

REVISION OF PORTUNOIDEA RAFINESQUE, 1815 (DECAPODA: BRACHYURA) WITH EMPHASIS ON THE FOSSIL GENERA AND FAMILIES

Hiroaki Karasawa, Carrie E. Schweitzer, and Rodney M. Feldmann

(HK) Mizunami Fossil Museum, Yamanouchi, Akeyo, Mizunami, Gifu 509-6132,
Japan (GHA06103@nifty.com);

(CES, correspondence) Department of Geology, Kent State University Stark Campus, 6000 Frank Ave. NW,
North Canton, Ohio 44720, U.S.A. (cschweit@kent.edu);

(RMF) Department of Geology, Kent State University, Kent, Ohio 44242, U.S.A. (rfeldman@kent.edu)

A B S T R A C T

The superfamily Portunoidea including extinct lineages is herein evaluated via cladistic analysis of adult morphological characters and traditional systematics. Nearly every fossil species has been examined via type material, or if this was not possible, through illustrations and original descriptions. The analyses indicate that the superfamily is much more diverse at the family level than has previously been recognized, and three subfamilies, Catoptrinae, Carcininae, and Macropipinae, are herein elevated to family status. One new family, Longusorbiidae; two new genera, *Euronectes* and *Viaophthalmus*; and two nomen nova are named herein in addition to the recognition of seven new combinations. The fossil record of each of the resulting families is evaluated and summarized, indicating that the superfamily extends into the Cretaceous but that many of the families are indeed much younger lineages.

KEY WORDS: Brachyura, Cretaceous, Neogene, Paleogene, Portunoidea, phylogeny, taxonomy

INTRODUCTION

Portunoidea embraces a diverse array of taxa known from a broad spectrum of marine and non-marine habitats. Martin and Davis (2001) included three extant families: Geryonidae Colosi, 1923; Portunidae Rafinesque, 1815; and Trichodactylidae H. Milne Edwards, 1853. The genus, *Sylviocarcinus* H. Milne Edwards, 1853, within the latter family is restricted to non-marine habitats. To this list, the extinct marine Carcineretidae Beurlen, 1930, has typically been assigned to the superfamily (Glaessner, 1969). Other authors, discussed below, have proposed other family-level arrangements. A compilation as a part of a broad study that is underway to develop a phylogeny of the decapod crustaceans based upon morphological, molecular, and paleontological evidence has resulted in the identification of approximately 88 genus-level taxa within the superfamily, most assigned to Portunidae. Recognition of this vast number of genera documents the wide range of variation within the superfamily. In order to assure that these taxa are arrayed phylogenetically, it is necessary to re-examine the current classification scheme and test the homogeneity of the family groupings. An initial study of extinct genera within Carcineretidae (Schweitzer et al., 2007) resulted in the reduction of genera that could legitimately be assigned to the family from seven to three; the other genera were either assigned to other portunoid families or were assigned to other superfamilies. This study clearly documented the need for a re-evaluation of the entire superfamily in a phylogenetic context.

In addition to the recognition that Portunoidea is an extremely diverse group, it was also abundantly clear that the current classification scheme(s) are based almost solely on criteria derived from study of extant organisms. Although this approach can be justified on the basis of availability of material and the wide range of morphological criteria that can be utilized in erecting a classification or

proposing a phylogenetic hypothesis, the results of these studies are that the geological history of the group is ignored and fossil taxa that are demonstrated to be members of the group are simply “inserted” into the classification. One of the consequences of this approach is that generic taxa known from the fossil record are placed within families on the basis of gross morphological similarity which can then foster misinterpretations of the geological history of taxa.

Recognizing the great breadth of taxa within Portunoidea; the long geological history of some of its members, extending into the Cretaceous; and the problems of classification of both extant and extinct forms; the present study has several objectives. Utilizing morphological data from a broad array of extinct and extant genera, it is the primary purpose of this study to develop a testable hypothesis to elucidate the phylogeny of Portunoidea. In so doing, a broad spectrum of characters is employed, some of which are rarely observable on fossil crabs, but all of which have been utilized in classification schemes of extant forms. This approach permits framing a second hypothesis, that the phylogenetic scheme derived from study of extinct and extant taxa will not differ significantly from one based solely upon extant forms. Stated another way, we propose to test whether or not the insertion of data from fossil forms, with all the attendant problems of missing information, will significantly perturb the resulting phylogenetic topology. Finally, having identified a reasonable phylogenetic array, we intend to propose a systematic framework that embraces monophyletic groups based upon morphological analyses, define a family and subfamily structure that reflects this arrangement, reassign generic-level taxa to their most appropriate family-level position, and refine the diagnoses of the resultant families and subfamilies.

The summation of the results of our work is that a very stable tree topology emerged, one that was not substantially perturbed by the addition of data from extinct taxa. Further,

the morphology-based phylogenetic analysis resulted in an array of monophyletic groups that rather strongly supported many aspects of existing systematic arrangements. Thus, the present results offer a phylogenetic arrangement that can be compared and contrasted to phylogenies derived from molecular studies. In addition, nearly every fossil species has been verified as to its generic placement either by examination of illustrations and descriptions in the literature, or examination of type or referred material where possible. Thus, this work represents the most comprehensive evaluation yet undertaken of the fossil record of Portunoidea.

HISTORY OF CLASSIFICATION

Beurlen (1930) first recognized the superfamily (as his tribus) Portunoidea containing two families, Carcineretidae Beurlen, 1930, and Portunidae Rafinesque, 1815, sensu Dana, 1851. Prior to Beurlen's work, Ortmann (1893) established his section Portuninea as the present superfamily-level name and he placed seven of his new families under the section: Platyonychidae, Polybiidae, Carupidae, Portunidae, Thalamitidae, Lissocarcinidae, and Podophthalmidae. Until the work presented herein, these families had been recognized as subfamilies of Portunidae. Subsequent to Beurlen's work (1930), most neontologists included only one family, Portunidae, within Portunoidea (Sakai, 1976), and paleontologists added the extinct family Carcineretidae to the superfamily (Glaessner, 1969; Guinot, 1978). Manning and Holthuis (1981) and Rice (1980) suggested that Geryonidae had close affinities with Portunidae, and subsequently, Bowman and Abele (1982) placed Geryonidae within Portunoidea. Since Rodríguez (1992) demonstrated that the freshwater crab family Trichodactylidae H. Milne Edwards, 1853, was the sister to Portunidae based upon a cladistic analysis, Von Sternberg et al. (1999), Von Sternberg and Cumberlidge (2001), and Martin and Davis (2001) placed Trichodactylidae within Portunoidea. More recently, Števcíč (2005) erected the new portunoid family Melybiidae Števcíč, 2005 (*non* Števcíč in Martin and Davis, 2001), removed Geryonidae to Goneplacoidea, and gave Trichodactylidae full superfamily status. Schubart and Reuschel (2005) also excluded Trichodactylidae from Portunoidea based upon molecular analyses. Most recently, Mathildellidae Karasawa and Kato, 2003, previously recognized as a goneplacid subfamily, was placed within Portunoidea (Karasawa and Schweitzer, 2006).

There have been numerous works on classification of Portunidae. In the 19th Century, Dana (1851) recognized three families, Portunidae with the subfamilies Lupinae, Arenaeinae, and Portuninae; Platyonychidae; and Podophthalmidae, under the present Portunoidea. A. Milne-Edwards (1860) divided the family into two subfamily-level groups: agèle des Portuniens Anormaux for *Podophthalmus* and agèle des Portuniens Normaux including six sub-groups, Lupéens, Thalamitiens, Carupiens, Lupocycliens, Carciniens, Lissocarciniens, and Polybiens. Paul'son (1875) largely accepted the classification of A. Milne-Edwards, and in his classification the family comprised eight subfamilies, Lupinae, Carcininae, Thalamitinae, Lissocarcininae, Caphyrinae, Lupocyclinae, Polybiinae [sic], and Podophthalminae. Miers (1886) also followed the concept of the classification of

A. Milne-Edwards and divided the group into two sections, Podophthalmidae and Portunidae with the subfamilies Lupinae, Thalamitinae, Carcininae, and Caphyrinae. Alcock (1899) placed four subfamilies, Carcininae, Portuninae, Caphyrinae, and Lupinae under Portunidae. Additionally, in his classification, each subfamily was subdivided into several alliances.

In the 20th century, Borradaile (1907) recognized eight subfamilies: Carcinidinae, Portumninae, Catoptrinae, Carupinae, Portuninae, Caphyrinae, Thalamitinae, and Podophthalminae. Klunzinger (1913) divided Portunidae into eight subfamilies: Carcininae, Pirimelinae, Portuninae, Carupinae, Lupinae, Thalamitinae, Caphirinae [sic], and Podophthalminae. Pirimelinae Alcock, 1899 was originally included within Cancridae (Alcock, 1899), and subsequently Bouvier (1940) gave it full family status. Pirimelidae is usually treated as a family of Cancroidea (Guinot, 1978; Bowman and Abele, 1982; Martin and Davis, 2001). In a recent molecular work, Schubart and Reuschel (2005) suggested that Pirimelidae should be assigned to Portunoidea. Beurlen (1930) included three extant subfamilies, Carcininae, Portuninae, and Lupinae, and one extinct family, Psammocarcininae Beurlen, 1930, within Portunidae.

Sakai (1939) recognized six subfamilies under Portunidae: Carcininae, Catoptrinae, Portuninae, Caphyrinae, Lupinae, and Podophthalminae. Balss (1957) divided the families into nine subfamilies: Carcineretinae, Psammocarcininae, Carcininae, Catoptrinae, Carupinae, Portuninae, Neptuninae (his replacement name of Lupinae), Caphyrinae, and Podophthalminae. The classification of Portunidae proposed by Sakai (1939) was largely accepted by subsequent workers (Edmondson, 1954; Stephenson and Campbell, 1960; Stephenson, 1972; Sakai, 1976). After that, Stephenson and Campbell (1960) proposed the replacement name, Macropipinae Stephenson and Campbell, 1960, for the currently used Portuninae and replaced Lupinae by Portuninae. Holthuis (1968) showed that Polybiinae Ortmann, 1893, is the correct name for Macropipinae. Subsequently, Apel and Spiridonov (1998) indicated that Carupinae Paul'son, 1875, was the senior name for Catoptrinae Borradaile, 1902, and separated Thalamitinae from Portuninae.

Within the above-mentioned works, the authorship for each subfamily has been confused. According to Davie (2002), Portunidae comprises seven subfamilies: Caphyrinae Paul'son, 1875; Carcininae MacLeay, 1838; Carupinae Paul'son, 1875; Podophthalminae Dana, 1851; Polybiinae Ortmann, 1893; Portuninae Rafinesque, 1815; and Thalamitinae Paul'son, 1875. However, in the most recent work, Števcíč (2005) divided Portunidae into eight subfamilies with 15 tribes: Carcininae with tribes Portumnini Ortmann, 1899, Carcinini, and Brusinini Števcíč, 1991; Polybiinae Paul'son, 1875 instead of Ortmann, 1893, with Platyonichini Dana, 1851, Polybiini, and Coenophthalmi Alcock, 1899; Carupinae with Carupini and Catoptrini Borradaile, 1902 (*non* Borradaile, 1907); Caphyrinae with Caphyrini, Lissocarcinini Paul'son, 1875, and Coelocarcinini Števcíč, 2005; Portuninae with Atoportunini Števcíč, 2005, Lupocyclini Paul'son, 1875, Portunini, and Thalamitini; Psammocarcininae Beurlen, 1930; Podophthalminae Dana, 1851; and Libystinae Števcíč, 2005 (*non* Serène, 1965[imprint 1966]).

Thus, based upon this convoluted history of the classification of the group, it is clear only that the superfamily is diverse and difficult to arrange in a meaningful systematic way.

MATERIALS AND METHODS

Thirty-nine extant and eleven fossil genera within Portunoidea as defined prior to this paper were examined (Appendix 1). The analyses were based upon the examination of material deposited in the following institutions (given with their abbreviations, used throughout this paper): BM, The Natural History Museum, London, UK; BSP, Bayerische Staatsammlung für Paläontologie und historische Geologie München (Munich), Germany; CAS, California Academy of Sciences, San Francisco, California; CBMZC, Natural History Museum and Institute, Chiba, Japan; GSC, Geological Survey of Canada Eastern Paleontology Division, Ottawa, Ontario; GHUNLPam, Geological Museum, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina; HNHM, Natural History Museum of Hungary, (Természettudományi Múzeum Föld-és Őslénytár), Budapest, Hungary; IG, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KMNH-IvP, Kitakyushu Museum and Institute of Natural History, Japan; KPM-NH, Kanagawa Prefectural Museum of Natural History, Odawara, Japan; KSU D, Kent State University Decapod Comparative Collection; MCZ, Museo Civico "G. Zannato" di Montecchio Maggiore (Vicenza), Italy; MFM, Mizunami Fossil Museum, Mizunami, Japan; MNHN, Museum National d'Histoire Naturelle, Paris, France; MNHNCu-P, National Museum of Natural History, Paleontological collection, Havana, Cuba; MHN-UABCS, Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Mexico; MPEF-PI, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; NMW, Naturhistorische Museum Wien (Natural History Museum of Vienna), Austria; PRI, Paleontological Research Institution, Ithaca, NY; RMNH D, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; RO, Muséum National d'Histoire Naturelle, Paris, France; RUMF-ZC, Department of Marine and Environmental Sciences, The University of Ryukyus, Okinawa, Japan; SDSNH, San Diego Natural History Museum, San Diego, California; SM, Sedgwick Museum, Cambridge University, UK; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC; and UT, University of Texas, Austin, Texas. 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 and subfamilial arrangement of Davie (2002) as well as our own observations. The out-groups were chosen from representatives of the superfamily Goneplacoidea MacLeay, 1838, because Karasawa and Schweitzer (2006) showed using cladistic analysis based upon adult morphology that Portunoidea is the sister to Goneplacoidea and Progeroidea Števíč, 2005.

Fifty-five adult morphological characters were used in the analysis (Appendix 2) (Figs. 1 and 2). The data matrix is provided in Appendix 3. Fifty characters were binary; five had multistate character states. The missing data were scored as unknown. The rate of missing data within examined fossil taxa was 15 to 42 per cent. 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 portunoid relationships; however, *Psammocarcinus* A. Milne-Edwards, 1860, was excluded from the analysis because of a large amount of missing data.

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: additional 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; tree unrooted; multistate taxa interpreted as polymorphism; character state optimization; and accelerated transformation (ACCTRAN). All characters were unordered, unscaled and equally weighted. Relative stability of clades was assessed using decay analyses (Bremer, 1994). The Bremer support was obtained using constraint trees generated in MacClade 4.08 for OSX (Maddison & Maddison, 2005) and analyzed using PAUP*.

RESULTS AND DISCUSSION

Analysis A produced only one most-parsimonious tree, 204 steps long with a consistency index (CI) of 0.4608, a retention index (RI) of 0.7791, and a rescaled consistency index (RC) of 0.3590 (Fig. 3). Analysis B yielded two most-parsimonious trees, 245 steps long with a consistency index (CI) of 0.4041, a retention index (RI) of 0.7671, and a rescaled consistency index (RC) of 0.3100. A strict consensus tree of the two most-parsimonious trees is given in Figure 4. The only difference in topology of the two trees is the relative position of the clade embracing genera traditionally assigned to Carcininae (Fig. 5: A, B). One of two most-parsimonious trees (Fig. 5A) is adopted in the present analysis because it has the lowest f-value (tree A = 11,317 and tree B = 12,127), and in this tree as well as the tree produced by analysis A, the "Carcininae" clade is derived as the sister to the clade containing genera traditionally assigned to Polybiinae. The relationships among the major groups indicating clade number are given in Figure 6. Character state changes are given in Appendix 4.

The monophyly of Portunoidea (clade 1) is supported by only one unambiguous character, male thoracic sternite 8 not visible in posterior view (41-0). In the phylogenetic analysis, the inclusion of the fossil taxa affects the resulting topologies (Figs. 3 and 6): the relationship between *Catoptrus* and *Libystes*, and the relative position of the clade we herein recognized as the family Macropipidae. In our analysis, Portunoidea consists of nine major clades, and each clade is principally construed as being of family status.

The most basal *Lithophylax* (clade 2) is derived as the sister to the remainder of the in-group taxa. *Lithophylax* is characterized by having a male pleomere 3 with a transverse keel (26-1) and a complete suture between thoracic sternites 6 and 7 (32-0), and by lacking a posterolateral prolongation of episternite 7 in males (39-0). A. Milne-Edwards and Brocchi (1879) originally placed *Lithophylax* under the tribu Gonéplaciens (= Goneplacidae). After that, Van Straelen (1936a) erected a new family Lithophylacidae for the sole included genus *Lithophylax*. Since Glaessner (1969) assigned *Lithophylax* to Carcineretidae, most subsequent workers (Schweitzer, Feldmann et al., 2002; Feldmann and Villamil, 2002) followed that placement. Most recently, Guinot and Breton (2006) redescribed the type species, *Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879, and redefined Lithophylacidae. They discussed the relationships between Lithophylacidae and other brachyuran families, but did not indicate its superfamily status. Our analysis suggests a basal position of *Lithophylax* within Portunoidea, but the inclusion of *Lithophylax* within Portunoidea shows weak branch support with the in-group taxa. Examination of a more complete data set will be necessary to confirm the systematic status of *Lithophylax*.

Clade 3 (remaining portunoids) shares three unambiguous characters: the presence of upper orbital fissures (8-0), the tip of the telson of the male pleon located on the posterior half of thoracic sternite 4 (20-0), and the cheliped shorter than pereopods 2-5 (47-1).

The second diverging lineage, *Longusorbis* (clade 4), has four apomorphic characters: carapace with tubercles (11-1), a relatively narrow thoracic sternum (29-1), a well marked

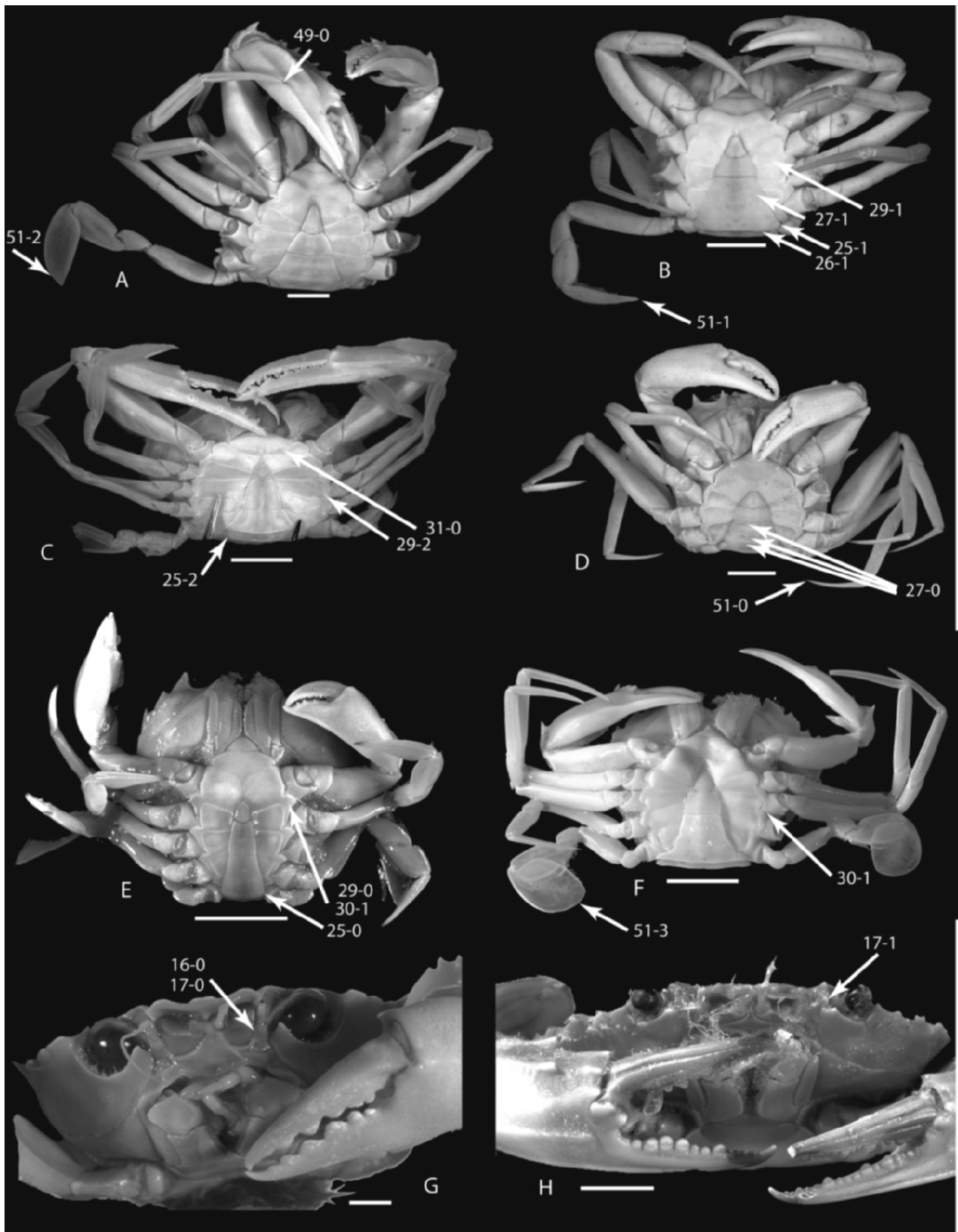


Fig. 1. Illustrations of selected portunoid crabs showing some characters used in preparing the character matrix for the cladistic analysis. Numbers (49-0, for example) denote the character illustrated (49) and the character state (0) keyed to the list of characters given in Appendix 2. Scale bars equal 1 cm. A, *Bathynectes* sp., USNM 186368; B, *Carcinus aestuarii*, USNM 257965; C, *Euphylax dovii*, USNM 85535; D, *Geryon longipes*, USNM 152241; E, *Portunus latipes*, USNM 221604; F, *Parathranites orientalis*, USNM 12709; G, *Benthochascon hemingi*, CBM-ZC specimen; H, *Charybdis japonica*, KSU D320.

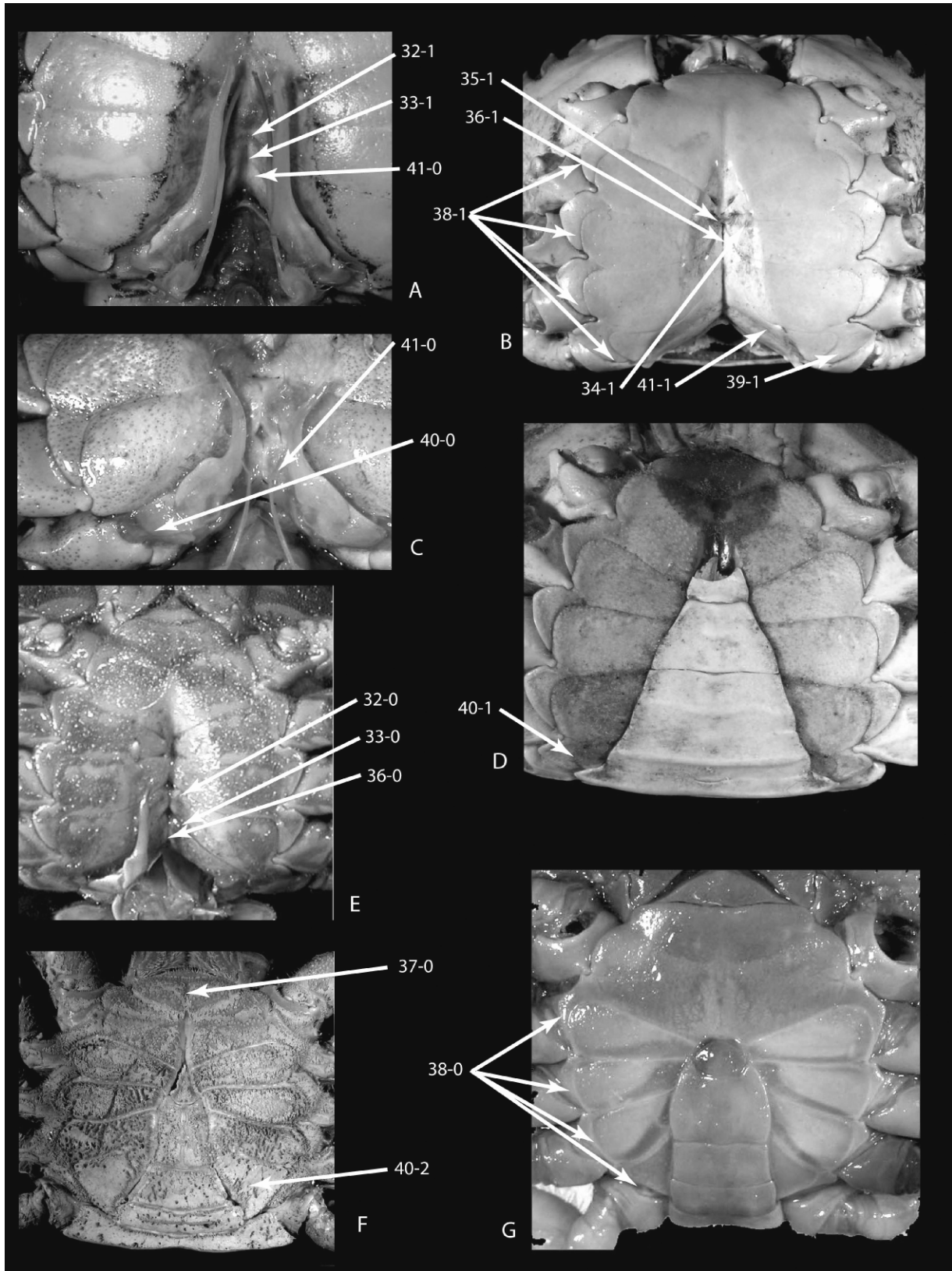


Fig. 2. Illustrations of the sterna of selected portunoid crabs showing some characters used in preparing the character matrix for the cladistic analysis. Numbers (41-0, for example) denote the character illustrated (41) and the character state (0) keyed to the list of characters given in Appendix 2. A, *Carcinoplax* sp.; B, *Charybdis* sp.; C, *Mathildella* sp.; D, *Necora* sp.; E, *Nectocarcinus* sp.; F, *Portunus* sp.; G, *Ovalipes* sp. All specimens deposited in the Mizunami Fossil Museum.

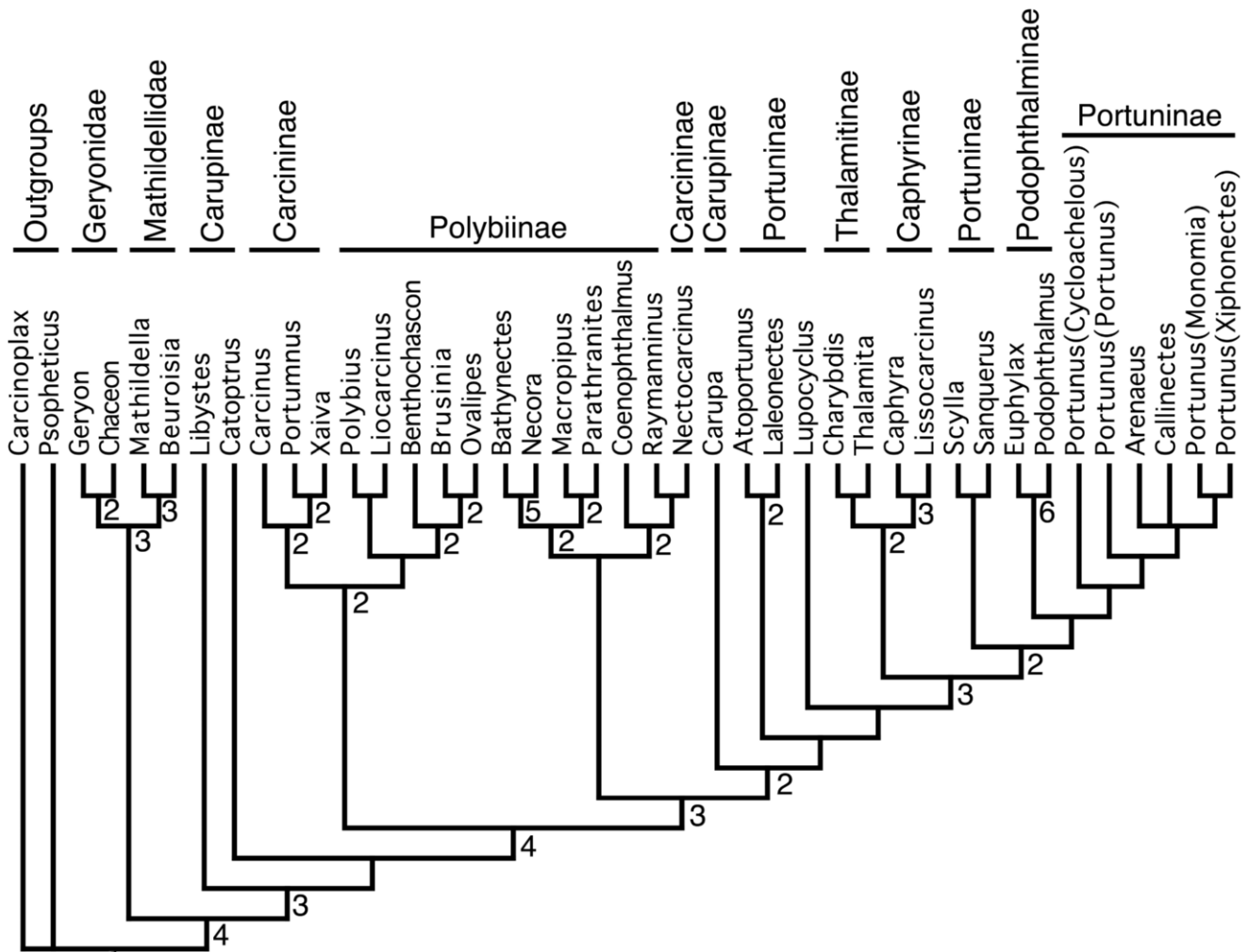


Fig. 3. A single most-parsimonious tree from analysis A (TL = 204; CI = 0.4608; RI = 0.7791; RC = 0.3590). Bremer support exceeding 1 indicated. Families and subfamilies as recognized previous to this work are indicated.

sulcus delimiting thoracic sternites 3 and 4 (31-0), and dark-colored fingers of the chelipeds (44-0). Richards (1975) erected a new monotypic genus, *Longusorbis*, for *L. cuniculosus* and placed it under Carcineretidae. Subsequent workers agreed with him concerning the systematic status of *Longusorbis*. Most recently, Schweitzer et al. (2007) excluded *Longusorbis* from Carcineretidae, but they did not assign it to a family and/or subfamily under Portunoidea. *Longusorbis* lacks a unique synapomorphy of clade 5, immovable male pleomeres 3-5 (28-1), and is derived as the sister to the remaining portunoid taxa. Therefore, the analysis supports the status of *Longusorbis* suggested by Schweitzer et al. (2007) and indicates that *Longusorbis* warrants its own family, Longusorbiidae.

Clade 6 (Mathildellidae + Geryonidae), with Bremer support 3, is well defined by three unambiguous characters: the inner orbital angle defined as teeth or spines (6-0), a complete sulcus separating thoracic sternites 7 and 8 (33-0), and the absence of a posterolateral prolongation of episternite 7 (39-0). Although Števič (2005) treated Mathildellidae as one of the tribes of the subfamily Geryoninae within Geryonidae, and Karasawa and Schweitzer (2006)

showed that Mathildellidae is the most basal within Portunoidea, the present analysis strongly suggests that Mathildellidae is derived as the sister to Geryonidae. Mathildellidae (clade 8), with Bremer support of 4, shares three synapomorphies: male pleomeres 4 and 5 with concave lateral margins (24-1), the possession of dark-colored fingers of chelipeds (44-0), and dactyli with a corneous tip (49-0). Geryonidae (clade 7), with Bremer support of 3, is well united by three synapomorphies: the possession of frontal teeth (4-0), a long lower orbital tooth (6-1), and male sternite 8 visible in posterior view (42-1).

Within Mathildellidae, the extinct genus *Coeloma* is derived as the sister to the extant *Beuroisia* (clade 9). A semicircular telson on the male pleon (22-1) unites the two taxa. A. Milne-Edwards (1865) established *Coeloma* under his "Galénides." After that, *Coeloma* was assigned to Goneplacidae (Glaessner, 1929). Since Beurlen (1930) assigned the genus to Geryonidae, most subsequent workers followed that precedent (Balss, 1957; Glaessner, 1969). The analysis suggests that *Coeloma* is placed within Mathildellidae. Examination of three species, *Coeloma vigil* A. Milne-Edwards, 1865, the type species of the genus,

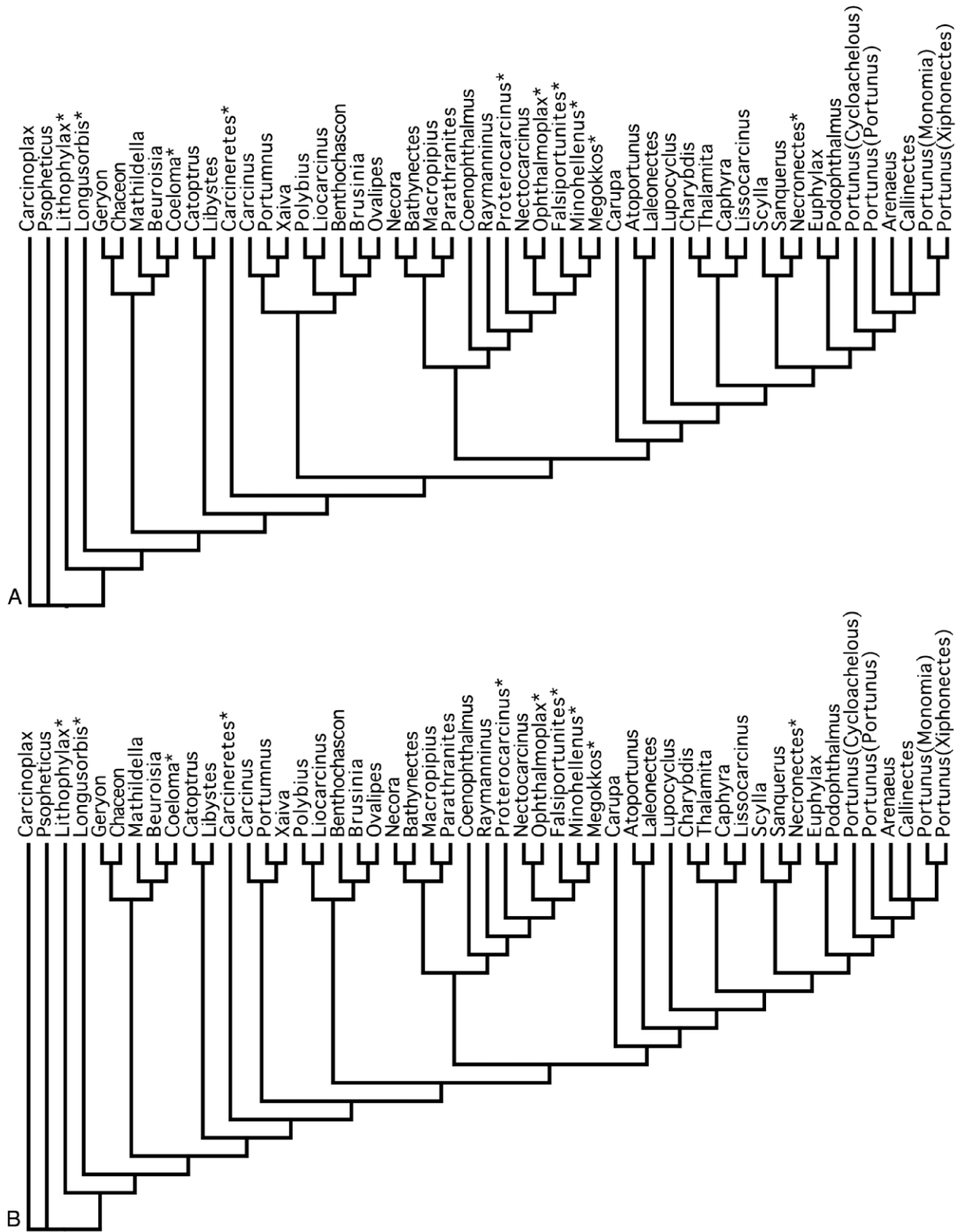


Fig. 5. Two most-parsimonious trees from analysis B. The f-value is 11,317 in tree A and is 12,127 in tree B.

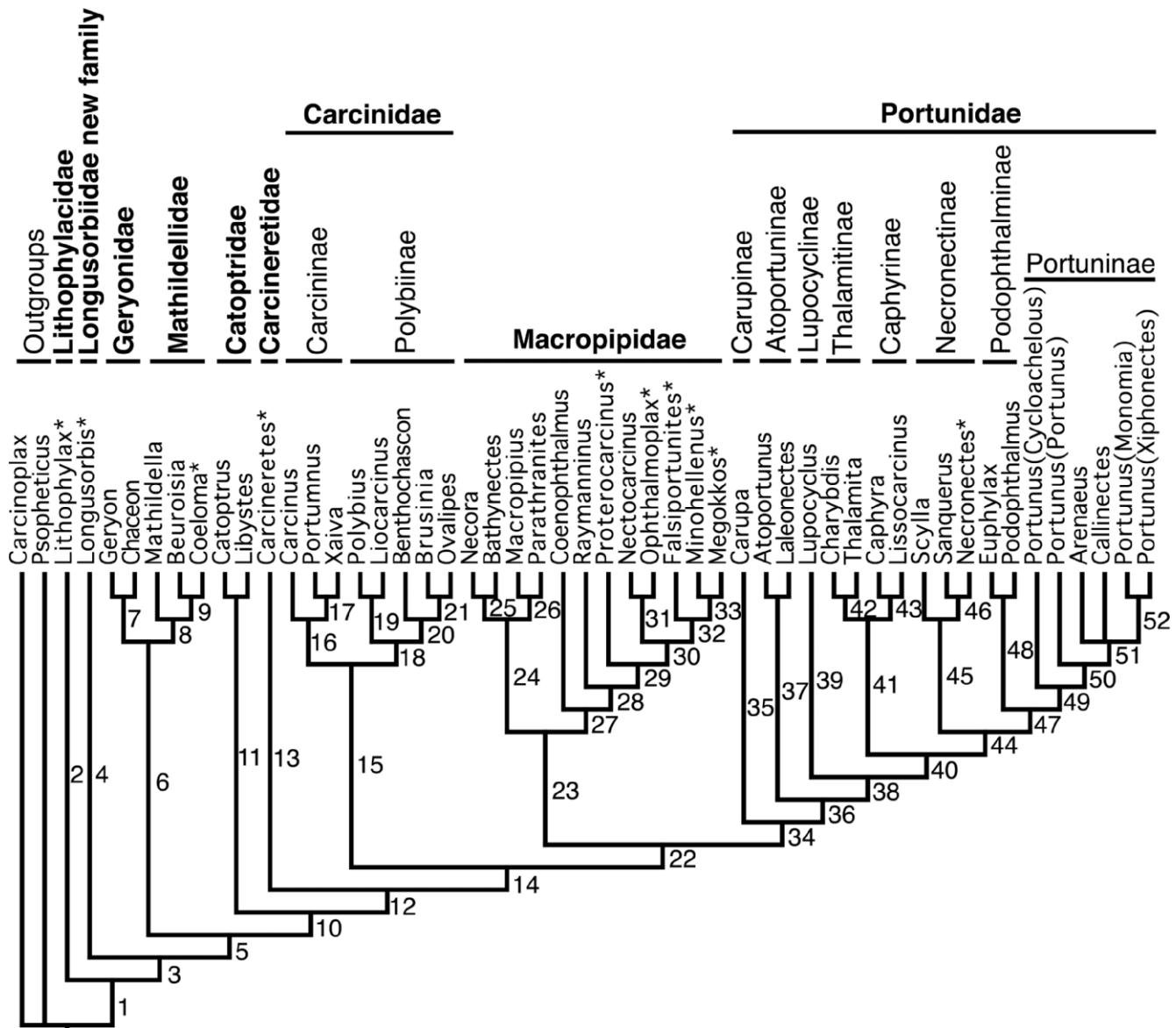


Fig. 6. One of two most-parsimonious trees from analysis B (TL = 245; CI = 0.4041; RI = 0.7671; RC = 0.3100). Clade number indicated. Families and subfamilies as recognized herein are indicated.

(1965[imprint 1966]) did not create a subfamily; therefore, the authorship of Libystinae should be cited as Števčić (2005). Our analysis strongly suggests the recognition of Catoptrinae including *Catoptrus* and *Libystes*. Additionally, Catoptrinae is elevated to full family status because it lacks the synapomorphies of clade 12 (“remaining Portunidae” + Carcineretidae). The distinction between Catoptridae and the portunid Carupinae lies in characters of the carapace and the sternum. Carupinae has unique synapomorphies of Portunidae, including secondary sulci delimiting thoracic sternites 6 and 7 (34-1), a median transverse ridge connecting secondary sulci (35-1), and a median line reaching the lateral ends of the sulci between thoracic sternites 5 and 6 (36-1), all of which Catoptridae lack. In Catoptridae, the suture between thoracic sternites 3 and 4 is indistinct,

whereas in Carupinae it is well defined. Additionally, Catoptridae is distinguished from Carupinae in that the front is nearly straight without teeth or lobes, the upper orbital margin is entire and does not bear a defined inner orbital angle, the lower orbital tooth is low and is not visible dorsally, and pereiopod 5 usually does not exhibit a foliaceous propodus and a lanceolate dactylus.

The extinct Carcineretidae and the remaining “Portunidae” (clade 12), with Bremer support of 5, is well defined by five unambiguous characters: a relatively narrow thoracic sternum (29-1), a well marked sulcus delimiting thoracic sternites 3 and 4 (31-0), pereiopod 5 with a foliaceous propodus (50-1), the possession of a lanceolate dactylus on pereiopod 5 (51-2), and the presence of a proximal insertion of the propodus of pereiopod 5 (53-1). *Carcineretes* stands

as its own clade (clade 11) and is defined by the presence of dorsal carapace ridges (10-1), a wide orbital margin (13-1), presence of sinuous lateral margins of male pleomeres 4-5 (24-1), presence of a median groove on male thoracic sternite 3 (37-0), presence of transverse ridges on the outer surface of the cheliped palm (46-1), and foliaceous-like propodi of pereopods 2-4 (48-1). Thus, Carcineretidae remain a legitimate family as in Schweitzer et al. (2007).

Clade 14 (remaining “Portunidae”) shares three synapomorphies, possession of frontal teeth (4-0), the inner orbital angles defined as lobes or teeth (17-0), and male pleomere 3 with a transverse keel (26-1). Our analysis shows that the three subfamilies, Carcininae, Polybiinae, and Portuninae, at least as traditionally defined, are polyphyletic. Von Sternberg and Cumberlidge (2001) and Karasawa and Schweitzer (2006) have already suggested the polyphyly of both Carcininae and Polybiinae based upon adult morphology-based cladistic analysis, but they did not evaluate both subfamilies. In our analysis, the “portunid” relationships are more fully resolved.

Clade 15 (Carcinidae) is united by only one unambiguous character, a trilobed front (3-1). We divide this clade into two subfamilies herein: Carcininae and Polybiinae. A single character, a complete suture between thoracic sternites 7 and 8 (33-0), supports the monophyly of Carcininae (clade 16) as defined herein. The analysis shows that *Benthochascon*, *Brusinia*, and *Nectocarcinus* are excluded from Carcininae. Alcock and Anderson (1899) originally included *Benthochascon* within Portuninae (= Polybiinae) and most subsequent workers (Balss, 1957; Stephenson, 1972; Davie, 2002) followed their opinion. Davie and Short (1989) mentioned that *Benthochascon* should be placed within Carcininae, and Moosa (1996) treated the genus as one of the members of Carcininae. Števc̃iĉ (1991) erected a new tribe Brusiniini Števc̃iĉ, 1991, for *Brusinia*, but did not assign it to any portunid subfamily. After that, Moosa (1996), Crosnier and Moosa (2002), and Števc̃iĉ (2005) included *Brusinia* within Carcininae. Since A. Milne-Edwards (1862) established the genus *Nectocarcinus*, it has been placed within Carcininae. The present analysis suggests that both *Benthochascon* and *Brusinia* belong to Polybiinae and *Nectocarcinus* should be moved to Macropipidae. One unambiguous character, an ovate thoracic sternum (30-1), unites clade 18 (Polybiinae). Most extant and fossil genera previously assigned to Polybiinae belong to the more derived clade of Macropipidae. D’Udekem d’Acoz (1999) placed three subgenera, *Macropipus*, *Necora*, and *Polybius* (= *Liocarcinus*), and an unnamed subgenus, under the genus *Polybius*. However, our analysis rejects the monophyly of his *Polybius*-relationship and removes *Necora* and *Macropipus* to Macropipidae. The monophyly of three genera, *Benthochascon*, *Brusinia*, and *Ovalipes*, is well supported by three unambiguous characters: a free basal article of the antenna that does not reach the front (14-1, 15-1), and all distinct pleonal sutures of the male (27-0). It is possible that future studies may indicate that this group warrants its own subfamily, for which Brusiniinae Števc̃iĉ, 1991, would be the available name.

A sister group relationship of Macropipidae and Portunidae (clade 22) is weakly supported by one unambiguous

character, the inner margin of the meri of the chelipeds with spines (45-1). Clade 24 (Macropipidae) is united by two synapomorphies: the telson of the male pleon reaching the anterior half of thoracic sternite 4 (20-1) and the possession of a median groove on thoracic sternite 3 (37-0). This clade contains seven extant genera (*Bathynectes*, *Coenophthalmus*, *Macropipus*, *Necora*, *Nectocarcinus*, *Parathranites*, and *Raymanninus*) and five fossil genera (*Proterocarcinus*, *Ophthalmoplax*, *Falsiportunites*, *Minohellenus*, and *Megokkos*). Alcock (1899) established the alliance Coenophthalmoida under his Portuninae (= Polybiinae). Stephenson and Campbell (1960) gave Macropipinae as a replacement name for a family-level group including *Macropipus*, *Ovalipes*, and *Parathranites*, and defined the subfamily in the same paper. Subsequently, Holthuis (1968) showed that Polybiinae Ortmann, 1893, replaced Macropipinae as the subfamily name. However, the first author to establish the name, Polybiidae or Polybiinae, was not Ortmann (1893), as has been used previously, but Paul’son (1875) (see also Števc̃iĉ, 2005). According to ICZN (1999), art. 35.5, the subfamily Macropipinae Stephenson and Campbell, 1960, predominates the alliance Coenophthalmoida Alcock, 1899. Therefore, Macropipidae is given as a family name for clade 23. Macropipidae is distinguished from Carcinidae in that the carapace is usually wider than long, the frontal margin consists of four teeth or lobes with a median notch (*Macropipus* as the exception), the anterior portion of the telson of the male pleon reaches to the anterior portion of thoracic sternite 4, and there is a median groove on thoracic sternite 3.

Portunidae as defined here (clade 34), with Bremer support of 4, is well defined by six unambiguous synapomorphies (12-1, 29-2, 34-1, 35-1, 36-1, 47-0), three of which are unique and never reversed: possession of secondary sulci delimiting thoracic sternites 6 and 7 (34-1), possession of a median transverse ridge connecting secondary sulci (35-1), and possession of a median line reaching lateral ends of sulci between thoracic sternites 5 and 6 (36-1). Within the taxa of Portunidae clade, the sulcus delimiting thoracic sternites 6 and 7 looks like a complete or nearly complete suture. However, this sulcus ends at a position lateral to the sterno-abdominal cavity, often ending in a deep pit, and a second sulcus extends from the end of the first and rises abruptly towards sulci delimiting the sternites 5 and 6 in the sterno-pleonal cavity. The end result is that it can be very difficult to determine whether or not sternal suture 6/7 is complete or incomplete. A long median line on the thoracic sternum reaches the lateral ends of the sulci between thoracic sternites 5 and 6. Other unambiguous characters include an anterolateral margin with six to nine teeth (12-1), a wide thoracic sternum (29-2), and chelipeds longer than pereopods (47-0).

Carupa (Carupinae) (clade 35) is the most basal within the clade Portunidae. Carupinae is characterized by having an elongate telson of the male pleon (21-1) and male pleomere 3 without a transverse keel (33-0). Paul’son (1875) included only *Carupa* within Carupinae, and Balss (1957) added *Lupocyclus* and *Carupella* Lenz, 1914, to it. Alternatively, Alcock (1899) erected his Alliance Lupocycloida Alcock, 1899, within his Lupinae (= Portuninae) for

Carupa and *Lupocyclus*. In most recent works, Carupinae contains *Carupa*, *Catoptrus*, and *Libystes* (Apel and Spiridonov, 1998), but the analysis does not support the monophyly of Carupinae, discussed above. The analysis suggests that Carupinae is represented by a single genus *Carupa*, although other genera not included in the analysis are placed within the subfamily. The clade of Carupinae is derived as the sister to the remaining portunid clade 36, united by two unambiguous characters: the carapace with dorsal ridges (10-1) and the cheliped with transverse ridges on the outer surface of the palm (46-1).

Portuninae as traditionally defined is polyphyletic. The analysis suggests that Portuninae is divided into four monophyletic groups, *Atoportunus* + *Laleonectes* (Atoportuninae), *Lupocyclus* (Lupocyclinae), *Scylla* + *Sanquerus* + *Necronectes* (Necronectinae), and *Callinectes* + *Arenaeus* + *Portunus* complex (Portuninae). Within the clade comprising Portunidae as defined here, clade 37 (*Atoportunus* + *Laleonectes*) share two unambiguous characters: a long, well-developed anterolateral spine (9-1) and the presence of a median groove on thoracic sternite 3 (37-0). *Laleonectes* was simply placed within Portunidae (Manning and Chace, 1990); subsequently, d'Udekem d'Acoz (1999) placed it in Portuninae. Ng and Takeda (2003) originally placed *Atoportunus* within Portuninae. Most recently, Števc̃iĉ (2005) erected a new tribe Atoportunini for *Atoportunus*. We treat the tribe Atoportunini as a subfamily containing *Atoportunus* and *Laleonectes*.

The ovate to elliptic dactyli of pereopods 5 (51-3) unites clade 38 with Bremer support of 2. The analysis shows that *Lupocyclus* warrants its own subfamily. A narrow carapace (1-1) and merus of pereopod 5 with a postero-distal spine (52-1) characterize the clade of *Lupocyclus*. Paul'son (1875) established Lupocyclinae for *Lupocyclus*; therefore, we use Lupocyclinae Paul'son, 1875, as the subfamily name for the clade.

Clade 40, with Bremer support of 2, shares one unambiguous character, a spined or lobed laterodistal area of the basal article of antenna (16-1). Clade 41 (Caphyrinae + Thalamitinae) is derived as the sister to Necronectinae + [Podophthalminae + Portuninae sensu stricto] clade (clade 41) and, with Bremer support of 3, is well defined by an unambiguous character, an indistinct sulcus delimiting thoracic sternites 3 and 4 (31-1), and a unique one, gonopods 1 with subterminal spines (as defined by Apel and Spiridonov, 1998; Davie, 2002) (55-1). The monophyly of Caphyrinae (clade 43), with Bremer support of 3, is well supported by three unambiguous characters: a narrow carapace (1-1), low lower orbital teeth (6-0), and a relatively narrow thoracic sternum (29-1). Thalamitinae (clade 42) is also monophyletic and shares a unique character, the presence of a laterodistal expansion of the basal article of antenna (17-1), and an unambiguous one, merus of pereopod 5 with a posterodistal spine (52-1).

Clade 44, with Bremer support of 4, is well defined by four synapomorphies: pleomere 3 of males with a rectangular, expanded lateral corner (25-2), a well-developed thoracic sternite 8 of males (40-2), foliaceous propodi of pereopods 2-4 (48-1), and meri of pereopods much shorter than propodi (54-1). One unambiguous character, palms of

chelipeds with smooth outer surface (43-0), supports the monophyly of *Scylla* + [*Sanquerus* + *Necronectes*] (clade 45). The analysis suggests that this monophyletic clade warrants its own subfamily, Necronectinae Glaessner, 1928. Traditionally, *Scylla* was believed to be a member of Portuninae, and the included species *S. validus* (Herklots, 1851) of the monotypic genus *Sanquerus* was included within *Portunus*.

Podophthalminae is derived as the sister to Portunidae sensu stricto (clade 47). Clade 47, with Bremer support of 2, is well defined by two synapomorphies: presence of an epistomial spine (18-1) and thoracic sternite 3 with a median groove (37-0). A well-developed epistomial spine (18-1) is a unique character. The monophyly of Podophthalminae (clade 48), with Bremer support of 6, is well supported by seven unambiguous characters: the front without a median notch (2-1), the absence of frontal teeth (4-1), a T-shaped front (5-1), the inner orbital angle not defined as a distinct tooth (7-1), the anterolateral margin with two or three teeth (12-0), a wide orbital margin (12-1), and meri of pereopods 5 with a postero-distal spine (52-1).

A narrow pleomere 6 of the male (23-1) defines Portuninae as defined herein (clade 49). The sister group relationship of the clade (*Portunus* (*Xiphonectes*) + *Portunus* (*Monomia*)), *Callinectes*, and *Arenaeus* remains unresolved. The genus *Portunus* is comprised of six subgenera, *Achelous* de Haan, 1833, *Cycloachelous* Ward, 1942, *Lupocycloporus* Alcock, 1899, *Monomia* Gistel, 1848, *Portunus*, and *Xiphonectes* A. Milne-Edwards, 1873 (Davie, 2002). In our study, four subgenera, *Cycloachelous*, *Monomia*, *Portunus*, and *Xiphonectes* were examined. The analysis suggests that the genus *Portunus* is a para- or polyphyletic group, but examination of additional taxa will be necessary to reevaluate the genus *Portunus*.

The recognition of the extinct subfamily Psammocarcininae is questionable. Psammocarcininae has previously contained four genera: *Psammocarcinus* (type genus), *Enoplonotus* A. Milne-Edwards, 1860; *Rhachiosoma* Woodward, 1871; and *Acanthoportunus* Schweitzer and Feldmann, 2002 (Schweitzer and Feldmann, 2002). *Psammocarcinus hericarti*, the type species of *Psammocarcinus*, is known from the carapace, thoracic sternum, chelipeds, and pereopods (A. Milne-Edwards, 1860). Examination of A. Milne-Edwards's original figures shows that the rate of missing data within *Psammocarcinus hericarti* is about 42.8 per cent, but the position of *Psammocarcinus* on the cladogram when run with the other data (41 trees; tree length = 247; Consistency index = 0.4008; Retention index = 0.7669; Rescaled consistency index = 0.3074) suggests possible placement within Carcinidae clade (Fig. 7). The other members of Psammocarcininae are removed herein to Portunidae. Therefore, Psammocarcininae might be synonymised with Carcinidae, but detailed examination of more complete specimens will be necessary to confirm the placement of *Psammocarcinus*.

Coelocarcinus Edmondson, 1930, has been placed within Portunidae, apparently based upon its paddle-like fifth pereopods, specifically within Caphyrinae (Edmondson, 1930; Ng, 2002). However, *Coelocarcinus* lacks a portunid lobe of maxilliped 1 and subterminal spines of gonopod 1.

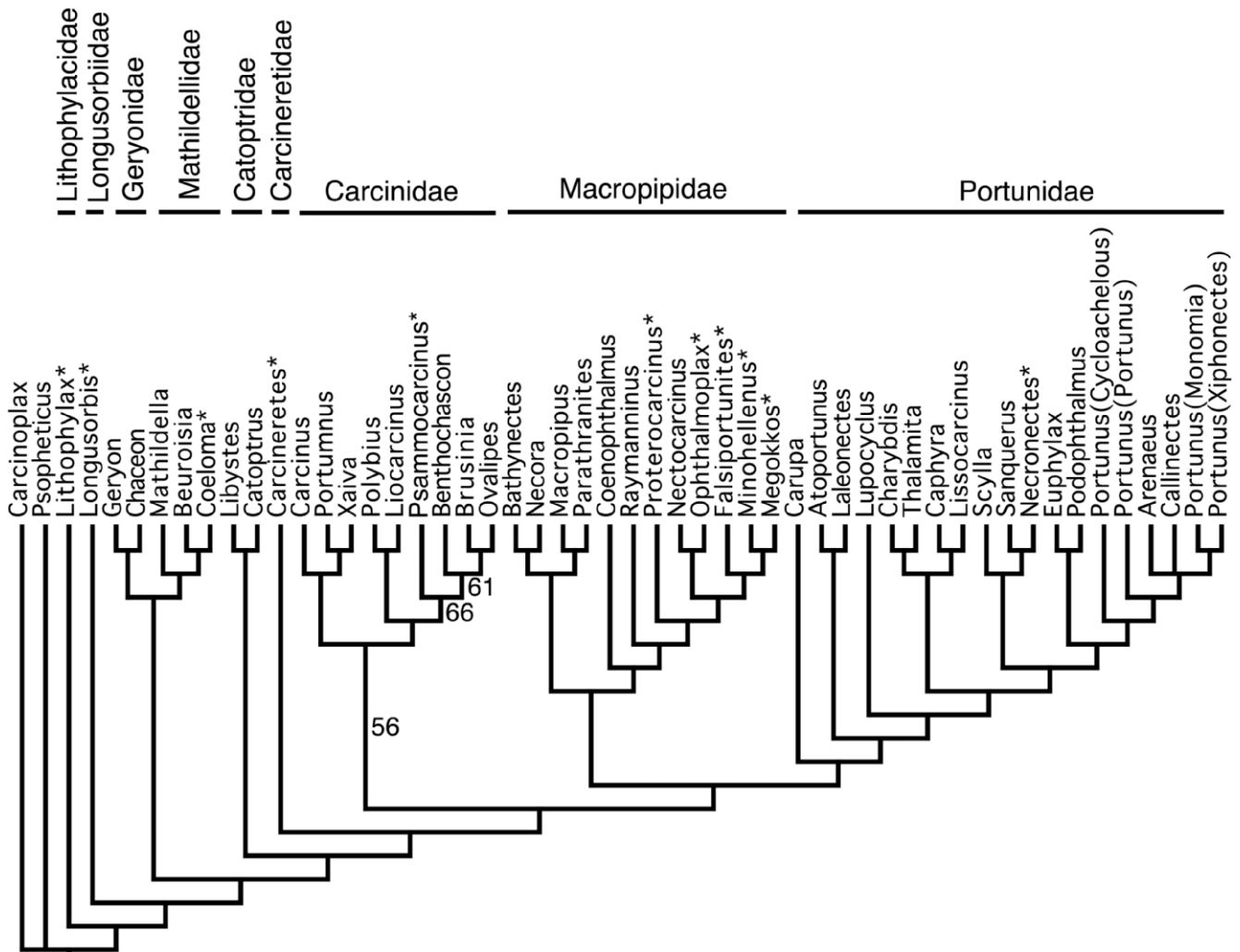


Fig. 7. A 50 percent majority-rule consensus tree from all extant and extinct genera including *Psammocarcinus hercarti* (41 trees; TL = 247; CI = 0.4008; RI = 0.7669; RC = 0.3074). Majority-rule consensus support excluding 100 percent indicated. Families as recognized herein are indicated.

In *Caphyra* and *Lissocarcinus*, the two included genera within Caphyrinae, the basal article of the antenna has a laterodistal lobe, but in *Coelocarcinus* it is simple. Thus, *Coelocarcinus* is not a member of Caphyrinae. Several features of this genus suggest that it is not a member of Portunoidea. The paddle-like fifth pereiopods are in fact unlike any seen within Portunoidea. The dactyls and propodi are each nearly circular (Ng, 2002); this shape of these elements is not seen in any portunoids, but the shape is in fact seen in many members of Matutidae Weber, 1795, for example. The shape of the carapace strongly suggests placement within Hepatidae Stimpson, 1871, or Aethridae Dana, 1851. The crispate anterolateral margins; strongly projected front; small, circular, forward directed orbits; and flattened lateral portions of the carapace are quite reminiscent of such hepatid genera as *Osachila* Stimpson, 1871. In addition, the sternum of *Coelocarcinus* is quite narrow, as in hepatids, and the chelae are somewhat concave on the inner surface, as in Calappoidea in general, to facilitate drawing the chelae close the anterior edge of the carapace. Thus, it seems that *Coelocarcinus* is best allied with Hepatidae for

now until more detailed studies can be undertaken. It is certainly not a portunoid.

Martins-Neto (1987) described *Araripecarcinus* from the early Cretaceous of Brazil. What he described and illustrated as the dorsal carapace is actually the ventral surface of the carapace (Martins-Neto, 1987, fig. 1, 2). Examination of those illustrations strongly suggests that *Araripecarcinus* is a raninid, based upon its long buccal cavity; large bulbous pterygostomial region; narrow sternum; and pleon that extends posteriorly from the carapace. Recovery of a dorsal carapace or better preserved material could help confirm this placement.

SYSTEMATICS

Among the symbols below: † indicates that the taxon has a fossil record and is also extant; †† indicates that the taxon is extinct; no dagger indicates that the taxon is extant only. The dagger is not used at the species level if the genus is extinct or extant only, which would obviously indicate that the species were extinct or extant only, respectively.

Infraorder Brachyura † Latreille, 1802

Section Heterotremata † Guinot, 1977

Cancroidea † Latreille, 1802

Cancridae † Latreille, 1802

Ceronnectes †† De Angeli and Beschin, 1998

Types Species.—*Cancer boeckhi* (Lörenthey, 1898), by original designation.

Included Species.—*Ceronnectes boeckhi*; *C. granulosa* Feldmann et al., 1998 (as *Pororaria?*); questionably *C. pusillinus* Secretan in Plaziat and Secretan, 1971 (as *Portunus*).

Material Examined.—*Ceronnectes boeckhi*, MCZ 1563.

Remarks.—De Angeli and Beschin (1998; 2001) originally placed their new genus *Ceronnectes* within Portunidae. Later, Schweitzer et al. (2006) placed the genus within Cancridae, closely allied with *Romaleon* Gistel, 1848, and *Anisospinos* Schweitzer and Feldmann, 2000a. De Angeli and Garassino (2006b) also moved *Ceronnectes* to Cancridae and showed that *Ceronnectes* is a senior synonym of *Anisospinos*. We concur with the placement of *Ceronnectes* within Cancridae but maintain *Ceronnectes* and *Anisospinos* as distinct genera based upon the generally more granular carapace, more attenuated spines, and broader orbits in *Anisospinos*. In addition, the spines of *Ceronnectes* do not appear to differ in size from one another as markedly as in *Anisospinos*.

Feldmann et al. (1998) described the new species, *Pororaria? granulosa*, from the Eocene of North Carolina. Examination of the illustrations of that specimen indicate that it is best placed within *Ceronnectes* De Angeli and Beschin, 1998, based upon the lobate nature of the anterolateral margins; development of the axial and protogastric regions; narrow posterior margin; and scabrous ornamentation. The Eocene occurrence of *C. granulosa* in North Carolina does not extend the geologic range but does extend the geographic range, suggesting a Tethyan distribution for the genus.

Secretan [in Plaziat and Secretan (1971)] described the new species *Portunus pusillinus* from the Ypresian of France. This species may also be placed within *Ceronnectes* based upon its trilobed front, lobate anterolateral margin with tiny spines, and the raised protogastric and axial regions and depressed lateral regions of the carapace. This general conformation of carapace regions is seen in *Ceronnectes*, *Romaleon*, and *Anisospinos*, suggesting a common ancestor for all three genera. *Portunus pusillinus* differs from the type species of *Ceronnectes* in having a narrower carapace, much smaller anterolateral spines, and a broader fronto-orbital width with respect to the maximum carapace width. It is possible that it may belong within a new genus, but type material will need to be examined. For now, it is placed within *Ceronnectes*.

Blow and Manning (1996) erected the genus *Sarahcarcinus*, which they questionably assigned to Cancridae. That genus has extremely broad orbits and an extremely broad fronto-orbital width, much broader than is typical for cancrids. *Sarahcarcinus* appears to possess eight anterolateral spines, and elevated axial and protogastric regions, not unlike the other cancrid genera under discussion.

However, the broad orbits are unique, suggesting that it should remain as a discrete genus. Family level placement will be confirmed only with more complete material.

Xanthoidea † MacLeay, 1838

Xanthidae † sensu stricto MacLeay, 1838

Nogarolia †† Beschin, Busulini,
De Angeli, and Tessier, 1994

Type Species.—*Nogarolia mirabilis* Beschin, Busulini, De Angeli, and Tessier, 1994.

Remarks.—*Nogarolia* is a monospecific genus described from the Eocene of Italy, and it displays an enigmatic combination of characters. It was originally referred to Portunidae, but the features it possesses, including a markedly wider than long carapace; five anterolateral spines; very stout chelae with black fingers; an eight-lobed front; and relatively small orbits with two fissures, do not place it within any known family or subfamily of Portunidae or Portunoidea as herein defined. The carapace shape and apparently raised protogastric and axial regions are reminiscent of Cancridae, but the cancrids generally possess many more anterolateral spines than does *Nogarolia*. The large, stout claws with black fingers suggest an affinity with some members of Xanthidae sensu stricto, especially *Etisus*. In addition, *Nogarolia* possesses other diagnostic features of Xanthidae sensu stricto as defined by Karasawa and Schweitzer (2006), including a transversely ovate carapace that is about 72 percent as long as wide; a position of maximum width anterior to the mid-length; a frontal margin with axial notch; a frontal width about 31 percent maximum carapace width; a fronto-orbital width slightly over half the maximum width; and an anterolateral margin with between 2 and 6 spines (5 in *Nogarolia*) and that is well-differentiated from the posterolateral margin. Unfortunately, none of the details of the sternum and pleon are known for *Nogarolia*. Thus, we place it within Xanthidae sensu stricto until more complete specimens can be recovered to confirm the arrangement.

Portunoidea † Rafinesque, 1815

Included Families.—Carcineretidae †† Beurlen, 1930; Carcinidae † MacLeay, 1838; Catoptridae † Borradaile, 1902; Geryonidae † Colosi, 1923; Lithophylacidae †† Van Straelen, 1936a; Longusorbiidae †† new family; Macropipidae † Stephenson and Campbell, 1960; Mathildellidae † Karasawa and Kato, 2003; Portunidae † Rafinesque, 1815; Psammocarcinidae †† Beurlen, 1930.

Diagnosis.—Carapace hexagonal, subhexagonal, rectangular, or transversely ovate, generally wider than long but occasionally equant, usually widest at position of last anterolateral spine; front typically with median notch but occasionally entire or with median spine; anterolateral margins almost always spinose, ranging from 3-9 spines or lobes; regions poorly or moderately defined, carapace with arcuate epibranchial ridge; lobe on endopod of first maxilliped (portunid lobe) sometimes present; male sternite 8 indistinctly visible posteriorly, sternal sutures 4/5, 5/6, 6/7, and 7/8 usually incomplete, sternite 8 usually visible in ventral view, with penial groove (Portunidae); telson of male

pleon usually reaching posterior part of sternite 4; sutures of male pleomeres, if present, usually immovable; male pleomere 3 almost always with transverse keel; chelipeds usually robust; last pair of pereopods may have ovate dactyls; gonopod 1 usually strongly curved, with inflated, strongly hooked base (after Karasawa and Schweitzer, 2006).

Lithophylacidae †† Van Straelen, 1936a

Included Genus.—*Lithophylax* †† A. Milne-Edwards and Brocchi, 1879.

Diagnosis.—A diagnosis for the family has just been published (Guinot and Breton, 2006, p. 600), and will not be repeated here. The characters that distinguish this clade in the present analysis include the presence of a keel on pleomere 3, a complete sulcus between sternites 6 and 7, and a weakly developed posterolateral prolongation of male episternite 7. It is interesting to note that the first of these characters, presence of a keel on pleomere 3, is one of the defining characters of clade 14, which includes all Portunoidea that are more derived than Carcineretidae, with only two reversals for *Ovalipes* and *Brusinia*, within Polybiinae, and for *Carupa* within Carupidae.

Remarks.—The history of placement of *Lithophylax* has been detailed by Guinot and Breton (2006) who noted the two general groups to which it has been allied, Goneplacidae and Carcineretidae within Portunoidea, but they failed to place the family within a superfamily so that their position on this matter remained unresolved. In our analysis, Lithophylacidae appear at the base of Portunoidea. One interesting character state that is shared with all taxa within clade 14, i.e., Carcinidae, Macropipidae, and Portunidae, is the presence of a keel on pleomere 3. However, the orbital margin in *Lithophylax* does not bear fissures and the front does not show an axial notch. The presence of the axial notch (character 2-0) is characteristic of nearly all extant portunoids.

One note of interest regarding *Lithophylax trigeri* is that it possesses a very distinctive, ovoid, elevated, stridulating device on the carapace margin just posterior to the outer-orbital tooth. The structure is inflated sufficiently that it can be observed from above. Stridulating devices are known in other portunoids, but they are commonly developed as an elongate rasping device on the pterygostomial region well below the margin of the carapace. Thus, those of *Lithophylax* are rather unusual within the superfamily.

The family is represented only by one species, *Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879, from the Upper Cretaceous of France. Thus, the short history of the group is confined to the Tethyan region.

Longusorbiidae †† new family

Type and Sole Included Genus.—*Longusorbis* †† Richards, 1975.

Diagnosis.—Carapace wider than long, maximum length ranging from 70 to 80 percent maximum width, widest at position of hepatic region, posterior to outer-orbital angle, about 30 percent the distance posteriorly; lateral margins of

carapace converging posteriorly; front interpreted to lie between interior-most orbital notches, axially produced into long, blunt-tipped rostrum, rostrum axially sulcate, strongly down-turned distally so that distal part is nearly perpendicular to dorsal carapace; frontal width about 40 percent maximum carapace width; orbits extremely broad, sinuous, with notches, spines, or blunt protuberances; orbits angling posteriorly; eyestalks apparently well calcified; fronto-orbital width about equal to maximum carapace width; mesogastric region merging with rostral sulcus; gastric regions short; branchial regions long; urogastric region about as wide as mesogastric and cardiac regions; epi-branchial region arcuate; metabranchial region with inflated oblique ridge parallel to margin. Carapace surface with tubercles. Sternum relatively narrow compared to other portunoids, about as long as wide, sternites 1/2 fused, no evidence of suture; sternal suture 2/3 entire; sternal suture 3/4 expressed as a marginal notch and weak groove, well marked; sternite 4 long; sternal sutures 4/5 and 5/6 not parallel; sternal suture 4/5 at high angle; sternite 8 not visible in ventral view. Male pleon extending to about middle of sternite 4 and about middle of coxae of pereopods 1; all male pleomeres free, entirely filling space between coxae of fifth pereopods. Chelae stout, markedly heterochelate, chelipeds shorter than pereopods; fingers with black tips; meri and carpi of fourth and fifth pereopods flattened; propodi of fourth and fifth pereopods elliptic; dactylus of fifth pereopod narrow, lanceolate (after Schweitzer et al., 2007, p. 29; and characters defined herein).

Material Examined.—*Longusorbis cuniculosus* Richards, 1975: PRI 55177, KSU D746, collected from near Shelter Point, late Campanian Northumberland Formation (Schweitzer et al., 2003); *L. eutychius* Schweitzer et al., 2007: MHN-UABCS/Te8/68-413, holotype.

Remarks.—Schweitzer et al. (2007) discussed the history of the taxonomic status of *Longusorbis* and placed it within Portunoidea, family uncertain. The analysis herein suggests that the genus differs significantly from other members of the superfamily. Specifically, *Longusorbis* is unique in possessing elliptical propodi of the fourth and fifth pereopods but lanceolate dactyli. Thus, the pereopods appear paddle-like as in many portunoids, but the paddle is developed on the propodus instead of the dactylus. In addition, all of the male pleomeres are free in *Longusorbis*, although it is not possible at this time to determine whether or not somites 3-5 are immovable, as they are in Geryonidae and Mathildellidae. Male sternite 8 is not visible in ventral view, differentiating it from all portunoids except Carcinidae. Well-calcified eyestalks as seen in *Longusorbis* appear to be common within extinct members of the Macropipidae, within Portunoidea. The broad orbits and well-ornamented carapace of *Longusorbis* are reminiscent of the goneplacoid and some portunoid groups. Thus, the unique combination of characters justifies placement of the genus within its own family within Portunoidea.

In the Late Cretaceous, the family was distributed along the coast of western North America from British Columbia, Canada, to Baja California Sur, Mexico in the eastern North

Pacific. The latest known record of the family is in Eocene rocks of Baja California Sur (Schweitzer et al., 2007).

Geryonidae † Colosi, 1923

Type Genus.—*Geryon* Kröyer, 1837.

Included Genera.—*Archaeogeryon* †† Colosi, 1923; *Archaeoplax* †† Stimpson, 1863; *Geryon*; *Chaceon* † Manning and Holthuis, 1989; *Zaraquieyon* Manning and Holthuis, 1989.

Diagnosis.—Carapace hexagonal, wider than long, smooth to granular, regions weakly or moderately defined, often with arcuate ridge on epibranchial area; front with even number of spines and axial notch; orbits only moderately wide, fissured, inner orbital angle defined by a node or spine, lower orbital spine long, visible dorsally; anterolateral margin convex with 3-5 spines; suture delimiting sternites 3 and 4 well marked, sternal sutures 4/5 and 5/6 incomplete, 6/7 barely incomplete, 7/8 complete; sternite 8 not visible ventrally but a small portion visible in posterior view; posterior prolongation of male episternite 7 not marked; pleon with seven pleomeres visible in males and females but pleomeres 3-5 immovable in males, pleomeres 2-3 or 1-3 with transverse keel; telson of male pleon reaches posterior of sternite 4; chelipeds unequal, shorter than pereopods, with distal, inner spine on carpus.

Material Examined.—*Chaceon erytheiae* (MacPherson, 1984), USNM 221963; *Chaceon granulatus* (Sakai, 1978), MFM; *Chaceon peruvianus* (d'Orbigny, 1842), BM In. 28002, GHUNLPam 16804-16814, MPEF-PI 1578-98 and 1603-1607; *Chaceon quinquedens* (Smith, 1879), USNM 5797, USNM 10589; *Geryon longipes* A. Milne-Edwards, 1882, USNM 152241; *Geryon trispinosus* (Herbst, 1803) USNM Acc. No. 38563.

Remarks.—The diagnosis given above is a composite of characters from Manning and Holthuis (1989), Davie (2002), Poore (2004), characters in the current cladistic analysis and of specimens listed above, and observations on specimens of *Chaceon peruvianus* (d'Orbigny, 1842) from the Miocene Monte Leon Formation, Argentina. Emphasis was placed on characters of external morphology in order to assure application to fossil members of the family as well as extant forms.

Manning and Holthuis (1989) restricted the extant representatives of the family to three genera, *Geryon*, *Chaceon*, and *Zaraquieyon*, a position that has been supported by subsequent workers. They did not consider fossil representatives at all.

Fossil representatives of the family have been assigned to four genera. *Archaeogeryon* was erected to embrace *A. fuegianus* Colosi, 1923, from the Cenozoic of Patagonia, South America. Subsequently, two additional species were assigned to the genus. Glaessner (1933) named *Archaeogeryon latus*, which has subsequently been assigned to *Proterocarcinus* Feldmann et al., 1995, by Schweitzer and Feldmann (2000b). *Archaeogeryon fuegianus*, type species of the genus, was reassigned (Aguirre Urreta, 1987) to *Coeloma* (*Coeloma*) by virtue of synonymizing the two genera. Analysis of the characters of *Coeloma* herein

confirms that it is not closely related to the Geryonidae. Specimens of *A. fuegianus* have not been examined and compared to other species within *Coeloma*, but for the time being we retain the species as originally defined. A line drawing of the outline of *A. fuegianus* (Aguirre Urreta, 1987, fig. 5B) closely resembles the outline of authentic geryonids. A single extinct species of *Chaceon*, *C. peruvianus*, is extremely abundant in Miocene rocks of Patagonia, and comparison of fossil forms with extant representatives of *Chaceon* in the U. S. National Museum of Natural History, Washington, confirms its generic affinities. Finally, *Archaeoplax* Stimpson, 1863, from the Miocene of the eastern United States, has been considered a geryonid (Rathbun, 1935; Glaessner, 1969). Although the dorsal carapace is not well preserved, particularly along the anterolateral margin, the material does exhibit features of the front and orbit that warrant placement of the genus within Geryonidae until more and better material is available.

The diagnosis refers to the length of chelipeds as being shorter than the other pereopods. Extant representatives of the family exhibit very long legs, longer than the chelipeds (Davie, 2002; Character 47 herein). However, examination of nearly complete specimens of *Chaceon peruvianus* confirms that in the Miocene specimens the pereopods may all be of about equal length. This observation is difficult to test because the terminal elements of the pereopods, the dactyls and often the propodi, are not preserved. It is clear, however, that the pereopods of *C. peruvianus* are stouter than those of extant species of the genus and the preserved elements are shorter. Modern species are confined to deep water habitats (Manning and Holthuis, 1989; Davie, 2002; Poore, 2004), and it is likely that elongation of the walking legs is an adaptation to life in deeper environments than was the case in the Miocene.

The earliest record of Geryonidae is in the Oligocene of Germany (Bachmayer and Mundlos, 1968). In the Miocene, another record in northern Europe, in Denmark (Fraaije et al., 2006), is overshadowed by numerous occurrences in southern South America, primarily in Argentina (Casadio et al., 2005; Feldmann and Schweitzer, 2006). Within the Pliocene and Pleistocene, the family is known from Japan (Kato and Koizumi, 2001), and the family has a cosmopolitan, deep-water distribution today. The geological occurrences are typical of an amphitropical distribution, originally confined to the Atlantic Ocean.

Mathildellidae † Karasawa and Kato, 2003

Included Genera.—*Mathildella* Guinot and Richer de Forges, 1981; *Beuroisia* Guinot and Richer de Forges, 1981; *Branchioplax* †† Rathbun, 1916; *Coeloma* †† A. Milne-Edwards, 1865; *Intesius* Guinot and Richer de Forges, 1981; *Neopilumnoplax* Serène in Guinot, 1969; *Platypilumnus* Alcock, 1894; *Tehuacana* †† Stenzel, 1944.

Diagnosis.—Carapace flattened with weakly defined dorsal carapace regions; front usually straight with shallow median notch, sometimes dentate; supraorbital angle separated from frontal margin; orbit usually relatively small, but sometimes wide, with upper orbital fissures; anterolateral margin with four or typically five spines including outer-orbital; eye

stalk short; antennular fossae broad laterally; merus of maxilliped 3 subquadrate, much longer than ischium; male pleon filling entire space between coxae of pereopods 5, usually with all pleomeres distinguishable, but male pleomeres 3-5 immovable; male pleomeres 4-5 with sinuous lateral margins; telson of male pleon semicircular or triangular; sternum wide with interrupted sutures except continuous suture 7/8; posterolateral prolongation of male episternite 7 not marked; sterno-pleonal cavity reaching posterior of sternite 4; chelipeds with dark-colored fingers; dactyli of pereopods 2-5 with corneous tips; dactyli of pereopod 5 spatulate with setae; gonopod 1 stout, curved, strongly inflated basally, with simple apex; gonopod 2 usually long with long flagellum (after Karasawa and Kato, 2003, and characters herein).

Material Examined.—*Branchioplax alberti* De Angeli and Beschin, 2002, holotype, MCZ 2062; *Branchioplax concinna* Quayle and Collins, 1981, holotype BM In. 61729; *Branchioplax washingtoniana* Rathbun, 1916, USNM 508244-508310, 508358-508365; *Coeloma vigil* A. Milne-Edwards, 1865, holotype MNHN R03822; *Coeloma balticum* Schlüter, 1879, IG 9271, IG 9219, SMNS drawer B16-6, NMW 1975/1726/10, BM I13525 and I13526; *Coeloma taunicum* von Meyer, 1862, syntypes SMF X/m 2g, X/m 2r, and X/m 2u; *Coeloma latifrons* Förster and Mundlos, 1982, BSP 1981 XI 26; *Coeloma macoveii* Lăzărescu, 1959, Univ. of Bucharest IIIart019; *Mathildella serrata* (Sakai, 1974), CBM-ZC2423; *Tehuacana tehuacana* Stenzel, 1944, BSP 1988 III 248.

Discussion.—The above diagnosis embraces the characters in the original definition of the taxon and also incorporates some of the characters defining the clades within the present analysis. For example, the form of the margin of male pleomeres 4-5 is diagnostic in the present phylogenetic analysis. One character that requires further consideration is the immovable condition of male pleomeres 3-5. Although a complete suture can be observed between these pleomeres, they are fused and are immobile. That particular character can be readily determined in extant taxa; however, no non-destructive test is available to determine that condition in fossil forms.

The extinct genera *Branchioplax* Rathbun, 1916, and *Tehuacana* Stenzel, 1944, had previously been placed with Mathildellinae (Karasawa and Kato, 2003), a position retained by Karasawa and Schweitzer (2006) as they elevated the subfamily to family rank. Both genera exhibit the characters used in the cladistic analysis to sustain that placement. However, the original diagnosis of Mathildellidae must be modified to allow the presence of four or five anterolateral spines or nodes in order that *Tehuacana* be included. Among the members of the family, it is also the one in which the regions are most strongly developed.

The genus *Coeloma* is also nested with Mathildellidae, based upon evaluation of three species, *C. vigil* A. Milne-Edwards, 1865, the type species, *C. taunicum* von Meyer, 1862, and *C. balticum* Schlüter, 1879. These three genera are quite similar to one another and clearly should be assigned to the same genus. To that list can be added *C. granulorum* A. Milne-Edwards, 1880, *C. latifrons* Förster

and Mundlos, 1982, and *C. macoveii* Lăzărescu, 1959. However, a vast array of other species has been assigned to *Coeloma* with the result that the genus in its broadest sense (Glaessner, 1969) is meaningless. Discussion of the placement of all species previously referred to *Coeloma* is not relevant here, but the group will be sorted out in future studies. Suffice it that the three species coded in the cladistic analysis and the others noted above form a well defined grouping consistent with the original description of the genus and, therefore, can be considered *Coeloma* sensu stricto. With that in mind, the genus clearly does belong within Mathildellidae and, as with *Tehuacana*, reinforces the extension of the diagnosis to embrace individuals with four as well as five anterolateral spines.

The earliest occurrences of the family are in Senegal (Remy in Remy and Tessier, 1954) and Texas, U.S.A. (Stenzel, 1944) in the Paleocene. Thus, a Tethyan origin for the family is indicated. In the Eocene, the genus *Branchioplax* is widely distributed in North Pacific, North Atlantic, and Tethyan sites. The youngest records for fossil mathildellids are in the Oligocene where they exhibit a similar North Pacific, North Atlantic, and Tethyan distributional pattern. None of the Eocene or Oligocene occurrences is in the Southern Hemisphere. Extant species are known from outer shelf to bathyal depths in the western Pacific and Indian oceans (Guinot and Richer de Forges, 1981). The absence of Neogene mathildellids may reflect a habitat change from shallower to deeper water settings, which are typically underrepresented in the fossil record.

Catoptridae † Borradaile, 1902

Included Genera.—*Libystes* † A. Milne-Edwards, 1867; *Catoptrus* A. Milne-Edwards, 1870.

Diagnosis.—Carapace moderately broad, transversely oval or rectangular, length about 60-75 percent maximum carapace width, widest one-fifth to one-third the distance posteriorly, always well before the mid-length, convex longitudinally and transversely; fronto-orbital width about 60 percent maximum carapace width, outer-orbital angle not defined as teeth or lobes; upper orbital fissures absent; front entire or bearing two truncated lobes, axially notched, about 30 percent maximum carapace width; anterolateral margin entire or with spines; dorsal carapace regions indistinct. Sternum broad, nearly parallel sided posteriorly, sternite 8 expanded laterally, clearly visible in ventral view; penial groove present on sternite 8; sternal sutures 6/7 and 7/8 incomplete; male pleomeres 3-5 fused, pleomere 3 lacking a transverse keel, sutures of male pleomeres indistinct. Basal article of antenna fixed, reaching front; portunid lobe present on maxilliped 1; chelipeds longer than pereopods; dactyli of pereopod 5 styliform or lanceolate.

Material Examined.—*Catoptrus inaequalis* (Rathbun, 1906), USNM 29661; *Catoptrus nitidus* A. Milne-Edwards, 1870, CBM-ZC4576, 3243, 3244; *Catoptrus* sp., CBM-ZC7119; *Libystes nitidus* A. Milne-Edwards, 1867, USNM 46379 (extant), USNM 518974-518978, 519523, 519524 (fossil); *Libystes edwardsi* Alcock, 1900, RUMF-ZC-283, 284.

Remarks.—The diagnosis above is based upon observations on male specimens of *Catoptrus inaequalis* (Rathbun) and *Libystes nitidus* in the U.S. National Museum of Natural History as well as the coded characters in the present study. Within the species of the family the front is nearly straight without teeth or lobes, the upper orbital margin is entire and does not bear a defined inner orbital angle, the lower orbital tooth is low and is not visible dorsally, pleomere 3 lacks a transverse keel, and pereopod 5 usually does not exhibit a foliaceous propodus and a lanceolate dactylus.

The sole fossil occurrence of the family is *Libystes nitidus* from the Pleistocene of Guam and Japan (Kesling, 1958; Karasawa, 2000; Schweitzer, Scott-Smith et al., 2002). The family seems to have had an Indo-Pacific distribution since that time, including all of the modern occurrences (Sakai, 1976; Apel and Spiridonov, 1998; Davie, 2002).

Carcineretidae †† Beurlen, 1930

Included Genera.—*Carcineretes* †† Withers, 1922; *Cancrixantho* †† Van Straelen, 1934; *Mascaranada* †† Vega and Feldmann, 1991.

Diagnosis.—Carapace quadrate, wider than long, flattened longitudinally and transversely; L/W about 90 percent, widest at position of hepatic region, just posterior to post-orbital angle. Rostrum straight in dorsal view, strongly downturned in anterior view, downturned portion nearly perpendicular to dorsal carapace; frontal width about half maximum carapace width, outer-most edges of front are inner-orbital spines. Orbits sinuous, long, with two or three intra-orbital projections and notches; outer-orbital spine triangular, directed forward; fronto-orbital width 90+ percent maximum carapace width. Anterolateral and posterolateral margins confluent, lateral margins with blunt protuberances or very short spines; posterolateral reentrants subtle but present; posterior margin rimmed, nearly straight. Protogastric regions and hepatic regions with transverse keels or swellings; epibranchial regions arcuate; mesobranchial region and cardiac region with weak transverse ridges; metabranchial region and intestinal region depressed below level of mesobranchial and cardiac regions.

Sternum ovate, moderately narrow but slightly wider than long; sternites 1 and 2 fused, no evidence of a suture; sternal suture 2/3 complete; sternite 3 with longitudinal groove extending anteriorly from axis of sterno-pleonal cavity, sternal suture 3/4 incomplete, well marked; lateral margin of sternite 4 at high angle to axis; sternal sutures 4/5 and 5/6 not parallel, 4/5 at high angle; sternite 8 not visible in ventral view. Male pleon with concave margins, reaching to about middle of sternite 4, reaching to about middle of coxae of first pereopods; pleomeres 3-5 appearing to be fused but with clear evidence of sutures; pleomere 3 very wide, completely filling space between coxae of fifth pereopods; pleomeres 1 and 2 and apparently part of pleomere 3 not visible in ventral view; pleomere 3 possibly with transverse keel, other pleomeres appearing to lack transverse keels. Chelipeds moderately heterochelate; chelae with one or more keels on outer surface; fingers with keels, lacking black tips. Propodi of pereopods 2-4 flattened. Fourth pereopod with flattened merus and carpus. Fifth

pereopod with elliptical propodus and dactyl and flattened merus and carpus; propodus not foliaceous, not inserted proximally (after Schweitzer et al., 2007).

Material Examined.—*Carcineretes woolacotti* Withers, 1922, holotype BM In. 20780, paratypes BM In. 20781-82.

Remarks.—Carcineretidae is the subject of a recent revision (Schweitzer et al., 2007) and will not be discussed in detail herein. Suffice it that the present inclusion of three genera, *Carcineretes*, *Cancrixantho*, and *Mascaranada* resulted from that study. The previously included genera, *Ophthalmoplax* and *Longusorbis*, were assigned to Portunidae, which is supported by the present analysis.

In the present analysis, emphasis was placed on the terminal elements of the pereopods perhaps to a greater degree than was done in the previous study. Determination of the foliaceous nature of the propodi and dactyli in fossils is extremely difficult and often impossible because these elements are less commonly preserved than are other parts of the animal. These elements have been coded based upon the best preserved examples of these elements in *Carcineretes*. They are not known in *Cancrixantho* and *Mascaranada* to our knowledge. Another potential discrepancy between the two studies is that the earlier work characterized the sternum as slightly wider than long, and in the present study the sternum is coded as moderately narrow. However, this discrepancy is largely semantic, as the sternum of Carcineretidae is moderately narrow in comparison to other members of Portunoidea studied herein. Schweitzer et al. (2007) considered the male pleomeres 3-5 to be fused, but examination of the holotype of *Carcineretes woolacotti* suggests that the fusion is partial. The sutures between the somites are quite evident, and there is in fact a small open space axially between somites 3/4 and 4/5. This suggests that there is indeed some fusion, resulting in this open hole axially. However, the sutures are clearly visible in this specimen, indicating that the fusion may be of the type in which the somites 3-5 behave as unit but in which the sutures are clearly visible, as in members of Geryonidae.

The family is restricted to Late Cretaceous age rocks in Mexico and the Caribbean (Vega et al., 1997) and Spain (Van Straelen, 1934). No members of the family survived the end-Cretaceous extinction event(s).

Carcinidae † MacLeay, 1838

Included Subfamilies.—Carcininae † MacLeay, 1838; Polybiinae † Paul'son, 1875.

Diagnosis.—Carapace not much wider than long, with length occupying from 80 to 100 percent maximum width and position of maximum width about half the distance posteriorly; front trifold or five-spined with an axial spine, or having a front that is entire, occupying from about 20-40 percent of the maximum width of the carapace; orbits with fissures; fronto-orbital width occupying about half but occasionally up to three-quarters maximum carapace width; usually five anterolateral spines including outer-orbital spines but may be fewer; posterior margin convex; arcuate epibranchial region; basal article of antenna free, without laterodistal spine (except some *Liocarcinus*); male pleomeres

3-5 fused (except *Brusinia*), with somite 3 always wider than other somites and with a transverse keel, anterior margin of pleomere 6 concave forward; posterior margin of telson convex to fit into somite 6; male pleon ranging from broadly triangular to narrow and nearly uniform in width; male gonopod 1 simple, without subterminal spines; sternum ovate, broad or narrow; chelipeds stout.

Discussion.—The phylogenetic position of Carcininae and Polybiinae and their included genera has been contentious. Historically, these two subfamilies have been treated as subfamilies of Portunidae, generally being defined as portunids with carapaces not much wider than long, with paddle-like fifth pereopods (Polybiinae) or with lanceolate fifth pereopods (Carcininae). Schweitzer et al. (2007) summarized the broad variation among extant members of Polybiinae and the resulting inherent difficulties of placing fossils into an appropriate portunid subfamily. Not surprisingly, for the genera within Polybiinae as historically recognized (Glaessner, 1969; Davie, 2002; Poore, 2004; Apel and Spiridonov, 1998), there have been four different subfamilies or tribes introduced (Davie, 2002; Števcíć, 2005), one for nearly every included extant genus, which demonstrates the variability even within the subfamily as defined herein. The situation is no better for Carcininae, for which a subfamily has been named for the three most commonly included extant genera as well as for some others that are herein removed to Macropipidae (Davie, 2002). Clearly, then, these subfamilies comprise a heterogeneous group, at least in terms of superficial characters.

The results of our analysis suggest that several of the taxa that have historically been assigned to either Carcininae or Polybiinae should be removed to Macropipidae, herein elevated to family level. The remaining genera form a family, Carcinidae, which is united by possession of the diagnostic features listed above. Each subfamily within Carcinidae defined below is clearly defined by possession of specific characters within this broad diagnosis. Interestingly, each subfamily embraces pairs of genera with similar superficial morphologies. As an example, two genera have a similar carapace form: *Brusinia* within the Polybiinae and *Portumnus* within Carcininae; an unpublished dissertation discusses these similarities further (Steudel, 1998) and relates them to the swimming habit of both genera. Two genera have almost identical superficial sternal shapes: *Polybius* within Polybiinae and *Carcinus* within Carcininae. Two genera have nearly identical superficial shapes of the male pleon, in which it is long, narrow, and uniformly wide along its width: *Portumnus* in Carcininae and *Ovalipes* in Polybiinae. We are unsure at this time as to why this is. It is possible that these pairs of genera demonstrate convergent evolution within the group; alternatively, they may represent ancestral features that are shared between genera within the family but that are not specific characteristics of the subfamilies. Another possibility is that Carcinidae as defined herein is polyphyletic, and that the clades defined herein are based upon convergent or homoplastic characters.

It is also important to note that *Brusinia* is an outlier in terms of many characters for the family and the subfamily, Polybiinae. It has all male pleomeres free, somite 3 lacks a transverse keel, and the carapace is longer than wide,

unique among the family. Sternite 8 is barely visible in ventral view, unique among the subfamily. It is notable that the placement of this genus has been contentious. Davie (2002) placed it within Polybiinae which the current analysis supports; however, Moosa (1996) and Števcíć (2005) placed it within Carcininae, apparently based upon its perceived similarity with *Portumnus* and *Xaiva*. Genetic studies may help to better resolve the placement of *Brusinia*.

Carcininae † MacLeay, 1838

Included Genera.—*Carcinus* † Leach, 1814; *Cicarnus* †† Karasawa and Fudouji, 2000; *Miopipus* †† Müller, 1979; *Portumnus* Leach, 1814, questionably fossil; *Xaiva* † MacLeay, 1838.

Diagnosis.—Carapace subhexagonal, somewhat wider than long or about as wide as long, length ranging from 80 to 100 percent maximum width; front with five lobes including inner orbital lobe, or nearly straight; front about one-quarter to one-third maximum carapace width; orbits small, orbital fissures reduced, fronto-orbital width about half maximum carapace width; anterolateral margin with five or fewer spines including outer-orbital spine; axial regions generally well-developed; carapace with arcuate epigastric ridge; posterolateral reentrant reduced or absent; posterior margin convex, not distinctly differentiated from posterolateral margin; basal antennal article narrow, fixed, longer than wide; portunid lobe not well-developed; chelipeds shorter than at least one other pereopod, generally smooth except for a spine on carpus; propodi of pereopod 4 may be ovate; dactyli of pereopod 5 styloform, ensiform, or lanceolate; male gonopod one without subterminal spines; sternite 8 not visible in ventral view; sternal sutures 4/5, 5/6, 6/7 interrupted, sternal suture 7/8 continuous; male abdomen ranging from broadly triangular to narrow and nearly uniform in width; male pleomeres 3-5 fused; male pleomere 3 widened laterally, with keel; anterior margin of somite 6 concave forward; posterior margin of telson convex posteriorly to fit into somite 6 (after Stephenson and Campbell, 1960; Apel and Spiridonov, 1998; Davie, 2002; Poore, 2004).

Material Examined.—*Carcinus maenas* (Linnaeus, 1758), USNM 119407, MFM, BM I3754, BM 59373, BM 38385, BM In. 59347; *Carcinus aestuarii* (Nardo, 1847), USNM 257965; *Portumnus latipes* (Pennant, 1777), USNM 20296, USNM 221604; *Xaiva biguttata* Risso, 1816, USNM 14499.

Remarks.—The subfamily as currently construed embraces a rather wide range of dorsal carapace and ventral morphology. Although united by the diagnostic characters above, it must be noted that there is a broad range in the morphology of the male pleon and sternum. The male pleon ranges from broadly triangular to narrow and nearly uniform in width along its length. The male sternum ranges from broadly ovate to narrowly ovate.

Carcinus has been reported from the fossil record from numerous Pliocene occurrences of the extant species *C. maenas* (Linnaeus, 1767) (Glaessner, 1929); indeed, the oldest occurrences of that species in the Natural History

Museum in London are Pliocene in age (BM In. 59347). Rathbun (1926) described *Carcinus minor* Rathbun, 1926, from Eocene rocks of Washington, USA. The specimen is not much wider than long and possesses five anterolateral spines that curve anteriorly; an arcuate epibranchial ridge; and moderately defined carapace regions (Rathbun, 1926, pl. 16, fig. 9). Examination of a specimen doubtfully ascribed to the species by Rathbun (CAS 12271) yields little information. Extant species of *Carcinus* do not exhibit well defined regions as does the illustration of the holotype of *C. minor*. It is notable that another genus, *Portunites* Bell, 1858, known from rocks of similar age of those of the occurrence of *Carcinus* in Washington, does exhibit well defined regions as well as all of the other features of *C. minor*. Thus, the type material of *C. minor* will need to be examined to determine whether it might be better placed within *Portunites* or some other taxon. Rathbun listed the repository as the University of Washington; investigation of the current whereabouts of that collection is ongoing. In any case, it seems prudent to restrict the confirmed fossil record of *Carcinus* to Pliocene and younger deposits at this time.

The holotype and sole specimen of *Portumnus tricarinatus* Lörenthey in Lörenthey and Beurlen, 1929, was reported to be lost (Müller, 1984). We have similarly been unable to locate the specimen in a variety of museums in Europe. It has also been suggested that the illustration of the species is inaccurate (Müller, 1984, p. 32). Thus, it is not possible to confirm the fossil record of *Portumnus*, and we regard it as questionable at this time. Certainly, summaries of the age and evolutionary history of the lineage should not be contingent upon this occurrence.

Modern records for Carcininae are largely northern hemisphere and Atlantic and Mediterranean (Ingle, 1980; Manning and Holthuis, 1981), although there are southern Atlantic occurrences (Manning and Holthuis, 1981) as well as Pacific occurrences. The extra-Atlantic/Mediterranean occurrences appear to be composed almost entirely of the introduced *Carcinus maenas* (Davie, 2002). The fossil occurrences largely follow this distribution, with nearly all from Tethyan localities in Hungary (Müller, 1984) or late Cenozoic North Atlantic occurrences (Glaessner, 1929). Exceptions include the Pacific *Cicarnus* and the doubtful occurrence of *Carcinus* in the Eocene of Washington, USA. Thus, the subfamily seems to be largely confined to the Atlantic and Mediterranean basins, based upon the records thus far.

Polybiinae Paul'son, 1875

Included Genera.—*Polybius* Leach, 1820 in 1815-1875; *Liocarcinus* † Stimpson, 1871; *Benthochascon* Alcock and Anderson, 1899; *Brusinia* Števíć, 1991; *Ovalipes* † Rathbun, 1898.

Diagnosis.—Carapace slightly wider than long or longer than wide, length ranging from 80 to 120 percent maximum width, position of maximum width about half or a little less the distance posteriorly on carapace, hexagonal or ovate in shape; front with three to five spines including inner orbital spines, always with an axial spine; orbits with one or two fissures, orbits generally moderate in size; anterolateral

margin with five spines including outer-orbital spines; posterolateral reentrant may be large; male pleon broadly triangular or narrow; male pleomeres 3-5 fused, fused but with sutures clearly visible (*Benthochascon*), or free (*Brusinia*), pleomeres 1-3 with transverse keels or lacking them (*Brusinia*), pleomere three markedly or slightly wider than other pleomeres; sternum ovate; sternal sutures all interrupted or with 6/7 continuous; fifth pereopods with broadly ovate dactyls.

Material Examined.—*Benthochascon hemingi* Alcock and Anderson, 1899, CBM (T. Komai coll.); *Brusinia profunda* Moosa, 1996, USNM 277519; *Ovalipes iridescens* (Miers, 1886), RUMF-ZC-521; *Ovalipes punctatus* (de Haan, 1833), MFM; *Ovalipes ocellatus* (Herbst, 1799), USNM 55556, USNM 185418; *Liocarcinus arcuatus* (Leach, 1814), USNM 205810; *Liocarcinus corrugatus* (Pennant, 1777), MFM; *Liocarcinus depurator* (Linnaeus, 1758), MFM, BM 42224; *Liocarcinus holsatus* (Fabricius, 1798), BM I8064; *Liocarcinus lancetidactylus* (Smirnov, 1929), syn-type BM In.36651; *Liocarcinus pusillus* (Leach, 1815), BM I8065; *Polybius henslowi* (Leach, 1820), USNM 6777.

Remarks.—*Liocarcinus* is well represented in the fossil record, mostly from Pliocene, Pleistocene, or sub-Recent occurrences but extending into the Miocene of Hungary (Müller, 1984) and the Oligocene of the Caucasus (Smirnov, 1929). *Ovalipes* has been reported from numerous occurrences in Australia, Taiwan, and Jamaica (Glaessner, 1960; Hu and Tao, 1996; Collins and Portell, 1998). The subfamily is widespread in today's oceans, including the Atlantic (Rathbun, 1930; Ingle, 1980; Manning and Holthuis, 1981) and the Indo-Pacific (Davie, 2002). The relatively limited fossil record, occurring largely only in localities in which the family is found today, does not shed much light on the historical distribution of the subfamily, although the Miocene occurrences in Hungary (Müller, 1984) suggest that a Tethyan distribution could account for the nearly cosmopolitan distribution seen today.

Macropipidae † Stephenson and Campbell, 1960 (= *Coenophthalmoida* Alcock, 1899)

Included Genera.—*Bathynectes* Stimpson, 1871; *Boschettia* †† Busulini et al., 2003; *Coenophthalmus* A. Milne-Edwards, 1879; *Echinolatus* Davie and Crosnier, 2006; *Falsiportunites* †† Collins and Jakobsen, 2003; *Macropipus* † Prestandrea, 1833; *Maeandricampus* †† Schweitzer and Feldmann, 2002; *Megokkos* †† Schweitzer and Feldmann, 2000b; *Minohellenus* †† Karasawa, 1990; *Necora* † Holthuis, 1987; *Nectocarcinus* A. Milne-Edwards, 1860; *Ophthalmoplax* †† Rathbun, 1935; *Parathranites* † Miers, 1886; *Pleolobites* †† Remy, 1960; *Pororaria* †† Glaessner, 1980; *Portunites* †† Bell, 1858; *Proterocarcinus* †† Feldmann et al., 1995; *Raymanninus* Ng, 2000; *Rhachiosoma* †† Woodward, 1871; Questionably *Portufuria* †† Collins et al., 2005.

Etymology.—The nomenclature surrounding the family name has been discussed above.

Diagnosis.—Carapace moderately broad, length about 65-80 percent maximum carapace width, widest between

50 and 60 percent the distance posteriorly, usually with longitudinal branchial ridges parallel to axis, often with large granules or tubercles ornamenting carapace; orbits usually moderate sized, with two fissures, fronto-orbital width usually 50-60 percent maximum carapace width, rarely approaching 90 percent (*Coenophthalmus* and some *Proterocarcinus*); front spined, number and size of spines variable, usually with an axial notch but sometimes with an axial spine (*Macropipus*), front ranging from 20-40 percent maximum carapace width but rarely reaching 60 percent (*Coenophthalmus*); anterolateral margins with three to five spines including outer-orbital spine, last anterolateral spine often long and directed laterally; epibranchial ridge arcuate, extending from last anterolateral spine to axial regions; large posterolateral reentrant for insertion of last pereopods; male pleomeres 3-5 fused and usually with clear evidence of sutures or indentations in the margins marking the position of pleomeres or all male pleomeres free, pleomere three and sometimes others with transverse keels, pleomere three generally markedly wider than other pleomeres, telson extending to middle or anterior of sternite 4; median groove present on male sternite 3; portion of male sternite 8 usually visible in ventral view but sometimes completely obscured by pleon; sternal sutures appearing to be incomplete with occasional exception of 6/7 and 7/8 (*Nectocarcinus*); portunid lobe usually present; basal antennal article fixed or free, usually lacking laterodistal spines; chelae usually keeled; some pereopods as long as chelipeds; dactylus of fifth pereopod oblongate or obovate, very rarely ovate and paddle-like in traditional sense (*Parathranites*).

Material Examined.—*Bathynectes superba* (Costa, 1853), USNM 136882, 186368; *B. maravigna* (Prestandrea, 1839), SMF 23642; *B. piperitus* Manning and Holthuis, 1981, SMF 19711; *Boschettia giampietroi* Busulini et al., 2003, holotype MCZ 2401; *Coenophthalmus tridentatus* A. Milne-Edwards, 1879, USNM 22050; *Macropipus australis* Guinot, 1961, USNM 173102; *Megokkos alaskensis* (Rathbun, 1926), USNM 534450-534451, GSC 124815-124817; *Megokkos hexagonalis* (Nagao, 1932), holotype, 4456 of Imaizumi Collection; *Megokkos feldmanni* (Nyborg et al., 2003), USNM 494682, 494688; *Maeandricampus triangulum* (Rathbun, 1926), holotype USNM 353567, USNM 534449; *Minohellenus inexpressus* Schweitzer and Feldmann, 2002, holotype SDSNH 81058; *Minohellenus macrocheilus* Kato and Karasawa, 1994, holotype KMNH IVP 300, 020; *Minohellenus minoensis* Karasawa, 1990, holotype MFM 9035; *Minohellenus quinquedentatus* Karasawa, 1993, holotype MFM 9030, paratype MFM 9031; *Necora puber* (Linnaeus, 1867), USNM 121969, BM 59372, BM I841, BM I 839, BM 59387; *Nectocarcinus integrifrons* (Latreille, 1825), USNM 17030; *Ophthalmoplax stephensoni* Rathbun, 1935, holotype USNM 73793, paratype, USNM 73794; UT 21258, 21262; *Parathranites orientalis* (Miers, 1886) USNM 41075, KPM-NH0106902; *Pleolobites erinaceus* Remy, 1960, cotypes RO 3781 and RO3782, unnumbered specimen in BSP; *Portunites incerta* Bell, 1858, lectotype, BM In.59104; *Portunites stintoni* Quayle, 1984, holotype BM In. 59105, BM In. 59102, 59103; *Portunites sylviae* Quayle and Collins, 1981, holotype BM In. 61713, paratype BM In. 61714, paratype

SM C84874; *Raymanninus schmitti* (Rathbun, 1931), USNM 136889; *Rhachiosoma bispinosa* Woodward, 1871, holotype SM C19132, SM 59223, SM C19170-84, BM I.2989, BM In.61406, BSP 1988 III 275, IG 4988, IG 4962; *Rhachiosoma echinata* Woodward, 1871, SM C19195.

Remarks.—Macropipidae as herein defined is separated into two clades, one composed of predominately extant forms and the other dominated by extinct forms. Interestingly, when the analysis is run without extinct taxa, the configuration of the extant forms is exactly the same as in the analysis run with extinct forms, except that all of the extinct macropipids fall within the second clade. In addition, nearly all of the extinct portunoids in general are grouped into the second clade of Macropipinae. We are unsure at this time as to why this is. A possible reason is that there is a very large number of Eocene and Oligocene portunoids with carapaces that are not much wider than long and that possess dorsal carapace ornamentation, placing them squarely with the extant Macropipidae. In addition, these extinct portunoids generally exhibit modestly flattened fifth pereopods that are not as markedly paddle-like as in Portunidae, and in the extant genera, the dactyl of the fifth pereopod ranges from paddle-like (only one genus) to oblongate. The extant members of Macropipidae as defined here exhibit a broad range of conformations of the fifth pereopod, from lanceolate to paddle-like, suggesting that at least in this family, the shape of the fifth pereopod may be entirely environmentally controlled and of no particular phylogenetic value. It is also possible that this family was particularly diverse and abundant in the past, yielding a robust fossil record.

All members of Macropipidae possess either all male pleomeres free or pleomeres 3-5 fused with some indication of sutures or marginal indentations between these pleomeres. The problem of fusion in pleomeres has been addressed previously, especially the issue of fusion of pleomeres 3-5 when sutures clearly remain between the somites (Schweitzer, 2003; 2005). In fossils, taxa with pleomeres 3-5 fused but retaining complete and clear sutures will appear as unfused somites. It is also unknown at this time what adaptive role the various degrees of fusion play in the organism, i.e., completely fused with no sutures; fused but with clear, complete sutures remaining; and all pleomeres free. Clearly, the degree of fusion of pleomeres, whether sutures are visible or not, affects the mobility and flexibility of the male pleon, suggesting an impact on reproductive strategy. However, this hypothesis has not been tested nor have observations been recorded in the neontological literature that could help resolve the issue. At this time, it is notable to observe that within the family, the somites are free or fused with clear evidence of sutures. Neither condition is widespread within Portunoidea. For example, within Geryonidae and Mathildellidae, male pleomeres 3-5 are generally fused into an inflexible unit, but the sutures between somites are clear and complete. Relicts of sutures between pleomeres 3-5 are visible in some members of other portunoid families, but this character is not found within all members of any other family.

The family is united by its possession of ornamented dorsal carapaces, often with large tubercles and/or ridges; long anterolateral spines, especially the last one; very large

posterolateral reentrants in which the coxae of pereopods 5 lie; and a generally hexagonal shape. Members of the family share some aspects of the male pleon and sternum, including lack of fusion of male pleomeres 3-5 or evidence of clear sutures between those somites in most forms and keels on male pleomere 3 and possibly 2 and 4.

There are several characteristics of the family that are shared by most members of the family, with one or two exceptions. Genera possess a dactyl of the fifth pereopod that is obovate to oblanceolate, not broadly ovate and paddle-like, with the exception of *Parathranites*. Most genera exhibit sternal sutures 4/5, 5/6, 6/7 and 7/8 incomplete except *Nectocarcinus*, in which 6/7 and 7/8 are complete. In almost all extant members, sternite 8 is visible in ventral view; in others, it is completely covered by the male pleon (*Nectocarcinus*) or barely visible (*Coenophthalmus*).

Because the family is diagnosed by a group of characteristics that fit the family in most cases but cannot diagnose each genus every time, we elect not to erect subfamilies at this time. It seems likely that this clade within Portunoidea, at least for the extant forms, may be further resolved best with genetic studies that can detect and resolve for characters that are primarily environmentally controlled (such as shape of the fifth pereopod). It should be noted that Steudel (1998) reported the portunid-lobe of maxilliped 1 as absent in *Parathranites* and *Coenophthalmus* but that the lobe was present in the material examined for this study. Thus, there appears to be some variability, perhaps in development or preservation after capture of the animal, in this feature.

Rhachiosoma had been previously placed within Psammocarcininae. Herein, we place it within Macropipidae, based upon its possession of all of the diagnostic characters of the dorsal carapace for the family, as well as a male pleon with keels on somite three. *Rhachiosoma* is unusual in the group in having a large swelling on each side of the fourth sternite, observed in all specimens in which the sternum is known. The function of the swelling is not known. *Pleolobites* is in many regards quite similar to *Rhachiosoma* in terms of the dorsal carapace; however, it differs from *Rhachiosoma* in lacking sternal swellings and possessing one orbital fissure and an indentation instead of two orbital fissures. An unnumbered specimen of *Pleolobites* deposited in BSP is noted as being Paleocene in age instead of Eocene as reported by Remy (1960); the origin of the information on the Paleocene age is unknown.

The placement of *Pororaria* has been problematic. Glaessner (1980) did not place it within a family but noted its resemblance to some members of Portunidae and Atelecyclidae among Crystoidea (it is uncertain what other families, if any, he believed referable to Crystoidea). Later, Feldmann and Maxwell (1990) referred the genus to Polybiinae of Portunidae based upon the shape of the anterior part of the sternum, the third maxilliped, and the cheliped. Although the data on *Pororaria* is quite incomplete because of the nature of the fossils, an analysis of our data run with *Pororaria* included placed it within Macropipidae, based upon its relatively narrow carapace, orbital fissures, small number of anterolateral spines, four-lobed front, and carapace with distinct ornamentation consisting of granules and keels. *Pororaria* differs from

other members of the family in lacking a long last anterolateral spine. More complete specimens, with male abdomen and sternum preserved, will be necessary to confirm the placement of *Pororaria* within Macropipidae.

Portufuria is questionably placed within Macropipidae. It is poorly preserved as a flattened, compression specimen, and little is known about the nature of the dorsal carapace morphology and the nature of the ventral surface. Thus, until better preserved specimens are recovered, the genus is placed within the family based upon its hexagonal shape and marked lateral spines. Secretan (1975) described the new species, *Macropipus ovalipes*, from the Eocene of Italy, based upon numerous flattened, compressed specimens. Those specimens are not particularly well preserved, and based upon her illustrations, appear to be ornamented with large, spherical swellings. However, *M. ovalipes* cannot be assigned to *Macropipus* because the carapace is about as long as wide, the fronto-orbital margin is wide, and the last anterolateral spine is short. More complete specimens will be necessary to confirm the generic or familial placement of this taxon.

The remainder of the fossil records for the family are well constrained and have been recently verified and summarized, including *Megokkos* (Schweitzer et al., 2006), *Maeandricampus* and *Minohellenus* (Schweitzer and Feldmann, 2002), *Ophthalmoplax* (Schweitzer et al., 2007), *Parathranites* (Karasawa, 1993), *Portunites* (Schweitzer and Feldmann, 2000b), and *Proterocarcinus* (Casadio et al., 2004; Feldmann et al., 2005). *Boschettiia*, *Falsiportunites* and *Pleolobites* are each monospecific and may be placed within the family based upon their possession of nodose carapace ornamentation, carapace ridges, and generally well-developed anterolateral spines, of which the last is longest. The extinct members of the family form a remarkably homogenous group in terms of dorsal carapace morphology with the exception of *Ophthalmoplax*, the only Cretaceous form. However, the features of the male sternum and abdomen of *Ophthalmoplax* are remarkably congruent with those of the other members of the family.

The earliest appearance of the family is from the Cretaceous of the Western Interior of North America, *Ophthalmoplax*, and it is later known from the Paleocene of Argentina, *Proterocarcinus* (Feldmann et al., 1995). The family underwent a major radiation during the Eocene and Oligocene, embracing numerous genera and species.

Genera within the family appear to be restricted either to the Indo-Pacific basin or the Atlantic basin, and this generalization holds for most of the fossil taxa as well as the extant taxa. Of the extinct taxa, *Boschettiia*, *Falsiportunites*, *Pleolobites*, and *Rhachiosoma* are North Atlantic taxa, and *Proterocarcinus* is a South Atlantic taxon; *Ophthalmoplax* is known from what would now be considered the central Atlantic area but during the Cretaceous, would have essentially been the central and southern Atlantic. *Maeandricampus*, *Megokkos*, *Minohellenus*, and *Pororaria* are all Pacific taxa, with only *Pororaria* being restricted to the Southern Pacific. Of the extinct taxa, *Portunites* is the only taxon found in both the Atlantic and Pacific basins, and only in the northern areas, suggesting a north Polar or Tethyan dispersal route (Schweitzer, 2001). Of the extant taxa, those with an

Indo-Pacific distribution include *Echinolatus*, *Nectocarcinus*, and *Parathranites*. Those with a primarily Atlantic distribution include *Bathynectes*, *Coenophthalmus*, *Macropipus*, *Necora*, and *Raymanninus*.

Portunidae † Rafinesque, 1815

Included Subfamilies.—*Atoportuninae* † Števčić, 2005; *Caphyrinae* † Paul'son, 1875; *Carupinae* † Paul'son, 1875; *Lupocyclinae* † Paul'son, 1875; *Necronectinae* † Glaessner, 1928; *Podophthalminae* † Dana, 1851; *Portuninae* † Rafinesque, 1815; *Thalamitinae* † Paul'son, 1875.

Diagnosis.—Carapace wider than long, often markedly so; often ornamented with an arcuate epibranchial keel; anterolateral margin with 3-9 spines including outer-orbital spine; orbits usually with two fissures; orbits generally moderate in size but can be very wide, directed forward or slightly anterolaterally; fronto-orbital width ranging from about half the maximum carapace width to the entire carapace width; sternum usually wide, ovate; secondary sulcus delimits sternites 6 and 7; median transverse ridge between sternite 6 and 7 present; median line on thoracic sternites up to sternite 6; sternite 8 clearly visible in ventral view, often markedly so; male pleon with somites 3-5 fused, weak remnants of sutures may remain, pleomere 3 markedly wider than other somites, pleomere 3 with transverse keel; lobe on endite of first maxilliped present (“portunid lobe”); chelipeds longer than other pereopods; chela often with keels but may be smooth; fifth pereopod with paddle-like dactyls and usually with ovate propodi; male first gonopod with or without subterminal spines.

Remarks.—Portunidae as herein defined is a well-constrained, homogeneous group. Numerous cladistic analyses were run based upon a variety of characters in the course of developing the final analysis, and in all cases, Portunidae as defined herein always formed a monophyletic group. This was also true whether or not fossils were added to the analysis. Thus, we feel confident in the monophyly of Portunidae *sensu stricto*, as herein defined. In addition, the subfamilies as defined are remarkably homogeneous, whether or not fossils were included in the analysis or the diagnoses. Thus, the subfamily arrangement is supported both by cladistic and by traditional systematic methods.

Atoportuninae † Števčić, 2005

Included Genera.—*Atoportunus* Ng and Takeda, 2003; *Euronectes* †† new genus; *Laleonectes* † Manning and Chace, 1990.

Diagnosis.—Carapace ovate, wider than long, length about two-thirds maximum width, widest about two-thirds the distance posteriorly on carapace at position of last anterolateral spine, carapace surface with poorly defined regions but with some granular ornamentation; front with four to six lobes including inner orbital lobes, axially notched, front about one-quarter to one-third maximum carapace width; orbits deep or very reduced, forward-directed, with one or two fissures, fronto-orbital width about half maximum carapace width; basal article of antenna without laterodistal spine; antennal flagellum excluded from orbit hiatus;

anterolateral margin with seven to nine spines including outer-orbital spine, last spine longest, anterolateral margin longer than posterolateral margin; longitudinal groove extending anteriorly onto sternite 4 from sterno-pleonal cavity, small portion of sternite 8 visible in ventral view; male pleon with somites 3-5 fused apparently without traces of fusion, somites 2 and 3 may have transverse keels; sternal sutures 4/5, 5/6, and 7/8 incomplete, 6/7 complete; male gonopod 1 thick at base and narrowing and curving distally; apex of gonopod 2 bifid; chelipeds stout or very slender; other pereopods slender; may possess obvious stridulating ridges on pterygostomial region.

Material Examined.—*Laleonectes nipponensis* (Sakai, 1938), USNM 190730, CBM-ZC5032; *Laleonectes vocans* (A. Milne-Edwards, 1878), BM In.61206.

Discussion.—Both species of *Euronectes* new genus are known from southern Europe, from Oligocene rocks of Italy and Miocene rocks of Spain. A single fossil occurrence of *Laleonectes* has been reported from Pleistocene or sub-Recent rocks of Barbados (Collins and Morris, 1976), but it is only a chela. Species of *Atoportunus* are known from various islands within the Indo-Pacific (Ng and Takeda, 2003), and *Laleonectes* exhibits a broad modern distribution, known from the eastern Atlantic (Manning and Chace, 1990) and the western Pacific (Sakai, 1938; Crosnier and Moosa, 2002). The combination of fossil and extant occurrences suggests a distribution pattern through the Tethyan Seaway, with a modern relict Tethyan distribution.

Euronectes †† n. gen.

Type Species.—*Rakosia grumiensis* Beschin, De Angeli, and Checchi, 2001, by original designation.

Other Species.—*Euronectes vocans* (Müller, 1993), as *Rakosia*.

Diagnosis.—Carapace wider than long, length about 64 percent maximum width, widest at about 65 percent maximum carapace length; front with six blunt lobes including inner-orbital lobes, about one-quarter to one-third carapace width; orbits appearing to have been fairly shallow, with broad rim, fronto-orbital width about 60 percent maximum carapace width; anterolateral margin longer than posterolateral margin, with nine short, triangular spines including outer-orbital spine, last spine longest, more attenuated than other spines; posterolateral margin concave; posterior margin nearly straight, rimmed; protogastric regions with very weak transverse keel; epibranchial ridge strongly arched anteriorly; axial regions well-marked; pterygostomial region may have stridulating ridges.

Etymology.—The genus name is derived from the word “nectes”, meaning swimmer and a common root within the family, and “euro,” with reference to the location of both known species thus far.

Material Examined.—*Rakosia grumiensis*, holotype, MCZ 2128; paratype, MCZ 2129.

Remarks.—Both species herein referred to the new genus were originally referred to *Rakosia*. They cannot be

accommodated within that genus based upon their possession of one more anterolateral spine than *Rakosia* spp.; the number of anterolateral spines is a critical diagnostic feature within Portunidae. The position of maximum width is located further posteriorly, at about 60-70 percent maximum carapace width, in species of *Euronectes* than in species of *Rakosia*, in which it is at the midlength. The last anterolateral spine of the species referred to *Euronectes* is longest, and the anterolateral margin is markedly longer than the posterolateral margin. In *Rakosia*, the anterolateral and posterolateral margins are about equal in length. These features place the species referred to *Rakosia* within Carupinae, and those referred to *Euronectes* within Atoportuninae, similar to *Laleonectes*.

Rakosia vocans Müller, 1993, herein referred to *Euronectes*, differs from the type species of *Rakosia* in several important ways. It possesses nine anterolateral spines instead of eight. In addition, *R. vocans* possesses a position of maximum width nearly two-thirds the distance posteriorly on the carapace, which is different than that seen in *R. carupoides*, the type species of *Rakosia*. *Rakosia vocans* also exhibits stridulating ridges on the pterygostomial region, which are unknown from the type species of *Rakosia*. *Rakosia grumiensis* Beschin et al., 2001, known from the Oligocene of Italy, exhibits similar features to *Rakosia vocans*. We suggest here that these two species belong to a *Euronectes* with affinities with *Laleonectes*.

Euronectes differs from *Laleonectes* because species of *Laleonectes* have longer last anterolateral spines and longer anterolateral margins than species of *Euronectes*. The dorsal carapace of *Laleonectes* is more distinctly ornamented with broad swellings than that of *Euronectes*. The frontal spines in *Laleonectes* are much longer and more produced than those of *Euronectes*, which are blunt and lobate. In species of *Atoportunus*, the front is bilobed instead of having four or six lobes as in *Euronectes*, and the anterolateral margin has eight spines including the outer-orbital spine instead of nine as in *Euronectes*. Although *Rakosia* sensu stricto has eight anterolateral spines, it belongs to an entirely different subfamily than *Euronectes* and *Atoportunus*. The front of *Atoportunus* is distinctly produced into a broad lobe, not seen in any other portunids. Thus, *Euronectes* is a unique genus.

Caphyrinae † Paul'son, 1875

Included Genera.—*Caphyra* Miers, 1886; *Lissocarcinus* † Adams and White, 1848; *Mioxaiva* †† Müller, 1979.

Diagnosis.—Carapace ovate, hexagonal, or sub-circular, not much wider than long, length ranging from 80 to 90 percent maximum width, position of maximum width about half or a little more the distance posteriorly, surface generally smooth or with epibranchial ridges; orbits small for family, forward directed, with two orbital fissures, fronto-orbital width 70-80 percent maximum carapace width; front wide, with axial notch, lobate, generally with four to eight lobes or spines including inner-orbital spines or nearly entire and without notch, front occupying half maximum carapace width; anterolateral margin with four to six spines including outer-orbital spine; posterolateral margin concave;

well-developed posterolateral reentrant; posterior margin rimmed; small portion of sternite 8 visible in ventral view; male pleomere 3-5 fused with no or little evidence of sutures, somites 1-3 may have transverse keels; sternal sutures 4/5, 5/6, and 7/8 discontinuous, 6/7 continuous; basal article of antenna with laterodistal spine; chelipeds as long as or slightly longer than other pereopods; pereopod 5 may be paddle-like or claw-like; first male gonopod with subterminal spines (after Vannini and Innocenti, 2000; Davie, 2002; Poore, 2004).

Material Examined.—*Caphyra rotundifrons* (A. Milne-Edwards, 1869), USNM 112160, CBM-ZC4576; *Lissocarcinus laevis* Miers, 1886, MFM; *Lissocarcinus orbicularis* Dana, 1852, USNM 267076, 267078, RUMF-ZC-285; *Lissocarcinus polybioides* Adams and White, 1849, KPM-NH0106901; *Mioxaiva psammophila* Müller, 1993, holotype, HNHM M.86.266.

Remarks.—*Mioxaiva*, known from the Miocene of Hungary, is represented only by a fragmental specimen, preserving the anterior half of the dorsal carapace. The small, forward directed spines; three, tiny frontal spines; and smooth dorsal carapace suggest an affinity with some species of *Lissocarcinus* (see illustrations in Poore, 2004). Indeed, the fragmentary specimen agrees well with many of the diagnostic characters of the family, including an ovate carapace that is not much wider than long, small orbits and eyestalks, and an anterolateral margin with five or six spines. *Mioxaiva* differs from other members of the subfamily in having an axial frontal spine; however, note that the front in extant members is variable and ranges from spined to entire. Thus, we place *Mioxaiva* within Caphyrinae until more complete specimens are collected.

Müller (1984) referred the Miocene *Thia szoeraenyia* Müller, 1974, to *Lissocarcinus*, on the advice of L. B. Holthuis (Müller, 1984, p. 86), based upon its subpentagonal, smooth carapace, small orbits, and lobate anterolateral margins. The specimens of *L. szoeraenyia* appear to be somewhat more inflated than extant *Lissocarcinus* and probably also somewhat narrower with respect to the carapace length. However, these are probably species-level differences, and we concur with the referral to *Lissocarcinus*.

Extant members of the subfamily are known from the Indo-Pacific (Davie, 2002). The occurrence of fossil species from the Miocene of Hungary, a Tethyan area, suggests that the subfamily dispersed from that area directly into its current range.

Carupinae † Paul'son, 1875

Included Genera.—*Carupa* † Dana, 1851; *Neptocarcinus* †† Lörenthey, 1898 (questionably referred); *Rakosia* †† Müller, 1984; *Richerellus* Crosnier, 2003.

Diagnosis.—Carapace transversely ovate, generally smooth, wider than long, length about 70-75 percent maximum width, position of maximum width about half the distance posteriorly on carapace; front lobate instead of with spines, with four to six lobes including inner orbital lobes, occupying about 30-35 percent maximum carapace width; orbits forward directed, with two orbital fissures, fronto-orbital

width occupying about 65-70 percent maximum carapace width; anterolateral margins with four to seven spines including outer-orbital spines; posterolateral reentrants large; basal antennal article much longer than wide, without laterodistal spine; antennal flagellum within orbit; chelipeds longer than other pereopods and stouter, chelae smooth or with weak keels; sternite 8 visible in ventral view, sternal sutures 4/5, 5/6, and 7/8 discontinuous, 6/7 continuous; male pleomeres 2-5 (*Carupa*) or 3-5 (*Richerellus*) fused, fusion may be incomplete, sutures not evident, at least somite 3 with transverse keel; pereopod five with ovate or obovate propodi and dactyl; first male gonopod stout.

Material Examined.—*Carupa tenuipes* Dana, 1851, USNM 143694, CBM-ZC4155, MFM; *Neptocarcinus millenaris* Lórenthey, 1898, MCZ 2300, 2380, 2351.

Remarks.—Crosnier (2003) recognized the affinities between *Carupa* and *Richerellus* and the necessity of reevaluating Carupinae as it was defined at that time. The results of our analysis support his observations, placing *Carupa* and *Richerellus* into a monophyletic grouping.

The fossil record for the subfamily is not extensive. Hu and Tao (1996) illustrated three specimens of *Carupa laeviuscula* Heller, 1862, of Pleistocene age from Taiwan (pl. 27, figs. 4, 13, 14). However, these specimens have dorsal ridges on the dorsal carapace and keeled male abdominal somites, whereas the extant *Carupa tenuipes* lacks both characters. Thus, it is possible that the specimens referred to *Carupa* are actually members of another genus, probably *Charybdis*, a genus for which Hu and Tao (1996) also illustrated numerous species. Subsequently, Hu and Tao (2000) reported *Carupa tenuipes* from the late Miocene of Taiwan and *C. laeviuscula* from the Pleistocene of Taiwan. *Carupa laeviuscula* was synonymised with *Carupa tenuipes* (Crosnier, 1962; Takeda, 1993; Davie, 2002); therefore, the stratigraphic range of *C. tenuipes* extends into the late Miocene. The middle Miocene specimen questionably referred to *Carupa* cf. *C. tenuipes* by Müller (1984) is quite fragmental. Thus, the confirmed fossil record for *Carupa* extends into the late Miocene.

Müller (1984) erected the genus *Rakosia* to accommodate a Miocene portunid fossil from Hungary. The type species of *Rakosia*, *R. carupoides*, is characterized by possession of a smooth, transversely ovate carapace that is about 70 percent as wide as long; a front with broad lobes that occupies about 40 percent the maximum carapace width; orbits with at least one closed fissure; a fronto-orbital width occupying 70 percent the maximum carapace width; eight anterolateral spines including the outer-orbital spine; and a smooth outer surface of the palm of chelipeds. These features are diagnostic of Portunidae and Carupinae, and the genus cannot be accommodated in any other subfamily based upon these characteristics. The only feature that is different in *Rakosia* from extant members of Carupinae is that it possesses eight anterolateral spines, one more than the maximum seen in extant members. However, note that in extant genera there is a range in number of anterolateral spines from four to seven, so the number itself is apparently not diagnostic at the subfamily level. Thus, we place *Rakosia* within Carupinae. Subsequent to Müller (1984),

several other species have been referred to *Rakosia*, but some are herein removed from the genus, discussed above. *Rakosia rectifrons* Müller, 1996, is rather fragmental but seems to retain the diagnostic features of the genus.

The extinct Eocene genus *Neptocarcinus* has been problematic since it was first named. Lórenthey (1898) originally placed the genus within Cancrinae, and later Lórenthey and Beurlen (1929) considered it to be allied with Xanthidae sensu lato, probably based upon its transversely ovate shape, lobate front, and reduced number of anterolateral spines (apparently four). Müller and Collins (1991) considered it as a member of Portunidae sensu lato, probably allied with Carupinae as then defined and the extinct *Rakosia* Müller, 1984. Based upon the features of *Neptocarcinus* noted above, it seems most prudent at this time to refer it to Carupinae as defined herein. However, more complete specimens will be necessary to confirm this placement.

Like other subfamilies within Portunidae, Carupinae is known largely from the Indo-Pacific in today's oceans (Davie, 2002), and the fossil record seems to be restricted to the Tethys.

Necronectinae † Glaessner, 1928

Included Genera.—*Scylla* † de Haan, 1833; *Sanquerus* Manning, 1989; *Necronectes* †† A. Milne-Edwards, 1881.

Diagnosis.—Carapace ovate; front with six spines including inner orbital spines; fronto-orbital width about 40-50 percent maximum carapace width; anterolateral margins with 8 or 9 spines including outer-orbital spine; regions poorly marked, carapace in general unornamented and relatively smooth, posterolateral and posterior margins rimmed; very small portion of sternite 8 visible in ventral view, sternum in general narrow for family, sternite 4 with axial groove extending anteriorly from sterno-pleonal cavity; male pleon triangular overall, weak remnants of sutures between pleomeres 3/4 and 4/5, transverse keels on somites 2 and 3 generally with well developed transverse keels, somites 4 and 5 with well or poorly developed transverse keels or swellings; basal antennal article with laterodistal spines; chelae stout, may lack keels; fingers with molariform teeth along occlusal surface; meri of fifth pereopods much shorter than propodi; dactyls and propodi of fifth pereopods ovate to obovate in shape.

Etymology.—Rathbun (1919) created a new family Gatuniidae for a single genus *Gatunia* Rathbun, 1919. Glaessner (1928) showed that *Gatunia* was a synonym of *Necronectes* and replaced Gatuniidae with Necronectidae Glaessner, 1928. Necronectidae is an available name under Article 40.2 of ICZN (1999). Therefore, we treat Necronectinae as the subfamily-level group including *Scylla*, *Sanquerus*, and *Necronectes* (type genus).

Material Examined.—*Scylla serrata* (Forskål, 1775), USNM 112335; *Scylla costata* Rathbun, 1919, USNM 527057; *Scylla olivacea* (Herbst, 1794), RUMF-ZC-521; *Scylla sindensis* (Stoliczka, 1871), casts of syntypes which are deposited in India, BM In. 60588 and 60589; *Scylla ozawai* Glaessner, 1933, holotype BM I.3469; *Necronectes*

proavita (Rathbun, 1918), holotype USNM 324289; *Necronectes drydeni* Rathbun, 1935, holotype USNM 109066; *Necronectes collinsi* Schweitzer et al., 2006, holotype USNM 527050; *Necronectes schafferi* Glaessner, 1928, BM In. 28049-51; *Necronectes summus* Collins and Donovan, 1995, holotype BMNH Pal. PI IC2, paratype BMNH Pal. PI IC3; *Sanquerus validus* (Herklots, 1851), RMNH D 21173.

Remarks.—Necronectinae has a well-verified, extensive fossil record. The fossil record of *Necronectes* and *Scylla* has each been recently summarized (Schweitzer et al., 2006). To the species list of *Necronectes* provided by Schweitzer et al. (2006) must only be added *N. batalleri* Vía, 1941, which, based upon the description and illustrations, appears to belong within the genus. Type material of that species has not been examined, however. *Scylla michelini* has been problematic and has been transferred between *Necronectes* and *Scylla*. Herein, we place it within *Scylla* based upon its large, smooth chelae (Schweitzer et al., 2006). Hu and Tao (1996) erected the species *S. marianae* for a fragmental specimen from the Plio-Pleistocene of Guam. It appears to possess the features of the genus, including the conformation of the front and anterolateral margins; thus, we retain it within the genus.

Neptunus sindensis was named by Stoliczka (1871) for well-preserved specimens from India. Examination of the illustrations of the specimen clearly indicate that it belongs to Necronectinae, based upon its possession of a carapace that is not much broader than long; six frontal spines; a rimmed posterior margin; a triangular male pleon with clear fusion of somites 3-5; a small portion of sternite 8 visible and a narrow sternum overall for the family; and stout chelae with molariform teeth. Glaessner (1933) placed the species within *Scylla*. Examination of specimens referred to the species by Glaessner, which are deposited in the Natural History Museum in London, indicate that it possesses nine anterolateral spines including the outer-orbital spines; thus, we concur with Glaessner's placement herein. Species of *Scylla* have previously been reported from the Miocene of India (Das Gupta, 1925) as well as other Indo-Pacific localities (Schweitzer et al., 2006); thus, this seems the best placement for *N. sindensis*. Species of *Sanquerus* also possess nine anterolateral spines; however, those spines are of a smaller and finer nature than those of *N. sindensis* and species of *Scylla*. In addition, *Sanquerus* is currently known only from one species from a rather small range of the West African coast. It seems most prudent at this time to refer *N. sindensis* to *Scylla* based upon these multiple factors.

The distribution of the fossil and extant taxa strongly suggests a Tethyan distribution during the Paleogene, with the modern occurrences in the Atlantic (Manning and Chace, 1990) and Indo-Pacific (Davie, 2002) as a relict of that distributional pathway.

Lupocyclusinae † Paul'son, 1875

Included Genera.—*Lupocyclus* † Adams and White, 1848; *Carupella* Lenz, 1914.

Diagnosis.—Carapace ovate, somewhat wider than long, length about 80 percent maximum width; carapace orna-

mented with ridges and sometimes with large, spherical swellings; front protruding anteriorly, with four to six spines or lobes including inner orbital; orbits directed forward, with two fissures, fronto-orbital width about 70-75 percent maximum carapace width; anterolateral margins tightly arched to nearly parallel to axis, usually bearing nine spines that may alternate in size, including the outer-orbital spine; anterolateral margins longer than posterolateral margins; posterolateral reentrant large; large portion of sternite 8 visible, slightly overlapping the third somite of the pleon in males; male pleon with somites 3-5 fused, somites 2 and 3 with transverse keels; basal antennal article simple; chelipeds slender, elongate, but shorter than other pereopods; second to fourth pereopods slender, elongate; meri of fifth pereopod about equal to propodi with postero-distal spine; fifth pereopod with oblongate dactyl.

Material Examined.—*Lupocyclus tugelae* Barnard, 1950, CBM-ZC2847, USNM 210826; *Lupocyclus philippinensis* Semper, 1880, CBM-ZC2956; *Lupocyclus rotundatus* Adams and White, 1849, CBM-ZC5844; *Lupocyclus karasawai* Collins et al., 2003 (now referred to *Saratunus*), holotype BM IC242.

Remarks.—Collins et al. (2003) named *Lupocyclus karasawai* for specimens recovered from the Pleistocene of Sarawak. Those specimens are referable to *Saratunus* Collins et al., 2003, based upon their T-shaped front, broad orbit with central orbital fissure, six anterolateral spines, and identical dorsal carapace ornamentation. The specimens referred to *Lupocyclus* appear to be more eroded specimens, with some layers of cuticle retained, whereas the holotype of *Saratunus longiorbis* retains more cuticle and is more complete. The specimens referred to *L. karasawai* have more slender anterolateral spines than those of *S. longiorbis*, and the anterolateral spines of *S. longiorbis* curve anteriorly whereas those of *L. karasawai* are directed laterally. Thus, *L. karasawai* is referable to *Saratunus*, resulting in two species in that genus. The subfamilial placement of *Saratunus* has been discussed (Schweitzer et al., 2006).

Lupocyclus tuberculatus Karasawa, 1993, is known from the early Pliocene of Japan. It possesses a nodose carapace, four anterolateral swellings, a fronto-orbital width between 70 and 80 percent the maximum width of the carapace, and the length is about 80 percent the width, a little more than in other Lupocyclusinae. It differs from other Lupocyclusinae in its possession of five anterolateral spines, apparently without interspersed smaller spines, and an anterolateral margin that is shorter than the posterolateral margin. It is also notable that the Japanese fossil species is very tiny in size. However, the prominent dorsal carapace swellings suggest that *Lupocyclus* is a good placement for the fossil species at this time. Such large swellings are not common in Portunidae.

Lupocyclusinae appears to be a largely Indo-Pacific subfamily (Karasawa, 1993; Vannini and Innocenti, 2000), including the sole fossil species known at this time.

Podophthalminae † Dana, 1851

Included Genera.—*Podophthalmus* † Lamarck, 1801; *Psyg-mophthalmus* †† Schweitzer et al., 2006; *Euphyllax* †



Fig. 8. *Viaophthalmus zariquieyi* (Vía, 1959). Cast (KSU D193) of holotype, MGSB 26404. Scale bar equals 1 cm.

Stimpson, 1860; *Sandomingia* †† Rathbun, 1919; *Saratunus* †† Collins, Lee, and Noad, 2003; *Viaophthalmus* †† new genus.

Diagnosis.—Carapace much broader than long, widest about one-quarter to one half the distance posteriorly on carapace; front narrow to extremely narrow at base and broadening distally to form a “T-shape;” orbits extremely broad, occupying about 80 percent to nearly entire anterior margin of carapace, entire or with fissures or notches; eyestalks very long, sometimes wider than carapace; anterolateral margin with two to five spines including outer-orbital spine; carapace often with transverse ridges on protogastric and branchial regions; epistomial spine well developed, visible dorsally; “antennules not completely retractile in fossae beneath front” (Davie, 2002, p. 456); basal article of antennae short and flagellum slender and long; sternum very broad, very broad portion of sternite 8 visible in ventral view, sternal suture 7/8 terminating well before sterno-abdominal cavity, sternal sutures 4/5, 5/6, 6/7, and 7/8 discontinuous; chelipeds very long, merus, carpus, and manus with spines, manus sometimes with keels; fifth pereopod with paddle-like dactylus and postero-distal spines of meri (modified after Ng, 1998; Apel and Spiridonov, 1998; Davie, 2002; Schweitzer et al., 2006).

Material Examined.—*Euphylax domingensis* (Rathbun, 1919), MNHNCu-P844, P1822; *Euphylax dovii* Stimpson, 1860, USNM 85535; *Euphylax fortispinosus* Collins et al., 2001, holotype, BM IC117; *Podophthalmus vigil* (Weber, 1795), RUMF-ZC-281, USNM 112121; *Podophthalmus fusiformis* Morris and Collins, 1991, holotype BM In. 62066, BM IC213; *Psygmophthalmus lares* Schweitzer et al., 2006, holotype USNM 527076; *Saratunus longiorbis* Collins et al., 2003, holotype BM IC246.

Remarks.—The fossil record for the subfamily has been recently summarized and exhibits a Central American, Caribbean, and Indo-Pacific distribution (Schweitzer, Scott-Smith et al., 2002; Schweitzer et al., 2006). Hu and Tao (1985) described the new species, *Podophthalmus taiwanicus*, from the middle Miocene of Taiwan. This species has

three short anterolateral spines including the outer-orbital spine, but the details of the fronto-orbital characters are unknown. Therefore, more complete specimens will be necessary to confirm this placement.

Viaophthalmus n. gen.

Fig. 8

Type and Sole Species.—*Ommatocarcinus zariquieyi* Vía, 1959.

Diagnosis.—Carapace not much wider than long; front triangular, orbits extremely elongate, extending beyond lateral margins of carapace into long, stout, outer-orbital spine; orbit with thickened rim, rim flared outward distally; lateral margins converging posteriorly; posterolateral reentrants moderately sized; protogastric regions with sharp, transverse keel extending continuously across both regions as well as mesogastric region, protogastric regions and anterior-most mesogastric region united into ovate field; mesogastric region with longitudinal keel between protogastric and epibranchial keels; epibranchial keel arcing forward distally and then arcing posteriorly to become nearly straight as it crosses the axis; cardiac region with sharp transverse keel; male pleomeres 3-5 fused, sutures weakly or not visible; sternum ovate, moderately wide, sternite 8 clearly visible in ventral view.

Etymology.—The genus name is a contraction of *Via*, honoring Luis Vía, a renowned decapod paleontologist and the person who originally named the species, and the Greek word “ophthalmos,” meaning eye and a common stem in the Brachyura.

Material Examined.—MGSB 26404, holotype.

Remarks.—Vía (1959) originally placed his new species within *Ommatocarcinus* White, 1852, based upon its extremely elongate orbits. Later, Karasawa and Kato (2003) placed it within *Euphylax*, but Schweitzer et al. (2006) excluded it from both of these genera based upon its narrow carapace, continuous carapace ridges, unusual orbital margins, and the shape of the front. Herein we place

it within a new genus, *Viaophthalmus*, in recognition of its unique characteristics.

It is not possible to assign the genus to a family and subfamily with certainty at this time. It certainly exhibits affinities with *Ommatocarcinus* within Goneplacidae MacLeay, 1838, but the extremely long orbits, elongate and laterally directed post-orbital spine, the narrow front, general shape of the carapace, and fused pleomeres 3-5 eliminate it from Goneplacidae. The shape of the orbits and the outer-orbital spine are reminiscent of *Lithophylax* of Lithophylacidae, but members of that family have all somites of the male pleon free. In addition, members of Lithophylacidae have much better developed carapace regions and lack complete, transverse ridges on the carapace. Podophthalminae possess broad orbits, narrow fronts, male pleomeres 3-5 fused, and may possess transverse keels on the dorsal carapace; it appears from the illustrations in Vía (1969, pl. 37, fig. 1b) and is clear on others (P. Artal and À. Ossó, personal communication) that part of sternite 8 is visible in ventral view. Thus, we place *Viaophthalmus* within that subfamily at this time. We note that *Viaophthalmus* displays some significant differences with the other podophthalminae, including a carapace that is about as long as wide, a lack of anterolateral spines except the long outer-orbital spine, and three complete, transverse keels. However, until more material of *Viaophthalmus* is examined, this placement is considered the best course.

Portuninae † Rafinesque, 1815

Included Genera.—*Portunus* (*Achelous*) † de Haan, 1833; *Portunus* (*Cycloachelous*) Ward, 1942; *Portunus* (*Lupocycloporus*) Alcock, 1899; *Portunus* (*Monomia*) Gistel, 1848; *Portunus* (*Portunus*) † Weber, 1795; *Portunus* (*Xiphonectes*) A. Milne-Edwards, 1873; *Acanthoportunus* †† Schweitzer and Feldmann, 2002; *Arenaeus* † Dana, 1851; *Callinectes* † Stimpson, 1860; *Colneptunus* †† Lörenthey in Lörenthey and Beurlen, 1929; *Cronius* † Stimpson, 1860; *Lupella* Rathbun, 1897; *Pseudoachelous* †† Portell and Collins, 2005.

Diagnosis.—Carapace markedly wider than long, length ranging from about 55 to 75 percent maximum carapace width, widest about 60 percent the distance posteriorly at position of last anterolateral spine, usually with arcuate epibranchial keel; front with six spines including inner orbital spines, front about one-quarter maximum carapace width but can range higher or lower (15-30 percent); orbits forward-directed, fronto-orbital width about half maximum carapace width but can range higher or lower (35-60 percent); epistomial spine usually well developed, visible dorsally; basal article of antenna with laterodistal lobe or spine; antennal flagellum within the orbit; anterolateral margins generally with 6-9 spines including outer-orbital spine, last spine usually notably longer or larger than other spines; male pleomeres 3-5 fused, sometimes with weak remnants of sutures, somites 2 and 3 with transverse keels; lateral margins of male pleon can be markedly concave so as to be nearly T-shaped; large portion of sternite 8 visible in males, sternal sutures 4/5, 5/6, 6/7, and 7/8 discontinuous or with 6/7 complete; cheliped markedly longer than other

pereiopods, chelae generally with marked keels on outer surface; propodi and dactyli of fifth pereiopod ovate; male first gonopod lacking subterminal spines.

Material Examined.—*Arenaeus cribrarius* (Lamarck, 1818), USNM 72191; *Cronius ruber* (Lamarck, 1818), USNM 76854; *Lupella forceps* (Fabricius, 1793), USNM 1072266; *Portunus gallicus* (A. Milne-Edwards in Bouillé, 1873), BM I.13745; *Portunus gibbesii* (Stimpson, 1859), BM In. 61204-05; *Portunus granulatus* (A. Milne-Edwards, 1860), BM In. 28042, 28043, 28048; *Portunus granulatus* (H. Milne Edwards, 1834), MFM; *Portunus haani* (Stimpson, 1858), MFM; *Portunus hastoides* Fabricius, 1798, MFM; *Portunus oblongus* Rathbun, 1920, BM In. 59980; *Portunus obvallatus* Morris and Collins, 1991, holotype BM In. 61947; *Portunus pelagicus* (Linnaeus, 1758), MFM; *Portunus sanguinolentus* (Herbst, 1783), USNM 243950, MFM; *Portunus withersi* (Glaessner, 1933), holotype BM In. 24479, In. 36049; *Portunus woodwardi* Morris and Collins, 1991, BM In. 61923; *Portunus wynneanus* (Stoliczka, 1871), cast of syntype BM In. 60596; *Callinectes jamaicensis* Withers, 1924, holotype BM In. 23016; *Callinectes sapidus*, KSU collection.

Remarks.—*Acanthoportunus* was originally placed within Psammocarcininae based upon its extremely long, ornamented last anterolateral spine (Schweitzer and Feldmann, 2002). It was favorably compared with *Colneptunus* at that time, based upon numerous dorsal carapace similarities. Herein we place *Acanthoportunus* within Portuninae, based upon its possession of eight anterolateral spines; a much wider than long carapace; two orbital fissures; and an arcuate epibranchial keel. *Acanthoportunus* differs from other members of the subfamily, like *Colneptunus*, in possessing tubercles on the dorsal carapace. Otherwise, both genera are quite similar in dorsal carapace conformation to other members of the subfamily and are placed within it with confidence. Both genera are known from Eocene occurrences, *Acanthoportunus* on the west coast of North America (Schweitzer and Feldmann, 2002) and *Colneptunus* in western and central Europe (Glaessner, 1969).

Examination of ten extinct species referred to *Portunus* housed in the Natural History Museum, London, as well as examination of illustrations and descriptions of living and extinct species of *Portunus* suggests that there is broad variation within the genus as currently construed. Neontologists sometimes use a subgeneric scheme to further classify the members of *Portunus*, but that scheme has not been applied to fossil species. Evaluation of all of the fossil species of *Portunus* is beyond the scope of this paper; suffice it that a revision of all of the species, at least the extinct ones, currently referred to the genus seems to be warranted.

During our systematic survey of fossil portunoids, we have discovered two fossil species of *Portunus*, both of which were a junior secondary homonym of an extant species of *Portunus*. Förster (1979) moved *Neptunus granulatus* A. Milne-Edwards, 1860, to *Portunus*. *Lupea granulata* H. Milne Edwards, 1834, was removed to *Portunus* by Rathbun (1906). *Lupea* H. Milne Edwards, 1834, was an erroneous spelling of *Lupa* Leach, 1814, and

Lupa is a junior objective synonym of *Portunus* (ICZN Opinion 394). *Portunus granulatus* (A. Milne-Edwards, 1860) was preoccupied by *Portunus granulatus* (H. Milne Edwards, 1834). Therefore, the new replacement name *Portunus alphonsei*, for the late A. Milne-Edwards, is here proposed for *P. granulatus* (A. Milne-Edwards, 1860). Allasinaz (1987) moved *Neptunus convexus* Ristori, 1889, to *Portunus* because *Neptunus* de Haan, 1833, is considered a junior objective synonym of *Portunus* (ICZN Opinion 394). *Portunus convexus* (Ristori, 1889) was preoccupied by *Portunus (Pontus) convexus* de Haan, 1833; thus, we herein provide the new substitute name *Portunus ristorii*, for the late G. Ristori, to replace *Portunus convexus* (Ristori, 1889).

The fossil record of *Callinectes* is neither robust nor well confirmed. The oldest reported occurrence of the genus is from the Eocene of Jamaica; however, that specimen is only a broken manus. It can be confirmed as a member of Portunidae, but not as a member of *Callinectes*. The Oligocene *C. alabamensis* Rathbun, 1935, and *C. reticulatus* Rathbun, 1918, are known only from claw fragments showing keels on the outer surface of the manus (Rathbun, 1918; 1935). The Miocene occurrences of *C. declivis* Rathbun, 1918, and *C. sapidus* Rathbun, 1896, are based only upon fingers (Rathbun, 1919; 1935). Thus, the fossil occurrences of *Callinectes* are almost exclusively from claw fragments. The occurrence of *Cronius* in Neogene rocks of Fiji is based on a fragment of manus only (Rathbun, 1945). *Pseudoachelous* is better known, from a partial dorsal carapace from Miocene rocks of the Caribbean (Portell and Collins, 2004).

Portuninae is a cosmopolitan subfamily in tropical and warm temperate waters. It is well-known from the eastern and western Atlantic (Rathbun, 1930; Manning and Holthuis, 1981; Williams, 1984) and the Indo-Pacific oceans (Davie, 2002). The fossil record is similarly widespread, with occurrences on nearly every continent.

Thalamitinae † Paul'son, 1875

Included Genera.—*Thalamita* † Latreille, 1829; *Charybdis* † de Haan, 1833; *Eocharybdis* †† Beschin et al., 2002; *Gonioinfradens* Leene, 1938; *Thalamitoides* A. Milne-Edwards, 1869.

Diagnosis.—Carapace wider than long; hexagonal in shape; front with 6 to 8 spines or lobes including inner orbital or rarely four truncated lobes (*Thalamita*); orbits generally broadly spaced, often positioned at the outer-most angles of the anterior margin of the carapace, orbits with two fissures, fronto-orbital width can range from about half maximum carapace width (some *Charybdis*) to nearly entire width (*Thalamitoides*); anterolateral margin with three to seven spines including outer-orbital spines, margin ranging from convex forward to nearly parallel to directed almost posterolaterally; posterolateral reentrant large; dorsal carapace often ornamented with transverse ridges on proto-gastric, hepatic, and epibranchial regions; basal article of antenna very wide, usually filling orbital hiatus, with laterodistal expansion; antennal peduncle and flagellum usually excluded from orbit; male sternum with crenate margins, lending overall unique sternum shape among Portunidae, shallow axial groove extending anteriorly from

sterno-pleonal cavity onto sternite 4; male pleon with somites 3-5 fused, sometimes weak remnants of sutures visible, somite 2 with transverse keel, sometimes somites 1 and 3 with transverse keels; cheliped longer than other pereiopods; fifth pereiopods with paddle-like propodi and dactyli, carpus with small distal spine; merus with posterodistal spine; male gonopod 1 with subterminal spines.

Material Examined.—*Thalamitoides tridens* A. Milne-Edwards, 1869, USNM 111813, RMNH D 483; *Thalamita crenata* Rüppell, 1830, USNM acc. number 99/798, MFM; *T. fragilis* Müller, 1979, HNHM M.86.497; *Thalamita sima* H. Milne Edwards, 1834, MFM; *Charybdis arabicus* (Woodward, 1905), BM I.14990; *Charybdis feriata bruneiensis* Morris and Collins, 1991, holotype BM In. 59015, paratype BM In. 59012; *Charybdis hellerii* (A. Milne-Edwards, 1867), USNM 93091; *Charybdis japonica* (A. Milne-Edwards, 1861), MFM; *Charybdis mathiasi* Müller, 1984, HNHM M.86.498; *Charybdis miles* de Haan, 1835, MFM; *Charybdis sinhaleya* Deraniyagala, 1958, holotype BM In.59305, paratype BM In.59318; *Eocharybdis cristata* Beschin et al., 2002, holotype MCZ 2275; *Gonioinfradens paucidentata* (A. Milne-Edwards, 1861), SMF 24384.

Remarks.—Many of the species of *Charybdis* from the fossil record are Indo-Pacific and Miocene or younger. *Charybdis gigantea* Hu and Tao, 1996; *C. minuta* Hu and Tao, 1996; *C. monsoonis* Hu and Tao, 1985; *C. kilmeri* Hu, 1984; *C. leei* Hu and Tao, 1996; *C. obtusa* Hu and Tao, 1996; and *C. preferiata* Hu and Tao, 1996, were all reported from the upper Miocene of Taiwan. All seven of these species are known from carapace material as well as chelae. Hu and Tao (1996) reported numerous other species that are also extant from the Pleistocene of Taiwan. Pleistocene and Holocene occurrences of extant species are known from Japan (Karasawa and Matsuoka, 1991; Karasawa and Tanaka, 1994; Karasawa and Kato, 1998). Rathbun (1945) named two species based upon dorsal carapaces and chelae from the Miocene of Fiji.

The only fossil species of *Charybdis* that are extralimital to the Indo-Pacific are *C. antiqua* from the Eocene of Italy and *Charybdis mathiasi* Müller, 1984, from the Miocene of Hungary. The Eocene occurrence has not been verified, because the holotype has been lost (De Angeli and Garassino, 2006b), the original description is very brief, and the original illustration is a rather odd line drawing (A. Milne-Edwards, 1860). The Miocene occurrence is certainly a member of the subfamily and a member of *Charybdis* based upon its dorsal carapace ridges, ovate shape, forward-arched anterolateral spines, and relatively narrow frontal width. Müller (1979) erected a species of *Thalamita*, *T. fragilis*. It superficially is quite similar to the species of *Charybdis* from rocks of the same age and general area, *C. mathiasi*. However, *T. fragilis* differs from *C. mathiasi* in having five anterolateral spines instead of seven as in *C. mathiasi* and in having those spines much larger than those of *C. mathiasi*. In addition, the front of *T. fragilis* appears to be more lobate, whereas that of *C. mathiasi* has lobes that are further projected into blunt spines. One of the defining features of *Thalamita* is that the orbits are very widely spaced, occupying much of the width of the carapace; this is not the case in *T. fragilis*. Thus, we place it

within *Charybdis*, in which the fronto-orbital width can range from about half to 70 percent the maximum carapace width, so that two Miocene species of *Charybdis* are known from Hungary. The presence of *Charybdis* in the Miocene of Hungary suggests a Tethyan distribution pattern in the past, with the modern Indo-Pacific distribution being a relict.

Eocharybdis was recorded from the Eocene of Italy. It is assigned to Thalamitinae based upon its broad, lobate front; anterolateral margins with five spines including the outer-orbital spines that curve anteriorly; thin ridges on the dorsal carapace that extend from anterolateral spines; and ovate carapace with concave posterolateral margins. No other portunoid family or subfamily can accommodate this combination of characters. Its presence in the Tethyan region echoes that of the fossil record for *Charybdis* and supports the notion of a relict Tethyan modern distribution for the subfamily.

Thalamita spp. have been reported from the Miocene of Taiwan (Hu and Tao, 1996); however, the specimens are fragmental and appear to lack margins. Thus, it is difficult to verify the placement of these species. Other occurrences of *Thalamita* in the fossil record are Pleistocene or sub-Recent occurrences of extant species. Thus, its fossil record is not extensive.

Portunidae Incertae sedis
Enoplonotus †† A. Milne-Edwards, 1860

Type Species.—*Enoplonotus armatus* A. Milne-Edwards, 1860, by original designation.

Material Examined.—*Enoplonotus armatus*, Verona M.1, M.2, deposited in the Museo Civico di Storia Naturale, Verona, Italy.

Remarks.—According to De Angeli and Garassino (2006b), the holotype of the type and only species of *Enoplonotus* is missing. Two specimens were illustrated by Secretan (1975) that appear to agree well with A. Milne-Edwards' illustration. The illustrations of Secretan (1975) show a crab with a much wider than long carapace; deep, arcuate branchiocardiac depressions; numerous spines on the anterolateral margins; and an extremely long, last anterolateral spine that is itself ornamented with spines. The rows of granules illustrated by A. Milne-Edwards are difficult to make out in the photographic images of Secretan (1975), although there do appear to be scattered granules on the carapace. Examination of the specimens indicates that there may indeed be a row of granules paralleling the anterolateral margin. These specimens do not show any evidence of fifth pereopods, which appear to be rather stylized in the drawing of A. Milne-Edwards (1860). It seems that based upon the spined anterolateral margin and wider than long carapace, the genus is best placed within Portunidae sensu lato, which can accommodate those features, until better preserved material is recovered. It may be similar to *Acanthoportunus*, herein referred to Portuninae.

Psammocarcinidae Beurlen, 1930††

Included Genus.—*Psammocarcinus* †† A. Milne-Edwards, 1860.

Description of Type Genus and Species (translated from French, A. Milne-Edwards, 1860).—[Beginning middle

paragraph, A. Milne-Edwards, 1860, p. 277] "... On the contrary, in *Psammocarcinus hericarti*, the last spine is not only much longer than the others, but also it presents anteriorly toward the middle part, a little secondary spine, and sometimes also one observes a second almost rudimentary spinelet. The general form of the carapace is much longer than in the Portunids. It is the genus *Platyonychus* that the fossil appears to approach the most; in effect, these Crustaceans present almost always an elongated form ranging to a very high degree toward *Platyonychus latipes* [now *Portumnus*] of our coasts. It is nevertheless not into this genus that *Portunus hericarti* should be placed; in effect, *Platyonychus* doesn't have lateral horns, and the spines which ornament the anterolateral borders are always equal among them. But that is not all; to this already very important character are added others of great value. Thus all of the portunids that we have examined up until the present have an orbital border divided into one or two lobes by more or less deep fissures. In the species at hand, the orbital margin is continuous, without any indication of division. The front of the latter advances more than in the genera *Portunus*, *Carcinus*, and *Platyonychus*. The inner sub-orbital tooth, very developed, attains the same level that the lateral teeth of the front do, and the result of this disposition is that the orbits present a considerable depth. The posterolateral borders of the carapace, in place of being concave in back to receive the base of the fifth pair of legs, are straight, and unite squarely with the posterior margin. Up until now we don't know any portunids with the cephalothoracic shield terminating in this manner; and if I had not observed a large number of articles of the legs disposed for swimming, I would have tended to attach *Portunus hericarti* to the genus *Pirimela*, of the family of the Cancériens. In effect, *Pirimela denticulata*, by the general disposition of the carapace, is attached to our fossil. The sternal plastron resembles a little the form of that which is ordinarily seen in *Neptunus* and in *Achelous*, that is to say the segment corresponding to the insertion of the anterior legs is very large, and cut squarely in front. The median suture does not occupy the two last segments of the plastron, like in all of the Carciniens. The endostome is deprived of crests as in the *Platyoniques* and in some *Portuniens* ..." [ending near end of p. 278]. [Species description following begins at bottom of p. 279]:

Psammocarcinus hericarti

"This pretty little species is found in enormous quantity in certain layers of the upper sand of the "large calcareous". At Gué-a-Tresmes, near Meaux, the sand is nearly completely composed of crustacean debris, among which one finds a large number of carapaces of *Psammocarcinus*. However, these parts are not all that are found, the hands are very common. In addition, upon looking with a little care, one can find pieces of the branchiostegite, the forward-arms, the arms, numerous articles of the following legs [pereopods], fragments of the sternal plastron, intact endostomes, and even the mandibles, which among all of the parts, despite their small size, are perfectly preserved. I have therefore reconstructed the entire animal, except the abdomen and the appendages of the head region.

“The carapace, among which the length varies from some mm to nearly 3 cm, or even more, doesn't have any granulations, punctations, and depending on the state of preservation is almost always perfect. The regions without being extremely projecting are very clearly marked. The gastric region is large and divided into lobes: the anteriors, or anterolaterals, are best marked. The mesogastric region merges posteriorly with the metagastric regions or posterolateral lobes, and is prolonged in front by a raised crest, which usually possesses three small swellings. The cardiac region is clearly indicated by a deep branchio-cardiac groove. The branchial regions have some traces of being divided into three lobes, of which the posterior is comparatively large. The hepatic regions are small, but well characterized.

“The anterolateral spines are ornamented with a very finely granular marginal line, which, after having followed the internal border of the longest lateral spine, prolongs onto the posterolateral border of the carapace, up until the junction of the posterior margin; their point of reunion is marked on each side by a small swelling.

“The front, very prominent, has three spiniform teeth: the middle one is the largest; the lateral ones merge with the inner orbital angle; the latter is constituted by a small swelling in the form of a lobe, which is found at the base of the external edge.

“The external angle of the orbit is very needle-like, very projected, and forms the first and the strongest of the anterolateral spines; the second is the smallest of all; finally the two following, of intermediate size, are equal to one another, and all are directed toward the front.

“I will not repeat the disposition of the orbits or of the endostome, they have already been described in the discussion of the generic characters of the species.

“The form of the anterior legs presents a great analogy with those of the Portunes and Carcines; in general, those of the left side are weaker than those of the right. The arms [meri], short and stout, should not pass beyond the anterolateral margins of the carapace; the form is that of a triangular prism, irregular. One never finds them in place; always they are isolated, and the upper surface is incomplete, because the complementary piece [carpus], in the form of a triangle, which one notices in all of the crabs, in the pagurids, etc., where it is imperfectly sutured to the rest of the arm, is always missing, I have not found a single arm which had it preserved. Finally, the article carries, toward the middle part of the posterior border, a small spine with its tip directed toward the front.

“The front-arm has on its upper and internal border a needle-like spine which it carries under the hand. The borders of this article are finely ridged.

“The hand is, proportional to the body, very large, and it is lightly curved following its length, with the result that it can be held against the facial region. The wrist, compared to the fingers, is short and stocky. On the external surface, near the articulation with the front-arm, one observes a line of little spines which are prolonged more or less toward the front. One notices also on this face a large number of small granulations, of which some of larger size form a rudimentary crest. The wrist is flattened underneath, and conse-

quently, in place of presenting a margin, it terminates superiorly by a surface inside and outside by a crest of granulations. The internal surface is smooth. The lower border is narrow and very granular. The fingers are remarkably strong; the index, laterally compressed, is directed a little downward, and does not recurve. . . .”

Remarks.—The systematic placement of *Psammocarcinus* is enigmatic. A. Milne-Edwards (1860) originally placed the genus among the other portunid genera and specifically with the polybiines. He based this placement on his interpretation of the last pair of pereopods as adapted for swimming, based upon the flattened nature of the propodus. The dactyl, however, was missing from his specimens. He also noted a general similarity in the sternum between *Psammocarcinus* and some other portunids. A. Milne-Edwards noted that *Psammocarcinus* shared several features with *Pirimela*, including the general shape of the carapace. Subsequently, Beurlen (1930) placed *Psammocarcinus* within its own subfamily in Portunidae, based upon its rounded to moderately widened carapace and four to five anterolateral spines with the last longest and strongest (Beurlen, 1930, p. 355). Along with *Psammocarcinus*, the two genera *Enoplonotus* A. Milne-Edwards, 1860, and *Rhachiosoma* Woodward, 1871, were placed within Psammocarcininae (Beurlen, 1930). This arrangement was maintained by later authors (Glaessner, 1969; Schweitzer and Feldmann, 2002). Schweitzer and Feldmann (2002) added an additional genus, *Acanthoportunus* Schweitzer and Feldmann, 2002, to the subfamily. *Rhachiosoma*, which possesses a long last anterolateral spine, is better placed within Macropipidae, discussed above. *Enoplonotus* and *Acanthoportunus* are each placed within Portunidae based upon their wider than long carapaces and numerous anterolateral spines, discussed above. Thus, *Psammocarcinus* remains the only genus within the family, and retains only one species, discussed below.

Examination of the original description and a specimen of the type species of *Psammocarcinus*, *P. hericarti*, in the BSP, as well as photographs of material deposited in MNHN suggests that the superfamily-level placement is questionable. Several features of *Psammocarcinus* are unlike that seen in any other portunoids. For example, *Psammocarcinus* possesses three frontal spines, with the axial spine longest. The orbits of *Psammocarcinus* lack orbital fissures and are deepest axially and shallow laterally, unlike any orbits within Portunoidea. The suborbital spine in *Psammocarcinus* is extremely long and well developed, unlike any portunoids. The conformation of the regions is unlike that of many portunoids in displaying well-defined axial, protogastric, hepatic, and branchial regions. Although A. Milne-Edwards (1860) illustrated the fifth pereopods as possessing paddlelike dactyls, there is no evidence that this is the case (G. Breton, personal communication). The propodus of the fifth pereopod is flattened and ob lanceolate in shape, which may have led him to believe that the dactyl would also be ovate. However, in Pirimelidae, for example, the propodus of the fifth pereopod is flattened and ob lanceolate, and the dactyl is lanceolate, not ovate and paddle-like. Thus, his reconstruction may be erroneous.

Taxa	Age	Cret.	Pal.	Eo.	Oligo.	Mio.	Plio.	Ple.	Rec.	Taxa	Age	Cret.	Pal.	Eo.	Oligo.	Mio.	Plio.	Ple.	Rec.
Family Lithophylacidae										Portunus									
Lithophylax										? <i>P. tricarينات</i>									★
<i>L. trigeri</i>		★								Xaiva									
Family Longusorbiidae										<i>X. bachmayeri</i>									★
Longusorbis										Subfamily Polybiinae									
<i>L. cuniculosus</i>		★								Liocarcinus									
<i>L. quadratus</i>		★								<i>L. atropatanus</i>									★
<i>L. eutychius</i>				★						<i>L. kuehni</i>									★
Family Geryonidae										<i>L. lancetidactylus</i>									★
Archaeogeryon										<i>L. oroszyi</i>									★
<i>A. fuegianus</i>						★				<i>L. praearcuatus</i>									★
Archaeoplax										<i>L. rakosensis</i>									★
<i>A. signifera</i>						★				<i>L. corrugatus</i>								★	★
Chaceon										<i>L. depurator</i>								★	★
<i>C. helmstedtense</i>					★					<i>L. holsatus</i>								★	★
<i>C. peruvianus</i>						★				<i>L. marmoreus</i>								★	★
<i>C. miocenicus</i>						★				<i>L. pusillus</i>								★	★
<i>C. matsushitai</i>							★	★		Ovalipes									
Family Mathildellidae										<i>O. punctatus</i>									★
Branchioplax										<i>O. formosanus</i>									★
<i>B. ballingi</i>			★							Family Macropipidae									
<i>B. concinna</i>				★						Boschetti									
<i>B. pentagonalis</i>				★						<i>B. giampietroi</i>				★					
<i>B. sulcatus</i>				★						Falsiportunites									
<i>B. albertii</i>				★						<i>F. longispinosus</i>				★					
<i>B. ? bidentata</i>				★						Macropipus									
<i>B. washingtoniana</i>				★						<i>M. ? ovalipes</i>				★					
<i>B. carmanahensis</i>				★						<i>M. tuberculatus</i>									★
Coeloma										Maeandricampus									
<i>C. balticum</i>					★					<i>M. granuliferum</i>				★					
<i>C. granulosum</i>					★					<i>M. triangulum</i>					★				
<i>C. macoveii</i>					★					Megokkos									
<i>C. taunicum</i>					★					<i>M. jeldmanni</i>				★					
<i>C. vigil</i>					★					<i>M. macrospinosus</i>				★					
<i>C. latifrons</i>					★					<i>M. alaskensis</i>					★				
Tehuacana										<i>M. hexagonalis</i>					★				
<i>T. tehuacana</i>			★							Minohellenus				★					
Family Catoptridae										<i>M. inexpressus</i>									
Libystes										<i>M. macrocheilus</i>									
<i>L. nitidus</i>										<i>M. sexdentatus</i>									★
Family Carcineretidae										<i>M. araucanus</i>									★
Carcinereutes										<i>M. chichibuensis</i>									★
<i>C. planetarius</i>		★								<i>M. minoensis</i>									★
<i>C. woolacotti</i>		★								<i>M. quinquedentatus</i>									★
Cancrinxantho										<i>M. umemotoi</i>									★
<i>C. pyrenaicus</i>		★								Necora									
Mascaranada										<i>N. puber</i>									★
<i>M. difuntaensis</i>		★								Ophthalmoplax									
Family Carcinidae										<i>O. brasiliانا</i>		★							
Subfamily Carcininae										<i>O. comancheensis</i>		★							
Carcinus										<i>O. stephensoni</i>		★							
<i>C. minor</i>				★						<i>O. ? spinosus</i>		★							
<i>C. maenus</i>							★	★		<i>O. triambonatus</i>		★							
Cicarnus										Parathranites									
<i>C. fumiae</i>				★						<i>P. shibatai</i>									★
Miopipus										Pleolobites									
<i>M. pygmeus</i>						★				<i>P. erinaceus</i>				★					

Fig. 9. Stratigraphic occurrence of each portunoid species occurring in the fossil record. Asterisk (*) indicates species of unknown age.

Age		Cret.	Pal.	Eo.	Oligo.	Mio.	Plio.	Ple.	Rec.	Age		Cret.	Pal.	Eo.	Oligo.	Mio.	Plio.	Ple.	Rec.
Taxa	Taxa																		
Pororaria										Scylla									
<i>P. eocenica</i>										<i>S. laevis</i>									
Portufuria										<i>S. sindensis</i>									
<i>P. enigmatica</i>										<i>S. hassiaca</i>									
Portunites										<i>S. costata</i>									
<i>P. angustata</i>										<i>S. floridana</i>									
<i>P. eocenica</i>										<i>S. michelini</i>									
<i>P. incerta</i>										<i>S. ozawai</i>									
<i>P. insculpta</i>										<i>S. serrata</i>									
<i>P. kattachiensis</i>										<i>S. marianae</i>									
<i>P. nodosus</i>										Subfamily Lupocyclusinae									
<i>P. rosenfeldi</i>										Lupocyclus									
<i>P. sylviae</i>										<i>L. tuberculosus</i>									
<i>P. stintoni</i>										Subfamily Podophthalminae									
Proterocarcinus										Euphylax									
<i>P. lophos</i>										<i>E. domingensis</i>									
<i>P. corsolini</i>										<i>E. septendentatus</i>									
<i>P. latus</i>										<i>E. callinectias</i>									
<i>P. navidad</i>										<i>E. fortis</i>									
Rhachiosoma										<i>E. maculatus</i>									
<i>R. bispinosa</i>										<i>E. fortispinosus</i>									
<i>R. echinata</i>										Podophthalmus									
Family Portunidae										<i>P. fusiformis</i>									
Enoplonotus										<i>P. taiwanicus</i>									
<i>E. armatus</i>										<i>P. vigil</i>									
Subfamily Atoportuninae										Psymgophthalmus									
Laleonectes										<i>P. lares</i>									
<i>L. vocans</i>										Sandomingia									
Euronectes										<i>S. yaquiensis</i>									
<i>E. grumiensis</i>										Saratunus									
<i>E. vocans</i>										<i>S. longiorbis</i>									
Subfamily Caphyrinae										<i>S. karasawai</i>									
Lissocarcinus										Viaophthalmus									
<i>L. szoeraenyiae</i>										<i>V. zariqueyi</i>									
Mioxaiva										Subfamily Portuninae									
<i>M. psammophila</i>										Acanthoportunus									
Subfamily Carupinae										<i>A. buchanani</i>									
Carupa										Arenaeus									
<i>C. tenuipes</i>										<i>A. cribrarius</i>									
Neptocarcinus										Callinectes									
<i>N. millenarus</i>										<i>C. alabamensis</i>									
Rakosia										<i>C. jamaicensis</i>									
<i>R. carupoides</i>										<i>C. reticulatus</i>									
<i>R. rectifrons</i>										<i>C. declivis</i>									
Subfamily Necronectinae										<i>C. sapidus</i>									
Necronectes										<i>C. bellicosus</i>									
<i>N. nodosus</i>										<i>C. toxodes</i>									
<i>N. summus</i>										Colneptunus									
<i>N. vicksburgensis</i>										<i>C. hungaricus</i>									
<i>N. vidalianus</i>										<i>C. hungaricus lutetianus</i>									
<i>N. collinsi</i>										<i>C. dalloni*</i>									
<i>N. batalleri</i>										Cronius									
<i>N. drydeni</i>										<i>C. obscurus</i>									
<i>N. proavitus</i>										Portunus									
<i>N. schafferi</i>										<i>P. catalanicus</i>									
<i>N. tajinensis</i>										<i>P. kochi</i>									
<i>N. beaumonti*</i>										<i>P. arcuatus</i>									

Fig. 9. Continued.

Taxa	Age	Cret.	Pal.	Eo.	Oligo.	Mio.	Plio.	Ple.	Rec.	Taxa	Age	Cret.	Pal.	Eo.	Oligo.	Mio.	Plio.	Ple.	Rec.	
<i>P. gallicus</i>					★					<i>P. gibbesii</i>									★	★
<i>P. incertus</i>					★					<i>P. pelagicus</i>									★	★
<i>P. larteti</i>					★					<i>P. xantusii</i>									★	★
<i>P. obtusus</i>					★					Pseudoachelous										
<i>P. ristorii</i>					★					<i>P. schindleri</i>										
<i>P. suessi</i>					★															
<i>P. tenuis</i>					★					Subfamily Thalamitinae										
<i>P. vectensis</i>					★					Charybdis										
<i>P. vicentinus</i>					★					<i>C. antiqua</i>					★					
<i>P. winneanus</i>					★					<i>C. arabica</i>									★	
<i>P. yaucoensis</i>					★					<i>C. fijiensis</i>									★	
<i>P. oligocaenicus</i>					★					<i>C. fragilis</i>									★	
<i>P. monspeliensis</i>					★	★				<i>C. hoffmeisteri</i>									★	
<i>P. stenaspis</i>					★	★				<i>C. kilmeri</i>									★	
<i>P. alphonsei</i>						★				<i>C. leei</i>									★	
<i>P. atecuicitlis</i>						★				<i>C. mathiasi</i>									★	
<i>P. brouweri</i>						★				<i>C. minuta</i>									★	
<i>P. delgadoi</i>						★				<i>C. monsoonis</i>									★	
<i>P. haitensis</i>						★				<i>C. obtuse</i>									★	
<i>P. kisslingi</i>						★				<i>C. preferiata</i>									★	
<i>P. krambergeri</i>						★				<i>C. gigantica</i>									★	
<i>P. levigatus</i>						★				<i>C. miles</i>									★	★
<i>P. miocaenicus</i>						★				<i>C. pleistocenica</i>									★	
<i>P. neogenicus</i>						★				<i>C. sinhaleya</i>									★	
<i>P. oblongus</i>						★				<i>C. acuta</i>									★	★
<i>P. obvallatus</i>						★				<i>C. annulata</i>									★	★
<i>P. pirabaensis</i>						★				<i>C. bimaculata</i>									★	★
<i>P. radobojanus</i>						★				<i>C. feriata</i>									★	★
<i>P. regulensis</i>						★				<i>C. granulata</i>									★	★
<i>P. sanshianus</i>						★				<i>C. japonica</i>									★	★
<i>P. thalae</i>						★				<i>C. orientalis</i>									★	★
<i>P. tongfai</i>						★				Eocharybdis										
<i>P. viai</i>						★				<i>E. cristata</i>										
<i>P. withersi</i>						★														
<i>P. woodwardi</i>						★				<i>T. fani</i>									★	
<i>P. gabbi</i>						★	★			<i>T. truncatata</i>									★	
<i>P. hastatus</i>						★	★	★	★	<i>T. admete</i>									★	★
<i>P. sayi</i>						★	★	★	★	<i>T. crenata</i>									★	★
<i>P. spinimanus</i>						★	★	★	★	Family Psammocarcinidae										
<i>P. edwardsi</i>						★				Psammocarcinus										
										<i>P. hericarti</i>										

Fig. 9. Continued.

The features of *Psammocarcinus* are suggestive of the families Atelecyclidae Ortmann, 1893; Matutidae de Haan, 1841; and Pirimelidae Alcock, 1899, but it does not appear to belong to any of these. The orbital features of *Psammocarcinus* are unlike those of Atelecyclidae, in which the orbits are facing anterolaterally, possess orbital fissures, and comprised of numerous articles. Pirimelidae lack the long suborbital spine of *Psammocarcinus* and the shape of the carapace and regions are somewhat different. The endostome of *Psammocarcinus* differs from that of members of Matutidae. Thus, the genus appears at this time to be unique and should remain within its own family within Portunoidea.

After the genus was named, two other species were referred to it, *Psammocarcinus laevis* Noetling, 1885, and *P. multispinatus* Noetling, 1885. Guinot (1976) placed these two species within the genus *Palaeotrichia* Guinot, 1976,

which she considered to be closely related to the extant *Trichia* de Haan, 1841 (= *Zalasia* Rathbun, 1897), a member of Xanthidae sensu stricto. *Palaeotrichia*, based upon the conformation of its carapace regions, its long last anterolateral spine, presence of posterolateral spines; and trilobed front seems especially similar to members of Atelecyclidae, in which we place it here.

Quayle and Collins (1981) described *Portunites subovata* from Eocene rocks of Britain. Schweitzer and Feldmann (1999) removed that species from the genus and later (Schweitzer and Feldmann, 2000b) suggested that it may have affinities with Cheiragonidae Ortmann, 1893. Examination of the holotype (BM In.61715) suggests that it may have affinities with *Palaeotrichia*. However, the holotype of *P. subovata* is fragmental, and more complete specimens will need to be recovered to test this hypothesis and determine the affinities of that species.

DISCUSSION OF FOSSIL RECORD

The fossil record for Portunoidea is well documented, going back to 18th century records. Each family within Portunoidea has fossil representatives, although of varying degrees of antiquity (Fig 9, Appendix 5). As for Xanthoidea s.l. (Karasawa and Schweitzer, 2006), the fossil records of some of the more derived groups within Portunoidea, i.e., genera within Macropipidae and Portunidae sensu stricto, suggests that there may be a more robust fossil record for the group than is currently recognized. More field work and study of museum collections will help to resolve these so-called ghost lineages in both superfamilies.

The only families within Portunoidea having confirmed Cretaceous records thus far are Lithophylacidae, Longusorbiidae, Carcineretidae, and Macropipidae. Of these, Longusorbiidae extends into the Eocene within the Central American region, surviving the K/T extinction event(s). *Ophthalmoplax* is the only member of Macropipidae known from the Cretaceous, and the family is extant. The positions of Carcineretidae and *Ophthalmoplax* in the cladogram suggest that Geryonidae, Mathildellidae, Catoptridae, and Carcinidae must have had Cretaceous origins, but as yet there are no fossils to support this hypothesis. Paleocene records are known within Mathildellidae and Macropipidae. However, a real radiation within the superfamily occurred within the Eocene, with occurrences of Longusorbiidae, Mathildellidae, and Macropipidae, and first occurrences of Carcinidae and Portunidae s.s. The Oligocene saw a continuation of this trend, with first occurrences of Geryonidae, followed by an explosive radiation within the superfamily, especially the more derived groups, in the Miocene. By Miocene time, every extant subfamily within Portunoidea had appeared in the fossil record. Pliocene, Pleistocene, and sub-Recent occurrences contain primarily extant species, and certainly extant genera. Thus, it appears that Portunoidea in general, and especially the more derived groups, are a geologically young group. Indeed they have geologically older relatives, extending into the Eocene and even the Cretaceous, but the major radiations within the superfamily seem to have been in Miocene and younger times. Investigation into this evolutionary pattern is ongoing.

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- **Carcineretes* Withers, 1922
- **Carcineretes planetarius* Vega et al., 1997
- **Carcineretes woolacotti* Withers, 1922
- Portunidae Rafinesque, 1815
- Carcininae MacLeay, 1838
- Carcinus* Leach, 1814
- Carcinus aestuari* Nardo, 1847
- Carcinus maenas* (Linnaeus, 1758)
- Nectocarcinus* A. Milne-Edwards, 1860
- Nectocarcinus bennettiae* Takeda and Miyake, 1969
- Nectocarcinus integrifrons* (Latreille, 1825)
- Nectocarcinus tuberculatus* A. Milne-Edwards, 1860
- Portumnus* Leach, 1814
- Portumnus latipes* (Pennant, 1777)
- Xaiva* MacLeay, 1838
- Xaiva biguttata* Risso, 1816
- Caphyrinae Paul'son, 1875
- Caphyra* Guerin-Méneville, 1832
- Caphyra rotundifrons* (A. Milne-Edwards, 1869)
- Lissocarcinus* Adams and White, 1849
- Lissocarcinus laevis* Miers, 1886
- Lissocarcinus orbiculatus* Dana, 1852
- Lissocarcinus polybioides* Adams and White, 1849
- Carupinae Paul'son, 1875
- Carupa* Dana, 1851
- Carupa tenuipes* Dana, 1851
- Catoptrus* A. Milne-Edwards, 1870
- Catoptrus inaequalis* (Rathbun, 1906)
- Catoptrus nitidus* A. Milne-Edwards, 1870
- Catoptrus* sp.
- Libystes* A. Milne-Edwards, 1867
- Libystes edwardsi* Alcock, 1900
- Libystes nitidus* A. Milne-Edwards, 1867
- Libystes villosus* Rathbun, 1924
- Polybiinae Paul'son, 1875
- Bathynectes* Stimpson, 1871
- Bathynectes maravigna* (Prestandrea, 1839)
- Bathynectes superba* (Costa, 1853)
- Benthochascon* Alcock and Anderson, 1899
- Benthochascon hemingi* Alcock and Anderson, 1899
- Brusinia* Števcic, 1991
- Brusinia profunda* Moosa, 1996
- Coenophthalmus* A. Milne-Edwards, 1879
- Coenophthalmus tridentatus* A. Milne-Edwards, 1879
- **Falsiportunites* Collins and Jakobsen, 2003
- **Falsiportunites longispinosus* Collins and Jakobsen, 2003
- Liocarcinus* Stimpson, 1871
- Liocarcinus corrugatus* (Pennant, 1777)
- Liocarcinus depurator* (Linnaeus, 1758)
- Liocarcinus arcuatus* (Leach, 1814)
- Macropipus* Prestandrea, 1833
- Macropipus tuberculatus* (Roux, 1830)
- Macropipus australis* Guinot, 1961
- **Megokkos* Schweitzer and Feldmann, 2000b
- **Megokkos alaskensis* (Rathbun, 1926)
- **Megokkos hexagonalis* (Nagao, 1932)
- **Megokkos feldmanni* (Nyborg et al., 2003)
- **Megokkos macrospinus* (Schweitzer et al., 2000)
- **Minohellenus* Karasawa, 1990
- **Minohellenus chichibuensis* (Kato, 1996)
- **Minohellenus macrocheilus* Kato and Karasawa, 1994
- **Minohellenus quinquedentatus* Karasawa, 1990
- Necora* Holthuis, 1987
- Necora puber* (Linnaeus, 1767)
- Ovalipes* Rathbun, 1898
- Ovalipes iridescens* (Miers, 1886)
- Ovalipes ocellatus* (Herbst, 1799)
- Ovalipes punctatus* (de Haan, 1833)
- **Ophthalmoplax* Rathbun, 1935
- **Ophthalmoplax stephensoni* Rathbun, 1935
- **Ophthalmoplax triambonatus* Feldmann and Villamil, 2002
- Parathranites* Miers, 1886
- Parathranites hexagonum* Rathbun, 1906

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APPENDIX I

Taxa used in the analysis. Classification in this table follows the traditional classification followed previous to the revision presented herein, following Davie (2002). Selection of taxa was based upon the prevailing classification. * indicates extinct taxa.

Goneplacoidea MacLeay, 1838

Goneplacidae MacLeay, 1838

- Carcinoplax* H. Milne Edwards, 1852
- Carcinoplax longimanus* (de Haan, 1833)
- Carcinoplax vestita* (de Haan, 1835)
- Psopheticus* Wood-Mason, 1892
- Psopheticus hughi* Rathbun, 1914

Portunoidea Rafinesque, 1815

Mathildellidae Karasawa and Kato, 2003

- Mathildella* Guinot and Richer de Forges, 1981
- Mathildella serrata* (Sakai, 1974)
- Beuroisia* Guinot and Richer de Forges, 1981
- Beuroisia major* Guinot and Richer de Forges, 1981

Geryonidae Colosi, 1923

- Chaceon* Manning and Holthuis, 1989
- Chaceon erythrae* (Macpherson, 1984)
- Chaceon granulatus* (Sakai, 1978)
- Chaceon quinquedens* (Smith, 1879)

- **Coeloma* A. Milne-Edwards, 1865
- **Coeloma balticum* Schlüter, 1879
- **Coeloma vigil* A. Milne-Edwards, 1865
- **Coeloma taunicum* (von Meyer, 1862)

Geryon Kröyer, 1837

- Geryon longipes* A. Milne-Edwards, 1882

- Parathranites orientalis* (Miers, 1886)
 **Proterocarcinus* Feldmann et al., 1995
 **Proterocarcinus corsolini* Casadío et al., 2004
 **Proterocarcinus latus* (Glaessner, 1933)
 **Proterocarcinus lophos* Feldmann et al., 1995
 **Proterocarcinus navidad* Feldmann et al., 2005
Polybius Leach, 1820
 Polybius henslowii Leach, 1820
Raymanninus Ng, 2000
 Raymanninus schmitti (Rathbun, 1931)
 Podophthalminae Dana, 1851
 Euphyllax Stimpson, 1862 [1860]
 Euphyllax dovii Stimpson, 1862 [1860]
 Podophthalmus Lamarck, 1801
 Podophthalmus vigil (Weber, 1795)
 Portuninae Rafinesque, 1815
 Arenaeus Dana, 1851
 Arenaeus cribrarius (Lamarck, 1818)
 Atoportunus Ng and Takeda, 2003
 Atoportunus gustavi Ng and Takeda, 2003
 Laleonectes Manning and Chace, 1990
 Laleonectes nipponensis (Sakai, 1938)
 Callinectes Stimpson, 1860
 Callinectes sapidus Rathbun, 1896
 Lupocyclus Adams and White, 1849
 Lupocyclus philippinensis Semper, 1880
 Lupocyclus rotundatus Adams and White, 1849
 Lupocyclus tugelae Barnard, 1950
 *Necronectes A. Milne-Edwards, 1881
 *Necronectes collinsi Schweitzer et al., 2006
 *Necronectes drydeni Rathbun, 1935
 *Necronectes proavitus (Rathbun, 1919)
 *Necronectes vicksburgensis (Stenzel, 1935)
 Portunus Weber, 1795
 Portunus (Cycloachelous) granulatus (H. Milne Edwards, 1834)
 Portunus (Monomia) haani (Stimpson, 1858)
 Portunus (Portunus) pelagicus (Linnaeus, 1758)
 Portunus (Portunus) sanguinolentus (Herbst, 1783)
 Portunus (Xiphonectes) hastoides Fabricius, 1798
 Sanquerus Manning, 1989
 Sanquerus validus (Herklots, 1851)
 Scylla de Haan, 1833
 Scylla olivacea (Herbst, 1794)
 Scylla serrata (Forskål, 1775)
 Thalamininae Paul'son, 1875
 Thalamita Latreille, 1829
 Thalamita crenata Rüppell, 1830
 Thalamita sima H. Milne Edwards, 1834
 Charybdis de Haan, 1833
 Charybdis hellerii (A. Milne-Edwards, 1867)
 Charybdis japonica (A. Milne-Edwards, 1861)
 Charybdis miles de Haan, 1835
 *Psammocarcininae Beurlen, 1830
 **Psammocarcinus* A. Milne-Edwards, 1860
 **Psammocarcinus hericarti* (Desmarest, 1822)
 *Portunidae incertae sedis
 **Longusorbis* Richards, 1975
 **Longusorbis cuniculosus* Richards, 1975
 Superfamily uncertain
 *Lithophylacidae Van Straelen, 1936a
 *Lithophylax A. Milne-Edwards and Brocchi, 1879
 *Lithophylax triggeri A. Milne-Edwards and Brocchi, 1879
 [2] Front with median notch: present (0), absent (1)
 [3] Front with median lobe: absent (0), present (1)
 [4] Frontal teeth: present (0), absent (1)
 [5] Front forming T-shape: absent (0), present (1)
 [6] Lower orbital tooth: low (0), long, visible dorsally (1)
 [7] Inner orbital angle defined as lobe or tooth: present (0), absent (1)
 [8] Upper orbital fissures: present (0), absent (1)
 [9] Epibranchial spine: short (0), long (1)
 [10] Carapace dorsal ridge: absent (0), present (1)
 [11] Carapace surface: smooth (0), with tubercles (1)
 [12] Anterolateral teeth: 1-5 (0), 6-9 (1)
 [13] Orbital length: normal (0), wide (1)
 [14] Basal article of antenna reaching front: present (0), absent (1)
 [15] Basal article of antenna: fixed (0), free (1)
 [16] Laterodistal area of basal article of antenna: absent (0), spine or lobed (1)
 [17] Laterodistal expansion of basal article of antenna: absent (0), present (1)
 [18] Epistomial spine: absent (0), present (1)
 [19] Portunid lobe of maxilliped 1: absent (0), present (1)
 [20] Telson of male pleon reaching: posterior of sternite 4 (0), anterior of sternite 4 (1)
 [21] Telson of male pleon about as long as wide (0), much longer than wide (1)
 [22] Telson shape of male pleon: triangular (0), semicircular (1)
 [23] Male pleomere 6: wide (0), narrow (1)
 [24] Lateral margin of male pleomeres 4-5: nearly straight (0), sinuous or concave (1)
 [25] Male pleomere 3: narrow (0), wider than somite 4 (1), wide with rectangular corner (2)
 [26] Male pleomere 3 with keel: absent (0), present (1)
 [27] Sutures of male pleomeres: distinct (0), indistinct (1)
 [28] Sutures of male pleomeres, if present: movable (0), immovable (1)
 [29] Sternum width: distinctly narrow (0), relatively narrow (1), wide (2)
 [30] Sternum shape: narrowly ovate (0), ovate (1), rather rectangular posteriorly (2)
 [31] Sulcus delimiting sternites 3 and 4: well marked (0), indistinct (1)
 [32] Sulcus delimiting sternites 6 and 7: complete (0), interrupted medially (1)
 [33] Sulcus delimiting sternites 7 and 8: complete (0), interrupted medially (1)
 [34] Secondary sulcus delimiting sternites 6 and 7: absent (0), present (1)
 [35] Median transverse ridge between sternites 6/7: present (0), absent (1)
 [36] Median line on thoracic sternites: up to sternite 7 (0), up to sternite 6 (1)
 [37] Median groove on male thoracic sternite 3: present (0), absent (1)
 [38] Episternites 4-7: narrow (0), wide (1)
 [39] Posterolateral prolongation of male episternite 7: not marked (0), well developed (1)
 [40] Sternite 8: reduced (0), expanded laterally (1), well developed (2)
 [41] Penial groove on male sternite 8: absent (0), present (1)
 [42] Male sternite 8 visible posteriorly: indistinct (0), distinct (1)
 [43] Male sternite 8 visible ventrally: indistinct (0), distinct (1)
 [44] Cheliped fingers dark in color: present (0), absent (1)
 [45] Inner margin of cheliped merus with spines: absent (0), present (1)
 [46] Outer surface of cheliped palm: smooth (0), transversely ridged (1)
 [47] Cheliped length: longer than pereopods (0), shorter than pereopods (1)
 [48] Pereiopods 2-4 propodi: normal (0), foliaceous-like (1)
 [49] Dactyli 2-4 with corneous tip: present (0), absent (1)
 [50] Pereiopod 5 with foliaceous propodus: absent (0), present (1)
 [51] Pereiopod 5 dactyli: ensiform (0), narrow, lanceolate (1), lanceolate (2), ovate-elliptic (3)
 [52] Pereiopod 5 merus with postero-distal spine: absent (0), present (1)
 [53] Proximal insertion of pereiopod 5 propodus: absent (0), present (1)
 [54] Pereiopod 5 merus: equal or longer than propodus (0), shorter than propodus (1)
 [55] Gonopod 1 with subterminal spines: absent (0), present (1)

APPENDIX II

Character list, indicating characters and their states.

- [1] Carapace proportion: much wider than long (0), slightly wider than long or longer than wide (1)

APPENDIX IV

Unambiguous character state changes for extant and extinct taxa (Fig. 4). Bold type indicates unique character changes.

- Clade 1 42: 1->0
 Clade 2 26: 0->1, 32: 1->0, 39: 1->0
 Clade 3 8: 1->0, 20: 1->0, 47: 0->1
 Clade 4 11: 0->1, 29: 2->1, 31: 1->0, 44: 1->0
 Clade 5 **28: 0->1**
 Clade 6 7: 1->0, 33: 1->0, 39: 1->0
 Clade 7 4: 1->0, 6: 0->1, 42: 0->1
 Clade 8 24: 0->1, 44: 1->0, **49: 1->0**
 Clade 9 22: 0->1
 Clade 10 14: 1->0, 15: 1->0, 19: 0->1, 27: 0->1, 30: 1->2, 40: 0->1, **41: 0->1**
 Clade 11 8: 0->1, 47: 1->0
 Clade 12 29: 2->1, 31: 1->0, 50: 0->1, 51: 0->2, 53: 0->1
 Clade 13 10: 0->1, 13: 0->1, 24: 0->1, 37: 1->0, 43: 1->0, 46: 0->1, 48: 0->1
 Clade 14 4: 1->0, 7: 1->0, 26: 0->1
 Clade 15 3: 0->1
 Clade 16 33: 1->0
 Clade 17 29: 1->0, 30: 2->0, 38: 1->0
 Clade 18 30: 2->1
 Clade 19 46: 0->1
 Clade 20 14: 0->1, 15: 0->1, 27: 1->0
 Clade 21 26: 1->0, 38: 1->0, 48: 0->1
 Clade 22 45: 0->1
 Clade 23 20: 0->1, 37: 1->0
 Clade 24 21: 0->1, 46: 0->1
 Clade 25 10: 0->1, 16: 0->1
 Clade 26 11: 0->1, 40: 1->2
 Clade 27 14: 0->1, 27: 1->0, 51: 2->1
 Clade 28 19: 1->0, 30: 2->1
 Clade 29 33: 1->0, 45: 1->0
 Clade 30 10: 0->1
 Clade 31 1: 0->1, 46: 0->1
 Clade 32 9: 0->1
 Clade 33 27: 0->1
 Clade 34 12: 0->1, 29: 1->2, **34: 0->1, 35: 0->1, 36: 0->1**, 47: 1->0
 Clade 35 21: 0->1, 26: 1->0
 Clade 36 10: 0->1, 46: 0->1
 Clade 37 9: 0->1, 37: 1->0
 Clade 38 51: 2->3
 Clade 39 1: 0->1, 52: 0->1
 Clade 40 16: 0->1
 Clade 41 31: 0->1, **55: 0->1**
 Clade 42 **17: 0->1**, 52: 0->1
 Clade 43 1: 0->1, 6: 1->0, 29: 2->1
 Clade 44 **25: 1->2**, 40: 1->2, 48: 0->1, 54: 0->1
 Clade 45 46: 1->0
 Clade 46 10: 1->0
 Clade 47 **18: 0->1**, 37: 1->0
 Clade 48 2: 0->1, 4: 0->1, **5: 0->1**, 7: 0->1, 12: 1->0, 13: 0->1, 52: 0->1
 Clade 49 23: 0->1
 Clade 50 9: 0->1
 Clade 51 21: 0->1
 Clade 52 11: 0->1

APPENDIX V

All species of portunoideans currently known from the fossil record and those herein or previously removed to other families. Classification follows new classification proposed herein.

- Cancroidea † Latreille, 1802
Atelecyclidae † Ortman, 1893
Palaeotrichia †† Guinot, 1976
P. laevis (Noetling, 1885) (as *Psammocarcinus*)
P. multispinatus (Noetling, 1885) (as *Psammocarcinus*)
Cancridae † Latreille, 1802

- Ceronnectes* †† De Angeli and Beschin, 1998
C. boeckhi (Lörenthey, 1898) (type species)
C. granulosa (Feldmann et al., 1998) (as *Pororaria*?)

new combination

?*C. pusillinus* (Secretan in Plaziat and Secretan, 1971) (as *Portunus*)

new combination

Xanthoidea † MacLeay, 1838

Xanthidae † MacLeay, 1838 sensu stricto

Nogarolia †† Beschin, Busulini, De Angeli, and Tessier, 1994

N. mirabilis Beschin, Busulini, De Angeli, and Tessier, 1994 (type species)

Portunoidea † Rafinesque, 1815

Lithophylacidae †† Van Straelen, 1936a

Lithophylax †† A. Milne-Edwards and Brocchi, 1879

L. trigeri A. Milne-Edwards and Brocchi, 1879 (type species)

Longosorbiidae †† new family

Longosorbis †† Richards, 1975

L. cuniculosus Richards, 1975 (type species)

L. quadratus Fraaije, Vega, van Bakel, and Garibay-Romero, 2006

L. eutychius Schweitzer, Feldmann, and Karasawa, 2007

Geryonidae † Colosi, 1923

Archaeogeryon †† Colosi, 1923

A. fuegianus Colosi, 1923 (type species)

Archaeoplax †† Stimpson, 1863

A. signifera Stimpson, 1863 (type species)

Chaceon † Manning and Holthuis, 1989

C. helmstedtense †† (Bachmayer and Mundlos, 1968)

C. matsushitai †† Kato and Koizumi, 2001

C. miocenicus †† Fraaije, Hansen, and Hansen, 2005

C. peruvianus †† (d'Orbigny, 1842)

Mathildellidae † Karasawa and Kato, 2003

Branchioplax †† Rathbun, 1916

B. albertii De Angeli and Beschin, 2002

B. ballingi Remy in Remy and Tessier, 1954

B. bidentata Birshtein, 1956

B. carmanahensis (Rathbun, 1926)

B. concinna Quayle and Collins, 1981

B. pentagonalis (Yokoyama, 1911)

B. sulcatus Müller and Collins, 1991

B. washingtoniana Rathbun, 1916 (type species)

Coeloma †† A. Milne-Edwards, 1865 (only confirmed species listed)

C. balticum Schlüter, 1879

C. granulatum A. Milne-Edwards, 1880

C. latifrons Förster and Mundlos, 1982

C. macoveii Lăzărescu, 1959

C. taunicum von Meyer, 1862

C. vigil A. Milne-Edwards, 1865 (type species)

Tehuacana †† Stenzel, 1944

T. tehuacana Stenzel, 1944 (type species)

Catoptridae † Borradaile, 1902

Libystes † A. Milne-Edwards, 1867 (= *Carcinoplacoides* Kesling, 1958)

L. nitidus † A. Milne-Edwards, 1867

Carcineretidae †† Beurlen, 1930

Carcineretes †† Withers, 1922

C. woolacotti Withers, 1922 (type species)

C. planetarius Vega et al., 1997

Cancrixantho †† Van Straelen, 1934

C. pyrenaicus Van Straelen, 1934 (type species)

Mascaranada †† Vega and Feldmann, 1991

M. difuntaensis Vega and Feldmann, 1991 (type species)

Carcinidae † MacLeay, 1838

Carcininae † MacLeay, 1838

Carcinus † Leach, 1814

C. maenus † (Linnaeus, 1767)

C. minor †† Rathbun, 1926

Cicarnus †† Karasawa and Fudouji, 2000

C. fumiae Karasawa and Fudouji, 2000 (type species)

Miopipus †† Müller, 1984

M. pygmeus (Brocchi, 1883) (type species)

Portumnus † Leach, 1814 (fossil record is questionable)

?*P. tricarinatus* †† Lörenthey in Lörenthey and Beurlen, 1929

Xaiva † MacLeay, 1838

X. bachmayeri †† Müller, 1984

- Polybiinae † Paul'son, 1875
Liocarcinus † Stimpson, 1871
L. atropatanus †† (Aslanova and Dschafarova, 1975) as *Portunus*
L. corrugatus † (Pennant, 1777)
L. depurator † (Linnaeus, 1758)
L. holsatus † (Fabricius, 1798)
L. kuehni †† (Bachmayer, 1953)
L. lancetidactylus †† (Smirnov, 1929) (*in* Garassino and Novati, 2001)
L. marmoreus † (Leach, 1814)
L. oroszyi †† (Bachmayer, 1953)
L. praeaeuatus †† Müller, 1996
L. pusillus † (Leach, 1815)
L. rakensis †† (Lórenthey *in* Lórenthey and Beurlen, 1929)
Ovalipes † Rathbun, 1898
O. formosanus †† Hu and Tao, 1996
O. punctatus † (de Haan, 1833) *in* Glaessner, 1960
- Macropipidae** Stephenson and Campbell, 1960
Boschettia †† Busulini et al., 2003
B. giampietroi Busulini et al., 2003 (type species)
Falsiportunites †† Collins and Jakobsen, 2003
F. longispinosus Collins and Jakobsen, 2003 (type species)
Macropipus † Prestandrea, 1833
?M. ovalipes †† Secretan, 1975
M. tuberculatus † (Roux, 1828)
Maeandricampus †† Schweitzer and Feldmann, 2002
M. triangulum (Rathbun, 1926) (type species)
M. granuliferum (Glaessner, 1960)
Megokkos †† Schweitzer and Feldmann, 2000b
M. alaskensis (Rathbun, 1926) (type species)
M. feldmanni (Nyborg et al., 2003)
M. hexagonalis (Nagao, 1932)
M. macrospinus (Schweitzer et al., 2000)
Minohellenus †† Karasawa, 1990
M. araucanus (Philippi, 1887)
M. chichibuensis Kato, 1996
M. inexpressus Schweitzer and Feldmann, 2002
M. macrocheilus Kato and Karasawa, 1994
M. minoensis (Karasawa, 1990)
M. quinquedentatus Karasawa, 1990 (type species)
M. sexdentatus (Karasawa, 1993)
M. umemotoi (Karasawa, 1993)
Necora † Holthuis, 1987
N. puber † (Linnaeus, 1767)
Ophthalmoplax †† Rathbun, 1935
O. brasiliensis (Mauray, 1930)
O. comancheensis Rathbun, 1935
O. stephensoni Rathbun, 1935 (type species)
O.? spinosus Feldmann et al., 1999
O. triambonatus Feldmann and Villamil, 2002
Parathranites † Miers, 1886
P. shibatai †† Karasawa, 1990
Pleolobites †† Remy, 1960
P. erinaceus Remy, 1960 (type species)
Pororaria †† Glaessner, 1980
P. eocenica Glaessner, 1980 (type species)
Portufuria †† Collins, Schulz, and Jakobsen, 2005
P. enigmatica Collins et al., 2005 (type species)
Portunites †† Bell, 1858
P. angustata Collins, Moody, and Sandman, 1999
P. eocenica Lórenthey *in* Lórenthey and Beurlen, 1929
P. incerta Bell, 1858 (type species)
P. insculpta Rathbun, 1926
P. kattachiensis Karasawa, 1992
P. nodosus Schweitzer and Feldmann, 2000b
P. rosenfeldi De Angeli and Garassino, 2006a
P. stintoni Quayle, 1984
P. sylviae Quayle and Collins, 1981
Proterocarcinus †† Feldmann et al., 1995
P. latus (Glaessner, 1933)
P. lophos Feldmann et al., 1995 (type species)
P. corsolini Casadio et al., 2004
P. navidad Feldmann et al., 2005
Rhachiosoma †† Woodward, 1871
R. bispinosa Woodward, 1871 (type species)
R. echinata Woodward, 1871
- Portunidae** † Rafinesque, 1815
Enoplonotus †† A. Milne-Edwards, 1860
E. armatus A. Milne-Edwards, 1860 (type species)
- Atoportuninae † Števcíć, 2005
Laleonectes † Manning and Chace, 1990
L. vocans † (A. Milne-Edwards, 1878)
- Euronectes* †† **new genus**
E. grumiensis (Beschlin et al., 2001) (*as* *Rakosia*) **new combination** (type species)
E. vocans (Müller, 1993) (*as* *Rakosia*) **new combination**
- Caphyrinae † Paul'son, 1875
Lissocarcinus † Adams and White, 1848
L. szoeraenyiae †† (Müller, 1974)
Mioxaiva †† Müller, 1984
M. psammophila Müller, 1979 (type species)
- Carupinae † Paul'son, 1875
Carupa † Dana, 1851
C. tenuipes † Dana, 1851 = *C. laeviuscula* Heller, 1861 *in* Hu and Tao, 1996
Neptocarcinus †† Lórenthey, 1898
N. millenarus Lórenthey, 1898 (type species)
Rakosia †† Müller, 1984
R. carupoides Müller, 1984 (type species)
R. rectifrons Müller, 1996
- Necronectinae † Glaessner, 1928
Necronectes †† A. Milne-Edwards, 1881
N. batalleri (Vía, 1941)
N. beaumonti (A. Milne-Edwards, 1864)
N. collinsi Schweitzer et al., 2006
N. drydeni Rathbun, 1935
N. nodosus Schweitzer, Feldmann et al., 2002
N. proavitus (Rathbun, 1918)
N. schafferi Glaessner, 1928
N. summus Collins and Donovan, 1995
N. tajinensis Vega et al., 1999
N. vicksburgensis (Stenzel, 1935)
N. vidalianus A. Milne-Edwards, 1881 (type species)
- Scylla* † de Haan, 1833
S. costata †† Rathbun, 1919
S. floridana †† Rathbun, 1935
S. hassiaca †† Ebert, 1887
S. laevis †† Böhm, 1922
S. marianae †† Hu and Tao, 1996
S. michelini †† A. Milne-Edwards, 1860
S. ozawai †† Glaessner, 1933
S. serrata † (Forskål, 1775)
S. sindensis †† (Stoliczka, 1871)
- Lupocyclusinae † Paul'son, 1875
Lupocyclus † Adams and White, 1848
L. tuberculatus †† Karasawa, 1993
- Podophthalminae † Dana, 1851
Euphylax † Stimpson, 1862
E. callinectias †† Rathbun, 1918
E. domingensis †† (Rathbun, 1919)
E. fortis †† Rathbun, 1918
E. fortispinosus †† Collins et al., 2001
E. maculatus †† Todd and Collins, 2005
E. septendentatus †† Beurlen, 1958
- Podophthalmus* † Lamarck, 1801
P. fusiformis †† Morris and Collins, 1991
P. taiwanicus †† Hu and Tao, 1985
P. vigil † (Fabricius, 1798) (type species)
Psygmophthalmus †† Schweitzer et al., 2006
P. lares Schweitzer et al., 2006 (type species)
- Sandomingia* †† Rathbun, 1919
S. yaquiensis Rathbun, 1919 (type species)
Saratunus †† Collins, Lee, and Noad, 2003
S. longiorbis Collins, Lee and Noad, 2003 (type species)
S. karasawai (Collins, Lee and Noad, 2003) **new combination**
- Viaophthalmus* †† **new genus**
V. zariqueyi (Vía, 1959) **new combination** (type species)
- Portuninae † Rafinesque, 1815

- Acanthoportunus* †† Schweitzer and Feldmann, 2002
A. buchanani Schweitzer and Feldmann, 2002 (type species)
Arenaeus † Dana, 1851
A. cribrarius † (Lamarck, 1818) in Távora et al. (2005)
Callinectes † Stimpson, 1862
C. alabamensis †† Rathbun, 1935 (claw only)
C. bellicosus † Stimpson, 1862
C. declivis †† Rathbun, 1918 (fingers only)
C. jamaicensis †† Withers, 1924 (claw fragment only)
C. reticulatus †† Rathbun, 1918 (claws only)
C. sapidus † Rathbun, 1896
C. toxodes † Ordway, 1863
Colneptunus †† Lörenthey in Lörenthey and Beurlen, 1929 (= *Allogoneplax* Van Straelen in Dalloni, 1930; *Gonioneptunites* Vía, 1959)
C. hungaricus Lörenthey in Lörenthey and Beurlen, 1929 (type species)
C. hungaricus lutetianus Remy in Remy and Tessier, 1954
C. dalloni (Van Straelen in Dalloni, 1930)
Cronius † Stimpson, 1860
C. obscurus † Rathbun, 1945 (claw only)
Portunus † Weber, 1795 (= *Neptunus* de Haan, 1833) (Subgenera not recognized for fossil species)
P. alphonsei †† **nomen novum** (= *P. granulatus* A. Milne-Edwards, 1860)
P. arcuatus †† (A. Milne-Edwards, 1860)
P. ateuicutilis †† Vega et al., 1999
P. brouweri †† Van Straelen, 1924
P. catalanicus †† (Vía, 1941)
P. delgadoi †† Fontannes, 1884
P. edwardsi †† Sismonda, 1861
P. gabbi †† Rathbun, 1919
P. gallicus †† (A. Milne-Edwards in Bouillé, 1873)
P. gibbesii † (Stimpson, 1859)
P. haitensis †† Rathbun, 1923
P. hastatus † (Linnaeus, 1767)
P. incertus †† (A. Milne-Edwards, 1860)
P. kisslingi †† Studer, 1892
P. kochi †† (Bittner, 1893)
P. krambergeri †† Bittner, 1893
P. larteti †† (A. Milne-Edwards, 1860)
P. levigatus †† Rathbun, 1945
P. miocaenicus †† Müller, 1984
P. monspeliensis †† (A. Milne-Edwards, 1860)
P. neogenicus †† Müller, 1979
P. oblongus †† Rathbun, 1920
P. obtusus †† A. Milne-Edwards, 1860
P. obvallatus †† Morris and Collins, 1991
P. oligocaenicus †† M. Paucă, 1929 (= *P. musceli* Paucă, 1929)
P. pelagicus † (Linnaeus, 1758) in Hu and Tao, 2000
P. pirabaensis †† Martins-Neto, 2001
P. radobojanus †† (Bittner, 1884)
P. regulensis †† Van Straelen, 1939
P. ristorii †† **nomen novum** (= *P. convexus*, Ristori, 1889)
P. sanshianus †† Hu, 1984
P. spinimanus † Latreille, 1819 in Távora et al., 2002
P. stenaspis †† (Bittner, 1884)
P. suessi †† (Bittner, 1875)
P. tenuis †† Rathbun, 1919 (claws only)
P. thalae †† Macarovic, 1970
P. tongfai †† Hu, 1981
P. vectensis †† (Carter, 1898) as *Neptunus*
P. viai †† Secretan in Philippe and Secretan, 1971
P. vicentinus †† (A. Milne-Edwards, 1860)
P. wynneanus †† (Stoliczka, 1871), as *Neptunus*
P. withersi †† (Glaessner, 1933), as *Neptunus*
P. woodwardi †† Morris and Collins, 1991
P. yaucoensis †† Schweitzer et al., 2006
P. xantusii † (Stimpson, 1862)
Pseudoachelous †† Portell and Collins, 2004
P. schindleri Portell and Collins, 2004 (type species)
Thalamitinae † Paul'son, 1875
Charybdis † de Haan, 1833
C. acuta † (A. Milne-Edwards, 1869)
C. annulata † (Fabricius, 1798)
C. antiqua †† (A. Milne-Edwards, 1860)
C. arabicus †† (Woodward, 1905), as *Neptunus*
C. bimaculata † (Miers, 1886)
C. feriatius † (Linnaeus, 1758) (2 subspecies also known)
C. fragilis †† (Müller, 1979) **new combination**
C. fijiensis †† Rathbun, 1945
C. gigantica †† Hu and Tao, 1996
C. granulata † (de Haan, 1833) in Hu and Tao (2000)
C. hoffmeisteri †† Rathbun, 1945
C. japonica † (A. Milne-Edwards, 1861)
C. kilmeri †† Hu, 1984
C. leei †† Hu and Tao, 1996
C. mathiasi †† Müller, 1984
C. miles † (de Haan, 1835)
C. minuta †† Hu and Tao, 1996
C. monsoonis †† Hu and Tao, 1985
C. obtuse †† Hu and Tao, 1996
C. orientalis † Dana, 1852
C. pleistocenica †† Hu and Tao, 1979
C. preferiata †† Hu and Tao, 1996
C. sinhaleya †† Deraniyagala, 1958
Eocharybdis †† Beschin et al., 2002
E. cristata Beschin et al., 2002 (type species)
Thalamita † Latreille, 1829
T. admete † (Herbst, 1803) (type species)
T. crenata † (Latreille, 1829)
T. truncata †† Hu and Tao, 1996
T. fani †† Hu and Tao, 1996
Psammocarcinidae †† Beurlen, 1930
Psammocarcinus †† A. Milne-Edwards, 1860
P. hericarti (Desmarest, 1822) (type species)