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XENOGRAPSIDAE, A NEW FAMILY OF GRAPSOID CRABS (CRUSTACEA: BRACHYURA) ASSOCIATED WITH SHALLOW WATER HYDROTHERMAL VENTS

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***ABSTRACT*. –** A new family, Xenograpsidae, is established to include an unusual genus of grapsoid crabs, *Xenograpsus* Takeda & Kurata, 1977, associated with shallow hydrothermal vents in the western Pacific Ocean. While *Xenograpsus* is related to other grapsoid crabs such as the Grapsidae, Varunidae, Sesarmidae, Gecarcinidae, and Plagusiidae, evidence from adult and larval morphology and DNA analyses show that the separation between lineages is very deep, and that it should be regarded as belonging to a distinct family. Key morphological differences relate to the structure of the sternum, orbit, basal antennal segment, shape of third maxillipeds, and gonopore position. The relationships amongst the grapsoid families, as currently conceived, are also briefly discussed.

***KEY WORDS*. –** Hydrothermal crab, Xenograpsidae, *Xenograpsus*, new family.

INTRODUCTION

Xenograpsus Takeda & Kurata, 1977, is a peculiar genus of grapsoid crabs which have been found thus far only in shallow-water, volcanically active, sulphur-rich hydrothermal vents. Three species are currently known, *X. novaeinsularis* Takeda & Kurata, 1977 (type species) from the Ogasawara Islands and the Marianas Arc; *X. testudinatus* Ng, Huang & Ho, 2000, from Kueishan Island, Taiwan Arc (Fig. 1A), and *X. ngatama* McLay, 2007, from Brothers Mount in New Zealand.

Xenograpsus novaeinsularis was collected from a depth of 5–120 m (Takeda & Kurata, 1977; Takeda et al., 1993; Türkay & Sakai, 1995); *X. testudinatus* from deeper waters immediately off Kueishan Island at depths of between 100–200 m (Jeng et al., 2004b); and *X. ngatama* from 239–270 m in depth (McLay, 2007). Little is known about the biology and ecology of species of *Xenograpsus*. *Xenograpsus novaeinsularis* has been observed to feed on the ocean floor with its setae-tipped pincers but its diet is not known (Takeda et al., 1993). A study by Jeng et al. (2004b) showed that *X. testudinatus* aggregates in large numbers around shallow water sulphur-rich vents (Fig. 1 B–C); and that twice daily, during slack water, they swarm out of their hiding places to feed on "marine snow", i.e. the zooplankton kill resulting from the toxic plumes discharged by the vents. Such feeding behaviour was the first ever reported for any hydrothermal vent species.

Takeda & Kurata (1977) referred *Xenograpsus* to the Varuninae in the Grapsidae, commenting that it had a ridge running parallel to the infra-orbital border, the third maxillipeds were quite broad and entirely closed the buccal cavern and the narrow male abdomen had an elongated telson; characters usually associated with members of this subfamily. Nevertheless, they stated that "Its systematic status is, however, highly puzzling in this subfamily since it is similar in general appearance of the carapace to *Planes* Bowdich, 1825, of the Grapsinae rather than to the genera of Varuninae, and as mentioned later, the chelipeds are related to those of Macrophthalminae of the Ocypodidae" (Takeda & Kurata, 1977: 100). In the discussion of *X. novaeinsularis*, they even compared the species to *Deiratonotus japonicum* (Sakai, 1934) (Camptandriidae, as *Camptandrium*) (Takeda & Kurata, 1977: 105).

Overall, the Grapsoidea has received considerable attention over the last few years following new evidence from genetic, larval and adult morphological research. The older system where the Grapsidae was divided into four subfamilies, viz. Grapsinae, Sesarminae, Plagusiinae and Varuninae (see Ng, 1998); or with an additional subfamily, Cyclograpsinae (Davie, 2002), has evolved into one which is considerably more complex, but probably a better reflection of phylogenetic realities.

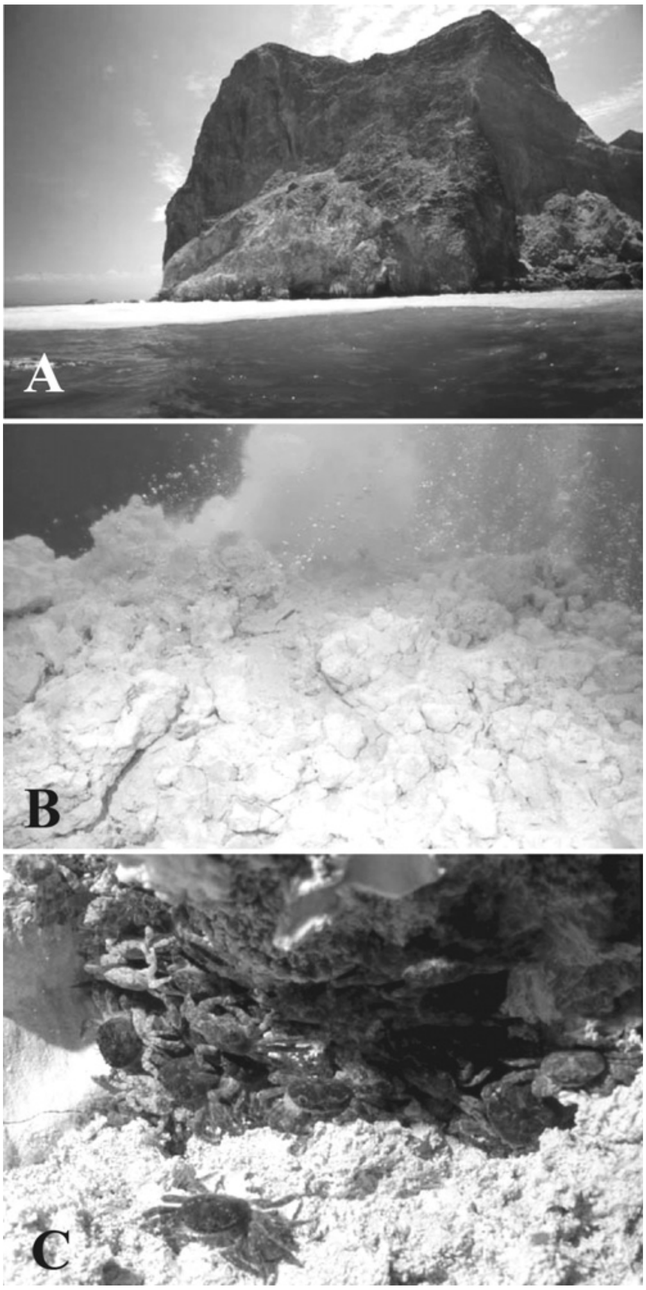

Fig. 1. Photographs on the habitats of *X. testudinatus* Ng, Huang & Ho, 2000: A, northeastern region of Kueishan Island, with sulphur particles; B, yellow smokers in Kueishan Island ; C, *X. testudinatus* crabs in situ, hiding in the crevices. (photographs courtsey of M.-S. Jeng).

The Plagusiidae traditionally has been treated as a subfamily of the Grapsidae, comprising three genera, *Plagusia*, *Percnon* and the newly described genus *Davusia* Guinot, 2007, which seem to be clearly united by the unusual cleft front, fused male abdominal segments 3–5 or 3–6, and third maxilliped with a reduced exopod which lacks a flagellum. To these character states can be added an unusual abdominal press-button locking mechanism with a rim-like sternal tubercle (see Guinot & Bouchard, 1998), and the suture between sternites 5/6 having a raised rim adjacent to the press-button. Sternberg & Cumberlidge (2000) conducted a cladistic study of grapsoid crabs, and concluded that *Plagusia* and *Percnon* form a distinctive monophyletic clade, and they formally raised it to full family status (see also Schubart & Ng, 2000; Schubart et al., 2000, 2002). Schubart et al. (2000, 2002) transferred the enigmatic 'varunid' genus *Euchirograpsus* into the Plagusiidae based on DNA and larval evidence (see also Cuesta & Schubart, 1997). Schubart et al. (2002: 42) commented that "... additional [constituent] genera (e.g. *Miersiograpsus* and *Xenograpsus*) will have to be removed from the Varunidae to make it a monophyletic group". Davie (2002) subsequently transferred *Miersiograpsus* into the Plagusiidae. Like other plagusiids *Euchirograpsus* and *Miersiograpsus* both have male abdominal segments 3–6 fused. Also there are shallow grooves on the frontal margin that appear to mark incipient antennular clefts. However, *Euchirograpsus* and *Miersiograpsus* retain a number of what must be considered as plesiomorphic grapsid features, such as the relatively broader front that overhangs the epistome, and the third maxilliped having a normal, long, grapsid-type exopod bearing a well-developed flagellum.

With regards to the other old subfamilies, Schubart et al. (2000, 2002) recognized the Varunidae and Sesarmidae as full families, distinct from the Grapsidae, and a new family, close to the Varunidae, Glyptograpsidae, was also recognized by Schubart et al. (2002). This new system for the grapsoids has seen increased recognition and use (e.g. see Ng et al., 2001; Martin & Davis, 2001). This system was also followed by Davie & Nguyen (2003), but to include two varunid subfamilies, the Varuninae and Cyclograpsinae. Števčić (2005) again recognised the older system of the Grapsidae with numerous subfamilies and tribes, although he included the Gecarcininae as a subfamily (not family as is usually done), and excluded the Plagusiidae. His decision was not explained. The subfamilial composition of the Varunidae is now being revised by two of the authors (PJFD and NKN).

Cyclograpsacea H. Milne Edwards, 1853, has long been treated as synonymous with Sesarminae Dana, 1851, but studies on the larval morphology and 16S mtDNA on a number of grapsoid genera by Schubart & Cuesta (1998), Schubart et al. (2000, 2002) and Kitaura et al. (2002) have shown that the type genus of the Cyclograpsacea, *Cyclograpsus,* along with *Chasmagnathus*, the *Helice*-group (sensu Sakai et al., 2006), *Helograpsus*, *Metaplax* and *Paragrapsus* have much greater affinities with the Varuninae than Sesarminae. Schubart et al. (2000: 183) commented "At this point, we therefore feel that there is strong enough evidence for transfer of *Cyclograpsus* and *Chasmagnathus* from the Sesarminae to the Varuninae… According to preliminary morphological and molecular data, several of the Indo-West Pacific sesarmine genera (*Helice*-group, *Helograpsus*, *Paragrapsus* and *Metaplax*) are also better classified within the Varuninae". In particular, Kitaura et al. (2002) studied the 16S mtDNA of four species of *Metaplax* and found them to be all firmly rooted in the clade with other cyclograpsine/varunine genera. They clearly belong to a different lineage from the Sesarminae, and from the ocypodoid family Macrophthalminae, whose species have broadly similar fascies and behaviour to those of *Metaplax* (see brief review of family status by Naruse & Kishino, 2006). Similarly a cladistic study by Sternberg & Cumberlidge (2000) found the Sesarminae to be paraphyletic and a number of genera (*Chasmagnathus*, *Cyclograpsus*, *Helice*, *Helograpsus*, *Metaplax*, and *Paragrapsus*) were "reassigned elsewhere within the Grapsoidea." Davie (2002) reported that these genera all have a different pattern of development of the grooves that direct respiratory water flow across the pterygostome, and in particular, have a more or less clearly defined vertical groove running subparallel with the buccal cavity that is not found in the Sesarminae sensu stricto. In addition, these genera have a strongly developed, typically stridulatory, sub-orbital crest that is relatively straight, and extends some distance across the lateral branchial region. In this latter feature, they are most similar to Varuninae, and this supports a putative sister-group relationship corroborating the results of Schubart et al. (2000, 2002) and Kitaura et al. (2002). A similar conclusion was reached independently by Karasawa & Kato (2001) after a phylogenetic analysis of 17 grapsoid genera. Both Karasawa & Kato (2001) and Davie (2002) recommended the recognition of a resurrected Cyclograpsinae to include the following extant genera: *Chasmagnathus* De Haan, 1833, *Cyclograpsus* H. Milne Edwards, 1837, *Helicana* Sakai & Yatsuzuka, 1980, *Helice* De Haan, 1833, *Helograpsus* Campbell & Griffin, 1966, *Metaplax* H. Milne Edwards, 1852, and *Paragrapsus* H. Milne Edwards, 1853. Their decisions were further supported by Sakai et al. (2006) during their revision of the *Helice*-complex of species.

Jeng et al. (2004a) described the larvae of *X. testudinatus* and commented that the "comparisons tabulated within this present study show that on the basis of zoeal morphology at least, *Xenograpsus* cannot be assigned to any of the currently recognised subfamilies of Varunidae… assigning *Xenograpsus* first stage zoeas to any of the existing families… is also not possible without substantially redefining these higher taxa… On the basis of the larval characters, the only systematic option may well be to accommodate *Xenograpsus* in a new family. However, establishing new families on the basis of larval characters alone is a poor taxonomic precedent. What is now required is alpha taxonomy based on adult material of *Xenograpsus* and another reappraisal of the grapsoid families." (Jeng et al., 2004a: 208).

In this paper, we examine the adult morphology of the three recognised species of *Xenograpsus* and report on several unique characters that clearly show the genus is not closely related to the Varunidae. Our proposal of a new family level taxon is supported by larval evidence and a DNA analysis of *Xenograpsus* species compared with taxa from other grapsoid families.

MATERIAL AND METHODS

Specimens of all described species of *Xenograpsus* were examined and compared critically with representatives of all other extant families of the Grapsoidea. A full list of comparative material is presented in the Appendix. Measurements provided are of carapace widths and lengths respectively. Abbreviations: G1, G2 = male first and second gonopods; p = penis; P1–P5 = pereiopods 1-5; s7 and s8 = sternites seven and eight; epi7 = episternite seven. For the larvae, the abbreviations, desciptions and explanation of setal formulae follow Clark et al. (1998).

Comparative material used for this study is listed in Appendix 1. Specimens examined are deposited in the following institutions: Institute of Zoology, Academia Sinica, Nankang (ASIZ), Taiwan; Museum für Naturkunde, Humbolt-Universität zu Berlin, Berlin (MNB), Germany; Muséum National d'Histoire Naturelle, Paris (MNHN), France; The Natural History Museum, London (NHM), United Kingdom; National Institute of Water and Atmospheric Research, (NIWA), New Zealand; National Museum, Manila (NMCR), Philippines; National Museum of Marine Biology and Aquarium, Kenting (NMMBA), Taiwan; United States National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., United States of America; National Museum of Natural Sciences, Taichung (NMNS), Taiwan; National Science Museum, Tokyo (NSMT), Japan; National Taiwan Ocean University, Keelung (NTOU), Taiwan; Institute of Oceanography, The Chinese Academy of Sciences, Qingdao (QIH), People's Republic of China; Queensland Museum, Brisbane (QMW), Australia; Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden (RMNH), The Netherlands; South African Museum, Cape Town (SAM), South Africa; Research Institute and Natural History Museum, Senkenberg, Frankfurt am Main (SFM), Germany; National Taiwan Museum, Taipei, (TMCD), Taiwan; Zoological Museum, University of Copenhagen, Copenhagen (ZMK), Denmark, and Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC), Singapore.

DNA extractions and selective amplification of a fragment of the mitochondrial large ribosomal subunits (16S rRNA) were performed as reported in Schubart et al. (2002, 2006). Most sequences were from previous studies by Schubart et al. (2002, 2006) and recovered from Genbank (see Fig. 7 for accession numbers). New sequence data of *Xenograpsus* sp., *Ptychognathus ishii* and *Discoplax hirtipes* have been submitted to the EMBL molecular database. DNA sequences of *Palicus caronii* (Palicidae) and of the blue crab *Callinectes sapidus* (Portunidae) were included as outgroups. The model of DNA substitution that fitted our data best was chosen using the software MODELTEST 3.6 (Posada & Crandall, 1998). Three methods of phylogenetic inference were applied to our dataset: minimum evolution (ME) with MEGA 3.1 (Kumar et al., 2004), maximum parsimony (MP) using the software package PAUP* (Swofford 1998) and Bayesian analysis (BI) as implemented in MrBayes v. 3.0b4 (Huelsenbeck & Ronquist, 2001). ME trees were calculated with Tamura-Nei distances applying the gamma correction as determined by Modeltest and the Interior-Branch Test with 2,000 replicates. The MP trees were obtained by a heuristic search with 10 replicates of random sequences addition and tree-bisection-reconnection as branch swapping options keeping multiple trees (MulTrees). Gaps were treated as a fifth character and transversions were weighted three times transitions. Confidence values for the proposed groups within the inferred trees were calculated with the nonparametric bootstrap method (2,000 pseudoreplicates). Only minimal trees were retained and zero-length branches were collapsed. The BI trees were calculated using the suggested model of evolution. The Bayesian analysis was run with four MCMC (Markov chain Monte Carlo) chains for 2,000,000 generations, saving a tree every 500 generations. The –lnL converged on a stable value between 5,000 and 15,000 generations (“burnin phase”). The first 20,000 generations were thus excluded from the analysis to avoid inclusion of sub-optimal trees. The posterior probabilities of the phylogeny were determined by constructing a 50% majority-rule consensus of the remaining trees. Consensus trees were obtained using the “sumpt” option in MrBayes.

SYSTEMATIC ACCOUNT

XENOGRAPSIDAE, new family

Type genus. – *Xenograpsus* Takeda & Kurata, 1977.

Diagnosis. – Carapace quadrate, almost rounded; surface finely granular, punctate; with fine posterolateral striations; completely lacking tomentum; regions poorly defined. Front broadly bilobed; single pair of small median postfrontal lobes, posterior to these, a second pair of small tubercular swellings below inner margin of orbit. Supraorbital margins without trace of cleft. Anterolateral margins short, oblique; with only trace of a single epibranchial tooth. Orbit a deep sunken cavity, almost complete; lower margin of exorbital tooth extending medially as a ridge to form new lower orbital margin, separated from large, broad, rounded infraorbital tooth by a narrow fissure; sub-orbital crest extending laterally beyond orbit as a slightly sinuous granular row, but not appearing to be stridulatory. Basal antennal segment immobile, locked against inner orbital tooth laterally. Interantennular septum in form of narrow keel, clasped by incision in lower frontal margin. Pterygostome with simple lateral groove, without supplementary grooves. Third maxilliped with merus and ischium together subrectangular, inner margins meeting medially, without leaving a rhomboidal gape; anteriorly reaching as far as epistome, completely closing buccal cavity; surface granular, without deep grooves, without oblique setose crest extending across outer distal corner of ischium. Exopod of third maxilliped normal, not swollen or enlarged. Chelipeds robust, swollen, absence of row of granules near posterior margin of cheliped; end of finger armed with subapical brush of setae; carpus unarmed with inner margin rounded, without spine. Ambulatory legs very flattened; meri anteriorly with bluntly rounded keel, with broad thick subdistal lobe; dactyli short, broad. Chelae and legs unarmed, tips of cheliped dactyli each with a tuft of short setae. Male abdomen with 7 free segments (including telson). Male gonopore narrowly separated from coxa of fifth ambulatory legs by an elongation of episternite 7 meeting thoracic sternite 8.

Remarks. – Takeda & Kurata (1977) recognized that the placement of *Xenograpsus* in the subfamily Varuninae was problematic, but nevertheless, left it there. Their classification has been followed by all subsequent workers (e.g. Ng et al., 2000; Ng et al., 2001; Jeng et al., 2004a, b; McLay, 2007). As discussed earlier, Jeng et al. (2004a) was the first to question this classification during their study of the larvae. Our present re-appaisal of *Xenograpsus* clearly demonstrates that while it is grapsoid in most characters, it is clearly not a varunid; and the deep split between *Xenograpsus* and other grapsoid families requires separate family recognition. The evidence for this is discussed fully later under the heading “Justification of Family Status”. Supplemenary evidence from larval morphology is presented in Tables 1–4, and from DNA in Figs. 8–10.

Xenograpsus Takeda & Kurata, 1977

Xenograpsus Takeda & Kurata, 1977: 100; Kido & Koike, 1975: 41; Nakamura & Koike, 1975: 37; Takeda et al., 1993: 59; Türkay & Sakai, 1995: 25; Ng et al., 2000: 191; Ng et al., 2001: 191; Schubart et al., 2002: 42; Jeng et al., 2004a: 188; Jeng et al., 2004b: 969.

Type species. – *Xenograpsus novaeinsularis* Takeda & Kurata, 1977, by monotypy.

Gender. – Masculine.

Diagnosis. – Carapace quadrate, convex, glabrous; anterolateral margin with or without teeth; epibranchial tubercle distinct; epigastric cristae prominent, protogastric cristae may be present, oblique granulate crista usually present on carapace above base of fifth ambulatory leg; cervical groove prominent. Anterolateral margin of third maxilliped merus weakly convex. Cheliped merus short, tips of fingers spoon-shaped with a tuft of short setae. Ambulatory legs with lateral margins of meri subparallel; propodi relatively short, stout; dactylus stout. Male telson broadly rounded distally. Male G1 strongly calcified, relatively short, stout. Female gonopore rounded.

Table 1. A comparison between the first stage zoeae of *Brachynotus sexdentatus*, *Eriocheir hepuensis*, *Johngarthia planatus* and *Xenograpsus testudinatus*

Zoea 1 characters	*Brachynotus sexdentatus* (after Cuesta et al., 2001a, b)	*Eriocheir hepuensis* (after Ng et al., 1998)	*Johngarthia planatus* (after Cuesta et al., 2007)	*Xenograpsus testudinatus* (after Jeng et al., 2004a)
Carapace – lateral spines	present	present	present	absent
Antenna – exopodpresent with 2 medial spines	present with 1 small, 1 median spine	absent	absent	
Maxillule – setation of proximal endopod segment	1	4	1	0
Maxilla – setation of bilobed coxa	3+3	4+2	4+4	5+3 & 1 spine
Maxilla – setation of bilobed basis	5+4	5+4	5+5	4 & 1 spine + 4
Maxilla – setation of bilobed endopod	2+2	2+2	2+2	2+3
Second maxilliped – setation of endopod	0,1,6	0,1,6	1,1,6	1,1,5
Abdomen – dorsal lateral process on somite 5	absent	absent	Absent	present
Telson – lateral spines on telson	0	0	0	1 minute spine

Table 2. A comparison between the first stage zoeas of *Gecarcinus lateralis* (Gecarcinidae); *Johngarthia planatus* (Gecarcinidae); *Glytograpsus impressus* (Glyptograpsidae); *Grapsus adscensionis* (Grapsidae); *Plagusia depressa* (Plagusiidae); *Sesarma aequatoriale* (Sesarmidae); *Brachynotus sexdentatus* (Varunidae); *Eriocheir hepuensis* (Varunidae) and *Xenograpsus testudinatus* (Xenograpsidae)

First stage zoeal characters	Gecarcinidae *Gecarcinus lateralis* (by Willems 1982)	Gercarcinidae *Jogngarthia planatus* (by Cuesta et al., 2007)	Glytograpsidae *Glytograpsus impressus* (by Cuesta & Schbart, 1997)	Grapsidae *Grapsus adscensionis* (by Schubart & Cuesta, 1998)	Plagusiidae *Plagusia depressa* (by Wilson & Gore, 1980)	Sesarmidae *Sesarma aequatoriale* (by Cuesta et al., 1997)	Varunidae *Brachynotus sexdentatus* (by Cuesta et al., 2001)	Varunidae *Eriocheir hepuensis* (by Ng et al., 1998)	Xenograpsidae *Xenograpsus testudinatus* (Jeng et al., 2004a)
Carapace – lateral spines	present	present	present	absent	present	absent	present	present	absent
Carapace – anterodorsal seta	absent	absent	absent	absent	absent	2 pairs present	absent	absent	absent
Antenna – exopod	present (2 unequal terminal setae)	present (1 long, 1 short & 2 minute)	Present (4 unequal terminal setae)	present (single seta)	present (2 unequal setae)	present (2 unequal setae)	present (2 medial spines)	present (1 small & 1 median spine)	absent
Maxillule – endopod setation	1,5 (1 subterminal + 4 terminal)	1,5 (2 terminal + 2 subterminal + 1 lateral)	1,5 (1 subterminal + 4 terminal)	1,5 (1 subterminal + 4 terminal)	1,5 (1 subterminal + 4 terminal)	1,5 (1 subterminal + 4 terminal)	1,5 (1 subterminal + 4 terminal)	1,5 (1 subterninal + 4 terminal)	0,4
Maxilla – coxal setation	5+4		5+4	5+4	5+4	4+4	3+3	4+2	5+3 & 1 spine
Maxilla – basial setation	5+4	4+4	4+4	5+4	5+4	4+4	5+4	5+4	4 & 1 spine + 4
Maxilla – endopod setation	2+2	2+2	1+2	2+2	2+2	2+3	2+2	2+2	2+3
First maxilliped – basial setation	10 2,2,3,3	10 2,2,3,3	8 2,2,2,2	8 2,2,2,2	8 2,2,2,2	10 2,2,3,3	10 2,2,3,3	10 2,2,3,3	10 2,2,3,3
First maxilliped – endopod setation	2,2,1,2,5	2,2,1,2,5	2,2,1,2,5	1,2,1,2,5	2,2,1,2,5	2,2,1,2,5	2,2,1,2,5	2,2,1,2,5	2,2,1,2,5
Second maxilliped – setation of endopod	1,1,6	1,1,6	1,1,6	0,1,5	1,1,5	0,1,6	0,1,6	0,1,6	1,1,5
Abdomen – dorsal lateral process present on somites	2,3	2,3	2,3,4	2,3,4,5	2,3,4,5	2,3	2,3	2,2,2,2	2,3,4,5
Telson – lateral spines on telson fork	absent	absent	absent	3 setae	absent	absent	absent	absent	1 minute spine

Table 3. A comparison between the zoeal characters of the Varunidae and *Xenograpsus testudinatus*

Zoeal Characters	Varunidae by Cuesta el al.. (2001a, b)	*Xenograpsus testudinatus* by Jeng et al. (2004a)
Antenna	Well developed exopod (≥ of the protopod length) and with 1 or 2 medial setae	Exopod absent
Maxilla, endopod setation	2,2	2,3
First maxilliped, basial setation	2,2,3,3	2,2,3,3
Second maxilliped, endopod setation	0,1,6	1,1,5
Abdomen, dorsal lateral process on somites	2, 2–3, or 2–4, but never 2–5	2–5
Telson	without lateral spines	with one lateral spine

Remarks. **–** Currently includes three species: *Xenograpsus novaeinsularis* Takeda & Kurata, 1977, from Ogasawara Islands, Japan and Mariana Arc; *X. testudinatus* Ng, Huang & Ho, 2000*,* from Taiwan; and *X. ngatama* McLay, 2007, from off New Zealand. All species are associated with hydrothermal vents — *X. novaeinsularis* and *X. ngatama* with black smokers (Türkay & Sakai, 1995; C. McLay, pers. comm.), and *X. testudinatus* from yellow smokers (Jeng et al., 2004b).

Key to species of *Xenograpsus*

1. Carapace with one distinct protogastric tubercle **2**
– Carapace with many distinct protogastric tubercles .... ***X. ngatama***
2. Carapace with anterolateral tooth present, oblique granulated crista absent on carapace above base of fifth ambulatory legs .... ***X. novaeinsularis***
– Carapace without anterolateral tooth, oblique granulated crista present on carapace above base of fifth ambulatory legs .... ***X. testudinatus***

Xenograpsus novaeinsularis Takeda & Kurata, 1977
(Fig. 2A)

Xenograpsus novaeinsularis Takeda & Kurata, 1977: 100; Kido & Koike, 1975: 41; Nakamura & Koike, 1975: 37; Takeda et al., 1993: 59; Türkay & Sakai, 1995: 25; Ng et al.*,* 2000: 46; Ng et al.*,* 2001: 191; Jeng et al., 2004b: 969.

Material examined. **– Holotype**: 1 male (7.3 × 6.4 mm) (NSMT-Cr.5427), Nishino-shima-shinto, Japan, coll. Y. Kurata, 25 Jul.1975. **Others**: 3 males (12.2–20.4 × 11.3–17.5 mm) (NSMT-Cr.6570), Tsukiura Wan, Nishino-shima-shinto, Nishi-no-shima, Japan, coll. Y. Kurata & K. Takenaga, 25 Oct.1979; 1 male (13.0 × 11.3 mm) (NSMT-Cr.12440), Sho-takara-jima, Ika-u Retto, Japan, coll. Y. Seyama, 2 May 1998; 11 males (5.6–12.3 × 4.9–11.2 mm), 7 females (ovig.) (5.5–10.0 × 5.0–9.0 mm) (SMF-22945), North Esmeralda, North Mariana, North Pacific, coll. F. S. Sonne, 12 Jul.1990; 1 male (5.9 × 5.1 mm), 1 female (ovigerous) (SMF-22946), Esmeralda, North Mariana, 114 m depth, coll. F. S. Sonne, 21 Jul.1990.

Remarks. **–** Takeda & Kurata (1977) described *Xenograpsus novaeinsularis* from Nishino-shima Island in the Ogasawara Islands, from an area with steep cliffs and violent waves; and this way only shortly after the island was first formed in 1973 (Kido & Koike, 1975; Nakamura & Koike, 1975; Takeda & Kurata, 1977). It was subsequently reported from the sediment of Esmeralda Bank, an active submarine volcano in the Mariana Arc (Türkay & Sakai, 1995).

All *X. novaeinsularis* specimens have been collected from hydrothermal environments. The specimens from the Mariana Arc are very similar to those from the Ogasawara Islands but there are very subtle differences in the form of the carapace, and ratio of the chelipeds and ambulatory legs. The parapatric occurrence of two distinct species, *X. novaeinsularis* and *X. testudinatus* from geographically close and yet distinct hydrothermal regions indicate that these crabs do not venture very far. The abbreviated larval development (Jeng et al., 2004a,) further indicates very limited ability for dispersal.

Distribution. **–** Japan (Ogasawara Islands) and Marianas Arc.

Xenograpsus testudinatus Ng, Huang & Ho, 2000
(Figs. 2B, 3A–J, 4A, 5A, 6A, 7A)

Xenograpsus testudinatus Ng, Huang & Ho, 2000: 192–198, Figs. 1–3; Ng et al., 2001: 46, 47; Jeng et al.*,* 2004a: 188; Jeng et al., 2004b: 969.

Material examined. **– Holotype**: 1 male (19.8 mm × 18.0 mm) (TMCD), Geng-Xin Fish Port, Pei-Kuan, 15 m depth in rocky reef, I-Lan County, Taiwan, coll. P.-H. Ho, 3 Oct.1991. **Paratypes**: 1 male (21.7 × 20.1 mm) (TMCD), same data as holotype; 1 male (15.8 × 14.4 mm) (NTOU), same data as holotype; 1 male (17.4 × 16.1 mm) (USNM), same data as holotype; 3 males, 4 females (ZRC), Kueishan (= Turtle Mountain) Island, I-Lan County, Taiwan; 5 males, 7 females (ASIZ-72116-2), 16 m depth, near thermal vent, coll. 18 Apr.1999.

Remarks. **–** This species was described from the vents of Kueishan Island in northeastern Taiwan, and separated from the allied *X. novaeinsularis* by differences in the carapaces, third maxillipeds, chelipeds, ambulatory legs, G1s and female gonopores (see Ng et al., 2000).

Ecological notes. **–** *Xenograpsus testudinatus* was found to occur in very high densities in shallow water around sulphur-rich hydrothermal vents in Taiwan. The crabs swarm out of their crevices during slack tide (Fig. 1C) to feed on the zooplankton kill (or "marine snow") resulting from the toxic

Table 4. A comparison between the more pronounced megalopa characters of *Brachynotus sexdentatus*, *Eriocheir hepuensis*, *Johngarthia planatus* and *Xenograpsus testudinatus*

Megalopal characters	Brachynotus sexdentatus (Cuesta et al., 2001a, b)	Eriocheir hepuensis (Ng et al., 1998)	Johngarthia planatus (Cuesta et al., 2007)	Xenograpsus testudinatus (Jeng et al., 2004a)
Antennule – setation of 3 segmented peduncle	6,3,1	6,3,1	4,7,1	4,2,0
Antennule – setation of endopod	1 subterminal, 2 terminal	1 subterminal, 2 terminal	1 subterminal, 3 terminal	1 subterminal, 3 terminal
Antenna – setation of 3-segmented penduncle	2,2,1	2,2,1	7,2,2	1,3,1
Antenna – flagellum	7-segmented with 0,0,4,1,5,3,3 (terminal) setae	10 segmented with 3,2,3,0,0,4,3,3,2,3 (terminal setae)	7 segmented with 0,2,4,1,4,2,3 (subterminal or terminal setae)	5-segmented with 0,0,3,1,8 (1 sub terminal + 7 terminal) setae
Maxillule – coxal endite setation	18 setae	17 setae	11 marginal, 12 submarginal setae	ca. 31 setae
Maxillule – setation of endopod 2-segmented	2,4 (2 subterminal & 2 terminal) setae	3,5,2 (5 subterminal & 2 terminal)	1,4,1 (1 proximal, 1 subterminal &	1,4 (2 subterminal & 2 terminal) setae
Maxillule – exopod setation	1 seta	2 setae	2 setae	2 setae
Maxilla – coxal endite setation	15+5	14,9	24+13	ca. 22+9
Maxilla – basial endite setation	11+16	11+14	12+18	8+12
Maxilla – endopod setation	0	0+(4 or 5)	8 setae & microtrichia	1 basal + 2 marginal
Maxilla – exopod (scaphognathite) margin setation	46	80-90	82-85	*ca.* 64
Maxilla – exopod (scaphognathite) lateral setation	5	5	5	3
First maxilliped – epipod setation	7	12	17	14
First maxilliped – coxal endite setation	17	17	27	12
First maxilliped – basial endite setation	17	23	26	12
First maxilliped – endopod setation	2 subterminal, 2 terminal	4 terminal	3 subterminal, 5 terminal	2 subterminal
Second maxilliped – endopod setation	0,2,1,8,11	1,0,1,5,10	2,2,9,15	0,0,2,6,10
Third maxillipeds – epipod	13 long setae	13 long setae	20 long setae	32 long setae

plumes discharged by the vents. Such feeding behaviour is a novel, and highly specialised, adaptation to living around hydrothermal vents (Jeng et al., 2004b).

At the type locality of *X. testudinatus*, Kueishan Island (24°50'N 121°57'E), shallow water vents in northeastern Taiwan (Fig. 1A) were discovered in 1997, and are part of the Okinawa Arc (Kido & Koike, 1975; Lee et al., 1980; Kuo, 2001). One of the unusual features of this system is that the discharges are highly acidic, and sulphur-rich. It has been demonstrated that vent discharges with high sulphide levels are integral to the establishment of a chemolithotrophic food-web and/or growth of sulphur-bacteria mats (Stüben et al., 1992; Dando et al., 1995). These food sources are absent in Kuei-shan, with the shallow water vent discharges having a high concentration of elemental sulphur (99.5% purity) (Jeng et al., 2004b). With most of the area covered with sulphur and the waters containing a high concentration of toxic volcanic gases, it is not surprising that the habitat is species-poor. The only macro-invertebrate associated with these vents is *Xenograpsus testudinatus.* The biology of this species is still under study (J.-F. Huang & J.-S. Hwang, pers. comm.)

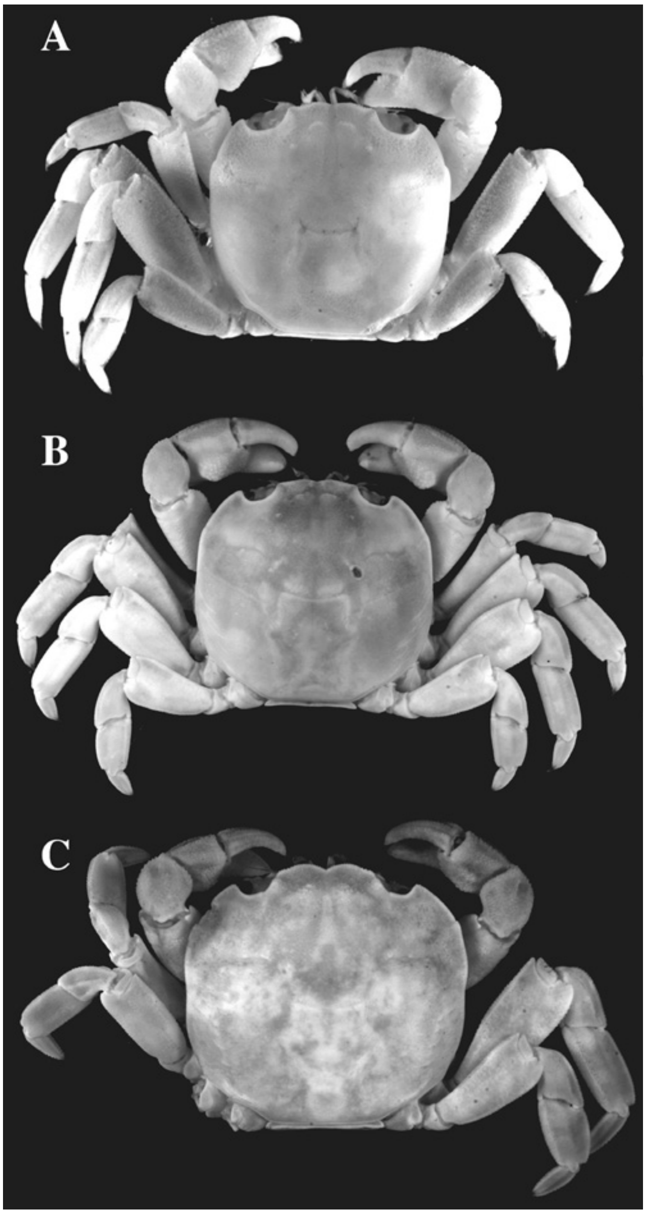

Fig. 2. Photographs of: A, *Xenograpsus novaeinsularis* Takeda & Kurata, 1977, male, holotype (7.3 × 6.4 mm) (NSMT-Cr.5427); B, *X. testudinatus* Ng, Huang & Ho, 2000, male, holotype (19.8 × 18.0 mm) (TMCD); C, *X. ngatama* McLay, 2007, male, paratype (17.3 × 15.7 mm) (ZRC).

***Distribution.* —** Taiwan (Kueishan Island).

Xenograpsus ngatama McLay, 2007
(Fig. 2C)

Xenograpsus ngatama McLay, 2007: 1.

***Material examined.* – Holotype:** 1 male (16.0 × 15.6 mm) (NIWA 18013)., Macauley Caldera, 30º2.06'S 181º17.36'E, 161 m, stn KOK0505/43, 15 Apr.2005. **Paratypes**: 1 male (19.7 × 19.0 mm) (NIWA 18022), Macauley Caldera, 30º2.16'S 181º17.63'E, 109 m, stn KOK0505/45, 16 Apr.2005; 1 female (12.8 × 11.7 mm) (NIWA 18021), Macauley Caldera, 30º2.01'S 181º17.37'E, 156 m, stn KOK0505/49, 17 Apr.2005.

Others: 5 males (11.0–15.2 × 10.5–14.4 mm) (NIWA 18020), Macauley Caldera, 30º2.01'S 181º17.37'E, 156 m, stn KOK0505/49, 17 Apr.2005; 1 male (27.1 × 25.8mm), 1 male (missing carapace, estimated 44.1 × 42.0 mm), 1 female (damaged) (34.8 × 33.1mm mm) (NIWA) Brothers Seamount, 35º44.22–44.04'S 178º29.72–29.63'E, 270–239 m, 21 May.2001; 2 males (16.8–17.8 × 15.3–16.5 mm) (NIWA 18014). Northwest of Kermadec Ridge, 25º53.41–53.61'S 177º11.10–11.07'E, 139–236 m, stn TAN0411/10, 4 Oct.2004; 1 male (17.3 × 15.7 mm) (ZRC), Brothers Seamount, near Kemadec Island, New Zealand, coll. C. M. McLay, 2005.

***Remarks.* –** This species can be easily separated from the other two, because the carapace has many distinct protogastric tubercles, although McLay (2007) also listed a number of other morphological differences. Preliminary study on 560 base-pairs of 16s rRNA of *X. ngatama* shows that this species clusters with *X. testudinatus* (see Figs. 8–10), but there are sufficient differences to support its separate species status (unpublished data).

***Distribution.* –** New Zealand (Brothers Seamount, near Kemadec Island) only.

JUSTIFICATION OF FAMILY STATUS

Morphological Evidence

Male gonopore position (Fig. 4A–H). Guinot (1979), in her landmark work on the phylogenetic relationships of the Brachyura, stressed the importance of the move of the male gonopore and penis from the plesiomorphic coxal position to the most apomorphic condition where they are fully sternal and completely isolated from the fifth pereiopod. This migration to the sternal position entails a re-organisation of the thorax, especially affecting muscle attachments and the structure of the exoskeleton, and which improves the mechanism of locomotion, particularly for walking and running. This in turn probably led to the major adaptative

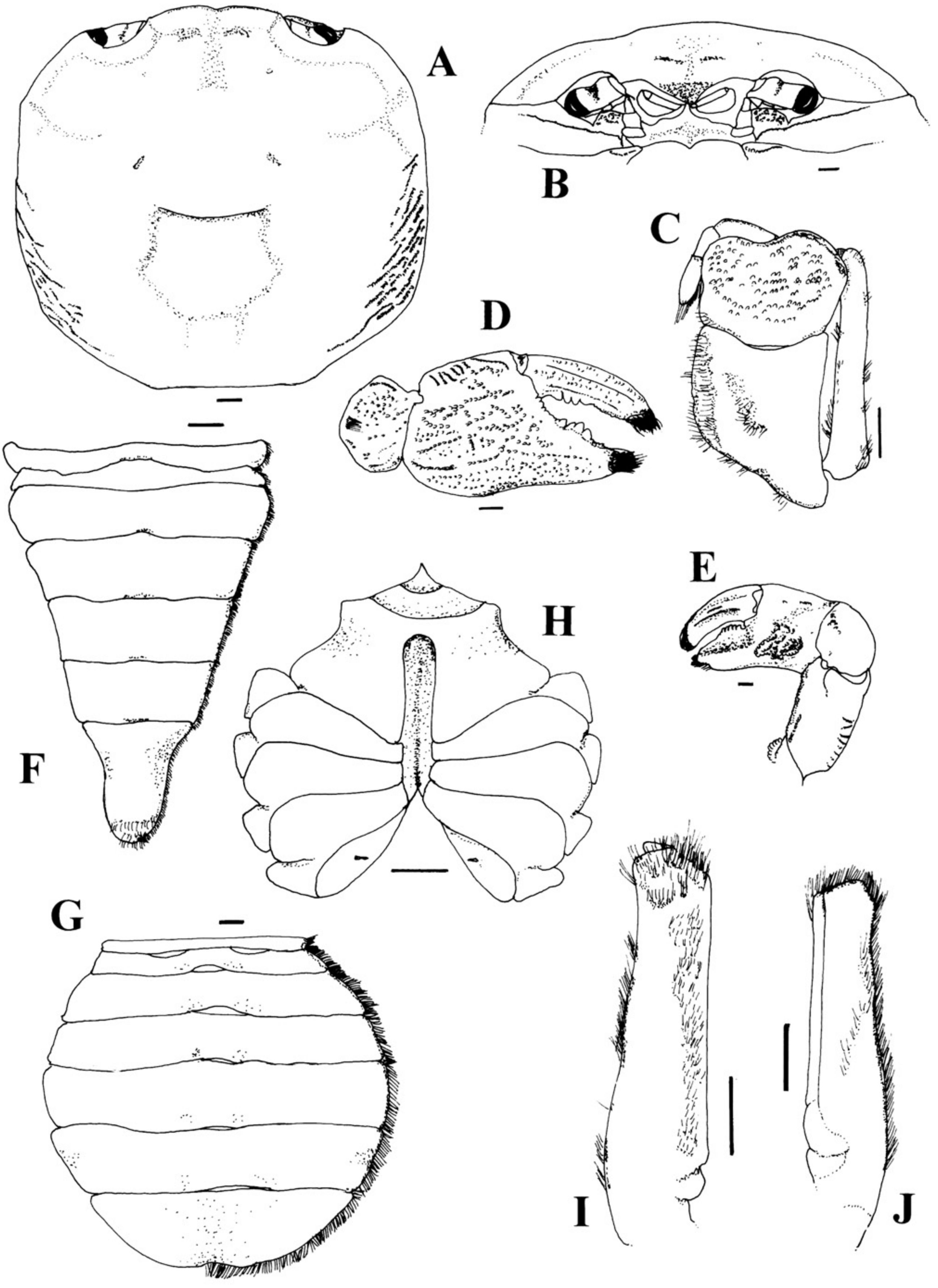

Fig. 3. *Xenograpsus testudinatus* Ng, Huang & Ho, 2000, male, holotype (19.8 × 18.0 mm) (TMCD): A, carapace; B, frontal view; C, third maxilliped; D, right cheliped; E, inner surface of chela; F, male abodmen; G, female abdomen; H, male sternum; I–J, different views of G1.

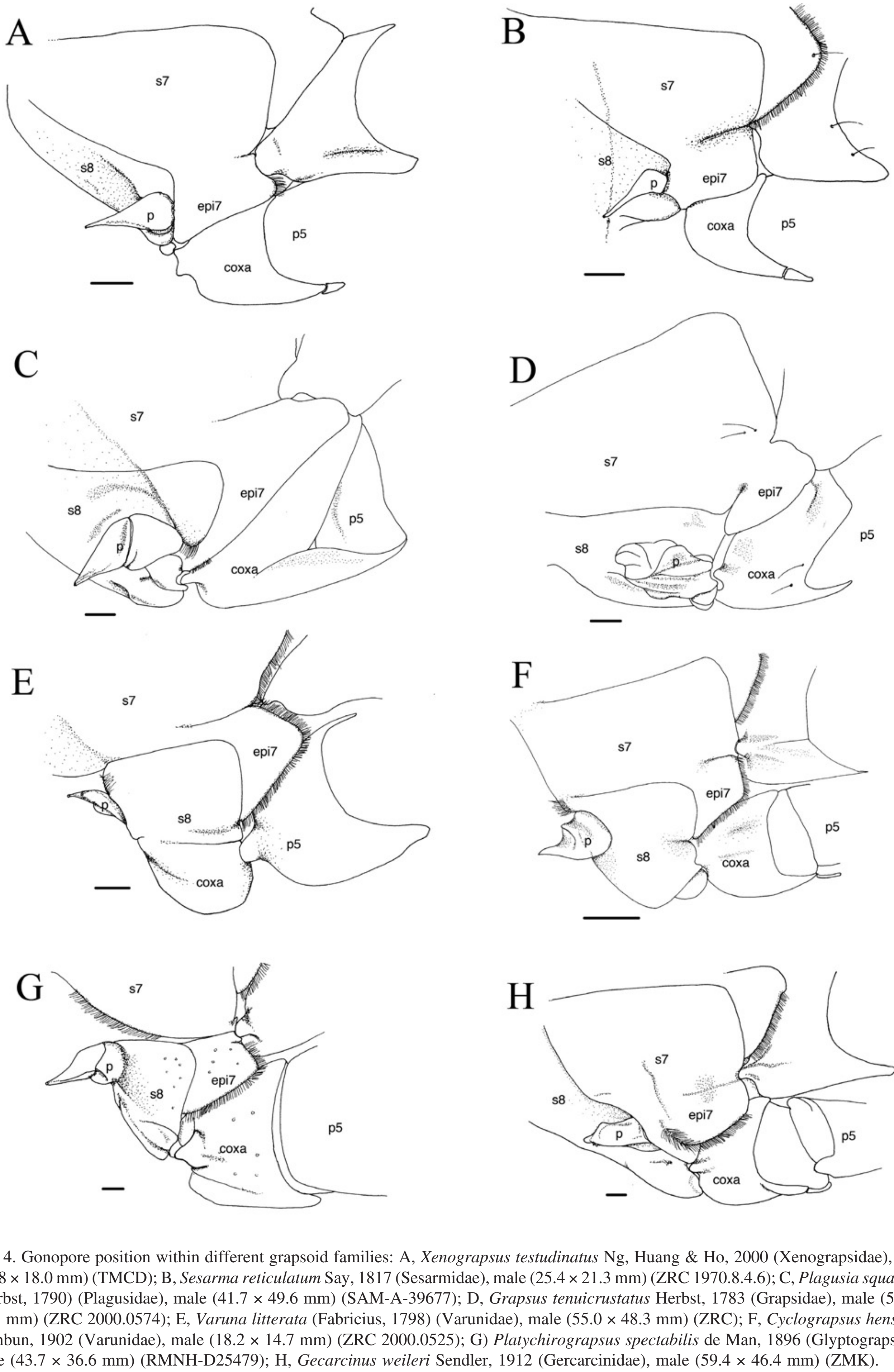

Fig. 4. Gonopore position within different grapsoid families: A, *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (Xenograpsidae), male (19.8 × 18.0 mm) (TMCD); B, *Sesarma reticulatum* Say, 1817 (Sesarmidae), male (25.4 × 21.3 mm) (ZRC 1970.8.4.6); C, *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7 × 49.6 mm) (SAM-A-39677); D, *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7 × 52.1 mm) (ZRC 2000.0574); E, *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0 × 48.3 mm) (ZRC); F, *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2 × 14.7 mm) (ZRC 2000.0525); G) *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae) male (43.7 × 36.6 mm) (RMNH-D25479); H, *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4 × 46.4 mm) (ZMK).

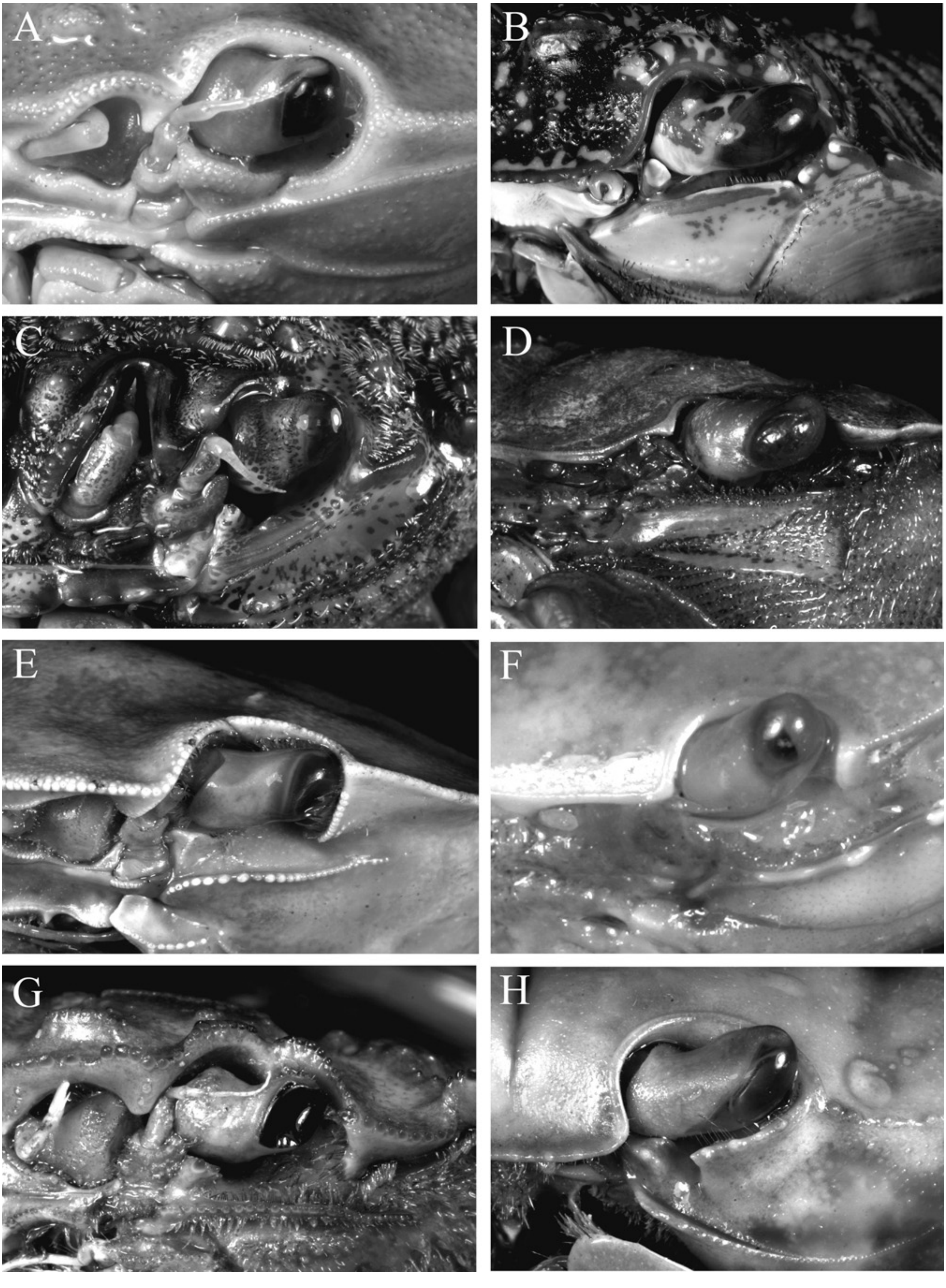

Fig. 5. Orbital structure within grapsoid families: A, *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (Xenograpsidae), male (19.8 × 18.0 mm) (TMCD); B, *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7 × 52.1 mm) (ZRC 2000.0574); C, *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7 × 49.6 mm) (SAM-A-39677); D, *Sesarma reticulatum* Say, 1817 (Sesarmindae), male (25.4 × 21.3 mm) (ZRC 1970.8.4.6); E, *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0 × 48.3 mm) (ZRC); F, *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2 × 14.7 mm) (ZRC 2000.0525); G, *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae), male (43.7 × 36.6 mm) (RMNH-D25479); H, *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4 × 46.4 mm) (ZMK).

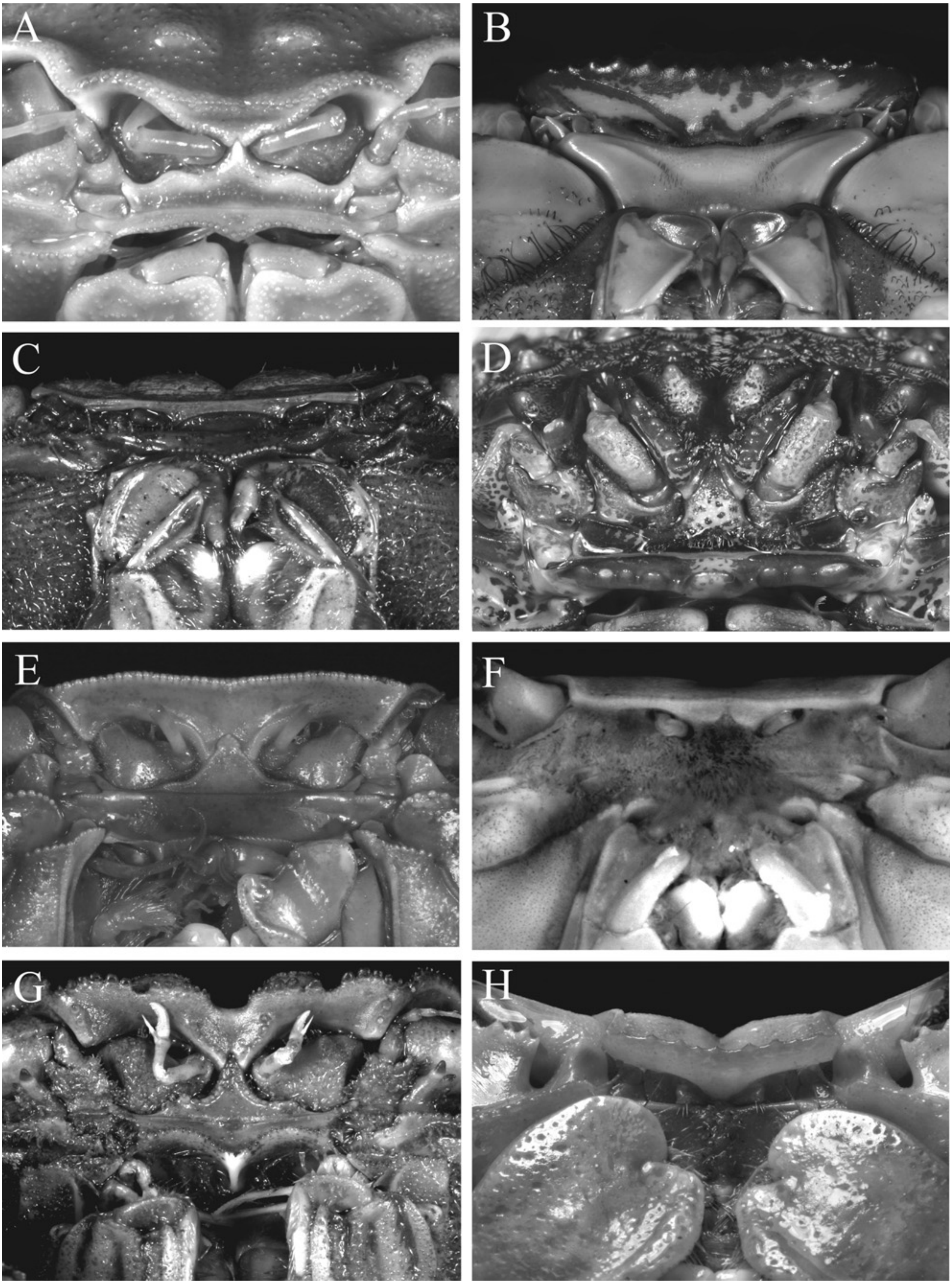

Fig. 6. Interantennular septum differences within grapsoid families: A, *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (Xenograpsidae), male (19.8 × 18.0 mm) (TMCD); B, *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7 × 52.1 mm) (ZRC 2000.0574); C, *Sesarma reticulatum* Say, 1817 (Sesarmindae), male (25.4 × 21.3 mm) (ZRC 1970.8.4.6); D, *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7 × 49.6 mm) (SAM-A-39677); E, *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0 × 48.3 mm) (ZRC); F, *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2 × 14.7 mm) (ZRC 2000.0525); G, *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae), male (43.7 × 36.6 mm) (RMNH-D25479); H, *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4 × 46.4 mm) (ZMK).

radiation of grapsoid crabs into the intertidal, terrestrial and freshwater habitats (Glaessner, 1957; Guinot, 1978). The grapsoid crab higher taxa show a number of different structural configurations that we believe, when taken with other characters, reflect their separate evolutionary lineages.

In the Xenograpsidae, the male gonopore and penis (p) is narrowly separated from the coxa of P5 by an elongation of episternite 7 (epi7) meeting, or nearly meeting, sternite 8 (s8), e.g., episternite 7 forms the lateral margin of the gonopore (Fig. 4A). This condition is almost identical for the Sesarmidae (Fig. 4B) and the Plagusiidae (Fig. 4C).

In this respect, the Grapsidae represent the most plesiomorphic condition with the gonopore/penis in free contact with the coxa of P5 (Fig. 4D). In the Varunidae, the gonopore is widely separated from P5, with the anterior and posterior lateral portions of sternite 8 (s8) meeting as a long suture line (Fig. 4E). This is true both for the two subfamilies of the Varunidae–Varuninae and the Cyclograpsinae (sensu Davie, 2002). Guinot (1979) was the first to recognise that the group of "sesarmine" genera around *Cyclograpsus* showed the same sternal gonopore structure as varunine genera (Fig. 4F), but failed to recognise how phylogenetically significant this was, and that it could be used to effectively separate these genera from the then Sesarminae sensu stricto (now Sesarmidae). This varunid condition is identical for the Glyptograpsidae (Fig. 4G). In the Gecarcinidae (e.g. *Johngarthia*), the gonopore is fully sternal, well separated from coxa of P5, but placed on the anterior border of sternite 8 in contact with sternite 7 (as is the condition, coincidentally, in the Ocypodidae) (Fig. 4H). It must be noted here, however, that *Cardisoma* and related genera such as *Discoplax* and *Epigrapsus* differ in their gonopore position from typical gecarcinids, and their status is also currently being reviewed.

Orbital structure (Fig. 5A–G). *Xenograpsus* is unusual in having an almost complete orbit in the form of a deep sunken cavity (Fig. 5A), a condition very different from all other grapsoids. The lower margin of the exorbital tooth of

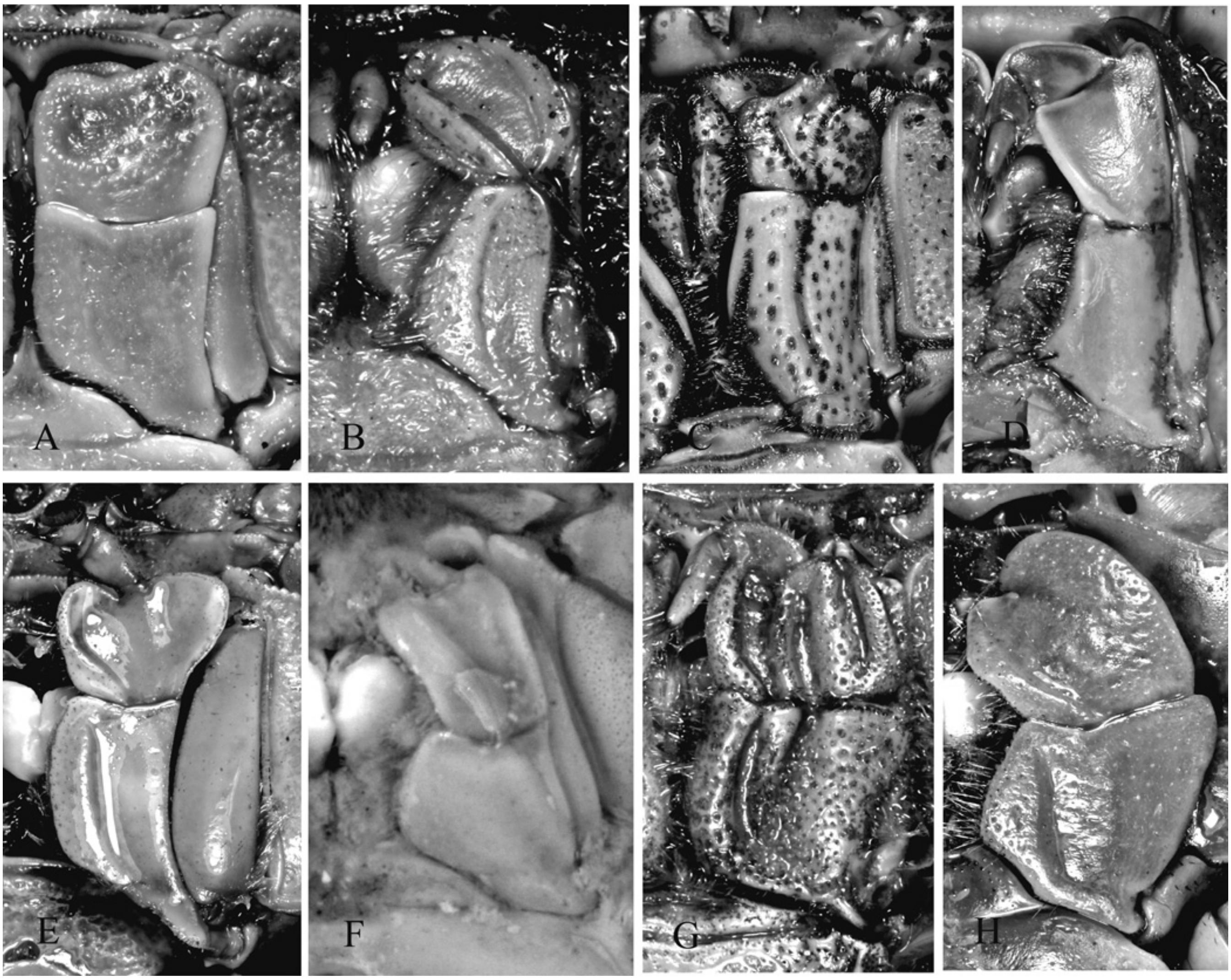

Fig. 7. Third maxilliped form within grapsoid families: A, *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (Xenograpsidae), male (19.8 × 18.0 mm) (TMCD); B) *Sesarma reticulatum* Say, 1817 (Sesarmindae), male (25.4 × 21.3 mm) (ZRC 1970.8.4.6); C, *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7 × 49.6 mm) (SAM-A-39677); D, *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7 × 52.1 mm) (ZRC 2000.0574); E, *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0 × 48.3 mm) (ZRC); F, *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2 × 14.7 mm) (ZRC 2000.0525); G, *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae), male (43.7 × 36.6 mm (RMNH-D25479); H, *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4 × 46.4 mm) (ZMK).

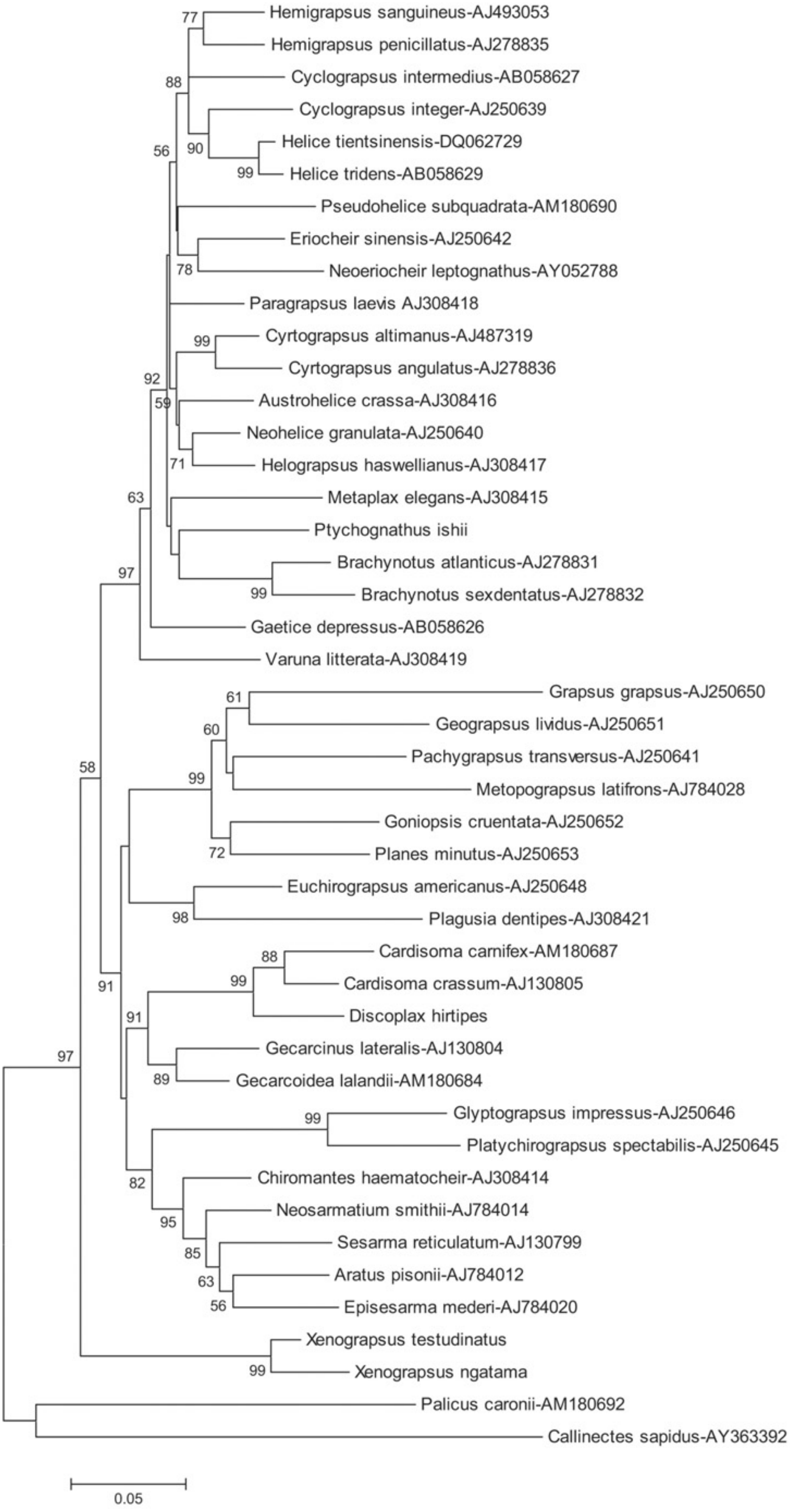

Fig. 8. Phylogenetic consensus tree of 45 brachyuran crabs constructed with the neighbor joining method. Tamura-Nei distances with a gamma correction of 0.5. Confidence values according to an Interior-Branch Test with 2000 replicates. *Callinectes sapidus* and *Palicus caronii* were included as outgroups. Only confidence values higher than 50% are shown. (See appendix for the familial arrangement of the species examined.)

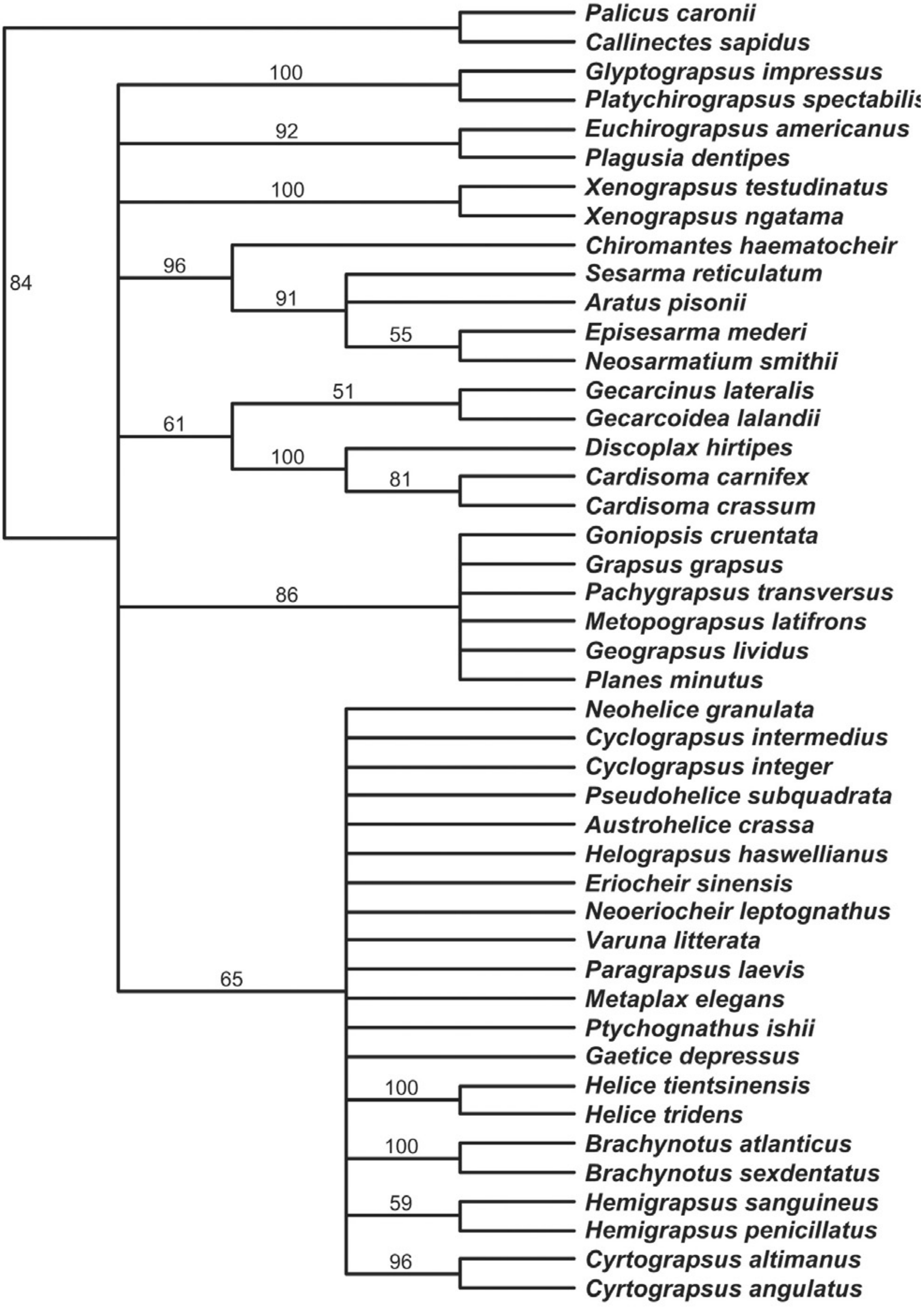

Fig. 9. Phylogenetic consensus tree of 45 brachyuran crabs constructed with the maximum parsimony method resulting in one shortest tree of the length 1989 (CI = 0.33, RI = 0.36). Tranversions were weighed three times transitions. Confidence values after running 2,000 bootstrap pseudoreplicates. *Callinectes sapidus* and *Palicus caronii* were defined as outgroups. Only confidence values higher than 50% are shown. (See Appendix 1 for the familial arrangement of the species examined.)

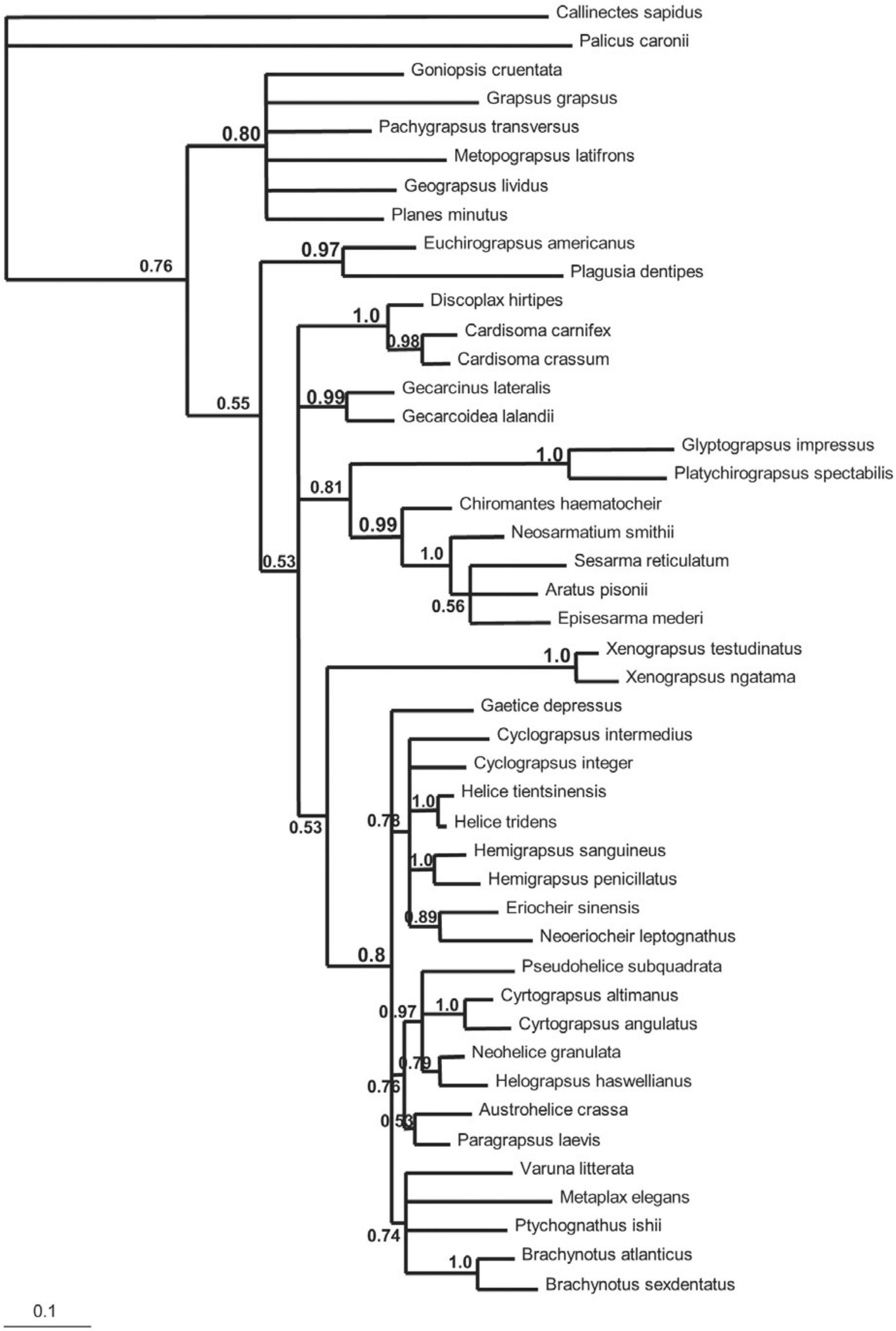

Fig. 10. Phylogenetic consensus tree of 45 brachyuran crabs constructed with Bayesian inference based on the General Time Reversible model (GTR+I+G) as calculated with MODELTEST. Confidence values reflect posterior probabilities after running 4 chains for 2 million generations, excluding 20 thousand as "burnin". *Callinectes sapidus* was defined as outgroup. Only confidence values higher than 0.5 are shown in the tree. (See Appendix 1 for the familial arrangement of the species examined.)

Xenograpsus extends medially as a ridge to form the lower orbital margin, which is separated from the large, broad, rounded infraorbital tooth by a narrow fissure. The true sub-orbital margin that is the homologue of that in the Grapsidae is deflected ventrally, and extends laterally beyond the orbit as a slightly sinuous granular row, but one that does not appear to have a stridulatory function as it does in the Varunidae.

In the Grapsidae (Fig. 5B) and Plagusiidae (Fig. 5C), the obit is also in the form of a distinct sunken cup and is almost complete, with only U- or V-shaped notch laterally adjacent to the exobital angle. The inner orbital tooth may be strong as in the Grapsidae, or more-or-less obsolete (as in the Plagusiidae), but is well separated, and placed internally from the true lower orbital margin which takes the form of a broad continuous, sometimes sinuous, projecting crest ending in a lateral sulcus adjacent the lower margin of the exorbital angle.

In the Sesarmidae (Fig. 5D), the inner orbital tooth is typically low to broadly triangular; well separated, and placed internally from the lower orbital margin; the lower orbital margin commences abutting the lateral edge of the epistome and forms a straight, broad, rounded, usually granular crest that continues for some distance below the exorbital tooth such that the orbit is open laterally in a wide sulcus. The orbit is thus fully open laterally, and the orbital floor is not conspicuously sunken and cupped.

In the Varunidae (Fig. 5E, F) and Glyptograpsidae (Fig. 5G), the inner orbital tooth is variably developed from small and low to broadly triangular and prominent; well separated, and placed internally from the lower orbital margin; the lower orbital margin may be similar to that in the Sesarmidae, or may be deflected ventrally and continued laterally as a granular (often stridulatory) ridge for some distance beyond and below the exorbital tooth. The orbit is generally open ventrally and laterally.

Members of the Gecarcinidae are highly adapted to a terrestrial existence and the orbital structure is extremely variable (see Fig. 5H), but none approach the condition in Xenograpsidae.

Interantennular Septum (Fig. 6A–H). The interantennular septum takes two major forms amongst the Grapsoidea. In the Xenograpsidae, it is narrow and inserted as a narrow tongue into lower margin of the front (Fig. 6A), and in this respect, it resembles all other families (Figs 6A–H) except the Grapsidae (Fig. 6B) and Sesarmidae (Fig. 6C). These latter two families have a broad anteriorly convex septum, meeting but not obviously inserted into the frontal margin.

Antenna. The basal antennal segment is immobile, being locked against the inner orbital tooth laterally. This is apparently a unique apomorphy amongst the grapsoid crabs. It is possible that the mobility and form of the basal segment could facilitate movement of water between the buccal cavity, the orbit, and the ptyerygostome in intertidal and terrestrial grapsoids.

Third maxillipeds (Fig. 7A–H). The broad flat subrectangular third maxillipeds of *Xenograpsus*, with their inner margins meeting and not leaving a rhomboidal gap (Fig. 7A) (versus a broad gap in all other families), also appears to be unique amongst the Grapsoidea (Fig. 7B–G). The merus and ischium are unusual within the grapsoids in being subquadrate. The merus is closest to that of the Glyptograpsidae but lacks a longitudinal sulcus (vs. with three sulci present in the Glyptograpsidae (Fig. 7G), and one sulcus present in the other families). The ischium also has only an indistinct sulcus (vs. two sulci present in Glyptograpsidae and one distinct sulcus in the other families). The palp (dactylus, propodus and carpus) of *Xenograpsus* is also unusually short amongst the Grapsoidea.

Larval Evidence

Jeng et al. (2004a) described the first stage zoea and megalopa of *X. testudinatus*, and compared the characters with other known varunid larvae (*Brachynotus sexdentatus*) as well as those of other grapsoids like Gecarcinidae, Glytograpsidae, Grapsidae (Cuesta et al., 1999), Plagusiidae (Wilson & Gore, 1980) and Sesarmidae (Cuesta et al., 1998) (Table 2). In addition, the larval characters of *Eriocheir hepuensis* (Ng et al., 1998) and *Johngarthia planatus* (Cuesta et al., 2007) are also compared with those of *X. testudinatus* (Table 1). The results are summarized in Tables 1–4.

A number of zoeal characters, including the absence of an antennal exopod; a 0,4 setal formula of the maxillular endopod, the presence of a spine each on the distal coxal and proximal basial lobes of the maxilla, and the presence of a spine on the lateral margin on the telson fork, are unique, and clearly distinguish *X. testudinatus* first stage zoea from those of all the other known grapsoids. On the basis of zoeal morphology, Jeng et al. (2004a) argued that *Xenograpsus* should be removed from the Varunidae and perhaps regarded as a separate family. They, however, deferred action as they preferred not to describe a new family from larval characters alone.

Certainly, the first zoeae of *X. testudinatus* also appear to share a number of conservative zoeal characters with some ocypodid genera like *Scopimera,* viz., the absence of an antennal exopod, and a setal formula of the maxillular endopod segment (see Jeng et al., 2004a). Other shared characters include the basal endite armature of the maxillule; the formula of the endopod setation of maxillule, maxilla and second maxilliped (Table 1); the setal formula on the basis of the first maxilliped (2,2,3,3) and the setal formula [2,2,1,2,5] on the endopod of the first maxilliped. However, the similarities between *Xenograpsus* and *Scopimera* first stage zoeas may well be convergent (see Jeng et al., 2004a). There are nevertheless some major differences between the two genera including the differences in spinulation of the antennal protopod (Jeng et al.*,* 2004a).

DNA Evidence

The trees in Figs 8–10 show both included species of *Xenograpsus* clustering together with high confidence (99/100/1.0 in NJ/MP/BI) as a separate clade. The position of this clade within the Grapsoidea is never resolved. In ME it stands basal relative to all other Grapsoidea; in MP it represents an independent clade in a polytomy at the base of the Grapsoidea; in BI it is linked to the Varunidae (sensu Davie & Nguyen, 2003), but with a low posterior probability of 0.53. Overall, its separation from the Varunidae is well corroborated. Otherwise, the Glyptograpsidae, Grapsidae, Plagusiidae, Sesarmidae and Varunidae are always reflected as monophyletic families with relatively high confidence values. The Gecarcinidae is monophyletic in ME (91) and MP (61), but not grouped together in MB, where it falls into two groups. However, in no analysis was a possibly closer relationship between Gecarcinidae and Plagusiidae observed, as was the case in the study by Schubart et al. (2006: Fig. 1), where the Gecarcinidae were represented as paraphyletic taxon. Within the large group of varunid genera, there is no clear support for the Cyclograpsinae (sensu Davie, 2002). However, there are still many varunid genera for which no sequences have yet been obtained, so it is too early to put much confidence in the topology of this section of the tree at the moment.

CONCLUSION

While the present study failed to clarify the phylogenetic relationships of the Xenograpsidae with other families within the Grapsoidea, nevertheless, the overall evidence (adult morphology, larval features and DNA datasets) clearly supports the recognition of a separate family for the genus *Xenograpsus*. We now believe the Grapsoidea contains seven families: Grapsidae, Sesarmidae, Varunidae, Plagusiidae, Gecarcinidae, Glyptograpsidae and Xenograpsidae.

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APPENDIX 1

Comparative grapsoid material

Varunidae H. Milne Edwards, 1853: *Acmaeopleura parvula* Stimpson, 1858: 1 male (8.4 × 6.2 mm) (TMCD-2525), Hsin-Gang, Tou-Cheng, I-Lan County, Taiwan, coll. C.-H. Wang, 13 Apr.1989; *Brachynotus sexdentatus* (Risso, 1827): 20 males (6.8–13.8 × 5.5–10.4 mm), 9 females (7.5–13.8 × 5.7–10.2 mm) (RMNH-D11067), Havan von Barcelona, Spain, coll. R. Zariguiey Alvarez, Nov.1955; *Cyrtograpsus angulatus* Dana, 1852: 7 males (15.4–47.4 × 13.3–41.7mm), 1 female (18.8 × 15.6 mm), 4 females (ovigerous) (27.1–34.4 × 23.5–30.6 mm), (USNM-173577), Rio Grande de Sal Lagon des Patos, Brazil, South Atlantic Ocean, coll. C. E. Bembenuti, & A. B. Willimans, 1979; *Eriocheir japonica* De Haan, 1835: 1 male (46.0 × 41.2 mm), 2 females (55.3–57.0 × 51.7–53.4 mm) (USNM-20177), Hakodate, Japan, coll. U. S. Fish Commission Steamer ALBATROSS, 19 Sep.1896; *Eriocheir hepuensis* Dai, 1991: 1 male (holotype) (70.2 × 63.0 mm) (ASIZ-GX899024A), Hepu, Guangxi Province, southern China, coll. 18 Nov.1989; *Hemigrapsus oregonensis* Dana, 1852: 2 males (13.1–15.4 × 11.3–13.2 mm), 1 female (13.4 × 11.0 mm) (RMNH-D9741), Mitchell Bay, northwest coast of San Juan Island, Washington State, United State of America, under stones, coll. L. B. Holthuis, 25 Jul.1952; *Hemigrapsus penicillatus* (De Haan, 1835): 3 males (11.8–22.2 × 10.8–19.3 mm), 2 females (13.5–25.6 × 11.8–21.7 mm) (TMCD-2705), De-Zhi-Kou, Zhu-An bridge, I-Lan County, coll. C.-H. Wang, 20 Mar.1991; *Noarograpsus lobulatus* (Manuel, Gonzales & Basmayor, 1991): 1 male (holotype) (8.5 × 7.5 mm) (NMCR-6383), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 23 Aug.1979; *Orcovita saltatrix* Ng & Tomascik, 1994: 1 male (paratype) (16.8 × 12.8 mm), 1 female (19.2 × 14.8 mm) (MNHN-B22891), 10 m depth, Kakaban, Indonesia, coll. T. Tomascik, 29 Sep.1993; *Parapyxidognathus deianira* (de Man, 1888): 10 males (8.8–14.6 × 6.3–11.5 mm), 2 females (9.0–10.0 × 6.8–8.0 mm) (TMCD), Lin-Bien estuary, Pingtung County, coll. H.-C. Liu, 14 Dec.1999; *Pseudograpsus setosus* (Fabricius, 1778): 2 males (37.3–39.5 × 32.8–34.5 mm) (IZAS-72487), Geng-Fang River, I-Lan County, coll. K.-X. Lee, 29 Apr.2000; *Ptychognathus glaber* Stimpson, 1858: 1 male (20.5 × 16.0 mm (NSMT), freshwater river, Chichijima island, Bonin Islands, coll. H. Suzuki, Mar.1972; *Ptychognathus dentatus* de Man, 1892: 1 male (34.3 × 32.5 mm), (RMNH-D2593), Lupa Lupa River, Celebes, coll. J.G. de Man, October, 1888, received on 26 Apr.1930; *Ptychognathus altimanus* Rathbun, 1913: 1 male (21.3 × 20.9 mm) (USNM-44558), Pt. Jamalo, Luzon, Philippines, coll. 13 Jul.1908; *Pyxidognathus granulosus* A. Milne-Edwards, 1878: 4 males (12.0–18.0 × 11.1–16.5 mm), 1 female (14.1 × 12.4 mm) (ZRC), Kawasan Fall, Matutinao, Cebu Island, Philippines, coll. P. K. L. Ng, 30 Jul.2003; *Scutumara enodis* Ng & Nakasone, 1993: 1 male (4.9 × 5.1 mm) (CBM-ZC 3604), beach near Fukido-gawa river-mouth, Ishigaki Island, Yaeyama group, Japan, coll. T. Komai, 24 Mar.1997; *Tetragrapsus jouyi* (Rathbun, 1893): 1 male (holotype) (12.9 × 10.2 mm) (USNM-17496), Guaymas, Mexico, Gulf of California, coll. P. L. Jouy, 27 Feb.1891; *Utica gracilipes* Adam & White, 1847: 1 female (14.0 × 13.8 mm) (ZRC), Inmabalcan River, Antequerra, Bohol Island, Philppines, coll. P. K. L. Ng et al., 27 Nov.2001; *Utica borneenensis* de Man, 1895: 1 male (14.5 × 12.4 mm) (ZRC), 300 m, West Irian, coll. 30 Mar.2000; *Varuna litterata* (Fabricius, 1798): 1 male (55.0 × 48.3 mm) (ZRC), Ta-Chi Fish Port, Taiwan, coll. P. K. L. Ng, 27 May.1997; *Cyclograpsus audouinii* H. Milne Edwards, 1837: 5 males (17.3–31.5 × 14.6-25.0 mm), 2 females (22.5–23.6 × 17.9–19.4 mm), 3 females (ovig.) (17.7–22.6 × 14.5–19.1 mm) (ZRC 1965.7.8.15–25), east coast of Tasmania, Australia, coll. W. W. F. Tweedie, 1940; *Cyclograpsus henshawi* Rathbun, 1902: 2 males (15.9–18.2 × 13.2–14.7 mm), 1 female (12.9 × 10.1 mm) (ZRC 2000.0525) (ex BPBM-1598), Kanana Bay, Oahu, Hawaii, coll. C. H. Edmondson, 22 Mar.1924; *Cyclograpsus integer* H. Milne Edwards, 1837: 4 males (7.0–9.4 × 5.4–7.7 mm), 2 females (9.6–11.0 × 7.4–8.7 mm) (TMCD-2514), Patouzhi, Keelung, coll. C.-H. Wang, 12 Apr.1989; *Cyclograpsus intermedius* Ortmann, 1894: 1 males (12.5 × 10.1 mm), 2 females (ovigerous) (18.1–21.5 × 14.5–17.6 mm), (TMCD-2557), Hsiao-Hsiang-Lan, Fu Lung, Taipei County, Taiwan, coll. C.-H. Wang, 21 Apr.1989; *Cyclograpsus cinereus* Dana, 1852: 1 female, paratype (13.8 × 11.4 mm) (USNM-2340), Valparaiso, Aconcagua, Chile, coll. J. D. Dana, U. S. Exploring Expedition, no collection date; *Cyclograpsus granulatus* Dana, 1852: 1 male (8.3 × 6.8 mm) (ZRC 2000.0523) (ex BPBM-3164), Maui, Hawaii, coll. P. St. Sure, 29 Aug.1928; *Chasmagnathus convexus* (De Haan, 1835): 1 male (41.0 × 30.0 mm), 1 female (42.4 × 32.2 mm) (ZRC), Hong Kong (purchased from market), coll. P. K. L. Ng, 28 Feb.2006; *Neohelice granulata* Sakai, Türkay & Yang, 2006: 1 males (28.0 × 23.4 mm), 1 female (25.8 × 21.6 mm) (ZRC), Sam Boromboin, Argentina, coll. R. Ribeiro, 17 Mar.2001; *Pseudohelice (Parahelice) pilimana* Sakai, Türkay & Yang, 2006: 1 male (26.0 × 22.3 mm), 1 female (23.0 × 19.8 mm) (MNHN-B-10996), New Caledonia, no collection date; *Pseudohelice* (*Pseudohelice*) *subquadrata* Sakai, Türkay & Yang, 2006: 2 males (18.0–18.7 × 16.3–15.5 mm), 2 females (12.5–16.4 × 10.0–14.4 mm) (NMMBA-CDA-652), Dongsha Island, Kaohsiung, Taiwan, coll. H.-P. Ho, 22 Aug.2004; *Helice tridens* De Haan, 1835: 9 males (13.4–18.8 × 10.6–15.0 mm), 2 females (13.7–14.5 × 10.6–11.4 mm) (NTOU), Fengshan river mouth, Hsinchu County, Taiwan, coll. J.-F. Huang, 27 Sep.1987; *Helice formosensis* Rathbun, 1931: 3 males (17.5–27.3 × 14.0–23.2 mm), 4 females (16.9–24.1 x 13.5–18.6 mm) (NMNS), Yanliao, Taichung, Taiwan, coll. H.-T. Shih, 20 May.2002; *Helice latimera* Parisi, 1918: 1 male (26.4 × 23.0 mm), 1 female (30.8 × 25.4 mm) (NMNS), Jinmen, Taiwan, coll. L.-R. Tung, 8 May.1989.; *Helice tientsinensis* Rathbun, 1931: 4 males (20.6–27.8 × 17.0–23.4 mm), 2 females (22.8–26.6 × 18.3–21.3 mm) (QIH), Yangkou market, Shandong Province, People's Rupblic of China, coll. R. Y. Liu, 24 Jul.1953; *Austrohelice crassa* (Dana, 1852): 5 males (9.2–16.9 × 7.2–13.1 mm) (NMNS), Avon-Heathcote Estuary, mudflat, Christchurch, New Zealand, coll. C. McLay, 5 Jun.2005; *Helicana japonica* Sakai & Yatsuzuka, 1980: 1 female (14.4 × 10.3 mm) (NTOU), Wuchao, Taichung County, Taiwan, coll. J.-F. Huang, 24 Apr.1988; *Helicana wuana* (Rathbun, 1931): 2 males (17.0–18.0 × 14.0–15.3 mm), 7 females (2.5–7.5 mm × 1.2–6.0 mm) (NMNS-004657-00107), Wuzaiwei, Taiwan, coll. H.-T. Shih & H.-T. Lung, 3 May.2003; *Metaplax elegans* de Man, 1888: 1 male (14.1 × 9.5 mm), 1 female (ovig.) (9.3 × 6.5 mm) (ZRC), Kranji Beach, Singapore, coll. May 1996; *Metaplax gocongensis* Davie & Nguyen, 2003: 2 males (18.9–29.1 × 14.2–20.7 mm) (ZRC), Phu Thanh Dong commune, ricefields near bank of Tan Thoi Island, Cua Tieu River (Mekong River estuary), ca. 70 km south of Ho Chi Minh City, Vietnam, 10°17'N 106°42'E, coll. Nguyen, 2 Feb.2002; *Metaplax tredecim* Tweedie, 1950: 3 males (14.1–21.3 × 10.8–16.0 mm), 1 female (15.3 × 11.5 mm), 1 female (ovig.) (13.0 × 9.0 mm) (ZRC), Tutong, Brunei, coll. 16 Sep.1990; *Metaplax crenulata* de Man, 1888: 2 males (33.8–44.0 × 26.4–32.6 mm), 1 female (ovig.) (22.6 × 18.2 mm) (ZRC 1997.696), Tanjong Kling mudflat, Singapore, coll. I. Polunin, no collection date; *Paragrapsus laevis* (Dana, 1852): 2 males (31.0–34.7 × 26.0–29.4 mm), 1 female (20.7 × 17.7 mm), 1 female (ovig.) (22.0 × 18.3 mm) (ZRC 1965.7.27.161–163), Sailor's Bay, Syndey, New South Wales, Australia, coll. M. W. F. Tweedie, 1941; *Gaetice depressus* (De Haan, 1833): 4 males (10.5–17.0 × 9.1–14.5 mm), 8 females (9.0–15.5 × 7.8–13.0 mm) (ZRC), Seashore along road from Changpo to Huiren, Hainan Island, China, coll. N. K. Ng & Y. Cai, 1 Dec.1998; *Thalassograpsus harpax* (Hilgendorf, 1892): 1 male (11.0 × 9.7 mm) (MMB-8472), Fundorf, Aden, leg Hildebrandt, no collection date.

Grapsidae MacLeay, 1838: *Grapsus albolineatus* Lamarck, 1818: 3 males (30.6–42.8 × 28.4–40.1 mm), 2 females (ovig.) (15.1–16.3 × 13.2–14.4 mm) (ZRC 2003.0709), southern coast of Palau Laut, Natuna, Indonesia, coll. 16 Mar.2002; *Grapsus tenuicrustatus* Herbst, 1783: 2 males (53.1–54.7 × 51.3–52.1 mm) (ZRC 2000.0574), Pago Bay, Guam, coll. P. K. L. Ng & C.-H. Wang, 15–18 Apr.2000; *Geograpsus crinipes* (Dana, 1852): 1 male (55.8 × 45.9 mm) (ZRC 2001.0727), Pago Bay, Guam, coll. P. K. L. Ng, 28 Jul.2001; *Planes cyaneus* Dana, 1852: 1 male (14.9 × 14.5 mm), 1 female (ovig.) (9.8 × 9.7 mm) (ZRC 2000.0453), Heeia, Hawaii, coll. D. Takada, 23 Jan.1999; *Metopograpus oceanicus* Jacquinot, 1852: 1 male (24.0 × 19.5 mm), 2 females (ovig.) (28.8–29.6 × 24.6–24.4 mm) (ZRC), Changi, Singapore, coll. Tweedie, Jun.1934; *Pachygrapsus fakaravensis* (Rathbun, 1907): 2 males (18.7–19.0 × 17.3–17.6 mm), 1 female (ovig.) (18.3 × 16.7 mm) (ZRC 2000.0406), Kewalo, on seawall, Ala Moana, Waikiki, Oahu, Hawaii, coll. S. H. Tan & P. K. L. Ng, 22 Jan.2000

Glytograpsidae Schubart, Cuesta & Felder, 2002: *Glyptograpsus impressus* Smith, 1870: 2 male (15.4–17.8 × 13.6–15.4 mm), 1 female (13.8 × 11.5 mm) (RMNH-D9745), El Salvador, coll. M. Boeseman, 27 Feb.1953; *Platychirograpsus spectabilis* de Man, 1896: 3 males (36.2–43.7 × 29.5–36.6 mm) (RMNH-D25479), Veracruz, Mexico, coll. E. A. Charex, 20 Sep.1965.

Sesarmidae Dana, 1851: *Sesarma reticulatum* Say, 1817: 1 male (25.4 × 21.3 mm) (ZRC 1970.8.4.6), Atlantic coast of North America, det. R. Serène, 10 Jul.1970; *Chiromantes haematocheir* (de Haan, 1833): 1 male (41.0 × 34.0 mm) (NHM-1880), Chufoo, Shangtung, People's Republic of China, coll. S. Hindle, no collection date; *Bresedium brevipes* (de Man, 1889): 1 male (21.9 × 19.9 mm) (QMW-8810), Daintree river, North Queensland, Australia, coll. B. Campbell, 3 Dec.1975; *Aratus pisoni* H. Milne Edwards, 1837: 1 male (18.9 × 18.8 mm) (NHM-1923.8.14.50-64), Marajo Island, Amazon, Brazil, no collection date; *Episesarma singaporense* (Tweedie, 1936): 1 male (19.1 × 16.5 mm), 1 female (15.1 × 12.0 mm) (ZRC 1999.0565), Chonburi Province, Thailand, coll. P. K. L. Ng, 29 Sep.1998; *Neosarmatium smithi* H. Milne Edwards, 1853: 1 male (36.6 × 35.8 mm) (ZRC 1971.7.29.2), Johore Straits, Singapore, coll. C. L. Soh, 18 Jul.1971.

Plagusiidae Dana, 1851: *Plagusia speciosa* Dana, 1852: 1 male (34.4 × 32.2 mm), 1 female (ovig.) (22.6 × 20.9 mm) (ZRC 2000.2234), Chuanfanshi, Hengchun, Pingtung County, Taiwan, coll. H.-C. Liu, 16 Oct.1997; *Plagusia chabrus* (Linnaeus, 1758): 1 male, 1 female (ZRC 1965.7.27.113-114), Bellambi, New South Wales, Australia, coll. M. W. F. Tweedie, May. 1941; *Plagusia immaculata* Lamarck, 1818: 1 male, neotype, (ZRC 1965.7.27.120), Cocos-Keeling Islands, coll. C. A. Gibbson-Hill, 1941; *Plagusia squamosa* (Herbst, 1790): 1 male (41.7 × 49.6 mm) (SAM-A-39677), Isipingo Natal, coll. ULT Ecological Survey, 12 Jul.1935; *Percnon affinis* Nobili, 1907: 2 males (28.8–37.3 × 30.4–41.1 mm), 1 female (40.4 × 41.6 mm) (ZRC), Kenting National Park, Taiwan, coll. 7 Apr.2004; *Miersiograpsus kingsleyi* (Miers, 1886): 4 males (6.5–12.1 × 6.2–11.3 mm), 2 females (ovig.) (8.1–8.1 × 7.8–8.2 mm) (SMF-13555), station 48, coll. 1 Aug.1984; *Echirograpsus madagascarensis* Türkay, 1978: 1 male (9.4 × 9.4 mm), 1 female (10.0 × 9.7 mm) (SMF-7794), Madagascar, coll. A. Crosnier, 3 Mar.1973; *Euchirograpsus americanus* H. Milne Edwards, 1880: 1 male (11.5 × 11.2 mm), 1 female (ovig.) (9.6 × 9.4 mm) (USNM-232638), off south Carolina, United States of America, coll. 9 Mar.1981; *Euchirograpsus liguricus* H. Milne Edwards, 1853: 7 males (8.8–20.4 × 7.9–17.8 mm), 4 females (8.3–10.9 × 7.4–9.2 mm) (SMF), Marokkan, station 8-13a, 120–180 m depth, coll. Meteor Expedition, 23 Jan.1967; *Euchirograpsus timorensis* Türkay, 1975: 1 male (18.1 × 17.1 mm), 3 female (12.8–23.5 × 12.7–22.5 mm) (USNM-308983), New Caledonia, coll. 18 Oct.1992; *Euchirograpsus tuerkayi* Crosnier, 2001: 2 males (34.1–37.8 × 33.2–36.7 mm) (ZRC), Balicasag Island, off Panglao Island, Bohol, the Phlilppines, coll. P. K. L. Ng, 25–30 Jul.2003.

Gecarcinidae MacLeay, 1838: *Epigrapsus notatus* (Heller, 1865): 1 male (33.8 × 28.8 mm) (ZRC), Siang-Chiao-Wan, Heng-Chun Peninsular, Pingtung County, Taiwan, coll. H.-C. Liu, 19 Jan.1998; *Gercarcinus weileri* Sendler, 1912: 2 males (52.7–59.4 × 41.6–46.4 mm), (ZMK), Sao Thome, West Africa, coll. Galathea Expedition, no collection date; *Cardisoma crassum* Smith 1870: 2 males (37.0–39.9 × 29.4–33.25 mm) (ZMK), Triunfo, El Salvador, coll. 20–21 Feb.1953; *Discoplax hirtipes* (Dana, 1852): 1 male (69.1 × 53.5 mm) (ZRC 2004.0462), Hinagdanan Cave, Panglao Island, Bohol, The Visayas, Philippines, coll. P. K. L. Ng, 3 Mar.2004.