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The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records

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Abstract. A phylogenetic analysis of 14 genera of the family Goneplacidae MacLeay (Decapoda: Brachyura: Xanthoidea) is presented based upon 45 adult morphological characters. Two most-parsimonious trees were obtained (length = 87, CI = 0.6667, RI = 0.8242, RC = 0.5495). The present analysis suggests that the Goneplacidae is divided into six subfamilies: Carinocarcinoidinae subfam. nov., Chasmocarcininae Serène, Euryplacinae Stimpson, Goneplacinae MacLeay, Mathildellinae subfam. nov., and Trogloplacinae Guinot. The Carcinoplacinae H. Milne Edwards is synonymised with the Goneplacinae. The family and six subfamilies are defined or redefined based upon the phylogenetic analysis. Within the Goneplacidae, the Trogloplacinae and Chasmocarcininae are sister groups nested as the most derived clade, followed by the Carinocarcinoidinae, Goneplacinae, Euryplacinae, and the most basal Mathildellinae. Our analysis supports recognition of the family Pseudoziidae Alcock by Ng and Liao and suggests that it is the sister to the Eriphiidae MacLeay. A reexamination of fossil records of the Goneplacidae shows that 62 species, 20 genera, and five subfamilies are recognized as fossils. A new monotypic genus *Viaplax* (Euryplacinae) is erected for *Pilumnoplax urpiniana* Via. *Chlinocephalus* Ristori and *Gillcarcinus* Collins and Morris are moved to the Goneplacidae. *Paleopsopheticus* Hu and Tao is synonymised with *Psopheticus* Wood-Mason. *Glaessneria* Takeda and Miyake is here the junior synonym of *Goneplax*. Eleven extinct genera previously assigned to the Goneplacidae are not referred to any subfamilies and are transferred out of the Goneplacidae. New combinations include: *Carcinoplax proavita* (Glaessner), *Goneplax arenicola* (Glaessner), *Euphylax zariquieri* (Via) (Portunidae Rafinesque), and *Psopheticus shujienae* (Hu and Tao).

Key words: Brachyura, Crustacea, Decapoda, Goneplacidae, phylogeny, systematics

Introduction

The family Goneplacidae MacLeay, 1838 (Brachyura: Heterotremata: Xanthoidea) has been traditionally recognized as a monophyletic group containing the five subfamilies, Carcinoplacinae H. Milne Edwards, 1852, Eucratopsinae Stimpson, 1871 (= Prionoplacinae Alcock, 1900), Goneplacinae MacLeay, 1838, Hexapodinae Miers, 1886, and Rhizopinae Stimpson, 1858 (Balss, 1957; Sakai, 1976). Guinot (1969a) suggested that the Goneplacidae *sensu* Balss (1957) was a polyphyletic group and first divided the Goneplacidae into three major groups; "Goneplacidae dérives des Xanthidae", "Goneplacidae euryplaciens (Euryplacinae)", and "Goneplacidae carcinoplaciens-gonéplaciens (Carcinoplacinae + Goneplacinae)". The subfamily Rhizopinae was removed to the Pilumnidae Samouelle, 1819 (Guinot, 1969c, 1978; Ng, 1987; Davie and Guinot, 1996), the Eucratopsinae was assigned to the Panopeidae Ortmann, 1893 (Guinot, 1978; Martin and Abele, 1986) and the Hexapodinae was treated as a family (Guinot, 1978; Manning and Holthuis, 1981). After Balss's (1957) work, two new subfamilies, Chasmocarcininae Serène, 1964 and Trogloplacinae Guinot, 1986, were added to the family. Ng and Wang (1994) moved the Pseudoziinae Alcock, 1898, from the Eriphiidae MacLeay, 1838, to the Goneplacidae. Therefore, the Goneplacidae is now represented by six subfamilies (Lemaitre *et al.*, 2001; Hsueh and Huang, 2002). Subsequently, Ng and Liao (2002) treated the Pseudoziinae as a distinct family.

Glaessner (1969) recognized 20 genera of the Goneplacidae as fossils and assigned 11 extinct genera to the family. Since then, 12 extinct genera have been added:

Caprocancer Müller and Collins, 1991a; *Corallicarcinus* Müller and Collins, 1991a; *Carinocarcinoides* Karasawa and Fudouji, 2000; *Chumaoia* Hu and Tao, 1996; *Orthakrolophos* Schweitzer and Feldmann, 2001a; *Eoplax* Müller and Collins, 1991a; *Lobogalenopsis* Müller and Collins, 1991a; *Orbitoplax* Tucker and Feldmann, 1990; *Paleopsopheticus* Hu and Tao, 1996; *Paracorallicarcinus* Tessier *et al.*, 1999; *Pregeryona* Hu and Tao, 1996; and *Stoaplax* Vega *et al.*, 2001. Karasawa and Kato (2001) moved two extinct genera, *Maingrapsus* Tessier *et al.*, 1999 and *Palaeograpsus* Bittner, 1875, from the Grapsidae MacLeay, 1838, to the Goneplacidae. They also referred *Telphusograpsus* Lőrenthey, 1902, to the family. Among these, *Carinocarcinoides* and *Stoaplax* were referred to the Carcinoplacinae (Karasawa and Fudouji, 2000; Vega *et al.*, 2001), *Orbitoplax* to the Euryplacinae (Tucker and Feldmann, 1990), and *Orthakrolophos* to the Chasmocarcininae (Schweitzer and Feldmann, 2001a). Remaining genera were not assigned to any subfamiles within the Goneplacidae because most genera were represented by only carapace specimens. Distinction between the goneplacid genera, and panopeid, pilumnid, and pseudorhombilid genera is difficult based solely upon carapace characters (Schweitzer, 2000).

The first aim of this paper is to provide an adult-morphology-based phylogenetic analysis for 14 genera within the Goneplacidae. A new classification and diagnoses of six subfamilies are presented based upon the phylogenetic analysis. The second aim of this paper is to review fossil taxa previously assigned to the family. All known fossil species and genera within the Goneplacidae are listed.

Phylogenetic analysis of family Goneplacidae

Materials and methods

Fourteen genera including one extinct genus, *Carinocarcinoides*, within the Goneplacidae, were examined. The analysis also includes *Epixanthus* Heller, 1861 (Eriphiidae MacLeay, 1838: Oziinae Dana, 1851), *Pilumnus* Leach, 1815 (Pilumnidae Samouelle, 1819: Pilumninae Samouelle, 1819), and *Pseudozius* Dana, 1851 (Pseudoziidae Alcock, 1898: Pseudoziinae Alcock, 1898) as ingroup taxa to analyze a sister-group relationship of the Goneplacidae. The analyses were based upon the examination of material deposited in the Kanagawa Prefectural Museum of Natural History, Odawara, Japan; the Mizunami Fossil Museum, Mizunami, Japan; the Natural History Museum and Institute, Chiba, Japan; and the National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A. The material examined is listed in Table 1. If material was unavailable, the descriptive information of taxa was obtained from the literature.

Table 1. Taxa included in the analysis. Abbreviations: CBM, Natural History Museum and Institute, Chiba; KPM, Kanagawa Prefectural Museum of Natural History; MFM, Mizunami Fossil Museum; NMNH, National Museum of Natural History, Smithsonian Institution; *1, Guinot (1989); *2, Guinot (1990); *3, Ikeda (1998), *4, Rathbun (1918); *5, Felder and Rabalais (1986); *6, Guinot (1986); *7, Guinot and Richer de Forges (1981).

- Family Goneplacidae MacLeay, 1838
  - Subfamily Carcinoplacinae H. Milne Edwards, 1852
    - Genus *Carcinoplax* H. Milne Edwards, 1852
      - *Carcinoplax indica* Doflein, 1904 *1
      - *Carcinoplax longimanus* (De Haan, 1833) CBM
      - *Carcinoplax vestita* (De Haan, 1835) CBM, MFM
    - Genus *Carinocarcinoides* Karasawa and Fudouji, 2000
      - *Carinocarcinoides angustus* (Karasawa, 1993) MFM
      - *Carinocarcinoides carinatus* Karasawa and Fudouji, 2000 MFM
    - Genus *Psopheticus* Wood-Mason, 1892
      - *Psopheticus hughi* Rathbun, 1914 CBM
      - *Psopheticus stridulans* Wood-Mason, 1892 *2, *3
  - Subfamily Chasmocarcininae Serène, 1964
    - Genus *Camatopsis* Alcock, 1899
      - *Camatopsis rubida* Alcock and Anderson, 1899 KPM
    - Genus *Chasmocarcinus* Rathbun, 1898
      - *Chasmocarcinus typicus* Rathbun, 1898 NMNH, *4
      - *Chasmocarcinus chacei* Felder and Rabalais, 1986 *5
  - Subfamily Euryplacinae Stimpson, 1871
    - Genus *Eucrate* De Haan, 1835
      - *Eucrate crenata* De Haan, 1835 CBM, MFM
    - Genus *Euryplax* Stimpson, 1859
      - *Euryplax nitida* Stimpson, 1859 NMNH, *4
    - Genus *Heteroplax* Stimpson, 1858
      - *Heteroplax nitida* Miers, 1879 CBM
  - Subfamily Goneplacinae MacLeay, 1838
    - Genus *Goneplax* Leach, 1814
      - *Goneplax rhomboides* (Linnaeus, 1758) NMNH
      - *Goneplax renoculis* Rathbun, 1914 CBM
    - Genus *Ommatocarcinus* White, 1852
      - *Ommatocarcinus macgillivrayi* White, 1852 CBM
  - Subfamily Trogloplacinae Guinot, 1986
    - Genus *Trogloplax* Guinot, 1986
      - *Trogloplax johliveti* Guinot, 1986 *6
  - Goneplacidae *incertae sedis*
    - Genus *Beuroisia* Guinot and Richer de Forges, 1981
      - *Beuroisia major* (Sakai, 1980) *3, *7
    - Genus *Intesius* Guinot and Richer de Forges, 1981
      - *Intesius pilosus* Guinot and Richer de Forges, 1981*3, *7
    - Genus *Mathildella* Guinot and Richer de Forges, 1981
      - *Mathildella serrata* (Sakai, 1974) CBM
- Family Pseudoziidae Alcock, 1898
  - Subfamily Pseudoziinae Alcock, 1898
    - Genus *Pseudozius* Dana, 1851
      - *Pseudozius caystrus* (Adams and White, 1852) CBM
- Family Eriphiidae MacLeay, 1838
  - Subfamily Oziinae Dana, 1851
    - Genus *Epixanthus* Heller, 1861
      - *Epixanthus frontalis* (H. Milne Edwards, 1834) MFM
- Family Pilumnidae Samouelle, 1819
  - Subfamily Pilumnidae Samouelle, 1819
    - Genus *Pilumnus* Leach, 1815
      - *Pilumnus vespertilio* (Fabricius, 1793) MFM

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

Carapace
1 Front with median notch: present (0), absent (1)
2 Front with median projection: absent (0), present (1)
3 Frontal teeth: present (0), absent (1)
4 Notch between frontal margin and supraorbital angle: distinct (0), indistinct (1)
5 Orbital width: narrow (0), moderate (1), wide (2)
6 Upper orbital fissure: present (0), absent (1)
7 Dorsal region: more or less distinct (0), indistinct (1)
8 Anterolateral teeth: >3 (0), 1–3 (1), 0 (2)

Antennule, antennae and eyes
9 Eye stalk: short (0), long (1)
10 Antennular fossae broad laterally: absent (0), present (1)
11 Basal article of antenna reaching front: present (0), absent (1)

Maxillipeds
12 Ischium longer than merus: long (0), short (1)
13 Merus of maxilliped 3: subquadrate (0), suboval (1)

Male abdomen
14 Telson about as long as wide (0), much longer than wide (1)
15 Telson: triangular (0), suboval (1)
16 Somites 4–6 much narrower than 3: absent (0), present (1)
17 Somite 3 much narrower than thoracic sternite 7: absent (0), present (1)
18 Somite 2 much narrower than 3: present (0), absent (1)
19 Somite 1 wider than 2: present (0), absent (1)
20 Somites 3–5: distinct (0), fused (1)

Thoracic sternum
21 Sternum width: narrow (0), wide (1)
22 Sulcus delimiting sternites 6 and 7: complete (0), interrupted medially (1)
23 Sulcus delimiting sternites 7 and 8: complete (0), interrupted medially (1)
24 Median sulcus on sternite 4: present (0), absent (1)
25 Anterior end of sterno-abdominal cavity: posterior on sternite 4 (0), anterior on 4 (1)
26 Prolongation of episternite 7 of male: absent (0), present (1)
27 Sternite 7 laterally covered with sternite 8: absent (0), present (1)
28 Sternite 8 with supplementary plate: absent (0), present (1)
29 Sternite 8 visible ventrally: indistinct (0), distinct (1)
30 Sternite 8 visible posteriorly: indistinct (0), distinct (1)

Gonopods
31 Gonopod 1: stout (0), slender (1)
32 Gonopod 1: sinuous (0), curved (1),
33 Gonopod 1 with hook-shaped apex: absent (0), present (1)
34 Gonopod 1 with truncated apex: absent (0), present (1)
35 Gonopod 1 strongly inflated proximally: absent (0), present (1)
36 Gonopod 2: long (0), short (1)
37 Flagellum of gonopod 2: long (0), very short (1)
38 Gonopod 2 with wing-like flagellum: absent (0), present (1)

Pereiopods
39 Fingers of pereiopod 1 elongate, much longer than palm: absent (0), present (1)
40 Fingers of pereiopod 1 dark in color: present (0), absent (1)
41 Carpus of pereiopod 1 with ventral spine: absent (0), present (1)
42 Meri of pereiopods 2–5 length: short (0), long (1)
43 Dactyli of pereiopods 2–5 with corneous tip: present (0), absent (1)
44 Dactyli of pereiopods 5: styliform (0), spatulate (1), sickle-shaped (2)
45 Dactyli of pereiopods 5 with setae: present (0), absent (1)

The subfamilial arrangement of the genera conforms to Guinot (1970 [1971]), Guinot and Richer de Forges (1981), Serène (1984), Davie and Guinot (1996), Karasawa and Fudouji (2000), and Ng and Liao (2002).

An outgroup was chosen to polarize the character states. The Goneplacidae does not have a reliable sister group. Ortmann (1893) thought that the Goneplacidae (= his Carcinoplacidae + Goneplacidae) were derived from the Eriphiidae (= his Menippidae). Guinot (1969c) and Stevcic *in* Martin and Davis (2001) mentioned that there is a close relationship between the Goneplacidae and Geryonidae Colosi, 1923 based upon adult morphology. Rice (1980)

Table 3. Input data matrix of 45 characters and 17 genera. Missing character states are shown by ?.

Taxa	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Carcinoplax	1	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0&1	0&1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0&1	1	1	1	1	0
Carinocarcinoides	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	?	1	1	1	1	0	1	?	?	?	?	?	?	?	?	?	1	1	0	1	?	?	?
Psopheticus	1	0	1	1	1&2	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1
Camatopsis	0	0	1	1	0	1	1	2	0	0	1	1	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	2	0
Chasmocarcinus	0	0	1	1	0	1	1	2	0	0	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	0	1	1	2	0
Eucrate	0	0	1	0	1&2	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	1	1	0	0
Euryplax	0	0	1	0	2	0	1	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0	1	0	1	1	0	0
Heteroplax	0	0	1	0	2	0	1	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0	1	0	1	1	0	1
Goneplax	1	0&1	1	1	2	1	1	1	1	0	1	0	0	0	0	0	0	0&1	0&1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0&1	1	1	0&1	1
Ommatocarcinus	1	1	1	1	2	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1
Trogloplax	0	0	1	1	0	1	1	2	0	0	1	1	0	0	0	0	1	?	?	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
Beurisia	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0
Intesius	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0
Mathildella	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0
Pseudozius	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Epixanthus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pilumnus	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Hypothetical Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

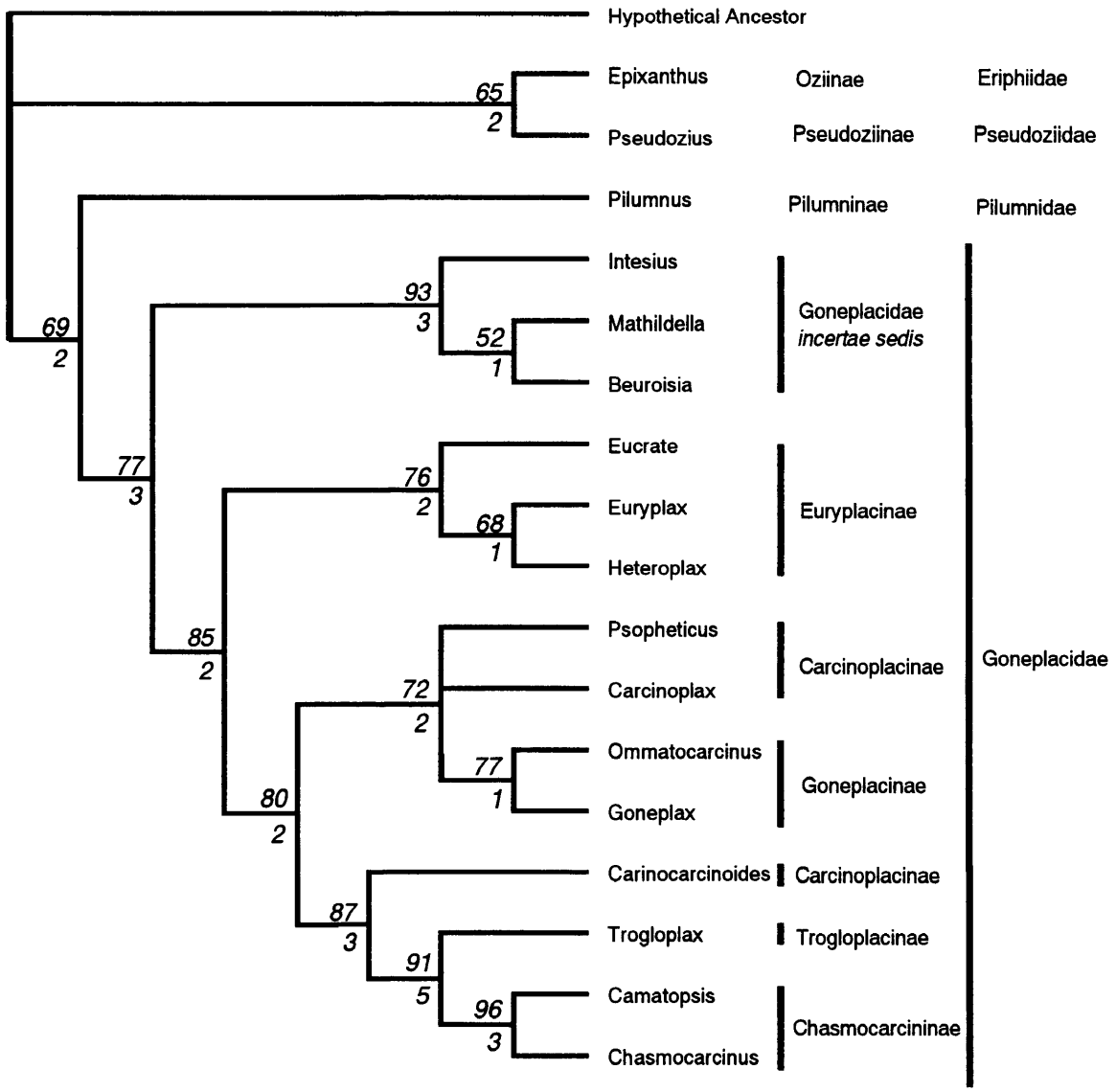

Figure 1. Strict consensus tree of two most-parsimonious trees of 14 genera within the Goneplacidae. Length = 87, Consistency index = 0.6667, Retention index = 0.8242, Rescaled consistency index = 0.5495. Numbers above branches are Bootstrap support and numbers below branches are Bremer support.

and Martin (1984) showed that the family is most similar to the Pilumnidae based upon zoeal morphology. Von Sternberg and Cumberlidge (2001) suggested based upon cladistic and phenetic analysis that the Goneplacidae may be more closely related to the Portunidae Rafinesque, 1815, than to any families of the Xanthoidea. Therefore, the cladogram was rooted against a "hypothetical ancestor". Table 2 lists 45 adult morphological characters and character states used in the analysis. The missing data were scored as unknown. The data matrix is provided in Table 3. Forty-five characters were included in the data matrix (Table 3). There are 42 binary characters and three multistate characters. In the text, characters and character states are indicated by numbers in parentheses (e.g., 1-0 = character 1 + character state 0).

The phylogenetic analysis used PAUP* 4.0b (Swofford, 1999), utilizing a data matrix originating in MacClade version 4.03 (Maddison and Maddison, 2001). Heuristic search analyses were performed with the following options in effect: addition sequence, 100 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 unor-

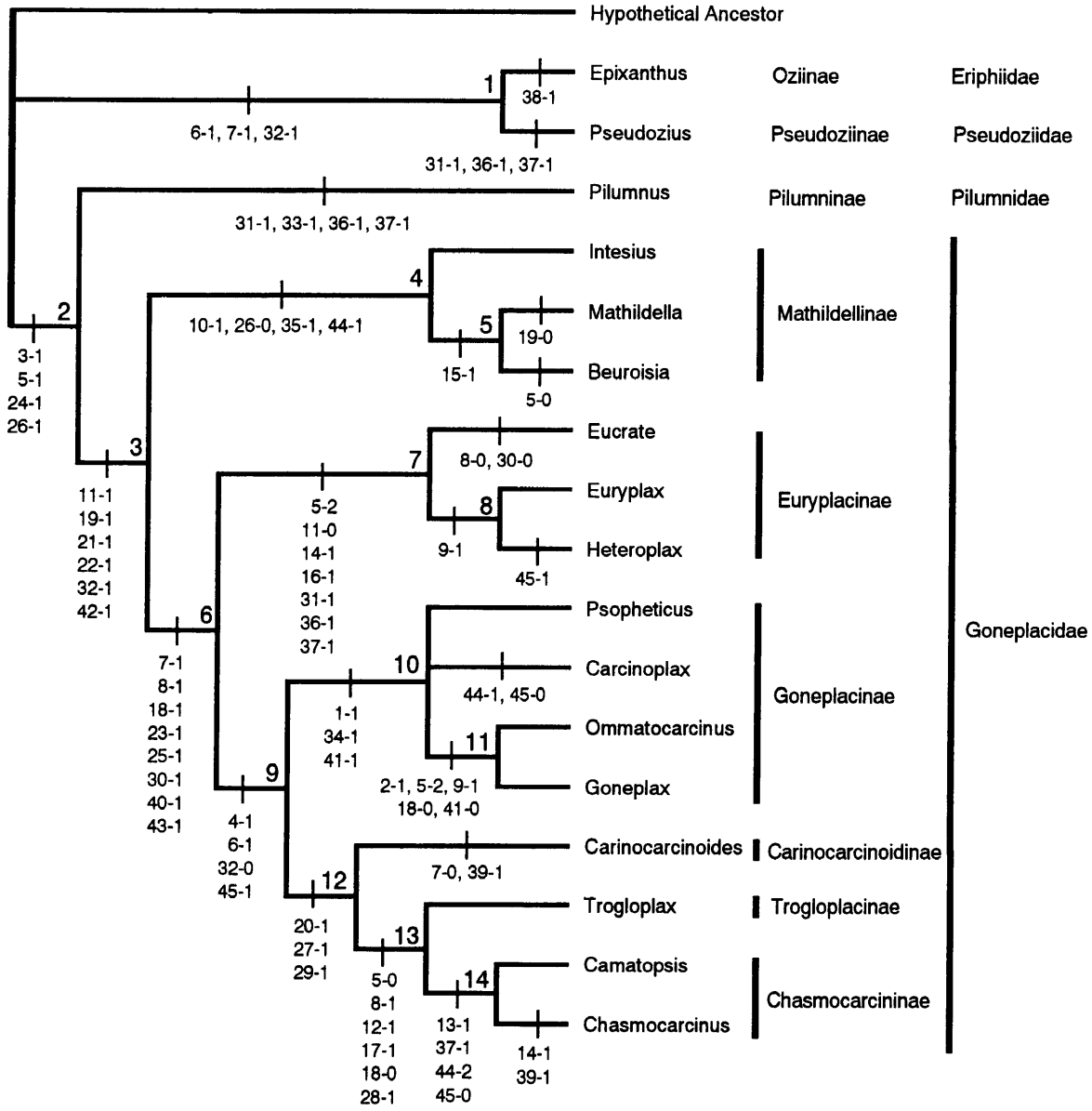

Figure 2. Strict consensus tree of two most-parsimonious trees of 14 genera within the Goneplacidae. Length = 87, Consistency index = 0.6667, Retention index = 0.8242, Rescaled consistency index = 0.5495. Character changes are indicated. Numbers above branches are clade numbers.

dered, unscaled and equally weighted. Relative stability of clades was assessed using bootstrap (Felsenstein, 1985) and decay analyses (Bremer, 1994). The bootstrapping was based on 100 replicates of random input order. The Bremer support was obtained using constraint trees generated by AutoDecay 4.02 (Eriksson, 1999) and analyzed using PAUP*.

Results

The present analysis yielded two most-parsimonious trees, 87 steps long with a consistency index (CI) of 0.6667, a retention index (RI) of 0.8242 and a rescaled consistency index (RC) of 0.5495. A strict consensus tree of two most-parsimonious trees, indicating bootstrap and Bremer support, is given in Figure 1. Fourteen distinct clades are recognized. Each clade is numbered with character state changes in Figure 2.

Clade 1: Epixanthus + Pseudozius (*Eriphiidae* + *Pseudoziidae*). In the examined material *Pseudozius* and *Epixanthus* are sister taxa nested as the most basal clade. This clade, with 65% bootstrap support and Bremer support of 2, is united by three synapomorphies (6-1, 7-1, 32-1). None is unique.

Clade 2: Pilumnus + *Goneplacidae*. *Pilumnus* and taxa of the Goneplacidae clade, with 69% bootstrap support and Bremer index of 2, share four synapomorphies, two of

which are unique and never reversed: the absence of frontal teeth (3-1) and the absence of a median sulcus on the thoracic sternite 4 (24-1).

Clade 3: *Goneplacidae*. The monophyly of the Goneplacidae, with 77% bootstrap support and Bremer index of 3, is well defined by seven synapomorphies, three of which are unique and unreversed: a wide thoracic sternum (21-1), a medially interrupted sulcus delimiting thoracic sternites 6 and 7 (22-1), and long meri of pereiopods 2-5 (42-1).

Clade 4: Mathildella + Beuroisia + Intesius (*Goneplacidae* incertae sedis). The *Mathildella* + *Beuroisia* + *Intesius* clade, with 93% bootstrap support and Bremer support of 3, is unambiguously united by four synapomorphies: laterally broad antennular fossae (10-1), the absence of a prolongation of the thoracic sternite 7 in male (26-0; reversal), a strongly inflated basal part of male gonopod 1 (35-1), and a spatulate dactylus of pereiopods 5 (44-1). Two synapomorphies (10-1, 35-1) are unique and never reversed.

Clade 5: Mathildella + Beuroisia. Only one unique synapomorphy, a semicircular male telson (15-1), defines this clade.

Clade 6: *Euryplacinae* + *Carcinoplacinae* + *Goneplacinae* + Carinocarcinoides + *Trogloplacinae* + *Chasmocarcininae*. This clade, with 85% bootstrap support and Bremer support of 2, shares eight synapomorphies, four of which are unique and never reversed: a medially interrupted sulcus delimiting thoracic sternites 7 and 8 (23-1), an anterior margin of the male sterno-abdominal cavity reaching the anterior part of the thoracic sternite 4 (25-1), the absence of dark-colored cheliped fingers (40-1) and the possession of dactyli of pereiopods 2-5 which terminate with acute chitinous tips (43-1).

Clade 7: Eucrate + Euryplax + Heteroplax (*Euryplacinae*). The Euryplacinae clade has 76% bootstrap support and Bremer support of 2. Seven synapomorphies (5-2, 11-0, 14-1, 16-1, 31-1, 36-1, 37-1) well define this clade. A unique synapomorphy is distinctly narrow male abdominal somites 4-6 (16-1). One synapomorphy, the presence of the basal article of antenna reaching the front (11-0), is a reversal.

Clade 8: Euryplax + Heteroplax. Only one synapomorphy, a long eye stalk (9-1), defines this clade.

Clade 9: *Carcinoplacinae* + *Goneplacinae* + Carinocarcinoides + *Trogloplacinae* + *Chasmocarcininae*. This clade, with 80% bootstrap support and Bremer index of 2, shares four synapomorphies: the supraorbital angle fused to the frontal margin (4-1), the absence of upper orbital fissures (6-1), a sinuous gonopod 1 (32-0; reversal), and the absence of marginal setae of dactyli of pereiopods 5 (45-0; reversal). The supraorbital angle fused to the frontal margin (4-1) is a unique synapomorphy.

Clade 10: Psopheticus + Carcinoplax + Ommatocarcinus + Goneplax (*Carcinoplacinae* + *Goneplacinae*). The Carcinoplacinae + Goneplacinae clade, with 72% bootstrap support and Bremer index of 2, is well defined by three synapomorphies, two of which are unique: the absence of a median notch on the frontal margin (1-1), and a truncated apex of gonopod 1 (34-1) and the possession of a ventral spine of the cheliped carpus (41-1). The sister-group relationship of the clade (*Psopheticus*, *Carcinoplax* and *Ommatocarcinus* + *Goneplax*) remained unresolved.

Clade 11: Ommatocarcinus + Goneplax (*Goneplacinae*). Five synapomorphies support this clade. Only one synapomorphy, the possession of the front with a median projection (2-1), is unique. Two synapomorphies, the male abdominal somite 2, which is much narrower than somite 3 (18-0), and the absence of a ventral spine of the carpus of the cheliped (41-0), are reversals.

Clade 12: Carinocarcinoides + *Trogloplacinae* + *Chasmocarcininae*. This clade, with 91% bootstrap support and Bremer index of 3, shares three unique synapomorphies: the possession of fused male abdominal somites 3-5 (20-1), the thoracic sternite 8 overlying posterolaterally sternite 7 (27-1), and the thoracic sternite 8 which is visible ventrally (29-1).

Clade 13: *Trogloplacinae* + *Chasmocarcininae*. The Trogloplacinae + Chasmocarcininae clade, with 88% bootstrap support and Bremer support of 5, is evidently united by five synapomorphies (5-0, 8-2, 12-1, 17-1, 18-0, 28-1). Three of these synapomorphies, the presence of maxilliped 3 ischium about equal to merus (12-1), male abdominal somite 3 much narrower than thoracic sternites 7 and 8 (17-1), and the presence of a supplementary plate of male thoracic sternite 8 (27-1), are unique.

Clade 14: Camatopsis + Chasmocarcinus (*Chasmocarcininae*). This clade, with 96% bootstrap support and Bremer support of 3, is well defined by four synapomorphies (13-1, 37-1, 44-2, 45-0). The possession of a suboval merus of maxilliped 3 (13-1) is a unique synapomorphy.

Discussion

Guinot (1969a, b, c; 1970 [1971]) divided the family Goneplacidae *sensu* Balss (1957) into three major groups; "Goneplacidae dérives des Xanthidae", "Goneplacidae euryplaciens (Euryplacinae)", and "Goneplacidae carcinoplaciens-gonéplaciens (Carcinoplacinae + Goneplacinae)". Glaessner (1969) and Sakai (1976) used the classification of the Goneplacidae *sensu* Balss, while Serène and Soh (1976), Manning and Holthuis (1981), and Williams (1984) partly accepted Guinot's concept for the classification of the family.

Since then, genera belonging to her "Goneplacidae dérives des Xanthidae" were removed to other families. Guinot (1978) and Martin and Abele (1986) transferred the

Eucratopsinae to the family Panopeidae. The Rhizopinae *sensu lato* is currently placed in the Pilumnidae (Guinot, 1969c, 1978; Ng, 1987; Davie and Guinot, 1996). *Litocheira* Kinaham, 1856 *sensu stricto* (see Guinot, 1970 [1971]; Türkay, 1975), is referred to her "Goneplacidae pilumniens *sensu stricto*", while the genus has not been assigned to any of the pilumnid subfamilies. Guinot (1969c, 1970 [1971]) referred *Galene* De Haan, 1833, to her "Goneplacidae pilumniens *sensu lato*", while Takeda (1976) included the genus within the subfamily Galeninae Alcock, 1898, of the Xanthidae *sensu lato*. Ng (1998) and Schweitzer (2000) classified *Galene* within the Pilumnidae, following Guinot (1969c, 1970 [1971]); therefore, species of the Galeninae are thought to be members of the Pilumnidae (Ng *et al.*, 2001; Hsueh and Huang, 2002). The Pseudorhombilinae Alcock, 1900, previously referred to the Goneplacidae, was also included in her "Goneplacidae dérives des Xanthidae" but Hendrickx (1998) treated it as a distinct family.

Davie and Guinot (1996) indicated that the Goneplacidae contains five subfamilies, Goneplacinae MacLeay, Carcinoplacinae H. Milne Edwards, Chasmocarcininae Serène, Trogloplacinae Guinot and Euryplacinae Stimpson. Ng and Wang (1994) transferred the Pseudoziinae Alcock from the Eriphiidae to the Goneplacidae. Therefore, Lemaitre *et al.* (2001) and Hsueh and Huang (2002) currently divided the Goneplacidae into six subfamilies. Subsequently, Ng and Liao (2002) excluded the Pseudoziinae from the Goneplacidae and treated it as a distinct family.

The present phylogenetic analysis well supports the monophyly of the Goneplacidae as envisioned by Davie and Guinot (1996). Six synapomorphies, three of which are unique and unreversed, well define the Goneplacidae (Figure 2, Clade 3). The present analysis suggests that the *Intesius* + *Mathildella* + *Beuroisia* (Goneplacidae *incertae sedis*) clade within the Goneplacidae is the most basal, followed by the Euryplacinae, the Carcinoplacinae + Goneplacinae, and the most advanced clade, *Carinocarcinoides* + Trogloplacinae + Chasmocarcininae.

Pseudozius, the type genus of the Pseudoziidae, is the sister to *Epixanthus* (Eriphiidae; Oziinae) (Figure 2; clade 1) and both genera are united by three synapomorphies. Alcock (1898) originally placed *Pseudozius* within his alliance Pseudozioida Alcock (= Pseudoziinae Alcock; *nom. transl.* of Takeda (1976)) within his Menippinae of the family Xanthidae *sensu lato* and subsequent workers (i.e., Guinot, 1970[1971]; Sakai, 1976; Takeda, 1976) also placed it within the Xanthidae *sensu lato*. Crosnier *in* Serène (1984) referred *Pseudozius* to *incertae sedis* within the Menippidae (= Eriphiidae). Ng and Wang (1995) moved the subfamily from the Eriphiidae to the Goneplacidae. Subsequently, Ng and Liao (2002) recognized the Pseudoziinae as a separate family and divided it into two subfamilies, Pseudoziinae and Planopilumninae Serène, 1984. In their work the Pseudoziinae contains four genera, *Euryozius* Miers, 1886, *Flindersoplax* Davie, 1989, *Platychelonion* Crosnier and Guinot, 1969, and *Pseudozius*, and the Planopilumninae is a monotypic subfamily. Our analysis supports the recognition of the Pseudoziidae by Ng and Liao (2002) and suggests that the family is the sister taxon of the Eriphiidae. Members of the subfamilies Eriphiinae, Oziinae, Menippinae Ortmann, 1893, and Dacryopilumninae Serène, 1984, within the Eriphiidae have a long gonopod 2 with a filamentous, long flagellum (36-0, 37-0, 38-1) while *Pseudozius* is characterized by having a short gonopod 2 and by lacking a filamentous, long flagellum of gonopod 2 (36-1, 37-1, 38-0).

The most basal *Intesius* + *Mathildella* + *Beuroisia* clade shares four synapomorphies, two of which are unique and never reversed: laterally broad antennular fossae (10-1) and a strongly inflated basal part of gonopod 1 (35-1) (Figure 2; clade 4). The subfamilial placement of three genera has not been well documented. Guinot and Richer de Forges (1981) erected two new genera, *Mathildella* and *Beuroisia*, based upon examination of new material and species previously assigned to *Neopilumnoplax* Serène *in* Guinot, 1969c, but did not designate subfamilial placement for *Mathildella* and *Beuroisia* or for another new genus, *Intesius*. Guinot (1970 [1971]) placed *Neopilumnoplax* within "Autres Carcinoplacinae-Goneplacinae" of the Goneplacidae, whereas Sakai (1976) placed it within the Carcinoplacinae. Poupin (1996) assigned *Intesius* to the Goneplacidae, and *Beuroisia* and *Mathildella* to "Xanthoidea *incertae sedis*". Ng *et al.* (2001) and Hsueh and Huang (2002) placed *Mathildella* within the Carcinoplacinae. The present analysis supports that these three genera should be included within the Goneplacidae. The three genera within this clade differ significantly from other goneplacid genera (Figure 2; clade 6) because they lack the diagnostic synapomorphies of clade 6; therefore, they cannot be placed within previously known subfamilies. A new subfamily, Mathildellinae, is erected herein for these genera.

Several workers did not recognize the Euryplacinae as a valid taxon. Indeed, Balss (1957) included *Eucrate* and *Heteroplax* within the Carcinoplacinae, and *Euryplax* within the Prionoplacinae, and Sakai (1976) classified *Eucrate* and *Heteroplax* within the Carcinoplacinae. However, the Euryplacinae (Figure 2, Clade 7) is well supported as monophyletic by seven synapomorphies, one of which is unique and never reversed, distinctly narrow male abdominal somites 4-6 (16-1). The present analysis strongly supports recognition of the subfamily by Guinot (1969a, b, c, 1970 [1971]), Manning and Holthuis (1981), Ng *et al.* (2001), and Hsueh and Huang (2002). The Euryplacinae clade is the sister to the Carcinoplacinae +

Goneplacinae + *Carinocarcinoides* + Trogloplacinae + Chasmocarcininae clade (Figure 2, Clade 9).

For the Carcinoplacinae, represented by *Psopheticus* and *Carcinoplax*, the analysis is unable to resolve the relationships between both taxa and other goneplacines, since they nest in a polytomy with the Goneplacinae clade (Figure 2, Clade 10). In one of the two most-parsimonious trees the subfamily is monophyletic whereas in another tree it is paraphyletic. The monophyly of the Goneplacinae is supported by five synapomorphies, but it is nested among the goneplacine genera (Figure 2, Clade 11). The Carcinoplacinae should either be synonymised with the Goneplacinae or divided into three subfamiles. In the latter scheme, a new monotypic subfamily would have to be proposed for *Psopheticus*. The Goneplacinae clade with Bremer support of 1 is more weakly defined than the Carcinoplacinae + Goneplacinae clade with Bremer support of 2. In the present analysis the Carcinoplacinae + Goneplacinae clade shares three synapomorphies, two of which are unique: the absence of a median notch on the frontal margin (1-1), and a truncated apex of gonopod 1 (34-1). Therefore, rather than proposing three subfamilies, each with weakly defined synapomorphies and with weak Bremer support, it is considered best to place *Carcinoplax* and *Psopheticus*, previously assigned to the Carcinoplacinae, within the Goneplacinae. Our phylogenetic analysis supports Guinot's concept of a "lignée Carcinoplacienne-Gonéplacienne" and "groupement *Carcinoplax - Psopheticus - Goneplax - Ommatocarcinus*" (Guinot, 1969b, c).

The *Carinocarcinoides* + Trogloplacinae + Chasmocarcininae clade is characterized by three unique synapomorphies: fused male abdominal somites 3-5 (20-1), thoracic sternite 8 overlying posterolaterally sternite 7 (27-1), and thoracic sternite 8 visible ventrally (29-1) (Figure 2, Clade 12). Karasawa and Fudouji (2000) originally placed *Carinocarcinoides* within the Carcinoplacinae; however, the present analysis suggests that the genus does not belong to the Carcinoplacinae. *Carinocarcinoides* is the first to diverge within the clade, characterized by having more or less defined dorsal regions of the carapace (7-0) and elongate chelipeds (39-1). The Trogloplacinae + Chasmocarcininae clade is unambiguously united by six synapomorphies, three of which are unique: ischium of maxilliped 3 about equal to merus (12-1), male abdominal somite 3 much narrower than thoracic sternites 7 and 8 (17-1), and the possession of the supplementary plate of thoracic sternite 8 in males (27-1) (Figure 2, Clade 13). On the basis of the phylogenetic analysis, *Carinocarcinoides* cannot be included in either subfamily, since it lacks their diagnostic synapomorphies, and the genus is here recognized as the type of a new monotypic subfamily, Carinocarcinoidinae.

The Trogloplacinae is here derived as the sister group to the Chasmocarcininae (Figure 2, Clade 14). Davie and Guinot (1996) suggested that the Trogloplacinae had close affinities with the Chasmocarcininae. We concur. The Trogloplacinae is a weakly defined subfamily lacking the diagnostic synapomorphies of the Chasmocarcininae. The Chasmocarcininae is a distinctive subfamily clearly defined by four autapomorphies (13-1, 37-1, 44-1, 45-1), one of which is unique: the possession of a suboval merus of maxilliped 3 (13-1).

Systematics

Family Goneplacidae MacLeay, 1838 *emend.*

Diagnosis.—Carapace transversely rectangular, trapezoidal or rounded; dorsal regions weakly distinct or indistinct; front straight, sometimes bearing median notch or median projection, without teeth; notch between frontal and supraorbital angle present or absent; upper orbital margin with or without fissures; anterolateral margin usually toothed; inner antennular septum a thin plate; buccal frame quadrangular; epistome well defined; palp of maxilliped 3 articulating on or near anteromesial corner of merus; exopod wide; male abdomen with all free somites or fused somites 3-5; thoracic sternum wide with all sutures interrupted, rarely with continuous suture delimiting sternites 7 and 8; sternite 4 lacking median sulcus; sternite 7 usually with posterolateral prolongation; chelipeds heterochelate; pereiopods 2-5 long; dactyli of pereiopods 2-5 with or without corneous tips; male genital openings coxal; gonopod 1 stout, sinuous or curved, usually with simple apex; gonopod 2 long or short.

Type genus.—*Goneplax* Leach, 1814.

Subfamilies included. — Carinocarcinoidinae subfam. nov.; Chasmocarcininae Serène, 1964; Euryplacinae Stimpson, 1871; Goneplacinae MacLeay, 1838; Mathildellinae subfam. nov.; Trogloplacinae Guinot, 1986.

Remarks.—The diagnosis is based upon Balss (1957) and the present phylogenetic analysis.

Subfamily Mathildellinae subfam. nov.

Diagnosis.—Carapace usually flattened with weakly defined dorsal regions; front straight with shallow median notch; supraorbital angle separated from frontal margin; orbit relatively small with upper orbital fissures; anterolateral margin bearing five teeth; eye stalk short; antennular fossae broad laterally; merus of maxilliped 3 subquadrate, much longer than ischium; male abdomen filling entire space between coxae of pereiopods 5, usually with all free somites; thoracic sternum wide with interrupted sutures excluding continuous suture delimiting sternites 7 and 8; sternite 7 without posterolateral prolongation; sterno-abdominal cavity reaching posterior of sternite

Table 4. Distributions and geologic ranges of recognized fossil species of the subfamily Mathildellinae.

Taxa	Range	locality
Genus *Branchioplax* Rathbun, 1916	PALAEOGENE	
Branchioplax ballingi Remy *in* Remy and Tessier, 1954	Palaeogene	Senegal
Branchioplax carmanahensis (Rathbun, 1926)	Oligocene	U.S.A.
Branchioplax concinna Quayle and Collins, 1981	M. Eocene	England
Branchioplax pentagonalis (Yokoyama, 1911)	M. Eocene	Japan
Branchioplax sulcata Müller and Collins, 1991a	U. Eocene	Hungary
Branchioplax washingtoniana Rathbun, 1916	U. Eocene - Oligocene	U.S.A.
Genus *Tehuacana* Stenzel, 1944	PALAEOGENE	
Tehuacana tehuacana Stenzel, 1944	Palaeogene	U.S.A.

4; chelipeds with dark-colored fingers; dactyli of pereiopods 2-5 with corneous tips; dactyli of pereiopods 5 spatulate with setae; gonopod 1 stout, curved, strongly inflated basally, with simple apex; gonopod 2 usually long with long flagellum.

Type genus.—*Mathildella* Guinot and Richer de Forges, 1981.

Genera included.—*Beuroisia* Guinot and Richer de Forges, 1981; *Branchioplax* Rathbun, 1916; *Intesius* Guinot and Richer de Forges, 1981; *Mathildella*; *Neopilumnoplax* Serène *in* Guinot, 1969; *Platypilumnus* Alcock, 1894; *Tehuacana* Stenzel, 1944.

Discussion.—The Mathildellinae is the most basal group within the Goneplacidae based upon the present phylogenetic analysis. The subfamily is well defined by the presence of more or less defined anterior dorsal regions, laterally broad antennular fossae, a complete sulcus delimiting thoracic sternites 7 and 8, an anterior end of the sterno-abdominal cavity located on the posterior half of the thoracic sternite 4, the absence of a posterolateral prolongation of the thoracic sternite 7, the presence of dark-colored cheliped fingers, dactyli of pereiopods 2-5 with corneous tips, and a strongly inflated basal part of gonopod 1, all of which other goneplacid subfamilies lack.

Alcock (1900) questionably referred *Platypilumnus* to the Goneplacidae. Guinot (1970 [1971]) placed *Platypilumnus* within the Geryonidae, while Manning and Holthuis (1989) did not include the genus within the Geryonidae. Richer de Forges (1996) showed that *Platypilumnus* has close affinities with *Neopilumnoplax* and *Intesius*. We concur. Crosnier and Guinot (1969) suggested that *Platychelonion* is similar to *Neopilumnoplax* whereas Guinot (1970 [1971]) questionably referred it to the Geryonidae. Manning and Holthuis (1989) excluded the genus from the Geryonidae and Davie (1989) suggested that the genus bears a close resemblance to the Goneplacidae. We place *Platychelonion* within the Pseudoziidae, following Ng and Liao (2002).

Tucker and Feldmann (1990), Schweitzer *et al.* (2000), and Schweitzer (2000) described well preserved specimens of *Branchioplax washingtoniana* Rathbun, 1916, the type species of *Branchioplax*, from Palaeogene rocks of the U.S.A. In her taxonomic review of *Branchioplax* Schweitzer (2000) synonymised *Pilumnoplax hannibalanus* Rathbun, 1926, with *B. washingtoniana* and moved *Pilumnoplax carmanahensis* Rathbun, 1926, to *Branchioplax*. Balss (1957) and Glaessner (1969) referred *Branchioplax* to the Carcinoplacinae, while Schweitzer (2000) suggested that the genus is similar to the extant *Chacellus* Guinot, 1969c. *Chacellus* is now placed within the family Pseudorhombilidae (Hendrickx, 1998). Examination of illustrations of *B. washingtoniana* and *B. pentagonalis* (Yokoyama, 1911) indicates that the genus belongs to the Mathildellinae. In *Branchioplax* the anterior dorsal regions are more or less defined; a nearly straight frontal margin bears a median notch; the supraorbital angle is developed; the upper orbital margin possesses two fissures; the anterior end of the sterno-abdominal cavity located on the posterior part of sternite 4; the sulcus delimiting thoracic sternites 7 and 8 is complete; the posterolaterally directed prolongation of thoracic sternite 7 is not developed; and the male abdomen consists of seven free somites. These characters are also definitive characters of the subfamily.

Stenzel (1944) established the monotypic genus *Tehuacana* based upon a male specimen from the Palaeogene of the U.S.A. and compared this new genus with "*Pilumnoplax* Stimpson, 1858". This genus has upper orbital fissures and more or less defined anterior dorsal regions, and lacks a prolongation of thoracic sternite 7. Therefore, the genus is here assigned to the Mathildellinae.

Fossil records.—Fossil records of the Mathildellinae are represented by two extinct genera known from the Palaeogene (Table 4).

Subfamily Euryplacinae Stimpson, 1871 *emend.*

Diagnosis.—Carapace usually with poorly defined dorsal regions; front straight with shallow median notch;

Table 5. Distributions and geologic ranges of recognized fossil species of the subfamily Euryplacinae. Asterisk indicates extant species.

Taxa	Range	locality
Genus *Chlinocephalus* Ristori, 1886	PLIOCENE	
Chlinocephalus demissifrons Ristori, 1886	Pliocene	Italy
Genus *Corallicarcinus* Müller and Collins, 1991a	EOCENE	
Corallicarcinus spinosus (Lörenthey *in* Lörenthey and Beurlen, 1929)	U. Eocene	Hungary
Corallicarcinus planus Müller and Collins, 1991a	U. Eocene	Hungary
Genus *Eucrate* De Haan, 1835	OLIGOCENE-RECENT	
Eucrate crenata De Haan, 1835*	Pleistocene	Japan
Eucrate martini Rathbun, 1926	Oligocene	U.S.A.
Eucrate puliensis Hu and Tao, 1996	Oligocene	Taiwan
Genus *Euryplax* Stimpson, 1859	OLIGOCENE-RECENT	
Euryplax culebrensis Rathbun, 1919	Oligocene	Panama
Genus *Orbitoplax* Tucker and Feldmann, 1990	EOCENE	
Orbitoplax plafkeri Tucker and Feldmann, 1990	U. Eocene	U.S.A.
Orbitoplax tuckerae Schweitzer, 2000	U. Eocene	U.S.A.
Orbitoplax weaveri (Rathbun, 1926)	U. Eocene	U.S.A.
Genus *Stoaplax* Vega *et al.*, 2001	EOCENE	
Stoaplax nandachare Vega *et al.*, 2001	M. Eocene	México
Genus *Viaplax* gen. nov.	EOCENE	
Viaplax urpiniana (Via, 1959) comb. nov.	Eocene	Spain

supraorbital angle distinct; orbit sometimes deep, large, with upper orbital fissures; anterolateral margin bearing two to five spines; eye stalk short or long; basal article of antenna reaching front; merus of maxilliped 3 subquadrate, much longer than ischium; male abdomen filling entire space between coxae of pereiopods 5, with all free somites; somites 4–6 much narrower than somite 3; telson usually longer than wide; thoracic sternum wide with sutures all interrupted; sternite 7 with posterolateral prolongation; sternite 8 visible in posterior view; sterno-abdominal cavity reaching anterior of sternite 4; chelipeds without dark-colored fingers; dactyli of pereiopods 2-5 without corneous tips; dactyli of pereiopods 5 usually styliform, with or without setae; gonopod 1 stout, curved, with simple apex; gonopod 2 very short with short flagellum.

Type genus.—*Euryplax* Stimpson, 1859.

Genera included.—*Chlinocephalus* Ristori, 1886; *Corallicarcinus* Müller and Collins, 1991a; *Euryplax*; *Eucrate* De Haan, 1835; *Fravillea* A. Milne Edwards, 1880; *Heteroplax* Stimpson, 1858; *Machaerus* Leach, 1818; *Nancyplax* Lemaitre *et al.*, 2001; *Orbitoplax* Tucker and Feldmann, 1990; *Psopheticoides* Sasaki, 1969; *Stoaplax* Vega *et al.*, 2001; *Trizocarcinus* Rathbun, 1914; *Viaplax* gen. nov.

Discussion.—Balss (1957) and Sakai (1976) placed members of the subfamily within the Carcinoplacinae, while Guinot (1970 [1971]), Serène and Soh (1976), Manning and Holthuis (1981), Williams (1984), Ng *et al.* (2001), and Hsueh and Huang (2002) indicated that the Euryplacinae is a valid taxon. The present analysis strongly supports the monophyly of the Euryplacinae.

Ristori (1886) described a new genus and species, *Chlinocephalus demissifrons*, from the Pliocene of Italy and originally placed it within the Cancridae Latreille, 1802. Glaessner (1929) referred *Chlinocephalus* to the Goneplacidae and in 1969 removed the genus to the Xanthidae *sensu lato*. The genus is reassigned to the Euryplacinae because the male abdomen consists of seven free somites, the telson of the male abdomen is much longer than wide, and the abdominal somites 4 and 5 are much narrower than the somite 3. The genus may resemble *Eucrate*, but differs by the presence of transverse ridges of the dorsal surface.

Via (1959) described a new species, *Pilumnoplax urpiniana* from the Eocene of Spain. Feldmann and Maxwell (1990) referred this species to *Carcinoplax* and Schweitzer (2000) assigned it to the Pilumnidae. Via (1959, 1969) indicated that *Pilumnoplax urpiniana* has three anterolateral teeth, while in the species a broken fourth anterolateral tooth (Via, 1969, pl. 36, figs. 2, 2b) is observed. *Pilumnoplax urpiniana* possesses carapace and male abdomen characters most like those of members of *Eucrate*; the front has a median notch; the supraorbital

angle is well marked; the upper orbital margin bears two shallow notches; the anterolateral margin has four anterolateral teeth; the male abdominal somites 5 and 6 are much narrower than somite 3; and the telson is much longer than wide. However, the species differs from species of *Eucrate* by having a flattened dorsal surface, well developed triangular anterolateral teeth, more or less defined cervical and branchiocardiac grooves, and well marked epibranchial regions. Therefore, *Viaplax* gen. nov. is here erected with a type species, *Pilumnoplax urpiniana* Via, 1959. The generic name is derived from the late Dr. L. Via, a Spanish paleontologist, and the suffix-*plax* (flat), which is used in names of related genera. The gender is feminine. The carapace of the new genus may also be similar to that of *Benthopanope* Davie, 1989, of the pilumnid Heteropanopinae Alcock, 1898 (*nom. correct. herein pro* Heteropanopeinae Alcock, 1898, *nom. transl.* Serène (1984)). It is readily distinguished from *Benthopanope* by the possession of a wider orbital margin and well developed anterolateral teeth, and the absence of granular dorsal crests on the carapace and prominent median lobes on the frontal margin.

Vega *et al.* (2001) erected a new monotypic genus, *Stoaplax*, containing *S. nandachare* Vega *et al.*, 2001, from the middle Eocene of México. They referred the genus to the Carcinoplacinae and indicated that it is most similar to *Orbitoplax*. Herein, the genus is removed to the Euryplacinae by having a medially notched frontal margin and a wide upper orbital margin with a fissure.

The Eocene genus *Corallicarcinus* possesses carapace characters like those of the extant *Euryplax*; however, in *Corallicarcinus* the carapace has distinct ridges extending onto the dorsal surface from the second and third anterolateral teeth.

Fossil records.—Seven genera including five extinct ones are known from the fossil record (Table 5). Four extinct genera are known from the Eocene and one is from the Pliocene. The geologic range of two extant genera, *Eucrate* and *Euryplax*, extend back to the Oligocene.

Subfamily Goneplacinae MacLeay, 1838 *emend.*
(= Subfamily Carcinoplacinae H. Milne Edwards, 1852)

Diagnosis.—Carapace with poorly defined dorsal regions; front straight without median notch, sometimes with low median projection; notch between frontal margin and supraorbital angle indistinct; orbit without upper orbital fissures; anterolateral margin bearing one to three spines; eye stalk short or long; merus of maxilliped 3 subquadrate, much longer than ischium; male abdomen filling entire space between coxae of pereiopods 5, with all free somites; thoracic sternum wide with sutures all interrupted; sternite 7 with posterolateral prolongation; sternite 8 visible in posterior view; sterno-abdominal cavity reaching anterior of sternite 4; chelipeds usually with lateral spine on carpus and without dark-colored fingers; dactyli of pereiopods 2–5 without corneous tips; dactyli of pereiopod 5 styliform or spatulate, with or without setae; gonopod 1 stout, sinuous, usually with truncated apex; gonopod 2 usually long with long flagellum.

Type genus.—*Goneplax* Leach, 1814.

Genera included.—*Bathyplax* A. Milne Edwards, 1880; *Carcinoplax* H. Milne Edwards, 1852; *Goneplax*; *Neommatocarcinus* Takeda and Miyake, 1969; *Ommatocarcinus* White, 1852; *Psopheticus* Wood-Mason, 1892; *Singhaplax* Serène and Soh, 1976.

Discussion.—The Goneplacinae was previously distinguished from the Carcinoplacinae by the following characters: carapace subquadrate in outline, greatest carapace width is at the outerorbital angle, front is usually narrow, and orbit is extremely elongate (Balss, 1957; Sakai, 1976; Hsueh and Huang, 2002). However, the Carcinoplacinae is herein recognized as a synonym of the Goneplacinae based upon the present analysis.

Via (1959) described a new species, *Ommatocarcinus zariquieri*, from the Eocene of Italy. In his 1969 work the present species was well figured. This species is not a member of *Ommatocarcinus* because the dorsal carapace possesses three well defined transverse ridges (Via, 1969, pl. 37, figs. 1, 1a, 2, 2a), the maximum carapace width is at the anterolateral angle (Via, 1969, pl. 37, figs. 1, 1a, 2, 2a), there is a well defined median groove on thoracic sternites 2 and 3 (Via, 1969, pl. 37, fig. 1b), and male abdominal somites 3–5 are fused (Via, 1969, pl. 37, fig. 1b). In the possession of fused abdominal somites 3–5 Takeda and Miyake (1969) and Jenkins (1975) noted that the species may be transferred to *Neommatocarcinus* Takeda and Miyake, 1969, but *O. zariquieri* apparently differs from the sole included species of *Neommatocarcinus*, *N. huttoni* (Filhol, 1885), by carapace and thoracic sternum characters. The species is here assigned to *Euphylax* Stimpson, 1860, of the family Portunidae Rafinesque, based upon the characters discussed above. In *Ommatocarcinus* there is only one transverse ridge on the dorsal surface, the maximum carapace width is at the outerorbital angle, a median groove is absent on thoracic sternites 2 and 3, and all male abdominal somites are free.

Glaessner (1960) described *Ommatocarcinus arenicola* Glaessner, 1960, from the lower Miocene of New Zealand and noted that "The new species is closer in the shape of its carapace to the less specialized genus *Goneplax* Leach, but the front is more like that of *Ommatocarcinus*, to which the species is assigned as an early primitive form". Takeda and Miyake (1969) proposed a new goneplacid genus, *Glaessneria*, for the species. We cannot concur. The carapace in this species bears two anterolateral teeth with an anterolaterally directed outerorbital tooth, has a rela-

Table 6. Distributions and geologic ranges of recognized fossil species of the subfamily Goneplacinae. Asterisk indicates extant species.

Taxa	Range	locality
Genus *Carcinoplax* H. Milne Edwards, 1852	EOCENE - RECENT	
Carcinoplax antiqua (Ristori, 1889)	L. - M. Miocene	Japan
Carcinoplax granulimanus Karasawa and Inoue, 1992	M. Miocene	Japan
Carcinoplax imperfecta Karasawa and Inoue, 1992	M. Miocene	Japan
Carcinoplax longimanus (De Haan, 1833) *	Pliocene - Pleistocene	Japan, Taiwan
Carcinoplax mongosungi Hu and Tao, 1985	unknown	Taiwan
Carcinoplax proavita (Glaessner, 1960) comb. nov.	L. Miocene	New Zealand
Carcinoplax prisca Imaizumi, 1961	U. Miocene - Pleistocene	Japan, Taiwan
Carcinoplax purpurea Rathbun, 1914*	Pliocene	Taiwan
Carcinoplax sp. aff. *C. purpurea* Rathbun, 1914	U. Pliocene	Japan
Carcinoplax shukumi Hu and Tao, 1985	Miocene	Taiwan
Carcinoplax temikoensis Feldmann and Maxwell, 1990	U. Eocene	New Zealand
Carcinoplax thongi Hu and Tao, 1985	Miocene	Taiwan
(*nom. correct. herein pro. Carcinoplax t-hongi* Hu and Tao, 1985)		
Carcinoplax tsengi Hu and Tao, 1996	Miocene	Taiwan
Carcinoplax sp., Feldmann and Keyes, 1992	U. Pliocene - L. Pleistocene	New Zealand
Carcinoplax sp., Karasawa, 1997	L. Pliocene	Japan
Carcinoplax sp., Kato, 1996	M. Miocene	Japan
Genus *Goneplax* Leach, 1814	MIOCENE - RECENT	
Goneplax arenicola (Glaessner, 1960) comb. nov.	L. Miocene	New Zealand
Goneplax craverii Crema, 1895	Pliocene	Italy
Goneplax formosa Ristori, 1886	Pliocene	Italy
Goneplax meneghinii Ristori, 1886	Pliocene	Italy
Goneplax gulderi Bachmayer, 1953a	Miocene - Pliocene	Bulgaria, Austria, Spain
Goneplax romboides (Linnaeus, 1758) *	Pliocene	England, Italy
Goneplax saccoi Crema, 1895	Pliocene	Italy
Goneplax sp. cfr. *G. saccoi* Crema, 1895	Miocene	Austria
Genus *Ommatocarcinus* White, 1852	MIOCENE - RECENT	
Ommatocarcinus corioensis (Creswell, 1886)	Miocene	Australia
Ommatocarcinus macgillivrayi White, 1852*	Pliocene - Pleistocene	Australia, Taiwan
Ommatocarcinus sp. cfr. *O. macgillivrayi* White, 1852	U. Pliocene - M. Pleistocene	Japan, New Zealand
Ommatocarcinus taiwanicus Hu and Tao, 1996	Miocene	Taiwan
Ommatocarcinus sp., Feldmann and Keyes, 1992	L. Miocene	New Zealand
Genus *Psopheticus* Wood-Mason, 1892	OLIGOCENE - RECENT	
Psopheticus shujenae (Hu and Tao, 1996) comb. nov.	Oligocene	Taiwan
Psopheticus sp. aff. *P. stridulans* Wood-Mason, 1892	U. Pliocene	Japan

Table 7. Distributions and geologic ranges of recognized fossil species of the subfamily Carinocarcinoidinae.

Taxa	Range	locality
Genus *Carinocarcinoides* Karasawa and Fudouji, 2000	OLIGOCENE	
Carinocarcinoides angustifrons (Karasawa, 1993)	L. Oligocene	Japan
Carinocarcinoides carinatus Karasawa and Fudouji, 2000	L. Oligocene	Japan

tively wide front without a median projection, and lacks a distinct transverse ridge dorsally; therefore, the species is here moved to *Goneplax*. *Glaessneria* thus becomes a junior subjective synonym of *Goneplax*.

Paleopsopheticus Hu and Tao, 1996, is a junior subjective synonym of *Psopheticus*. Hu and Tao (1996) distinguished the present monotypic genus from *Psopheticus* by having a small-sized carapace, a nearly straight anterolateral margin, a rounded posterior margin, and equal-sized anterolateral spines (modified from Hu and Tao, 1996, p. 102). We believe that these characters cannot define the genus but define *Psopheticus shujenae* (Hu and Tao, 1996) comb. nov. Examination of their figures (Hu and Tao, 1996, pl. 49, figs. 1, 2, 5, 6) suggests that the

species is quite similar to most members of *Psopheticus* (i.e. *P. stridulans* Wood-Mason, 1892, *P. vocans* Guinot, 1985).

Glaessner (1960) described a new species, *Galene proavita*, from the Miocene of New Zealand. This species is here moved to *Carcinoplax* because the carapace has smooth, poorly defined anterior dorsal regions with a straight frontal margin, the thoracic sternum and male abdomen are wide, and the telson of the male abdomen is about as long as wide. In members of *Galene* the frontal margin is bilobed; the anterior mesogastric process is more or less defined; the cardiac region is longer than wide; the thoracic sternum is much longer than wide with a narrow sterno-abdominal cavity; the male abdominal somites 4–6 are much narrower than somite 3 with a long, elongate telson. *Pilumnoplax petrificus* Hu and Tao, 1996, from the Pleistocene of Taiwan, is identical with *Carcinoplax prisca* Imaizumi, 1961, because the carapace is rounded-hexagonal in outline and slightly wider than long, and a large outerorbital tooth is directed sharply forwards. Hu and Tao (1996) described a new species, *Carcinoplax linae*, from the upper Pliocene of Taiwan. They compared the species with *Carcinoplax longimanus* (De Haan, 1833) rather than with the quite similar extant species *Carcinoplax purpurea* Rathbun, 1914, and in fact no substantive difference between *C. linae* and *C. purpurea* can be found. *Carcinoplax linae* is here regarded as a junior synonym of *C. purpurea*.

Fossil records.—Four genera, *Carcinoplax, Goneplax, Ommatocarcinus*, and *Psopheticus*, are recognized as fossils (Table 6). Most species of these genera are known from the Neogene and two species, *Carcinoplax temikoensis* and *Psopheticus shujense*, are from the Palaeogene.

Subfamily Carinocarcinoidinae subfam. nov.

Diagnosis.—Carapace with more or less defined dorsal regions; front straight without median notch; notch between frontal margin and supraorbital angle indistinct; upper orbital margin without fissures; anterolateral margin bearing three spines; merus of maxilliped 3 subquadrate, much longer than ischium; male abdomen filling entire space between coxae of pereiopods 5, with somites 3–5 fused; thoracic sternum wide; sternite 7 with posterolateral prolongation; sternite 8 visible in ventral view, overlying posterior of sternite 7; sterno-abdominal cavity reaching anterior of sternite 4; fingers of chelipeds long, elongate, not dark in color.

Type and sole included genus. — *Carinocarcinoides* Karasawa and Fudouji, 2000.

Discussion.—Karasawa and Fudouji (2000) originally placed *Carinocarcinoides* within the Carcinoplacinae. However, the phylogenetic analysis strongly suggests that the genus should not be assigned to the Carcinoplacinae (= Goneplacinae) based upon examination of type and newly obtained specimens. *Carinocarcinoides* is derived as the sister to the Trogloplacinae and Chasmocarcininae, and lacks diagnostic synapomorphies of both subfamilies. *Carinocarcinoides* is here treated as the type of a new subfamily. Based upon the present phylogenetic analysis, the Carinocarcinoidinae belongs in a monophyletic group with the Trogloplacinae and Chasmocarcininae within the Goneplacidae.

Fossil records.—Two species have been recorded from the lower Oligocene of Japan (Table 7).

Subfamily Trogloplacinae Guinot, 1986

Diagnosis.—Carapace rounded, sometimes poorly calcified; dorsal regions poorly defined; front straight with shallow median indentation; notch between frontal margin and supraorbital angle indistinct; upper orbital margin narrow without fissures; anterolateral margin cristate, entire or toothed; eye stalk short; merus of maxilliped 3 subquadrate, about as long as ischium; male abdomen not filling entire space between coxae of pereiopods 5, with somites 3–5 fused; thoracic sternum wide with sutures all interrupted; sternite 7 with posterolateral prolongation; sternite 8 visible in ventral view, overlying posterior part of sternite 7, with supplementary plate; chelipeds without dark-colored fingers; dactyli of pereiopods 2–5 with or without corneous tips; dactyli of pereiopods 5 styliform with or without setae; gonopod 1 stout, sinuous, with simple apex; gonopod 2 long, about as long as gonopod 1, with flagellum about same length as peduncle (from Davie and Guinot, 1996).

Type genus.—*Trogloplax* Guinot, 1986.

Genera included. — *Australocarcinus* Davie, 1987; *Trogloplax*.

Remarks.—The Trogloplacinae is derived as the sister group to the Chasmocarcininae based upon the present phylogenetic analysis. Davie and Guinot (1996) showed that the subfamily is most closely related to the Chasmocarcininae and is separated from it by the suture of the antennular region and differences in length and shape of the male gonopods.

Fossil records.—None.

Subfamily Chasmocarcininae Serène, 1964 *emend.*

Diagnosis.—Carapace with poorly defined dorsal regions; front straight with shallow median notch; notch between frontal margin and supraorbital angle indistinct; orbit usually small without upper orbital fissures; anterolateral margin entire or toothed, tapering anteriorly; eye stalk short; merus of maxilliped 3 suboval, about as long as ischium; male abdomen not filling entire space between coxae of pereiopods 5, with somites 3–5 fused; thoracic sternum wide with sutures all interrupted; sternite 7 with posterolateral prolongation; sternite 8 visible in ventral

Table 8. Distributions and geologic ranges of recognized fossil species of the subfamily Chasmocarcininae.

Taxa	Range	locality
Genus *Chasmocarcinus* Rathbun, 1898	EOCENE - Recent	
Chasmocarcinus robertsi Blow and Bailey, 1992	Miocene	U.S.A.
Chasmocarcinus seymourensis Feldmann and Zinsmeister, 1984	Eocene	Antarctica
Genus *Collinsius* Karasawa, 1993	L. OLIGOCENE	
Collinsius simplex Karasawa, 1993	L. Oligocene	Japan
Genus *Gillcarcinus* Collins and Morris, 1978	M. EOCENE	
Gillcarcinus amphora Collins and Morris, 1978	M. EOCENE	Pakistan
Genus *Falconoplax* Van Straelen, 1933	Eocene	
Falconoplax bicarinella Collins and Morris, 1976	Eocene	Barbados
Falconoplax kugleri Van Straelen, 1933	Eocene	Venezuela
Genus *Mioplax* Bittner, 1884	MIOCENE	
Mioplax socialis Bittner, 1884	Miocene	Austria
Genus *Orthakrolophos* Schweitzer and Feldmann, 2001a	EOCENE - PLIOCENE	
Orthakrolophos bartonensis (Quayle and Collins, 1981)	Eocene	England
Orthakrolophos bittneri (Morris and Collins, 1991)	Pliocene	Brunei
Orthakrolophos depressus (Quayle and Collins, 1981)	Eocene	England

view, overlying posterior part of sternite 7, with supplementary plate; sterno-abdominal cavity reaching anterior of sternite 4; chelipeds without dark-colored fingers; fingers sometimes elongate, deflexed; dactyli of pereiopods 2–5 without corneous tips; dactyli of pereiopods 5 sickle-shaped with setae; gonopod 1 stout, sinuous, with simple apex; gonopod 2 long, but shorter than gonopod 1, with flagellum much shorter than peduncle.

Type genus.—*Chasmocarcinus* Rathbun, 1898.

Genera included.—*Camatopsis* Alcock and Anderson, 1899, *Chasmocarcinus*; *Chasmocarcinops* Alcock, 1900, *Collinsius* Karasawa, 1993; *Falconoplax* Van Straelen, 1933, *Gillcarcinus* Collins and Morris, 1978; *Hephthopelta* Alcock, 1899; *Mioplax* Bittner, 1884; *Orthakrolophos* Schweitzer and Feldmann, 2001a; *Parapilumnus* Kossmann, 1877; *Scalopidia* Stimpson, 1858.

Discussion.—Serène (1964) originally included *Megaesthesius* Rathbun, 1909, within the Chasmocarcininae while Davie and Guinot (1996) excluded this genus from the subfamily. We concur with Davie and Guinot. Ng (2002) moved *Parapilumnus*, previously assigned to the Pilumnidae, to the Chasmocarcininae.

Schweitzer and Feldmann (2001a) recognized three extinct genera within the Chasmocarcininae. It is here expanded to include two genera *Gillcarcinus* and *Mioplax*. Collins and Morris (1978) erected the monotypic genus *Gillcarcinus* from the middle Eocene of Pakistan and referred the genus to the Xanthidae. The genus is moved to the Chasmocarcininae by having a narrow upper orbital margin without notches, a wide thoracic sternum, a narrow male abdominal somite 3, which does not fill the entire space between pereiopods 5, and fused male abdominal somites 3–5. Glaessner (1969) placed *Mioplax* from the Miocene of Austria within the Goneplacinae; however, the genus possesses a small orbit and long, slender deflexed fingers of chelipeds. Both characters strongly suggest that *Mioplax* should be assigned to the Chasmocarcininae. *Gillcarcinus* has three weakly developed anterolateral spines and *Mioplax* bears a well developed anterolateral spine. Most members of the Chasmocarcininae lack anterolateral spines, while the extant *Hephthopelta aurita* Rathbun, 1932, has two sharp anterolateral spines.

Fossil records.—Six genera are known from the fossil record (Table 8). *Collinsius*, *Falconoplax*, and *Orthakrolophos* are extinct genera. Fossil members of *Chasmocarcinus* are known from the Eocene of Antarctica and Miocene of the U.S.A.

A review of remaining fossil genera

"*Pilumnoplax* Stimpson, 1858"

Guinot (1969a, b, c; Tucker and Feldmann, 1990) have already discussed the nomenclatural status of the generic name *Pilumnoplax*, and have shown that the genus was a heterogenous group. Bachmayer (1953b) described a new species, *Pilumnoplax carnuntinus*, from the Miocene of Austria based upon a single incomplete specimen. In this specimen the front, a part of the upper orbital margin, and a part of the gastric region have been preserved; therefore, the species is not classified within any known genus of the

Goneplacidae (Müller, 1984; 1998). *Pilumnoplax soledadensis* Rathbun, 1926, described from the Eocene of the U.S.A., was moved to the panopeid genus *Panopeus* H. Milne Edwards, 1834 (Schweitzer, 2000).

Glyphithyreus Reuss, 1859 (= *Plagiolophus* Bell, 1858 *non* Pomel, 1847)

Glyphithyreus Reuss, 1859, has been placed within the goneplacid Carcinoplacinae (Balss, 1957, Glaessner, 1969 and many subsequent workers). *Glyphithyreus* lacks the poorly defined dorsal carapace regions, a straight front margin without median notch, the upper orbital margin with an indistinct supraorbital angle and without fissures, and a wide male abdomen with all free somites, all of which are diagnostic characters of the Goneplacinae (= Carcinoplacinae). *Glyphithyreus* is here placed in the panopeid Eucratopsinae because the carapace has well defined dorsal regions, the front consists of two rounded lobes, and the narrow male abdomen has fused somites 3–5. Previously known species of *Glyphithyreus* include: *G. ellipticus* Bittner, 1875, from the Eocene of Italy; *G. markgrafi* (Lőrenthey, 1907 [1909]), from the Eocene of Egypt; *G. sturgeoni* Feldmann *et al.*, 1998, from the Eocene of the U.S.A.; *G. weaveri* (Rathbun, 1926) from the Eocene of the U.S.A.; *G. wetherelli* (Bell, 1858) (type species) from the Eocene of Europe, Senegal, and Pakistan; and ? *G. wichmanni* Feldmann *et al.*, 1995, from the Danian of Argentina. Among these, *Glyphithyreus weaveri* was moved to the euryplacine *Orbitoplax* (Schweitzer, 2000).

Galenopsis A. Milne Edwards, 1865

A. Milne Edwards (1865) erected the genus *Galenopsis* containing five species within his "Galénides". Subsequently, Glaessner (1929) placed the genus within the Xanthidae, Balss (1957) and Glaessner (1969) removed it to the goneplacid Carcinoplacinae, and Schweitzer (2000) reassigned it to the Pilumnidae. We agree with Schweitzer's opinion. In *Galenopsis* a narrow, deflexed frontal margin is medially interrupted with prominent median lobes, and the narrow upper orbital margin possesses a distinct supraorbital angle. These characters do not match the diagnostic characters of the Goneplacinae (= Carcinoplacinae) but match those of the Pilumnidae as defined by Schweitzer (2000).

Galenopsis contains numerous species (Via, 1969) from the Eocene-Pliocene of Europe, Africa, India, and Fiji (Glaessner, 1969). Among these Müller and Collins (1991a) proposed a new monotypic genus, *Lobogalenopsis*, for *Galenopsis quadrilobatus* Lőrenthey, 1897, from the upper Eocene of Hungary. *Lobogalenopsis* was also excluded from the Goneplacidae and has been transferred to the Pilumnidae (Schweitzer, 2000).

Palaeograpsus Bittner, 1875

Palaeograpsus has long been placed within the Grapsidae MacLeay, 1838 (Glaessner, 1969). Previously known species of the genus are *Palaeograpsus attenuatus* Bittner, 1875, *P. bartonensis* Quayle and Collins, 1981, *P. depressus* Quayle and Collins, 1981, *P. guerini* Via, 1959, *P. inflatus* Bittner, 1875 (type species), *P. loczyanus* Lőrenthey, 1898a and *P. parvus* (Müller and Collins, 1991b) from the Eocene of Europe; and *P. bittneri* Morris and Collins, 1991 from the Pliocene of Brunei. Among these, Schweitzer and Feldmann (2001a) moved three species, *P. bartonensis, P. bittneri* and *P. depressus*, to *Orthakrolophos* within the Goneplacidae. *Palaeograpsus guerini* is similar to members of *Orthakrolophos*, but is characterized by having transverse ridges on the dorsal carapace, which are absent in *Orthakrolophos*; therefore, Schweitzer and Feldmann (2001a) did not include the species in *Orthakrolophos*.

Via (1969) suggested that *P. loczyanus* closely resembles members of *Carcinoplax* within the Goneplacinae. Karasawa and Kato (2001) also suggested that *P. inflatus* and *P. loczyanus* possess carapace and cheliped characters most like those of *Carcinoplax* and moved *Palaeograpsus* to the Goneplacidae. Reexamination of *P. inflatus* described by De Angeli (1995) strongly suggests that the genus does not belong within the Goneplacinae but within the panopeid Eucratopsinae or the Pseudorhombilidae because the front has a median notch (De Angeli, 1995, figs. 3.2, 3.4, pl. 2, figs. 2, 4), there are two fissures on the upper orbital margin (De Angeli, 1995, figs. 3.2, 3.4, pl. 2, figs. 2, 4), male abdominal somites 3 and 4 are incompletely fused (De Angeli, 1995, fig. 3.4, pl. 2, fig. 4) and male abdominal somite 1 fills the entire space between the coxae of pereiopods 5 (De Angeli, 1995, pl. 2, figs. 2–4). The panopeid Eucratopsinae is quite similar to the Pseudorhombilidae, and the differentiation between them is mainly based upon the male gonopod morphology (Hendrickx, 1998). However, male abdominal somite 1 in members of the Eucratopsinae does not fill the entire space between coxae of pereiopods 5; it is therefore considered best to place *Palaeograpsus inflatus* within the Pseudorhombilidae.

The monotypic genus *Carinocarcinus* Lőrenthey, 1898b, described from the middle Eocene of Germany, possesses carapace and cheliped characters like those of *Palaeograpsus sensu stricto*; however, in *Carinocarcinus* the carapace is much wider than long with four anterolateral teeth. *Carinocarcinus* may be also referred to the Pseudorhombilidae.

Telphusograpsus Lőrenthey, 1902

Glaessner (1969) showed that *Telphusograpsus* Lőrenthey, 1902, from the Eocene of Rumania, was synonymous with the grapsid genus *Varuna* H. Milne Edwards, 1830;

Table 9. The current status of the remaining extinct genera previously assigned to the Goneplacidae.

Genus	Previous study	Present study
Caprocancer Müller and Collins, 1991a	Goneplacidae	Xanthoidea *incertae sedis*
Carcinoplacoides Kesling, 1958	Goneplacidae: Carcinoplacinae	Portunidae
Carinocarcinus Lőrenthey, 1898b	Goneplacidae: Carcinoplacinae	Pseudorhombilidae
Chumaoia Hu and Tao, 1996	Goneplacidae	Leucosiidae
Eoplax Müller and Collins, 1991	Goneplacidae	Xanthoidea *incertae sedis*
Galenopsis A. Milne Edwards, 1865	Goneplacidae: Carcinoplacinae	Pilumnidae
Glyphithyreus Reuss, 1859	Goneplacidae: Carcinoplacinae	Panopeidae
Laevicarcinus Lőrenthey *in* Lőrenthey and Beurlen, 1929	Goneplacidae: Carcinoplacinae	Panopeidae
Lobogalenopsis Müller and Collins, 1991a	Goneplacidae	Pilumnidae
Maingrapsus Tessier *et al.*, 1999	Goneplacidae	Pilumnidae
Martinezicancer Van Straelen, 1939	Goneplacidae: Carcinoplacinae	Retroplumidae
Palaeograpsus Bittner, 1875	Goneplacidae	Pseudorhombilidae
Paracorallicarcinus Tessier *et al.*, 1999	Goneplacidae	Pilumnidae
Progeryona Hu and Tao, 1996	Goneplacidae	Xanthoidea *incertae sedis*
Styrioplax Glaessner, 1969	Goneplacidae *incertae sedis*	Xanthoidea *incertae sedis*
Telphusograpsus Lőrenthey, 1902	Goneplacidae	Xanthoidea *incertae sedis*

however, Karasawa and Kato (2001) suggested that *Telphusograpsus* is an independent genus and probably belongs to the Goneplacidae. *Telphusograpsus*, represented only by a carapace specimen, has a distinct supraorbital angle and upper orbital fissures; therefore, it could be referred to the Mathildellinae, the Euryplacinae, the Panopeidae or the Pseudorhombilidae. Complete familial and subfamilial arrangements of the genus must await discovery of the thoracic sternum and the male abdomen.

Laevicarcinus Lőrenthey *in* Lőrenthey and Beurlen, 1929

Laevicarcinus was originally placed within the Carcinoplacidae (= Goneplacidae), and within the goneplacid Carcinoplacinae by Balss (1957) and Glaessner (1969). Crosnier and Guinot (1969) indicated that the genus has a close resemblance to *Platychelonion*. Müller and Collins (1991a) reexamined the type specimen of the type species, *Laevicarcinus egerensis* Lőrenthey *in* Lőrenthey and Beurlen, 1929, from the upper Eocene of Hungary and removed *Laevicarcinus* to the Panopeidae.

Martinezicancer Van Straelen, 1939

Van Straelen (1939) described a new genus and species, *Martinezicancer schencki*, from the Palaeogene of California and suggested that the genus might represent a new family. Glaessner (1969) placed the genus within the Carcinoplacinae. *Martinezicancer schencki* has well defined dorsal regions, an arcuate protogastric ridge, an epibranchial region with two ovoid swellings, a mesogastric region with low transverse ridge, and a broad cardiac region with lobate swellings along lateral margins; therefore, it is assigned to *Archaeopus* Rathbun, 1908, redefined by Schweitzer and Feldmann (2001b), of the Retroplumidae Gill, 1894, and *Martinezicancer* becomes a junior synonym of *Archaeopus*.

Carcinoplacoides Kesling, 1958

The monotypic genus, *Carcinoplacoides*, erected with *C. flottei* Kesling, 1958, from the Pleistocene of Guam, was placed within the Carcinoplacinae (Kesling, 1958; Glaessner, 1969). Schweitzer *et al.* (2002) indicated that the species is synonymous with *Libystes nitidus* A. Milne Edwards, 1867, of the Portunidae.

Styrioplax Glaessner, 1969

Glaessner (1969) gave *Styrioplax* as a replacement generic name for *Microplax* Glaessner, 1928. This monotypic genus contains *S. exiguus* (Glaessner, 1928) from the Miocene of Austria. Glaessner (1969) did not place it in any known subfamily within the Goneplacidae. This genus is characterized by a small-sized carapace, a straight frontal margin with a median notch, small orbits, and a distinctly narrowed male abdomen. These characters indicate that the genus may belong to the Trogloplacinae, Chasmocarcininae, or pilumnid Rhizopinae *sensu lato*. The familial and subfamilial placements of *Styrioplax* remain obscure because detailed characters of the male abdomen of *S. exiguus* are poorly known.

Caprocancer Müller and Collins, 1991a and *Eoplax* Müller and Collins, 1991a

Müller and Collins (1991a) erected the two new goneplacid genera, *Caprocancer* and *Eoplax*, from the upper Eocene of Hungary. However, Müller and Collins (1991a) did not make any comparisons between *Caprocancer* and any known genera of decapods and indicated that there was a similarity between *Eoplax* and the grapsid

genus *Pachygrapsus* Randall, 1840. The familial placement of both genera remains obscure because they are based upon poorly preserved carapace specimens.

Chumaoia Hu and Tao, 1996

Hu and Tao (1996) erected a new monotypic genus, *Chumaoia*, with *C. johnferi* Hu and Tao, 1996, from the Miocene of Taiwan. Karasawa (1997, p. 67, footnote) showed that the genus is a junior synonym of *Typilobus* Stoliczka, 1871, of the Leucosiidae Samouelle, 1819.

Pregeryona Hu and Tao, 1996

Hu and Tao (1996) described a new genus and species, *Pregeryona taiwanica*, from the Miocene of Taiwan. The familial placement of the genus is doubtful because their description was brief and their materials poorly preserved.

Maingrapsus Tessier *et al.*, 1999 and *Paracorallicarcinus* Tessier *et al.*, 1999

Tessier *et al.* (1999) erected a new grapsid genus, *Maingrapsus*, from the Eocene of Italy. Karasawa and Kato (2001) suggested that the genus resembles *Paracorallicarcinus* Tessier *et al.*, 1999 and moved it to the Goneplacidae. *Maingrapsus* and *Paracorallicarcinus* possess carapace characters like those of the extant *Georgeoplax* Türkay, 1983 of the Pilumnidae (as Goneplacidae by Karasawa and Kato, 2001); therefore, both genera are removed to the Pilumnidae.

The current status of the sixteen genera discussed above is listed in Table 9.

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