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The systematic status of the genus *Miosesarma* Karasawa, 1989 with a phylogenetic analysis within the family Grapsidae and a review of fossil records (Crustacea: Decapoda: Brachyura)

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Abstract. **The genus *Miosesarma* Karasawa (Decapoda: Brachyura: Grapsidae) known from the Miocene of Japan is redefined. A phylogenetic analysis of 22 genera of the family Grapsidae MacLeay is provided based on 41 adult morphological characters. A single tree is produced (length = 85, CI = 0.565, RI = 0.807, RC = 0.456). The analysis supports the monophyly of the subfamilies Plagusiinae Dana, Grapsinae MacLeay and Varuninae H. Milne Edwards. The analysis suggests that the Sesarminae Dana is polyphyletic and that *Cyclograpsus* H. Milne Edwards, *Helice* De Haan, *Metaplax* H. Milne Edwards and *Miosesarma* are derived as sister taxa to varunines. The tribe Cyclograpscaea H. Milne Edwards is treated as a subfamily Cyclograpsinae (*nomen. transl.*) consisting of *Cyclograpsus* (type genus), *Helice*, *Heterograpsus* Campbell and Griffin, *Metaplax*, *Miosesarma* and *Paragrapsus* H. Milne Edwards, which were previously placed within the Sesarminae. Within the Grapsidae, the Varuninae and Cyclograpsinae are sister groups nested as the most derived clade, followed by the Sesarminae, Grapsinae, and the most basal Plagusiinae. Five subfamilies within the Grapsidae are redefined based on the phylogenetic analysis. During a review of fossil records of the Grapsidae, 25 species, 17 genera and four subfamilies are recognized as fossils. *Maingrapsus* Tessier *et al.*, *Palaeograpsus* Bittner, and *Telphusograpsus* Lőrenthey, known from the European Eocene, are referred to the family Goneplacidae H. Milne Edwards and *Sculptoplax* Müller and Collins from the Eocene of Hungary is referred to the Xanthidae MacLeay. Fossil grapsids exhibiting the dorsal carapace only can not confidently be referred to subfamilies.**

Key words: Brachyura, Crustacea, Decapoda, Grapsidae, Phylogeny

Introduction

The genus *Miosesarma* Karasawa, 1989 is an endemic genus known from the lower-middle Miocene of Japan (Karasawa, 1989, 1999; Kato, 1996). Karasawa (1989) originally placed the genus within the subfamily Sesarminae Dana, 1851 (Decapoda: Brachyura: Grapsidae) and demonstrated its close resemblance to extant sesarmines, *Helice* De Haan, 1835 and *Metaplax* H. Milne Edwards, 1852. Pereyra Lago (1993) and Schubart and Cuesta (1998) indicated that larval characters of *Helice* were similar to those of the grapsid subfamily Varuninae H. Milne Edwards, 1853. Schubart *et al.* (2000) suggested reclassification and phylogeny of the Grapsidae based upon molecular data, and that *Helice* and *Metaplax* should be classified within Varuninae.

The purpose of the present paper is to redefine the genus *Miosesarma* based on newly obtained specimens and to provide an adult morphology-based phylogenetic analysis for 22 genera of the Grapsidae. A review of fossil records of the Grapsidae is included.

Phylogenetic analysis of the family Grapsidae MacLeay, 1838

Materials and methods

A total of 25 species were examined with representatives from 22 genera including one extinct genus, *Miosesarma*, within the Grapsidae. Among these, extant species were collected from Japan, Thailand and Malaysia. The analyses were based on the examination of material deposited in the Mizunami Fossil Museum, Mizunami, Japan and the

Table 1. Taxa included in the analysis.

Family Grapsidae MacLeay, 1838
Subfamily Grapsinae MacLeay, 1838
Genus *Geograpsus* Stimpson, 1858
Geograpsus grayi (H. Milne Edwards, 1853)
Genus *Grapsus* Lamarck, 1801
Grapsus albolineatus Lamarck, 1818
Grapsus tenuicrustatus (Herbst, 1783)
Genus *Metopograpsus* H. Milne Edwards, 1853
Metopograpsus thukuhar (Owen, 1839)
Genus *Pachygrapsus* Randall, 1840
Pachygrapsus minutus A. Milne Edwards, 1873
Genus *Planes* Bowdich, 1825
Planes cyaneus Dana, 1851
Subfamily Sesarminae Dana, 1851
Genus *Chasmagnathus* De Haan, 1833
Chasmagnathus convexus De Haan, 1833
Genus *Cyclograpsus* H. Milne Edwards, 1837
Cyclograpsus intermedius Ortmann, 1894
Genus *Helice* de Haan, 1835
Helice leachi Hess, 1865
Genus *Metaplax* H. Milne Edwards, 1852
Metaplax crenulata (Gerstecker, 1856)
Genus *Miosesarma* Karasawa, 1989
Miosesarma japonicum Karasawa, 1989
Miosesarma naguraense Kato, 1996
Genus *Nanosesarma* Tweedie, 1950
Nanosesarma minutum (De Man, 1887)
Genus *Sesarma* Say, 1817
Sesarma (*Perisesarma*) *bidens* (De Haan, 1835)
Sesarma (*Parasesarma*) *pictum* (De Haan, 1835)
Genus *Sesarmops* Sèrene and Soh, 1970
Sesarmops intermedium (De Haan, 1835)
Subfamily Varuninae H. Milne Edwards, 1853
Genus *Acmaeopleura* Stimpson, 1858
Acmaeopleura parvula Stimpson, 1858
Genus *Eriocheir* De Haan, 1835
Eriocheir japonica (De Haan, 1835)
Genus *Gaetice* Gistl, 1848
Gaetice depressus (De Haan, 1833)
Genus *Hemigrapsus* Dana, 1851
Hemigrapsus sanguinensis (De Haan, 1835)
Genus *Pseudograpsus* H. Milne Edwards, 1837
Pseudograpsus sp.
Genus *Ptychognathus* Stimpson, 1858
Ptychognathus sp. aff. *P. ishii* Sakai, 1939
Genus *Varuna* H. Milne Edwards, 1830
Varuna litterata (Fabricius, 1798)
Subfamily Plagusiinae Dana, 1851
Genus *Percnon* Gistl, 1848
Percnon planissimum (Herbst, 1804)
Genus *Plagusia* Latreille, 1804
Plagusia dentipes De Haan, 1833

Family Xanthidae MacLeay, 1838
Genus *Leptodius* A. Milne Edwards, 1873
Leptodius nudipes (Dana, 1852)
Family Cancridae Latreille, 1803
Genus *Cancer* Linnaeus, 1758
Cancer amphioetus Rathbun, 1898

Natural History Museum and Institute, Chiba, Japan. The material examined is listed in Table 1. The subfamilial arrangement of the genera conforms to Sakai (1976), Manning and Holthuis (1981) and Karasawa (1989). Outgroups included two heterotrematous crabs, *Cancer amphioetus* Rathbun, 1898 (Cancridae) and *Leptodius nudipes* (Dana, 1852) (Xanthidae) outside of the Grapsidae (Table 1). Table 2 lists 41 adult morphological characters and character states used in the analysis. The missing data were scored unknown. The data matrix is provided in Table 3.

The phylogenetic analysis used PAUP version 3.1.1 (Swofford, 1993), utilizing a data matrix originating in MacClade version 3 (Maddison and Maddison, 1992). Heuristic search analyses were performed with the following options in effect: addition sequence, simple; one tree held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch stepping performed; MULPARS 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 uncertain; character state optimization, accelerated transformation (ACCTRAN). All characters were unordered, unscaled and equally weighted.

Characters

Forty-one characters were included in the data matrix (Table 3). There are 34 binary characters and 7 multistate characters. In the text, characters and character states are indicated by numbers in parentheses (e.g. 1-0 = character 1+character state 0).

Carapace.—In examined material the carapace is usually smooth (3-0; Figures 1.1, 1.2, 1.5-1.8, 4.11, 4.12, 4.15); however, all grapsine genera and a sesarmine *Sesarma* bear oblique ridges dorsally (3-1; Figure 1.3, 1.4). One outgroup taxon, *Cancer*, and two plagusiines, *Plagusia* and *Percnon*, possess frontal teeth (4-0; Figure 1.1, 1.2), while all other examined taxa have a straight frontal margin without teeth (4-1; Figure 1.3-1.8). Most taxa have a narrow orbital margin (5-0; Figure 1.1-1.4, 1.6), but a varunine *Hemigrapsus* and three sesarmines, *Chasmagnathus*, *Metaplax* and *Miosesarma*, possess wide orbital margins (5-1: Figures 1.5, 1.7, 1.8, 4.5, 4.11, 4.12, 4.15). Both outgroup taxa, all plagusiines and all grapsines lack infraorbital ridges (6-0; Figure 2.9-2.11); however, all sesarmines and all varunines bear infraorbital ridges (6-1;

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

Carapace

1 Ratio of carapace length/width: wider than long (0); about equal (1); long (2)
2 Maximum carapace width: midlength (0); anterior (1); posterior (2)
3 Carapace with oblique ridges dorsally: absent (0); present (1)
4 Frontal margin with frontal teeth: present (0); absent (1)
5 Orbital width: narrow (0); wide (1)
6 Infraorbital ridge: absent (0); present (1)
7 Upper orbital margin with notch: present (0); absent (1)
8 Lateral teeth: present (0); absent (1)
9 Pterygostomian and ventrolateral surfaces with oblique striae: absent (0); present (1)

Eye stalk and antennule

10 Eye stalk: short (0); long (1)
11 Antennule: not visible dorsally (0); visible dorsally (1)

Maxilliped 3

12 Ratio of merus/ischium: short (0); subequal (1); very short (2)
13 Anterolateral margin of merus: quadrate (0); expanded (1); convex (2)
14 merus and ischium with oblique, hairy ridge: absent (0); present (1)
15 Maxilliped 3 with wide rhomboidal gap: absent (0); present (1)
16 Exopod: wide (0); narrow (1)
17 Articulation of palp: anteromesial angle of merus (0); anterior margin of merus (1)
18 Dactylus: long (0); short (1)

Abdomen

19 Male abdomen: fused somites (0); 7 somites (1)
20 Male abdomen width; narrow (0); wide (1)

Thoracic sternum

21 Thoracic sternum width: narrow (0); wide (1)
22 Sternites 1 and 2: distinct (0); indistinct (1)
23 Suture between sternites 3 and 4: distinct (0); indistinct (1)
24 Median groove on sternite 3: present (0); absent (1)
25 Median groove on sternite 4: present (0); absent (1)
26 Button: present (0); absent (1)
27 Anterior end of sterno-abdominal cavity: shallow (0); sternite 4 (1); sternite 3 (2)
28 Cristiform margin of anterior sterno-abdominal cavity: absent (0); present (1)
29 Deeply concave lateral margin of sternites 3-4: absent (0); present (1)
30 Transverse groove on sternite 8: absent (0); present (1)
31 Sternite 8 visible in ventral view: indistinct (0); distinct (1)
32 Sternite 8 visible in posterior view: indistinct (0); distinct (1)
33 Location of male gonopore: coxae (0); sternite 8 (1)
34 Location of male gonopore on sternite 8: excluded (0); lateral (1); inner (2)

Gonopod

35 Gonopods 1: sinuous (0); twist (1); linear (2)

Pereiopods

36 Cheliped with elongate, slender palm: absent (0): present (1)
37 Chelipeds with pectinated crests on dorsal margin of propodus: absent (0); present (1)
38 Chelipeds with hairs on lateral surfaces of propodus near base of fingers: absent (0); present (1)
39 Chelipeds with tubercles on dorsal margin of dactylus: absent (0); present (1)
40 Pereiopods 2-5 meri with longitudinal ridge on lateral surface: absent (0); present (1)
41 Pereiopods 2-5 meri with oblique ridges on lateral surface: absent (0); present (1)

Table 3. Input data matrix of 41 characters and 24 genera. The last two taxa are outgroups. Missing character states are shown by ?.

Characters	0 0 0 0 0 0 0 0 0 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4
Taxa	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1
Geograpsus	0 1 1 1 0 0 1 0 0 0	0 1 1 0 1 1 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Grapsus	1 2 1 1 0 0 1 0 0 0	0 1 1 0 1 1 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Metopograpsus	0 1 1 1 0 0 1 1 0 0	0 0 1 0 1 1 1 0 1 1	1 0 1 1 1 0 2 1 0 0	0 0 1 1 1 0 0 0 0 0	1
Pachygrapsus	0 1 1 1 0 0 1 1 0 0	0 0 1 0 1 1 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Planes	2 0 1 1 0 0 1 0 0 0	0 0 1 0 1 0 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Chasmagnathus	0 0 0 1 1 1 1 0 0 1	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 0 2 1 1 0	0 0 1 1 2 0 0 0 0 0	0
Cyclograpsus	0 0 0 1 0 1 1 0 0 0	0 1 2 1 1 1 1 1 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Helice	0 0 0 1 1 1 1 0 0 1	0 1 2 1 1 1 1 1 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Metaplax	0 0 0 1 1 1 1 0 0 1	0 1 2 1 1 1 1 1 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 1 0 0 0 0	0
Miosesarma	0 0 0 1 1 1 1 0 0 1	0 1 2 ? 1 1 1 ? 1 0	1 ? 1 1 1 ? 2 1 0 1	1 1 1 2 2 1 0 ? 0 0	0
Nanosesarma	0 1 0 1 0 1 1 0 1 0	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 1 2 1 1 0	0 0 1 1 2 0 0 0 0 0	0
Sesarma	0 1 1 1 0 1 1 0&1 1 0	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 0 2 1 1 0	0 0 1 1 2 0 1 0 1 0	1
Sesarmops	1 0 0 1 0 1 1 0 1 0	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 1 2 1 1 0	0 0 1 1 2 0 1 0 1 0	0
Acmaeopleura	0 0 0 1 0 1 1 1 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 1 0 0	0
Eriocheir	1 2 0 1 0 1 1 0 0 0	0 0 1 0 0 0 1 0 1 1	1 0 1 1 1 0 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Gaetice	0 0 0 1 0 1 1 0 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 0 1 1 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Hemigrapsus	0 0 0 1 1 1 1 0 0 1	0 1 1 0 1 1 1 0 1 0	1 0 1 1 1 0 2 1 0 1	1 1 1 2 2 0 0 1 0 0	0
Pseudograpsus	1 0 0 1 0 1 1 0 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 1 0 0	0
Ptychognathus	0 1 0 1 0 1 1 0 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 1 1 1 2 1 0 0	1 1 1 2 2 0 0 1 0 0	0
Varuna	1 0 0 1 0 1 1 0 0 0	0 0 1 0 0 0 1 0 1 1	1 0 1 1 1 0 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Percnon	2 2 0 0 0 0 1 0 0 0	1 2 2 0 0 1 0 0 0 1	1 1 1 1 1 0 1 0 0 0	1 0 1 1 2 0 0 0 0 1	0
Plagusia	2 2 0 0 0 0 1 0 0 0	1 0 2 0 0 1 0 0 0 1	1 0 1 1 1 0 1 0 0 0	1 0 1 1 1 0 0 0 0 1	0
Leptodius	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0
Cancer	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

Figures 2.12–2.16, 4.5, 4.8). Upper orbital fissures are present in both outgroup taxa (7–0), and absent in all taxa of the Grapsidae (7–1; Figures 1.1–1.8, 4.11, 4.12, 4.15). Two grapsines, *Metopograpsus* and *Pachygrapsus*, and a varunine *Acmaeopleura* possess the anterolateral margin without teeth (8–1), but all other taxa have anterolateral teeth (8–0; Figures 1.1–1.8, 4.11, 4.12, 4.15). The pterygostomian and ventrolateral surfaces in three sesarmines, *Nanosesarma*, *Sesarma*, and *Sesarmops*, are ornamented with oblique striae (9–1), while those in remaining taxa are without oblique striae (9–0). A ratio of the carapace width/length [character 1; Figure 1.1–1.8] and a maximum carapace width [character 2, Figure 1.1–1.8] are variable in examined taxa and both characters seem to be consistent at the generic level.

Eye stalk and antennule.—In examined taxa a varunine *Hemigrapsus* and three sesarmines, *Chasmagnathus*, *Metaplax* and *Miosesarma* have slender, long eye stalks (10–1; Figures 1.5, 1.7, 1.8, 4.15), but others have stout, short ones (10–0; Figure 1.1–1.4, 1.6). The antennule in all plagusiines is visible dorsally in deep clefts of the front (11–1; Figure 1.1, 1.2), and this character defines the Plagusiinae (Alcock, 1900 and subsequent workers). In all other taxa antennules are not visible dorsally (11–0; Figures 1.3–1.8, 4.11, 4.12, 4.15).

Maxilliped 3.—The merus is shorter than the ischium in both outgroup taxa, three grapsines, *Metopograpsus*, *Pachygrapsus* and *Planes*, a plagusiine *Plagusia*, and two varunines, *Gaetice* and *Varuna* (12–0; Figure 2.9); it is much shorter than the ischium in only plagusiine *Percnon* (12–2; Figure 2.10). In remaining taxa its length is about equal to the ischium length (12–1; Figures 2.11–2.16, 4.10). The anterolateral corner of the merus is quadrate in both outgroups (13–0), is more or less expanded and strongly convex anterolaterally in all grapsines and all varunines (13–1; Figure 2.11, 2.15, 2.16), and is not expanded but convex in all plagusiines and all sesarmines (13–2; Figures 2.9, 2.10, 2.12–2.14, 4.10). The possession of an oblique, hairy ridge on the merus and ischium is a definitive character of the Sesarminae (Alcock, 1900 and subsequent workers). In examined taxa, all extant sesarmines possess this oblique, hairy ridge (14–1; Figure 2.12–2.14), which all other taxa lack. In all grapsines, all sesarmines and a varunine *Hemigrapsus*, a wide rhomboidal gap separates maxillipeds 3 (15–1; Figure 2.11–2.15), while maxillipeds 3 are completely closed together or leave a narrow gape in all other taxa (15–0; Figures 2.9, 2.10, 2.16, 4.10). The exopods are wide in two outgroup taxa and most varunines (16–0; Figure 2.16), but narrow in most grapsines, all plagusiines and all sesarmines (16–1; Figures 2.9–2.15, 4.10). In both

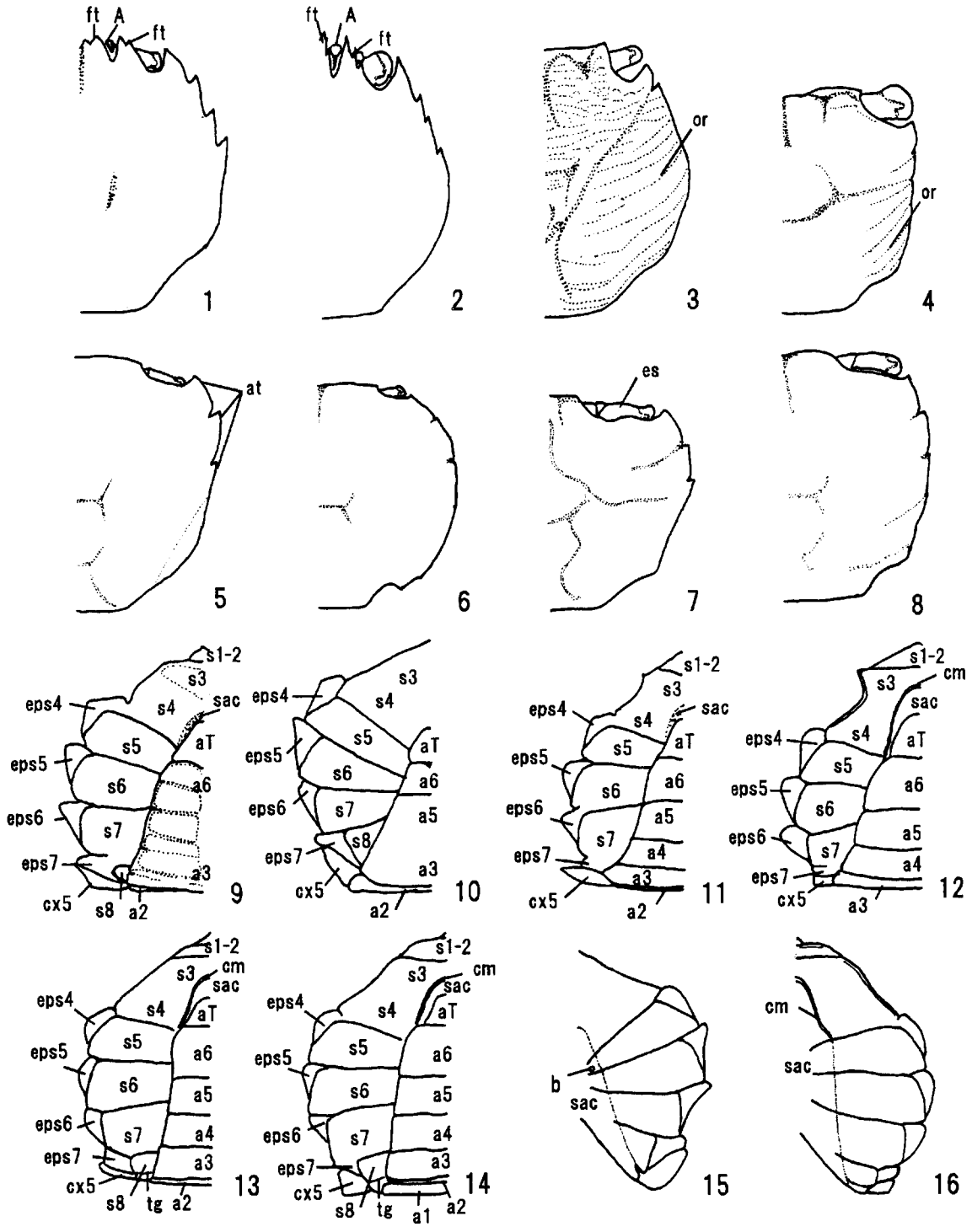

Figure 1. Diagrammatic representation of selected extant grapsid morphological characters. **1–8.** Dorsal view of carapace. **9–14.** Thoracic sternum and abdomen of male. **15, 16.** Thoracic sternum of male. **1, 9**: *Plagusia dentipes* De Haan, 1833 (CL = 43.5 mm). **2, 10, 15**: *Percnon planissimum* (Herbst, 1804) (CL = 33.8 mm). **3**: *Grapsus albolineatus* Lamarck, 1818 (CL = 57.6 mm). **4**: *Sesarma (Perisesarma) bidens* (De Haan, 1835) (CL = 12.5 cm). **5, 13, 16**: *Hemigrapsus sanguinensis* (De Haan, 1835) (CL = 18.9 mm). **6, 13**: *Cyclograpsus intermedius* Ortmann, 1894 (CL = 18.3 mm). **7**: *Metaplax crenulata* (Gerstecker, 1856) (CL = 29.4 mm). **8**: *Helice leachi* Hess, 1865 (CL = 14.6 mm). **12**: *Sesarmops intermedium* (De Haan, 1835) (CL = 24.1 cm). **Abbreviations**: **A**, antennule; **a1**, abdominal somite 1; **a2**, abdominal somite 2; **a3**, abdominal somite 3; **a4**, abdominal somite 4; **a5**, abdominal somite 5; **a6**, abdominal somite 6; **aT**, telson; **at**, anterolateral tooth; **b**, button; **cm**, cristiform margin of anterior sterno-abdominal cavity; **cx5**, coxa of pereiopod 5; **eps4**, episternite 4; **eps5**, episternite 5; **eps6**, episternite 6; **eps7**, episternite 7; **es**, eye stalk; **ft**, frontal tooth; **or**, oblique ridge; **s1-2**, thoracic sternites 1–2; **s3**, thoracic sternite 3; **s4**, thoracic sternite 4; **s5**, thoracic sternite 5; **s6**, thoracic sternite 6; **s7**, thoracic sternite 7; **s8**, thoracic sternite 8; **sac**, sterno-abdominal cavity; **tg**, transverse groove on sternite 8.

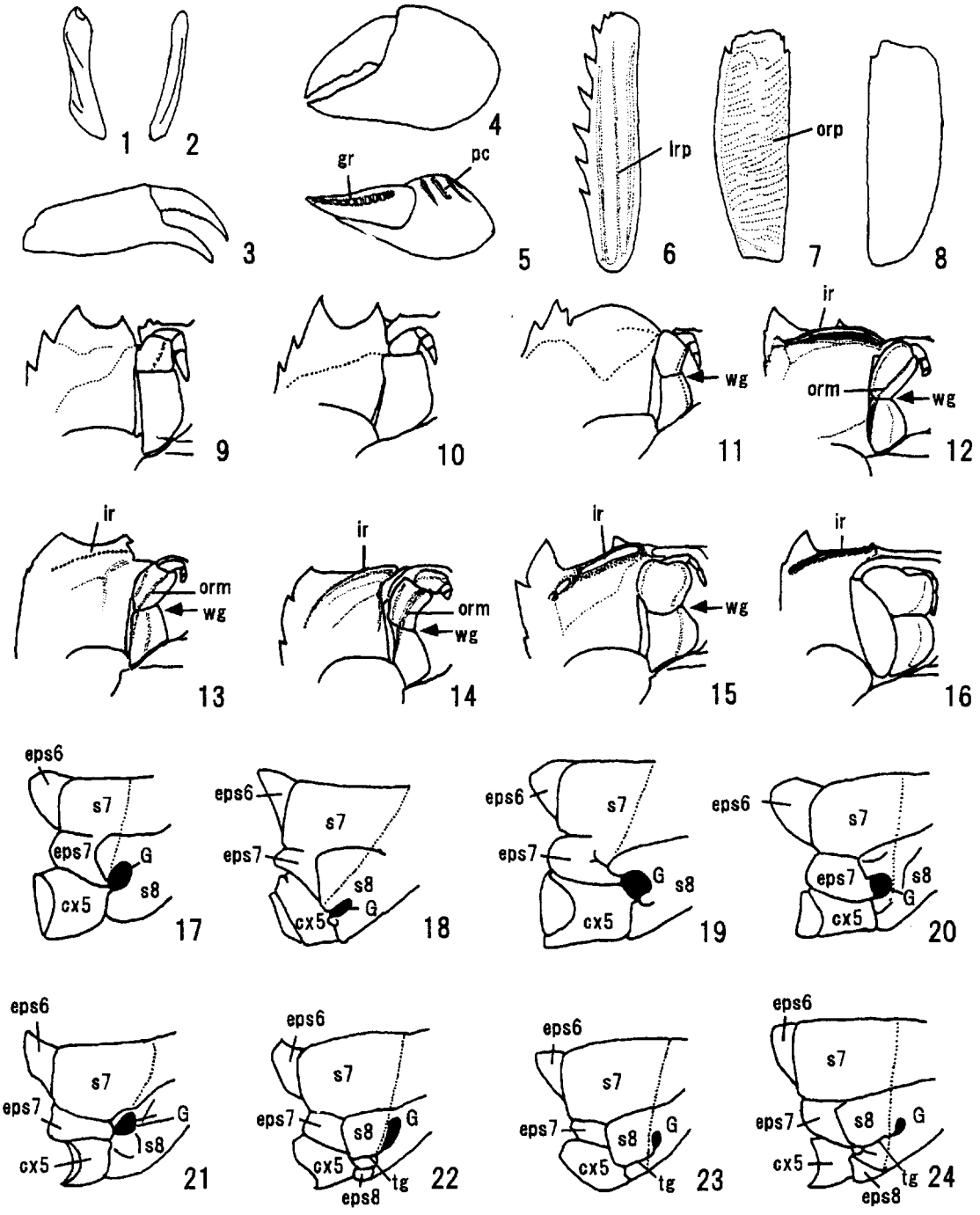

Figure 2. Diagrammatic representation of selected extant grapsid morphological characters. **1, 2.** Gonopod 1. **3–5.** Cheliped. **6–8.** Merus of pereiopod 4. **9–16.** Ventral view of carapace and maxilliped 3. **17–24.** Thoracic sternites 7 and 8. **1, 11, 19**: *Grapsus tenuicrustatus* (Herbst, 1783) (CL = 36.1 mm). **2, 13, 23**: *Cyclograpsus intermedius* Ortmann, 1894 (CL = 18.3 mm). **4, 5**: *Sesarma (Parasesarma) pictum* (De Haan, 1835) (CL = 17.4 mm). **6, 9, 17**: *Plagusia dentipes* De Haan, 1833 (CL = 43.5 mm). **7**: *Grapsus albolineatus* Lamarck, 1818 (CL = 57.6 mm). **8**: *Helice leachi* Hess, 1865 (CL = 14.6 mm). **10, 18**: *Percnon planissimum* (Herbst, 1804) (CL = 33.8 mm). **12, 20**: *Sesarmops intermedium* (De Haan, 1835) (CL = 24.1 mm). **14, 24**: *Metaplax crenulata* (Gerstecker, 1856) (CL = 29.4 mm). **15, 22**: *Hemigrapsus sanguinensis* (De Haan, 1835) (CL = 18.9 mm). **16**: *Ptychognathus* sp. aff. *P. ishii* Sakai, 1939 (CL = 8.3 mm). **21**: *Chasmagnathus convexus* De Haan, 1833 (CL = 40.1 mm). **Abbreviations**: **cx5**, coxa of pereiopod 5; **eps6**, episternite 6; **eps7**, episternite 7; **eps8**, episternite 8; **G**, gonopore; **gr**, tubercles on dorsal margin of dactylus; **ir**, infraorbital ridge; **lrp**, longitudinal ridge on lateral surface of pereiopod 4; **orm**, oblique, hairy ridge on merus and ischium of maxilliped 3; **orp**, oblique ridge on lateral surface of pereiopod 4; **pc**, pectinated crests on dorsal margin of propodus; **s7**, thoracic sternite 7; **s8**, thoracic sternite 8; **tg**, transverse groove on sternite 8; **wg**, wide rhomboidal gap between maxillipeds 3.

outgroup taxa and all plagusiines the palp articulates at an anteromesial angle of the merus (17-0; Figure 2.9, 2.10); however, in all other taxa it articulates at an anterior margin (17-1; Figures 2.11-2.16, 4.10). The dactyli are long in both outgroup taxa, all plagusiines, all grapsines and all varunines (18-0; ; Figure 2.9-2.11, 2.15, 2.16), but is reduced and short in all extant sesarmines (18-1; Figure 2.12-2.14).

Abdomen.—In all grapsines, all sesarmines and all varunines, the male abdomen consists of seven unfused abdominal somites (19-1; Figures 1.11-1.14, 4.9, 4.14), while the outgroup taxa and all plagusiines possess fused somites (19-0; Figure 1.9, 1.10). The outgroup taxa, most varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma*, have a narrow male abdomen (20-0; Figures 1.13, 1.14, 4.3, 4.9, 4.14), while the male abdomen is wide and fills the entire space between pereiopods 5 in all grapsines, all plagusiines, two varunines, *Varuna* and *Eriocheir*, and three sesarmines, *Nanosesarma*, *Sesarma* and *Sesarmops* (20-1; Figure 1.9-1.12).

Thoracic sternum.—All grapsids possess a wide thoracic sternum (21-1; Figures 1.9-1.14, 4.2, 4.3, 4.6, 4.7, 4.9, 4.10, 4.13, 4.14, 4.16), but the two outgroup taxa have a narrow sternum (21-0). In the outgroup taxa and most extant grapsids, thoracic sternites 1-2 are distinct (22-0; Figure 1.9, 1.11-1.14), while in only plagusiine *Percnon* they are reduced and indistinct (22-1; Figure 1.10). In both outgroup taxa, a suture between sternites 2 and 3 is distinct and well defined as a deep groove (23-0); however, the suture in all grapsids is indistinct and poorly defined (23-1; Figures 1.9-1.14, 4.13, 4.14). A median groove on sternite 3 is present in one outgroup taxon, *Cancer*, and a varunine *Gaetice* (24-0) , but it is absent in all other examined taxa (24-1; Figures 1.9-1.14, 4.6, 4.13). A median groove on sternite 4 is present in both outgroup taxa (25-0), but is absent in all grapsid taxa (25-1; Figures 1.9-1.14, 4.6). Guinot and Bouchard (1998) described the button on the male thoracic sternum within the Brachyura and indicated that in their examined material plagusiines and grapsines possessed the button on the sternum (Figure 1.15), but that the button was either present or absent within the Varuninae and Sesarminae (Figures 1.16, 4.6). In our examined material the button [character 26] is present in both outgroup taxa, all grapsines and all plagusiines, and present or absent in sesarmines and varunines. The outgroup taxon, *Cancer*, possesses a shallow sterno-abdominal cavity (27-0), while all other examined taxa have a deep sterno-abdominal cavity (Figures 1.9-1.16, 4.6). The anterior end of the sterno-abdominal cavity reaches the anterior sternite 4 in one outgroup, *Leptodius*, most grapsines and all plagusiines (27-1; Figure 1.9-1.11, 1.15), and reaches sternite 3 in all sesarmines, all varunines and a grapsine *Metopograpsus* (27-2; Figures 1.12-1.14, 1.16, 4.6, 4.13, 4.14). Guinot and Bouchard (1998) mentioned that in the Thoracotremata a deep sterno-abdominal cavity was often anteriorly delimited by a cristiform margin. In our examined material, the cristiform margin is well defined in all sesarmines, all varunines and a grapsine *Metopograpsus* (28-1; Figures 1.12-1.14, 1.16, 4.6, 4.13), but absent in both outgroup taxa, all plagusiines and most grapsines (28-0; Figure 1.9-1.11, 1.15). *Nanosesarma*, *Sesarma* and *Sesarmops*, members of the Sesarminae, possess deeply concave lateral margins of sternites 3-4 (29-1; Figure 1.12). In both outgroup taxa and the sesarmine genera, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops*, the male abdomen covers entirely the sternite 8 (31-0, 32-0; Figure 1.9-1.12). The sternite 8 is not covered entirely by the abdomen and is visible in ventral and posterior view in all varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma* (31-1, 32-1; Figures 1.13, 1.14, 4.14), but in both plagusiine taxa the male abdomen fills the entire space between pereiopods 5 (31-0; Figure 1.9, 1.10) and is visible in ventral view (32-1; Figure 1.9, 1.10).

In members of the section Heterotremata Guinot, 1977, male gonopores are located on coxae and/or the thoracic sternite 8, and the gonopores in all representatives within the Thoracotremata Guinot, 1977 are on sternite 8 (Guinot, 1977; Guinot and Richer de Forges, 1997). If male gonopores are situated on the inner part of sternite 8, the sternite is traversed by a groove which arises from the coxa and joins the gonopore or is interrupted (Figure 2.22-2.24) (Guinot, 1979; Tavares, 1992; Jamieson, Guinot and Richer de Forges, 1996). Both outgroups, all grapsines, all plagusiines, and the sesarmine genera, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops*, lack a transverse groove on the sternite 8 (30-0; Figure 2.17-2.20); however, most varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma*, have a groove on sternite 8 (30-1; Figures 2.22-2.24, 4.13, 4.14). In all grapsids of the Thoracotremata male gonopores are opened on thoracic sternite 8 (34-1; Figures 2.17-2.24, 4.13, 4.14), but in both outgroup taxa belonging to the Heterotremata they are located on the coxae (34-0). When male gonopores are situated on sternite 8, they are opened on lateral parts of sternite 8 in all plagusiines, all grapsines and the sesarmines, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops* (34-1; Figure 2.17-2.21). The male gonopores are located on the inner part of sternite 8 (34-2; Figures 2.22-2.24, 4-13, 4.14) in all varunines and the sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma*.

Gonopod.—Only one character is found to be informative. Male gonopods 1 are sinuous (35-0) in both outgroup taxa, twisted (35-1; Figure 2.1) in a plagusiine *Plagusia* and all grapsines, and linear (35-2; Figures 2.2, 4.7, 4.13, 4.14, 4.16) in a plagusiine *Percnon*, all sesarmines and all varunines.

Pereiopods. — Two sesarmine genera, *Metaplax* and *Miosesarma*, possess a slender, elongate palm of the male chelipeds (36-1; Figures 2.3, 4.4), while all other taxa possess a short, massive palm (36-0; Figure 2.4). In examined material two sesarmines, *Sesarma* and *Sesarmops*, have chelipeds with pectinated crests on the dorsal margin of the propodus (37-1; Figure 2.5) and with tubercles on the dorsal margin of the dactylus (39-1; Figure 2.5). Four varunines, *Acmaeopleura*, *Hemigrapsus*, *Pseudograpsus* and *Ptychognathus*, bear hairs on the lateral surface of the propodus of the cheliped near the base of fingers (38-1), which all other extant taxa lack. Longitudinal ridges on the lateral surface of meri of pereiopods 2-5 are present in the Plagusiinae (40-1; Figure 2.6), but absent in all other taxa (40-0; Figures

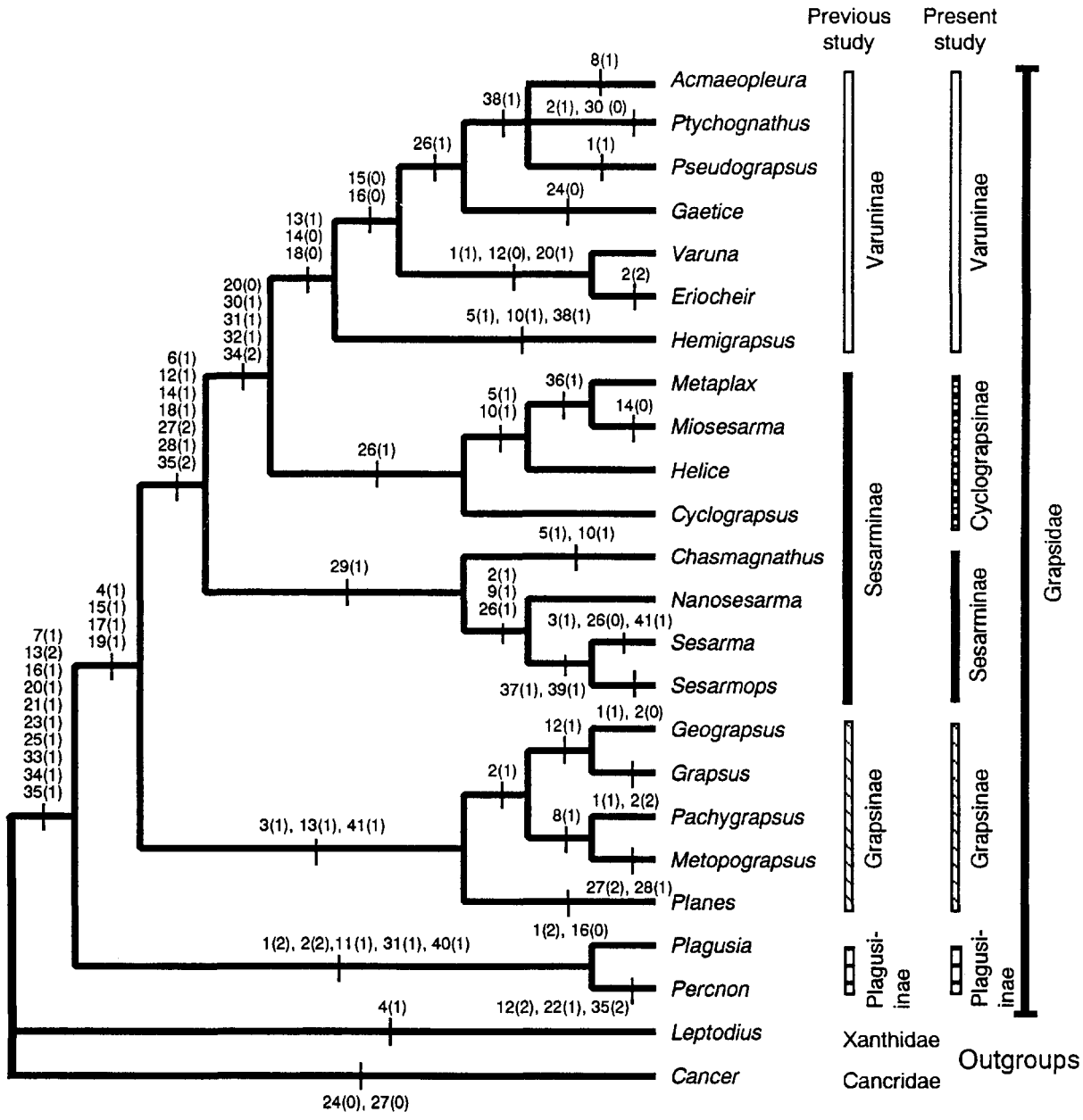

Figure 3. Single parsimonious tree of 22 genera within the Grapsidae. Length = 85, Consistency index = 0.565, Retention index = 0.807, Rescaled consistency index = 0.456. Character changes are indicated.

2.8, 4.15). All taxa within the Grapsinae and a sesarmine *Sesarma* possess oblique ridges on the lateral surface of meri of pereiopods 2–5 (41–1; Figure 2.7), which all other taxa lack.

Results

The present analysis yielded a single parsimonious tree, 85 steps long with a consistency index (CI) of 0.565, a retention index (RI) of 0.807 and a rescaled consistency index (RC) of 0.456 (Figure 3). The monophyly of the Grapsidae is well supported by ten characters, five of which are unique and unreversed: the upper orbital margin without distinct notches (7–1), a wide thoracic sternum (21–1), the absence of a suture between thoracic sternites 3 and 4 (23–1), the absence of a median groove on the thoracic sternite 4 (25–1), and male gonopores opened on thoracic sternites 8 (33–1). Our analysis suggests that within the Grapsidae the Plagusiinae is the most basal clade, followed by the Grapsinae, Sesarminae and the most derived Varuninae. The Plagusiinae is united by five characters, three of which are unique: antennules which are visible dorsally (11–1), sternite 8 which is visible ventrally (31–1), and the posses-

sion of longitudinal ridges on meri of pereiopods 2–5 (40–1).

The Grapsinae+Sesarminae+Varuninae clade is unambiguously united by four synapomorphies, three of which are never reversed: the absence of frontal teeth (4–1), the palp of the maxilliped 3 which articulates at an anterior margin of the merus (17–1), and the male abdomen with seven free somites (19–1). Three synapomorphies, the carapace with oblique ridges dorsally (3–1), an expanded anterolateral corner of the merus of the maxilliped 3 (13–1), and the presence of meri of pereiopods with oblique ridges on the lateral surface (41–1), well support the monophyly of the Grapsinae. The analysis shows the sister-group relationship of the Grapsinae and Sesarminae+Varuninae clades. The Sesarminae+Varuninae clade is unambiguously united by seven characters of which four are never reversed: the possession of the infraorbital ridge (6–1), an anterior margin of the sterno-abdominal cavity reaching the thoracic sternite 3 (27–2), the presence of the cristiform margin of an anterior sterno-abdominal cavity (28–1), and linear gonopods 1 (35–2).

Our analysis suggests that the Sesarminae as customarily defined is a polyphyletic group. The monophyly of the *Chasmagnathus+Nanosesarma+Sesarma+Sesarmops* clade is united by only one character, deeply concave lateral margins of thoracic somites 3 and 4 (29–1), and is derived as the sister to the Varuninae+four remaining sesarmines (*Cyclograpsus*, *Metaplax*, *Helice*, *Miosesarma*) clade. The Varuninae and *Metaplax+Miosesarma+Helice+Cyclograpsus* clades are unambiguously united by four unique synapomorphies: the presence of a transverse groove on the thoracic sternite 8 (30–1), the thoracic sternite 8 which is visible in ventral and posterior view (31–1, 32–1), and male gonopores located on the inner part of the thoracic sternite 8 (34–2). The Varuninae clade is the sister to the *Metaplax +Miosesarma+Helice+Cyclograpsus* clade and is united by three characters, an expanded anterolateral corner of the merus of maxilliped 3 (13–1), the absence of oblique, hairy ridges on the merus and ischium of maxilliped 3 (14–0) and a long dactylus of maxilliped 3 (18–0).

Discussion

The family Grapsidae is presently divided into four subfamilies, Grapsinae, Plagusiinae, Sesarminae and Varuninae, based on the adult morphology (i.e., Alcock, 1900, Rathbun, 1918, Sakai, 1976, Guinot, 1979, Manning and Holthuis, 1981). However, the subfamilial arrangement of some genera within the Grapsidae has been questioned by recent contributions based on larval morphology (Pereyra Lago, 1993, Schubart and Cuesta, 1998 and many more) and molecular data using the 16S rRNA (Schubart *et al.*, 2000). Guinot and Bouchard (1998) mentioned that both Sesarminae and Varuninae were artificial groups. Rice (1980) noted that the Grapsinae seemed to have the most advanced zoeae within the Grapsidae and thought that the four subfamilies within the Grapsidae evolved independently from a more primitive stock of which there is no larval evidence. Schubart, Neigel and Felder (2000) and Schubart *et al.* (2000) provided molecular phylogenies of the Grapsidae. Although Schubart *et al.* (2000) treated four subfamilies within the Grapsidae as families, we place four subfamilies within the Grapsidae according to previous studies of Alcock (1900), Sakai (1976), Manning and Holthuis (1981) and others.

The adult morphology-based phylogeny presented herein and the molecular phylogeny of Schubart *et al.* (2000) each of which supports monophyly of the Grapsidae, are each largely supported, but they differ somewhat in topology. Ten characters, five of which are unique and unreversed, well support the monophyly of the family Grapsidae in this study. Schubart, Neigel and Felder (2000) showed the paraphyly of the family based on molecular data using 16S rRNA but the subsequent study of Schubart *et al.* (2000) suggested the monophyly of the family; we concur that the Grapsidae is monophyletic.

Our morphology-based phylogenetic analysis suggests the Plagusiinae is the earliest derived crown-group subfamily, followed by the Grapsinae. These results support the molecular phylogeny of the family by Schubart *et al.* (2000). The Plagusiinae and Grapsinae are monophyletic by our analysis. The monophyly of the Grapsinae is well supported by molecular data (Schubart *et al.*, 2000) and larval morphology (Rice, 1980, Cuesta and Schubart, 1999). Schubart *et al.* (2000) showed that the Plagusiinae was polyphyletic and that only *Percnon* was the most basal clade. However, the larval morphology of *Percnon* is most similar to that of *Plagusia* within the Grapsidae (Rice, 1980) which supports our tree in which *Percnon* and *Plagusia* occur together on one clade.

The subfamily Sesarminae is polyphyletic. The *Metaplax +Miosesarma+Helice+Cyclograpsus* clade is readily distinguished from the *Chasmagnathus+Nanosesarma+Sesarma +Sesarmops* clade by having four unique synapomorphies and the former is derived as the sister to the Varuninae clade. One unique synapomorphy supports the monophyly of the latter sesarmine clade. The Sesarminae was previously discriminated from the other three subfamilies by the possession of an oblique, hairy ridge on the merus and ischium of the maxilliped 3 (Alcock, 1900 and subsequent workers). In our analysis the presence of this ridge [character 14] is not a unique character and the character state in the Varuninae clade is the absence of the ridge, a reversal of the state identified as a synapomorphy of the Sesarminae+Varuninae clade. Guinot (1979) indicated that male gonopores of *Cyclograpsus*, *Helice* and *Metaplax* together with those of varunine genera were located on the inner part of thoracic sternite 8. Examination of American sesarmine genera based on molecular data (Schubart *et al.*, 2000) suggested that *Chasmagnathus* and *Cyclograpsus* should be classified within the Varuninae and that the remaining Sesarminae group was monophyletic. Pereyra Lago (1993) and Schubart and Cuesta (1998) also showed that larval characters of three genera, *Chasmagnathus*, *Cyclograpsus* and *Helice*, were similar to those of members within the Varuninae rather than *Sesarma* sensu lato. However, our adult-morphology based analysis indicates that *Chasmagnathus* remains within the "Sesarminae" clade and that *Cyclograpsus* and *Helice* belong to another clade which is derived as the sister to the Varuninae clade and are more derived than the "Sesarminae" clade.

The present analysis separates the *Metaplax+Miose-*

sarma+Helice+Cyclograpsus clade from the "Sesarminae" clade and strongly suggests that genera placed within the clade should be classified in another subfamily. H. Milne Edwards (1853) erected a new tribe Cyclograpscaea within his subfamily Grapsinae (= Grapsidae see Alcock, 1900). Six genera, *Pseudograpsus, Heterograpsus* Lucas, 1849 (= *Brachynotus* de Haan, 1833), *Cyclograpsus, Paragrapsus* H. Milne Edwards, 1853, *Pralynotus* de Haan, 1835 (= *Gaetice*), and *Chasmagnathus* were originally included in the Cyclograpscaea. Subsequently, Alcock (1900) redefined four subfamilies within the Grapsidae, and synonymized the Cyclograpscaea with the Sesarminae and Varuninae. He moved *Pseudograpsus, Brachynotus* and *Gaetice* to the Varuninae and *Cyclograpsus* and *Chasmagnathus* to the Sesarminae. Tesch (1918) referred *Paragrapsus* to the Sesarminae. In our phylogenetic analysis, *Pseudograpsus* and *Gaetice* are classified within the Varuninae, and *Chasmagnathus* is placed within the Sesarminae. Two genera, *Brachynotus* and *Paragrapsus*, were not examined in our analysis. We treat the tribe Cyclograpscaea which contains a remaining genus *Cyclograpsus* as a subfamily Cyclograpsinae H. Milne Edwards, 1853 *nomen. transl. herein* (type genus: *Cyclograpsus* by present designation). Three additional genera, *Helice, Miosesarma* and *Metaplax* are included in the Cyclograpsinae based on the present analysis. The Cyclograpsinae is distinguished from the Sesarminae in that male gonopores are located on the inner part of thoracic sternite 8, sternite 8 is visible in ventral and poserior view, and bears a distinct transverse groove that extends from the articulation of the coxa-sternal junction to the gonopore. The present subfamily differs from the Varuninae derived as its sister group by the presence of an oblique, hairy ridge on the merus and ischium and a short, reduced dactylus of maxilliped 3, and the absence of an anterolateral expansion of the merus of maxilliped 3. *Paragrapsus and Heterograpsus* Campbell and Griffin, 1966 have an oblique, hairy ridge on the merus and ischium of maxilliped 3, male gonopores located on the inner part of the thoracic sternite 8, and a transverse groove on sternite 8; therefore, it is suggested that both genera should be referred to the Cyclograpsinae.

Within examined material the Varuninae is at least monophyletic. However, Schubart *et al.* (2000) showed using molecular data that the subfamily was polyphyletic, *Euchirograpsus* H. Milne Edwards, 1853, a non Northwestern Pacific genus, was the sister taxon of *Plagusia*, and *Platychirograpsus* de Man, 1896 and *Glyptograpsus* Smith, 1870, which both are American endemic genera, were derived as the sister to the Sesarminae. The reexamination of the systematic position of these three genera is beyond the scope of our study, whilst examination of the detail adult morphology would be necessary to confirm the reassignment of these genera.

The location of gonopores on thoracic sternite 8 [character 34] and the possession of the infraorbital ridge [character 6] are supported as useful phylogenetic characters. The gonopores are located on the lateral margin of sternite 8 in the Plagusiinae, Grapsinae and Sesarminae, and on the inner part of sternite 8 in the Cyclograpsinae and Varuninae. The Plagusiinae and Grapsinae lack the infraorbital ridge, while the Sesarminae, Cyclograpsinae and Varuninae possess the infraorbital ridge.

The following diagnosis is given for five subfamilies based on our phylogenetic analysis:

Subfamily Plagusiinae Dana, 1851. — Front with teeth. Antennule visible dorsally. Infraorbital ridge absent. Maxillipeds 3 without wide rhomboidal gap and oblique, hairy ridge on merus and ischium; anterolateral corner not expanded, convex; palp articulating at anteromesial corner of merus; exopod narrow. Male abdomen wide, filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 4. Sternal button present in male. Male gonopore located on lateral margin of thoracic sternite 8. Meri of pereiopods usually bearing longitudinal ridges laterally and spines dorsally (modified from Rathbun, 1918).

Subfamily Grapsinae MacLeay, 1838. — Front usually strongly deflexed. Carapace usually with oblique ridges dorsally. Infraorbital ridge absent. Maxillipeds 3 usually separated by wide rhomboidal gap, without oblique, hairy ridge on merus and ischium; anterolateral corner of merus usually expanded; palp articulating at anterior margin of merus; exopod narrow. Male abdomen wide, filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity usually reaching thoracic sternite 4. Strernal button present in male. Male gonopore located on lateral margin of thoracic sternite 8 (modified from Rathbun, 1918).

Subfamily Sesarminae Dana, 1851. — Front strongly deflexed. Infraorbital ridge present. Maxillipeds 3 separated by wide rhomboidal gap, and with oblique, hairy ridge on merus and ischium; anterolateral corner of merus not expanded, convex; palp articulating at anterior margin of merus; exopod narrow. Male abdomen wide, filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 3. Sternal button present or absent in male. Male gonopore located on lateral margin of thoracic sternite 8 (modified from Rathbun, 1918).

Subfamily Varuninae H. Milne Edwards, 1853. — Front moderately or little deflexed. Infraorbital ridge present. Maxillipeds 3 moderately or slightly gaping, without oblique, hairy ridge on merus and ischium; anterolateral corner of merus expanded; palp articulating at anterior margin of merus; exopod usually wide. Male abdomen rarely filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 3. Transverse groove usually present on sternite 8. Sternal button usually present in male. Male gonopore located on inner part of thoracic sternite 8 (modified from Rathbun, 1918).

Subfamily Cyclograpsinae H. Milne Edwards, 1853 [nom. transl. *of Tribe Cyclograpscaea*]. — Front strongly deflexed. Infraorbital ridge present. Maxillipeds 3 separated by wide rhomboidal gap, with oblique, hairy ridge on merus and ischium; anterolateral corner of merus not expanded, convex; palp articulating at anterior margin of merus; exopod narrow. Male abdomen not filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity

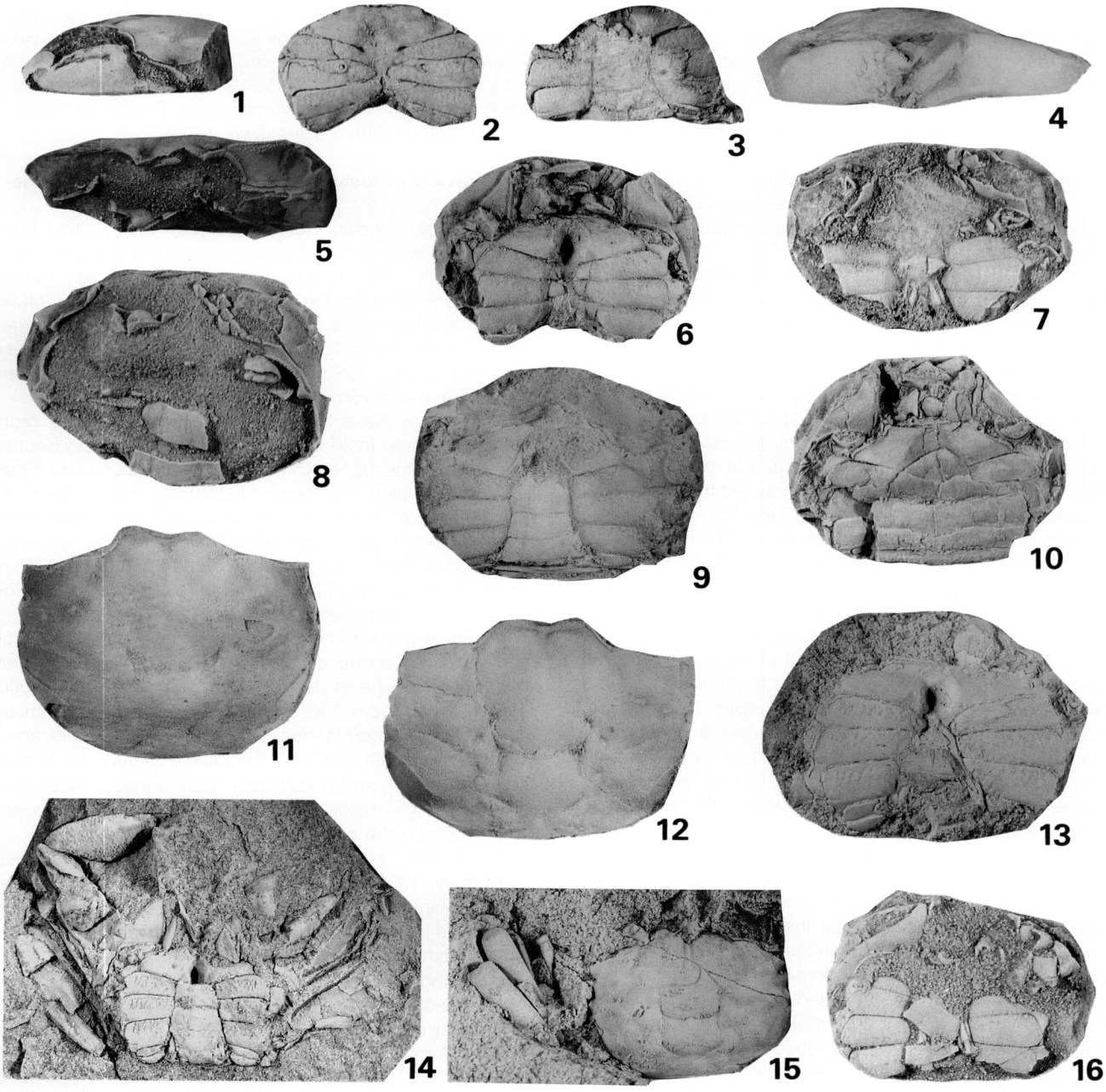

Figure 4. **1–13, 15, 16.** *Miosesarma japonicum* Karasawa, 1989. **1:** MFM83343, middle Miocene Masuda Group, frontal view of carapace and lateral view of cheliped, female, ×2.5. **2:** MFM39154, middle Miocene Bihoku Group, ventral view of thoracic sternum, female, ×2.5. **3:** MFM39155, middle Miocene Bihoku Group, ventral view of thoracic sternum and abdomen, male, ×2.5. **4:** MFM9146, lower Miocene Mizunami Group, lateral view of chelipeds, male, ×1.5. **5:** MFM83344, middle Miocene Masuda Group, frontal view of carapace, male, ×2.5. **6:** MFM39156, middle Miocene Bihoku Group, ventral view of carapace, thoracic sternum and maxillipeds 3, male, ×2.5. **7:** MFM83345, middle Miocene Masuda Group, ventral view of carapace, thoracic sternum and gonopods 1, male, ×2.5. **8:** MFM83344, middle Miocene Masuda Group, ventral view of carapace and abdomen, male, ×2.5. **9:** MFM9017 (paratype), lower Miocene Mizunami Group, ventral view of thoracic sternum and abdomen, male, ×2.5. **10:** MFM39157, middle Miocene Bihoku Group, ventral view of carapace, thoracic sternum, abdomen and maxillipeds 3, female, ×2.5. **11:** MFM9016 (paratype), lower Miocene Mizunami Group, dorsal view of carapace, male, ×2.5. **12:** MFM9015 (holotype), lower Miocene Mizunami Group, dorsal view of carapace, male, ×2.5. **13:** MFM9147, lower Miocene Mizunami Group, ventral view of thoracic sternum, abdomen and gonopods 1, male, ×2.5. **15:** MFM39158, middle Miocene Bihoku Group, dorsal view of carapace and eye stalk, and lateral view of pereiopods, male, ×2.5. **16:** MFM83346, middle Miocene Masuda Group, ventral view of carapace, thoracic sternum, abdomen and gonopods 1, male, ×2.5. **14.** *Miosesarma naguraense* Kato, 1996, MFM83347, middle Miocene Nagura Formation, ventral view of thoracic sternum, abdomen and gonopods 1, male, ×1.5.

reaching thoracic sternite 3. Transverse groove present on sternite 8. Sternal button usually absent in male. Male gonopore located on inner part of thoracic sternite 8 (redefined here).

Redefinition of the genus *Miosesarma* Karasawa, 1989

Subfamily Cyclograpsinae H. Milne Edwards, 1853
Genus ***Miosesarma*** *Karasawa, 1989*

Type species.—*Miosesarma japonica* Karasawa, 1989 by monotypy.

Species included. — *Miosesarma japonicum* Karasawa, 1989 (Figure 4.1 - 4.13, 4.15, 4.16) and *Miosesarma naguraense* Kato, 1996 (Figure 4.14).

Revised diagnosis. — Carapace rectangular in outline, length about 3/4 width, widest at midlength. Front deflexed, about 1/4 carapace width. Frontal margin bilobed. Upper orbital margin sinuous, occupying about 3/4 carapace width. Anterolateral margins nearly straight, almost parallel, with 4 forwardly directed teeth. Posterolateral margin sinuous. Dorsal surface smooth, moderately vaulted transversely and weakly vaulted longitudinally. Regions well defined; epibranchial lobe more inflated; mesobranchial lobe with ridge extending from 4th anterolateral tooth; metabranchial lobe with weak ridge parallel to posterolateral margin. Infraorbital ridge present with prominence laterally. Thoracic sternum wide; sterno-abdominal cavity of male deep, reaching sternite 3; sternite 8 of male with transverse groove. Male abdomen narrow, not filling entire space between pereiopods 5. Merus of maxilliped 3 subequal to ischium with convex anterolateral margin; exopod narrow. Male gonopod linear; gonopore opened on inner part of thoracic sternite 8. Chelipeds dissimilar in both sexes; female chelae much smaller than male; propodus slender, elongate. Pereiopods flattened.

Remarks. — Karasawa (1989) originally placed *Miosesarma* in the subfamily Sesarminae. Examination of new specimens shows that the genus is referred to the subfamily Cyclograpsinae because the infraorbital ridge is present, the gonopore is located on the inner part of the thoracic sternite 8, a narrow male abdomen does not fill all of the space between pereiopods 5, and the merus of maxilliped 3 has a convex anterolateral margin. Karasawa (1989) showed that the genus had close affinities with Recent cyclograpsines, *Helice* and *Metaplax*. Our phylogenetic analysis also suggests that *Miosesarma* and *Metaplax* are sister taxa nested as the most derived clade, followed by *Helice* and the most basal *Cyclograpsus* within the Cyclograpsinae.

Most extant members of the Grapsidae live in intertidal waters and adapt to freshwater or terrestrial habitats (Guinot and Bouchard, 1998); however, *Planes* is known from pelagic waters (Manning and Holthuis, 1981) and *Euchirograpsus* from depths between 10 and 359 m (Manning and Holthuis, 1981). *Miosesarma* appears to have inhabited sublittoral and upper bathyal waters based on associated decapods and molluscs (Karasawa, 1993; Kato, 1996).

Distribution. — Early-early Middle Miocene of Honshu, Japan; Ayugawa Group (Karasawa, 1997), Bihoku Group (Karasawa, 1993), Hokutan Group (Karasawa, 1997), Katsuta Group (Karasawa, 1993), Masuda Group (Karasawa, 1993), Mizunami Group (Karasawa, 1989), Chichibumachi Group (Kato, 1996), Nenokami Sandstone Member (Kato, 1996), Numanouchi Formation (Kato in prep.), Yatsuo Group (Karasawa, 1993).

A review of fossil records of the family Grapsidae

Previously known fossil records within the family Grapsidae have included 34 species and 21 genera. Fossil records of the Grapsinae comprise three genera: *Metopograpsus* from the lower Miocene of Hungary (Müller, 1998); *Pachygrapsus* from the middle Miocene of Hungary and Poland (Müller, 1974, 1996) and from the Pleistocene of Jamaica (Morris, 1993); and *Planes* from the lower Miocene of the Caucasus (Smirnov, 1929; Glaessner, 1969).

The genus *Sesarma* (s.l.) of the Sesarminae is represented by three fossil species, *Sesarma paraensis* Beurlen, 1958, from the upper Oligocene-lower Miocene of Brazil, *Sesarma smithi* H. Milne Edwards, 1853, from the Pleistocene of Australia (Etheridge and McCulloch, 1916) and *Sesarma* sp. from the middle Miocene of Japan (Karasawa, 1993). According to Serène and Soh's 1970 reclassification of the genus *Sesarma* (s.l.), *S. smithi* now belongs to *Neosarmatium* Serène and Soh, 1970.

Varunine genera known as fossils are *Brachynotus* from the middle Miocene of Hungary (Müller, 1974), *Eriocheir* from the Pliocene of Japan (Karasawa and Narita, 2000), *Hemigrapsus* from the Pleistocene of U.S.A. (Rathbun, 1926), *Miograpsus* Fleming, 1981 from the upper Miocene of New Zealand, *Varuna* from the middle Eocene of Jamaica (Withers, 1924), and *Utica* White, 1847 from the Pleistocene of Australia (Wintle, 1886). Among these genera *Miograpsus* is the only known extinct genus.

Glaessner (1969) showed that *Telphusograpsus* Lőrenthey, 1902, from the Eocene of Rumania, was referable to *Varuna*; however, *Telphusograpsus* is an independent genus by virture of having an inflated carapace with two upper orbital fissures and with a distinct inner orbital angle, and lacking a posterolateral facet on the branchial region. Members of the Grapsidae lack a distinct inner orbital angle and upper orbital fissures. The genus is probably referred to the family Goneplacidae H. Milne Edwards, 1852. Withers (1924) reported *Varuna* ? sp. from the Eocene of Jamaica, but that occurrence was based only upon a portion of the merus of the cheliped; therefore, the systematic position of the species is doubtful. Karasawa (1993) described a new species, *Varuna angustifrons*, from the lower Oligocene of Japan; however, the species was moved from *Varuna* to *Carinocarcinoides* Karasawa and Fudouji, 2000 of the family Goneplacidae (Karasawa and Fudouji, 2000).

Fossil records of the Cyclograpsinae comprise three genera, *Cyclograpsus*, *Miosesarma* and *Helice*, all known from the Miocene of Japan (Karasawa, 1989; Karasawa and Inoue, 1992; Karasawa, 1993; Kato, 1996).

The extinct genus *Palaeograpsus* Bittner, 1875 has not been placed within any of the grapsid subfamilies (Glaessner, 1969). Previously known species of the genus include: *Palaeograpsus attenuatus* Bittner, 1875, *P.*

Table 4. Distributions and geologic ranges of recognized fossil species of the family Grapsidae.

Taxa	Range	Locality
Family Grapsidae MacLeay, 1838		
Subfamily Grapsinae MacLeay, 1838		
Genus *Metopograpsus* H. Milne Edwards, 1853		
Metopograpsus traxleri Müller, 1998	L. Miocene	Austria
Genus *Pachygrapsus* Randall, 1840		
Pachygrapsus hungaricus Müller, 1974	M. Miocene	Hungary, Poland
Pachygrapsus sp., Morris, 1993	Pleistocene	Jamaica
Genus *Planes* Bowdich, 1825		
Planes prior (Smirnov, 1929)	L. Miocene	Caucasus
Subfamily Sesarminae Dana, 1851		
Genus *Sesarma* Say, 1917		
Sesarma paraensis Beurlen, 1958	U. Oligo.- L. Mio.	Brazil
Sesarma (s.l.) ? sp., Karasawa, 1993	M. Miocene	Japan
Genus *Neosarmatium* Sèrene and Soh, 1970		
Neosarmatium smithi (H. Milne Edwards, 1853)	Pleistocene	Australia
Subfamily Cyclograpsinae H. Milne Edwards, 1853		
Genus *Cyclograpsus* H. Mine Edwards, 1837		
Cyclograpsus directus Karasawa, 1989	L. Miocene	Japan
Cyclograpsus rectangularis Karasawa, 1989	M. Miocene	Japan
Genus *Helice* De Haan, 1835		
Helice sp., Karasawa and Inoue, 1992	M. Miocene	Japan
Genus *Miosesarma* Karasawa, 1989		
Miosesarma japonicum Karasawa, 1989	L.- M. Miocene	Japan
Miosesarma naguraense Kato, 1996	M. Miocene	Japan
Subfamily Varuninae H. Milne Edwards, 1853		
Genus *Brachynotus* De Haan, 1833		
Brachynotus febrarius Müller, 1974	M. Miocene	Hungary
Genus *Eriocheir* De Haan, 1835		
Eriocheir japonica (De Haan, 1835), Karasawa and Narita, 2000	L. Pliocene	Japan
Genus *Hemigrapsus* Dana, 1851		
Hemigrapsus oregonensis (Dana, 1851), Rathbun, 1926	Pleistocene	U.S.A.
Hemigrapsus nudus (Dana, 1851), Rathbun, 1926	Pleistocene	U.S.A.
Hemigrapsus sp., Rathbun, 1926	Pleistocene	U.S.A.
Genus *Miograpsus* Fleming, 1981		
Miograpsus papaka Fleming, 1981	L. Miocene	New Zealand
Genus *Varuna* H. Milne Edwards, 1830		
Varuna ? sp., Withers, 1924	M. Eocene	Jamaica
Genus *Utica* White, 1847		
Utica haswelli Wintle, 1886	Pleistocene	Australia
Utica yarraensis Wintle, 1886	Pleistocene	Australia
Subfamily uncertain		
Genus *Daragrapsus* Müller and Collins, 1991		
Daragrapsus trispinosus Müller and Collins, 1991	U. Eocene	Hungary
Genus *Daranyia* Lõrenthey, 1901		
Daranyia granulata Lõrenthey, 1901	U. Eocene	Hungary
Daranyia fabiani Di Salvo, 1933	M. Eocene	Italy
Genus *Pseudodaranyia* Tessier et al., 1999		
Pseudodaranyia carinata Tessier et al., 1999	M. Eocene	Italy

bartonensis Quayle and Collins, 1981, *P. depressus* Quayle and Collins, 1981, *P. guerini* Via, 1959, *P. inflatus* Bittner, 1875 (type species), *P. loczyanus* Lőrenthey, 1898 and *P. parvus* Müller and Collins, 1991 from the Eocene of Europe; *P. bittneri* Morris and Collins, 1991 from the Pliocene of Brunei. Among these, Schweitzer and Feldmann (2001) moved three species, *P. bartonensis, P. bittneri* and *P. depressus*, to the chasmocarcine genus *Orthakrolophos* Schweitzer and Feldmann, 2001, within the Goneplacidae. *Palaeograpsus guerini* is similar to members of *Orthakrolophos*, but is characterized by having transverse ridges on the dorsal carapace which are lacking in *Orthakrolophos*; therefore, Schweitzer and Feldmann (2001) did not include the species in *Orthakrolophos*. The species remains doubtfully placed within *Palaeograpsus*.

In his original description of the genus, Bittner (1875) indicated that *Palaeograpsus* had a close affinity with *Varuna* and *Pseudograpsus* within the Varuninae. Via (1959) suggested that *P. loczyanus* closely resembles members of *Carcinoplax* H. Milne Edwards, 1852 within the Goneplacidae. Beschin *et al.* (1994) reported well preserved carapaces associated with chelipeds and pereiopods of *P. loczyanus*. De Angeli (1995) also described carapaces, abdominal sternites, chelipeds and pereiopods of *P. inflatus*, the type species of the genus. We agree with the opinion of Via (1959). Examination of their specimens and the type specimen of *P. loczyanus* by one of us (Karasawa) strongly suggests that *Palaeograpsus* should be placed within the Goneplacidae. In *P. inflatus* and *P. loczyanus* the infraorbital ridge is absent; a median depression on thoracic sternite 3 is present, and a groove between sternites 3 and 4 is deep and well defined. However, in members of the Grapsidae sternite 3 usually lacks a median depression and a well defined groove between sternites 3 and 4 is absent. *Varuna* and *Pseudograpsus* possess the infraorbital ridge which *Palaeograpsus* lacks, a unique character of the Varuninae. *Palaeograpsus inflatus* and *P. loczyanus* have slender meri of the pereiopods while genera within the Grapsidae usually possess broad, flattened meri. *Palaeograpsus inflatus* and *P. loczyanus* possess carapace and cheliped characters most like those of *Carcinoplax*. However, the male abdominal somites 3 and 4 of *P. inflatus* are fused, while members of *Carcinoplax* have seven free abdominal somites in males.

The genus *Daranyia* Lőrenthey, 1901 was found in the Eocene of Hungary (Lőrenthey, 1901; Lőrenthey and Beurlen, 1929) and Italy (Di Salvo, 1933). Lőrenthey (1901) and Lőrenthey and Beurlen (1929) compared *Daranyia* with the extant genus *Euchirograpsus*, but the genus differs from *Euchirograpsus* by having a wide, sinuous frontal margin and well separated anterolateral teeth. Glaessner (1969) did not classify the genus in a known subfamily. We agree with Glaessner's opinion. Only the dorsal carapace of the genus is yet known. The subfamilial arrangement of the genus must await discovery of a ventral carapace and thoracic sternites.

Müller and Collins (1991) erected two monotypic genera, *Daragrapsus* and *Sculptoplax*, within the Grapsidae, based on material from the Hungarian Eocene. *Sculptoplax* does not appear to be a member of the Grapsidae. *Sculptoplax* resembles the xanthid genus *Carpilodes* Dana, 1851(= *Liomera* Dana, 1851; ICZN Opinion 73) (Müller and Collins,1991: 90); therefore, the genus is referred to the Xanthidae s.l. Müller and Collins (1991) indicated that *Daragrapsus* resembled *Daranyia*, but because the genus is represented by only a dorsal carapace specimen, subfamilial placement remains obscure.

Tessier *et al.* (1999) described two new grapsid genera, *Maingrapsus* and *Pseudodaranyia*, from the Eocene of Italy. Although Tessier *et al.* (1999) compared *Maingrapsus* with *Palaeograpsus*, the systematic position of the genus is doubtful. *Maingrapsus* is characterized by having a strongly inflated carapace with three transverse ridges and a wide, anteriorly protruded front, and lacking the infraorbital ridge and anterolateral teeth. There is no similarity between *Maingrapsus* and any known extant members of the Grapsidae. The genus has a resemblance to *Paracorallicarcinus* Tessier *et al.*,1999, but differs in having a longer carapace without anterolateral teeth. *Paracorallicarcinus* possesses carapace characters like those of the extant *Georgeoplax* Türkay,1983 of the family Goneplacidae; however, the carapace in *Paracorallicarcinus* is more inflated with weak transverse ridges and bears well defined anterolateral teeth. Therefore, *Maingrapsus* is placed within the family Goneplacidae. The subfamilial placement of *Pseudodaranyia* awaits the discovery of better material.

Thus 25 species in 17 genera of the family Grapsidae are recognized as fossils (Table 4). Three species in three extinct genera are not referred to any known subfamilies. Only the Plagusiinae lacks fossil records.

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