pseudoziidae (Wolfe & others, 2023). Members of Potamoidea, which are heterotrematous in terms of gonopores, are often recovered as sister to thoracotreme crabs (Chen & others, 2019; Wolfe & others, 2023). As the mitogenome of various lineages is elucidated, the lineages within Eubrachyura will be clarified (presumably). The classification for Eubrachyura used here must be construed as the current best estimate of the composition of the various groups.

The basis for the recognized families within each brachyuran subsection and of genera within the families is based on many works. The initial framework was taken from Ng, Guinot, and Davie (2008), De Grave and others (2009), and Schweitzer and others (2010) and revised according to Davie & others (2015b), in addition to references cited in the Eriphioidea, Majoidea, Portunoidea, Potamoidea, and Xanthoidea systematic chapters (Schweitzer & Feldmann, 2020; Schweitzer, Feldmann, & Karasawa, 2020a, 2020b, 2021a, 2021b). Portunoidea, in particular, has undergone

many recent rearrangements, so that our classification follows that of Evans (2018), as noted in that section. Several differences with DecaNet now exist in our portunoid classification; however, we note that we included as subfamilies most of those groups now recognized as families in DecaNet. Thus, our classification, at least for extant forms, largely follows that of Poore and Ahyong (2023) and DecaNet. Placement of fossil taxa within extinct families follows the publication in which the family was erected in nearly all cases.

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